BIOLOGY FOR MAJORS II (LUMEN)



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Book- Biology for Majors II (Lumen)

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TABLE OF CONTENTS

Licensing

1: Course Contents

- 1.1: About This Course
- 1.2: Course Contents at a Glance
- 1.3: Learning Outcomes
- 1.4: Teaching this Course

2: Faculty Resources

- 2.1: Faculty Resource Overview
- 2.2: Pacing
- 2.3: PDF
- 2.4: PowerPoints
- 2.5: Assignments
- 2.6: Question Banks
- 2.7: I Need Help

3: Resources- Course Assignments

- 3.1: Assignment- Build a Cell
- 3.2: Assignment- Nature's Recyclers
- 3.3: Assignment- Hobby Horticulturalist
- 3.4: Assignment- Morphological Phylogenetics
- 3.5: Assignment- Public Relations- Invertebrates are Awesome!
- 3.6: Assignment- Medical Experience
- 3.7: Assignment- Synesthesia is an HR Issue?
- 3.8: Assignment- Infertility- What's to Blame
- 3.9: Assignment- High Altitude Athletic Training Advertisement
- 3.10: Assignment- New AIDS Treatment Protocol
- 3.11: Assignment- Celiac Disease vs IBS
- 3.12: Assignment- Ecotourism

4: Module 1- Introduction to Biology

- 4.1: Why It Matters- Introduction to Biology
- 4.2: Introduction to Characteristics of Life
- 4.3: Properties of Life
- 4.4: Levels of Organization of Living Things
- 4.5: Introduction to Prokaryotes and Eukaryotes
- 4.6: Comparing Prokaryotic and Eukaryotic Cells
- 4.7: Introduction to Taxonomy
- 4.8: The Diversity of Life
- 4.9: Phylogenetic Trees
- 4.10: Taxonomy
- 4.11: Introduction to the Study of Biology
- 4.12: The Branches of Biology

- 4.13: Scientific Inquiry
- 4.14: Experiments and Hypotheses
- 4.15: Interpreting Results
- 4.16: Putting It Together- Introduction to Biology

5: Module 2- Viruses

- 5.1: Why It Matters- Viruses
- 5.2: Introduction to Viral Evolution, Morphology, and Classification
- 5.3: History of Viruses
- 5.4: Viral Morphology
- 5.5: Virus Classification
- 5.6: Introduction to Virus Infections and Hosts
- 5.7: Steps of Virus Infections
- 5.8: Different Hosts and Their Viruses
- 5.9: Introduction to Prevention and Treatment of Viral Infections
- 5.10: Vaccines for Prevention
- 5.11: Vaccines and Anti-Viral Drugs for Treatment
- 5.12: Introduction to Prions and Viroids
- 5.13: Prions and Viroids
- 5.14: Putting It Together- Viruses
- 5.15: Cerego- Viruses

6: Module 3- History of Life

- 6.1: Why It Matters- History of Life
- 6.2: Introduction to Evolution
- 6.3: Natural Selection
- 6.4: Theory of Evolution
- 6.5: Evidence of Evolution
- 6.6: Misconceptions of Evolution
- 6.7: Introduction to Speciation
- 6.8: What is a Species?
- 6.9: Types of Speciation
- 6.10: Reconnection
- 6.11: Rates of Speciation
- 6.12: Introduction to the Evolution of Populations
- 6.13: Population Genetics
- 6.14: Hardy-Weinberg Principle of Equilibrium
- 6.15: Genetic Variation and Drift
- 6.16: Adaptive Evolution
- 6.17: Introduction to Phylogenies and the History of Life
- 6.18: Phylogenetic Trees
- 6.19: Taxonomy
- 6.20: Homologous and Analogous Traits
- 6.21: Cladistics
- 6.22: Perspectives on the Phylogenetic Tree
- 6.23: Putting It Together- History of Life
- 6.24: Cerego- History of Life

7: Module 4- Prokaryotes

- 7.1: Why It Matters- Prokaryotes
- 7.2: Introduction to Prokaryotic Diversity
- 7.3: Evolutionary History of Prokaryotes
- 7.4: Life in Moderate and Extreme Environments
- 7.5: Culturing Prokaryotes
- 7.6: Prokaryotic Biofilms
- 7.7: Introduction to the Structure of Prokaryotes
- 7.8: The Prokaryotic Cell
- 7.9: Archaea vs. Bacteria
- 7.10: Introduction to Prokaryotic Metabolism
- 7.11: Needs of Prokaryotes
- 7.12: How Prokaryotes Get Energy
- 7.13: Role of Prokaryotes in Ecosystems
- 7.14: Introduction to Bacterial Diseases in Humans
- 7.15: Long History of Bacterial Disease
- 7.16: Biofilms and Foodborne Diseases
- 7.17: Antibiotic Resistance
- 7.18: Introduction to Beneficial Prokaryotes
- 7.19: Nitrogen Fixation
- 7.20: Food from Bacteria
- 7.21: Bioremediation
- 7.22: Microbes and the Human Body
- 7.23: Putting It Together- Prokaryotes
- 7.24: Cerego- Prokaryotes

8: Module 5- Protists

- 8.1: Why It Matters- Protists
- 8.2: Introduction to the Characteristics of Protists
- 8.3: Cell Structure and Motility
- 8.4: Metabolism
- 8.5: Life Cycles and Habitats
- 8.6: Introduction to Groups of Protists
- 8.7: Excavata
- 8.8: Chromalveolata
- 8.9: Rhizaria
- 8.10: Archaeplastida
- 8.11: Amoebozoa
- 8.12: Opisthokonta
- 8.13: Introduction to the Ecology of Protists
- 8.14: Primary Producers
- 8.15: Protists as Decomposers
- 8.16: Pathogenic Protists
- 8.17: Putting It Together- Protists
- 8.18: Cerego- Protists

9: Module 6- Fungi

- 9.1: Why It Matters- Fungi
- 9.2: Introduction to the Characteristics of Fungi
- 9.3: Fungal Structure and Habitats
- 9.4: Nutrition and Growth
- 9.5: Reproduction
- 9.6: Introduction to the Classifications of Fungi
- 9.7: Chytridiomycota- The Chytrids
- 9.8: Zygomycota- The Conjugated Fungi
- 9.9: Ascomycota- The Sac Fungi
- 9.10: Basidiomycota- The Club Fungi
- 9.11: Glomeromycota
- 9.12: Deuteromycota- The Imperfect Fungi
- 9.13: Introduction to the Ecology of Fungi
- 9.14: Decomposers and Recyclers
- 9.15: Mutualistic Relationships
- 9.16: Introduction to Fungal Parasites and Pathogens
- 9.17: Infections in Plants
- 9.18: Infections in Humans
- 9.19: Antifungal Therapy
- 9.20: Putting It Together- Fungi
- 9.21: Cerego- Fungi

10: Module 7- Plant Diversity

- 10.1: Why It Matters- Plant Diversity
- 10.2: Introduction to Seedless Plants
- 10.3: Early Plant Life
- 10.4: Green Algae- Precursors of Land Plants
- 10.5: Bryophytes
- 10.6: Seedless Vascular Plants
- 10.7: Introduction to Seed Plants
- 10.8: Evolution of Seed Plants
- 10.9: Gymnosperms
- 10.10: Angiosperms
- 10.11: The Role of Seed Plants
- 10.12: Putting It Together- Plant Diversity
- 10.13: Cerego- Plant Diversity

11: Module 8- Plant Structure and Function

- 11.1: Why It Matters- Plant Structure and Function
- 11.2: Introduction to Plant Structures
- 11.3: Plant Cells
- 11.4: Plant Tissues and Organs
- 11.5: Stems
- 11.6: Leaves
- 11.7: Roots
- 11.8: Introduction to Transport of Water and Solutes in Plants
- 11.9: Water Potential

- 11.10: Transpiration
- 11.11: Photosynthates
- 11.12: Introduction to Plant Sensory Systems and Responses
- 11.13: Plant Responses to Light
- 11.14: Plant Responses to Gravity
- 11.15: Plant Responses to Wind and Touch
- 11.16: Defense Responses against Herbivores and Pathogens
- 11.17: Introduction to Plant Growth
- 11.18: How Plants Grow
- 11.19: Stem Growth
- 11.20: Growth Responses
- 11.21: Introduction to Plant Nutrition
- 11.22: Nutritional Requirements
- 11.23: Autotrophic Plants
- 11.24: Heterotrophic Plants
- 11.25: Putting It Together- Plant Structure and Function
- 11.26: Cerego- Plant Structure and Function

12: Module 9- Plant Reproduction

- 12.1: Why It Matters- Plant Reproduction
- 12.2: Introduction to Reproductive Development and Structure
- 12.3: Stages of a Plant's Life Cycle
- 12.4: Flower Structure
- 12.5: Sexual Reproduction in Angiosperms
- 12.6: Sexual Reproduction in Gymnosperms
- 12.7: Angiosperms versus Gymnosperms
- 12.8: Introduction to Asexual Reproduction in Plants
- 12.9: Asexual Plants
- 12.10: Natural and Artificial Asexual Reproduction
- 12.11: Plant Life Spans
- 12.12: Introduction to Sexual Reproduction in Plants
- 12.13: Self-Pollination and Cross-Pollination
- 12.14: Methods of Pollination
- 12.15: Double Fertilization
- 12.16: Development Seeds and Fruit
- 12.17: Fruit and Seed Dispersal
- 12.18: Putting It Together- Plant Reproduction
- 12.19: Cerego- Plant Reproduction

13: Module 10- Animal Diversity

- 13.1: Why It Matters- Animal Diversity
- 13.2: Introduction to the Evolutionary History of the Animal Kingdom
- 13.3: Pre-Cambrian Animal Life
- 13.4: The Cambrian Explosion
- 13.5: Post-Cambrian Evolution
- 13.6: Introduction to Animal Phylogeny
- 13.7: Classifying Animals
- 13.8: Constructing an Animal Phylogenetic Tree
- 13.9: Modern Revisions of Phylogeny

- 13.10: Introduction to Animal Form and Function
- 13.11: Body Plans
- 13.12: Limits on Animal Size and Shape
- 13.13: Animal Bioenergetics
- 13.14: Introduction to Animal Primary Tissues
- 13.15: Complex Tissue Structure
- 13.16: Epithelial Tissues
- 13.17: Connective Tissues
- 13.18: Muscle and Nervous Tissues
- 13.19: Introduction to Animal Reproduction
- 13.20: Processes of Animal Reproduction and Development
- 13.21: Embryological Development
- 13.22: Hox Genes
- 13.23: Introduction to Homeostasis
- 13.24: What is Homeostasis?
- 13.25: Control of Homeostasis
- 13.26: Thermoregulation
- 13.27: Putting It Together- Animal Diversity
- 13.28: Cerego- Animal Diversity

14: Module 11- Invertebrates

- 14.1: Why It Matters- Invertebrates
- 14.2: Introduction to Phylum Porifera
- 14.3: Morphology of Sponges
- 14.4: Physiological Processes in Sponges
- 14.5: Introduction to Phylum Cnidaria
- 14.6: Characteristics of Phylum Cnidaria
- 14.7: Classes in the Phylum Cnidaria
- 14.8: Introduction to Superphylum Lophotrochozoa
- 14.9: Characteristics of Superphylum Lophotrochozoa
- 14.10: Phylum Platyhelminthes
- 14.11: Phylum Rotifera
- 14.12: Phylum Nemertea
- 14.13: Phylum Mollusca
- 14.14: Phylum Annelida
- 14.15: Introduction to Superphylum Ecdysozoa
- 14.16: Phylum Nematoda
- 14.17: Nematodes in Research
- 14.18: Phylum Arthropoda
- 14.19: Subphylums of Arthropoda
- 14.20: Introduction to Superphylum Deuterostomia
- 14.21: Characteristics of Superphylum Deuterostomia
- 14.22: Phylum Echinodermata
- 14.23: Putting It Together- Invertebrates
- 14.24: Cerego- Invertebrates

15: Module 12- Vertebrates

- 15.1: Why It Matters- Vertebrates
- 15.2: Introduction to Chordates

- 15.3: Characteristics of Chordates
- 15.4: Invertebrate Chordates
- 15.5: Craniates
- 15.6: Introduction to Fishes
- 15.7: Jawless Fishes
- 15.8: Jawed Fishes
- 15.9: Introduction to Amphibians
- 15.10: Amphibians
- 15.11: The Life Cycle of Amphibians
- 15.12: Clades of Amphibians
- 15.13: Introduction to Amniotes
- 15.14: Amniotic Animals
- 15.15: Evolution of Amniotes
- 15.16: Introduction to Reptiles
- 15.17: Characteristics of Reptiles
- 15.18: Classes of Reptiles
- 15.19: Evolutionary History of Reptiles
- 15.20: Introduction to Birds
- 15.21: Characteristics of Birds
- 15.22: Evolutionary History of Birds
- 15.23: Introduction to Mammals
- 15.24: Mammals
- 15.25: Primates
- 15.26: Evolution of Humans
- 15.27: Putting It Together- Vertebrates
- 15.28: Cerego- Vertebrates

16: Module 13- Overview of Body Systems

- 16.1: Why It Matters- Overview of Body Systems
- 16.2: Introduction to Integration of Systems
- 16.3: How Bodies Work
- 16.4: Maintaining Homeostasis
- 16.5: Blood Calcium and Glucose Levels
- 16.6: Introduction to Control Systems
- 16.7: Nervous System
- 16.8: Endocrine System
- 16.9: Reproductive System
- 16.10: Sensory Systems
- 16.11: Introduction to Cell Maintenance Systems
- 16.12: Circulatory System
- 16.13: Respiratory System
- 16.14: Immune System
- 16.15: Digestive System
- 16.16: Introduction to Support Systems
- 16.17: The Muscular System
- 16.18: The Skeletal System
- 16.19: Integumentary System
- 16.20: Putting It Together- Overview of Body Systems
- 16.21: Cerego- Overview of Body Systems

17: Module 14- The Nervous System

- 17.1: Why It Matters- The Nervous System
- 17.2: Introduction to Components of the Nervous System
- 17.3: Diversity of Nervous Systems
- 17.4: The Central and Peripheral Nervous Systems
- 17.5: Neurons
- 17.6: Neurogenesis
- 17.7: Glial Cells
- 17.8: Introduction to Neuron Communication
- 17.9: Resting Membrane Potential
- 17.10: Action Potential
- 17.11: Chemical and Electrical Synapses
- 17.12: Signal Summation
- 17.13: Synaptic Plasticity
- 17.14: Introduction to the Central Nervous System
- 17.15: Components of the Central Nervous System
- 17.16: Brain
- 17.17: Spinal Cord
- 17.18: Introduction to the Peripheral Nervous System
- 17.19: Autonomic Nervous System
- 17.20: Sensory-Somatic Nervous System
- 17.21: Introduction to Nervous System Disorders
- 17.22: Neurodegenerative Disorders
- 17.23: Neurodevelopmental Disorders
- 17.24: Mental Illnesses
- 17.25: Other Neurological Disorders
- 17.26: Putting It Together- The Nervous System
- 17.27: Cerego- The Nervous System

18: Module 15- The Endocrine System

- 18.1: Why It Matters- The Endocrine System
- 18.2: Introduction to Types of Hormones
- 18.3: Lipid-Derived Hormones
- 18.4: Amino Acid-Derived Hormones
- 18.5: Peptide Hormones
- 18.6: Hormone Regulation
- 18.7: Introduction to How Hormones Work
- 18.8: Hormones
- 18.9: Intracellular Hormone Receptors
- 18.10: Plasma Membrane Hormone Receptors
- 18.11: Introduction to Regulation of Body Processes
- 18.12: Hormonal Regulation of the Excretory System
- 18.13: Hormonal Regulation of the Reproductive System
- 18.14: Hormonal Regulation of Metabolism
- 18.15: Blood Calcium Levels and Growth
- 18.16: Hormonal Regulation of Stress
- 18.17: Introduction to Endocrine Glands
- 18.18: Hypothalamic-Pituitary Axis
- 18.19: Thyroids

- 18.20: Adrenal Glands
- 18.21: The Pancreas, Pineal Gland, and Gonads
- 18.22: Organs with Secondary Endocrine Functions
- 18.23: Putting It Together- The Endocrine System
- 18.24: Cerego- The Endocrine System

19: Module 16- The Reproductive System

- 19.1: Why It Matters- The Reproductive System
- 19.2: Introduction to Reproduction Methods
- 19.3: Asexual Reproduction
- 19.4: Sexual Reproduction
- 19.5: Introduction to Human Reproductive Anatomy
- 19.6: Male Reproductive Anatomy
- 19.7: Female Reproductive Anatomy
- 19.8: Sexual Response
- 19.9: Gametogenesis
- 19.10: Introduction to Hormonal Control of Human Reproduction
- 19.11: Reproductive Hormones
- 19.12: The Ovarian Cycle, the Menstrual Cycle, and Menopause
- 19.13: Introduction to Fertilization
- 19.14: Fertilization
- 19.15: External and Internal Fertilization
- 19.16: The Evolution of Reproduction
- 19.17: Introduction to Early Embryonic Development
- 19.18: Cleavage and Blastula Stage
- 19.19: Gastrulation
- 19.20: Organogenesis
- 19.21: Vertebrate Axis Formation
- 19.22: Introduction to Human Pregnancy and Birth
- 19.23: Human Gestation
- 19.24: Labor and Birth
- 19.25: Contraception and Birth Control
- 19.26: Infertility
- 19.27: Putting It Together- The Reproductive System
- 19.28: Cerego- The Reproductive System

20: Module 17- Sensory Systems

- 20.1: Why It Matters- The Sensory Systems
- 20.2: Introduction to the Senses
- 20.3: Human Senses
- 20.4: Sensation
- 20.5: Just-Noticeable Difference
- 20.6: Introduction to Somatosensation
- 20.7: Somatosensory Receptors
- 20.8: Thermoreception and Pain
- 20.9: Introduction to Taste and Smell
- 20.10: Tastes and Odors
- 20.11: Tastes
- 20.12: Smell and Taste in the Brain

- 20.13: Introduction to Hearing and Vestibular Sensation
- 20.14: Sound and Reception
- 20.15: Transduction of Sound
- 20.16: Vestibular Information
- 20.17: Introduction to Vision
- 20.18: Light
- 20.19: Anatomy of the Eye
- 20.20: Transduction of Light
- 20.21: Vision in the Brain
- 20.22: Putting It Together- The Sensory System
- 20.23: Cerego- Sensory Systems

21: Module 18- The Circulatory System

- 21.1: Why It Matters- The Circulatory System
- 21.2: Introduction to the Circulatory System
- 21.3: Circulatory System Architecture
- 21.4: Circulatory System Variation in Animals
- 21.5: Introduction to Structure and Function of Blood
- 21.6: The Role of Blood in the Body
- 21.7: Blood Cells
- 21.8: Components of Blood
- 21.9: Introduction to the Mammalian Heart
- 21.10: Structure of the Heart
- 21.11: The Cardiac Cycle
- 21.12: Introduction to Blood Flow and Blood Pressure Regulation
- 21.13: Blood Vessels
- 21.14: Blood Circulation
- 21.15: Blood Pressure
- 21.16: Putting It Together- The Circulatory System
- 21.17: Cerego- The Circulatory System

22: Module 19- The Respiratory System

- 22.1: Why It Matters- The Respiratory System
- 22.2: Introduction to Systems of Gas Exchange
- 22.3: Different Types of Respiratory Systems
- 22.4: Mammalian Systems
- 22.5: Protective Mechanisms
- 22.6: Introduction to Gas Exchange across Respiratory Surfaces
- 22.7: Breathing Capacity
- 22.8: Gas Pressure and Respiration
- 22.9: Gas Exchange across the Alveoli
- 22.10: Introduction to Breathing
- 22.11: Types of Breathing
- 22.12: The Mechanics of Human Breathing
- 22.13: The Work of Breathing
- 22.14: Dead Space
- 22.15: Introduction to Transport of Gases in Human Bodily Fluids
- 22.16: Transport of Oxygen in the Blood
- 22.17: Transport of Carbon Dioxide in the Blood

- 22.18: Putting It Together- The Respiratory System
- 22.19: Cerego- The Respiratory System

23: Module 20- The Immune System

- 23.1: Why It Matters- The Immune System
- 23.2: Introduction to the Innate Immune Response
- 23.3: Physical and Chemical Barriers
- 23.4: Pathogen Recognition
- 23.5: Natural Killer Cells
- 23.6: Complement System
- 23.7: Introduction to the Adaptive Immune Response
- 23.8: Antigen-Presenting Cells
- 23.9: T and B Lymphocytes
- 23.10: Mucosal Surfaces and Immune Tolerance
- 23.11: Immunological Memory
- 23.12: Primary Centers of the Immune System
- 23.13: Introduction to Antibodies
- 23.14: Antibody Structure
- 23.15: Antibody Classes
- 23.16: Antibody Functions
- 23.17: Disruptions in the Immune System
- 23.18: Putting It Together- The Immune System
- 23.19: Cerego- The Immune System

24: Module 21- The Digestive System

- 24.1: Why It Matters- The Digestive System
- 24.2: Introduction to Digestive Systems
- 24.3: Herbivores, Carnivores, and Omnivores
- 24.4: Invertebrates and Vertebrate Digestive Systems
- 24.5: Parts of the Digestive System
- 24.6: Introduction to Nutrition and Energy Production
- 24.7: Food Requirements
- 24.8: Essential Nutrients
- 24.9: Food Energy and ATP
- 24.10: Introduction to Digestive System Processes and Regulation
- 24.11: Digestive System Processes
- 24.12: Neural Responses to Food
- 24.13: Hormonal Responses to Food
- 24.14: Putting It Together- The Digestive System
- 24.15: Cerego- The Digestive System

25: Module 22- The Excretory System

- 25.1: Why It Matters- The Excretory System
- 25.2: Introduction to Osmoregulation and Osmotic Balance

Index

Glossary

Detailed Licensing

Licensing

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

CHAPTER OVERVIEW

1: Course Contents

1.1: About This Course

1.2: Course Contents at a Glance

1.3: Learning Outcomes

1.4: Teaching this Course

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1.1: About This Course

This gateway biology course provides a strong foundation in the principles of biology for students majoring in Natural Science, medical and healthcare fields. It is the first of a two-course sequence. Primary topics include biochemistry, cell structure and function, genetics, heredity, evolution, and modern applications of biology. The course incorporates Cerego practice sets to aid students as they learn relevant vocabulary.

This course was developed by Lumen Learning, with contributing work from Shelli Carter and Monisha Scott. The course is based on the OpenStax textbook Biology, supplemented with relevant materials from Khan Academy and videos from multiple sources. Original practice activities were authored by Shelli Carter and Lumen Learning in the development of this course.

What's New?

We believe in making continuous improvements to our courses in order to enhance and facilitate student learning. This newest version of the course includes a number of data-driven improvements to assessment questions and text content in order to better illustrate, clarify, and evaluate concepts.

About Lumen

Lumen Learning's mission is to make great learning opportunities available to all students, regardless of socioeconomic background.

We do this by using open educational resources (OER) to create well-designed and low-cost course materials that replace expensive textbooks. Because learning is about more than affordability and access, we also apply learning science insights and efficacy research to develop learning activities that are engineered to improve subject mastery, course completion and retention.

If you'd like to connect with us to learn more about adopting this course, please Contact Us.

You can also make an appointment for OER Office Hours to connect virtually with a live Lumen expert about any question you may have.

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1.2: Course Contents at a Glance

The following list shows a summary of the topics covered in this course. To see all of the course pages, visit the Table of Contents.

Module 1: Introduction to Biology

- Characteristics of Life
- Prokaryotes and Eukaryotes
- Taxonomy
- The Study of Biology

Module 2: Viruses

- Viral Evolution, Morphology, and Classification
- Virus Infections and Hosts
- Prevention and Treatment of Viral Infections
- Prions and Viroids

Module 3: History of Life

- Evolution
- Speciation
- The Evolution of Populations
- Phylogenies and the History of Life

Module 4: Prokaryotes

- Prokaryotic Diversity
- The Structure of Prokaryotes
- Prokaryotic Metabolism
- Bacterial Diseases in Humans
- Beneficial Prokaryotes

Module 5: Protists

- Characteristics of Protists
- Groups of Protists
- Ecology of Protists

Module 6: Fungi

- Characteristics of Fungi
- Classifications of Fungi
- Ecology of Fungi
- Fungal Parasites and Pathogens

Module 7: Plant Diversity

- Seedless Plants
- Seed Plants

Module 8: Plant Structure and Function

- Plant Structures
- Transport of Water and Solutes in Plants
- Plant Sensory Systems and Responses
- Plant Growth
- Plant Nutrition

Module 9: Plant Reproduction

- Reproductive Development and Structure
- Asexual Reproduction in Plants
- Sexual Reproduction in Plants

Module 10: Animal Diversity

- Evolutionary History of the Animal Kingdom
- Animal Phylogeny
- Animal Form and Function
- Animal Primary Tissues
- Animal Reproduction
- Homeostasis

Module 11: Invertebrates

- Phylum Porifera
- Phylum Cnidaria
- Superphylum Lophotrochozoa
- Superphylum Ecdysozoa
- Superphylum Deuterostomia

Module 12: Vertebrates

- Chordates
- Fishes
- Amphibians
- Amniotes
- Reptiles
- Birds
- Mammals

Module 13: Overview of Body Systems

- Integration of Systems
- Control Systems
- Cell Maintenance Systems
- Support Systems

Module 14: The Nervous System

- Components of the Nervous System
- Neuron Communication
- The Central Nervous System
- The Peripheral Nervous System
- Nervous System Disorders

Module 15: The Endocrine System

- Types of Hormones
- How Hormones Work
- Regulation of Body Processes
- Endocrine Glands

Module 16: The Reproductive System

- Reproduction Methods
- Human Reproductive Anatomy
- Hormonal Control of Human Reproduction
- Fertilization
- Early Embryonic Development
- Human Pregnancy and Birth

Module 17: Sensory Systems

- The Senses
- Somatosensation
- Taste and Smell
- Hearing and Vestibular Sensation
- Vision

Module 18: The Circulatory System

- The Circulatory System
- Structure and Function of Blood
- The Mammalian Heart
- Blood Flow and Blood Pressure Regulation

Module 19: The Respiratory System

- Systems of Gas Exchange
- Gas Exchange across Respiratory Surfaces
- Breathing
- Transport of Gases in Human Bodily Fluids

Module 20: The Immune System

- The Innate Immune Response
- The Adaptive Immune Response
- Antibodies

Module 21: The Digestive System

- Digestive Systems
- Nutrition and Energy Production
- Digestive System Processes and Regulation

Module 22: The Excretory System

- Osmoregulation and Osmotic Balance
- Kidneys and Osmoregulatory Organs
- Excretion Systems

Module 23: The Musculoskeletal System

- Skeletal Systems
- Bones
- Joints and Skeletal Movement
- Muscle Contraction and Locomotion

Module 24: The Integumentary System

- Structure and Function of Skin
- Accessory Structures of the Skin
- Functions of the Integumentary System
- Diseases, Disorders, and Injuries of the Integumentary System

Module 25: Ecology of Living Things

- The Scope of Ecology
- Biotic and Abiotic Factors
- Biomes
- Population Ecology
- Community Ecology

Module 26: Ecology and the Environment

- Energy in the Environment
- Biogeochemical Cycles
- Climate Change
- Conservation Biology and Biodiversity

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1.3: Learning Outcomes



The content, assignments, and assessments for Biology for Majors II are aligned to the following learning outcomes. A full list of course learning outcomes can be viewed here: Biology for Majors II Learning Outcomes.

Module 1: Introduction to Biology

Define biology and apply its principles

- List the defining characteristics of biological life
- Identify the different kinds of cells that make up different kinds of organisms
- Describe classification and organizational tools biologists use, including modern taxonomy
- Describe biology as a science and identify the key components of scientific inquiry

Module 2: Viruses

Identify different viruses and the methods they use to infect humans

- Discuss the basics of virus discovery, evolution, and classification
- Describe a viral infection and explain what impact an infection has on its host
- Compare vaccinations and antiviral drugs as medical approaches to viruses
- Describe prions and viroids

Module 3: History of Life

Discuss the history of life on Earth

- Explain the theory of evolution
- Define species and identify how species form
- Discuss the ways populations evolve
- Read and analyze a phylogenetic tree that documents evolutionary relationships

Module 4: Prokaryotes

Identify the different kinds of prokaryotes and common bacteria that infect humans

- Discuss the diversity of prokaryotic cells
- Describe the structure of prokaryotic cells
- Identify the metabolic needs of prokaryotes
- Identify common bacterial diseases in humans
- Identify common prokaryotes that are beneficial to humans

Module 5: Protists

Discuss the organisms in Kingdom Protista

- Identify the common characteristics of protists
- Classify protists into unique categories
- Describe the role that protists play in the ecosystem

Module 6: Fungi

Discuss the organisms in Kingdom Fungi

- Identify the common characteristics of fungi
- Classify fungi into unique categories
- Describe the role that fungi play in the ecosystem
- Identify common fungal parasites and pathogens

Module 7: Plant Diversity

Differentiate between different types of plants

- Classify seedless plants
- Classify seed plants

Module 8: Plant Structure and Function

Discuss the structure and function of plants

- Identify basic common structures of plants
- Describe how water and solutes are transported in plants
- Identify common sensory systems and responses in plants
- Identify the key elements and processes in plant growth
- Discuss the common nutritional needs of plants

Module 9: Plant Reproduction

Differentiate between different types of plants

- Discuss the reproductive development and structure of plants
- Describe how plants reproduce asexually
- Describe how plants reproduce sexually

Module 10: Animal Diversity

Discuss the importance of animal diversity

- Discuss the evolutionary history of the animal kingdom
- Chart animal phylogeny
- Describe the various types of body plans that occur in animals
- Discuss the tissue structures found in animals
- Discuss methods and features of animal reproduction
- Discuss the importance of homeostasis in animals

Module 11: Invertebrates

Classify different types of invertebrates

- Identify the common characteristics of phylum Porifera
- Identify the common characteristics of phylum Cnidaria
- Identify the common characteristics of superphylum Lophotrochozoa
- Identify the common characteristics of superphylum Ecdysozoa
- Identify the common characteristics of superphylum Deuterostomia

Module 12: Vertebrates

Classify different types of vertebrates

- Identify the common characteristics of chordates
- Identify characteristics of fishes

- Identify characteristics of amphibians
- Identify characteristics of amniotes
- Identify characteristics of reptiles
- Identify characteristics of birds
- Identify characteristics of mammals

Module 13: Overview of Body Systems

Describe different body systems

- Discuss how different body systems interact with one another
- Describe the nervous, endocrine, reproductive, and sensory systems
- Describe the circulatory, immune, respiratory, and digestive systems
- Describe the muscular, skeletal, and integumentary systems

Module 14: The Nervous System

Describe the components and role of the nervous system

- Identify the two primary parts of the nervous system and describe the function and structure of neurons and glial cells
- Explain the way neurons communicate
- Identify the components of the central nervous system
- Identify the components of the peripheral nervous system
- Describe the symptoms, potential causes, and treatment of several examples of nervous system disorders

Module 15: The Endocrine System

Describe the components and role of the endocrine system

- Identify different types of hormones and explain the regulation of hormone production
- Describe the two types of hormone receptors
- Describe how hormones regulate body processes
- Describe the role of different glands in the endocrine system

Module 16: The Reproductive System

Describe the components and role of the reproductive system

- Describe advantages and disadvantages of asexual and sexual reproduction
- Describe human male and female reproductive anatomies
- Describe the roles of male and female reproductive hormones
- Discuss internal and external methods of fertilization
- Explain how the embryo forms from the zygote
- Explain fetal development during the three trimesters of gestation

Module 17: Sensory Systems

Describe the components and role of the sensory system

- Identify the general and special senses in humans
- Describe how somatosensation, the sense of touch, works
- Explain how taste and smell work together
- Trace the path of sound through the auditory system to the site of transduction of sound
- Trace the path of light through the eye to the point of the optic nerve

Module 18: The Circulatory System

Describe the components and role of the circulatory system

- Describe the organization of the vertebrate circulatory system
- Describe the structure and function of blood in the body
- Describe the structure of the heart and explain how cardiac muscle is different from other muscles
- Explain the structure of arteries, veins, and capillaries, and how blood flows through the body

Module 19: The Respiratory System

Describe the components and role of the respiratory system

- Describe the passage of air from the outside environment to the lungs
- Understand how gas pressure influences how gases move into and out of the body
- Describe how the structures of the respiratory system control the mechanics of breathing
- Explain how gases are transported in the body

Module 20: The Immune System

Describe the components and role of the immune system

- Explain immediate and induced innate immune responses
- Explain adaptive immunity
- Describe the structure and function of antibodies

Module 21: The Digestive System

Describe the components and role of the digestive system

- Compare and contrast different types of digestive systems
- Explain how energy is produced through diet and digestion
- Discuss the processes and regulations involved in digestion

Module 22: The Excretory System

Describe the components and role of the excretory system

- Explain why osmoregulation and osmotic balance are important body functions
- Describe the structure of the kidneys and the functions of the parts of the kidney
- Explain how different excretion systems function

Module 23: The Musculoskeletal System

Describe the components and role of the musculoskeletal system

- Discuss the different types of skeletal systems
- Discuss the structure and function of bones
- Classify the different types of joints on the basis of structure
- Explain the role of muscles in locomotion

Module 24: The Integumentary System

Describe the components and role of the integumentary system

- Describe the layers of the skin and the functions of each layer
- Identify the accessory structures of the skin
- Describe the different functions of the skin
- Identify different diseases, disorders, and injuries of the integumentary system

Module 25: Ecology of Living Things

Define the scope and components of ecology

- Identify the scope of ecology
- Distinguish between abiotic and biotic components of the environment
- Identify different biomes of our world
- Discuss the scope and study of population ecology
- Discuss the scope and study of community ecology

Module 26: Ecology and the Environment

Discuss the ecology as it relates to the environment

- Describe how organisms acquire energy
- Discuss the biogeochemical cycles of water, carbon, nitrogen, phosphorus, and sulfur
- Identify evidence of climate change
- Explain why conservation biology and biodiversity are important

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1.4: Teaching this Course

This course has been designed to fill the needs of different instructors across multiple institutions. As such, there are more modules than can be taught in a single semester.

We have two primary recommendations for teaching the course. One method has a broad coverage, while the other focuses more on the human body, with in-depth focus on each body system. Please note that we do **NOT** recommend teaching all 26 modules in a single semester.

Broad Approach

This first method has a broad coverage, discussing the the scope and diversity of life. Below are recommended modules to include in this approach.

- Module 1: Introduction to Biology
- Module 2: Viruses
- Module 3: History of Life
- Module 4: Prokaryotes
- Module 5: Protists
- Module 6: Fungi
- Module 7: Plant Diversity
- Module 8: Plant Structure and Function
- Module 9: Plant Reproduction
- Module 10: Animal Diversity
- Module 11: Invertebrates
- Module 12: Vertebrates
- Module 13: Overview of Body Systems
- Module 25: Ecology of Living Things
- Module 26: Ecology and the Environment

Optional: You can also include a deeper focus on one or two body systems of your choosing, from modules 14–24.

Human-Centric Approach

This second method has a light discussion of the diversity of life, but is largely focused on the human body. In this method, we focus in on the human body systems. Below are recommended modules to include in this approach.

- Module 1: Introduction to Biology
- Module 3: History of Life
- Module 7: Plant Diversity
- Module 10: Animal Diversity
- Module 14: Nervous System
- Module 15: Endocrine System
- Module 16: Reproductive System
- Module 17: Sensory Systems
- Module 18: Circulatory System

- Module 19: Respiratory System
- Module 20: Immune System
- Module 21: Digestive System
- Module 22: Excretory System
- Module 23: Musculoskeletal System
- Module 24: Integumentary System
- Module 25: Ecology of Living Things
- Module 26: Ecology and the Environment

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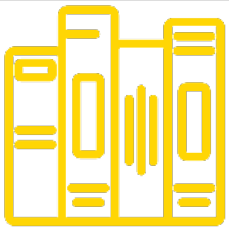
CHAPTER OVERVIEW

2: Faculty Resources

2.1: Faculty Resource Overview
2.2: Pacing
2.3: PDF
2.4: PowerPoints
2.5: Assignments
2.6: Question Banks
2.7: I Need Help

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2.1: Faculty Resource Overview



We've seen overwhelming demand for high quality, openly-licensed course materials, including supplemental resources to enrich teaching and learning and to make life easier for instructors. To support this need, we've developed and curated faculty resources to use with this course.

Free and Open Supplemental Materials

On the following pages, you will find supplemental resources that are freely available to use with the interactive learning materials for this course. Since these resources are openly licensed, you may use them as is or adapt them to your needs.

Additional Faculty Resources

Additional supplemental resources, learning tools, and support services are available to faculty who adopt Waymaker, OHM, or Candela courses with paid support from Lumen Learning. For many courses, these include some combination of summative assessments, answer keys, solutions manuals, or other materials shared only with authorized instructors in order to protect academic integrity.

Click here to learn more about additional instructor tools and resources available to faculty who adopt Lumen-supported courseware. Information about pricing and payment options is available on this page. Lumen's low-cost support fees replace the cost of expensive textbooks and may be paid by students or by the institution directly.

Continuously Improving Learning Materials

Are you interested in collaborating with us to make these course materials better? We use learning data to identify where content improvements are needed, and then we invite faculty and subject matter experts to work with us developing continuous improvements aimed at increasing learning.

Learn more from this blog post, or sign up here to join our continuous improvement mailing list and stay up to date about upcoming OER hackathons and other continuous improvement activities.

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2.2: Pacing



The Biology for Majors II textbook contains twenty-six chapters. As mentioned in Teaching this Course, we do not recommend teaching all twenty-six chapters in a single semester. There are two primary approaches we recommend:

Broad Approach

This first method has a broad coverage, discussing the the scope and diversity of life. Below are recommended modules to include in this approach.

- Module 1: Introduction to Biology
- Module 2: Viruses
- Module 3: History of Life
- Module 4: Prokaryotes
- Module 5: Protists
- Module 6: Fungi
- Module 7: Plant Diversity
- Module 8: Plant Structure and Function
- Module 9: Plant Reproduction
- Module 10: Animal Diversity
- Module 11: Invertebrates
- Module 12: Vertebrates
- Module 13: Overview of Body Systems
- Module 25: Ecology of Living Things
- Module 26: Ecology and the Environment

Optional: You can also include a deeper focus on one or two body systems of your choosing, from modules 14–24. This approach has 15 modules (with an optional 16th module)—roughly one chapter per week for a sixteen-week semester. If you need to modify the pace and cover the material more quickly, the following chapters work well together:

- Module 1: Introduction to Biology and Module 2: Viruses
- Module 3: History of Life and Module 4: Prokaryotes
- Module 5: Protists and Module 6: Fungi
- Module 7: Plant Diversity and Module 9: Plant Reproduction
- Module 25: Ecology of Living Things and Module 26: Ecology and the Environment

We recommend NOT doubling up the following modules, because they are long and especially challenging. Students will need more time for mastery and completion of assignments.

- Module 11: Invertebrates
- Module 13: Vertebrates

Human-Centric Approach

This second method has a light discussion of the diversity of life, but is largely focused on the human body. In this method, we focus in on the human body systems. Below are recommended modules to include in this approach.

- Module 1: Introduction to Biology

- Module 3: History of Life
- Module 7: Plant Diversity
- Module 10: Animal Diversity
- Module 14: Nervous System
- Module 15: Endocrine System
- Module 16: Reproductive System
- Module 17: Sensory Systems
- Module 18: Circulatory System
- Module 19: Respiratory System
- Module 20: Immune System
- Module 21: Digestive System
- Module 22: Excretory System
- Module 23: Musculoskeletal System
- Module 24: Integumentary System
- Module 25: Ecology of Living Things
- Module 26: Ecology and the Environment

This approach has 17 modules—roughly one chapter per week for a sixteen-week semester. If you need to modify the pace and cover the material more quickly, the following chapters work particularly well together:

- Module 1: Introduction to Biology and Module 3: History of Life
- Module 7: Plant Diversity and Module 10: Animal Diversity
- Module 18: Circulatory System and Module 19: Respiratory System
- Module 21: Digestive System and Module 22: Excretory System
- Module 23: Musculoskeletal System and Module 24: Integumentary System
- Module 25: Ecology of Living Things and Module 26: Ecology and the Environment

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2.3: PDF



Lumen makes significant investments to ensure our digital courseware is accessible, allowing students to learn using superior interactivity, multimedia, and a variety of accommodations for individuals with varying abilities.

PDFs offer an inferior learning experience compared to the richness and interactivity in our digital courseware. A PDF version of the textbook is available as a print alternative. The PDF does not include interactive content such as simulations, videos, and quizzes and is not vetted for accessibility. For these reasons, **we do not recommend using the textbook in the PDF form**. The offline version should be used as a print backup rather than as the primary textbook.

You can download the PDF using the following link:

1. All Module PDFs
2. Broad Approach PDFs (Modules 1–13; 25–26)
3. Humanistic Approach PDFs (Modules 1, 3, 7, 10; 14–26)

To share these files with your students, copy and paste the text and download link above into a page or announcement in your learning management system (Blackboard, Canvas, etc.).

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2.4: PowerPoints

This course includes PowerPoint slide decks organized by chapter and aligned to course content.

Since the slides are openly licensed, you are welcome to retain, reuse, revise, remix, and redistribute them. They are also accessible. If you do revise them, make sure to follow these guidelines for creating accessible PowerPoints.

Use the following link to download all PowerPoint decks in a single .zip file (110 MB), or download each individual deck below:

1. Introduction to Biology
2. Viruses
3. History of Life
4. Prokaryotes
5. Protists
6. Fungi
7. Plant Diversity
8. Plant Structure and Function
9. Plant Reproduction
10. Animal Diversity
11. Invertebrates
12. Vertebrates
13. Overview of Body Systems
14. Nervous System
15. Endocrine System
16. Reproductive System
17. Sensory Systems
18. Circulatory System
19. Respiratory System
20. Immune System
21. Digestive System
22. Excretory System
23. Musculoskeletal System
24. Integumentary System
25. Ecology of Living Things
26. Ecology and the Environment

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2.5: Assignments

The assignments in this course are openly licensed, and are available as-is, or can be modified to suit your students' needs. If you import this course into your learning management (Blackboard, Canvas, etc.), the assignments will automatically be loaded into the assignment tool.

The assignments in this course cover content taught multiple modules. The alignment of each assignment can be seen below, and you can download print files of each assignment.

Assignment Files and Alignment		
Assignment	Student File	Covered Modules
Build a Cell	.docx, .rtf	Module 1: Introduction to Biology, Module 2: Viruses, and Module 4: Prokaryotes
Nature's Recyclers	.docx, .rtf	Module 5: Protists, Module 6: Fungi, and Module 26: Ecology and the Environment
Hobby Horticulturalist	.docx, .rtf	Module 7: Plant Diversity, Module 8: Plant Structure and Function, and Module 9: Plant Reproduction
Morphological Phylogenetics	.docx, .rtf	Module 3: History of Life, Module 10: Animal Diversity, and Module 12: Vertebrates
Public Relations: Invertebrates are Awesome!	.docx, .rtf	Module 11: Invertebrates
Medical Experience	.docx, .rtf	Module 13: Overview of Body Systems
Synesthesia is an HR Issue?	.docx, .rtf	Module 14: The Nervous System and Module 17: Sensory Systems
Infertility: What's to Blame	.docx, .rtf	Module 15: The Endocrine System and Module 16: The Reproductive System
High Altitude Athletic Training Advertisement	.docx, .rtf	Module 18: The Circulatory System and Module 19: The Respiratory System
New AIDS Treatment Protocol	.docx, .rtf	Module 20: The Immune System and Module 23: The Musculoskeletal System
Infographic: Celiac Disease vs IBS	.docx, .rtf	Module 21: The Digestive System, Module 22: The Excretory System, and Module 24: The Integumentary System
Ecotourism	.docx, .rtf	Module 25: Ecology and the Biosphere and Module 26: Ecology and the Environment

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2.6: Question Banks

The machine-graded assessments in this course are organized by module and are aligned to specific learning outcomes. Waymaker courses assess students in three locations: Show What You Know (ungraded pretests at the beginning of each module), Self-Checks (short, ungraded practice tests), and end-of-module quizzes (graded).

Authorized faculty may edit and delete quiz questions and also add new ones using the quiz editing tool inside their Waymaker course(s). To learn more about editing the assessments in Waymaker, visit the Waymaker Faculty User Guide AFTER the course package has been imported to your learning management system (Blackboard, Canvas, etc.).

Optional Download

The Show What You Know and Self-Check questions are also available as a separate file that can be downloaded and imported into the assessment tool in your LMS. This format and extra step are needed ONLY if you want to make your own customized quiz, midterm, or final exam that combines quiz questions from multiple modules.

There are 26 question banks with a total of 1268 multiple choice questions.

We provide quiz banks as QTI files, a standard format that allows you to import questions, build, and customize quizzes in most learning management systems (Canvas, Blackboard, etc.). **These files cannot be opened outside of an LMS.**

According to Lumen company policy, we do not provide quizzes in written (e.g. MS Word) form, in order to preserve the academic integrity of our quiz banks on behalf of everyone using our materials. We adopted this policy after observing how easy it is for quiz banks in written formats to find their way onto websites that promote academic cheating.

Click the name of your LMS to prompt the download of the file.

- Canvas
- Blackboard
- D2L
- Moodle

Once you've downloaded the file, visit the Quiz Imports page and click through to the directions for your LMS.

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2.7: I Need Help



Need more information about this course? Have questions about faculty resources? Can’t find what you’re looking for? Experiencing technical difficulties?

We’re here to help! Take advantage of the following Lumen customer-support resources:

- Check out one of Lumen’s Faculty User Guides here.
- Submit a support ticket here and tell us what you need.
- Talk and screen-share with a live human during Lumen’s OER office hours. See available times here.

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CHAPTER OVERVIEW

3: Resources- Course Assignments

3.1: Assignment- Build a Cell
3.2: Assignment- Nature’s Recyclers
3.3: Assignment- Hobby Horticulturalist
3.4: Assignment- Morphological Phylogenetics
3.5: Assignment- Public Relations- Invertebrates are Awesome!
3.6: Assignment- Medical Experience
3.7: Assignment- Synesthesia is an HR Issue?
3.8: Assignment- Infertility- What’s to Blame
3.9: Assignment- High Altitude Athletic Training Advertisement
3.10: Assignment- New AIDS Treatment Protocol
3.11: Assignment- Celiac Disease vs IBS
3.12: Assignment- Ecotourism

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3.1: Assignment- Build a Cell

Build a model of a prokaryotic cell using any material of your choice. In your model be sure to include all the structures appropriate to your cell. You may model a bacterial cell or an archaea. You will model at least 4 structures in any model.

Next, build a model of a virus using the same type of materials. You may choose any type of virus but be sure you can illustrate the key features of a virus (head shape for example).

Once complete, take multiple photographs of your models from all angles. Include these images in a document that also contains the following completed table format. You may need to add rows to your table depending on the type of prokaryote you model.

Structure	Model Key	Function	Found in Virus	Different in Virus

Once your model is complete, write a brief description of your cell and your virus. Emphasize features that are absent in viruses that classify them as non-living. You can refer to specific structures in your table in this explanation.

Some suggestions for 3D models include Legos, a decorated cake with candy toppings, or standard Styrofoam base with appropriate pieces attached. You can also draw or illustrate a model.

Rubric: Build a Cell

Criteria	Ratings			Pts
Prokaryotic model provided	Model includes nucleoid, DNA, ribosomes, and cell membrane and other structures such as cilia, flagella or cell wall	Model includes nucleoid, DNA, ribosomes, and cell membrane	Model does not include nucleoid, DNA, ribosomes, and cell membrane	3 pts
Viral model provided	Model includes nucleic acid, coat, shaped head, and tail	Model includes nucleic acid, coat, and tail	Model does not include nucleic acid, coat, and tail	3 pts
Table is fully completed	All structures include a key and detailed function description; viral structures are also included/labeled	All structures are not fully described or functions are incomplete	Not all structures are included or viral differences are not noted	3 pts
Written description	Written description fully outlines and discusses both models and emphasizes the features of viruses that classify them as non-living. Specific features of the models are referenced in description	Written description is brief or terse but does address required points	Written description is incomplete or absent	3 pts
Total points: 12				

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3.2: Assignment- Nature's Recyclers

Humans consider themselves amazingly clever and innovative, constantly developing "new" ways of altering the world around us. As material consumption has increased, many have turned to the ideas of recycling and reuse as a means to minimize some negative aspects of our modern consumerism. Mother Nature though is the ultimate innovator and, more importantly, the ultimate recycler.

Write a brief paper that summarizes the key role that protists and fungi play as nature's recyclers. Focus your paper on your local environment or perhaps your favorite location. Emphasize their specific ecological functions, using appropriate terminology, within food webs and biogeochemical cycles. Identify at least one species of each within your paper.

Rubric: Nature's Recyclers

Criteria	Ratings			Pts
Role of fungi and protists as recyclers is discussed	Protists and fungi are identified as decomposers; the terms saprobes and decomposer are accurately applied. Specific mention is made of how these organisms serve as "recyclers." At least 1 species of each is identified.	Protists and fungi are identified as decomposers; discussion includes why this is "recycling." One species of each is identified.	Protists and fungi are identified as decomposers only; no specific species are named.	3 pts
Discussion focuses on single location	Multiple protists/fungi and their roles are identified appropriate to the specified location.	Specific role of protists/fungi is identified for a specified location.	No specific location is discussed	3 pts
Role of fungi/protists in food webs are discussed	Role of fungi/protists as the decomposer level of food webs is discussed in relation to other levels of food webs.	Role of fungi/protists as the decomposer level of food webs is discussed.	Role of fungi/protists as the decomposer level of food webs is not discussed.	3 pts
Role of fungi/protists in biogeochemical cycles is identified	Role of fungi/protists in multiple specific biogeochemical cycles is discussed.	Role of fungi/protists in at least one biogeochemical cycle is discussed.	Fungi/protists are not discussed in terms of biogeochemical cycles.	3 pts
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3.3: Assignment- Hobby Horticulturalist

You have decided to take up horticulture as a hobby. The first thing you will do in pursuit of this new passion is identifying a plant found in your yard or local environment. If you do not have a yard or live in an urban environment, visit a local park or botanical garden. Collect a field journal on your chosen plant (this means take lots of photos and measurements as you can).

Conduct appropriate research to provide the following information.

1. Scientific and common name of your plant
2. Classification of the plant (vascular vs. non-vascular, seedless vs. seed, flowering vs. non-flowering)
3. Dominant stage in life cycle (gametophyte vs. sporophyte)
4. Life span
5. Reproductive frequency
6. Method of reproduction (self vs. cross, artificial vs. natural reproduction)
7. Method of pollen distribution
8. Natural environment/distribution
9. Type of root system
10. Is your plant considered invasive or alien to your area?

Provide images (photographs, sketches, or even scans will work) of the following structures and label them appropriately.

1. Shape of leaf (be sure to label all the parts of a leaf on one of your images)
2. Primary and secondary growth (if appropriate)
3. Flower or seed (if appropriate and available)

Rubric: Hobby Horticulturalist

Criteria	Ratings			Pts
Plant is identified	Scientific and multiple common names provided	Scientific and common name provided	Scientific and common name are not both provided	3 pts
Plant is classified	Plant is fully classified (vascularity, seeds, flowering)	Plant is classified at only a high level (i.e. stop as vascular)	Plant is not classified	3 pts
Life cycle is identified	Dominant and secondary stage are identified	Dominant stage is identified specific to plant at time of examination	No life stage is identified	3 pts
Life span is noted	Full life span is identified, along with “guess” as to current likely life span	Average life span is identified	Life span is not identified	3 pts
Reproductive frequency is identified	Reproductive frequency is identified, along with current status (varies by plant and season)	Reproductive frequency is identified	Reproductive frequency is not identified	3 pts
Method of reproduction is identified	Natural and artificial reproduction methods are both identified	Typical reproduction method identified	No reproductive method is identified	3 pts
Pollen distribution is noted	Pollinators and pollination identified	Pollen distribution is identified	Pollen distribution is not discussed	3 pts
Natural environment	Natural distribution and environmental requirements are noted	Natural distribution is listed	Distribution is not identified	3 pts
Root system identified	Root system is identified and illustrated	Root system is identified	Root system is not identified	3 pts
Images are provided	Leaf, growth, flower/seed are all photographed or imaged from multiple views and each image is clearly labeled	Images are provided and gross features labeled	Images are not provided or are not labeled	3 pts
Total points: 30				

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3.4: Assignment- Morphological Phylogenetics

You have returned to college to become a phylogeneticist. One of the first things you wish to do is determine how mammals, birds, and reptiles are related.

Like any good scientist, you need to consider all available data objectively and without a preconceived “correct” answer. In pursuit of that, you should produce a phylogenetic tree based only on morphological features that show birds and mammals are more closely related. You will then produce a totally different tree, also using morphological features, that shows birds and reptiles are more closely related. Do not forget to include all three groups in both your trees.

Based solely off the trees you produce, which relationship would you consider the more likely and why? Once you have answered that question, provide a brief summary of the “modern” understanding of the relationship between these three groups.

Rubric: Morphological Phylogenetics

Criteria	Ratings			Pts
Mammalian/avian tree is provided	Tree includes full relationship with all 3 groups sharing multiple characteristics until the mammal/bird split from reptiles	Tree includes relationships between all 3 groups on a minimal number of features	Tree does not include all 3 groups	3 pts
Reptilian/avian tree is provided	Tree includes full relationship with all 3 groups sharing multiple characteristics until the reptile/bird split from mammals	Tree includes relationships between all 3 groups on a minimal number of features	Tree does not include all 3 groups	3 pts
One tree is identified as most likely	Discussion outlines multiple features for the “chosen” tree	Discussion outlines at least 1 reason for the chosen tree	Discussion does not use the trees to argue for a closer relationship	3 pts
Modern understanding is discussed	At least 2 pieces of modern evidence (not only morphological) is discussed	Modern evidence is discussed	Modern evidence is not discussed or the current relationships are not properly identified	3 pts
Total points: 12				

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3.5: Assignment- Public Relations- Invertebrates are Awesome!

You have been hired as a public relations specialist to give invertebrates a good name. After all, they are much more than just creepy crawly bugs!

Your first task though is to convince yourself that is true. The best way to do that is to start close to home. Find something in your house that is a product obtained directly from an invertebrate or only due to an invertebrate's actions. Describe the product, its function and utility, as well as any human manufactured alternatives. Be sure to highlight the advantages of obtaining this directly from nature.

Keep in mind, a product can be something you use, wear, eat, or enjoy for its visual appeal.

Rubric: Public Relations: Invertebrates are Awesome!

Criteria	Ratings			Pts
Home product is identified	A non-obvious product is identified	An obvious home product is identified	No product is identified	3 pts
Function and utility	Full functions and uses are discussed	One function/use is discussed	No function or use is discussed	3 pts
Human alternatives	At least one manufactured alternative is identified or suggested	A manufactured alternative is identified or suggested	No alternative is identified	3 pts
Natural advantages	Advantages and disadvantages are identified for obtaining this product naturally	Advantages are identified for obtaining this product naturally	No advantages are identified for the natural product	3 pts
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3.6: Assignment- Medical Experience

Identify a medical condition that affects you or a close family member. Research and write a summary of the condition that addresses the following points:

1. Signs and symptoms of the condition
2. How the condition is diagnosed
3. Body system directly impacted by the condition
4. At least one other body system impacted by the condition or its symptoms
5. Treatment options (traditional and holistic are appropriate here)
6. On-going medical research on this condition
7. Prognosis of condition
8. Personal impact of this condition

Rubric: Medical Experience

Criteria	Ratings			Pts
Condition	Signs, symptoms, and specific tests used in diagnosis are discussed, including rare symptoms or timeline of progression	Signs, symptoms, and tests used in diagnosis are discussed	Major signs/symptoms or diagnosis not discussed	3 pts
Body systems	Major and secondary body systems directly impacted and then connected systems are identified	Major body system impacted and one connected system identified	Major body system or connected system not identified	3 pts
Treatment	Current, experimental and holistic treatment options are all identified	Current standard treatment is identified	Treatments are not identified or discussed	3 pts
Medical research	A summary of specific medical research is provided	A high level overview of ongoing medical research is provided	Medical research is not discussed	3 pts
Prognosis	Typical and atypical prognosis is discussed, including impact of treatment options	Typical prognosis is discussed	Prognosis is not provided	3 pts
Personal impact	Personal impact is discussed		Personal impact is not discussed	3 pts
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3.7: Assignment- Synesthesia is an HR Issue?

You are an occupational nurse for a large corporation. One day the manager of a team rushes into your office in a panic. At a team building exercise, one of the employees mentions she has synesthesia. The manager is now concerned that some type of reasonable accommodation needs to be made to ensure she can perform her job fully. There have been some issues recently with this employee missing deadlines. Could it be due to her synesthesia?

You tell the manager you have never heard of this condition before but will do some research and get back to her. Once she leaves your office you begin your investigation. At the end of it, you need to prepare a brief (1–2 page) report for the manager explaining the following:

- What is synesthesia
- Medically how does it occur (be sure to focus on neuronal and sensory system features here)
- What are the more common types of synesthesia
- Could this condition be impacting the employee's ability to meet deadlines
- Any types of work projects that could be given to the employee that actually take advantage of her synesthesia

Rubric: Synesthesia is an HR Issue?

Criteria	Ratings			Pts
Synesthesia Definition	Signs, symptoms, and specific tests used in diagnosis are discussed	Signs and symptoms, and tests are discussed	Major signs or symptoms not discussed	3 pts
Medical explanation	Specific discussion focused on neuronal interpretation of sensory signals	High level discussion that touches upon mismatch between sensory signals and neuronal perception	Mismatch between sensory and neuronal systems not addressed	3 pts
Types of synesthesia	At least 3 types of synesthesia are highlighted, with specific symptoms	At least 2 types of synesthesia are highlighted, with specific symptoms	0–1 types of different synesthesia discussed	3 pts
Deadlines	Possible impact of specific types of synesthesia on "time perceptions" are discussed	General statement on synesthesia's general impact on work performance	Does not address work performance concerns	3 pts
Work Projects	Specific skillsets or strengths of different forms of synesthesia are identified with "work projects"	Different work projects suggested that may not be associated with specific types of synesthesia	No specific work projects are suggested	3 pts
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3.8: Assignment- Infertility- What's to Blame

You have been hired as a medical assistant at an infertility clinic. One day a couple comes to a consultation appointment to discuss their inability to conceive. They desperately want children but are concerned about the "level" of medical intervention that may be necessary. Rather than just accepting a standard treatment plan, they insist that the underlying cause for their infertility needs to be determined. They do not care about associated costs or time; they absolutely insist upon knowing why they have this problem before deciding how to treat it.

The doctor you assist tasks you with developing a list of possible causes, focused on endocrine as well as reproductive system issues. You need to consider both the male and female system. In addition to outlining the possible underlying cause, you need to suggest a test for each factor you identify. You should complete a table as shown below, identifying at least 3 causes from the endocrine system and 3 from the reproductive system for each sexes.

System	Organ/Tissue	Function	Impact on Conception	Test

Rubric: Infertility: What's to Blame

Criteria	Ratings			Pts
Endocrine system	At least 3 possible endocrine organs/tissues are identified that relate to human conception	3 possible endocrine organs/tissues are identified that relate to human conception but at a high level of detail	2 or fewer possible endocrine organs/tissues are identified that relate to human conception but not to specific infertility issues	3 pts
Reproductive system	At least 3 possible reproductive organs/tissues are identified that relate to human conception	3 possible reproductive organs/tissues are identified that relate to human conception but at a high level of detail	2 or fewer possible reproductive organs/tissues are identified that relate to human conception but not to specific infertility issues	3 pts
Sexual differences	Both sexes are covered fully in both systems		Both sexes are not fully addressed in both systems	3 pts
Conception	Each identified organ/tissue is associated with a specific impact on the process of fertilization through implantation	Not all organ/tissue is associated with a specific impact on the process of fertilization through implantation	Not organ/tissue is associated with a specific impact on the process of fertilization through implantation	3 pts
Tests	Each identified organ/tissue is associated with a test (even if not truly available medically)	Not all organs/tissues are associated with a test	No specific testing plan is suggested	3 pts
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3.9: Assignment- High Altitude Athletic Training Advertisement

You have been hired to develop a promotional brochure for a fitness destination camp located at a high altitude. This camp wishes to attract athletes from around the world to train and live at the facility before their big event. In the promotional brochure you should focus on attracting competitors by highlighting specific circulatory and respiratory changes that can be induced by high altitude training. Be sure to note how far in advance of the big event competitors should plan to move into the facility and how early they can plan to leave without losing their physiological boosts.

And because this is a reputable facility, be sure to provide references for all those intense athletes to check.

Rubric: High Altitude Athletic Training Advertisement

Criteria	Ratings			Pts
Circulatory system	More than 2 positive circulatory system changes identified that occur from high altitudes	1–2 positive circulatory system changes identified that occur from high altitudes	0 positive circulatory system changes identified that occur from high altitudes	3 pts
Respiratory system	More than 2 positive respiratory system changes identified that occur from high altitudes	1–2 positive respiratory system changes identified that occur from high altitudes	0 positive respiratory system changes identified that occur from high altitudes	3 pts
Timing	Timing for both latest arrival and earliest departure from high altitude training identified for both sports	Timing for latest arrival or earliest departure from high altitude training identified for both sports	No timing considerations addressed	3 pts
References	At least 1 study is referenced for each system benefits noted		No references provided supporting health claims	3 pts
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3.10: Assignment- New AIDS Treatment Protocol

The “Berlin patient” is a medical case frequently discussed in which a patient received a bone marrow transplant as a treatment for a blood cancer. The unique part of the Berlin patient is that he was also cured of an HIV infection. Over the years there have been a number of tests to determine what about the bone marrow transplant addressed a systemic immunity failure such as AIDS.

Summarize the Berlin patient information, focused on the connection between the skeletal and immune systems. Specifically note factors that likely contributed to curing the Berlin patient’s HIV infection. Finally, discuss why this type of treatment approach is unlikely to become a widespread solution to ongoing HIV infections and AIDS epidemic.

Rubric: New AIDS Treatment Protocol

Criteria	Ratings			Pts
Berlin patient	Original treatment (why and what) discussed, along with the timeline for AIDS “cure”	Original treatment addressed at a high level with specific comments about AIDS outcome	Original treatment not discussed or not connected to AIDS cure	3 pts
AIDS outcome	All possible explanations for AIDS “cure” are summarized, specifically emphasizing the connection between the immune and skeletal systems	Limited summary of possible causes of AIDS cure, with only basic connections made between immune and skeletal systems	Possible explanations for AIDS cure are not discussed, or both skeletal and immune system are not addressed	3 pts
General Cure	Risks and success rates are discussed as arguments against the Berlin patient scenario as a general AIDS cure	Limited discussion of risks and success rates against the Berlin patient scenario as a general AIDS cure	No discussion of why this will not be a general AIDS cure	3 pts
Total points: 9				

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3.11: Assignment- Celiac Disease vs IBS

You volunteer for a doctor's office developing infographic handouts for patients. After a recent episode of "Celebrity Diagnosis Face Off" a number of patients have come into the office convinced they have celiac disease. Others believe they have irritable bowel syndrome. The doctor and nursing staff have become so frustrated that they asked you to develop an infographic for patients focused on the two diseases.

Be sure to focus on digestive, excretory and integumentary symptoms of each as well as how they are diagnosed.

Rubric: Celiac Disease vs IBS

Criteria	Ratings			Pts
Celiac disease	Signs and symptoms of celiac disease are highlighted, including impacts in digestive, excretory, and integumentary systems	Signs and symptoms of celiac disease are highlighted, including impacts in at least 2 of systems	Celiac disease is poorly explained, or only 1 system is discussed	3 pts
Irritable Bowel Syndrome	Signs and symptoms of IBS are highlighted, including impacts in digestive, excretory, and integumentary systems	Signs and symptoms of IBS are highlighted, including impacts in at least 2 of systems	IBS is poorly explained, or only 1 system is discussed	3 pts
Infographic	Information on both conditions is presented as an infographic, not as plain text		Information is not presented as an infographic	3 pts
Total points: 9				

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3.12: Assignment- Ecotourism

You have decided to start a travel agency focused on ecotourism with a positive impact on the natural world. One of the first items on your to-do list is to create a brochure highlighting a biome that your clients can visit.

In your brochure, be sure to address the following points:

1. Location
2. Major biotic components
3. Major abiotic components
4. Energy flow/food web (don’t forget the detritivores!)
5. Relative biodiversity
6. Impact/risk from climate change
7. Impact/risk from invasive species
8. Impact/risk from human activities
9. How your ecotours will have a positive impact

Remember, good brochures have lots of photos highlighting the natural wonders, so be sure to provide appealing graphics or images.

Rubric: Ecotourism

Criteria	Ratings			Pts
Location	Location is identified geographically, including similar (and unique) characteristics	Location is identified geographically	A specific location is not identified	3 pts
Biotic components	Biotic components at all tropic levels are identified	Biotic components are identified	Few or no biotic components are identified	3 pts
Abiotic components	Multiple abiotic components are identified	Abiotic components are identified	Few or no abiotic components are identified	3 pts
Food web	All levels of the food web are identified, with multiple species	All levels of the food web are identified	Not all levels of the food web are identified	3 pts
Biodiversity	Specific unique biodiversity features are mentioned	Biodiversity is summarized	Biodiversity is not addressed	3 pts
Climate change	Potential/actual impact of climate change is discussed with specific evidence	Potential impact of climate change is discussed	Climate change is not addressed specifically	3 pts
Invasive species	Potential/actual impact of invasive species discussed with specific evidence and species identified	Potential impact of invasive species discussed	Invasive species not addressed specifically	3 pts
Human activities	Potential/actual impact of human activity discussed with specific evidence	Potential impact of human activity discussed	Human activity not addressed specifically	3 pts
Positive impact	Specific environmental activities discussed	Positive impacts addressed at a high level, such as economically	Positive impacts not discussed	3 pts
Total points: 27				

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CHAPTER OVERVIEW

4: Module 1- Introduction to Biology

4.1: Why It Matters- Introduction to Biology
4.2: Introduction to Characteristics of Life
4.3: Properties of Life
4.4: Levels of Organization of Living Things
4.5: Introduction to Prokaryotes and Eukaryotes
4.6: Comparing Prokaryotic and Eukaryotic Cells
4.7: Introduction to Taxonomy
4.8: The Diversity of Life
4.9: Phylogenetic Trees
4.10: Taxonomy
4.11: Introduction to the Study of Biology
4.12: The Branches of Biology
4.13: Scientific Inquiry
4.14: Experiments and Hypotheses
4.15: Interpreting Results
4.16: Putting It Together- Introduction to Biology

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4.1: Why It Matters- Introduction to Biology

Why define biology and apply its principles?



Figure 1. The pangolin (also known as the scaly anteater) is a unique animal. It walks on just its hind legs and uses its front claws to tear open termite mounds.

One night while she was scrolling through her social media feeds, Cristina saw that her brother had linked to an article about some of the world's weirdest animals. As she paged through the article, Cristina became increasingly interested in the different features these animals had: some were eyeless, some were colorless, and others had even stranger features.

Before Cristina could dig deeper into these animals, she got a message from her cousin Samuel. He'd sent a link to an article that said scientists had discovered a new organ in the human body called the mesentery. Cristina watched a short video attached to the article, but before she began to read the article itself, she remembered that she had a paper due the next day. She made a mental note to come back to the article from her cousin, and she bookmarked the animals article.

Though Cristina might not realize it, she's just been presented with two different biological questions. How did these animals develop such unique characteristics? How could scientists just now be discovering a new organ?

Cristina still has to come to her own conclusions and make her own choices, but having an understanding of biology will help her make the best choices she can.

Learning Outcomes

- List the defining characteristics of biological life
- Identify the different kinds of cells that make up different kinds of organisms
- Describe classification and organizational tools biologists use, including modern taxonomy
- Describe biology as a science and identify the key components of scientific inquiry

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4.2: Introduction to Characteristics of Life

List the defining characteristics of biological life

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

What You'll Learn to Do

- List the properties of life
- Order the levels of organization of living things

Learning Activities

The learning activities for this section include the following:

- Properties of Life
- Levels of Organization of Living Things
- Self Check: Characteristics of Life

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4.3: Properties of Life

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

Order



Figure 1. A toad represents a highly organized structure consisting of cells, tissues, organs, and organ systems.

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

In multicellular organisms (Figure 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.

Sensitivity or Response to Stimuli



Figure 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)

Organisms respond to diverse stimuli. For example, plants can bend toward a source of light, climb on fences and walls, or respond to touch (Figure 2). Even tiny bacteria can move toward or away from chemicals (a process called *chemotaxis*) or light (*phototaxis*). Movement toward a stimulus is considered a positive response, while movement away from a stimulus is considered a negative response.

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

Reproduction

Single-celled organisms reproduce by first duplicating their DNA, and then dividing it equally as the cell prepares to divide to form two new cells. Multicellular organisms often produce specialized reproductive germline cells that will form new individuals. When reproduction occurs, 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



Figure 3. Although no two look alike, these puppies have inherited genes from both parents and share many of the same characteristics.

Organisms grow and develop following specific instructions coded for by their genes. These genes provide instructions that will direct cellular growth and development, ensuring that a species' young (Figure 3) will grow up to exhibit many of the same characteristics as its parents.

Regulation

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

Homeostasis



Figure 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)

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 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.

Energy Processing

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



Figure 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.

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4.4: 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), which contains the instructions for the structure and functioning of all living organisms.

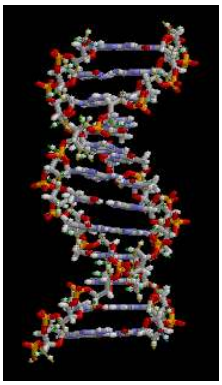


Figure 1. All molecules, including this DNA molecule, are composed of atoms. (credit: “brian0918″/Wikimedia Commons)

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 or organelles; in contrast, the cells of **eukaryotes** do have membrane-bound organelles and a membrane-bound nucleus.

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

All the individuals of a species living within a specific area are collectively called a **population**. For example, a forest may include many pine trees. All of these pine trees represent the population of pine trees in this forest. Different populations may live in the same specific area. For example, the forest with the pine trees includes populations of flowering plants and also insects and microbial populations. A **community** is the sum of populations inhabiting a particular area. For instance, all of the trees, flowers, insects, and other populations in a forest form the forest’s community. 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 rain water. At the highest level of organization (Figure 2), the **biosphere** is the collection of all ecosystems, and it represents the zones of life on earth. It includes land, water, and even the atmosphere to a certain extent.

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

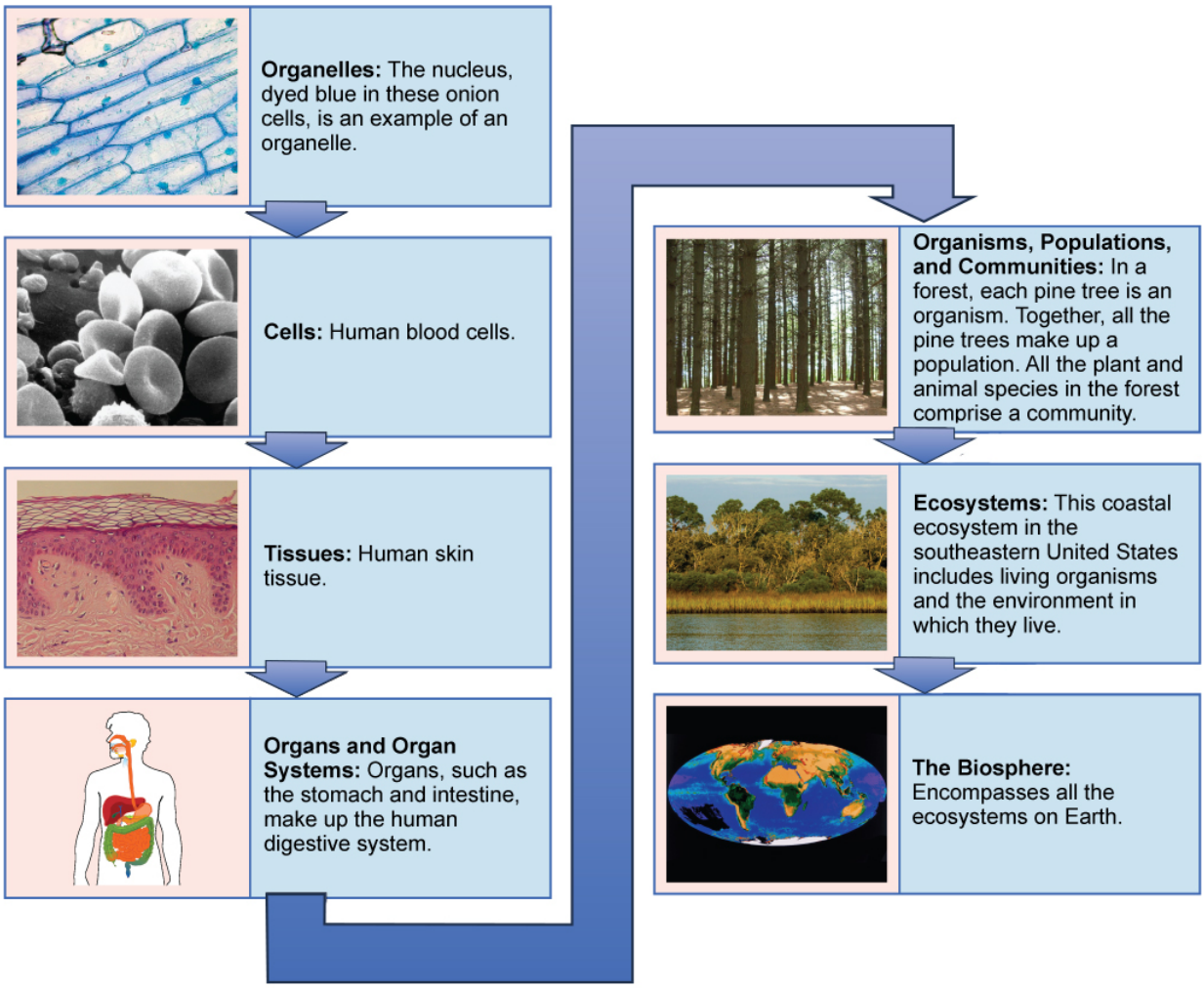


Figure 7. The biological levels of organization of living things are shown. From a single organelle to the entire biosphere, living organisms are parts of a highly structured hierarchy. (credit “organelles”: modification of work by Umberto Salvagnin; credit “cells”: modification of work by Bruce Wetzel, 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)

Practice Question

Which of the following statements is false?

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.

[reveal-answer q=”750531″]**Show Answer**[/reveal-answer]
[hidden-answer a=”750531″]Statement b is false: populations exist within communities.[/hidden-answer]

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4.5: Introduction to Prokaryotes and Eukaryotes

Identify the different kinds of cells that make up different kinds of organisms

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

What You'll Learn to Do

- Identify features common to all cells
- Contrast the composition and size of prokaryotic and eukaryotic cells

Learning Activities

The learning activities for this section include the following:

- Comparing Prokaryotic and Eukaryotic Cells
- Self Check: Prokaryotes and Eukaryotes

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4.6: Comparing Prokaryotic and Eukaryotic Cells

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

Components of Prokaryotic Cells

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

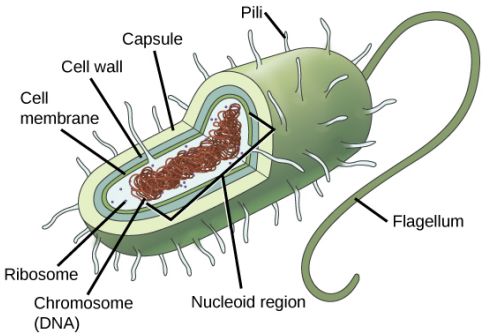


Figure 1. This figure shows the generalized structure of a prokaryotic cell.

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

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

Eukaryotic Cells

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

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

Cell Size

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

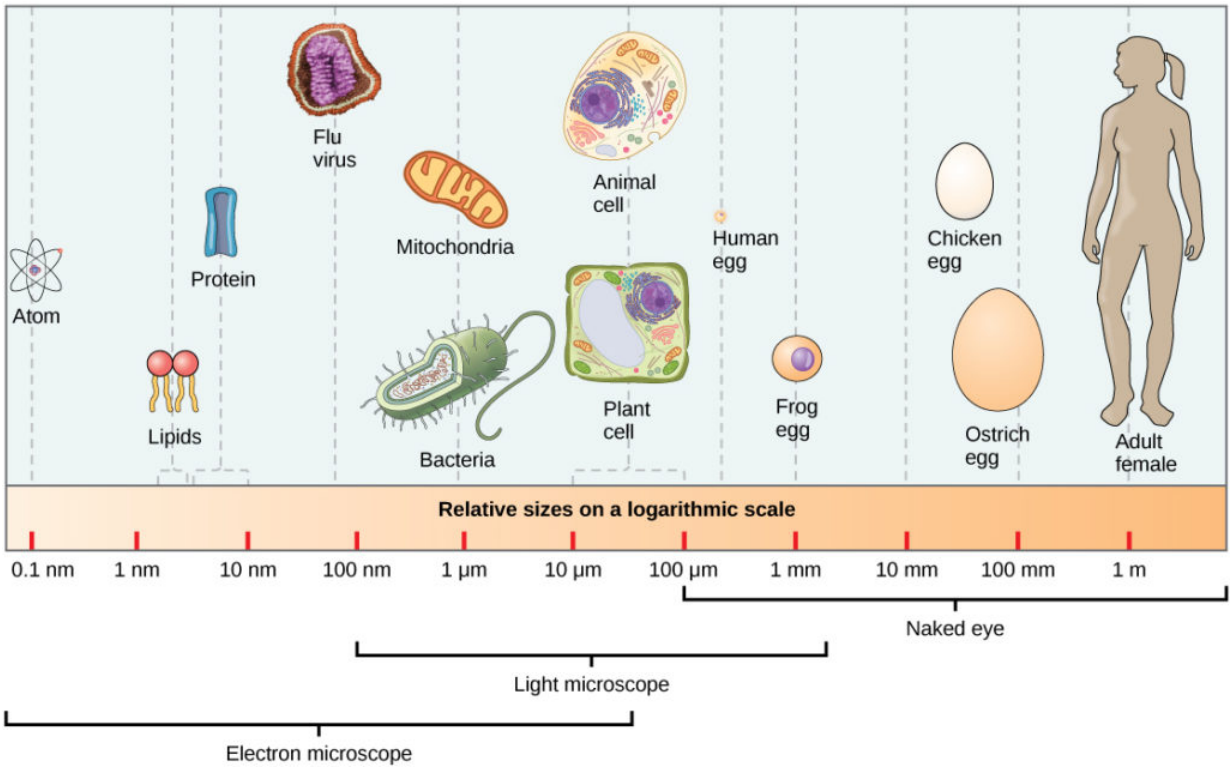


Figure 2. This figure shows the relative sizes of different kinds of cells and cellular components. An adult human is shown for comparison.

Learning Objectives

Prokaryotes are single-celled organisms of the domains Bacteria and Archaea. All prokaryotes have plasma membranes, cytoplasm, ribosomes, a cell wall, DNA, and lack membrane-bound organelles. Many also have polysaccharide capsules. Prokaryotic cells range in diameter from 0.1–5.0 µm.

Like a prokaryotic cell, a eukaryotic cell has a plasma membrane, cytoplasm, and ribosomes, but a eukaryotic cell is typically larger than a prokaryotic cell, has a true nucleus (meaning its DNA is surrounded by a membrane), and has other membrane-bound organelles that allow for compartmentalization of functions. Eukaryotic cells tend to be 10 to 100 times the size of prokaryotic cells.

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4.7: Introduction to Taxonomy

Describe classification and organizational tools biologists use, including modern taxonomy



Figure 1. Our planet

Viewed from space, Earth offers no clues about the diversity of life forms that reside there. The first forms of life on Earth are thought to have been microorganisms that existed for billions of years in the ocean before plants and animals appeared. The mammals, birds, and flowers so familiar to us are all relatively recent, originating 130 to 200 million years ago. Humans have inhabited this planet for only the last 2.5 million years, and only in the last 200,000 years have humans started looking like we do today.

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

What You'll Learn to Do

- Explain the "diversity of life"
- Explain the purpose of phylogenetic trees
- Explain how relationships are indicated by the binomial naming system

Learning Activities

The learning activities for this section include the following:

- The Diversity of Life
- Phylogenetic Trees
- Taxonomy
- Self Check: Taxonomy

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4.8: The Diversity of Life



Figure 1. Life on earth is incredibly diverse.

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

The sheer amount of biological diversity on the Earth is incredible. There are approximately 8.7 different species on the earth today!

What Is Biodiversity?

Biodiversity refers to the variety of life and its processes, including the variety of living organisms, the genetic differences among them, and the communities and ecosystems in which they occur. Scientists have identified about 1.9 million species alive today. They are divided into the six kingdoms of life shown in Figure 2. Scientists are still discovering new species. Thus, they do not know for sure how many species really exist today. Most estimates range from 5 to 30 million species.

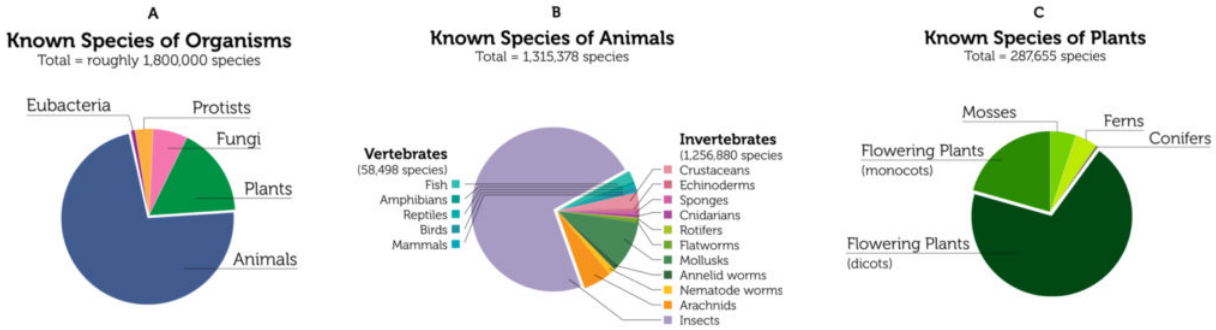


Figure 2. Known life on earth

Cogs and Wheels

To save every cog and wheel is the first precaution of intelligent tinkering.

—Aldo Leopold, Round River: from the Journals of Aldo Leopold, 1953

What are the “cogs” and “wheels” of life?

Although the concept of biodiversity did not become a vital component of biology and political science until nearly 40 years after Aldo Leopold’s death in 1948, Leopold – often considered the father of modern ecology – would have likely found the term an appropriate description of his “cogs and wheels.” Literally, biodiversity is the many different kinds (diversity) of life (bio-). Biologists, however, always alert to levels of organization, have identified three measures of life’s variation. Species diversity best fits the literal translation: the number of different species in a particular ecosystem or on Earth. A second measure recognizes variation within a species: differences among individuals or populations make up genetic diversity. Finally, as Leopold clearly understood, the “cogs and wheels” include not only life but also the land, sea, and air that support life. Ecosystem diversity describes the many types of functional units formed by living communities interacting with their environments. Although all three levels of diversity are important, the term biodiversity usually refers to species diversity.

Watch this discussion about biodiversity:

A link to an interactive elements can be found at the bottom of this page.

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

? Try It



Figure 2. The short-beaked echidna is endemic to Australia. This animal—along with the platypus and three other species of echidnas—is one of the five surviving species of egg-laying mammals.

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

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

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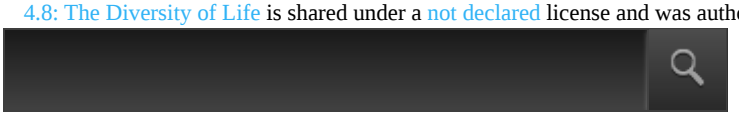
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4.9: Phylogenetic Trees

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

Phylogenetic Trees

Scientists use a tool called a phylogenetic tree to show the evolutionary pathways and connections among organisms. A **phylogenetic tree** is a diagram used to reflect evolutionary relationships among organisms or groups of organisms. Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past since one cannot go back to confirm the proposed relationships. In other words, a "tree of life" can be constructed to illustrate when different organisms evolved and to show the relationships among different organisms (Figure 1).



Figure 1. Both of these phylogenetic trees shows the relationship of the three domains of life—Bacteria, Archaea, and Eukarya—but the (a) rooted tree attempts to identify when various species diverged from a common ancestor while the (b) unrooted tree does not. (credit a: modification of work by Eric Gaba)

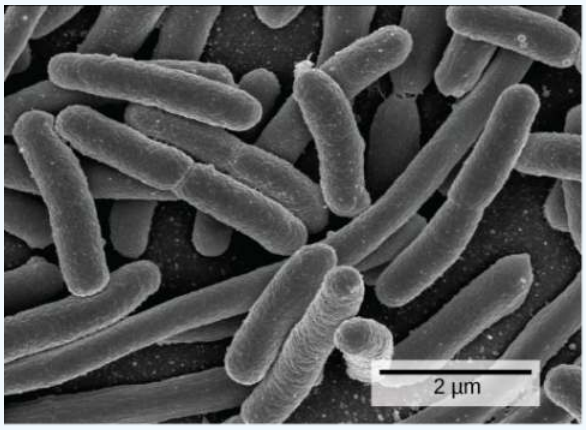
A phylogenetic tree can be read like a map of evolutionary history. Many phylogenetic trees have a single lineage at the base representing a common ancestor. Scientists call such trees rooted, which means there is a single ancestral lineage (typically drawn from the bottom or left) to which all organisms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

? Try It

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 groups of 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 1a). 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 2). 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.



(a)



(b)



(c)



(d)

Figure 2. These organisms 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)

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4.10: Taxonomy

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

The taxonomic classification system (also called the Linnaean system after its inventor, Carl Linnaeus, a Swedish botanist, zoologist, and physician) uses a hierarchical model. Moving from the point of origin, the groups become more specific, until one branch ends as a single species. For example, after the common beginning of all life, scientists divide organisms into three large categories called a domain: Bacteria, Archaea, and Eukarya. Within each domain is a second category called a **kingdom**. After kingdoms, the subsequent categories of increasing specificity are: **phylum**, **class**, **order**, **family**, **genus**, and **species** (Figure 1).

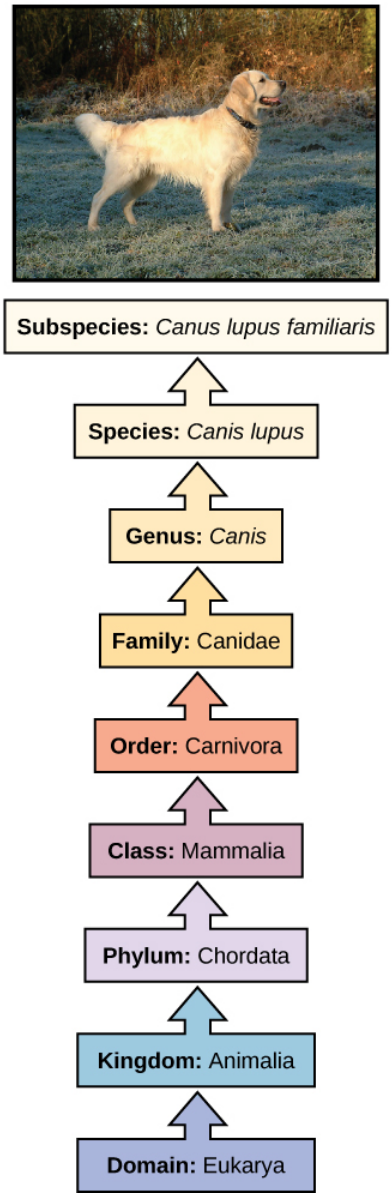


Figure 1. The taxonomic classification system uses a hierarchical model to organize living organisms into increasingly specific categories. The common dog, Canis lupus familiaris, is a subspecies of Canis lupus, which also includes the wolf and dingo. (credit “dog”: modification of work by Janneke Vreugdenhil)

The kingdom Animalia stems from the Eukarya domain. For the common dog, the classification levels would be as shown in Figure 1. Therefore, the full name of an organism technically has eight terms. For the dog, it is: Eukarya, Animalia, Chordata, Mammalia, Carnivora, Canidae, *Canis*, and *lupus*. Notice that each name is capitalized except for species, and the genus and species names are italicized. Scientists generally refer to an organism only by its genus and species, which is its two-word scientific name, in what is called **binomial nomenclature**. Therefore, the scientific name of the dog is *Canis lupus*. The name at each level is also called a **taxon**. In other words, dogs are in order Carnivora. Carnivora is the name of the taxon at the order level; Canidae is the taxon at the family level, and so forth. Organisms also have a common name that people typically use, in this case, dog. Note that the dog is additionally a subspecies: the "*familiaris*" in *Canis lupus familiaris*. Subspecies are members of the same species that are capable of mating and reproducing viable offspring, but they are considered separate subspecies due to geographic or behavioral isolation or other factors.

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4.11: Introduction to the Study of Biology

Describe biology as a science and identify the key components of scientific inquiry

The scope of biology is vast. Biologists may study anything from the microscopic (Figure 1a) or submicroscopic view of a cell to ecosystems (Figure 1b) and the whole living planet.

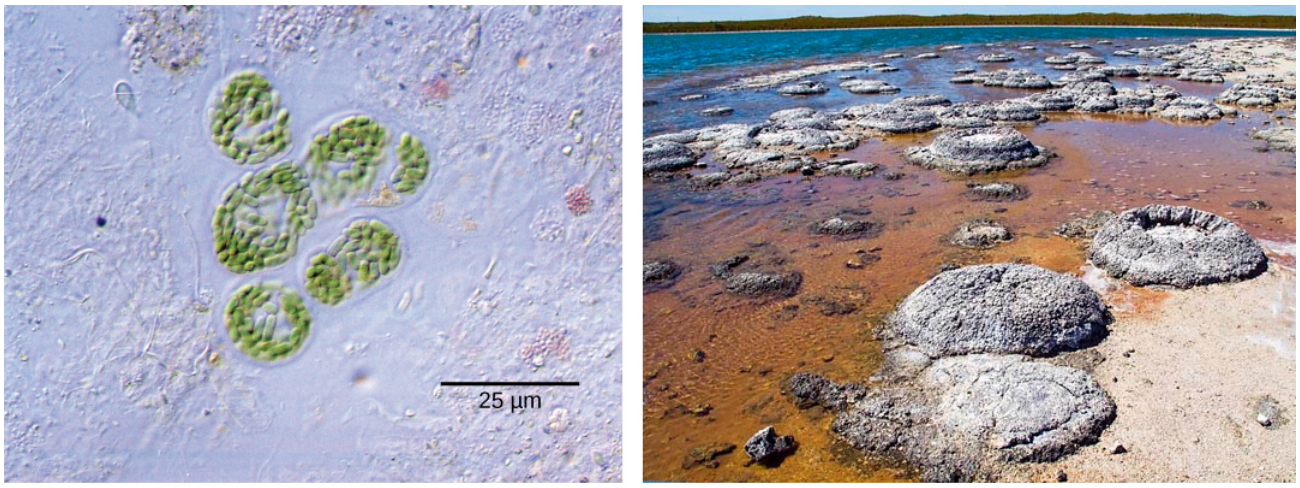


Figure 1. (a) Formerly called blue-green algae, these cyanobacteria, shown here at 300× magnification under a light microscope, are some of Earth's oldest life forms. (b) These stromatolites along the shores of Lake Thetis in Western Australia are ancient structures formed by the layering of cyanobacteria in shallow waters.

Listening to the daily news, you will quickly realize how many aspects of biology are discussed every day. You may hear about *E. coli (Escherichia coli)* outbreaks in spinach or listeria contamination in ice cream. Or you may hear about efforts toward finding a cure for Ebola, 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.

Regardless of their particular focus of study, all biologists use the same methodology as they seek new discoveries: scientific inquiry.

What You'll Learn to Do

- Identify the main branches of biology
- Describe "scientific inquiry" and identify its scope of coverage
- Form a hypothesis and use it to design a scientific experiment
- Analyze simple data and graphed results

Learning Activities

The learning activities for this section include the following:

- The Branches of Biology
- Scientific Inquiry
- Experiments and Hypotheses
- Interpreting Results
- Self Check: The Study of Biology

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- Stromatolites at Lake Thetis. **Authored by**: Ruth Ellison. **Located at**: https://flic.kr/p/ezabK. **License**: *CC BY-NC: Attribution-NonCommercial*

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- Modification of Cyanobacteria; scale-bar data from Matt Russell. **Provided by**: NASA. **Located at**: https://commons.wikimedia.org/wiki/File:Cyanobacteria_guerrero_negro.jpg. **License**: *Public Domain: No Known Copyright*

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4.12: The Branches of Biology

The scope of biology is broad and therefore contains many branches and sub-disciplines. Biologists may pursue one of those sub-disciplines 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 itself, and depending on the subject of study, there are also microbial physiologists, ecologists, and geneticists, among others.

Forensic Science



Figure 1. This forensic scientist works in a DNA extraction room at the U.S. Army Criminal Investigation Laboratory at Fort Gillem, GA. (credit: United States Army CID Command Public Affairs)

Forensic science is the application of science to answer questions related to the law. Biologists as well as chemists and biochemists can be forensic scientists. Forensic scientists provide scientific evidence for use in courts, and their job involves examining trace materials associated with crimes. Interest in forensic science has increased in the last few years, possibly because of popular television shows that feature forensic scientists on the job. Also, the development of molecular techniques and the establishment of DNA databases have expanded the types of work that forensic scientists can do.

Their job activities are primarily related to crimes against people such as murder, rape, and assault. Their work involves analyzing samples such as hair, blood, and other body fluids and also processing DNA (Figure 1) found in many different environments and materials.

Forensic scientists also analyze other biological evidence left at crime scenes, such as insect larvae or pollen grains. Students who want to pursue careers in forensic science will most likely be required to take chemistry and biology courses as well as some intensive math courses.

Another field of biological study, neurobiology, studies the biology of the nervous system, and although it is considered a branch of biology, it is also recognized as an interdisciplinary field of study known as neuroscience. Because of its interdisciplinary nature, this sub-discipline studies different functions of the nervous system using molecular, cellular, developmental, medical, and computational approaches.



Figure 2. Researchers work on excavating dinosaur fossils at a site in Castellón, Spain. (credit: Mario Modesto)

Paleontology, another branch of biology, uses fossils to study life's history (Figure 2). Zoology and botany are the study of animals and plants, respectively. Biologists can also specialize as biotechnologists, ecologists, or physiologists, to name just a few areas. This is just a small sample of the many fields that biologists can pursue.

Biology is the culmination of the achievements of the natural sciences from their inception to today. Excitingly, it is the cradle of emerging sciences, such as the biology of brain activity, genetic engineering of custom organisms, and the biology of evolution that uses the laboratory tools of molecular biology to retrace the earliest stages of life on earth. A scan of news headlines—whether reporting on immunizations, a newly discovered species, sports doping, or a genetically modified food—demonstrates the way biology is active in and important to our everyday world.

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4.13: Scientific Inquiry

Science deals with testable knowledge about physical phenomena in the universe. The goal of science is to understand how the universe works. Biology focuses on understanding living things. To gain knowledge about nature and physical phenomena, scientists use a particular approach called “scientific inquiry.”

Scientific inquiry is the best approach we have to understanding the natural world and predicting natural phenomena. Evidence for this claim can be found in the successes of science-based technologies. Take medicine, for example. Prior to the 1700s, most medical practices were based on folk traditions or on ideas promoted by religious leaders. Some of these prescientific remedies worked, but the process for discovering new treatments was a slow and haphazard system of trial and error. Ineffective treatments were often accepted simply because there was no clear procedure for evaluating them. Today, with science-based medicine and public health practices, we have gained unprecedented control over threats to our health. According to the Centers for Disease Control, the average life expectancy in the United States has increased by more than 30 years since 1900.

Scientific inquiry has not displaced faith, intuition, and dreams. These traditions and ways of knowing have emotional value and provide moral guidance to many people. But hunches, feelings, deep convictions, old traditions, or dreams cannot be accepted directly as scientifically valid. Instead, science limits itself to ideas that can be tested through verifiable observations. Supernatural claims that events are caused by ghosts, devils, God, or other spiritual entities cannot be tested in this way.

Practice Question

Your friend sees this image of a circle of mushrooms and excitedly tells you it was caused by fairies dancing in a circle on the grass the night before. Can your friend’s explanation be studied using the process of science?



Figure 1. A fairy ring

[practice-area rows=”2″][/practice-area]
[reveal-answer q=”665464″]**Show Answer**[/reveal-answer]
[hidden-answer a=”665464″]In theory, you might try to observe the fairies. But fairies are magical or supernatural beings. We have never observed them using any verifiable method, so scientists agree that they cannot be studied using scientific tools. Instead, science has an explanation supported by strong evidence: “fairy rings” result when a single colony of fungus spreads out into good habitat over a period of many years. The core area is clear of mushrooms because the soil nutrients have been partly depleted there. This idea can be evaluated with repeated observations over time using chemical soil tests and other verifiable measurements.
[/hidden-answer]

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4.14: Experiments and Hypotheses

Now we'll focus on the methods of scientific inquiry. Science often involves making observations and developing hypotheses. Experiments and further observations are often used to test the hypotheses.

A scientific experiment is a carefully organized procedure in which the scientist intervenes in a system to change something, then observes the result of the change. Scientific inquiry often involves doing experiments, though not always. For example, a scientist studying the mating behaviors of ladybugs might begin with detailed observations of ladybugs mating in their natural habitats. While this research may not be experimental, it is scientific: it involves careful and verifiable observation of the natural world. The same scientist might then treat some of the ladybugs with a hormone hypothesized to trigger mating and observe whether these ladybugs mated sooner or more often than untreated ones. This would qualify as an experiment because the scientist is now making a change in the system and observing the effects.

Forming a Hypothesis

When conducting scientific experiments, researchers develop hypotheses to guide experimental design. A hypothesis is a suggested explanation that is both testable and falsifiable. You must be able to test your hypothesis, and it must be possible to prove your hypothesis true or false.

For example, Michael observes that maple trees lose their leaves in the fall. He might then propose a possible explanation for this observation: "cold weather causes maple trees to lose their leaves in the fall." This statement is testable. He could grow maple trees in a warm enclosed environment such as a greenhouse and see if their leaves still dropped in the fall. The hypothesis is also falsifiable. If the leaves still dropped in the warm environment, then clearly temperature was not the main factor in causing maple leaves to drop in autumn.

In the Try It below, you can practice recognizing scientific hypotheses. As you consider each statement, try to think as a scientist would: can I test this hypothesis with observations or experiments? Is the statement falsifiable? If the answer to either of these questions is "no," the statement is not a valid scientific hypothesis.

? Practice Questions

Determine whether each following statement is a scientific hypothesis.

1. Air pollution from automobile exhaust can trigger symptoms in people with asthma.
    a. No. This statement is not testable or falsifiable.
    b. No. This statement is not testable.
    c. No. This statement is not falsifiable.
    d. Yes. This statement is testable and falsifiable.
2. Natural disasters, such as tornadoes, are punishments for bad thoughts and behaviors.
    a. No. This statement is not testable or falsifiable.
    b. No. This statement is not testable.
    c. No. This statement is not falsifiable.
    d. Yes. This statement is testable and falsifiable.

[reveal-answer q="429550″]**Show Answers**[/reveal-answer]
[hidden-answer a="429550″]

1. d: Yes. This statement is testable and falsifiable. This could be tested with a number of different kinds of observations and experiments, and it is possible to gather evidence that indicates that air pollution is not linked with asthma.
2. a: No. This statement is not testable or falsifiable. "Bad thoughts and behaviors" are excessively vague and subjective variables that would be impossible to measure or agree upon in a reliable way. The statement might be "falsifiable" if you came up with a counterexample: a "wicked" place that was not punished by a natural disaster. But some would question whether the people in that place were really wicked, and others would continue to predict that a natural disaster was bound

to strike that place at some point. There is no reason to suspect that people's immoral behavior affects the weather unless you bring up the intervention of a supernatural being, making this idea even harder to test.

[/hidden-answer]

Testing a Vaccine

Let's examine the scientific process by discussing an actual scientific experiment conducted by researchers at the University of Washington. These researchers investigated whether a vaccine may reduce the incidence of the human papillomavirus (HPV). The experimental process and results were published in an article titled, "A controlled trial of a human papillomavirus type 16 vaccine."

Preliminary observations made by the researchers who conducted the HPV experiment are listed below:

- Human papillomavirus (HPV) is the most common sexually transmitted virus in the United States.
- There are about 40 different types of HPV. A significant number of people that have HPV are unaware of it because many of these viruses cause no symptoms.
- Some types of HPV can cause cervical cancer.
- About 4,000 women a year die of cervical cancer in the United States.

? Practice Question

Researchers have developed a potential vaccine against HPV and want to test it. What is the first testable hypothesis that the researchers should study?

a. HPV causes cervical cancer.
b. People should not have unprotected sex with many partners.
c. People who get the vaccine will not get HPV.
d. The HPV vaccine will protect people against cancer.

[reveal-answer q="20917"]**Show Answer**[/reveal-answer]
[hidden-answer a="20917"]Hypothesis A is not the best choice because this information is already known from previous studies. Hypothesis B is not testable because scientific hypotheses are not value statements; they do not include judgments like "should," "better than," etc. Scientific evidence certainly might support this value judgment, but a hypothesis would take a different form: "Having unprotected sex with many partners increases a person's risk for cervical cancer." Before the researchers can test if the vaccine protects against cancer (hypothesis D), they want to test if it protects against the virus. This statement will make an excellent hypothesis for the next study. The researchers should first test hypothesis C—whether or not the new vaccine can prevent HPV.[/hidden-answer]

Experimental Design

You've successfully identified a hypothesis for the University of Washington's study on HPV: People who get the HPV vaccine will not get HPV.

The next step is to design an experiment that will test this hypothesis. There are several important factors to consider when designing a scientific experiment. First, scientific experiments must have an experimental group. This is the group that receives the experimental treatment necessary to address the hypothesis.

The experimental group receives the vaccine, but how can we know if the vaccine made a difference? Many things may change HPV infection rates in a group of people over time. To clearly show that the vaccine was effective in helping the experimental group, we need to include in our study an otherwise similar control group that does not get the treatment. We can then compare the two groups and determine if the vaccine made a difference. The control group shows us what happens in the absence of the factor under study.

However, the control group cannot get "nothing." Instead, the control group often receives a placebo. A *placebo* is a procedure that has no expected therapeutic effect—such as giving a person a sugar pill or a shot containing only plain saline solution with no drug. Scientific studies have shown that the "placebo effect" can alter experimental results because when individuals are told that they

are or are not being treated, this knowledge can alter their actions or their emotions, which can then alter the results of the experiment.

Moreover, if the doctor knows which group a patient is in, this can also influence the results of the experiment. Without saying so directly, the doctor may show—through body language or other subtle cues—his or her views about whether the patient is likely to get well. These errors can then alter the patient's experience and change the results of the experiment. Therefore, many clinical studies are "double blind." In these studies, neither the doctor nor the patient knows which group the patient is in until all experimental results have been collected.

Both placebo treatments and double-blind procedures are designed to prevent bias. Bias is any systematic error that makes a particular experimental outcome more or less likely. Errors can happen in any experiment: people make mistakes in measurement, instruments fail, computer glitches can alter data. But most such errors are random and don't favor one outcome over another. Patients' belief in a treatment can make it more likely to appear to "work." Placebos and double-blind procedures are used to level the playing field so that both groups of study subjects are treated equally and share similar beliefs about their treatment.

? Practice Questions

The scientists who are researching the effectiveness of the HPV vaccine will test their hypothesis by separating 2,392 young women into two groups: the control group and the experimental group. Answer the following questions about these two groups.

1. Which of the following groups most likely represents the control group?
    a. This group is given a placebo.
    b. This group is deliberately infected with HPV.
    c. This group is given nothing.
    d. This group is given the HPV vaccine.
2. Which of the following groups most likely represents the experimental group?
    a. This group is given a placebo.
    b. This group is deliberately infected with HPV.
    c. This group is given nothing.
    d. This group is given the HPV vaccine.

[reveal-answer q="918962"]**Show Answers**[/reveal-answer]
[hidden-answer a="918962"]

1. a: This group is given a placebo. A placebo will be a shot, just like the HPV vaccine, but it will have no active ingredient. It may change peoples' thinking or behavior to have such a shot given to them, but it will not stimulate the immune systems of the subjects in the same way as predicted for the vaccine itself.
2. d: This group is given the HPV vaccine. The experimental group will receive the HPV vaccine and researchers will then be able to see if it works, when compared to the control group.

[/hidden-answer]

Experimental Variables

A variable is a characteristic of a subject (in this case, of a person in the study) that can vary over time or among individuals. Sometimes a variable takes the form of a category, such as male or female; often a variable can be measured precisely, such as body height. Ideally, only one variable is different between the control group and the experimental group in a scientific experiment. Otherwise, the researchers will not be able to determine which variable caused any differences seen in the results. For example, imagine that the people in the control group were, on average, much more sexually active than the people in the experimental group. If, at the end of the experiment, the control group had a higher rate of HPV infection, could you confidently determine why? Maybe the experimental subjects were protected by the vaccine, but maybe they were protected by their low level of sexual contact.

To avoid this situation, experimenters make sure that their subject groups are as similar as possible in all variables except for the variable that is being tested in the experiment. This variable, or factor, will be deliberately changed in the experimental group. The

one variable that is different between the two groups is called the independent variable. An independent variable is known or hypothesized to cause some outcome. Imagine an educational researcher investigating the effectiveness of a new teaching strategy in a classroom. The experimental group receives the new teaching strategy, while the control group receives the traditional strategy. It is the teaching strategy that is the independent variable in this scenario. In an experiment, the independent variable is the variable that the scientist deliberately changes or imposes on the subjects.

Dependent variables are known or hypothesized consequences; they are the effects that result from changes or differences in an independent variable. In an experiment, the dependent variables are those that the scientist measures before, during, and particularly at the end of the experiment to see if they have changed as expected. The dependent variable must be stated so that it is clear how it will be observed or measured. Rather than comparing "learning" among students (which is a vague and difficult to measure concept), an educational researcher might choose to compare test scores, which are very specific and easy to measure.

In any real-world example, many, many variables MIGHT affect the outcome of an experiment, yet only one or a few independent variables can be tested. Other variables must be kept as similar as possible between the study groups and are called *control variables*. For our educational research example, if the control group consisted only of people between the ages of 18 and 20 and the experimental group contained people between the ages of 30 and 35, we would not know if it was the teaching strategy or the students' ages that played a larger role in the results. To avoid this problem, a good study will be set up so that each group contains students with a similar age profile. In a well-designed educational research study, student age will be a controlled variable, along with other possibly important factors like gender, past educational achievement, and pre-existing knowledge of the subject area.

? Practice Questions

What is the independent variable in this experiment?

a. Sex (all of the subjects will be female)
b. Presence or absence of the HPV vaccine
c. Age
d. Presence or absence of HPV (the virus)

[reveal-answer q="68680"]Show Answer[/reveal-answer]
[hidden-answer a="68680"]Answer b. Presence or absence of the HPV vaccine. This is the variable that is different between the control and the experimental groups. All the subjects in this study are female, so this variable is the same in all groups. In a well-designed study, the two groups will be of similar age. The presence or absence of the virus is what the researchers will measure at the *end* of the experiment. Ideally the two groups will both be HPV-free at the start of the experiment.

[/hidden-answer]

List three control variables other than age.

[practice-area rows="3"][/practice-area]
[reveal-answer q="903121"]Show Answer[/reveal-answer]
[hidden-answer a="903121"]Some possible control variables would be: general health of the women, sexual activity, lifestyle, diet, socioeconomic status, etc.

[/hidden-answer]

What is the dependent variable in this experiment?

a. Sex (male or female)
b. Rates of HPV infection
c. Age (years)

[reveal-answer q="907103"]Show Answer[/reveal-answer]
[hidden-answer a="907103"]Answer b. Rates of HPV infection. The researchers will measure how many individuals got infected with HPV after a given period of time.[/hidden-answer]

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4.15: Interpreting Results

Gathering Data

After the experiment is completed, the data gathered are carefully interpreted. This involves the measurement of the dependent variable. In the case of our HPV experiment, remember, the dependent variable is the rate of HPV infection.

? Practice Question

The researchers found that, of the 1,200 women in the control group, nine were infected with HPV at the end of the study. Of the 1,200 women in the experimental group, zero were infected with HPV. Does this result support the original hypothesis, that the HPV vaccine would reduce HPV infection?

[practice-area rows="2"][/practice-area]
[reveal-answer q="318356"]**Show Answer**[/reveal-answer]
[hidden-answer a="318356"]The results demonstrate that fewer individuals who got the vaccine were infected with HPV when compared to the number of infected individuals who did not get the vaccine. This supports the hypothesis that the new vaccine protects against HPV.[/hidden-answer]

Significance

Although the HPV study suggests that the vaccine protects against infection by HPV, is the finding significant? In science, as in life, things can happen for many different reasons. A convincing study will rule out "luck" (random chance) as an explanation for the results. Strong results are said to be significant: very unlikely to occur by chance or random events.

Whether the outcome is significant often depends on the size of study; the larger the number of individuals enrolled, the more convincing the results are likely to be. For example, imagine only 10 women were enrolled in the study. In the control group, 2 in 5 of the women became infected. In the experimental group, 0 in 5 were infected. At first you might think this proves the vaccine's effectiveness, but it is NOT a convincing or significant result. Why not? Random events could easily explain the difference between the groups. For example, perhaps none of the five women in the experimental group were sexually active over the study period. They therefore stood no chance of acquiring HPV. The vaccine might appear to work, but a skeptical reader could account for the results by proposing many other scenarios.

However, imagine if the same study were done with 10,000 women, and the infection rates were 2,000 of 5,000 in the control group and zero of 5,000 in the experimental group. Random events would be spread out among a very large group of people in this study; on average, the two big groups should have similar sexual behavior and other factors influencing infection rates. If there is a big difference at the end of the study, it is very unlikely that *this* result occurred by random chance.

Statistical analyses did support the significance of the HPV vaccine result.

? Practice Question

Researchers reported significant results from the HPV vaccine experiment. If the results had NOT been significant, what would this mean?

[practice-area rows="2"][/practice-area]
[reveal-answer q="185159"]**Show Answer**[/reveal-answer]
[hidden-answer a="185159"]If the results from this experiment were not significant, it would mean that the number of women who did not get HPV after being vaccinated was the same number that would be seen just from random chance.[/hidden-answer]

After the results are interpreted and conclusions are drawn, researchers often return to their work and begin asking further questions. In this way, scientific inquiry is a powerful tool for exploration.

? Practice Question

What would be a good next question the HPV vaccine researchers may want to test? (*More than one answer is correct.*)

a. At what age is this vaccine most effective (what age group should be vaccinated)?
b. Does the HPV vaccine protect males as well as females?
c. Does protecting against HPV protect against cancer?
d. Should young girls be forced to get the vaccine against their parents' wishes?

[reveal-answer q="689643"]**Show Answers**[/reveal-answer]
[hidden-answer a="689643"]

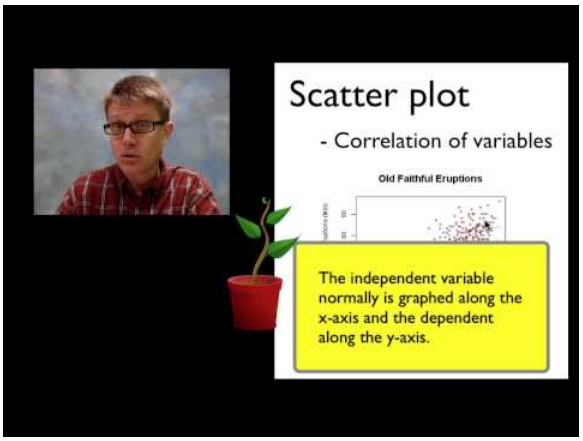
Questions a, b, anc c are the best questions. These questions are currently being studied.

Although question d is important and has generated a lot of political heat, it is not a scientific question. Scientists can predict what will happen if girls are or are not vaccinated, but cannot decide whether disease risk or parental authority is more important.

[/hidden-answer]

Graphing Data

Watch this ten-minute video about simple graphing:



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=106

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4.16: Putting It Together- Introduction to Biology

Biology is the study of life. As we've learned, this field covers a broad scope of subjects. As you progress through this course, you'll gain the knowledge you need to make informed decisions. Let's think back to the articles Cristina encountered at the beginning of this module: how could a knowledge of biological principle help with her understanding of each article?

Think about It

Cristina read an article about some of the world's weirdest animals. What biological principle would help her understand why these animals have the features they do?

[practice-area rows="4"][/practice-area]
[reveal-answer q="775039"]See Our Thoughts[/reveal-answer]
[hidden-answer a="775039"]By learning about evolution and natural selection, Cristina could begin to see the different evolutionary reasons behind the extreme features some animals have. For example, the aye-aye, a mammal native to Madagascar, has evolved to have an extra long middle finger, which it can use to dig grubs out of trees. Throughout the course we'll learn about different organisms and how their unique features allow them to survive and thrive in different environments.

[/hidden-answer]

Cristina also found an article about a "new" organ called the mesentery. How could scientists just now be discovering a new organ?

[practice-area rows="4"][/practice-area]
[reveal-answer q="781328"]See Our Thoughts[/reveal-answer]
[hidden-answer a="781328"]While our scientific understanding is much broader than it once was, our understanding is always expanding—we are always learning more things.

Clarifications of the mesenteric anatomy have facilitated a clearer understanding of diseases involving the mesentery—which include malrotation and Crohn's disease (CD). In CD, the mesentery is frequently thickened, rendering haemostasis challenging. Some authors say that CD is mainly a mesenteric disorder that secondarily affects the GIT and systemic circulation.[1]

As scientists researched the mesentery more and more, they found that it should be reclassified as an organ. As we will see in the chapter "Body Systems," having a better understanding of bodies can dramatically improve our ability to detect and prevent illness.
[/hidden-answer]

1. Sahebally SM, Burke JP, Chang KH, Kiernan MG, O'Connell PR, Coffey JC (November 2013). "Circulating fibrocytes and Crohn's disease". *The British Journal of Surgery*. **100** (12): 1549–56. doi:10.1002/bjs.9302. PMID 24264775↵

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CHAPTER OVERVIEW

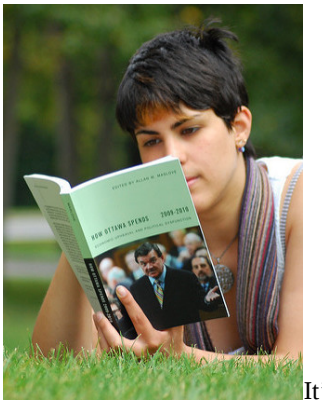
5: Module 2- Viruses

5.1: Why It Matters- Viruses
5.2: Introduction to Viral Evolution, Morphology, and Classification
5.3: History of Viruses
5.4: Viral Morphology
5.5: Virus Classification
5.6: Introduction to Virus Infections and Hosts
5.7: Steps of Virus Infections
5.8: Different Hosts and Their Viruses
5.9: Introduction to Prevention and Treatment of Viral Infections
5.10: Vaccines for Prevention
5.11: Vaccines and Anti-Viral Drugs for Treatment
5.12: Introduction to Prions and Viroids
5.13: Prions and Viroids
5.14: Putting It Together- Viruses
5.15: Cerego- Viruses

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5.1: Why It Matters- Viruses

Why identify different viruses and the methods they use to infect humans?



It's late October and Kendra's studying when she gets a text from her mom: "Have you gotten your flu shot yet?" Kendra sets down her book to text her mom that, no she hasn't had the time yet; classes have been keeping her really busy this semester. Besides, she got her flu shot last year. Her mom responds informing Kendra that her local drug store has a flu shot kiosk—one that promises a quick and easy vaccination. "If there's a line, you could study while you wait!" her mom concludes.

Kendra tells her mom she'll think about it, but that she really needs to get back to studying. A few minutes later, Kendra gets a text from her mom: it's an article explaining why people should get a flu shot every year. As Kendra reads on, she learns that the flu virus changes from year to year. She pauses in her reading: does this mean viruses are alive? They would have to be to change, right?

In this module, we'll learn about viruses: how they function and how they infect people and animals. And, of course, we'll determine whether or not they're alive.

Learning Outcomes

- Discuss the basics of virus discovery, evolution, and classification
- Describe a viral infection and explain what impact an infection has on its host
- Compare vaccinations and antiviral drugs as medical approaches to viruses
- Describe prions and viroids

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5.2: Introduction to Viral Evolution, Morphology, and Classification

Discuss the basics of virus discovery, evolution, 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.

What You'll Learn to Do

- Describe how viruses were first discovered and how they are detected
- Discuss three hypotheses about how viruses evolved
- Recognize the basic shapes of viruses
- Understand past and emerging classification systems for viruses

Learning Activities

The learning activities for this section include the following:

- History of Viruses
- Viral Morphology
- Viral Classification
- Self Check: Viral Evolution, Morphology, and Classification

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5.3: History of Viruses

No one knows exactly when viruses emerged or from where they came, since viruses do not leave historical footprints such as fossils. Modern viruses are thought to be a mosaic of bits and pieces of nucleic acids picked up from various sources along their respective evolutionary paths. Viruses are acellular, parasitic entities that are not classified within any kingdom. Unlike most living organisms, viruses are not cells and cannot divide. Instead, they infect a host cell and use the host's replication processes to produce identical progeny virus particles. Viruses infect organisms as diverse as bacteria, plants, and animals. They exist in a netherworld between a living organism and a nonliving entity. Living things grow, metabolize, and reproduce. Viruses replicate, but to do so, they are entirely dependent on their host cells. They do not metabolize or grow, but are assembled in their mature form.

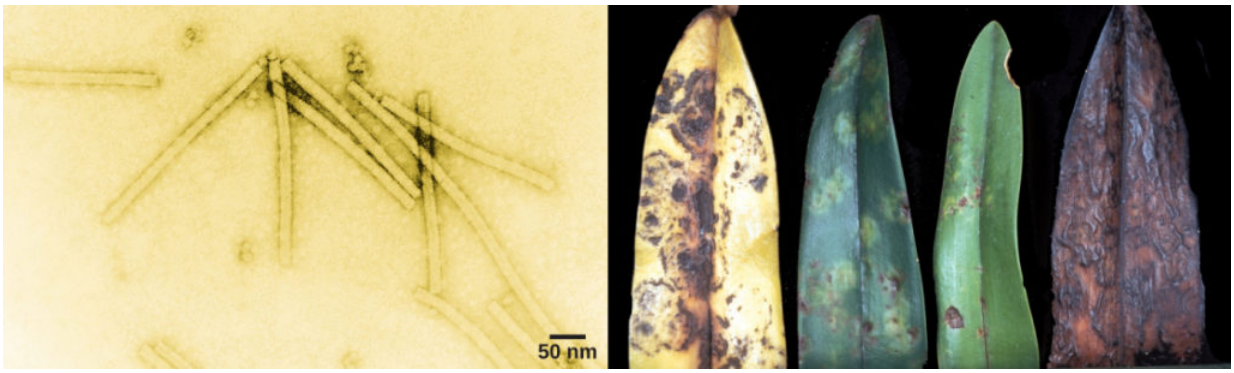


Figure 1. The tobacco mosaic virus (left), seen here by transmission electron microscopy, was the first virus to be discovered. The virus causes disease in tobacco and other plants, such as the orchid (right). (credit a: USDA ARS; credit b: modification of work by USDA Forest Service, Department of Plant Pathology Archive North Carolina State University; scale-bar data from Matt Russell)

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, 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 100 times larger), we cannot see viruses with a light microscope, with the exception of 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 good view of the structure of the tobacco mosaic virus (TMV) (Figure 1) and other viruses (Figure 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 of 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.

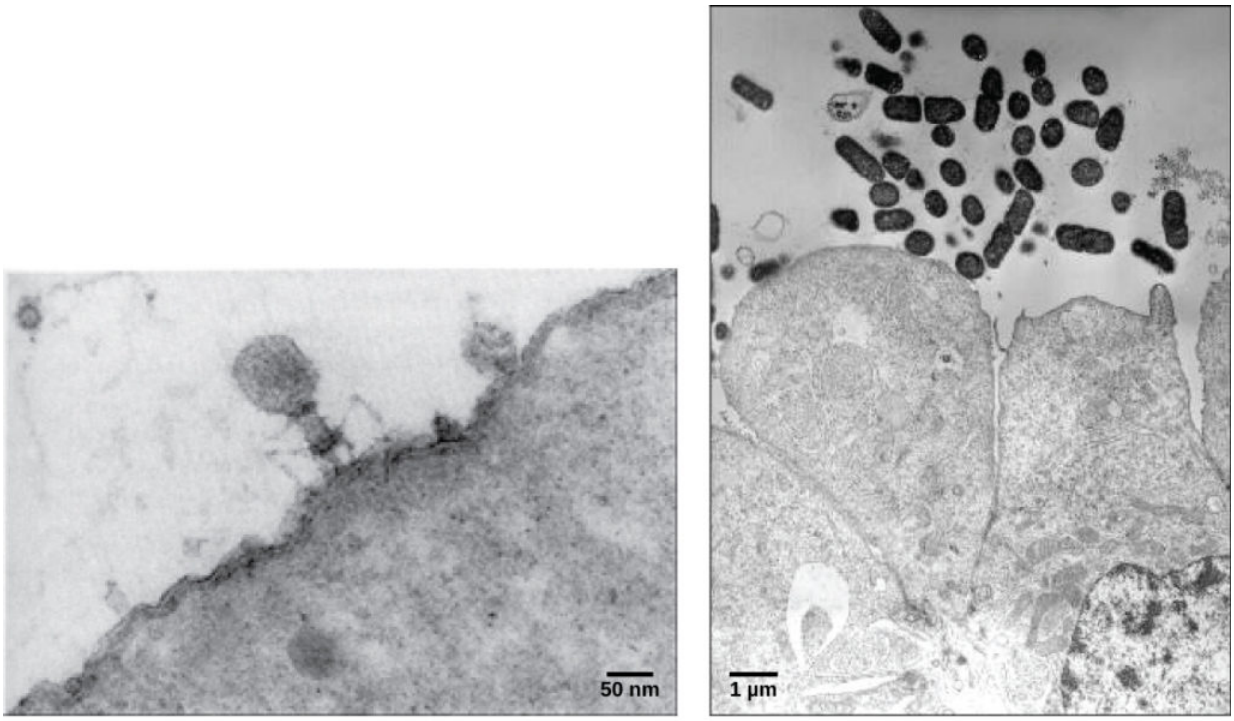


Figure 2. In these transmission electron micrographs, (a) a virus is dwarfed by the bacterial cell it infects, while (b) these E. coli cells are dwarfed by cultured colon cells. (credit a: modification of work by U.S. Dept. of Energy, Office of Science, LBL, PBD; credit b: modification of work by J.P. 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 historic evidence. However, viruses do not fossilize, so researchers can only hypothesize about viruses' evolutionary history 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 don't have a single common ancestor, scholars have yet to find a single hypothesis about virus origins that is fully accepted in the field—and that fully explains viruses and their characteristics. There are, however, three hypotheses that have risen as the most accepted:

- **Devolution** or **regressive hypothesis**. This hypothesis proposes to explain the origin of viruses by suggesting that viruses evolved from free-living cells. However, many components of how this process might have occurred are a mystery.
- **Escapist** or **progressive hypothesis**. This hypothesis accounts for viruses having either an RNA or a DNA genome and suggests that viruses originated from RNA and DNA molecules that escaped from a host cell. However, this hypothesis doesn't explain the complex capsids and other structures on virus particles.
- **Self-replication hypothesis**. This 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.

Another problem for those studying viral origins and evolution is their high rate of mutation, particularly the case in RNA retroviruses like HIV/AIDS.

As technology advances, scientists will develop and refine further hypotheses to explain the origin of viruses—or create new hypotheses. The emerging field called virus molecular systematics attempts to do just that through comparisons of sequenced genetic material. These researchers hope to one day better understand the origin of viruses, a discovery that could lead to advances in the treatments for the ailments they produce.

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5.4: Viral Morphology

Viruses are **acellular**, meaning they are biological entities that do not have a cellular structure. They therefore 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 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.

Types of Nucleic Acid

Unlike nearly all living organisms that use DNA as their genetic material, viruses may use either DNA or RNA as theirs. 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. This genetic material may be single- or double-stranded. It may also be linear or circular. While most viruses contain a single nucleic acid, others have genomes that have several, which are called segments.

In DNA viruses, the viral DNA directs the host cell's replication proteins to synthesize new copies of the viral genome and to transcribe and translate that genome into viral proteins. DNA viruses cause human diseases, such as chickenpox, hepatitis B, and some venereal diseases, like herpes and genital warts.

RNA viruses contain only RNA as their genetic material. To replicate their genomes in the host cell, the RNA viruses encode enzymes that can replicate RNA into DNA, which cannot be done by the host cell. These RNA polymerase enzymes are more likely to make copying errors than DNA polymerases, and therefore often make mistakes during transcription. For this reason, mutations in RNA viruses occur more frequently than in DNA viruses. This causes them to change and adapt more rapidly to their host. Human diseases caused by RNA viruses include hepatitis C, measles, and rabies.

Morphology

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.

In general, the shapes of viruses are classified into four groups: filamentous, isometric (or icosahedral), enveloped, and head and tail. Filamentous viruses are long and cylindrical. Many plant viruses are filamentous, including TMV. Isometric viruses have shapes that are roughly spherical, such as poliovirus or herpesviruses. Enveloped viruses have membranes surrounding capsids. Animal viruses, such as HIV, are frequently enveloped. Head and tail viruses infect bacteria and have a head that is similar to icosahedral viruses and a tail shape like filamentous viruses.

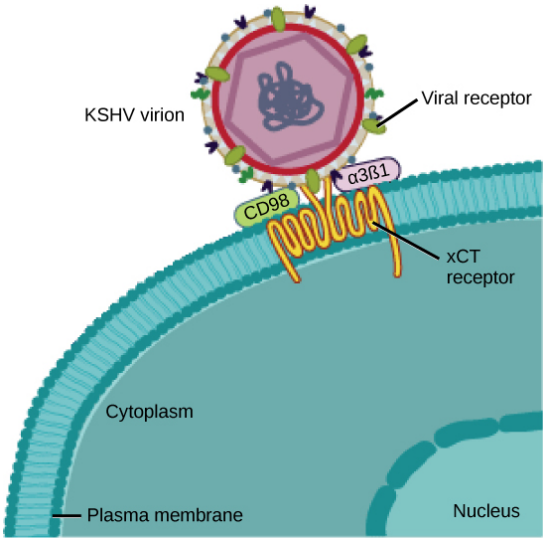


Figure 1. The KSHV virus binds the xCT receptor on the surface of human cells. xCT receptors protect cells against stress. Stressed cells express more xCT receptors than non-stressed cells. The KSHV virion causes cells to become stressed, thereby increasing expression of the receptor to which it binds. (credit: modification of work by NIAID, NIH)

Many viruses use some sort of glycoprotein to attach to their host cells via molecules on the cell called **viral receptors** (Figure 1). For these viruses, attachment is a requirement for later penetration of the cell membrane, so they can complete their replication inside the cell. The receptors that viruses use are molecules that are normally found on cell surfaces and have their own physiological functions. Viruses have simply evolved to make use of these molecules for their own replication. For example, HIV uses the CD4 molecule on T lymphocytes as one of its receptors. CD4 is a type of molecule called a cell adhesion molecule, which functions to keep different types of immune cells in close proximity to each other during the generation of a T lymphocyte immune response.

Among the most complex virions known, the T4 bacteriophage, which infects the *Escherichia coli* bacterium, has a tail structure that the virus uses to attach to host cells and a head structure that houses its DNA.

Adenovirus, a non-enveloped animal virus that causes respiratory illnesses in humans, uses glycoprotein spikes protruding from its capsomeres to attach to host cells. Non-enveloped viruses also include those that cause polio (poliovirus), plantar warts (papillomavirus), and hepatitis A (hepatitis A virus).

Enveloped virions like HIV, the causative agent in AIDS, consist of nucleic acid (RNA in the case of HIV) and capsid proteins surrounded by a phospholipid bilayer envelope and its associated proteins. Glycoproteins embedded in the viral envelope are used to attach to host cells. Other envelope proteins are the **matrix proteins** that stabilize the envelope and often play a role in the assembly of progeny virions. Chicken pox, influenza, and mumps are examples of diseases caused by viruses with envelopes. Because of the fragility of the envelope, non-enveloped viruses are more resistant to changes in temperature, pH, and some disinfectants than enveloped viruses.

Overall, the shape of the virion and the presence or absence of an envelope tell us little about what disease the virus may cause or what species it might infect, but they are still useful means to begin viral classification (Figure 2).

Practice Question

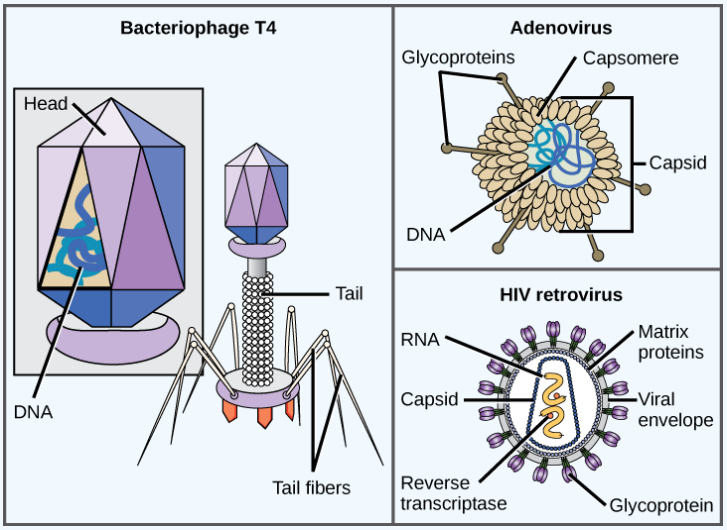


Figure 2. Viruses can be either complex in shape or relatively simple. This figure shows three relatively complex virions: the bacteriophage T4, with its DNA-containing head group and tail fibers that attach to host cells; adenovirus, which uses spikes from its capsid to bind to host cells; and HIV, which uses glycoproteins embedded in its envelope to bind to host cells. Notice that HIV has proteins called matrix proteins, internal to the envelope, which help stabilize virion shape. (credit "bacteriophage, adenovirus": modification of work by NCBI, NIH; credit "HIV retrovirus": modification of work by NIAID, NIH)

Which of the following statements about virus structure is true?

a. All viruses are encased in a viral membrane.
b. The capsomere is made up of small protein subunits called capsids.
c. DNA is the genetic material in all viruses.
d. Glycoproteins help the virus attach to the host cell.

[reveal-answer q="243497"]Show Answer[/reveal-answer]
[hidden-answer a="243497"]Statement d is true.[/hidden-answer]

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5.5: Virus Classification

To understand the features shared among different groups of viruses, a classification scheme is necessary. As most viruses are not thought to have evolved from a common ancestor, however, the methods that scientists use to classify living things are not very useful. Biologists have used several classification systems in the past, based on the morphology and genetics of the 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 particular type of virus.

Past Systems of Classification

Viruses are classified in several ways: by factors such as their core content (Table 1 and Figure 1), the structure of their capsids, and whether they have an outer envelope. The type of genetic material (DNA or RNA) and its structure (single- or double-stranded, linear or circular, and segmented or non-segmented) are used to classify the virus core structures.

Table 1. Virus Classification by Genome Structure and Core

Core Classifications	Examples
RNA	Rabies virus, retroviruses
DNA	Herpesviruses, smallpox virus
Single-stranded	Rabies virus, retroviruses
Double-stranded	Herpesviruses, smallpox virus
Linear	Rabies virus, retroviruses, herpesviruses, smallpox virus
Circular	Papillomaviruses, many bacteriophages
Non-segmented: genome consists of a single segment of genetic material	Parainfluenza viruses
Segmented: genome is divided into multiple segments	Influenza viruses

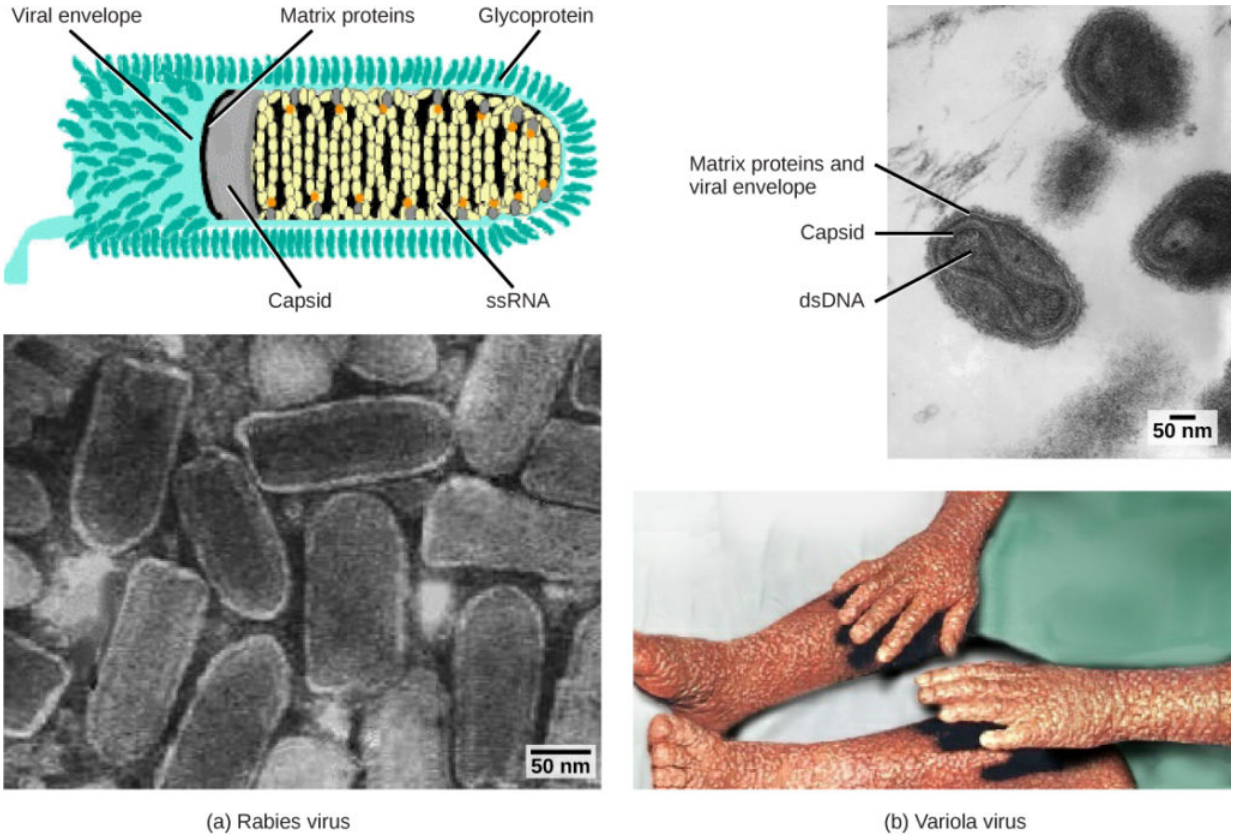


Figure 1. Viruses are classified based on their core genetic material and capsid design. (a) Rabies virus has a single-stranded RNA (ssRNA) core and an enveloped helical capsid, whereas (b) variola virus, the causative agent of smallpox, has a double-stranded DNA (dsDNA) core and a complex capsid. (credit "rabies diagram": modification of work by CDC; "rabies micrograph": modification of work by Dr. Fred Murphy, CDC; credit "small pox micrograph": modification of work by Dr. Fred Murphy, Sylvia Whitfield, CDC; credit "smallpox photo": modification of work by CDC; scale-bar data from Matt Russell)

Viruses can also be classified by the design of their capsids (Figure 1). Capsids are classified as naked icosahedral, enveloped icosahedral, enveloped helical, naked helical, and complex (Figure 2 and Figure 3). The type of genetic material (DNA or RNA) and its structure (single- or double-stranded, linear or circular, and segmented or non-segmented) are used to classify the virus core structures (Table 2).

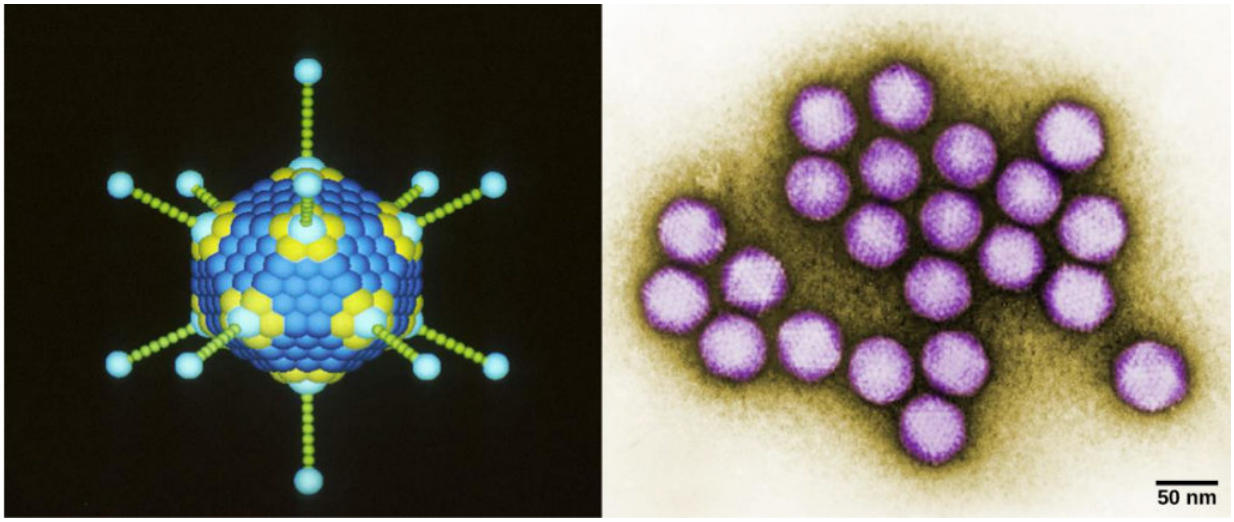


Figure 2. Adenovirus (left) is depicted with a double-stranded DNA genome enclosed in an icosahedral capsid that is 90–100 nm across. The virus, shown clustered in the micrograph (right), is transmitted orally and causes a variety of illnesses in vertebrates, including human eye and respiratory infections. (credit "adenovirus": modification of work by Dr. Richard Feldmann, National Cancer Institute; credit "micrograph": modification of work by Dr. G. William Gary, Jr., CDC; scale-bar data from Matt Russell)

Table 2. Virus Classification by Capsid Structure	
Capsid Classification	Examples
Naked icosahedral	Hepatitis A virus, polioviruses
Enveloped icosahedral	Epstein-Barr virus, herpes simplex virus, rubella virus, yellow fever virus, HIV-1
Enveloped helical	Influenza viruses, mumps virus, measles virus, rabies virus
Naked helical	Tobacco mosaic virus
Complex with many proteins; some have combinations of icosahedral and helical capsid structures	Herpesviruses, smallpox virus, hepatitis B virus, T4 bacteriophage

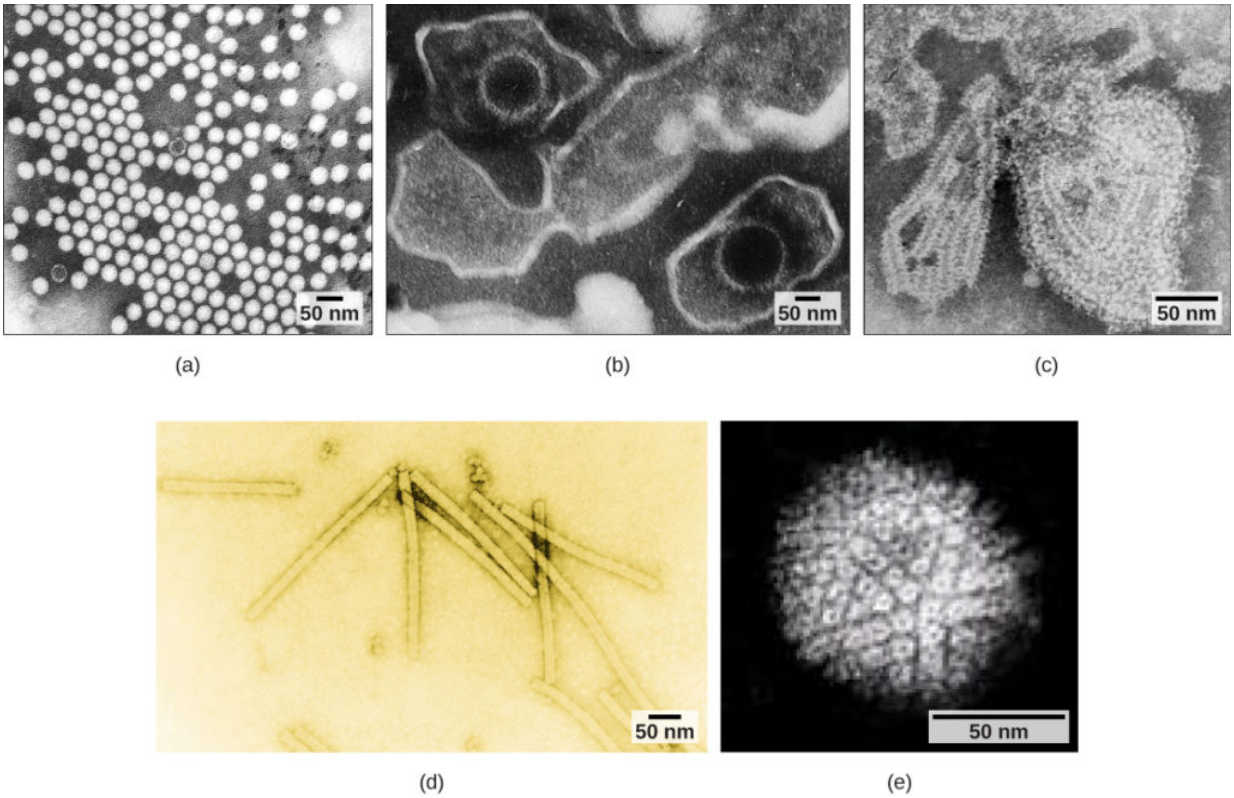


Figure 3. Transmission electron micrographs of various viruses show their structures. The capsid of the (a) polio virus is naked icosahedral; (b) the Epstein-Barr virus capsid is enveloped icosahedral; (c) the mumps virus capsid is an enveloped helix; (d) the tobacco mosaic virus capsid is naked helical; and (e) the herpesvirus capsid is complex. (credit a: modification of work by Dr. Fred Murphy, Sylvia Whitfield; credit b: modification of work by Liza Gross; credit c: modification of work by Dr. F. A. Murphy, CDC; credit d: modification of work by USDA ARS; credit e: modification of work by Linda Stannard, Department of Medical Microbiology, University of Cape Town, South Africa, NASA; scale-bar data from Matt Russell)

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.

Group I viruses contain double-stranded DNA (dsDNA) as their genome. Their mRNA is produced by transcription in much the same way as with cellular DNA.

Group II viruses have single-stranded DNA (ssDNA) as their genome. They convert their single-stranded genomes into a dsDNA intermediate before transcription to mRNA can occur.

Group III viruses use dsRNA as their genome. The strands separate, and one of them is used as a template for the generation of mRNA using the RNA-dependent RNA polymerase encoded by the virus.

Group IV viruses have ssRNA as their genome with a positive polarity. **Positive polarity** means that the genomic RNA can serve directly as mRNA. Intermediates of dsRNA, called **replicative intermediates**, are made in the process of copying the genomic RNA. Multiple, full-length RNA strands of negative polarity (complimentary to the positive-stranded genomic RNA) are formed from these intermediates, which may then serve as templates for the production of RNA with positive polarity, including both full-length genomic RNA and shorter viral mRNAs.

Group V viruses contain ssRNA genomes with a **negative polarity**, meaning that their sequence is complementary to the mRNA. As with Group IV viruses, dsRNA intermediates are used to make copies of the genome and produce mRNA. In this case, the negative-stranded genome can be converted directly to mRNA. Additionally, full-length positive RNA strands are made to serve as templates for the production of the negative-stranded genome.

Group VI viruses have diploid (two copies) ssRNA genomes that must be converted, using the enzyme **reverse transcriptase**, to dsDNA; the dsDNA is then transported to the nucleus of the host cell and inserted into the host genome. Then, mRNA can be produced by transcription of the viral DNA that was integrated into the host genome.

Group VII viruses have partial dsDNA genomes and make ssRNA intermediates that act as mRNA, but are also converted back into dsDNA genomes by reverse transcriptase, necessary for genome replication. The characteristics of each group in the Baltimore classification are summarized in Table 3 with examples of each group.

Table 3. 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)

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5.6: Introduction to Virus Infections and Hosts

Describe a viral infection and explain what impact an infection has on its host

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. 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 which cells a virus may target for replication. The permissive cell must make the substances that the virus needs or the virus will not be able to replicate there.

What You'll Learn to Do

- List the steps of replication and explain what occurs at each step
- Explain the transmission and diseases of viruses that infect animals
- Explain the transmission and diseases of viruses that infect plants

Learning Activities

The learning activities for this section include the following:

- Steps of Virus Infections
- Different Hosts and Their Viruses
- Self Check: Virus Infections and Hosts

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5.7: Steps of Virus Infections

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. Most productive viral infections follow similar steps in the virus replication cycle: attachment, penetration, uncoating, replication, assembly, and release. In Figure 1, the host cell is destroyed at the end of the replication cycle—it's important to remember that this doesn't always happen: sometimes the host cell lives on and continues to replicate the virus.

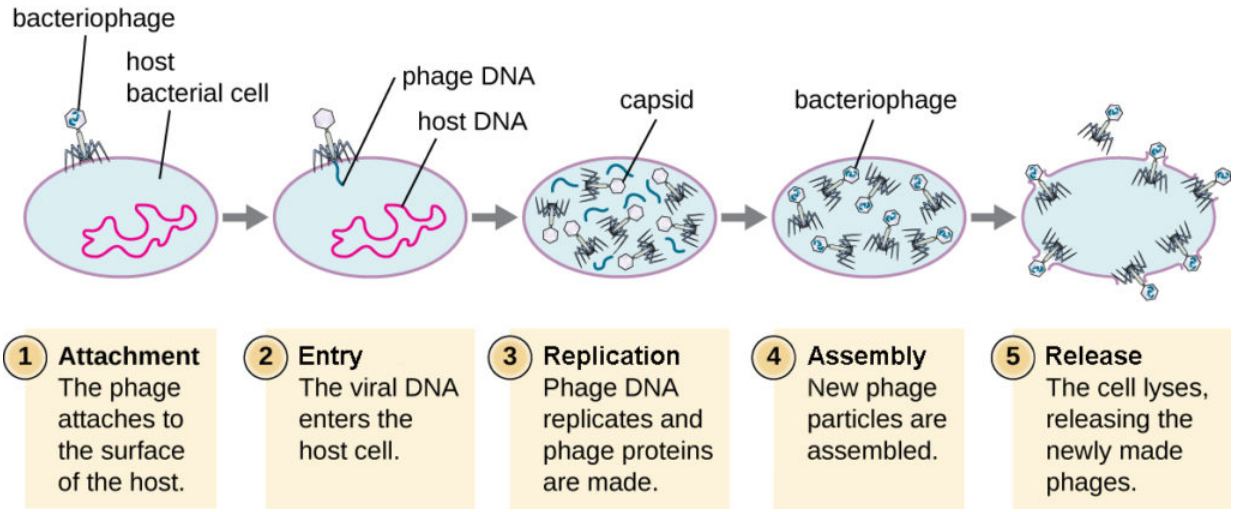


Figure 1. A bacteriophage replicates and lyses (bursts) the host cell.

Attachment

A virus attaches to a specific receptor site on the host cell membrane through attachment proteins in the capsid or via glycoproteins embedded in the viral envelope. The specificity of this interaction determines the host—and the cells within the host—that can be infected by a particular virus. This can be illustrated by thinking of several keys and several locks, where each key will fit only one specific lock.

Entry (Penetration and Uncoating)

The nucleic acid of bacteriophages enters the host cell naked, leaving the capsid outside the cell. Plant and animal viruses can enter through endocytosis, in which the cell membrane surrounds and engulfs the entire virus. Some enveloped viruses enter the cell when the viral envelope fuses directly with the cell membrane. Once inside the cell, the viral capsid is degraded, and the viral nucleic acid is released, which then becomes available for replication and transcription.

Replication and Assembly

The replication mechanism depends on the viral genome. DNA viruses usually use host cell proteins and enzymes to make additional DNA that is transcribed to messenger RNA (mRNA), which is then used to direct protein synthesis. RNA viruses usually use the RNA core as a template for synthesis of viral genomic RNA and mRNA. The viral mRNA directs the host cell to synthesize viral enzymes and capsid proteins, and assemble new virions. Of course, there are exceptions to this pattern. If a host cell does not provide the enzymes necessary for viral replication, viral genes supply the information to direct synthesis of the missing proteins.

Retroviruses, such as HIV, have an RNA genome that must be reverse transcribed into DNA, which then is incorporated into the host cell genome. They are within group VI of the Baltimore classification scheme. To convert RNA into DNA, retroviruses must contain genes that encode the virus-specific enzyme reverse transcriptase that transcribes an RNA template to DNA. Reverse transcription never occurs in uninfected host cells—the needed enzyme reverse transcriptase is only derived from the expression of viral genes within the infected host cells.

The fact that HIV produces some of its own enzymes not found in the host has allowed researchers to develop drugs that inhibit these enzymes. These drugs, including the reverse transcriptase inhibitor **AZT**, inhibit HIV replication by reducing the activity of the enzyme without affecting the host's metabolism. This approach has led to the development of a variety of drugs used to treat HIV and has been effective at reducing the number of infectious virions (copies of viral RNA) in the blood to non-detectable levels in many HIV-infected individuals.

Egress (Release)

The last stage of viral replication is the release of the new virions produced in the host organism, where they are able to infect adjacent cells and repeat the replication cycle. As you've learned, some viruses are released when the host cell dies, and other viruses can leave infected cells by budding through the membrane without directly killing the cell.

Steps of Virus Infections

The following activity will show you just how the flu virus can infect your body.

A link to an interactive elements can be found at the bottom of this page.

Click here for a text-only version of the activity.

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5.8: Different Hosts and Their Viruses

As you've learned, viruses are often very specific as to which hosts and which cells within the host they will infect. This feature of a virus makes it specific to one or a few species of life on Earth. On the other hand, so many different types of viruses exist on Earth that nearly every living organism has its own set of viruses that tries to infect its cells. Even the smallest and simplest of cells, prokaryotic bacteria, may be attacked by specific types of viruses. Viruses that target bacteria are known as **bacteriophages**.

When a temperate bacteriophage infects a bacterial cell, it replicates by means of a **lysogenic cycle** (Figure 1), and the viral genome is incorporated into the genome of the host cell. When the phage DNA is incorporated into the host cell genome, it is called a **prophage**. An example of a lysogenic bacteriophage is the λ (lambda) virus, which infects the *E. coli* bacterium. Viruses that infect plant or animal cells may also undergo infections where they are not producing virions for long periods. An example is the animal herpesviruses, including herpes simplex viruses, the cause of oral and genital herpes in humans. In a process called **latency**, these viruses can exist in nervous tissue for long periods of time without producing new virions, only to leave latency periodically and cause lesions in the skin where the virus replicates. Even though there are similarities between lysogeny and latency, the term lysogenic cycle is usually reserved to describe bacteriophages. Latency will be described in more detail below.

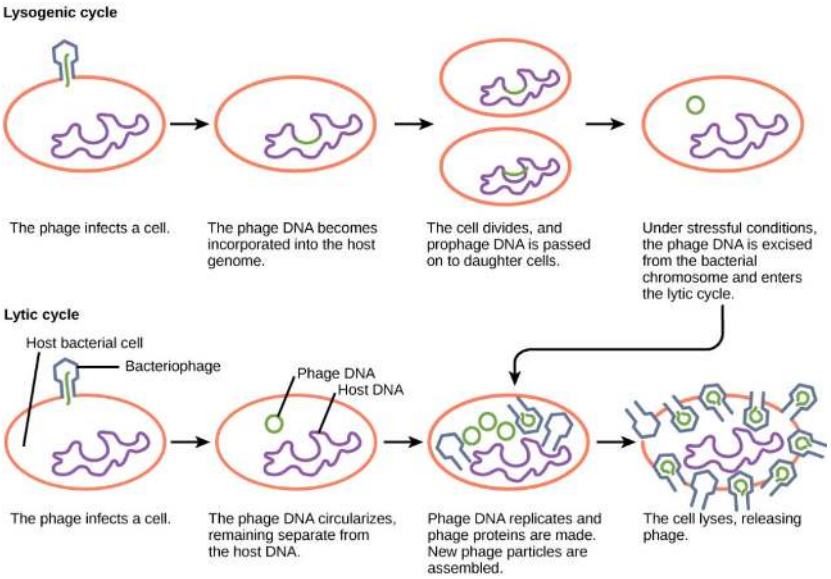


Figure 1. Click for a larger image. A temperate bacteriophage has both lytic and lysogenic cycles. In the lytic cycle, the phage replicates and lyses the host cell. In the lysogenic cycle, phage DNA is incorporated into the host genome, where it is passed on to subsequent generations. Environmental stressors such as starvation or exposure to toxic chemicals may cause the prophage to excise and enter the lytic cycle.

? Practice Question

Which of the following statements is false?

a. In the lytic cycle, new phage are produced and released into the environment.
b. In the lysogenic cycle, phage DNA is incorporated into the host genome.
c. An environmental stressor can cause the phage to initiate the lysogenic cycle.
d. Cell lysis only occurs in the lytic cycle.

[reveal-answer q="191487"]Show Answer[/reveal-answer]
[hidden-answer a="191487"]Statement c is false.[/hidden-answer]

Animal Viruses

Animal viruses, unlike the viruses of plants and bacteria, do not have to penetrate a cell wall to gain access to the host cell. Non-enveloped or "naked" animal viruses may enter cells in two different ways. As a protein in the viral capsid binds to its receptor on the host cell, the virus may be taken inside the cell via a vesicle during the normal cell process of receptor-mediated endocytosis. An

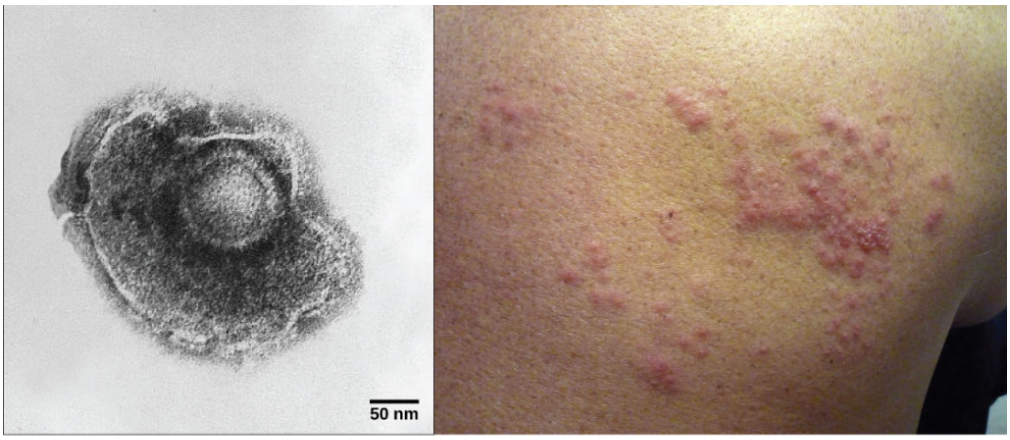
alternative method of cell penetration used by non-enveloped viruses is for capsid proteins to undergo shape changes after binding to the receptor, creating channels in the host cell membrane. The viral genome is then “injected” into the host cell through these channels in a manner analogous to that used by many bacteriophages. Enveloped viruses also have two ways of entering cells after binding to their receptors: receptor-mediated endocytosis, or **fusion**. Many enveloped viruses enter the cell by receptor-mediated endocytosis in a fashion similar to some non-enveloped viruses. On the other hand, fusion only occurs with enveloped virions. These viruses, which include HIV among others, use special fusion proteins in their envelopes to cause the envelope to fuse with the plasma membrane of the cell, thus releasing the genome and capsid of the virus into the cell cytoplasm.

After making their proteins and copying their genomes, animal viruses complete the assembly of new virions and exit the cell. As we have already discussed using the example of HIV, enveloped animal viruses may bud from the cell membrane as they assemble themselves, taking a piece of the cell’s plasma membrane in the process. On the other hand, non-enveloped viral progeny, such as rhinoviruses, accumulate in infected cells until there is a signal for lysis or apoptosis, and all virions are released together.

Animal viruses are associated with a variety of human diseases. Some of them follow the classic pattern of **acute disease**, where symptoms get increasingly worse for a short period followed by the elimination of the virus from the body by the immune system and eventual recovery from the infection. Examples of acute viral diseases are the common cold and influenza. Other viruses cause long-term **chronic infections**, such as the virus causing hepatitis C, whereas others, like herpes simplex virus, only cause **intermittent** symptoms. Still other viruses, such as human herpesviruses 6 and 7, which in some cases can cause the minor childhood disease roseola, often successfully cause productive infections without causing any symptoms at all in the host, and thus we say these patients have an **asymptomatic infection**.

In hepatitis C infections, the virus grows and reproduces in liver cells, causing low levels of liver damage. The damage is so low that infected individuals are often unaware that they are infected, and many infections are detected only by routine blood work on patients with risk factors such as intravenous drug use. On the other hand, since many of the symptoms of viral diseases are caused by immune responses, a lack of symptoms is an indication of a weak immune response to the virus. This allows for the virus to escape elimination by the immune system and persist in individuals for years, all the while producing low levels of progeny virions in what is known as a chronic viral disease. Chronic infection of the liver by this virus leads to a much greater chance of developing liver cancer, sometimes as much as 30 years after the initial infection.

As already discussed, herpes simplex virus can remain in a state of latency in nervous tissue for months, even years. As the virus “hides” in the tissue and makes few if any viral proteins, there is nothing for the immune response to act against, and immunity to the virus slowly declines. Under certain conditions, including various types of physical and psychological stress, the latent herpes simplex virus may be reactivated and undergo a lytic replication cycle in the skin, causing the lesions associated with the disease. Once virions are produced in the skin and viral proteins are synthesized, the immune response is again stimulated and resolves the skin lesions in a few days by destroying viruses in the skin. As a result of this type of replicative cycle, appearances of cold sores and genital herpes outbreaks only occur intermittently, even though the viruses remain in the nervous tissue for life. Latent infections are common with other herpesviruses as well, including the varicella-zoster virus that causes chickenpox. After having a chickenpox infection in childhood, the varicella-zoster virus can remain latent for many years and reactivate in adults to cause the painful condition known as “shingles” (Figure 2).



(a) (b)

Figure 2. (a) Varicella-zoster, the virus that causes chickenpox, has an enveloped icosahedral capsid visible in this transmission electron micrograph. Its double-stranded DNA genome becomes incorporated in the host DNA and can reactivate after latency in the form of (b) shingles, often exhibiting a rash. (credit a: modification of work by Dr. Erskine Palmer, B. G. Martin, CDC; credit b: modification of work by "rosmary"/Flickr; scale-bar data from Matt Russell)

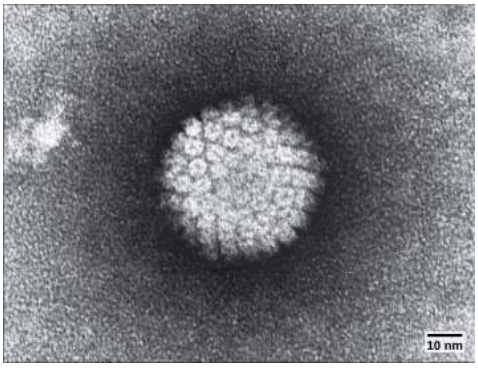


Figure 3. HPV, or human papillomavirus (credit: modification of work by NCI, NIH; scale-bar data from Matt Russell)

Some animal-infecting viruses, including the hepatitis C virus discussed above, are known as **oncogenic viruses**: They have the ability to cause cancer. These viruses interfere with the normal regulation of the host cell cycle either by either introducing genes that stimulate unregulated cell growth (oncogenes) or by interfering with the expression of genes that inhibit cell growth. Oncogenic viruses can be either DNA or RNA viruses.

Cancers known to be associated with viral infections include cervical cancer caused by human papillomavirus (HPV) , liver cancer caused by hepatitis B virus, T-cell leukemia, and several types of lymphoma.

HPV, or human papillomavirus (as seen in Figure 3), has a naked icosahedral capsid visible in this transmission electron micrograph and a double-stranded DNA genome that is incorporated into the host DNA. The virus, which is sexually transmitted, is oncogenic and can lead to cervical cancer.

Visit the interactive animations showing the various stages of the replicative cycles of animal viruses and click on the flash animation links.

Plant Viruses

Plant viruses, like other viruses, contain a core of either DNA or RNA. You have already learned about one of these, the tobacco mosaic virus. As plants have a cell wall to protect their cells, these viruses do not use receptor-mediated endocytosis to enter host cells as is seen with animal viruses. For many plant viruses to be transferred from plant to plant, damage to some of the plants' cells must occur to allow the virus to enter a new host. This damage is often caused by weather, insects, animals, fire, or human activities like farming or landscaping. Additionally, plant offspring may inherit viral diseases from parent plants. Plant viruses can be transmitted by a variety of vectors, through contact with an infected plant's sap, by living organisms such as insects and nematodes, and through pollen. When plants viruses are transferred between different plants, this is known as **horizontal transmission**, and when they are inherited from a parent, this is called **vertical transmission**.

Symptoms of viral diseases vary according to the virus and its host (see the table below). One common symptom is **hyperplasia**, the abnormal proliferation of cells that causes the appearance of plant tumors known as **galls**. Other viruses induce **hypoplasia**, or decreased cell growth, in the leaves of plants, causing thin, yellow areas to appear. Still other viruses affect the plant by directly killing plant cells, a process known as **cell necrosis**. Other symptoms of plant viruses include malformed leaves, black streaks on the stems of the plants, altered growth of stems, leaves, or fruits, and ring spots, which are circular or linear areas of discoloration found in a leaf.

Table 1. Some Common Symptoms of Plant Viral Diseases

Symptom	Appears as
Hyperplasia	Galls (tumors)
Hypoplasia	Thinned, yellow splotches on leaves
Cell necrosis	Dead, blackened stems, leaves, or fruit
Abnormal growth patterns	Malformed stems, leaves, or fruit
Discoloration	Yellow, red, or black lines, or rings in stems, leaves, or fruit

Plant viruses can seriously disrupt crop growth and development, significantly affecting our food supply. They are responsible for poor crop quality and quantity globally, and can bring about huge economic losses annually. Others viruses may damage plants used in landscaping. Some viruses that infect agricultural food plants include the name of the plant they infect, such as tomato spotted wilt virus, bean common mosaic virus, and cucumber mosaic virus. In plants used for landscaping, two of the most common viruses are peony ring spot and rose mosaic virus. There are far too many plant viruses to discuss each in detail, but symptoms of bean common mosaic virus result in lowered bean production and stunted, unproductive plants. In the ornamental rose, the rose mosaic disease causes wavy yellow lines and colored splotches on the leaves of the plant.

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5.9: Introduction to Prevention and Treatment of Viral Infections

Compare vaccinations and antiviral drugs as medical approaches to viruses

Viruses cause a variety of diseases in animals, including humans, ranging from the common cold to potentially fatal illnesses like meningitis (Figure 1). 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.

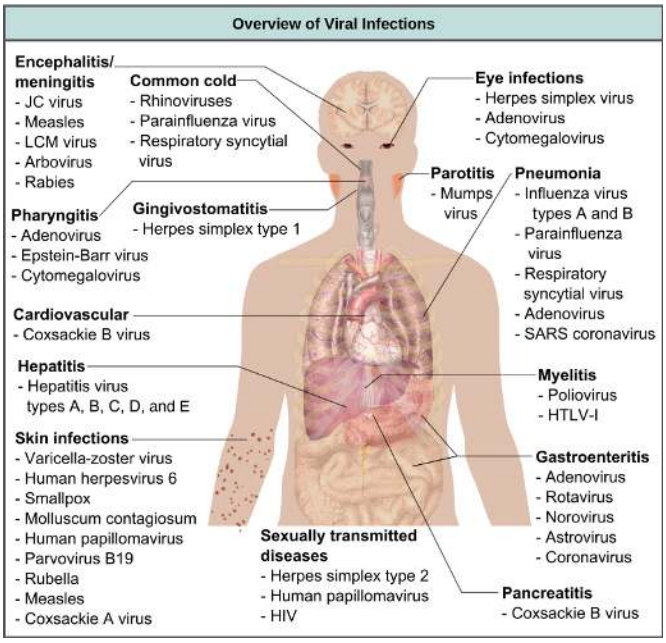


Figure 1. Viruses can cause dozens of ailments in humans, ranging from mild illnesses to serious diseases. (credit: modification of work by Mikael Häggström)

What You'll Learn to Do

- Identify the advantages of vaccines as a preventative measure
- Discuss the effectiveness of vaccines and antiviral drugs as treatment for infections

Learning Activities

The learning activities for this section include the following:

- Vaccines for Prevention
- Vaccines and Anti-Viral Drugs for Treatment
- Self Check: Prevention and Treatment of Viral Infections

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5.10: 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 (Figure 1). **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.



Figure 1. Vaccinations are designed to boost immunity to a virus to prevent infection. (credit: USACE Europe District)

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.

The danger of using live vaccines, which are usually more effective than killed vaccines, is the low but significant danger that these viruses will revert to their disease-causing form by **back mutations**. Live vaccines are usually made by **attenuating** (weakening) the “wild-type” (disease-causing) virus by growing it in the laboratory in tissues or at temperatures different from what the virus is accustomed to in the host. Adaptations to these new cells or temperatures induce mutations in the genomes of the virus, allowing it to grow better in the laboratory while inhibiting its ability to cause disease when reintroduced into conditions found in the host. These attenuated viruses thus still cause infection, but they do not grow very well, allowing the immune response to develop in time to prevent major disease. Back mutations occur when the vaccine undergoes mutations in the host such that it readapts to the host and can again cause disease, which can then be spread to other humans in an epidemic. This type of scenario happened as recently as 2007 in Nigeria where mutations in a polio vaccine led to an epidemic of polio in that country.

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.

Watch this NOVA video to learn how microbiologists are attempting to replicate the deadly 1918 Spanish influenza virus so they can understand more about virology.

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5.11: 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. Thus, the potentially fatal neurological consequences of the disease are averted, and the individual only has to recover from the infected bite. This approach is also being used for the treatment of Ebola, one of the fastest and most deadly viruses on earth. Transmitted by bats and great apes, this disease can cause death in 70–90 percent of infected humans within 2 weeks. Using newly developed vaccines that boost the immune response in this way, there is hope that affected individuals will be better able to control the virus, potentially saving a greater percentage of infected persons from a rapid and very painful death.

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. In this way, viral growth is inhibited without damaging the host. There are large numbers of antiviral drugs available to treat infections, some specific for a particular virus and others that can affect multiple viruses.

Antivirals have been developed to treat genital herpes (herpes simplex II) and influenza. For genital herpes, drugs such as acyclovir can reduce the number and duration of episodes of active viral disease, during which patients develop viral lesions in their skin cells. As the virus remains latent in nervous tissue of the body for life, this drug is not curative but can make the symptoms of the disease more manageable. For influenza, drugs like Tamiflu (oseltamivir) (Figure 1) can reduce the duration of “flu” symptoms by 1 or 2 days, but the drug does not prevent symptoms entirely. Tamiflu works by inhibiting an enzyme (viral neuraminidase) that allows new virions to leave their infected cells. Thus, Tamiflu inhibits the spread of virus from infected to uninfected cells. Other antiviral drugs, such as Ribavirin, have been used to treat a variety of viral infections, although its mechanism of action against certain viruses remains unclear.

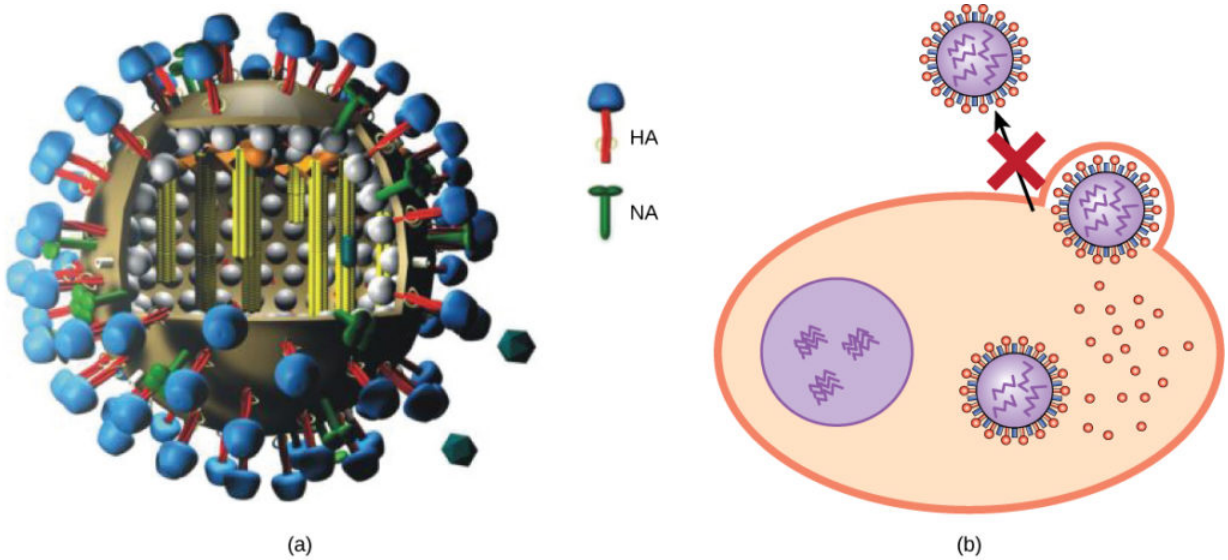


Figure 1. (a) Tamiflu inhibits a viral enzyme called neuraminidase (NA) found in the influenza viral envelope. (b) Neuraminidase cleaves the connection between viral hemagglutinin (HA), also found in the viral envelope, and glycoproteins on the host cell surface. Inhibition of neuraminidase prevents the virus from detaching from the host cell, thereby blocking further infection. (credit a: modification of work by M. Eickmann)

By far, the most successful use of antivirals has been in the treatment of the retrovirus HIV, which causes a disease that, if untreated, is usually fatal within 10–12 years after infection. Anti-HIV drugs have been able to control viral replication to the point that individuals receiving these drugs survive for a significantly longer time than the untreated.

Anti-HIV drugs inhibit viral replication at many different phases of the HIV replicative cycle (Figure 2). Drugs have been developed that inhibit the fusion of the HIV viral envelope with the plasma membrane of the host cell (fusion inhibitors), the conversion of its RNA genome into double-stranded DNA (reverse transcriptase inhibitors), the integration of the viral DNA into the host genome (integrase inhibitors), and the processing of viral proteins (protease inhibitors).

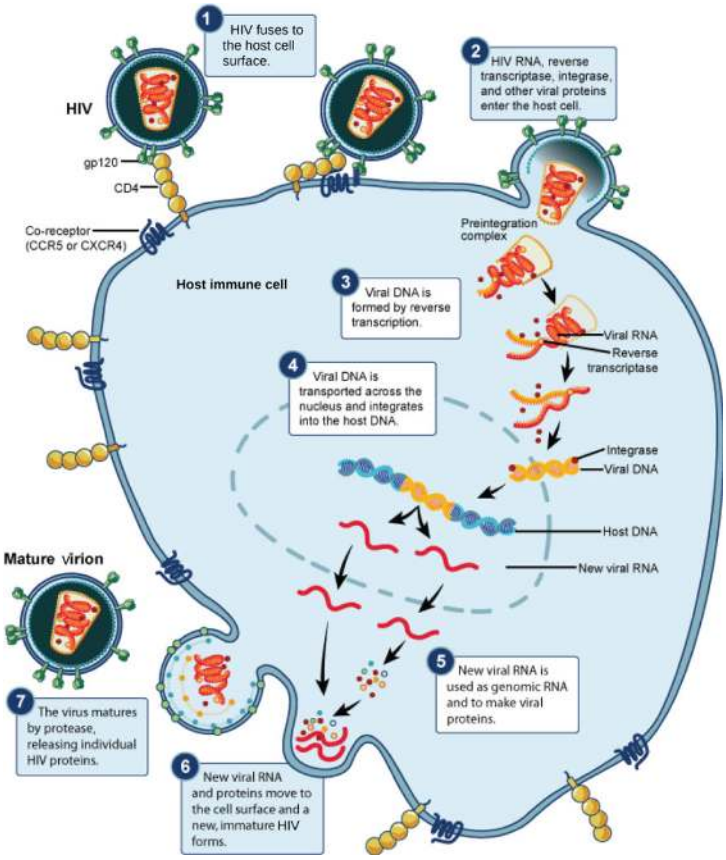


Figure 2. Click for a larger image. HIV, an enveloped, icosahedral virus, attaches to the CD4 receptor of an immune cell and fuses with the cell membrane. Viral contents are released into the cell, where viral enzymes convert the single-stranded RNA genome into DNA and incorporate it into the host genome. (credit: NIAID, NIH)

When any of these drugs are used individually, the high mutation rate of the virus allows it to easily and rapidly develop resistance to the drug, limiting the drug's effectiveness. The breakthrough in the treatment of HIV was the development of HAART, highly active anti-retroviral therapy, which involves a mixture of different drugs, sometimes called a drug "cocktail." By attacking the virus at different stages of its replicative cycle, it is much more difficult for the virus to develop resistance to multiple drugs at the same time. Still, even with the use of combination HAART therapy, there is concern that, over time, the virus will develop resistance to this therapy. Thus, new anti-HIV drugs are constantly being developed with the hope of continuing the battle against this highly fatal virus.

Applied Virology

The study of viruses has led to the development of a variety of new ways to treat non-viral diseases. Viruses have been used in **gene therapy**. Gene therapy is used to treat genetic diseases such as severe combined immunodeficiency (SCID), a heritable, recessive disease in which children are born with severely compromised immune systems. One common type of SCID is due to the lack of an enzyme, adenosine deaminase (ADA), which breaks down purine bases. To treat this disease by gene therapy, bone marrow cells are taken from a SCID patient and the ADA gene is inserted. This is where viruses come in, and their use relies on their ability to penetrate living cells and bring genes in with them. Viruses such as adenovirus, an upper respiratory human virus, are modified by the addition of the ADA gene, and the virus then transports this gene into the cell. The modified cells, now capable of making ADA, are then given back to the patients in the hope of curing them. Gene therapy using viruses as carrier of genes (viral

vectors), although still experimental, holds promise for the treatment of many genetic diseases. Still, many technological problems need to be solved for this approach to be a viable method for treating genetic disease.

Another medical use for viruses relies on their specificity and ability to kill the cells they infect. **Oncolytic viruses** are engineered in the laboratory specifically to attack and kill cancer cells. A genetically modified adenovirus known as H101 has been used since 2005 in clinical trials in China to treat head and neck cancers. The results have been promising, with a greater short-term response rate to the combination of chemotherapy and viral therapy than to chemotherapy treatment alone. This ongoing research may herald the beginning of a new age of cancer therapy, where viruses are engineered to find and specifically kill cancer cells, regardless of where in the body they may have spread.

A third use of viruses in medicine relies on their specificity and involves using bacteriophages in the treatment of bacterial infections. Bacterial diseases have been treated with antibiotics since the 1940s. However, over time, many bacteria have developed resistance to antibiotics. A good example is methicillin-resistant *Staphylococcus aureus* (MRSA, pronounced “mersa”), an infection commonly acquired in hospitals. This bacterium is resistant to a variety of antibiotics, making it difficult to treat. The use of bacteriophages specific for such bacteria would bypass their resistance to antibiotics and specifically kill them. Although **phage therapy** is in use in the Republic of Georgia to treat antibiotic-resistant bacteria, its use to treat human diseases has not been approved in most countries. However, the safety of the treatment was confirmed in the United States when the U.S. Food and Drug Administration approved spraying meats with bacteriophages to destroy the food pathogen *Listeria.* As more and more antibiotic-resistant strains of bacteria evolve, the use of bacteriophages might be a potential solution to the problem, and the development of phage therapy is of much interest to researchers worldwide.

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5.12: Introduction to Prions and Viroids

Describe 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.

What You'll Learn to Do

- Describe prions and their basic properties
- Define viroids and their targets of infection

Learning Activities

The learning activities for this section include the following:

- Prions and Viroids
- Self Check: Prions and Viroids

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5.13: Prions and Viroids

Prions

Prions, so-called because they are proteinaceous, 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 the majority of biologists that such agents do indeed exist.

Fatal neurodegenerative diseases, such as kuru in humans and bovine spongiform encephalopathy (BSE) in cattle (commonly known as “mad cow disease”), were shown to be transmitted by prions. The disease was spread by the consumption of meat, nervous tissue, or internal organs between members of the same species. Kuru, native to humans in Papua New Guinea, was spread from human to human via ritualistic cannibalism. BSE, originally detected in the United Kingdom, was spread between cattle by the practice of including cattle nervous tissue in feed for other cattle. 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. Kuru was controlled by inducing the population to abandon its ritualistic cannibalism.

On the other hand, 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 on in the outbreak, however, it was shown that a similar encephalopathy in humans known as variant Creutzfeldt-Jakob disease (CJD) could be acquired from eating beef from animals with BSE, sparking bans by various countries on the importation of British beef and causing considerable economic damage to the British beef industry (Figure 1). BSE still exists in various areas, and although a rare disease, CJD is difficult 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.

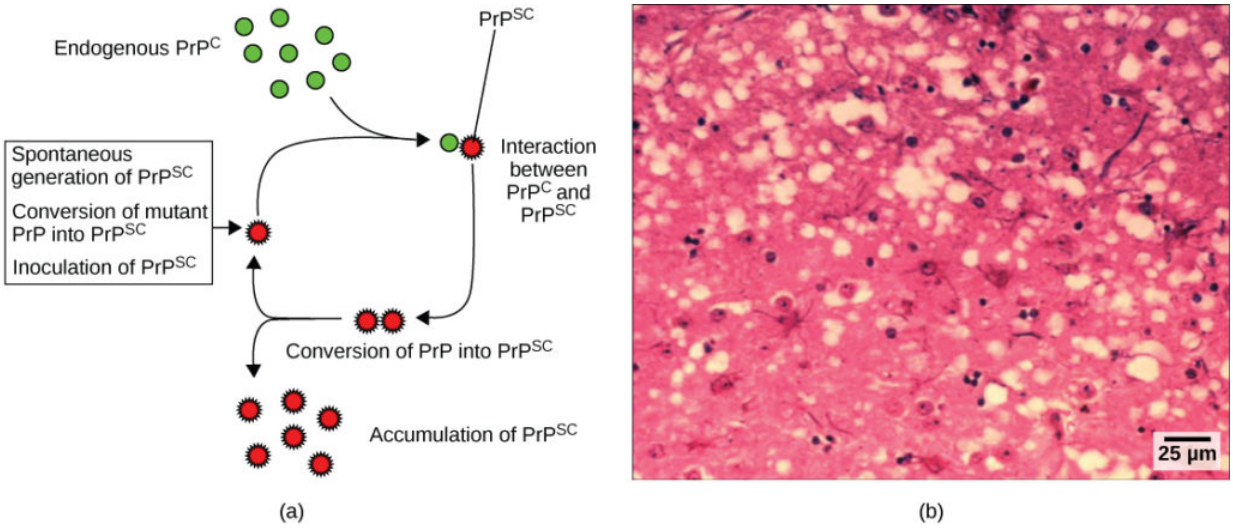


Figure 1. (PrP^{SC}) when it encounters this variant form of the protein. PrP^{SC} may arise spontaneously in brain tissue, especially if a mutant form of the protein is present, or it may occur via the spread of misfolded prions consumed in food into brain tissue. (b) This prion-infected brain tissue, visualized using light microscopy, shows the vacuoles that give it a spongy texture, typical of transmissible spongiform encephalopathies. (credit b: modification of work by Dr. Al Jenny, USDA APHIS; scale-bar data from Matt Russell)

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} contained within the prion binds to PrP^{C} and converts it to PrP^{SC}. This leads to an exponential increase of the PrP^{SC} protein, which aggregates. PrP^{SC} is folded abnormally, and the resulting conformation (shape) is directly responsible for the lesions seen in the brains of infected cattle. Thus, although not fully accepted among scientists, the prion seems likely 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.

Viroids



Figure 2. These potatoes have been infected by the potato spindle tuber viroid. (credit: Pamela Roberts, University of Florida Institute of Food and Agricultural Sciences, USDA ARS)

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 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. For example, the potato spindle tuber viroid (PSTVd), which typically spreads when infected knives cut healthy potatoes in preparation for planting, can affect potatoes and tomatoes. The symptoms of PSTVd can be seen in Figure 2.

Learning Objectives

Prions are infectious agents that consist of protein, but no DNA or RNA, and seem to produce their deadly effects by duplicating their shapes and accumulating in tissues. They are thought to contribute to several progressive brain disorders, including mad cow disease and Creutzfeldt-Jakob disease. Viroids are single-stranded RNA pathogens that infect plants. Their presence can have a severe impact on the agriculture industry.

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5.14: Putting It Together- Viruses

At this stage hopefully you realize life isn't actually all that simple to define. Let's look at our enemy Mr. Flu Virus. Is the flu a living organism? According to the definition of life: no. The flu virus (or any virus) is not capable of reproducing on its own. Well then, you may be thinking, what about a drone bee or a mule (the offspring of a male donkey and a female horse)? Neither of these organisms can reproduce, but they are living creatures. The difference here is that they are made up of parts that meet all the requirements of biological life, including having cells that reproduce and grow. Viruses, on the other hand, don't have any self-replicating parts: copying any part of a virus requires a host cell. Viruses must hijack the cellular machinery of the host in order to make more parts to assemble into new viral particles.

Viruses cause a variety of diseases in humans. Many of these diseases can be prevented by the use of viral vaccines, which stimulate protective immunity against the virus without causing major disease. Viral vaccines may also be used in active viral infections, boosting the ability of the immune system to control or destroy the virus. A series of antiviral drugs that target enzymes and other protein products of viral genes have been developed and used with mixed success. Combinations of anti-HIV drugs have been used to effectively control the virus, extending the lifespans of infected individuals. Viruses have many uses in medicines, such as in the treatment of genetic disorders, cancer, and bacterial infections.

Virology



Figure 1. 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)

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 generation and production of vaccines. They might participate in epidemiologic studies (Figure 1) or become science writers, to name just a few possible careers.

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.

The American Society of Virology's website is a good resource for information regarding training and careers in virology.

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5.15: Cerego- Viruses

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for Viruses. You'll need to create a free log-in to practice these items, if you haven't already.

https://cerego.com/sets/796507/learn

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CHAPTER OVERVIEW

6: Module 3- History of Life

6.1: Why It Matters- History of Life
6.2: Introduction to Evolution
6.3: Natural Selection
6.4: Theory of Evolution
6.5: Evidence of Evolution
6.6: Misconceptions of Evolution
6.7: Introduction to Speciation
6.8: What is a Species?
6.9: Types of Speciation
6.10: Reconnection
6.11: Rates of Speciation
6.12: Introduction to the Evolution of Populations
6.13: Population Genetics
6.14: Hardy-Weinberg Principle of Equilibrium
6.15: Genetic Variation and Drift
6.16: Adaptive Evolution
6.17: Introduction to Phylogenies and the History of Life
6.18: Phylogenetic Trees
6.19: Taxonomy
6.20: Homologous and Analogous Traits
6.21: Cladistics
6.22: Perspectives on the Phylogenetic Tree
6.23: Putting It Together- History of Life
6.24: Cerego- History of Life

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6.1: Why It Matters- History of Life

Why discuss the history of life on Earth?

Human beings are just one of countless examples of life on Earth. The sheer amount of diversity can seem overwhelming. However, over the years, scientists have developed tools and methods to organize all known living organisms. With the phylogenetic tree and the taxonomic classification system, scientists have grouped and organized organisms by domain, kingdom, phylum, class, order, family, genus, and species.

The term *kingdom* is likely familiar to you, and you may even know the genus and species names of some organisms, as these names are used to create scientific names such as *Canis lupus familiaris* (dogs) and *Felis catus* (cats). But how does this type of organization matter in everyday life?

Evolutionary biologists could list many reasons why understanding phylogeny is important to everyday life in human society. For botanists, phylogeny acts as a guide to discovering new plants that can be used to benefit people. Think of all the ways humans use plants—food, medicine, and clothing are a few examples. If a plant contains a compound that is effective in treating disease, scientists might want to examine all of the relatives of that plant for other useful drugs.

Learning Outcomes

- Explain the theory of evolution
- Define species and identify how species form
- Discuss the ways populations evolve
- Read and analyze a phylogenetic tree that documents evolutionary relationships

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6.2: Introduction to Evolution

Explain the theory of evolution

All species of living organisms, from bacteria to baboons to blueberries, evolved at some point from a different species. Although it may seem that living things today stay much the same, that is not the case—evolution is an ongoing process.

The theory of evolution is the unifying theory of biology, meaning it is the framework within which biologists ask questions about the living world. Its power is that it provides direction for predictions about living things that are borne out in experiment after experiment. The Ukrainian-born American geneticist Theodosius Dobzhansky famously wrote that "nothing makes sense in biology except in the light of evolution."[1] He meant that the tenet that all life has evolved and diversified from a common ancestor is the foundation from which we approach all questions in biology.

What You'll Learn to Do

- Define natural selection
- Describe the basis of the present-day theory of evolution
- Describe how the theory of evolution by natural selection is supported by evidence
- Refute common misconceptions about evolution

Learning Activities

The learning activities for this section include the following:

- Natural Selection
- Theory of Evolution
- Evidence of Evolution
- Misconceptions of Evolution
- Self Check: Evolution

1. Theodosius Dobzhansky. "Biology, Molecular and Organismic." *American Zoologist* 4, no. 4 (1964): 449. ↵

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6.3: Natural Selection

Darwin and Descent with Modification

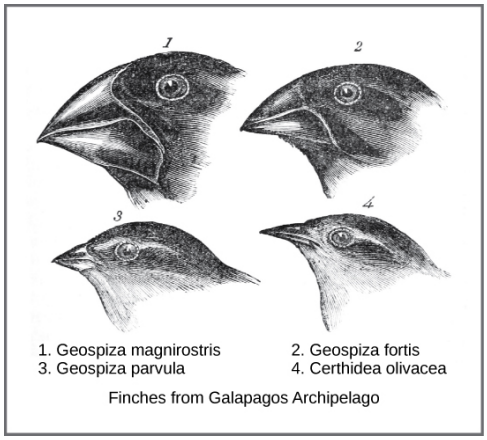


Figure 1. Darwin observed that beak shape varies among finch species. He postulated that the beak of an ancestral species had adapted over time to equip the finches to acquire different food sources.

Charles Darwin is best known for his discovery of natural selection. In the mid-nineteenth century, the actual 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 on *H.M.S. Beagle*, including stops in 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, like 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 species of organisms on different islands that were clearly similar, yet had distinct differences. For example, the ground finches inhabiting the Galápagos Islands comprised several species with a unique beak shape (Figure 1).

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 species 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, and insect-eating finches had spear-like beaks for stabbing their prey.

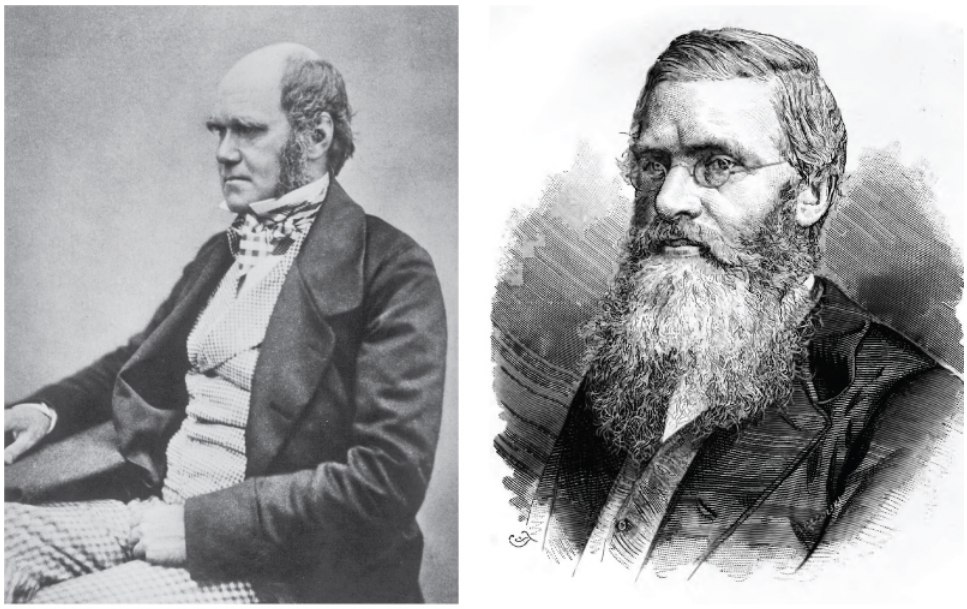
Wallace and Darwin both observed similar patterns in other organisms and they independently developed the same explanation for how and why such changes could take place. Darwin called this mechanism natural selection. **Natural selection**, also known as "survival of the fittest," is the more prolific reproduction of individuals with favorable traits that survive environmental change because of those traits; this leads to evolutionary change.

For example, a population of giant tortoises found in the Galapagos Archipelago was observed by Darwin to 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 couldn't reach the food source. Consequently, long-necked tortoises would be more likely to be reproductively successful 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 no one, including Darwin and Wallace, knew how this happened at the time, it was a common understanding. Second, more offspring are produced than are able to survive, so resources for survival and reproduction are limited. 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. Both Darwin and Wallace's understanding of this principle came from reading an essay by the economist Thomas Malthus who discussed this principle in relation to human populations. Third, offspring vary among each other in regard to their characteristics and those variations are inherited. Darwin and

Wallace reasoned that offspring with inherited characteristics which 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 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.

Papers by Darwin and Wallace (Figure 2) 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. His book outlined in considerable detail his arguments for gradual changes and adaptive survival by natural selection.



(a) (b)

Figure 2. Both (a) Charles Darwin and (b) Alfred Wallace wrote scientific papers on natural selection that were presented together before the Linnean Society in 1858.

Demonstrations of evolution by natural selection are time consuming and difficult to obtain. One of the best examples has been demonstrated in the very birds that helped to inspire Darwin's 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 natural selection. The Grants found changes from one generation to the next in the distribution of beak shapes with the medium ground finch on the Galápagos island of Daphne Major. The birds have inherited variation in the bill shape with some birds having wide deep bills and others having thinner bills. During a period in which rainfall was higher than normal because of an El Niño, the large hard seeds that large-billed birds ate were reduced in number; however, there was an abundance of the small soft seeds which the small-billed birds ate. Therefore, survival and reproduction were much better in the following years for the small-billed birds. In the years following this El Niño, the Grants measured beak sizes in the population and found that the average bill size was smaller. Since bill size is an inherited trait, parents with smaller bills had more offspring and the size of bills had evolved to be smaller. As conditions improved in 1987 and larger seeds became more available, the trend toward smaller average bill size ceased.

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6.4: Theory of Evolution

Natural selection can only take place if there is **variation**, or differences, among individuals in a population. Importantly, these differences must have some genetic basis; otherwise, the 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 being taller because of better nutrition rather than different genes.

Genetic diversity in a population comes from two main mechanisms: mutation and sexual reproduction. Mutation, a change in DNA, 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 on the phenotype. A mutation affects the phenotype of the organism in a way that gives it reduced fitness—lower likelihood of survival or fewer offspring. A mutation may produce a phenotype with a beneficial effect on fitness. And, many mutations will also have no effect on the fitness of the phenotype; these are called neutral mutations. Mutations may also have a whole range of effect sizes on the fitness of the organism that expresses them in their phenotype, from a small effect to a great effect. Sexual reproduction also leads to genetic diversity: when two parents reproduce, unique combinations of alleles assemble to produce the unique genotypes and thus phenotypes in each of the offspring.

A heritable trait that helps the survival and reproduction of an organism in its present environment is called an **adaptation**. Scientists describe groups of organisms becoming adapted to their environment when a change in the range of genetic variation occurs over time that increases or maintains the “fit” of the population to its environment. The webbed feet of platypuses are an adaptation for swimming. The snow leopards’ thick fur is an adaptation for living in the cold. The cheetahs’ fast speed is an adaptation for catching prey.

Whether or not a 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.

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. When two species evolve in diverse directions from a common point, it is called divergent evolution. Such **divergent evolution** can be seen in the forms of the reproductive organs of flowering plants which share the same basic anatomies; however, they can look very different as a result of selection in different physical environments and adaptation to different kinds of pollinators (Figure 1).



Figure 1. 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. (credit a: modification of work by Drew Avery; credit b: modification of work by Cory Zanker)

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, 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. The two species came to the same function, flying, but did so separately from each other.

These physical changes occur over enormous spans of time and help explain how evolution occurs. Natural selection acts on individual organisms, which in turn can 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 the genotype of an entire species to evolve. It is over these large time spans that life on earth has changed and continues to change.

Our Modern Understanding

The mechanisms of inheritance, or genetics, were not understood at the time Charles Darwin and Alfred Russel Wallace were developing their idea of natural selection. This lack of understanding was a stumbling block to understanding many aspects of evolution. In fact, the predominant (and incorrect) genetic theory of the time, blending inheritance, made it difficult to understand how natural selection might operate. Darwin and Wallace were unaware of the genetics work done by Austrian monk Gregor Mendel, which was published in 1866, not long after publication of Darwin's book, *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 in 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 processes, 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 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**.

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6.5: Evidence of Evolution

The evidence for evolution is compelling and extensive. Looking at every level of organization in living systems, biologists see the signature of past and present evolution. Darwin dedicated a large portion of his book, *On theOrigin of Species*, to identifying patterns in nature that were consistent with evolution, and since Darwin, our understanding has become clearer and broader.

Physical Evidence

Fossils

Fossils provide solid evidence that organisms from the past are not the same as those found today, and fossils show a progression of evolution. Scientists determine the age of fossils and categorize them from all over the world to determine when the organisms lived relative to each other. The resulting fossil record tells the story of the past and shows the evolution of form over millions of years (Figure 1a). For example, scientists have recovered highly detailed records showing the evolution of humans and horses (Figure 1b).



Figure 1. In this (a) display, fossil hominids are arranged from oldest (bottom) to newest (top). As hominids evolved, the shape of the skull changed. An artist's rendition of (b) extinct species of the genus Equus reveals that these ancient species resembled the modern horse (Equus ferus) but varied in size.

Anatomy and Embryology

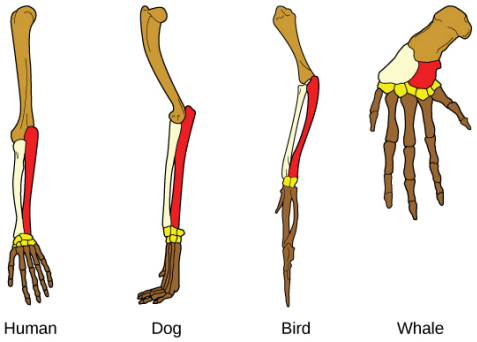


Figure 2. The similar construction of these appendages indicates that these organisms share a common ancestor.

Another type of evidence for evolution is the presence of structures in organisms that share the same basic form. For example, the bones in the appendages of a human, dog, bird, and whale all share the same overall construction (Figure 2) resulting from their origin in the appendages of a common ancestor. Over time, evolution led to changes in the shapes and sizes of these bones in different species, but they have maintained the same overall layout. Scientists call these synonymous parts homologous structures.

Some structures exist in organisms that have no apparent function at all, and appear to be residual parts from a past common ancestor. These unused structures without function are called vestigial structures. Some examples of vestigial structures are wings

on flightless birds, leaves on some cacti, and hind leg bones in whales.

Visit this interactive site to guess which bones structures are homologous and which are analogous. There are also examples of evolutionary adaptations that illustrate these concepts.

Another evidence of evolution is the convergence of form in organisms that share similar environments. For example, species of unrelated animals, such as the arctic fox and ptarmigan, living in the arctic region have been selected for seasonal white phenotypes during winter to blend with the snow and ice (Figure 3). These similarities occur not because of common ancestry, but because of similar selection pressures—the benefits of not being seen by predators.



(a) (b)

Figure 3. The white winter coat of the (a) arctic fox and the (b) ptarmigan's plumage are adaptations to their environments. (credit a: modification of work by Keith Morehouse)

Embryology, the study of the development of the anatomy of an organism to its adult form, also provides evidence of relatedness between now widely divergent groups of organisms. Mutational tweaking in the embryo can have such magnified consequences in the adult that embryo formation tends to be conserved. As a result, structures that are absent in some groups often appear in their embryonic forms and disappear by the time the adult or juvenile form is reached. For example, all vertebrate embryos, including humans, exhibit gill slits and tails at some point in their early development. These disappear in the adults of terrestrial groups but are maintained in adult forms of aquatic groups such as fish and some amphibians. Great ape embryos, including humans, have a tail structure during their development that is lost by the time of birth.

Biological Evidence

Biogeography

The geographic distribution of organisms on the planet follows patterns that are best explained by evolution in conjunction with the movement of tectonic plates over geological time. Broad groups that evolved before the breakup of the supercontinent Pangaea (about 200 million years ago) are distributed worldwide. Groups that evolved since the breakup appear uniquely in regions of the planet, such as the unique flora and fauna of northern continents that formed from the supercontinent Laurasia and of the southern continents that formed from the supercontinent Gondwana. The presence of members of the plant family Proteaceae in Australia, southern Africa, and South America is best due to their appearance prior to the southern supercontinent Gondwana breaking up.

The great diversification of marsupials in Australia and the absence of other mammals reflect Australia's long isolation. Australia has an abundance of endemic species—species found nowhere else—which is typical of islands whose isolation by expanses of water prevents species migration. Over time, these species diverge evolutionarily into new species that look very different from their ancestors that may exist on the mainland. The marsupials of Australia, the finches on the Galápagos, and many species on the Hawaiian Islands are all unique to their one point of origin, yet they display distant relationships to ancestral species on mainlands.

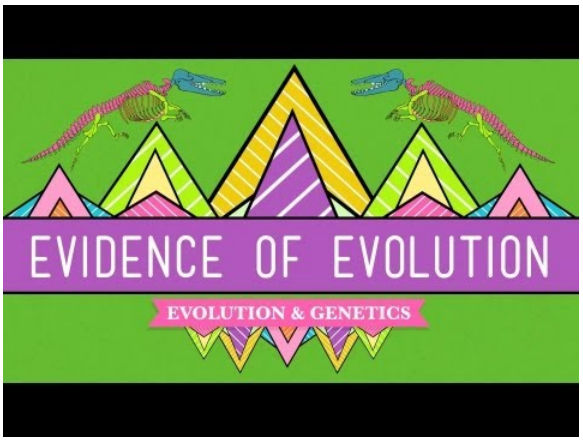
Molecular Biology

Like anatomical structures, the structures of the molecules of life reflect descent with modification. Evidence of a common ancestor for all of life is reflected in the universality of DNA as the genetic material and in the near universality of the genetic code and the machinery of DNA replication and expression. Fundamental divisions in life between the three domains are reflected in major structural differences in otherwise conservative structures such as the components of ribosomes and the structures of membranes. In general, the relatedness of groups of organisms is reflected in the similarity of their DNA sequences—exactly the pattern that would be expected from descent and diversification from a common ancestor.

DNA sequences have also shed light on some of the mechanisms of evolution. For example, it is clear that the evolution of new functions for proteins commonly occurs after gene duplication events that allow the free modification of one copy by mutation, selection, or drift (changes in a population's gene pool resulting from chance), while the other copy continues to produce a functional protein.

Evolution—It's a Thing

This video defines evolution and discusses several varieties of evidence that support the Theory of Evolution:



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=152

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6.6: Misconceptions of Evolution

Although the theory of evolution generated some controversy when it was first proposed, it was almost universally accepted by biologists, particularly younger biologists, within 20 years after publication of *On theOrigin of Species*. Nevertheless, the theory of evolution is a difficult concept and misconceptions about how it works abound.

This site addresses some of the main misconceptions associated with the theory of evolution.

Evolution Is Just a Theory

Critics of the theory of evolution dismiss its importance by purposefully confounding the everyday usage of the word "theory" with the way scientists use the word. In science, a "theory" is understood to be a body of thoroughly tested and verified explanations for a set of observations of the natural world. Scientists have a theory of the atom, a theory of gravity, and the theory of relativity, each of which describes understood facts about the world. In the same way, the theory of evolution describes facts about the living world. As such, a theory in science has survived significant efforts to discredit it by scientists. In contrast, a "theory" in common vernacular is a word meaning a guess or suggested explanation; this meaning is more akin to the scientific concept of "hypothesis." When critics of evolution say evolution is "just a theory," they are implying that there is little evidence supporting it and that it is still in the process of being rigorously tested. This is a mischaracterization.

Individuals Evolve

Evolution is the change in genetic composition of a population over time, specifically over generations, resulting from differential reproduction of individuals with certain alleles. Individuals do change over their lifetime, obviously, but this is called development and involves changes programmed by the set of genes the individual acquired at birth in coordination with the individual's environment. When thinking about the evolution of a characteristic, it is probably best to think about the change of the average value of the characteristic in the population over time. For example, when natural selection leads to 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, this average value will be different as a result of evolution. Although some individuals may survive from the first time to the second, they will still have the same bill size; however, there will be many new individuals that contribute to the shift in average bill size.

Organisms Evolve on Purpose

Statements such as "organisms evolve in response to a change in an environment" are quite common, but such statements can lead to two types of misunderstandings. First, the statement must not be understood to mean that individual organisms evolve. The statement is shorthand for "a population evolves in response to a changing environment." However, a second misunderstanding may arise by interpreting the statement to mean that the evolution is somehow intentional. A changed environment results in some individuals in the population, those with particular phenotypes, benefiting and therefore producing proportionately more offspring than other phenotypes. This results in change in the population if the characteristics are genetically determined.

It is also important to understand that the variation that natural selection works on is already in a population and does not arise in response to an environmental change. For example, applying antibiotics to a population of bacteria will, over time, select a population of bacteria that are resistant to antibiotics. The resistance, which is caused by a gene, did not arise by mutation because of the application of the antibiotic. The gene for resistance was already present in the gene pool of the bacteria, likely at a low frequency. The antibiotic, which kills the bacterial cells without the resistance gene, strongly selects 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 antibiotic.

In a larger sense, evolution is not goal directed. Species do not become "better" over time; they simply track their changing environment with adaptations that maximize their reproduction in a particular environment at a particular time. Evolution has no goal of making faster, bigger, more complex, or even smarter species, despite the commonness of this kind of language in popular discourse. What characteristics evolve in a species are a function of the variation present and the environment, both of which are

constantly changing in a non-directional way. What trait is fit in one environment at one time may well be fatal at some point in the future. This holds equally well for a species of insect as it does the human species.

Evolution Explains the Origin of Life

It is a common misunderstanding that evolution includes an explanation of life's origins. Conversely, some of the theory's critics believe that it cannot explain the origin of life. The theory does not try to explain the origin of life. The theory of evolution explains how populations change over time and how life diversifies the origin of species. It does not shed light on the beginnings of life including the origins of the first cells, which is how life is defined. The mechanisms of the origin of life on Earth are a particularly difficult problem because it occurred a very long time ago, and presumably it just occurred once. Importantly, biologists believe that the presence of life on Earth precludes the possibility that the events that led to life on Earth can be repeated because the intermediate stages would immediately become food for existing living things.

However, once a mechanism of inheritance was in place in the form of a molecule like DNA either within a cell or pre-cell, these entities would be subject to the principle of natural selection. More effective reproducers would increase in frequency at the expense of inefficient reproducers. So while evolution does not explain the origin of life, it may have something to say about some of the processes operating once pre-living entities acquired certain properties.

Learning Objectives

Many misconceptions exist about the theory of evolution—including some perpetuated by critics of the theory. First, evolution as a scientific theory means that it has years of observation and accumulated data supporting it. It is not "just a theory" as a person may say in common vernacular.

Another misconception is that individuals evolve, though in fact it is populations that evolve over time. Individuals simply carry mutations. Furthermore, these mutations neither arise on purpose nor do they arise in response to an environmental pressure. Instead, mutations in DNA happen spontaneously and are already present in individuals of a population when a selective pressure occurs. Once the environment begins to favor a particular trait, then those individuals already carrying that mutation will have a selective advantage and are likely to survive better and outproduce others without the adaptation.

Finally, the theory of evolution does not in fact address the origins of life on this planet. Scientists believe that we cannot, in fact, repeat the circumstances that led to life on Earth because at this time life already exists. The presence of life has so dramatically changed the environment that the origins cannot be totally produced for study.

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6.7: Introduction to Speciation

Define species and identify how species form

Although all life on earth shares various genetic similarities, only certain organisms combine genetic information by sexual reproduction and have offspring that can then successfully reproduce. Scientists call such organisms members of the same biological species.

What You'll Learn to Do

- Define species and describe how species are identified as different
- Differentiate between types of speciation
- Describe the process of reconnection
- Explain the two major theories on rates of speciation

Learning Activities

The learning activities for this section include the following:

- What is a Species?
- Types of Speciation
- Reconnection
- Rates of Speciation
- Self Check: Speciation

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6.8: What is a Species?

A **species** is a group of individual organisms that interbreed and produce fertile, viable offspring. According to this definition, one species is distinguished from another when, in nature, it is not possible for matings between individuals from each species to produce fertile offspring.

Members of the same species share both external and internal characteristics, which develop from their DNA. The closer 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 similar to their father or mother's DNA than their cousin or grandparent's DNA. Organisms of the same species have the highest level of DNA alignment and therefore share characteristics and behaviors that lead to successful reproduction.

Species' appearance can be misleading in suggesting an ability or inability to mate. For example, even though domestic dogs (*Canis lupus familiaris*) display phenotypic differences, such as size, build, and coat, most dogs can interbreed and produce viable puppies that can mature and sexually reproduce (Figure 1).



(a) (b) (c)

Figure 1. The (a) poodle and (b) cocker spaniel can reproduce to produce a breed known as (c) the cockapoo. (credit a: modification of work by Sally Eller, Tom Reese; credit b: modification of work by Jeremy McWilliams; credit c: modification of work by Kathleen Conklin)

In other cases, individuals may appear similar although they are not members of the same species. For example, even though bald eagles (*Haliaeetus leucocephalus*) and African fish eagles (*Haliaeetus vocifer*) are both birds and eagles, each belongs to a separate species group (Figure 2). If humans were to artificially intervene and fertilize the egg of a bald eagle with the sperm of an African fish eagle and a chick did hatch, that offspring, called a **hybrid** (a cross between two species), would probably be infertile—unable to successfully reproduce after it reached maturity. Different species may have different genes that are active in development; therefore, it may not be possible to develop a viable offspring with two different sets of directions. Thus, even though hybridization may take place, the two species still remain separate.



(a) (b)

Figure 2. The (a) African fish eagle is similar in appearance to the (b) bald eagle, but the two birds are members of different species. (credit a: modification of work by Nigel Wedge; credit b: modification of work by U.S. Fish and Wildlife Service)

Populations of species share a gene pool: a collection of all the variants of genes in the species. Again, the basis to any changes in a group or population of organisms must be genetic for this is the only way to share and pass on traits. When variations occur within a species, they can only be passed to the next generation along two main pathways: asexual reproduction or sexual reproduction. The change will be passed on asexually simply if the reproducing cell possesses the changed trait. For the changed trait to be passed on by sexual reproduction, a gamete, such as a sperm or egg cell, must possess the changed trait. In other words, sexually-reproducing organisms can experience several genetic changes in their body cells, but if these changes do not occur in a sperm or egg cell, the changed trait will never reach the next generation. Only heritable traits can evolve. Therefore, reproduction plays a paramount role for genetic change to take root in a population or species. In short, organisms must be able to reproduce with each other to pass new traits to offspring.

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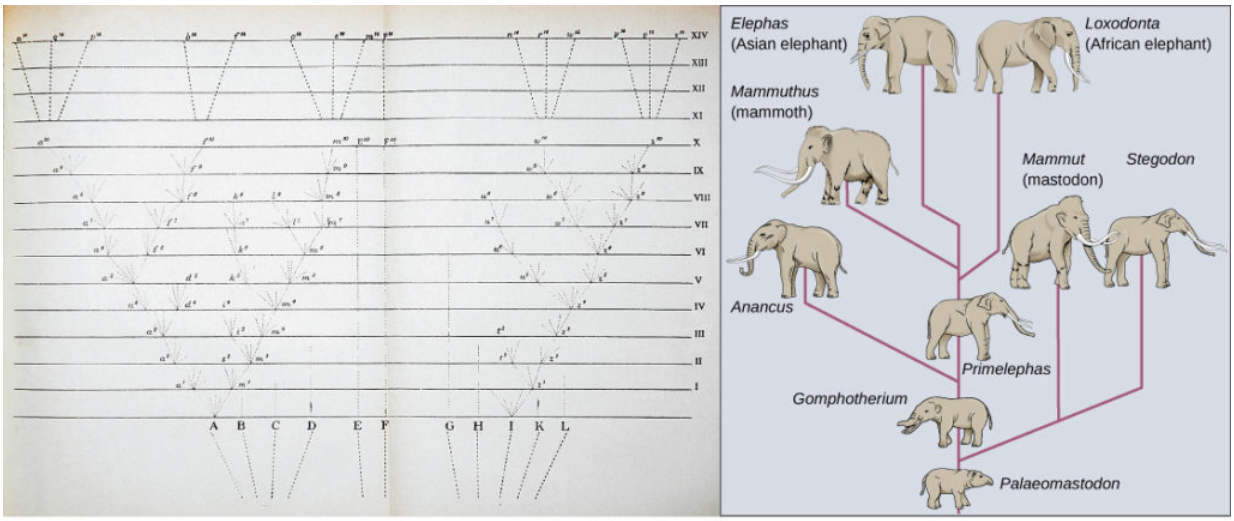
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6.9: Types of Speciation

The biological definition of species, which works for sexually reproducing organisms, is a group of actually or potentially interbreeding individuals. There are exceptions to this rule. Many species are similar enough that hybrid offspring are possible and may often occur in nature, but for the majority of species this rule generally holds. In fact, the presence in nature of hybrids between similar species suggests that they may have descended from a single interbreeding species, and the speciation process may not yet be completed.

Given the extraordinary diversity of life on the planet there must be mechanisms for **speciation**: the formation of two species from one original species. Darwin envisioned this process as a branching event and diagrammed the process in the only illustration found in *On the Origin of Species* (Figure 1a). Compare this illustration to the diagram of elephant evolution (Figure 1b), which shows that as one species changes over time, it branches to form more than one new species, repeatedly, as long as the population survives or until the organism becomes extinct.



(a) (b)

Figure 1. The only illustration in Darwin's *On the Origin of Species* is (a) a diagram showing speciation events leading to biological diversity. The diagram shows similarities to phylogenetic charts that are drawn today to illustrate the relationships of species. (b) Modern elephants evolved from the *Palaeomastodon*, a species that lived in Egypt 35–50 million years ago.

For speciation to occur, two new populations must be formed from one original population and they must evolve in such a way that it becomes impossible for individuals from the two new populations to interbreed. Biologists have proposed mechanisms by which this could occur that fall into two broad categories. **Allopatric speciation** (*allo–* = "other"; *–patric* = "homeland") involves geographic separation of populations from a parent species and subsequent evolution. **Sympatric speciation** (*sym–* = "same"; *–patric* = "homeland") involves speciation occurring within a parent species remaining in one location.

Biologists think of speciation events as the splitting of one ancestral species into two descendant species. There is no reason why there might not be more than two species formed at one time except that it is less likely and 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 a distribution will be similar to the frequency of the allele at the other end. When populations become geographically discontinuous, that free-flow of alleles is prevented. When that separation lasts for a period of time, the two populations are able to evolve along different trajectories. Thus, their allele frequencies at numerous genetic loci gradually become more and more different as new alleles independently arise by mutation in each population. Typically, environmental conditions, such as climate, resources, predators, and competitors for the two populations will differ causing natural selection to favor divergent adaptations in each group.

Isolation of populations leading to allopatric speciation can occur in a variety of ways: a river forming a new branch, erosion forming a new valley, a group of organisms traveling to a new location without the ability to return, or seeds floating over the ocean to an island. The nature of the geographic separation necessary to isolate populations depends entirely on the 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 unlikely; therefore, speciation would be more likely.

Biologists group allopatric processes into two categories: dispersal and vicariance. **Dispersal** is when a few members of a species move to a new geographical area, and **vicariance** is when a natural situation arises to physically divide organisms.



Figure 2. The northern spotted owl and the Mexican spotted owl inhabit geographically separate locations with different climates and ecosystems. The owl is an example of allopatric speciation. (credit “northern spotted owl”: modification of work by John and Karen Hollingsworth; credit “Mexican spotted owl”: modification of work by Bill Radke)

Scientists have documented numerous cases of allopatric speciation taking place. 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 (Figure 2).

Additionally, scientists have found that the further the distance between two groups that once were the same species, the more likely it is that speciation will occur. This seems logical because as the distance increases, the various environmental factors would likely have less in common than locations in close proximity. Consider the two owls: in the north, the climate is cooler than in the south; the types of organisms in each ecosystem differ, as do their behaviors and habits; also, the hunting habits and prey choices of the southern owls vary from the northern owls. These variances can lead to evolved differences in the owls, and speciation likely will occur.

Adaptive Radiation

In some cases, a population of one species disperses throughout an area, and each finds a distinct niche or isolated habitat. Over time, the varied demands of their new lifestyles lead to multiple speciation events originating from a single species. This is called **adaptive radiation** because many adaptations evolve from a single point of origin; thus, causing the species to radiate into several new ones. Island archipelagos like the Hawaiian Islands provide an ideal context for adaptive radiation events because water surrounds each island which leads to geographical isolation for many organisms. The Hawaiian honeycreeper illustrates one example of adaptive radiation. From a single species, called the founder species, numerous species have evolved, including the six shown in Figure 3.



Figure 3. The honeycreeper birds illustrate adaptive radiation. From one original species of bird, multiple others evolved, each with its own distinctive characteristics.

Notice the differences in the species' beaks in Figure 3. Evolution in response to natural selection based on specific food sources in each new habitat led to evolution of a different beak suited to the specific food source. The seed-eating bird has a thicker, stronger beak which is suited to break hard nuts. The nectar-eating birds have long beaks to dip into flowers to reach the nectar. The insect-eating birds have beaks like swords, appropriate for stabbing and impaling insects. Darwin's finches are another example of adaptive radiation in an archipelago.

Click through this interactive site to see how island birds evolved in evolutionary increments from 5 million years ago to today.

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; the prefix "sym" means same, so "sympatric" means "same homeland" in contrast to "allopatric" meaning "other homeland." A number of mechanisms for sympatric speciation have been proposed and studied.

One form of sympatric speciation can begin with a serious chromosomal error during cell division. In a normal cell division event chromosomes replicate, pair up, and then separate so that each new cell has the same number of chromosomes. However, sometimes the pairs separate and the end cell product has too many or too few individual chromosomes in a condition called **aneuploidy** (Figure 4).

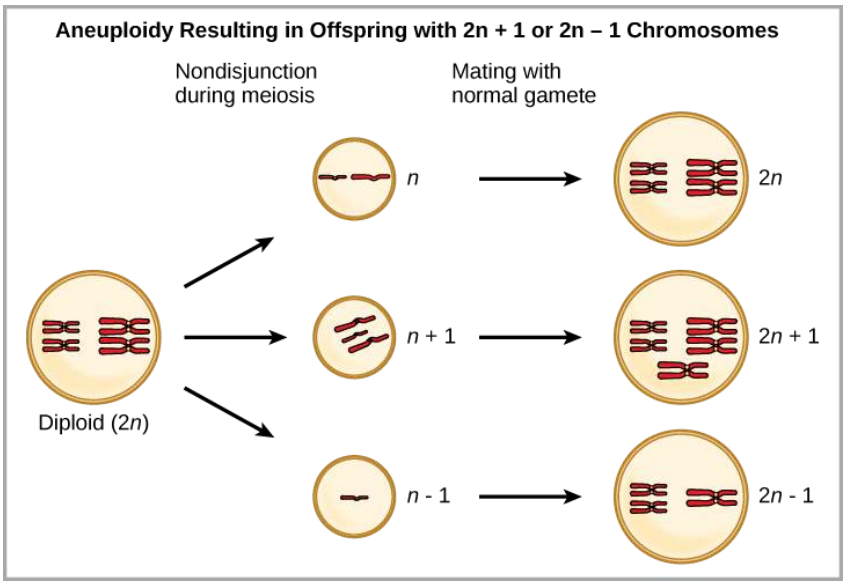


Figure 4. Aneuploidy results when the gametes have too many or too few chromosomes due to nondisjunction during meiosis. In the example shown here, the resulting offspring will have $2n+1$ or $2n-1$ chromosomes

? Practice Question

In Figure 4, which is most likely to survive, offspring with $2n+1$ chromosomes or offspring with $2n-1$ chromosomes?

[practice-area rows="2"][/practice-area]
[reveal-answer q="462162"]Show Answer[/reveal-answer]
[hidden-answer a="462162"]Loss of genetic material is almost always lethal, so offspring with $2n+1$ chromosomes are more likely to survive.[/hidden-answer]

Polyploidy is a condition in which a cell or organism has an extra set, or sets, of chromosomes. Scientists have identified two main types of polyploidy that can lead to reproductive isolation of an individual in the polyploidy state. Reproductive isolation is the inability to interbreed. In some cases, a polyploid individual will have two or more complete sets of chromosomes from its own species in a condition called **autopolyploidy** (Figure 5). The prefix "auto-" means "self," so the term means multiple chromosomes from one's own species. Polyploidy results from an error in meiosis in which all of the chromosomes move into one cell instead of separating.

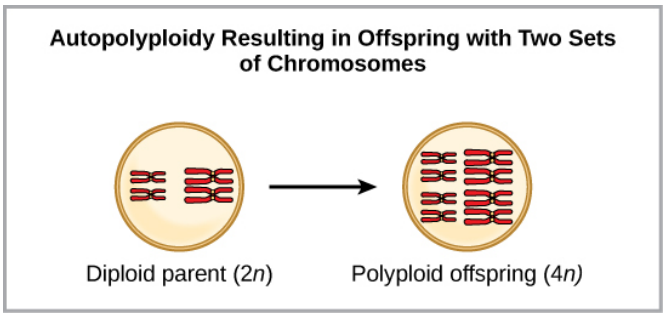


Figure 5. Autopolyploidy results when mitosis is not followed by cytokinesis.

For example, if a plant species with $2n = 6$ produces autopolyploid gametes that are also diploid ($2n = 6$, when they should be $n = 3$), the gametes now have twice as many chromosomes as they should have. These new gametes will be incompatible with the normal gametes produced by this plant species. However, they could either self-pollinate or reproduce with other autopolyploid plants with gametes having the same diploid number. In this way, sympatric speciation can occur quickly by forming offspring with $4n$ called a tetraploid. These individuals would immediately be able to reproduce only with those of this new kind and not those of the ancestral species.

The other form of polyploidy occurs when individuals of two different species reproduce to form a viable offspring called an **allopolyploid**. The prefix “allo-” means “other” (recall from allopatric): therefore, an allopolyploid occurs when gametes from two different species combine. Figure 6 illustrates one possible way an allopolyploid can form. Notice how it takes two generations, or two reproductive acts, before the viable fertile hybrid results.

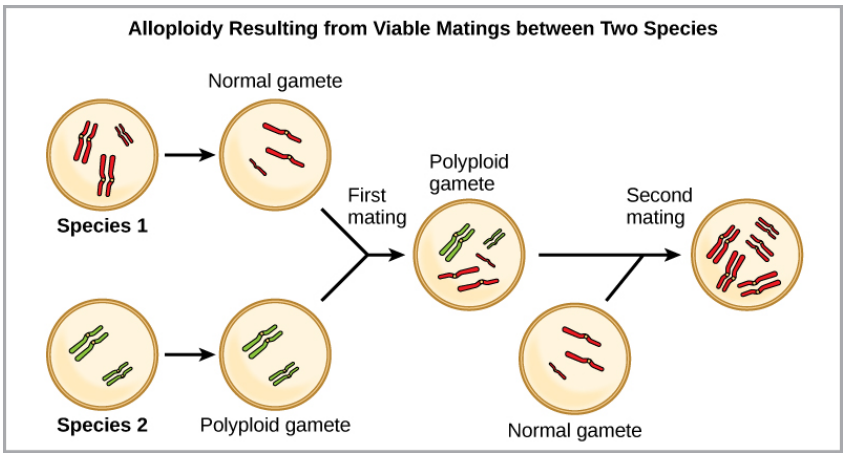


Figure 6. Alloploidy results when two species mate to produce viable offspring. In the example shown, a normal gamete from one species fuses with a polyploidy gamete from another. Two matings are necessary to produce viable offspring.

The cultivated forms of wheat, cotton, and tobacco plants are all allopolyploids. Although polyploidy occurs occasionally in animals, it takes place most commonly in plants. (Animals with any of the types of chromosomal aberrations described here are unlikely to survive and produce normal offspring.) Scientists have discovered more than half of all plant species studied relate back to a species evolved through polyploidy. With such a high rate of polyploidy in plants, some scientists hypothesize that this mechanism takes place more as an adaptation than as an error.

Reproductive Isolation

Given enough time, the genetic and phenotypic divergence between populations will affect characters that influence reproduction: if individuals of the two populations were to be brought together, mating would be less likely, but if mating occurred, offspring would be non-viable or infertile. Many types of diverging characters may affect the **reproductive isolation**, the ability to interbreed, of the two populations.

Reproductive isolation can take place in a variety of ways. Scientists organize them into two groups: 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 don’t survive the embryonic stage and those that are born sterile.

Some types of prezygotic barriers prevent reproduction entirely. Many organisms only reproduce at certain times of the year, often just annually. Differences in breeding schedules, 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 (Figure 7).



(a) (b)

Figure 7. These two related frog species exhibit temporal reproductive isolation. (a) *Rana aurora* breeds earlier in the year than (b) *Rana boylii*. (credit a: modification of work by Mark R. Jennings, USFWS; credit b: modification of work by Alessandro Catenazzi)

In some cases, populations of a species move or are moved to a new habitat and take up residence in a place that no longer overlaps with the other populations of the same species. This situation 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 8).

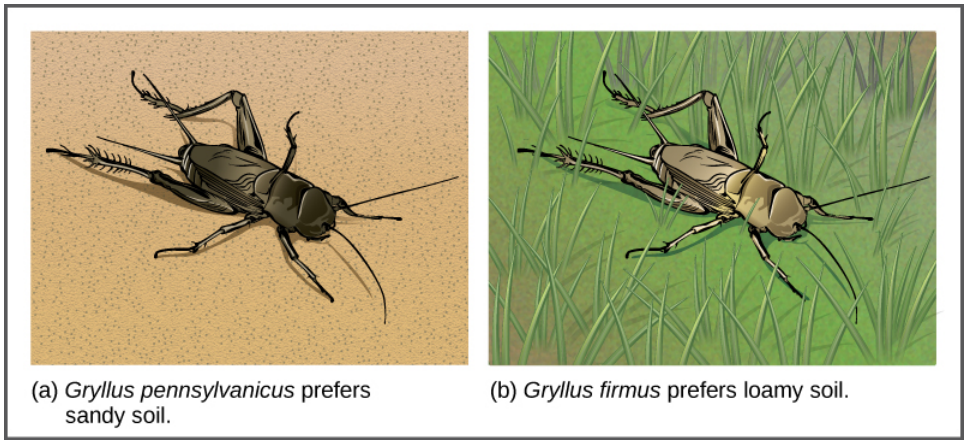


Figure 8. Speciation can occur when two populations occupy different habitats. The habitats need not be far apart. The cricket (a) *Gryllus pennsylvanicus* prefers sandy soil, and the cricket (b) *Gryllus firmus* prefers loamy soil. The two species can live in close proximity, but because of their different soil preferences, they became genetically isolated.

Behavioral isolation occurs when the presence or absence of a specific behavior prevents reproduction from taking place. For example, male fireflies use specific light patterns to attract females. Various species of fireflies display their lights differently. If a male of one species tried to attract the female of another, she would not recognize the light pattern and would not mate with the male.

Other prezygotic barriers work when differences in their gamete cells (eggs and sperm) prevent fertilization from taking place; this is called a **gametic barrier**. Similarly, in some cases closely related organisms try to mate, but their reproductive structures simply do not fit together. For example, damselfly males of different species have differently shaped reproductive organs. If one species tries to mate with the female of another, their body parts simply do not fit together. (Figure 9).



Figure 9. The shape of the male reproductive organ varies among male damselfly species, and is only compatible with the female of that species. Reproductive organ incompatibility keeps the species reproductively isolated.

In plants, certain structures aimed to attract one type of pollinator simultaneously prevent a different pollinator from accessing the pollen. The tunnel through which an animal must access nectar can vary widely in length and diameter, which prevents the plant from being cross-pollinated with a different species (Figure 10).



(a) Honeybee drinking nectar from a foxglove flower

(b) Ruby-throated hummingbird drinking nectar from a trumpet creeper flower

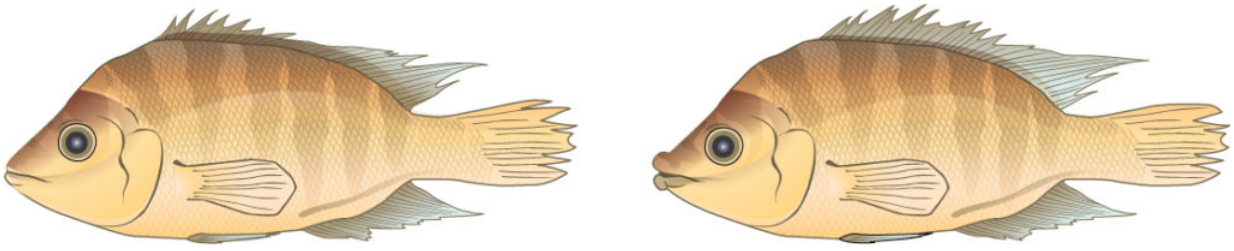
Figure 10. Some flowers have evolved to attract certain pollinators. The (a) wide foxglove flower is adapted for pollination by bees, while the (b) long, tube-shaped trumpet creeper flower is adapted for pollination by humming birds.

When fertilization takes place and a zygote forms, postzygotic barriers can prevent reproduction. Hybrid individuals in many cases cannot form normally in the womb and simply do not survive past the embryonic stages. This is called **hybrid inviability** because the hybrid organisms simply are not viable. In another postzygotic situation, reproduction leads to the birth and growth of a hybrid that is sterile and unable to reproduce offspring of their own; this is called hybrid sterility.

Habitat Influence on Speciation

Sympatric speciation may also take place in ways other than polyploidy. For example, consider a species of fish that lives in a lake. As the population grows, competition for food also grows. Under pressure to find food, suppose that a group of these fish had the genetic flexibility to discover and feed off another resource that was unused by the other fish. What if this new food source was found at a different depth of the lake? Over time, those feeding on the second food source would interact more with each other than the other fish; therefore, they would breed together as well. Offspring of these fish would likely behave as their parents: feeding and living in the same area and keeping separate from the original population. If this group of fish continued to remain separate from the first population, eventually sympatric speciation might occur as more genetic differences accumulated between them.

This scenario does play out in nature, as do others that lead to reproductive isolation. One such place is Lake Victoria in Africa, famous for its sympatric speciation of cichlid fish. Researchers have found hundreds of sympatric speciation events in these fish, which have not only happened in great number, but also over a short period of time. Figure 11 shows this type of speciation among a cichlid fish population in Nicaragua. In this locale, two types of cichlids live in the same geographic location but have come to have different morphologies that allow them to eat various food sources.



Thin-lipped cichlid

Thick-lipped cichlid

Figure 11. Cichlid fish from Lake Apoyeque, Nicaragua, show evidence of sympatric speciation. Lake Apoyeque, a crater lake, is 1800 years old, but genetic evidence indicates that the lake was populated only 100 years ago by a single population of cichlid fish. Nevertheless, two populations with distinct morphologies and diets now exist in the lake, and scientists believe these populations may be in an early stage of speciation.

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6.10: Reconnection

After speciation, two species may recombine or even continue interacting indefinitely. Individual organisms will mate with any nearby individual who they are capable of breeding with. 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 of the hybrids and the reproductive barriers (Figure 1). If the hybrids are less fit than the parents, reinforcement of speciation occurs, and the species continue to diverge until they can no longer mate and produce viable offspring. If reproductive barriers weaken, fusion occurs and the two species become one. Barriers remain the same if hybrids are fit and reproductive: stability may occur and hybridization continues.

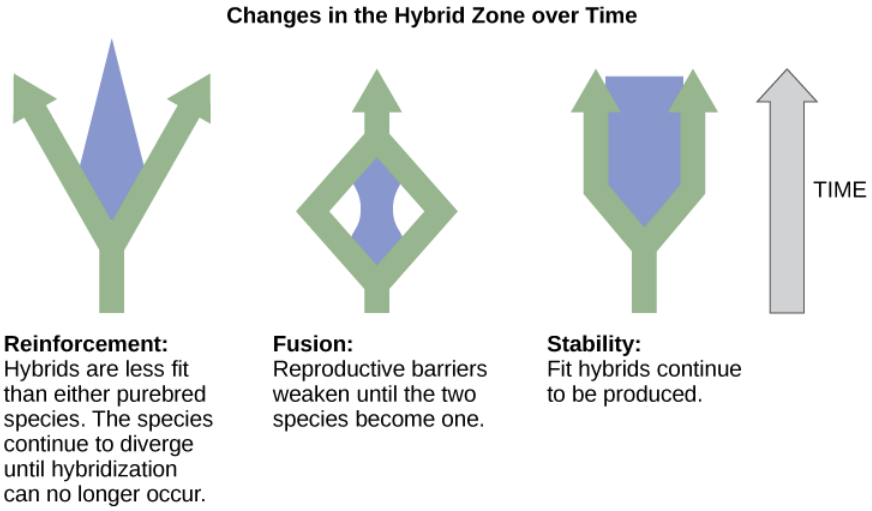


Figure 1. After speciation has occurred, the two separate but closely related species may continue to produce offspring in an area called the hybrid zone. Reinforcement, fusion, or stability may result, depending on reproductive barriers and the relative fitness of the hybrids.

Practice Question

If two species eat a different diet but one of the food sources is eliminated and both species are forced to eat the same foods, what change in the hybrid zone is most likely to occur?

[practice-area rows="2"][/practice-area]
[reveal-answer q="839665"]Show Answer[/reveal-answer]
[hidden-answer a="839665"]Fusion is most likely to occur because the two species will interact more and similar traits in food acquisition will be selected.[/hidden-answer]

Hybrids can be either less fit than the parents, more fit, or about the same. Usually hybrids tend to be less fit; therefore, such reproduction diminishes over time, nudging the two species to diverge further in a process called **reinforcement**. This term is used because the low success of the hybrids reinforces the original speciation. If the hybrids are as fit or more fit than the parents, the two species may fuse back into one species. Scientists have also observed that sometimes two species will remain separate but also continue to interact to produce some hybrid individuals; this is classified as stability because no real net change is taking place.

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6.11: 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: gradual speciation model and punctuated equilibrium model.

In the **gradual speciation model**, species diverge gradually over time in small steps. In the **punctuated equilibrium** model, a new species undergoes changes quickly from the parent species, and then remains largely unchanged for long periods of time afterward (Figure 1). 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.

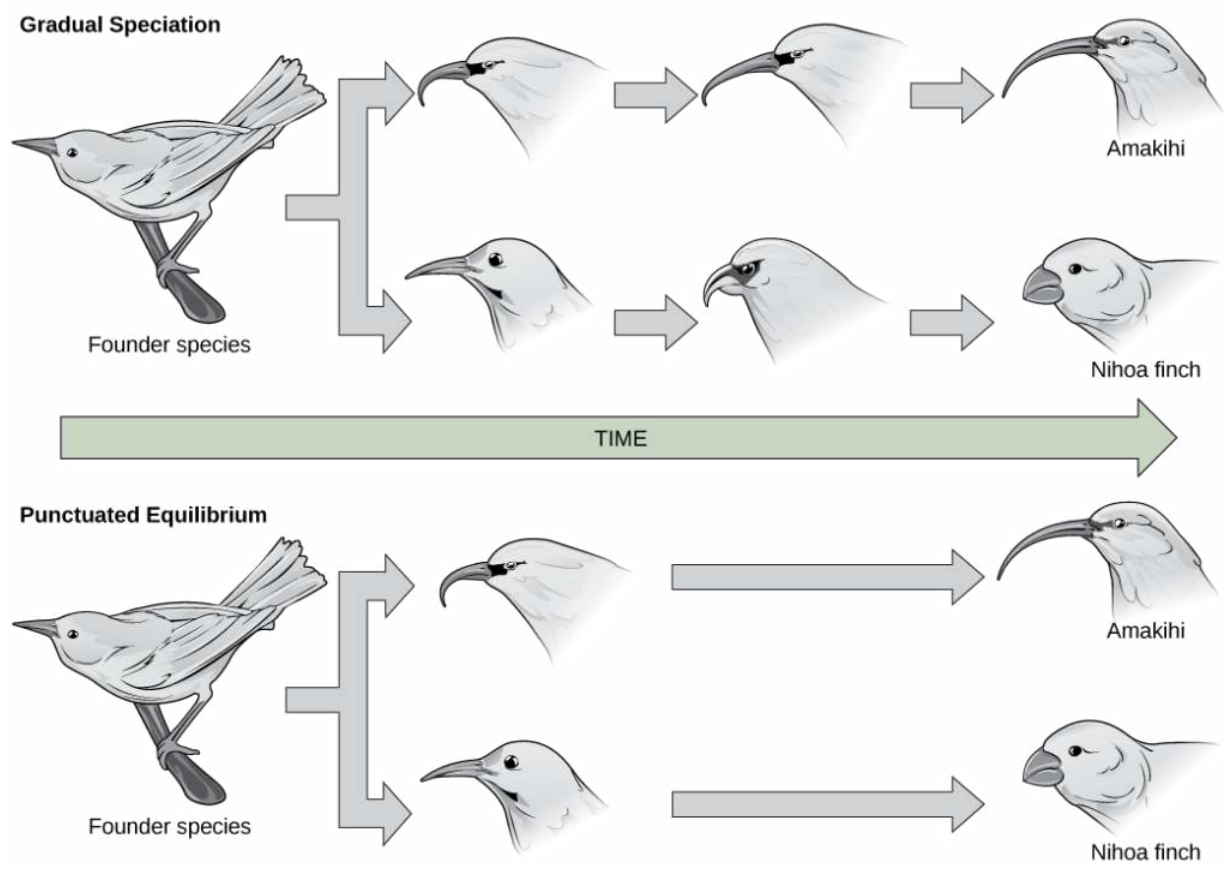


Figure 1. In (a) gradual speciation, species diverge at a slow, steady pace as traits change incrementally. In (b) punctuated equilibrium, species diverge quickly and then remain unchanged for long periods of time.

Practice Question

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.

[reveal-answer q="912830"]Show Answer[/reveal-answer]
[hidden-answer a="912830"]Answer b is false.[/hidden-answer]

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. Layers of 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 surfaces and that aids in surviving the new conditions becomes the predominant form.

Visit this website to continue the speciation story of the snails.

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6.12: Introduction to the Evolution of Populations

Discuss the ways populations evolve

All life on Earth is related. Evolutionary theory states that humans, beetles, plants, and bacteria all share a common ancestor, but that millions of years of evolution have shaped each of these organisms into the forms seen today. Scientists consider evolution a key concept to understanding life. Natural selection is one of the most dominant evolutionary forces. Natural selection acts to promote traits and behaviors that increase an organism's chances of survival and reproduction, while eliminating those traits and behaviors that are to the organism's detriment. But natural selection can only, as its name implies, select—it cannot create. The introduction of novel traits and behaviors falls on the shoulders of another evolutionary force—mutation. Mutation and other sources of variation among individuals, as well as the evolutionary forces that act upon them, alter populations and species. This combination of processes has led to the world of life we see today.

What You'll Learn to Do

- Describe how population genetics is used in the study of the evolution of populations
- Define the Hardy-Weinberg principle and discuss its importance
- Describe the different types of variation in a population
- Explain the different ways natural selection can shape populations

Learning Activities

The learning activities for this section include the following:

- Population Genetics
- Hardy-Weinberg Principle of Equilibrium
- Genetic Variation and Drift
- Adaptive Evolution
- Self Check: The Evolution of Populations

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6.13: Population Genetics

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

The **allele frequency** (or gene frequency) is the rate at which a specific allele appears within a population. Until now we have discussed evolution as a change in the characteristics of a population of organisms, but behind that phenotypic change is genetic change. In population genetics, the term evolution is defined as a change in the frequency of an allele in a population. Using the ABO blood type system as an example, the frequency of one of the alleles, I^A, is the number of copies of that allele divided by all the copies of the ABO gene in the population. For example, a study in Jordan[1] found a frequency of I^A to be 26.1 percent. The $I^B$and I^0 alleles made up 13.4 percent and 60.5 percent of the alleles respectively, and all of the frequencies added up to 100 percent. A change in this frequency over time would constitute evolution in the population.

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

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

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

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6.14: Hardy-Weinberg Principle of Equilibrium

In the early twentieth century, English mathematician Godfrey Hardy and German physician Wilhelm Weinberg stated the principle of equilibrium to describe the genetic makeup of a population. 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. The Hardy-Weinberg principle assumes conditions with no mutations, migration, emigration, or selective pressure for or against genotype, plus an infinite population; while no population can satisfy those conditions, the principle offers a useful model against which to compare real population changes.

Working under this theory, population geneticists represent different alleles as different variables in their mathematical models. The variable p, for example, often represents the frequency of a particular allele, say Y for the trait of yellow in Mendel's peas, while the variable q represents the frequency of y alleles that confer the color green. If these are the only two possible alleles for a given locus in the population, $p + q = 1$. In other words, all the p alleles and all the q alleles make up all of the alleles for that locus that are found in the population.

But what ultimately interests most biologists is not the frequencies of different alleles, but the frequencies of the resulting genotypes, known as the population's **genetic structure**, from which scientists can surmise the distribution of phenotypes. If the phenotype is observed, only the genotype of the homozygous recessive alleles can be known; the calculations provide an estimate of the remaining genotypes. Since each individual carries two alleles per gene, if the allele frequencies (p and q) are known, predicting the frequencies of these genotypes is a simple mathematical calculation to determine the probability of getting these genotypes if two alleles are drawn at random from the gene pool. So in the above scenario, an individual pea plant could be pp (YY), and thus produce yellow peas; pq (Yy), also yellow; or qq (yy), and thus producing green peas (Figure 1). In other words, the frequency of pp individuals is simply p^2; the frequency of pq individuals is 2pq; and the frequency of qq individuals is q^2. And, again, if p and q are the only two possible alleles for a given trait in the population, these genotypes frequencies will sum to one: $p^2 + 2pq + q^2 = 1$.

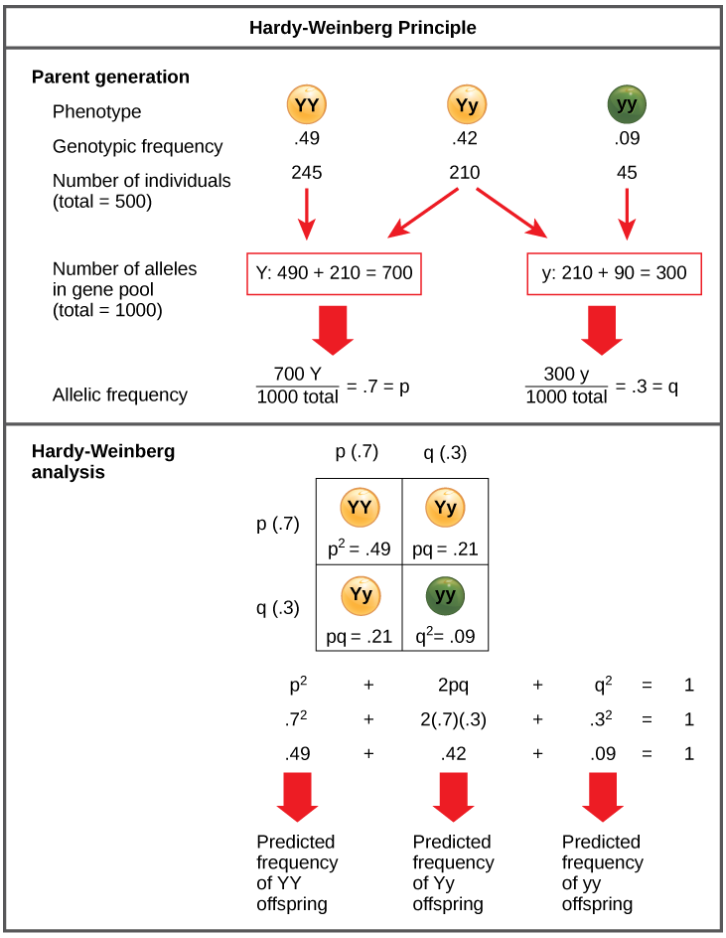


Figure 1. When populations are in the Hardy-Weinberg equilibrium, the allelic frequency is stable from generation to generation and the distribution of alleles can be determined from the Hardy-Weinberg equation. If the allelic frequency measured in the field differs from the predicted value, scientists can make inferences about what evolutionary forces are at play.

Practice Question

In plants, violet flower color (V) is dominant over white (v). If p = 0.8 and 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?

[practice-area rows="2"][/practice-area]
[reveal-answer q="84391"]Show Answer[/reveal-answer]
[hidden-answer a="84391"]The expected distribution is 320 VV, 160Vv, and 20 vv plants. Plants with VV or Vv genotypes would have violet flowers, and plants with the vv genotype would have white flowers, so a total of 480 plants would be expected to have violet flowers, and 20 plants would have white flowers.[/hidden-answer]

In theory, if a population is at equilibrium—that is, there are no evolutionary forces acting upon it—generation after generation would have the same gene pool and genetic structure, and these equations would all hold true all of the time. Of course, even Hardy and Weinberg recognized that no natural population is immune to evolution. Populations in nature are constantly changing in genetic makeup due to drift, mutation, possibly migration, and selection. As a result, the only way to determine the exact distribution of phenotypes in a population is to go out and count them. But the Hardy-Weinberg principle gives scientists a mathematical baseline of a non-evolving population to which they can compare evolving populations and thereby infer what evolutionary forces might be at play. If the frequencies of alleles or genotypes deviate from the value expected from the Hardy-Weinberg equation, then the population is evolving.

Use this online calculator to determine the genetic structure of a population.

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6.15: Genetic Variation and Drift



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

Individuals of a population often display different phenotypes, or express different alleles of a particular gene, referred to as polymorphisms. Populations with two or more variations of particular characteristics 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 1). 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.

Genetic Variance

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 body builder. If there is a genetic basis for the ability to run fast, on the other hand, this may be passed to a child.

Before Darwinian evolution became the prevailing theory of the field, French naturalist Jean-Baptiste Lamarck theorized that acquired traits could, in fact, be inherited; while this hypothesis has largely been unsupported, scientists have recently begun to realize that Lamarck was not completely wrong. Visit this site to learn more.

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

The diversity of alleles and genotypes within a population is called **genetic variance**. 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**.

Changes in allele frequencies that are identified in a population can shed light on how it is evolving. In addition to natural selection, there are other evolutionary forces that could be in play: genetic drift, gene flow, mutation, nonrandom mating, and environmental variances.

Genetic Drift

The theory of natural selection stems from the observation that some individuals in a population are more likely to survive longer and have more offspring than others; thus, they will pass on more of their genes to the next generation. A big, powerful male gorilla, for example, is much more likely than a smaller, weaker one to become the population's silverback, the pack's leader who mates far more than the other males of the group. The pack leader will father more offspring, who share half of his genes, and are likely to also grow bigger and stronger like their father. Over time, the genes for bigger size will increase in frequency in the population, and the population will, as a result, grow larger on average. That is, this would occur if this particular **selection pressure**, or driving selective force, were the only one acting on the population. In other examples, better camouflage or a stronger resistance to drought might pose a selection pressure.

Another way a population's allele and genotype frequencies can change is **genetic drift** (Figure 2), which is simply the effect of chance. By chance, 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).

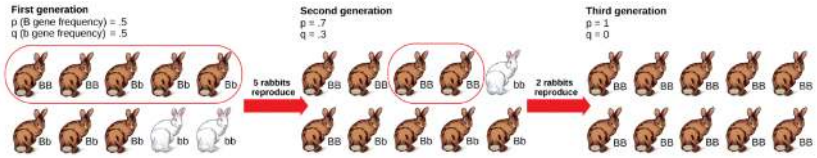


Figure 2. Click for a larger image. Genetic drift in a population can lead to the elimination of an allele from a population by chance. In this example, rabbits with the brown coat color allele (*B*) are dominant over rabbits with the white coat color allele (*b*). In the first generation, the two alleles occur with equal frequency in the population, resulting in p and q values of .5. Only half of the individuals reproduce, resulting in a second generation with p and q values of .7 and .3, respectively. Only two individuals in the second generation reproduce, and by chance these individuals are homozygous dominant for brown coat color. As a result, in the third generation the recessive b allele is lost.

? Practice Question

Do you think genetic drift would happen more quickly on an island or on the mainland?

[practice-area rows="2"][/practice-area]
[reveal-answer q="949142"]Show Answer[/reveal-answer]
[hidden-answer a="949142"]Genetic drift is likely to occur more rapidly on an island where smaller populations are expected to occur.[/hidden-answer]

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 it leaves any offspring to the next generation, all of its genes—1/10 of the population's gene pool—will be suddenly lost. In a population of 100, that's only 1 percent of the overall gene pool; therefore, it is much less impactful on the population's genetic structure.

Watch this animation of random sampling and genetic drift in action:



Bottleneck Effect

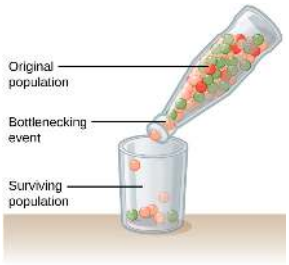


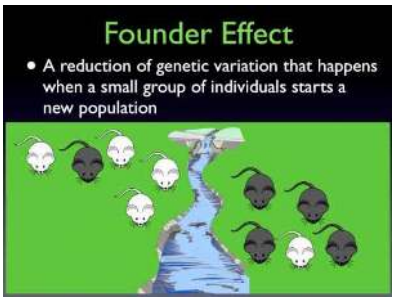
Figure 3. A chance event or catastrophe can reduce the genetic variability within a population.

Genetic drift can also be magnified by natural events, such as a natural disaster that kills—at random—a large portion of the population. Known as the **bottleneck effect**, it results in a large portion of the genome suddenly being wiped out (Figure 3). In one fell swoop, the genetic structure of the survivors becomes the genetic structure of the entire population, which may be very different from the pre-disaster population.

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. In this situation, those individuals are unlikely to be 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 is likely due to the fact that a higher-than-normal proportion of the founding colonists carried these mutations. As a result, the population expresses unusually high incidences of Huntington's disease (HD) and Fanconi anemia (FA), a genetic disorder known to cause blood marrow and congenital abnormalities—even cancer.

Watch this short video to learn more about the founder and bottleneck effects. Note that the video has no audio.



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=172

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 the original population 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 1/3 of the bottle's contents into a bowl. This represents the surviving individuals after a natural disaster kills a majority 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 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 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 Mississippi Gulf Coast? How do the seabirds that live on the beach fare?

Gene Flow

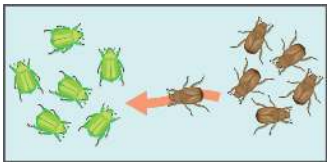


Figure 4. Gene flow can occur when an individual travels from one geographic location to another.

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). 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 it can also introduce new genetic variation to populations in different geological locations and habitats.

Mutation

Mutations are changes to an organism's DNA and are an important driver of diversity in populations. Species 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. Some mutations are unfavorable or harmful and are quickly eliminated from the population by natural selection. 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. Some can have a dramatic effect on a gene and the resulting phenotype.

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 peahens may prefer peacocks with bigger, brighter tails. 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.

Environmental Variance



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

Genes are not the only players involved in determining population variation. Phenotypes are also influenced by other factors, such as the environment (Figure 5). A beachgoer is likely to have darker skin than a city dweller, for example, due to regular exposure to the sun, an environmental factor. Some major characteristics, such as sex, 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.

Geographic separation between populations can lead to differences in the phenotypic variation between those populations. Such **geographical variation** is seen between most populations and can be significant. One type of geographic variation, called a **cline**, can be seen as populations of a given species vary gradually across an ecological gradient. Species of warm-blooded animals, for example, tend to have larger bodies in the cooler climates closer to the earth's poles, allowing them to better conserve heat. This is considered a latitudinal cline. 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.

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

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6.16: Adaptive Evolution

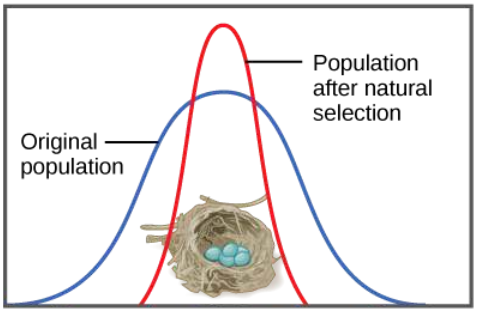
Natural selection only acts on the population's heritable traits: selecting for beneficial alleles and thus increasing their frequency in the population, while selecting against deleterious alleles and thereby decreasing their frequency—a process known as **adaptive evolution**. Natural selection does 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 (fecundity), but if that same individual also carries an allele that results in a fatal childhood disease, that 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 (Darwinian) fitness**.

Fitness is often quantifiable and is measured by scientists in the field. 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.

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

Stabilizing Selection

If natural selection favors an average phenotype, selecting against extreme variation, the population will undergo **stabilizing selection** (Figure 1). In a population of mice that live in the woods, for example, natural selection is likely 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 is most closely matched to that color will be most likely to survive and reproduce, passing on their genes for their brown coat. Mice that carry alleles that make them a bit lighter or a bit darker will stand out against the ground and be more likely to fall victim to predation. As a result of this selection, the population's genetic variance will decrease.

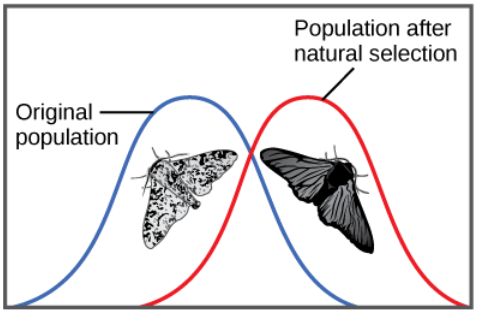


Robins typically lay four eggs, an example of stabilizing selection. Larger clutches may result in malnourished chicks, while smaller clutches may result in no viable offspring.

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

Directional Selection

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



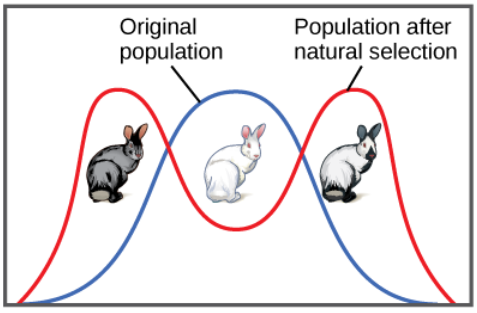
Light-colored peppered moths are better camouflaged against a pristine environment; likewise, dark-colored peppered moths are better camouflaged against a sooty environment. Thus, as the Industrial Revolution progressed in nineteenth-century England, the color of the moth population shifted from light to dark, an example of directional selection.

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

In science, sometimes things are believed to be true, and then new information comes to light that changes our understanding. The story of the peppered moth is an example: the facts behind the selection toward darker moths have recently been called into question. Read this article to learn more.

Diversifying Selection

Sometimes two or more distinct phenotypes can each have their advantages and be selected for by natural selection, while the intermediate phenotypes are, on average, less fit. Known as **diversifying selection** (Figure 3), this is seen in many populations of animals that have multiple male forms. 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 can't overtake the alpha males and are too big to sneak copulations, are selected against. Diversifying selection can also occur when environmental changes favor individuals on either end of the phenotypic spectrum. Imagine a 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 would thus be more likely to be eaten by predators. The result of this type of selection is increased genetic variance as the population becomes more diverse.



In a hyphothetical population, gray and Himalayan (gray and white) rabbits are better able to blend with a rocky environment than white rabbits, resulting in diversifying selection.

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

? Practice Question

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

[practice-area rows="2"][/practice-area]
[reveal-answer q="771182"]Show Answer[/reveal-answer]
[hidden-answer a="771182"]Moths have shifted to a lighter color.[/hidden-answer]

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). An interesting example of this type of selection is seen in a

unique group of lizards of the Pacific Northwest. Male common side-blotched lizards come in three throat-color patterns: orange, blue, and yellow.



Figure 4. A yellow-throated side-blotched lizard is smaller than either the blue-throated or orange-throated males and appears a bit like the females of the species, allowing it to sneak copulations. (credit: “tinyfroglet”/Flickr)

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 (Figure 4) are the smallest, and look a bit like females, which allows them to sneak copulations. Like a game of rock-paper-scissors, orange beats blue, blue beats yellow, and yellow beats orange in the competition for females. That is, the big, strong orange males can fight off the blue males to mate with the blue’s pair-bonded females, the blue males are successful at guarding their mates against yellow sneaker males, and the yellow males can sneak copulations from the potential mates of the large, polygynous orange males.

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.

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

Sexual Selection

Males and females of certain species are often quite different from one another in ways beyond the reproductive organs. Males are often larger, for example, and display many elaborate colors and adornments, like the peacock’s tail, while females tend to be smaller and duller in decoration. Such differences are known as **sexual dimorphisms** (Figure 5), which arise from the fact that in many populations, particularly animal populations, there is more variance in the reproductive success of the males than there is of the females. That is, some males—often the bigger, stronger, or more decorated males—get the vast majority of the total matings, while others receive none. This can occur because the males are better at fighting off other males, or because females will choose to mate with the bigger or more decorated males. In either case, this variation in reproductive success generates a strong selection pressure among males to get those matings, resulting in the evolution of bigger body size and elaborate ornaments to get the females’ attention. Females, on the other hand, tend to get a handful of selected matings; therefore, they are more likely to select more desirable males.

Sexual dimorphism varies widely among species, of course, and some species are even sex-role reversed. In such cases, females tend to have a greater variance in their reproductive success than males and are correspondingly selected for the bigger body size and elaborate traits usually characteristic of males.



(a) (b) (c)

Figure 5. Sexual dimorphism is observed in (a) peacocks and peahens, (b) *Argiope appensa* spiders (the female spider is the large one), and in (c) wood ducks. (credit "spiders": modification of work by "Sanba38"/Wikimedia Commons; credit "duck": modification of work by Kevin Cole)

The selection pressures on males and females to obtain matings is known as sexual selection; it can result in the development of secondary sexual characteristics that do not benefit the individual's likelihood of survival but help to maximize its reproductive success. Sexual selection can be so strong that it selects for traits that are actually detrimental to the individual's survival. Think, once again, about the peacock's tail. While it is beautiful and the male with the largest, most colorful tail is more likely to win the female, it is not the most practical appendage. In addition to being more visible to predators, it makes the males slower in their attempted escapes. There is some evidence that this risk, in fact, is why females like the big tails in the first place. The speculation is that large tails carry risk, and only the best males survive that risk: the bigger the tail, the more fit the male. This idea is known as the **handicap principle**.

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 picky 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.

In 1915, biologist Ronald Fisher proposed another model of sexual selection: the Fisherian runaway model, which suggests that selection of certain traits is a result of sexual preference.

In both the handicap principle and the good genes hypothesis, the trait is said to be an **honest signal** of the males' quality, thus giving females a way to find the fittest mates—males that will pass the best genes to their offspring.

No Perfect Organism

Natural selection is a driving force in evolution and can generate populations that are better adapted to survive and successfully reproduce in their environments. But natural selection cannot produce the perfect organism. Natural selection can only select on existing variation in the population; it does not create anything from scratch. Thus, it is limited by a population's existing genetic variance and whatever new alleles arise through mutation and gene flow.

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

Furthermore, natural selection can be constrained by the relationships between different polymorphisms. One morph may confer a higher fitness than another, but may not increase in frequency due to the fact that going from the less beneficial to the more beneficial trait would require going through a less beneficial phenotype. Think back to the mice that live at the beach. Some are light-colored and blend in with the sand, while others are dark and blend in with the patches of grass. The dark-colored mice may be, overall, more fit than the light-colored mice, and at first glance, one might expect the light-colored mice be selected for a darker

coloration. But remember that the intermediate phenotype, a medium-colored coat, is very bad for the mice—they cannot blend in with either the sand or the grass and are more likely to be eaten by predators. As a result, the light-colored mice would not be selected for a dark coloration because those individuals that began moving in that direction (began being selected for a darker coat) would be less fit than those that stayed light.

Finally, it is important to understand that not all evolution is adaptive. While natural selection selects the fittest individuals and often results in a more fit population overall, other forces of evolution, including genetic drift and gene flow, often do the opposite: introducing deleterious alleles to the population's gene pool. Evolution has no purpose—it is not changing a population into a preconceived ideal. It is simply the sum of the various forces described in this chapter and how they influence the genetic and phenotypic variance of a population.

? Practice Questions

Give an example of a trait that may have evolved as a result of the handicap principle and explain your reasoning.

[practice-area rows="2"][/practice-area]
[reveal-answer q="232026"]Show Answer[/reveal-answer]
[hidden-answer a="232026"]The peacock's tail is a good example of the handicap principle. The tail, which makes the males more visible to predators and less able to escape, is clearly a disadvantage to the bird's survival. But because it is a disadvantage, only the most fit males should be able to survive with it. Thus, the tail serves as an honest signal of quality to the females of the population; therefore, the male will earn more matings and greater reproductive success.

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List the ways in which evolution can affect population variation and describe how they influence allele frequencies.

[practice-area rows="2"][/practice-area]
[reveal-answer q="880085"]Show Answer[/reveal-answer]
[hidden-answer a="880085"]There are several ways evolution can affect population variation: stabilizing selection, directional selection, diversifying selection, frequency-dependent selection, and sexual selection. As these influence the allele frequencies in a population, individuals can either become more or less related, and the phenotypes displayed can become more similar or more disparate.[/hidden-answer]

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6.17: Introduction to Phylogenies and the History of Life

Read and analyze a phylogenetic tree that documents evolutionary relationships

This bee and *Echinacea* flower (Figure 1) could not look more different, yet they are related, as are all living organisms on Earth. By following pathways of similarities and changes—both visible and genetic—scientists seek to map the evolutionary past of how life developed from single-celled organisms to the tremendous collection of creatures that have germinated, crawled, floated, swam, flown, and walked on this planet.



Figure 1. The life of a bee is very different from the life of a flower, but the two organisms are related. Both are members the domain Eukarya and have cells containing many similar organelles, genes, and proteins. (credit: modification of work by John Beetham)

What You'll Learn to Do

- Discuss the components and purpose of a phylogenetic tree
- List the different levels of the taxonomic classification system
- Compare homologous and analogous traits
- Discuss the purpose of cladistics
- Identify different perspectives and criticisms of the phylogenetic tree

Learning Activities

The learning activities for this section include the following:

- Phylogenetic Trees
- Taxonomy
- Homologous and Analogous Traits
- Cladistics
- Perspectives on the Phylogenetic Tree
- Self Check: Phylogenies and the History of Life

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6.18: Phylogenetic Trees

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

Scientists use a tool called a phylogenetic tree to show the evolutionary pathways and connections among organisms. A **phylogenetic tree** is a diagram used to reflect evolutionary relationships among organisms or groups of organisms. Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past since one cannot go back to confirm the proposed relationships. In other words, a "tree of life" can be constructed to illustrate when different organisms evolved and to show the relationships among different organisms (Figure 1).



Figure 1. Both of these phylogenetic trees shows the relationship of the three domains of life—Bacteria, Archaea, and Eukarya—but the (a) rooted tree attempts to identify when various species diverged from a common ancestor while the (b) unrooted tree does not. (credit a: modification of work by Eric Gaba)

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

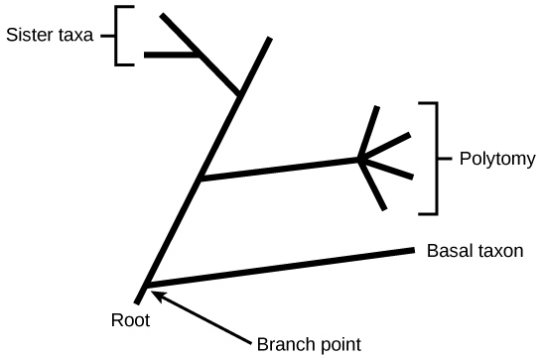


Figure 2. The root of a phylogenetic tree indicates that an ancestral lineage gave rise to all organisms on the tree. A branch point indicates where two lineages diverged. A lineage that evolved early and remains unbranched is a basal taxon. When two lineages stem from the same branch point, they are sister taxa. A branch with more than two lineages is a polytomy.

In a rooted tree, the branching indicates evolutionary relationships (Figure 2). The point where a split occurs, called a **branch point**, represents where a single lineage evolved into a distinct new one. A lineage that evolved early from the root and remains unbranched is called **basal taxon**. When two lineages stem from the same branch point, they are called **sister taxa**. A branch with more than two lineages is called a **polytomy** and serves to illustrate where scientists have not definitively determined all of the

relationships. It is important to note that although sister taxa and polytomy do share an ancestor, it does not mean that the groups of organisms split or evolved from each other. Organisms in two taxa may have split apart at a specific branch point, but neither taxa gave rise to the other.

The diagrams above 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 branch points does not change the information. For example, if a branch point was rotated and the taxon order changed, this would not alter the information because the evolution of each taxon from the branch point was independent of the other.

Many disciplines within the study of biology contribute to understanding how past and present life evolved over time; these disciplines together contribute to building, updating, and maintaining the "tree of life." Information is used to organize and classify organisms based on evolutionary relationships in a scientific field called **systematics**. Data may be collected from fossils, from studying the structure of body parts or molecules used by an organism, and by DNA analysis. By combining data from many sources, scientists can put together the phylogeny of an organism; since phylogenetic trees are hypotheses, they will continue to change as new types of life are discovered and new information is learned.

Limitations of Phylogenetic Trees

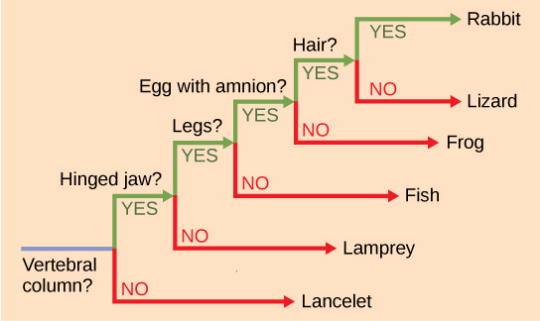


Figure 3. This ladder-like phylogenetic tree of vertebrates is rooted by an organism that lacked a vertebral column. At each branch point, organisms with different characters are placed in different groups based on the characteristics they share.

It may be easy to assume that more closely related organisms look more alike, and while this is often the case, it is not always true. If two closely related lineages evolved under significantly varied surroundings or after the evolution of a major new adaptation, it is possible for the two groups to appear more different than other groups that are not as closely related. For example, the phylogenetic tree in Figure 3 shows that lizards and rabbits both have amniotic eggs, whereas frogs do not; yet lizards and frogs appear more similar than lizards and rabbits.

Another aspect of phylogenetic trees is that, unless otherwise indicated, the branches do not account for length of time, only the evolutionary order. In other words, the length of a branch does not typically mean more time passed, nor does a short branch mean less time passed— unless specified on the diagram. For example, in Figure 3, 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 3, the tree shows that the oldest trait is the vertebral column, followed by hinged jaws, and so forth. Remember that any phylogenetic tree is a part of the greater whole, and like a real tree, it does not grow in only one direction after a new branch develops. So, for the organisms in Figure 3, just because a vertebral column evolved does not mean that invertebrate evolution ceased, it only means that a new branch formed. Also, groups that are not closely related, but evolve under similar conditions, may appear more phenotypically similar to each other than to a close relative.

Head to this website to see interactive exercises that allow you to explore the evolutionary relationships among species.

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6.19: Taxonomy

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

The taxonomic classification system (also called the Linnaean system after its inventor, Carl Linnaeus, a Swedish botanist, zoologist, and physician) uses a hierarchical model. Moving from the point of origin, the groups become more specific, until one branch ends as a single species. For example, after the common beginning of all life, scientists divide organisms into three large categories called a domain: Bacteria, Archaea, and Eukarya. Within each domain is a second category called a **kingdom**. After kingdoms, the subsequent categories of increasing specificity are: **phylum**, **class**, **order**, **family**, **genus**, and **species** (Figure 1).

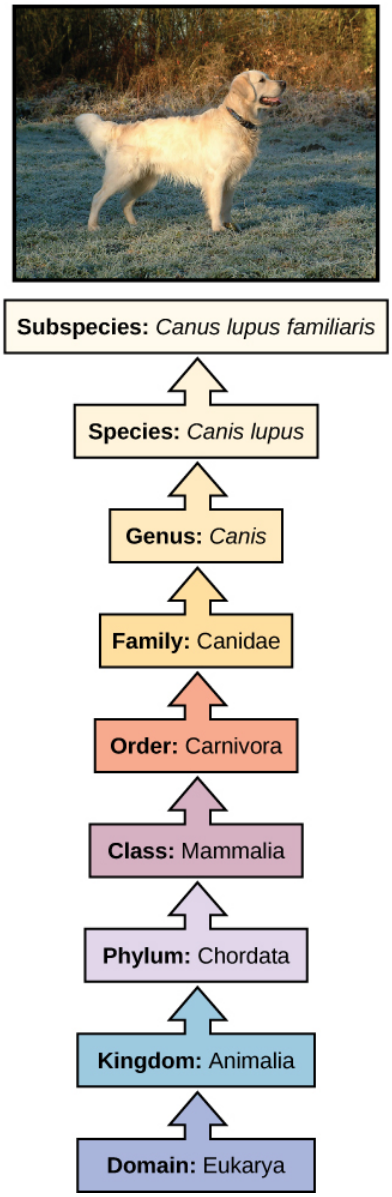


Figure 1. The taxonomic classification system uses a hierarchical model to organize living organisms into increasingly specific categories. The common dog, *Canis lupus familiaris*, is a subspecies of *Canis lupus*, which also includes the wolf and dingo. (credit “dog”: modification of work by Janneke Vreugdenhil)

The kingdom Animalia stems from the Eukarya domain. For the common dog, the classification levels would be as shown in Figure 1. Therefore, the full name of an organism technically has eight terms. For the dog, it is: Eukarya, Animalia, Chordata, Mammalia, Carnivora, Canidae, *Canis*, and *lupus*. Notice that each name is capitalized except for species, and the genus and species names are italicized. Scientists generally refer to an organism only by its genus and species, which is its two-word scientific name, in what is called **binomial nomenclature**. Therefore, the scientific name of the dog is *Canis lupus*. The name at each level is also called a **taxon**. In other words, dogs are in order Carnivora. Carnivora is the name of the taxon at the order level; Canidae is the taxon at the family level, and so forth. Organisms also have a common name that people typically use, in this case, dog. Note that the dog is additionally a subspecies: the "*familiaris*" in *Canis lupus familiaris*. Subspecies are members of the same species that are capable of mating and reproducing viable offspring, but they are considered separate subspecies due to geographic or behavioral isolation or other factors.

Figure 2 shows how the levels move toward specificity with other organisms. Notice how the dog shares a domain with the widest diversity of organisms, including plants and butterflies. At each sublevel, the organisms become more similar because they are more closely related. Historically, scientists classified organisms using characteristics, but as DNA technology developed, more precise phylogenies have been determined.

Practice Question

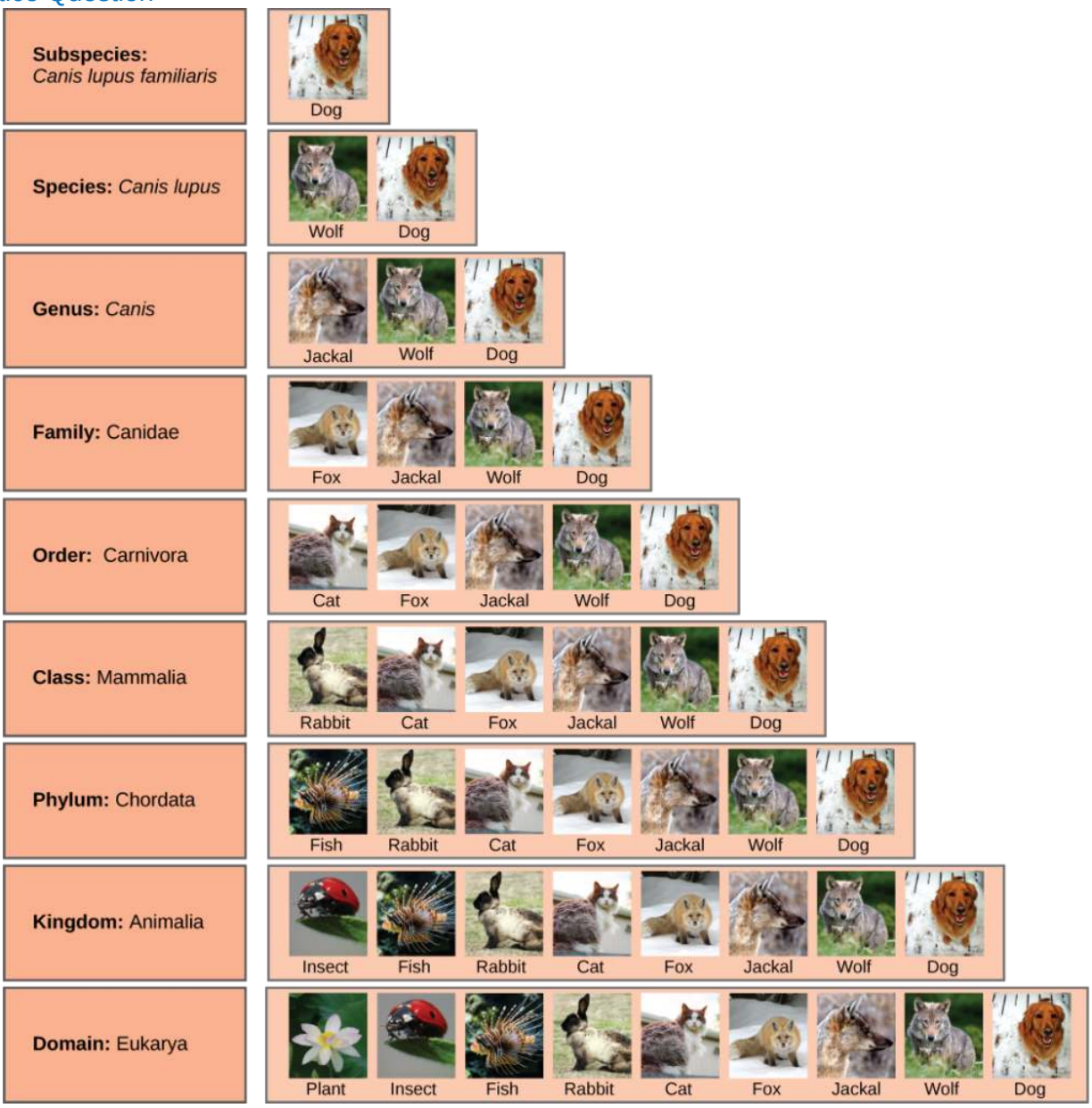


Figure 2. At each sublevel in the taxonomic classification system, organisms become more similar. Dogs and wolves are the same species because they can breed and produce viable offspring, but they are different enough to be classified as different subspecies. (credit “plant”: modification of work by “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)

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

[practice-area rows=”2″][/practice-area]
[reveal-answer q=”614472″]Show Answer[/reveal-answer]
[hidden-answer a=”614472″]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.[/hidden-answer]

Visit this website to classify three organisms—bear, orchid, and sea cucumber—from kingdom to species. To launch the game, under Classifying Life, click the picture of the bear or the Launch Interactive button.

Recent genetic analysis and other advancements have found that some earlier phylogenetic classifications do not align with the evolutionary past; therefore, changes and updates must be made as new discoveries occur. 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 of the whale.

Video Summary

This video provides another introduction to taxonomy and just how it works:



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=180

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6.20: Homologous and Analogous Traits

Scientists must collect accurate information that allows them to make evolutionary connections among organisms. Similar to detective work, scientists must use evidence to uncover the facts. In the case of phylogeny, evolutionary investigations focus on two types of evidence: morphologic (form and function) and genetic. In general, organisms that share similar physical features and genomes tend to be more closely related than those that do not. Such features that overlap both morphologically (in form) and genetically are referred to as homologous structures; they stem from developmental similarities that are based on evolution. For example, the bones in the wings of bats and birds have homologous structures (Figure 1).

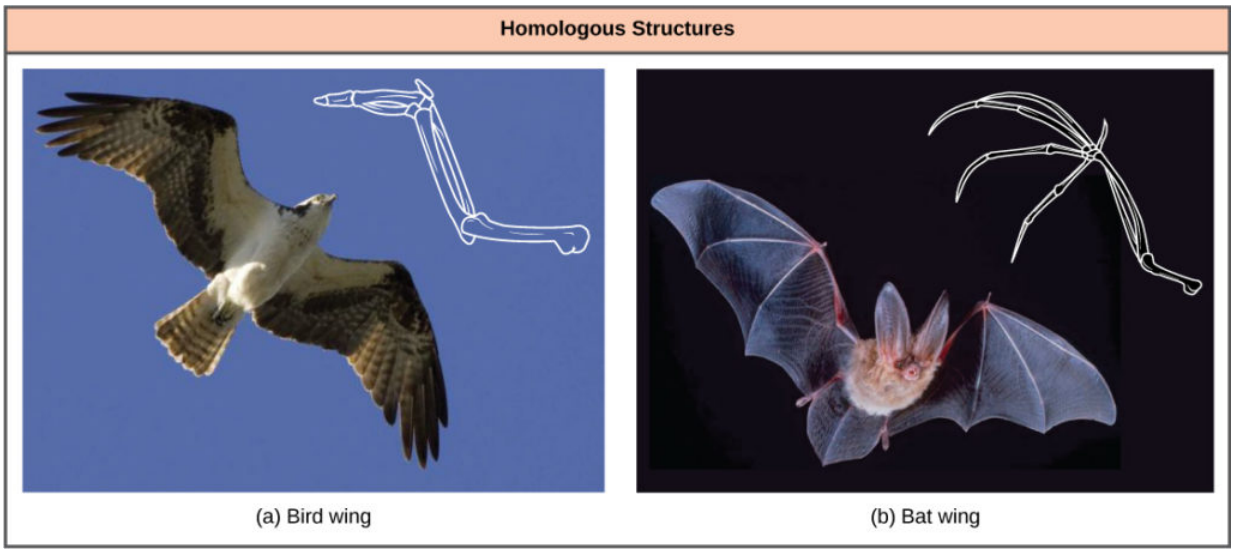


Figure 1. Bat and bird wings are homologous structures, indicating that bats and birds share a common evolutionary past. (credit a: modification of work by Steve Hillebrand, USFWS; credit b: modification of work by U.S. DOI BLM)

Notice it is not simply a single bone, but rather a grouping of several bones arranged in a similar way. The more complex the feature, the more likely any kind of overlap is due to a common evolutionary past. Imagine two people from different countries both inventing a car with all the same parts and in exactly the same arrangement without any previous or shared knowledge. That outcome would be highly improbable. However, if two people both invented a hammer, it would be reasonable to conclude that both could have the original idea without the help of the other. The same relationship between complexity and shared evolutionary history is true for homologous structures in organisms.

Misleading Appearances

Some organisms may be very closely related, even though a minor genetic change caused a major morphological difference to make them look quite different. Similarly, unrelated organisms may be distantly related, but appear very much alike. This usually happens because both organisms were in common adaptations that evolved within similar environmental conditions. When similar characteristics occur because of environmental constraints and not due to a close evolutionary relationship, it is called an **analogy** or **homoplasy**. For example, insects use wings to fly like bats and birds, but the wing structure and embryonic origin is completely different. These are called analogous structures (Figure 2).

Similar traits can be either homologous or analogous. Homologous structures share a similar embryonic origin; analogous organs have a similar function. For example, the bones in the front flipper of a whale are homologous to the bones in the human arm. These structures are not analogous. The wings of a butterfly and the wings of a bird are analogous but not homologous. Some structures are both analogous and homologous: the wings of a bird and the wings of a bat are both homologous and analogous. Scientists must determine which type of similarity a feature exhibits to decipher the phylogeny of the organisms being studied.

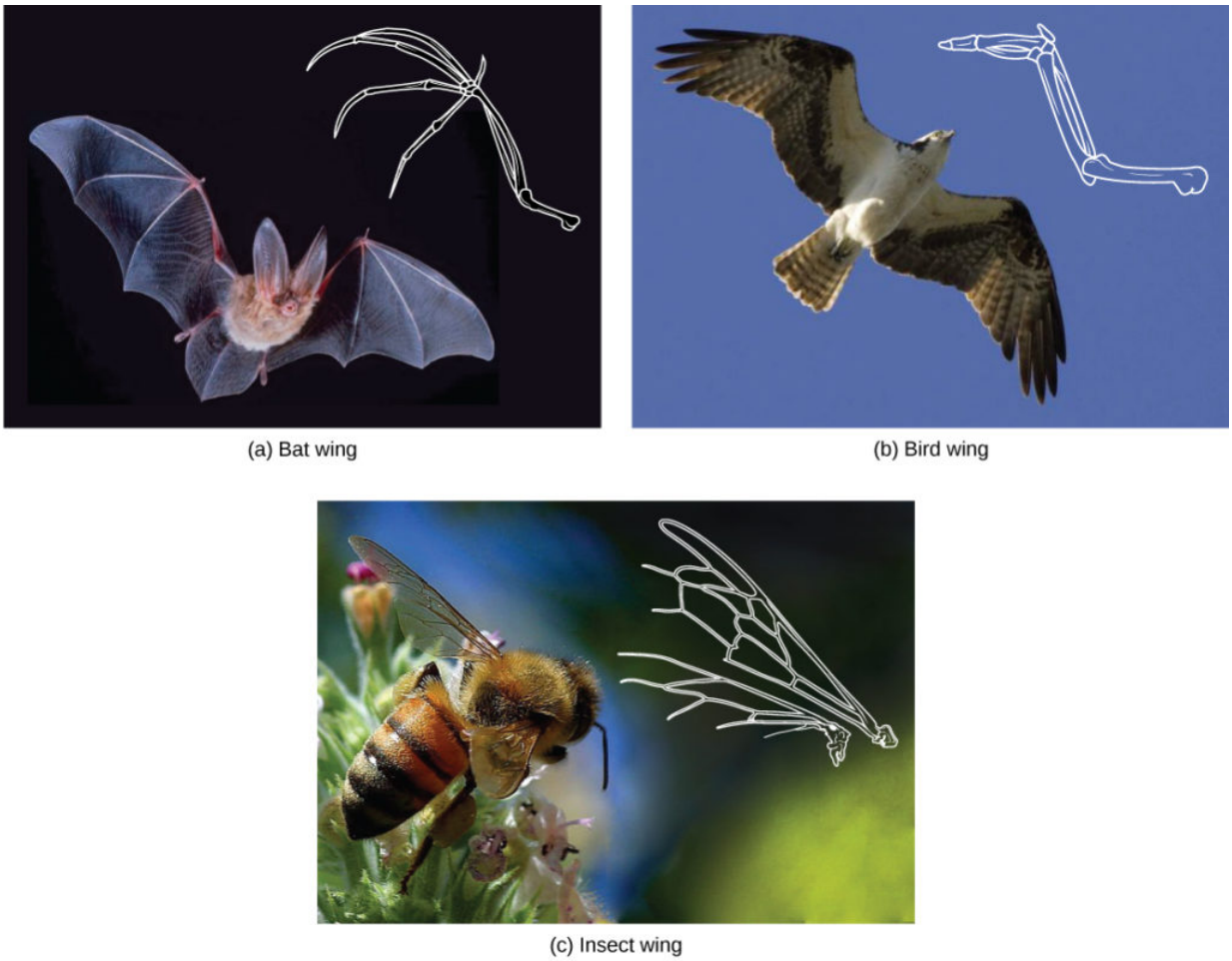


Figure 2. The (c) wing of a honeybee is similar in shape to a (b) bird wing and (a) bat wing, and it serves the same function. However, the honeybee wing is not composed of bones and has a distinctly different structure and embryonic origin. These wing types (insect versus bat and bird) illustrate an analogy—similar structures that do not share an evolutionary history. (credit a: modification of work by Steve Hillebrand, USFWS; credit b: modification of work by U.S. DOI BLM; credit c: modification of work by Jon Sullivan)

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 analysis, has blossomed. New computer programs not only confirm many earlier classified organisms, but also uncover previously made errors. As with physical characteristics, even the DNA sequence can be tricky to read in some cases. For some situations, two very closely related organisms can appear unrelated if a mutation occurred that caused a shift in the genetic code. An insertion or deletion mutation would move each nucleotide base over one place, causing two similar codes to appear unrelated.

Sometimes two segments of DNA code 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 both of these situations, computer technologies have been developed to help identify the actual relationships, and, ultimately, the coupled use of both morphologic and molecular information is more effective in determining phylogeny.

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6.21: Cladistics

How do scientists construct phylogenetic trees? After the homologous and analogous traits are sorted, scientists often organize the homologous traits using a system called **cladistics**. This system sorts organisms into clades: groups of organisms that descended from a single ancestor. For example, in Figure 1, all of the organisms in the orange region evolved from a single ancestor that had amniotic eggs. Consequently, all of these organisms also have amniotic eggs and make a single clade, also called a **monophyletic group**. Clades must include all of the descendants from a branch point.

? Practice Question

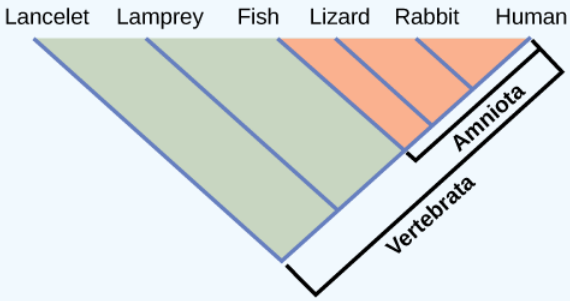


Figure 1. Lizards, rabbits, and humans all descend from a common ancestor that had an amniotic egg. Thus, lizards, rabbits, and humans all belong to the clade Amniota. Vertebrata is a larger clade that also includes fish and lamprey.

Which animals in this figure belong to a clade that includes animals with hair? Which evolved first, hair or the amniotic egg?

[practice-area rows="2"][/practice-area]
[reveal-answer q="74182"]Show Answer[/reveal-answer]
[hidden-answer a="74182"]Rabbits and humans belong in the clade that includes animals with hair. The amniotic egg evolved before hair because the Amniota clade is larger than the clade that encompasses animals with hair.[/hidden-answer]

Clades can vary in size depending on which branch point is being referenced. The important factor is that all of the 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. Figure 2 shows various examples of clades. Notice how each clade comes from a single point, whereas the non-clade groups show branches that do not share a single point.

? Practice Question

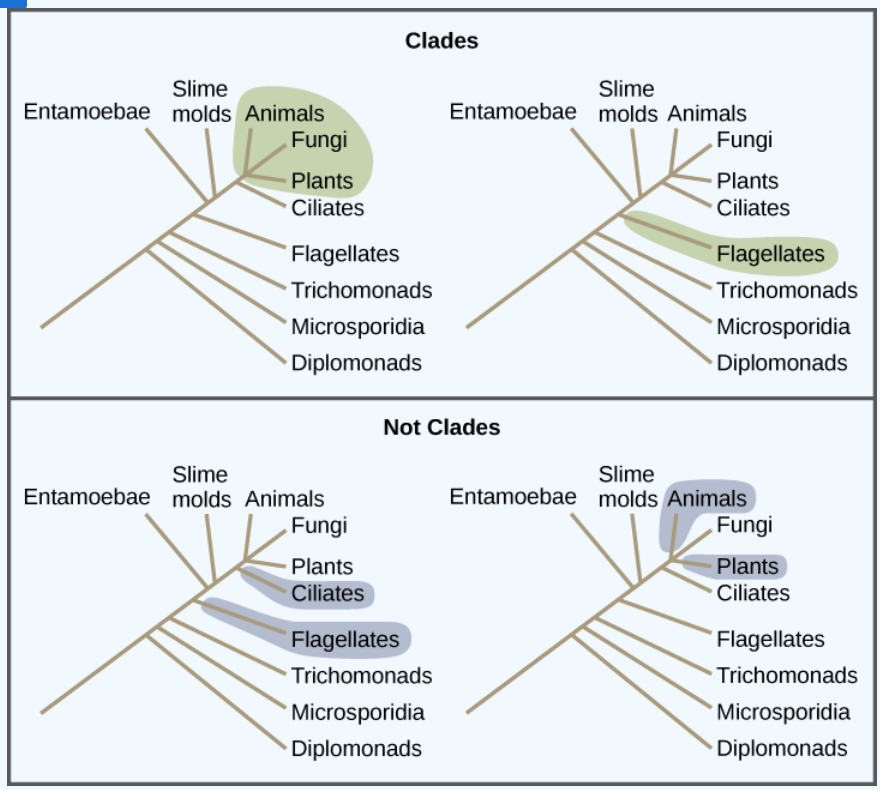


Figure 2. All the organisms within a clade stem from a single point on the tree. A clade may contain multiple groups, as in the case of animals, fungi and plants, or a single group, as in the case of flagellates. Groups that diverge at a different branch point, or that do not include all groups in a single branch point, are not considered clades.

What is the largest clade in this diagram?

[practice-area rows="2"][/practice-area]
[reveal-answer q="549784"]Show Answer[/reveal-answer]
[hidden-answer a="549784"]The largest clade encompasses the entire tree.[/hidden-answer]

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 over and over as one goes through the phylogenetic tree of life:

1. A change in the genetic makeup of an organism leads to a new trait which becomes prevalent in the group.
2. Many organisms descend from this point and have this trait.
3. New variations continue to arise: some are adaptive and persist, leading to new traits.
4. With new traits, a new branch point is determined (go back to step 1 and repeat).

If a characteristic is found in the ancestor of a group, it is considered a **shared ancestral character** because all of the organisms in the taxon or clade have that trait. The vertebrate in Figure 1 is a shared ancestral character. Now consider the amniotic egg characteristic in the same figure. Only some of the organisms in Figure 1 have this trait, and to those that do, it is called a **shared derived character** because this trait derived at some point but does not include all of the ancestors in the tree.

The tricky aspect to shared ancestral and shared derived characters is the fact that these terms are relative. The same trait can be considered one or the other depending on the particular diagram being used. Returning to Figure 1, note that the amniotic egg is a shared ancestral character for the Amniota clade, while having hair is a shared derived character for some organisms in this group. These terms help scientists distinguish between clades in the building of phylogenetic trees.

Choosing the Right Relationships

Imagine being the person responsible for organizing all of the items in a department store properly—an overwhelming task. Organizing the evolutionary relationships of all life on Earth proves much more difficult: scientists must span enormous blocks of time and work with information from long-extinct organisms. Trying to decipher the proper connections, especially given the presence of homologies and analogies, makes the task of building an accurate tree of life extraordinarily difficult. Add to that the advancement of DNA technology, which now provides large quantities of genetic sequences to be used and analyzed. Taxonomy is a subjective discipline: many organisms have more than one connection to each other, so each taxonomist will decide the order of connections.

To aid in the tremendous task of describing phylogenies accurately, scientists often use a concept called **maximum parsimony**, which means that events occurred in the simplest, most obvious way. For example, if a group of people entered a forest preserve to go hiking, based on the principle of maximum parsimony, one could predict that most of the people would hike on established trails rather than forge new ones.

For scientists deciphering evolutionary pathways, the same idea is used: the pathway of evolution probably includes the fewest major events that coincide with the evidence at hand. Starting with all of the homologous traits in a group of organisms, scientists look for the most obvious and simple order of evolutionary events that led to the occurrence of those traits.

Head to this website to learn how maximum parsimony is used to create phylogenetic trees.

These tools and concepts are only a few of the strategies scientists use to tackle the task of revealing the evolutionary history of life on Earth. Recently, newer technologies have uncovered surprising discoveries with unexpected relationships, such as the fact that people seem to be more closely related to fungi than fungi are to plants. Sound unbelievable? As the information about DNA sequences grows, scientists will become closer to mapping the evolutionary history of all life on Earth.

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6.22: Perspectives on the Phylogenetic Tree

The concepts of phylogenetic modeling are constantly changing. It is one of the most dynamic fields of study in all of biology. Over the last several decades, new research has challenged scientists' ideas about how organisms are related. New models of these relationships have been proposed for consideration by the scientific community.

Many phylogenetic trees have been shown as models of the evolutionary relationship among species. Phylogenetic trees originated with Charles Darwin, who sketched the first phylogenetic tree in 1837 (Figure 1a), which served as a pattern for subsequent studies for more than a century. The concept of a phylogenetic tree with a single trunk representing a common ancestor, with the branches representing the divergence of species from this ancestor, fits well with the structure of many common trees, such as the oak (Figure 1b). However, evidence from modern DNA sequence analysis and newly developed computer algorithms has caused skepticism about the validity of the standard tree model in the scientific community.



(a) (b)

Figure 1. The (a) concept of the "tree of life" goes back to an 1837 sketch by Charles Darwin. Like an (b) oak tree, the "tree of life" has a single trunk and many branches. (credit b: modification of work by "Amada44"/Wikimedia Commons)

Limitations to the Classic Model

Classical thinking about prokaryotic evolution, included in the classic tree model, is that species evolve clonally. That is, they produce offspring themselves with only random mutations causing the descent into the variety of modern-day and extinct species known to science. This view is somewhat complicated in eukaryotes that reproduce sexually, but the laws of Mendelian genetics explain the variation in offspring, again, to be a result of a mutation within the species. The concept of genes being transferred between unrelated species was not considered as a possibility until relatively recently. Horizontal gene transfer (HGT), also known as lateral gene transfer, is the transfer of genes between unrelated species. HGT has been shown to be an ever-present phenomenon, with many evolutionists postulating a major role for this process in evolution, thus complicating the simple tree model. 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.

Horizontal Gene Transfer

Horizontal gene transfer (HGT) is the introduction of genetic material from one species to another species by mechanisms other than the vertical transmission from parent(s) to offspring. These transfers allow even distantly related species to share genes, influencing their phenotypes. It is thought that HGT is more prevalent in prokaryotes, but that only about 2% of the prokaryotic genome may be transferred by this process. Some researchers believe such estimates are premature: the actual importance of HGT to evolutionary processes must be viewed as a work in progress. As the phenomenon is investigated more thoroughly, it may be revealed to be more common. Many scientists believe that HGT and mutation appear to be (especially in prokaryotes) a significant source of genetic variation, which is the raw material for the process of natural selection. These transfers may occur between any two species that share an intimate relationship (Table 1).

Table 1. Summary of Mechanisms of Prokaryotic and Eukaryotic HGT

	Mechanism	Mode of Transmission	Example
Prokaryotes	transformation	DNA uptake	many prokaryotes
	transduction	bacteriophage (virus)	bacteria
	conjugation	pilus	many prokaryotes
	gene transfer agents	phage-like particles	purple non-sulfur bacteria
Eukaryotes	from food organisms	unknown	aphid
	jumping genes	transposons	rice and millet plants
	epiphytes/parasites	unknown	yew tree fungi
	from viral infections		

HGT in Prokaryotes

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.

The fact that genes are transferred among common bacteria is well known to microbiology students. 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:

1. Transformation: naked DNA is taken up by a bacteria
2. Transduction: genes are transferred using a virus
3. Conjugation: the use a hollow tube called a pilus to transfer genes between organisms

More recently, a fourth mechanism of gene transfer between prokaryotes has been discovered. Small, virus-like particles called **gene transfer agents (GTAs)** transfer random genomic segments from one species of prokaryote to another. GTAs have been shown to be responsible for genetic changes, sometimes at a very high frequency compared to other evolutionary processes. The first GTA was characterized in 1974 using purple, non-sulfur bacteria. These GTAs, which are thought to be bacteriophages that lost the ability to reproduce on their own, carry random pieces of DNA from one organism to another. The ability of GTAs to act with high frequency has been demonstrated in controlled studies using marine bacteria. Gene transfer events in marine prokaryotes, either by GTAs or by viruses, have been estimated to be as high as 10^{13} per year in the Mediterranean Sea alone. GTAs and viruses are thought to be efficient HGT vehicles with a major impact on prokaryotic evolution.

As a consequence of this modern DNA analysis, the idea that eukaryotes evolved directly from Archaea has fallen out of favor. While eukaryotes share many features that are absent in bacteria, such as the TATA box (found in the promoter region of many genes), the discovery that some eukaryotic genes were more homologous with bacterial DNA than Archaea DNA made this idea

less tenable. Furthermore, the fusion of genomes from Archaea and Bacteria by endosymbiosis has been proposed as the ultimate event in eukaryotic evolution.

HGT in Eukaryotes

Although it is easy to see how prokaryotes exchange genetic material by HGT, it was initially thought that this process was absent in eukaryotes. After all, prokaryotes are but single cells exposed directly to their environment, whereas the sex cells of multicellular organisms are usually sequestered in protected parts of the body. It follows from this idea that the gene transfers between multicellular eukaryotes should be more difficult. Indeed, it is thought that this process is rarer in eukaryotes and has a much smaller evolutionary impact than in prokaryotes. In spite of this fact, HGT between distantly related organisms has been demonstrated in several eukaryotic species, and it is possible that more examples will be discovered in the future.

In plants, gene transfer has been observed in species that cannot cross-pollinate by normal means. Transposons or “jumping genes” have been shown to transfer between rice and millet plant species. Furthermore, fungal species feeding on yew trees, from which the anti-cancer drug TAXOL® is derived from the bark, have acquired the ability to make taxol themselves, a clear example of gene transfer.

In animals, a particularly interesting example of HGT occurs within the aphid species (Figure 2). 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. A carotenoid enzyme called a desaturase is responsible for the red coloration seen in certain aphids, and it has been further shown that when this gene is inactivated by mutation, the aphids revert back to their more common green color (Figure 2).



(a) (b)

Figure 2. (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. (credit a: modification of work by Benny Mazur; credit b: modification of work by Mick Talbot)

Genome Fusion and the Evolution of Eukaryotes

Scientists believe the ultimate in HGT occurs through **genome fusion** between different species of prokaryotes when two symbiotic organisms become endosymbiotic. This occurs when one species is taken inside the cytoplasm of another species, which ultimately results in a genome consisting of genes from both the endosymbiont and the host. This mechanism is an aspect of the Endosymbiont Theory, which is accepted by a majority of biologists as the mechanism whereby eukaryotic cells obtained their mitochondria and chloroplasts. However, the role of endosymbiosis in the development of the nucleus is more controversial. Nuclear and mitochondrial DNA are thought to be of different (separate) evolutionary origin, with the mitochondrial DNA being derived from the circular genomes of bacteria that were engulfed by ancient prokaryotic cells. Mitochondrial DNA can be regarded

as the smallest chromosome. Interestingly enough, mitochondrial DNA is inherited only from the mother. The mitochondrial DNA degrades in sperm when the sperm degrades in the fertilized egg or in other instances when the mitochondria located in the flagellum of the sperm fails to enter the egg.

Within the past decade, the process of genome fusion by endosymbiosis has been proposed by James Lake of the UCLA/NASA Astrobiology Institute to be responsible for the evolution of the first eukaryotic cells (Figure 3**a**). Using DNA analysis and a new mathematical algorithm called conditioned reconstruction (CR), his laboratory proposed that eukaryotic cells developed from an endosymbiotic gene fusion between two species, one an Archaea and the other a Bacteria. As mentioned, some eukaryotic genes resemble those of Archaea, whereas others resemble those from Bacteria. An endosymbiotic fusion event, such as Lake has proposed, would clearly explain this observation. On the other hand, this work is new and the CR algorithm is relatively unsubstantiated, which causes many scientists to resist this hypothesis.

More recent work by Lake (Figure 3**b**) proposes that gram-negative bacteria, which are unique within their domain in that they contain two lipid bilayer membranes, indeed resulted from an endosymbiotic fusion of archaeal and bacterial species. The double membrane would be a direct result of the endosymbiosis, with the endosymbiont picking up the second membrane from the host as it was internalized. This mechanism has also been used to explain the double membranes found in mitochondria and chloroplasts. Lake's work is not without skepticism, and the ideas are still debated within the biological science community. In addition to Lake's hypothesis, there are several other competing theories as to the origin of eukaryotes. How did the eukaryotic nucleus evolve? One theory is that the prokaryotic cells produced an additional membrane that surrounded the bacterial chromosome. Some bacteria have the DNA enclosed by two membranes; however, there is no evidence of a nucleolus or nuclear pores. Other proteobacteria also have membrane-bound chromosomes. If the eukaryotic nucleus evolved this way, we would expect one of the two types of prokaryotes to be more closely related to eukaryotes.

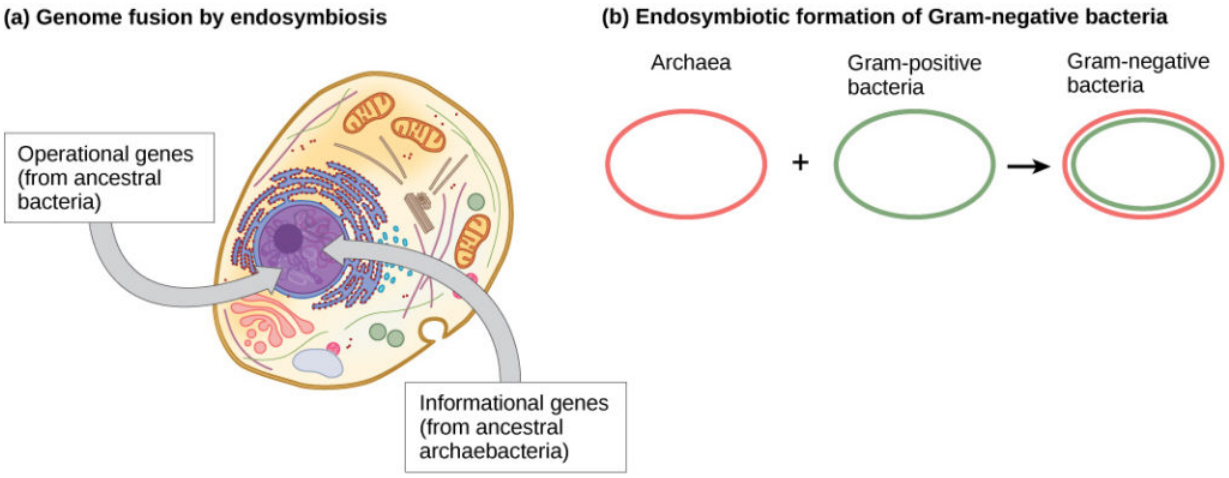


Figure 3. The theory that mitochondria and chloroplasts are endosymbiotic in origin is now widely accepted. More controversial is the proposal that (a) the eukaryotic nucleus resulted from the fusion of archaeal and bacterial genomes, and that (b) Gram-negative bacteria, which have two membranes, resulted from the fusion of Archaea and Gram-positive bacteria, each of which has a single membrane.

The **nucleus-first** hypothesis proposes that the nucleus evolved in prokaryotes first (Figure 4**a**), followed by a later fusion of the new eukaryote with bacteria that became mitochondria. The **mitochondria-first** hypothesis proposes that mitochondria were first established in a prokaryotic host (Figure 4**b**), which subsequently acquired a nucleus, by fusion or other mechanisms, to become the first eukaryotic cell. Most interestingly, the **eukaryote-first** hypothesis proposes that prokaryotes actually evolved from eukaryotes by losing genes and complexity (Figure 4**c**). All of these hypotheses are testable. Only time and more experimentation will determine which hypothesis is best supported by data.

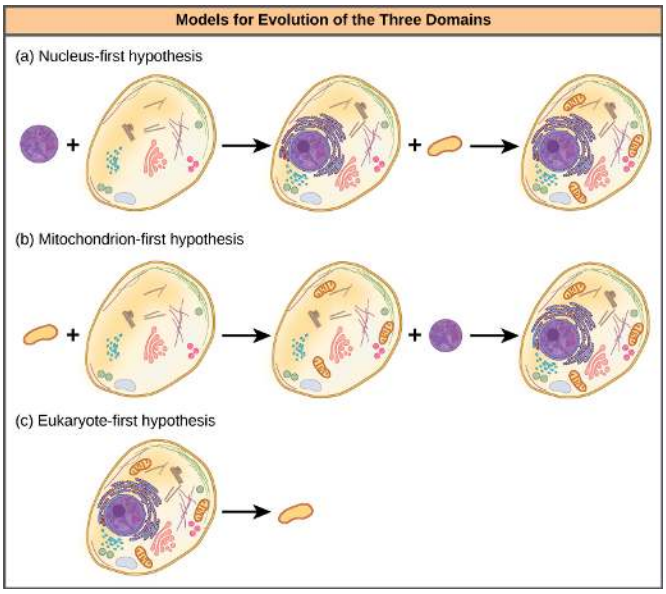


Figure 4. Three alternate hypotheses of eukaryotic and prokaryotic evolution are (a) the nucleus-first hypothesis, (b) the mitochondrion-first hypothesis, and (c) the eukaryote-first hypothesis.

Web and Network Models

The recognition of the importance of HGT, especially in the evolution of prokaryotes, has caused some to propose abandoning the classic "tree of life" model. In 1999, W. Ford Doolittle proposed a phylogenetic model that resembles a web or a network more than a tree. The hypothesis is that eukaryotes evolved not from a single prokaryotic ancestor, but from a pool of many species that were sharing genes by HGT mechanisms. As shown in Figure 5**a**, some individual prokaryotes were responsible for transferring the bacteria that caused mitochondrial development to the new eukaryotes, whereas other species transferred the bacteria that gave rise to chloroplasts. This model is often called the "**web of life**." In an effort to save the tree analogy, some have proposed using the *Ficus* tree (Figure 5**b**) with its multiple trunks as a phylogenetic to represent a diminished evolutionary role for HGT.

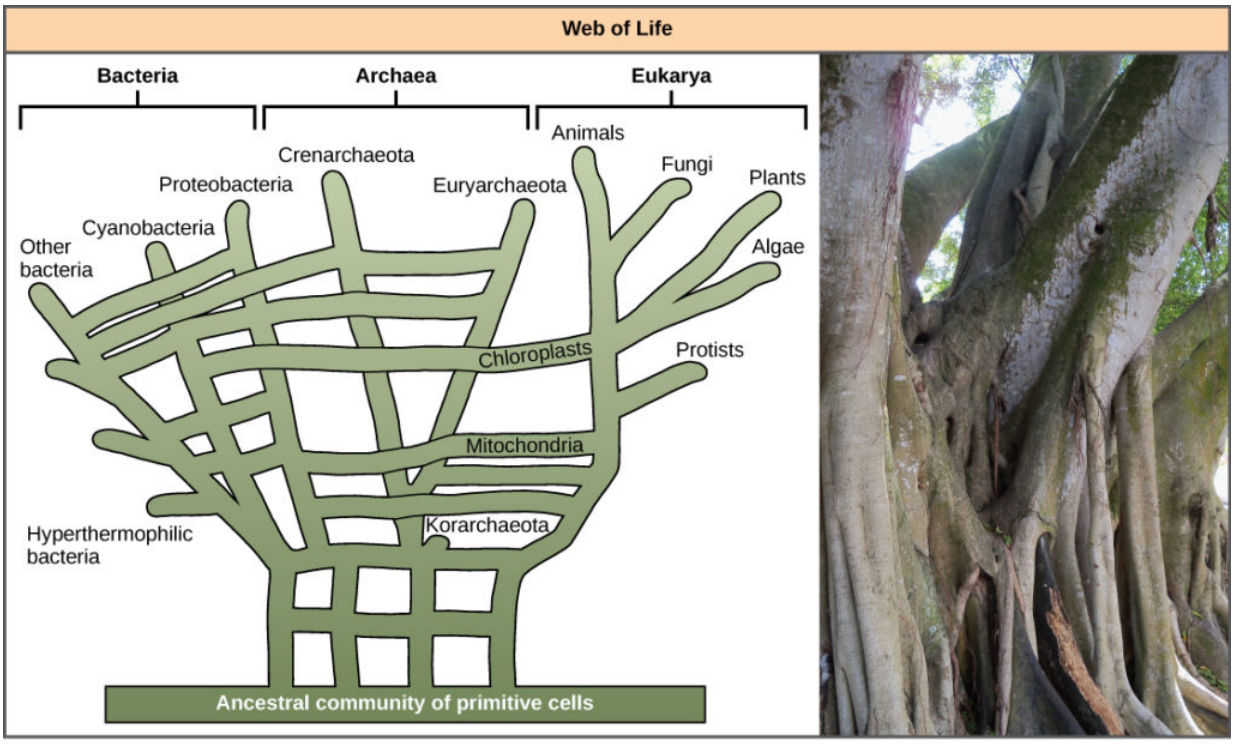


Figure 5. In the (a) phylogenetic model proposed by W. Ford Doolittle, the "tree of life" arose from a community of ancestral cells, has multiple trunks, and has connections between branches where horizontal gene transfer has occurred. Visually, this concept is better represented by (b) the multi-trunked Ficus than by the single trunk of the oak similar to the tree drawn by Darwin Figure 1. (credit b: modification of work by "psyberartist"/Flickr)

Ring of Life Models

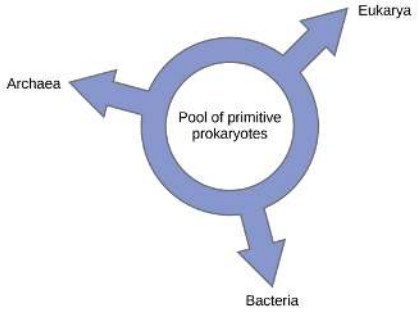


Figure 6. According to the "ring of life" phylogenetic model, the three domains of life evolved from a pool of primitive prokaryotes.

Others have proposed abandoning any tree-like model of phylogeny in favor of a ring structure, the so-called "**ring of life**" (Figure 6); a phylogenetic model where all three domains of life evolved from a pool of primitive prokaryotes. Lake, again using the conditioned reconstruction algorithm, proposes a ring-like model in which species of all three domains—Archaea, Bacteria, and Eukarya—evolved from a single pool of gene-swapping prokaryotes. His laboratory proposes that this structure is the best fit for data from extensive DNA analyses performed in his laboratory, and that the ring model is the only one that adequately takes HGT and genomic fusion into account. However, other phylogeneticists remain highly skeptical of this model.

In summary, the "tree of life" model proposed by Darwin must be modified to include HGT. Does this mean abandoning the tree model completely? Even Lake argues that all attempts should be made to discover some modification of the tree model to allow it to accurately fit his data, and only the inability to do so will sway people toward his ring proposal.

This doesn't mean a tree, web, or a ring will correlate completely to an accurate description of phylogenetic relationships of life. A consequence of the new thinking about phylogenetic models is the idea that Darwin's original conception of the phylogenetic tree is too simple, but made sense based on what was known at the time. However, the search for a more useful model moves on: each

model serving as hypotheses to be tested with the possibility of developing new models. This is how science advances. These models are used as visualizations to help construct hypothetical evolutionary relationships and understand the massive amount of data being analyzed.

Learning Objectives

The phylogenetic tree, first used by Darwin, is the classic “tree of life” model describing phylogenetic relationships among species, and the most common model used today. New ideas about HGT and genome fusion have caused some to suggest revising the model to resemble webs or rings.

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6.23: Putting It Together- History of Life



Figure 1. *Dalbergia sissoo*

At the start of this module, we stated that if a plant contains a compound that is effective in treating disease, scientists might want to examine all of the relatives of that plant for other useful drugs. Let's take a look at one example of this.

Dalbergia sissoo (D. sissoo) is in the Fabaceae, or legume family. A research team in China identified a segment of DNA that was thought to be common to some medicinal plants in the family Fabaceae (Figure 1). They then worked to identify which species had this segment. After testing plant species in this family, the team found a DNA marker (a known location on a chromosome that enabled them to identify the species) present.

Then, using the DNA to uncover phylogenetic relationships, the team could identify whether a newly discovered plant was in this family and assess its potential medicinal properties.

Subsequently, scientists found that *D. sissoo* and other species with this DNA marker did, in fact, share fungicidal activity, supporting the idea that DNA markers can be used to screen for plants with potential medicinal properties.

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6.24: Cerego- History of Life

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for History of Life. You'll need to create a free log-in to practice these items, if you haven't already.

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CHAPTER OVERVIEW

7: Module 4- Prokaryotes

7.1: Why It Matters- Prokaryotes
7.2: Introduction to Prokaryotic Diversity
7.3: Evolutionary History of Prokaryotes
7.4: Life in Moderate and Extreme Environments
7.5: Culturing Prokaryotes
7.6: Prokaryotic Biofilms
7.7: Introduction to the Structure of Prokaryotes
7.8: The Prokaryotic Cell
7.9: Archaea vs. Bacteria
7.10: Introduction to Prokaryotic Metabolism
7.11: Needs of Prokaryotes
7.12: How Prokaryotes Get Energy
7.13: Role of Prokaryotes in Ecosystems
7.14: Introduction to Bacterial Diseases in Humans
7.15: Long History of Bacterial Disease
7.16: Biofilms and Foodborne Diseases
7.17: Antibiotic Resistance
7.18: Introduction to Beneficial Prokaryotes
7.19: Nitrogen Fixation
7.20: Food from Bacteria
7.21: Bioremediation
7.22: Microbes and the Human Body
7.23: Putting It Together- Prokaryotes
7.24: Cerego- Prokaryotes

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7.1: Why It Matters- Prokaryotes

Why identify the different kinds of prokaryotes and common bacteria that infect humans?

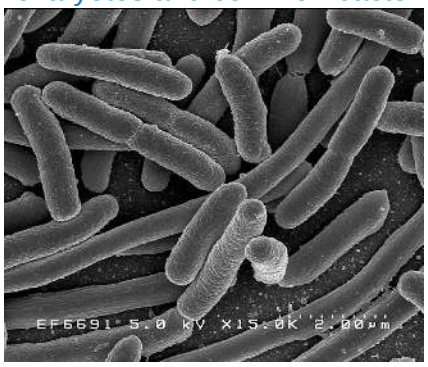


Figure 1. *Escherichia coli*, one of the many species of bacteria present in the human gut

In August 2016, a woman in Nevada died from an incurable bacterial infection. She was infected with a strain of *Klebsiella* that was resistant to all twenty-six of the antibiotics at the hospital. Doctors suspect she picked up the bacteria in India, where this kind of resistance is particular prevalent.[1] How do you think this resistance came about? Aren't antibiotics supposed to kill all bacteria?

However, not all prokaryotes are dangerous—in fact, some strains are essential for our bodies to function correctly. For example, each person has a normal microbial flora (also known as a gut microbiota) in our stomachs. In other words, we have approximately 100 trillion bacteria living in our stomachs. These bacteria help us with digestion, synthesizing vitamins, and producing hormones.

Learning Outcomes

- Discuss the diversity of prokaryotic cells
- Describe the structure of prokaryotic cells
- Identify the metabolic needs of prokaryotes
- Identify common bacterial diseases in humans
- Identify common prokaryotes that are beneficial to humans

---

1. MacKenzie, Debora. "Woman dies from infection resistant to all available antibiotics." *New Scientist*. January 16, 2017. https://www.newscientist.com/article/2118046-woman-dies-from-infection-resistant-to-all-available-antibiotics/. ↵

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7.2: Introduction to Prokaryotic Diversity

Discuss the diversity of prokaryotic cells



Figure 1. Certain prokaryotes can live in extreme environments such as the Morning Glory pool, a hot spring in Yellowstone National Park. The spring's vivid blue color is from the prokaryotes that thrive in its very hot waters. (credit: modification of work by Jon Sullivan)

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, and so on. In the late 20th century, the pioneering work of Carl Woese and others compared sequences of small-subunit ribosomal RNA (SSU rRNA), which resulted in a more fundamental way to group organisms on Earth. Based on differences in the structure of cell membranes and in rRNA, Woese and his colleagues proposed that all life on Earth evolved along three lineages, called domains. 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.

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 present everywhere. 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, such as Chernobyl. Prokaryotes reside in the human digestive system and on the skin, are responsible for certain illnesses, and serve an important role in the preparation of many foods.

What You'll Learn to Do

- Describe the evolutionary history of prokaryotes
- Discuss the distinguishing features of extremophiles
- Understand why it is difficult to culture prokaryotes
- Discuss why prokaryotes often form biofilms

Learning Activities

The learning activities for this section include the following:

- Evolutionary History of Prokaryotes
- Life in Moderate and Extreme Environments
- Culturing Prokaryotes
- Prokaryotic Biofilms
- Self Check: Prokaryotic Diversity

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7.3: Evolutionary History of Prokaryotes

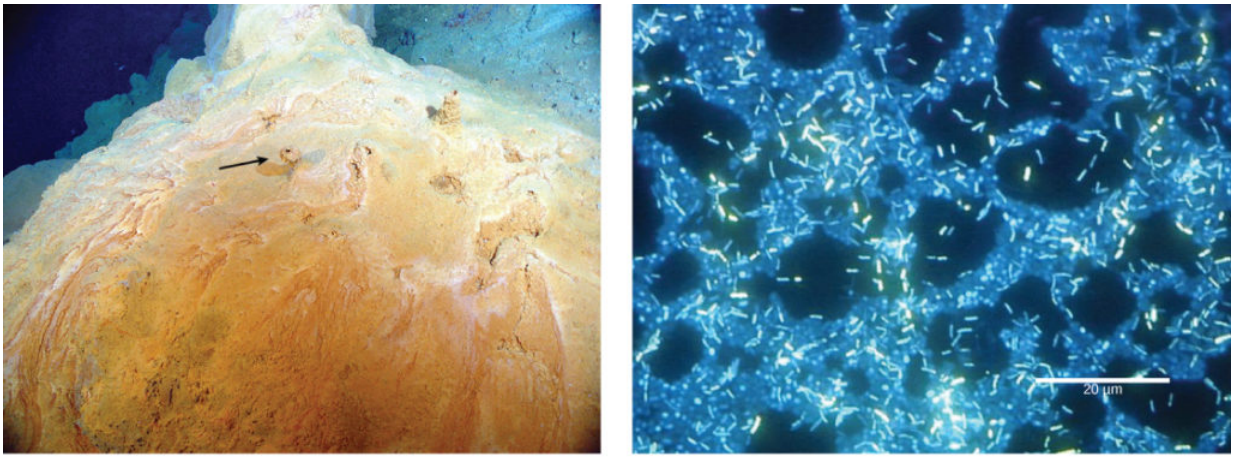
Prokaryotes are ubiquitous. They cover every imaginable surface where there is sufficient moisture, and they live on and inside of other living things. In the typical human body, prokaryotic cells outnumber human body cells by about ten to one. They comprise the majority of living things in all ecosystems. Some prokaryotes thrive in environments that are inhospitable for most living things. Prokaryotes recycle **nutrients**—essential substances (such as carbon and nitrogen)—and they drive the evolution of new ecosystems, some of which are natural and others man-made. Prokaryotes have been on Earth since long before multicellular life appeared.

When and where did life begin? What were the conditions on Earth when life began? Prokaryotes were the first forms of life on Earth, and they existed for billions of years before plants and animals appeared. The Earth and its moon are thought to be about 4.54 billion years old. This estimate is based on evidence from radiometric dating of meteorite material together with other substrate material from Earth and the moon. Early Earth had a very different atmosphere (contained less molecular oxygen) than it does today and was subjected to strong radiation; thus, the first organisms would have flourished where they were more protected, such as in ocean depths or beneath the surface of the Earth. At this time too, strong volcanic activity was common on Earth, so it is likely that these first organisms—the first prokaryotes—were adapted to very high temperatures. Early Earth was prone to geological upheaval and volcanic eruption, and was subject to bombardment by mutagenic radiation from the sun. The first organisms were prokaryotes that could withstand these harsh conditions.

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 (Figure 1) that includes mostly bacteria, but also archaea. Microbial mats are a few centimeters thick, and they typically grow where different types of materials interface, mostly on moist surfaces. The various types of prokaryotes that comprise them carry out different metabolic pathways, and that is the reason for their various colors. Prokaryotes in a microbial mat are held together by a glue-like sticky substance that they secrete called extracellular matrix.

The first microbial mats likely obtained their energy from chemicals found near hydrothermal vents. A **hydrothermal vent** is a breakage or fissure in the Earth's surface that releases geothermally heated water. 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.



(a) (b)

Figure 1. This (a) 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, bacteria are visualized using fluorescence microscopy. (credit a: modification of work by Dr. Bob Embley, NOAA PMEL, Chief Scientist; credit b: modification of work by Ricardo Murga, Rodney Donlan, CDC; scale-bar data from Matt Russell)

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 2). 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.



(a) (b)

Figure 2. (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. (credit a: Robert Young; credit b: P. Carrara, NPS)

The Ancient Atmosphere



Figure 3. This hot spring in Yellowstone National Park flows toward the foreground. Cyanobacteria in the spring are green, and as water flows down the gradient, the intensity of the color increases as cell density increases. The water is cooler at the edges of the stream than in the center, causing the edges to appear greener. (credit: Graciela Brelles-Mariño)

Evidence indicates that during the first two billion years of Earth's existence, the atmosphere was **anoxic**, meaning that there was no molecular oxygen. Therefore, only those organisms that can grow without oxygen—**anaerobic** organisms—were able to live. Autotrophic organisms that convert solar energy into chemical energy are called **phototrophs**, and they appeared within one billion years of the formation of Earth. Then, **cyanobacteria**, also known as blue-green algae, evolved from these simple phototrophs one billion years later. Cyanobacteria (Figure 3) began the oxygenation of the atmosphere. Increased atmospheric oxygen allowed the development of more efficient O_2-utilizing catabolic pathways. It also opened up the land to increased colonization, because some O_2 is converted into O_3 (ozone) and ozone effectively absorbs the ultraviolet light that would otherwise cause lethal mutations in DNA. Ultimately, the increase in O_2 concentrations allowed the evolution of other life forms.

? Practice Questions

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. are all of the above

[reveal-answer q="125455"]Show Answer[/reveal-answer]
[hidden-answer a="125455"]Answer d. Microbial mats **are all of the above**.

[/hidden-answer]

The first organisms that oxygenated the atmosphere were

a. cyanobacteria
b. phototrophic organisms
c. anaerobic organisms
d. all of the above

[reveal-answer q="566688"]Show Answer[/reveal-answer]
[hidden-answer a="566688"]Answer a. The first organisms that oxygenated the atmosphere were **cyanobacteria**.[/hidden-answer]

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7.4: 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 are able to form endospores that resist heat and drought, thereby allowing the organism to survive until favorable conditions recur. These adaptations, along with others, allow bacteria to be the most abundant life form in all terrestrial and aquatic ecosystems.

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 Earth, in harsh chemical environments, and in high radiation environments, just to mention a few.

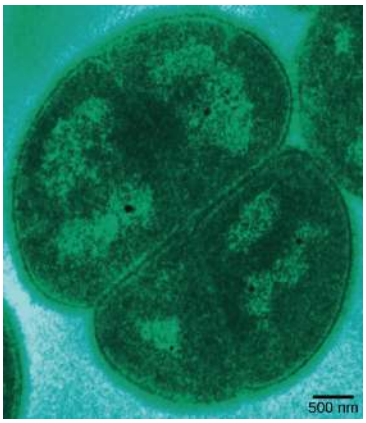


Figure 1. *Deinococcus radiodurans*, visualized in a false color transmission electron micrograph (credit: modification of work by Michael Daly; scale-bar data from Matt Russell)

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. For example, *Deinococcus radiodurans*, shown in Figure 1, is a prokaryote that can tolerate very high doses of ionizing radiation. It has developed DNA repair mechanisms that allow it to reconstruct its chromosome even if it has been broken into hundreds of pieces by radiation or heat.

These organisms give us a better understanding of prokaryotic diversity and open up the possibility of finding new prokaryotic species that may lead to the discovery of new therapeutic drugs or have 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, and several 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 (Table 1).

Table 1. Extremophiles and Their Preferred Conditions	
Extremophile Type	Conditions for Optimal Growth
Acidophiles	pH 3 or below
Alkaliphiles	pH 9 or above
Thermophiles	Temperature 60–80 °C (140–176 °F)
Hyperthermophiles	Temperature 80–122 °C (176–250 °F)
Psychrophiles	Temperature of −15–10 °C (5–50 °F) or lower
Halophiles	Salt concentration of at least 0.2 M
Osmophiles	High sugar concentration

Prokaryotes in the Dead Sea

One example of a very harsh environment is the Dead Sea, a hypersaline basin that is located between Jordan and Israel. Hypersaline environments are essentially concentrated seawater. In the Dead Sea, the sodium concentration is 10 times higher than that of seawater, and the water contains high levels of magnesium (about 40 times higher than in seawater) that would be 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 uniquely hostile, ecosystem[1] (Figure 2).



Figure 2. (a) The Dead Sea is hypersaline. Nevertheless, salt-tolerant bacteria thrive in this sea. (b) These halobacteria cells can form salt-tolerant bacterial mats. (credit a: Julien Menichini; credit b: NASA; scale-bar data from Matt Russell)

What sort of prokaryotes do we find in the Dead Sea? The extremely salt-tolerant bacterial mats include *Halobacterium*, *Haloferax volcanii* (which is found in other locations, not only the Dead Sea), *Halorubrum sodomense*, and *Halobaculum gomorrense*, and the archaea *Haloarcula marismortui*, among others.

1. Bodaker, I, Itai, S, Suzuki, MT, Feingersch, R, Rosenberg, M, Maguire, ME, Shimshon, B, and others. Comparative community genomics in the Dead Sea: An increasingly extreme environment. *The ISME Journal* 4 (2010): 399–407, doi:10.1038/ismej.2009.141. published online 24 December 2009. ↵

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7.5: Culturing Prokaryotes



Figure 1. In these agar plates, the growth medium is supplemented with red blood cells. Blood agar becomes transparent in the presence of hemolytic *Streptococcus*, which destroys red blood cells and is used to diagnose *Streptococcus* infections. The plate on the left is inoculated with non-hemolytic *Staphylococcus* (large white colonies), and the plate on the right is inoculated with hemolytic *Streptococcus* (tiny clear colonies). If you look closely at the right plate, you can see that the agar surrounding the bacteria has turned clear. (credit: Bill Branson, NCI)

Microbiologists typically grow prokaryotes in the laboratory using an appropriate culture medium containing all the nutrients needed by the target organism. The medium can be liquid, broth, or solid. After an incubation time at the right temperature, there should be evidence of microbial growth (Figure 1).

The process of culturing bacteria is complex and is one of the greatest discoveries of modern science. German physician Robert Koch is credited with discovering the techniques for pure culture, including staining and using growth media. His assistant Julius Petri invented the Petri dish whose use persists in today's laboratories. Koch worked primarily with the *Mycobacterium tuberculosis* bacterium that causes tuberculosis and developed postulates to identify disease-causing organisms that continue to be widely used in the medical community. Koch's postulates include that an organism can be identified as the cause of disease when it is present in all infected samples and absent in all healthy samples, and it is able to reproduce the infection after being cultured multiple times. Today, cultures remain a primary diagnostic tool in medicine and other areas of molecular biology.

Some prokaryotes, however, cannot grow in a laboratory setting. In fact, over 99 percent of bacteria and archaea are unculturable. For the most part, this is due to a lack of knowledge as to what to feed these organisms and how to grow them; they have special requirements for growth that remain unknown to scientists, such as needing specific micronutrients, pH, temperature, pressure, co-factors, or co-metabolites. Some bacteria cannot be cultured because they are obligate intracellular parasites and cannot be grown outside a host cell.

In other cases, culturable organisms become unculturable under stressful conditions, even though the same organism could be cultured previously. Those organisms that cannot be cultured but are not dead are in a **viable-but-non-culturable** (VBNC) state. The VBNC state occurs when prokaryotes respond to environmental stressors by entering a dormant state that allows their survival. The criteria for entering into the VBNC state are not completely understood. In a process called **resuscitation**, the prokaryote can go back to "normal" life when environmental conditions improve.

Is the VBNC state an unusual way of living for prokaryotes? In fact, most of the prokaryotes living in the soil or in oceanic waters are non-culturable. It has been said that only a small fraction, perhaps one percent, of prokaryotes can be cultured under laboratory conditions. If these organisms are non-culturable, then how is it known whether they are present and alive? Microbiologists use molecular techniques, such as the polymerase chain reaction (PCR), to amplify selected portions of DNA of prokaryotes, demonstrating their existence. Recall that PCR can make billions of copies of a DNA segment in a process called amplification.

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7.6: Prokaryotic Biofilms



Figure 1. A biofilm on the surface of the water in the on the edge of the Port of Saint-Goustan in Auray

Until a couple of decades ago, microbiologists used to think of prokaryotes as isolated entities living apart. This model, however, does not reflect the true ecology of prokaryotes, most of which prefer to live in communities where they can interact. A biofilm is a microbial community (Figure 1) held together in a gummy-textured matrix that consists primarily of polysaccharides secreted by the organisms, together with some proteins and nucleic acids. Biofilms grow attached to surfaces. 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.

Biofilms are present almost everywhere: they can cause the clogging of pipes and readily colonize surfaces in industrial settings. In recent, large-scale outbreaks of bacterial contamination of food, biofilms have played a major role. 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.

Interactions among the organisms that populate a biofilm, together with their protective exopolysaccharidic (EPS) environment, make these communities more robust than free-living, or planktonic, prokaryotes. The sticky substance that holds bacteria together also excludes most antibiotics and disinfectants, making biofilm bacteria hardier than their planktonic counterparts. Overall, biofilms are very difficult to destroy because they are resistant to many common forms of sterilization.

Practice Question

There are five stage of biofilm development:

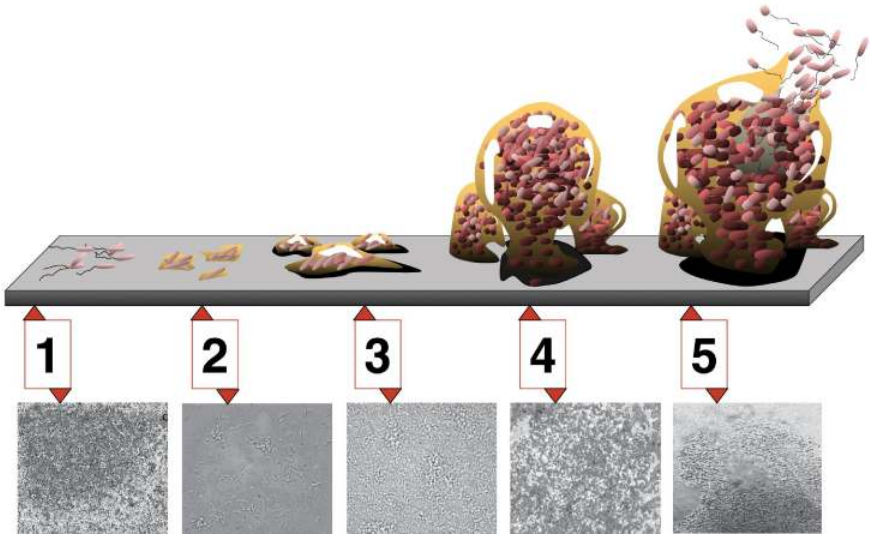


Figure 2. Five stages of biofilm development are shown. Micrographs of a *Pseudomonas aeruginosabiofilm* in each of the stages of development are shown. (credit: D. Davis, Don Monroe, PLoS)

- During stage 1, initial attachment, bacteria adhere to a solid surface via weak van der Waals interactions.
- During stage 2, irreversible attachment, hairlike appendages called pili permanently anchor the bacteria to the surface.
- During stage 3, maturation I, the biofilm grows through cell division and recruitment of other bacteria. 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 bacteria to escape and colonize another surface.

Compared to free-floating bacteria, bacteria in biofilms often show increased resistance to antibiotics and detergents. Why do you think this might be the case?

[practice-area rows="4"][/practice-area]
[reveal-answer q="805834"]Show Answer[/reveal-answer]
[hidden-answer a="805834"]The extracellular matrix and outer layer of cells protects the inner bacteria. The close proximity of cells also facilitates lateral gene transfer, a process by which genes such as antibiotic resistance genes are transferred from one bacterium to another. And even if lateral gene transfer does not occur, one bacterium that produces an exo-enzyme that destroys antibiotic may save neighboring bacteria.[/hidden-answer]

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7.7: Introduction to the Structure of Prokaryotes

Describe the structure of prokaryotic cells

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 various shapes, but many fall into three categories: cocci (spherical), bacilli (rod-shaped), and spirilli (spiral-shaped) (Figure 1).

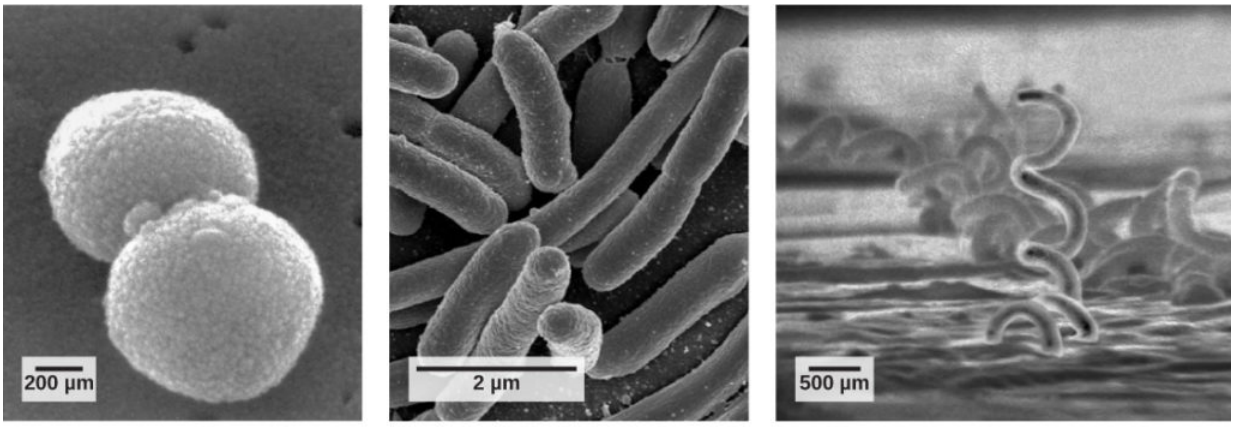


Figure 1. Prokaryotes fall into three basic categories based on their shape, visualized here using scanning electron microscopy: (a) cocci, or spherical (a pair is shown); (b) bacilli, or rod-shaped; and (c) spirilli, or spiral-shaped. (credit a: modification of work by Janice Haney Carr, Dr. Richard Facklam, CDC; credit c: modification of work by Dr. David Cox; scale-bar data from Matt Russell)

What You'll Learn to Do

- Describe the basic structure of a typical prokaryote
- Describe important differences in structure between Archaea and Bacteria

Learning Activities

The learning activities for this section include the following:

- The Prokaryotic Cell
- Archaea vs. Bacteria
- Self Check: Structure of Prokaryotes

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7.8: The Prokaryotic Cell

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

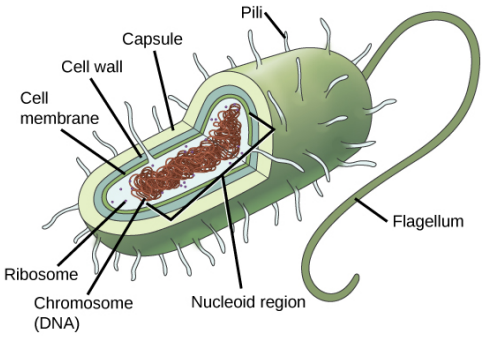


Figure 1. The features of a typical prokaryotic cell are shown.

A prokaryotic cell is a simple, single-celled (unicellular) organism that lacks a nucleus, or any other membrane-bound organelle. Prokaryotic DNA is found in the central part of the cell: a darkened region called the nucleoid (Figure 1).

Some prokaryotes have flagella, pili, or fimbriae. Flagella are used for locomotion, while most pili are used to exchange genetic material during a type of reproduction called conjugation. Many prokaryotes also have a cell wall and capsule. 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.

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 genetic diversity, but prokaryotes can share genes by three other mechanisms.

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 too may become pathogenic. In **transduction**, bacteriophages, the viruses that infect bacteria, sometimes also 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, a small circular piece of extrachromosomal DNA, or as a hybrid, containing both plasmid and chromosomal DNA. These three processes of DNA exchange are shown in Figure 2.

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 result in the rapid evolution of prokaryotes, allowing them to respond to environmental changes (such as the introduction of an antibiotic) very quickly.

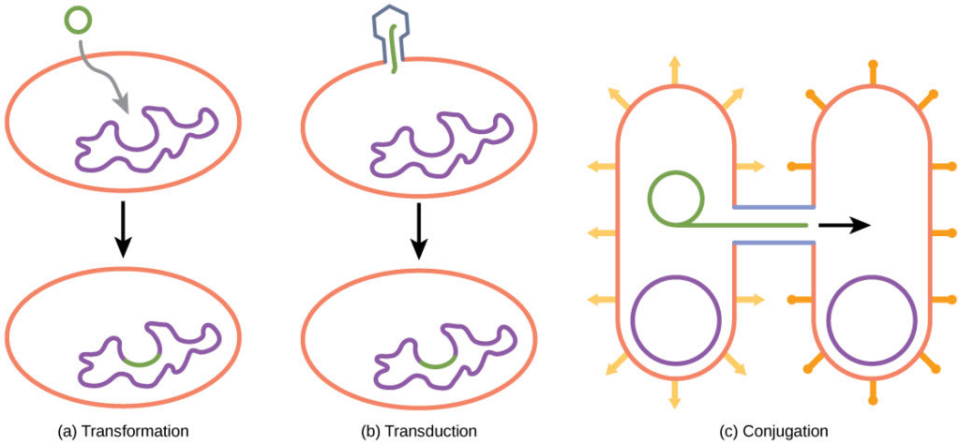


Figure 2. Besides binary fission, there are three other mechanisms by which prokaryotes can exchange DNA. In (a) transformation, the cell takes up prokaryotic DNA directly from the environment. The DNA may remain separate as plasmid DNA or be incorporated into the host genome. In (b) transduction, a 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.

Try It

How do scientists answer questions about the evolution of prokaryotes? Unlike with animals, artifacts in the fossil record of prokaryotes offer very little information. Fossils of ancient prokaryotes look like tiny bubbles in rock. Some scientists turn to genetics and to the principle of the molecular clock, which 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 more genes that are dissimilar.

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. (Recall that *Deinococcus* is a genus of prokaryote—a bacterium—that is highly resistant to ionizing radiation.) Cyanobacteria are photosynthesizers, while Actinobacteria are a group of very common bacteria that include species important in decomposition of organic wastes.

The timelines of divergence suggest that bacteria (members of the domain 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 (resistance to drying and the possession of compounds that protect the organism from excess light), photosynthesis using oxygen may be closely linked to adaptations to survive on land.

Learning Objectives

Prokaryotes (domains Archaea and Bacteria) are single-celled organisms lacking a nucleus. They have a single piece of circular DNA in the nucleoid area of the cell. Most prokaryotes have a cell wall that lies outside the boundary of the plasma membrane. Some prokaryotes may have additional structures such as a capsule, flagella, and pili.

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. ↵

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7.9: Archaea vs. Bacteria

Prokaryotes are divided into two different domains, Bacteria and Archaea, which together with Eukarya, comprise the three domains of life (Figure 1).

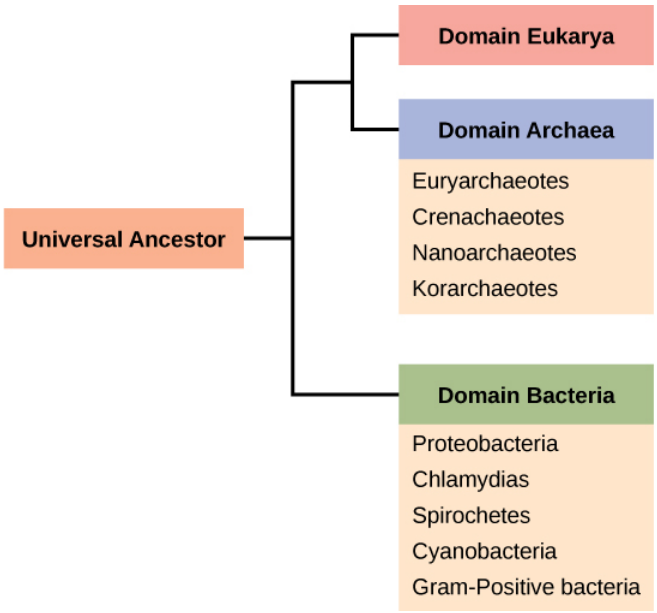


Figure 1. Bacteria and Archaea are both prokaryotes but differ enough to be placed in separate domains. An ancestor of modern Archaea is believed to have given rise to Eukarya, the third domain of life. Archaeal and bacterial phyla are shown; the evolutionary relationship between these phyla is still open to debate.

The composition of the cell wall differs significantly between the domains Bacteria and Archaea. The composition of their cell walls also differs from the eukaryotic cell walls found in plants (cellulose) or fungi and insects (chitin). The cell wall functions as a protective layer, and it is responsible for the organism's shape. Some bacteria have an outer **capsule** outside the cell wall. Other structures are present in some prokaryotic species, but not in others. For example, the capsule found in some species enables the organism to attach to surfaces, protects it from dehydration and attack by phagocytic cells, and makes pathogens more resistant to our immune responses. Some species also have flagella (singular, flagellum) used for locomotion, and **pili** (singular, pilus) used for attachment to surfaces. Plasmids, which consist of extra-chromosomal DNA, are also present in many species of bacteria and archaea.

Phylum Proteobacteria is one of up to 52 bacteria phyla. Proteobacteria is further subdivided into five classes, Alpha through Epsilon (Table 1).

Table 1. Bacteria of Phylum Proteobacteria

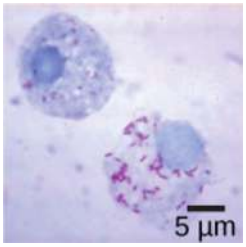
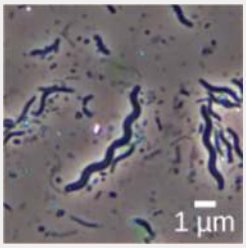
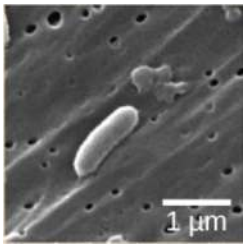
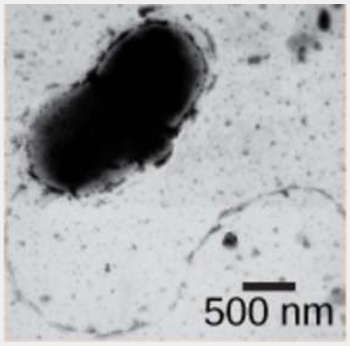
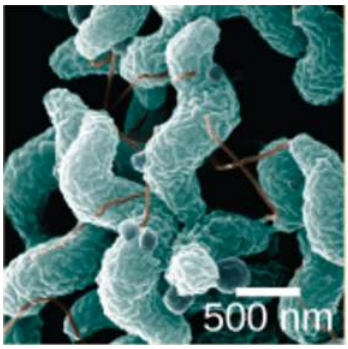
Class	Representative organisms	Representative micrograph
Alpha proteobacteria Some species are photoautotrophic, but some are symbionts of plants and animals, and others are pathogens. Eukaryotic mitochondria are thought to be derived from bacteria in this group.	*Rhizobium*: Nitrogen-fixing endosymbiont associated with roots of legumes *Rickettsia*: Obligate intracellular parasite that causes typhus and Rocky Mountain Spotted Fever	 *Rickettsia rickettsia*, staid red, growing inside a host cell
Beta proteobacteria This group of bacteria is divers. Some species play an important role in the nitrogen cycle.	*Nitrosomas*: Species from this group oxidize ammonia into nitrite *Spirillum minus*: Causes rat-bite fever	 *Spirillum minus*
Gamma proteobacteria Many are beneficial symbionts that populate the human gut, but others are familiar human pathogens. Some species from this subgroup oxidize sulfur compounds.	*E. coli*: Normally beneficial microbe of the human gut, but some strains cause disease *Salmonella*: Certain strains cause food poisoning or typhoid fever *V. cholera*: Causative agent of cholera *Chromatium*: Sulfur-producing bacteria that oxidize sulfur, producing H_2S	 *Vibrio cholera*
Delta proteobacteria Some species generate a spore-forming fruiting body in adverse conditions. Others reduce sulfate and sulfur.	*Myxobacteria*: Generate spore-forming fruiting bodies in adverse conditions *Desulfovibrio vulgaris*: Anaerobic, sulfate-reducing bacterium	 *Desulfovibrio vulgaris*

Table 1. Bacteria of Phylum Proteobacteria

Class	Representative organisms	Representative micrograph
Epsilon proteobacteria Many species inhabit the digestive tract of animals as symbionts or pathogens. Bacteria from this group have been found in deep-sea hydrothermal vents and cold seep habitats.	*Campylobacter*: Causes blood poisoning and intestinal inflammation *H. pylori*: Causes stomach ulcers	 *Campylobacter*

(credit “Rickettsia rickettsia”: modification of work by CDC; credit “Spirillum minus”: modification of work by Wolframm Adlassnig; credit “Vibrio cholera”: modification of work by Janice Haney Carr, CDC; credit “Desulfovibrio vulgaris”: modification of work by Graham Bradley; credit “Campylobacter”: modification of work by De Wood, Pooley, USDA, ARS, EMU; scale-bar data from Matt Russell)

Chlamydia, Spirochetes, Cyanobacteria, and Gram-positive bacteria are described in Table 2. Note that bacterial shape is not phylum-dependent; bacteria within a phylum may be cocci, rod-shaped, or spiral.

Table 2. Bacteria: Chlamydia, Spirochetes, Cyanobacteria, and Gram-positive

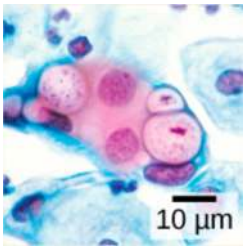
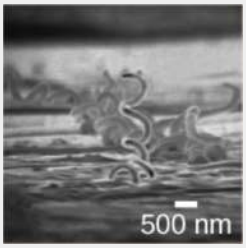
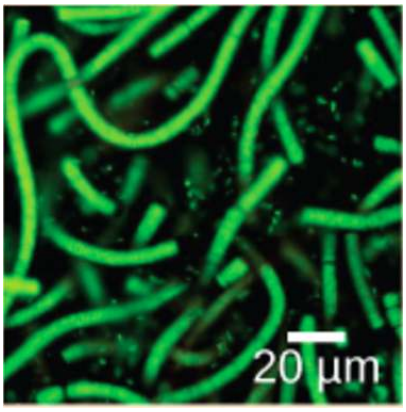
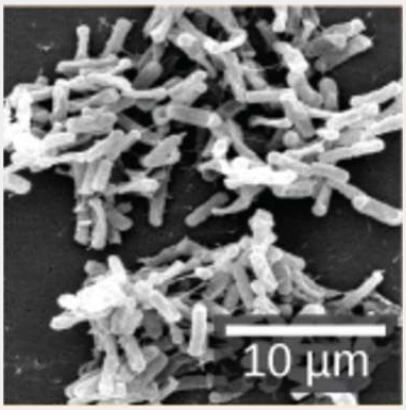
Phylum	Representative organisms	Representative micrograph
Chlamydias All members of this group are obligate intracellular parasites of animal cells. Cell walls lack peptidoglycan	*Chlamydia trachomatis*: Common sexually transmitted disease that can lead to blindness	 In this pap smear, *Chlamydia trachomatis* appear as pink inclusions inside cells
Spirochetes Most members of this phylum, which has spiral-shaped cells, are free-living anaerobes, but some are pathogenic. Flagella run lengthwise in the periplasmic space between the inner and outer membrane	*Treponema pallidum:* Causative agent of syphillis *Borrelia burgdorferi*: Causative agent of Lyme disease	 *Treponema pallidum*
Cyanobacteria Also known as blue-green algae, these bacteria obtain their energy through photosynthesis. They are ubiquitous, found in terrestrial, marine, and freshwater environments. Eukaryotic chloroplasts are thought to be derived from bacteria in this class.	*Prochlorococcus*: Believed to be the most abundant photosynthetic organism on earth, it is responsible for generating half the world's oxygen	 *Phormidium*
Gram-positive Bacteria Soil-dwelling members of this subgroup decompose organic matter. Some species cause disease. They have a thick cell wall and lack an outer membrane.	*Clostridium botulinum*: Causes Botullism *Steptomyces:* Many antibiotics, including streptomyocin, are derived from these bacteria *Mycoplasmas*: These tiny bacteria, the smallest known, lack a cell wall. Some are free-living, and some are pathogenic	 *Clostridium difficile*

Table 2. Bacteria: Chlamydia, Spirochetes, Cyanobacteria, and Gram-positive		
Phylum	Representative organisms	Representative micrograph
(credit “Chlamydia trachomatis”: modification of work by Dr. Lance Liotta Laboratory, NCI; credit “Treponema pallidum”: modification of work by Dr. David Cox, CDC; credit “Phormidium”: modification of work by USGS; credit “Clostridium difficile”: modification of work by Lois S. Wiggs, CDC; scale-bar data from Matt Russell)		

Archaea are separated into four phyla: the Euryarchaeota, Crenarchaeota, Nanoarchaeota, and Korarchaeota.

Table 3. Archaea

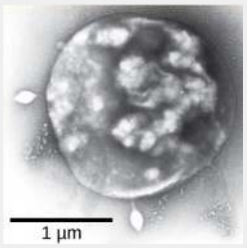
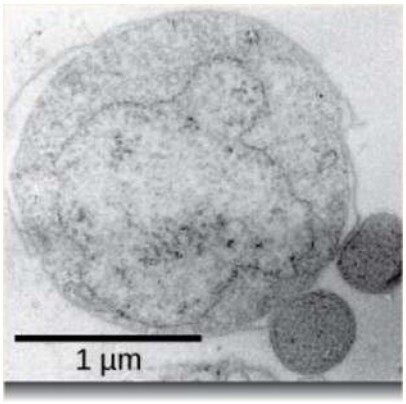
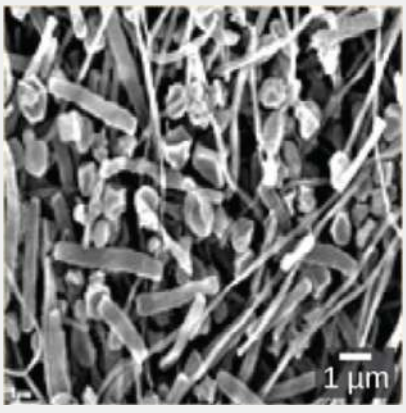
Phylum	Representative organisms	Representative micrograph
Euryarchaeota This phylum includes methanogens, which produce methane as a metabolic waste product, and halobacteria, which live in an extreme saline environment.	*Methanogens*: Methane production causes flatulence in humans and other animals. *Halobacteria*: Large blooms of this salt-loving archaea appear reddish due to the presence of bacteriorhodopsin in the membrane. Bacteriorhodopsin is related to the retinal pigment rhodopsin.	 *Halobacterium* strain NRC-1
Crenarchaeota Members of this ubiquitous phylum play an important role in the fixation of carbon. Many members of this group are sulfur-dependent extremophiles. Some are thermophilic or hyperthermophilic.	*Sulfolobus*: Members of this genus grow in volcanic springs at temperatures between 75º and 80º C and at a pH between 2 and 3.	 *Sulfolobus* being infected by bacteriophage
Nanoarchaeota This group currently contains only one species: *Nanoarchaeum equitans*.	*Nanoarchaeum equitans*: This species was isolated from the bottom of the Atlantic Ocean and from a hydrothermal vent at Yellowstone National Park. It is an obligate symbiont with *Ignicoccus*, another species of archaea.	 *Nanoarchaeum equitans* (small dark spheres) are in contact with their larger host, *Ignococcus*
Korarchaeota This group is considered to be one of the most primitive forms of life. Members of this phylum have only been found in the Obsidian Pool, a hot spring at Yellowstone National Park.	No members of this species have been cultivated.	

Table 3. Archaea		
Phylum	Representative organisms	Representative micrograph
		This image shows a variety of korarchaeota species from the Obsidian Pool at Yellowstone National Park.
(credit “Halobacterium”: modification of work by NASA; credit “Nanoarchaeotum equitans”: modification of work by Karl O. Stetter; credit “korarchaeota”: modification of work by Office of Science of the U.S. Dept. of Energy; scale-bar data from Matt Russell)		

The Plasma Membrane

The plasma membrane is a thin lipid bilayer (6 to 8 nanometers) that completely 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 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, isoprene (phytanyl) chains linked to glycerol replace the fatty acids linked to glycerol in bacterial membranes. Some archaeal membranes are lipid monolayers instead of bilayers (Figure 2).

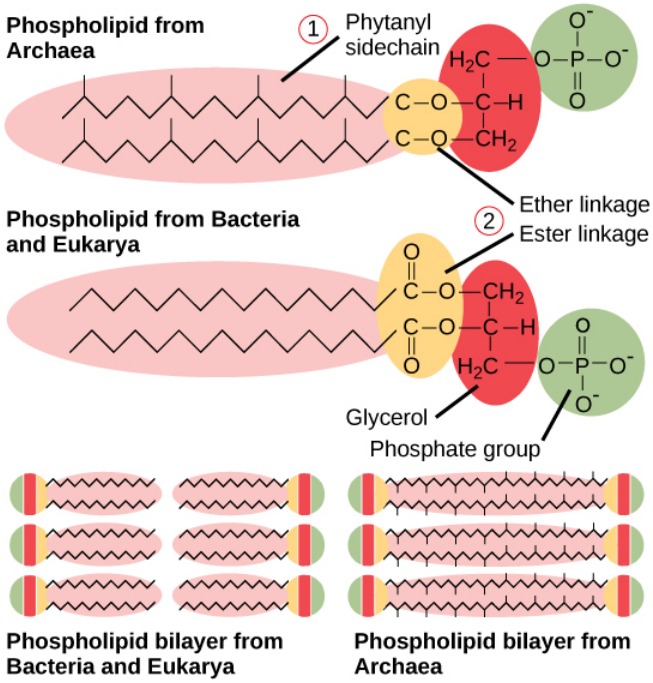


Figure 2. Archaeal phospholipids differ from those found in Bacteria and Eukarya in two ways. First, they have branched phytanyl sidechains instead of linear ones. Second, an ether bond instead of an ester bond connects the lipid to the glycerol.

The Cell Wall

The cytoplasm of prokaryotic cells has a high concentration of dissolved solutes. Therefore, the osmotic pressure within the cell is relatively high. The 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 also varies between bacterial species.

Bacterial cell walls contain **peptidoglycan**, composed of polysaccharide chains that are cross-linked by unusual peptides containing both L- and D-amino acids including D-glutamic acid and D-alanine. Proteins normally have only L-amino acids; as a consequence, many of our antibiotics work by mimicking D-amino acids and therefore have specific effects on bacterial cell wall development. There are more than 100 different forms of peptidoglycan. **S-layer** (surface layer) proteins are also present on the outside of cell walls of both archaea and bacteria.

Bacteria are divided into two major groups: **Gram positive** and **Gram negative**, based on their reaction to Gram staining. Note that all Gram-positive bacteria belong to one phylum; bacteria in the other phyla (Proteobacteria, Chlamydias, Spirochetes, Cyanobacteria, and others) are Gram-negative. The Gram staining method is named after its inventor, Danish scientist Hans Christian Gram (1853–1938). The different bacterial responses to the staining procedure are ultimately due to cell wall structure. Gram-positive organisms typically lack the outer membrane found in Gram-negative organisms (Figure 3). Up to 90 percent of the cell wall in Gram-positive bacteria is composed of peptidoglycan, and 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. Gram-negative bacteria 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.

? Practice Question

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.

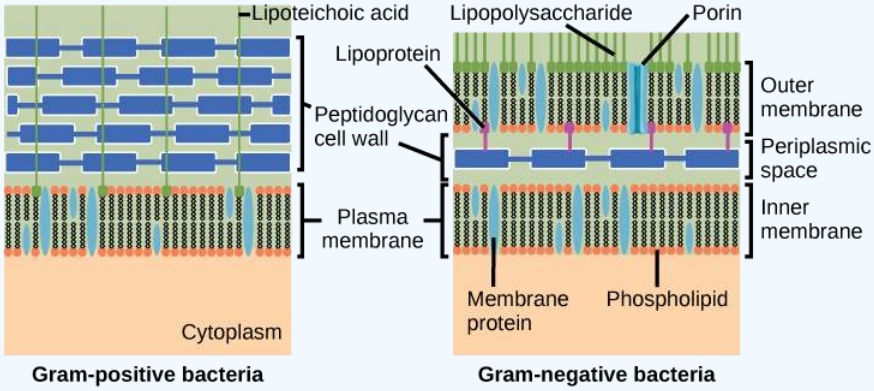


Figure 3. Gram-positive and -negative bacteria (credit: modification of work by “Franciscosp2″/Wikimedia Commons)

Which of the following statements is true?

a. Gram-positive bacteria have a single cell wall anchored to the cell membrane by lipoteichoic acid.
b. Porins allow entry of substances into both Gram-positive and Gram-negative bacteria.
c. The cell wall of Gram-negative bacteria is thick, and the cell wall of Gram-positive bacteria is thin.
d. Gram-negative bacteria have a cell wall made of peptidoglycan, whereas Gram-positive bacteria have a cell wall made of lipoteichoic acid.

[reveal-answer q=”765650″]Show Answer[/reveal-answer]
[hidden-answer a=”765650″]Statement a is true: **Gram-positive bacteria have a single cell wall anchored to the cell membrane by lipoteichoic acid.**[/hidden-answer]

Archaean cell walls do not have peptidoglycan. 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.

Learning Objectives

Table 4. 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

Bacteria and Archaea differ in the lipid composition of their cell membranes and the characteristics of the cell wall. In archaeal membranes, phytanyl units, rather than fatty acids, are linked to glycerol. Some archaeal membranes are lipid monolayers instead of bilayers.

The cell wall is located outside the cell membrane and prevents osmotic lysis. The chemical composition of cell walls varies between species. Bacterial cell walls contain peptidoglycan. Archaean cell walls do not have peptidoglycan, but they may have pseudopeptidoglycan, polysaccharides, glycoproteins, or protein-based cell walls. Bacteria can be divided into two major groups: Gram positive and Gram negative, based on the Gram stain reaction. Gram-positive organisms have a thick cell wall, together with teichoic acids. Gram-negative organisms have a thin cell wall and an outer envelope containing lipopolysaccharides and lipoproteins.

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7.10: Introduction to Prokaryotic Metabolism

Identify the metabolic needs of prokaryotes

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. The very broad range of environments that prokaryotes occupy is possible because they have diverse metabolic processes.

What You'll Learn to Do

- 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 cycle
- Describe the roles of prokaryotes in the nitrogen cycle

Learning Activities

The learning activities for this section include the following:

- Needs of Prokaryotes
- How Prokaryotes Get Energy
- Role of Prokaryotes in Ecosystems
- Self Check: Prokaryotic Metabolism

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7.11: Needs of Prokaryotes

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.

Macronutrients

Cells are essentially a well-organized assemblage of macromolecules and water. Recall that macromolecules are produced by the polymerization of smaller units called monomers. For cells to build all of the molecules required to sustain life, they need certain substances, collectively called **nutrients**. When prokaryotes grow in nature, they obtain their nutrients from the environment. Nutrients that are required in large amounts are called macronutrients, whereas those required in smaller or trace amounts are called micronutrients. Just a handful of elements are considered macronutrients—carbon, hydrogen, oxygen, nitrogen, phosphorus, and sulfur. (A mnemonic for remembering these elements is the acronym *CHONPS*.)

Why are these macronutrients needed in large amounts? They are the components of organic compounds in cells, including water. Carbon is the major element in all macromolecules: carbohydrates, proteins, nucleic acids, lipids, and many other compounds. Carbon accounts for about 50 percent of the composition of the cell. Nitrogen represents 12 percent of the total dry weight of a typical cell and is a component of proteins, nucleic acids, and other cell constituents. Most of the nitrogen available in nature is either atmospheric nitrogen (N_2) or another inorganic form. Diatomic (N_2) nitrogen, however, can be converted into an organic form only by certain organisms, called nitrogen-fixing organisms. Both hydrogen and oxygen are part of many organic compounds and of water. Phosphorus is required by all organisms for the synthesis of nucleotides and phospholipids. Sulfur is part of the structure of some amino acids such as cysteine and methionine, and is also present in several vitamins and coenzymes. Other important macronutrients are potassium (K), magnesium (Mg), calcium (Ca), and sodium (Na). Although these elements are required in smaller amounts, they are very important for the structure and function of the prokaryotic cell.

Micronutrients

In addition to these macronutrients, prokaryotes require various metallic elements in small amounts. These are referred to as micronutrients or trace elements. For example, iron is necessary for the function of the cytochromes involved in electron-transport reactions. Some prokaryotes require other elements—such as boron (B), chromium (Cr), and manganese (Mn)—primarily as enzyme cofactors.

? Practice Question

The substances needed to sustain life are _____.

a. trace elements
b. DNA and proteins
c. nutrients
d. building blocks

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[hidden-answer a="957849"]Answer c. Nutrients are the substances needed to sustain life.[/hidden-answer]

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7.12: How Prokaryotes Get Energy

Prokaryote Metabolism

Like all living things, prokaryotes need energy and carbon. They meet these needs in a variety of ways. In fact, prokaryotes have just about every possible type of **metabolism**. They may get energy from light (photo) or chemical compounds (chemo). They may get carbon from carbon dioxide (**autotroph**) or other living things (**heterotroph**). Most prokaryotes are **chemoheterotrophs**. They depend on other organisms for both energy and carbon. Many break down organic wastes and the remains of dead organisms. They play vital roles as decomposers and help recycle carbon and nitrogen. **Photoautotrophs** are important producers. They are especially important in aquatic ecosystems.

Classification of Prokaryotes Based on Metabolism

Two major nutritional needs can be used to group prokaryotes. These are (1) carbon metabolism, their source of carbon for building organic molecules within the cells, and (2) energy metabolism, their source of energy used for growth.

In terms of carbon metabolism, prokaryotes are classified as either heterotrophic or autotrophic:

- **Heterotrophic** organisms use organic compounds, usually from other organisms, as carbon sources.
- **Autotrophic** organisms use carbon dioxide (CO_2) as their only source or their main source of carbon. Many autotrophic bacteria are photosynthetic, and get their carbon from the carbon dioxide in the atmosphere. This process of capturing inorganic carbon and converting it to organic sugar molecules is known as carbon fixation.

Energy metabolism in prokaryotes is classified as one of the following:

- **Phototrophic** organisms capture light energy from the sun and convert it into chemical energy inside their cells.
- **Chemotrophic** organisms break down either organic or inorganic molecules to supply energy for the cell. Some chemotrophic organisms can also use their organic energy-supplying molecules as a carbon supply, which would make them chemoheterotrophs.

Organisms are then classified as follows:

- **Photoheterotrophs** are organisms that capture light energy to convert to chemical energy in the cells, but they get carbon from organic sources (other organisms). Examples are purple non-sulfur bacteria, green non-sulfur bacteria and heliobacteria.
- **Chemoheterotrophs** are organisms that get their energy source and carbon source from organic sources. Chemoheterotrophs must consume organic building blocks that they are unable to make themselves. Most get their energy from organic molecules such as sugars. This nutritional mode is very common among eukaryotes, including humans.
- **Photoautotrophs** are cells that capture light energy, and use carbon dioxide as their carbon source. There are many photoautotrophic prokaryotes, which include cyanobacteria. Photoautotrophic prokaryotes use similar compounds to those of plants to trap light energy.
- **Chemoautotrophs** are cells that break down inorganic molecules to supply energy for the cell, and use carbon dioxide as a carbon source. Chemoautotrophs include prokaryotes that break down hydrogen sulfide (H_2S the “rotten egg” smelling gas), and ammonia (NH_4). Nitrosomonas, a species of soil bacterium, oxidizes NH_4^+ to nitrite (NO_2^-). This reaction releases energy that the bacteria use. Many chemoautotrophs also live in extreme environments such as deep sea vents (extremophiles).

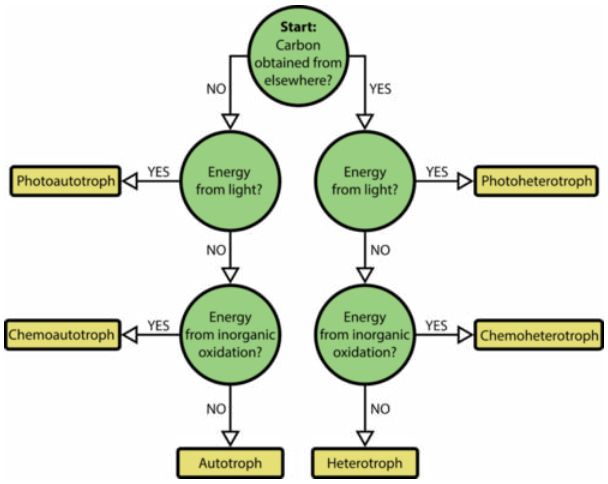


Figure 1. This flowchart helps to determine if a species is an autotroph or a heterotroph, a phototroph or a chemotroph. For example, “Obtain carbon elsewhere?” asks if the source of carbon is another organism. If the answer is “yes”, the organism is heterotrophic. If the answer is “no,” the organisms is autotrophic.

Learning Objectives

Prokaryotes fulfill their carbon and energy needs in various ways. They may be photoautotrophs, chemoautotrophs, photoheterotrophs, or chemoheterotrophs.

Nutritional mode	Energy source	Carbon source
Photoautotroph	Light	Carbon dioxide (or related compounds)
Photoheterotroph	Light	Organic compounds
Chemoautotroph	Chemical compounds	Carbon dioxide (or related compounds)
Chemoheterotroph	Chemical compounds	Organic compounds

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7.13: Role of Prokaryotes in Ecosystems

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.

Prokaryotes and the Carbon Cycle

Carbon is one of the most important macronutrients, and prokaryotes play an important role in the carbon cycle (Figure 1). 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, 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. Related to this, one very significant source of carbon compounds is humus, which is a mixture of organic materials from dead plants and prokaryotes that have resisted decomposition. Consumers such as animals use organic compounds generated by producers and release carbon dioxide to the atmosphere. 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) that undergo 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, which then returns to the atmosphere.

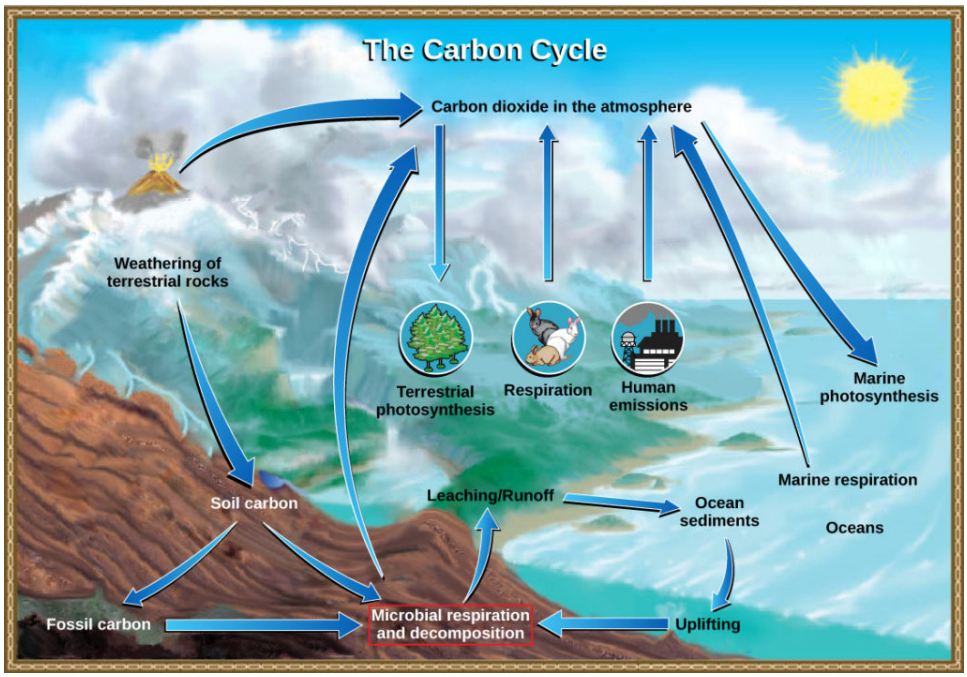


Figure 1. Prokaryotes play a significant role in continuously moving carbon through the biosphere. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

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, ammonium ions, nitrate, nitrite, and nitrogen gas by myriad processes, many of which are carried out only by prokaryotes. As illustrated in Figure 2, 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**. 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. Ammonia released to the atmosphere, however, represents only 15 percent of the total nitrogen released; the rest is as N_2 and N_2O. Ammonia is catabolized anaerobically by some prokaryotes, yielding N_2 as the final product. 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**.

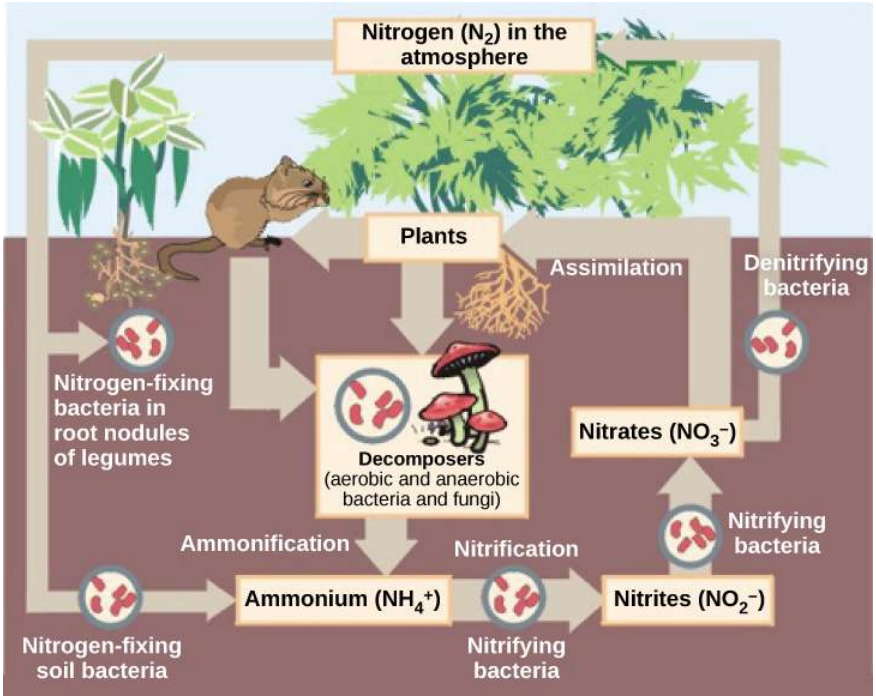


Figure 2. Prokaryotes play a key role in the nitrogen cycle. (credit: Environmental Protection Agency)

Practice Questions

Which of the following statements about the nitrogen cycle is false?

a. Nitrogen fixing bacteria exist on the root nodules of legumes and in the soil.
b. Denitrifying bacteria convert nitrates (NO_3^-) into nitrogen gas (N_2).
c. Ammonification is the process by which ammonium ion (NH_4^+) is released from decomposing organic compounds.
d. Nitrification is the process by which nitrites (NO_2^-) are converted to ammonium ion (NH_4^+).

[reveal-answer q=”123240″]Show Answer[/reveal-answer]
[hidden-answer a=”123240″]Answer d is false.

[/hidden-answer]

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?

[practice-area rows=”4″][/practice-area]
[reveal-answer q=”566708″]See Our Thoughts[/reveal-answer]
[hidden-answer a=”566708″]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. [/hidden-answer]

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7.14: Introduction to Bacterial Diseases in Humans

Identify common 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.

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.

What You'll Learn to Do

- Identify bacterial diseases that caused historically important plagues and epidemics
- Identify common foodborne illnesses
- Explain how overuse of antibiotic may be creating "superbugs"

Learning Activities

The learning activities for this section include the following:

- Long History of Bacterial Disease
- Biofilms and Foodborne Diseases
- Antibiotic Resistance
- Self Check: Bacterial Diseases in Humans

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7.15: Long History of Bacterial Disease

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 twenty-first 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



Figure 1. *Salmonella enterica* serovar Typhi, the causative agent of Typhoid fever. (credit: modification of work by NCI, CDC)

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 1), which causes typhoid fever.[1] This disease is commonly seen in overcrowded areas and has caused epidemics throughout recorded history.

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.

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 2). 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.

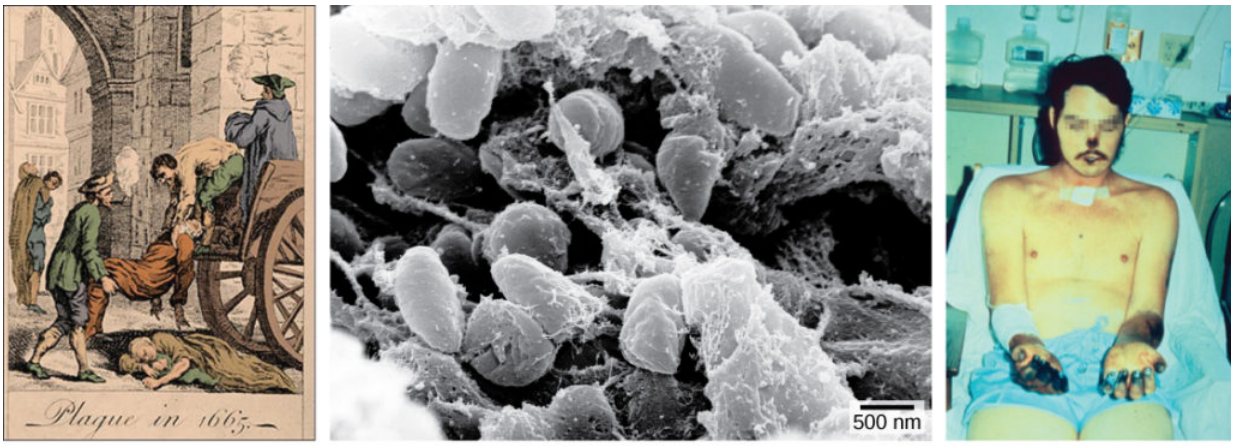


Figure 2. The (a) Great Plague of London killed an estimated 200,000 people, or about twenty percent of the city's population. The causative agent, the (b) bacterium *Yersinia pestis*, is a Gram-negative, rod-shaped bacterium from the class Gamma Proteobacteria. The disease is transmitted through the 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)

Watch a video on the modern understanding of the Black Death—bubonic plague in Europe during the fourteenth century.

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** (Figure 3) 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.

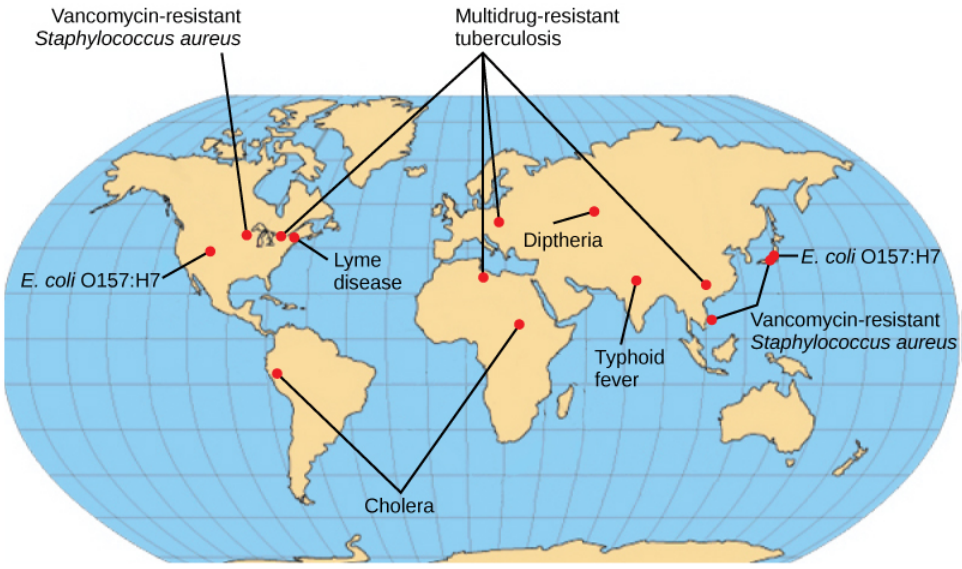


Figure 3. The map shows regions where bacterial diseases are emerging or reemerging. (credit: modification of work by NIH)

Some of the present emerging diseases are not actually new, but are diseases that were catastrophic in the past (Figure 4). 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.

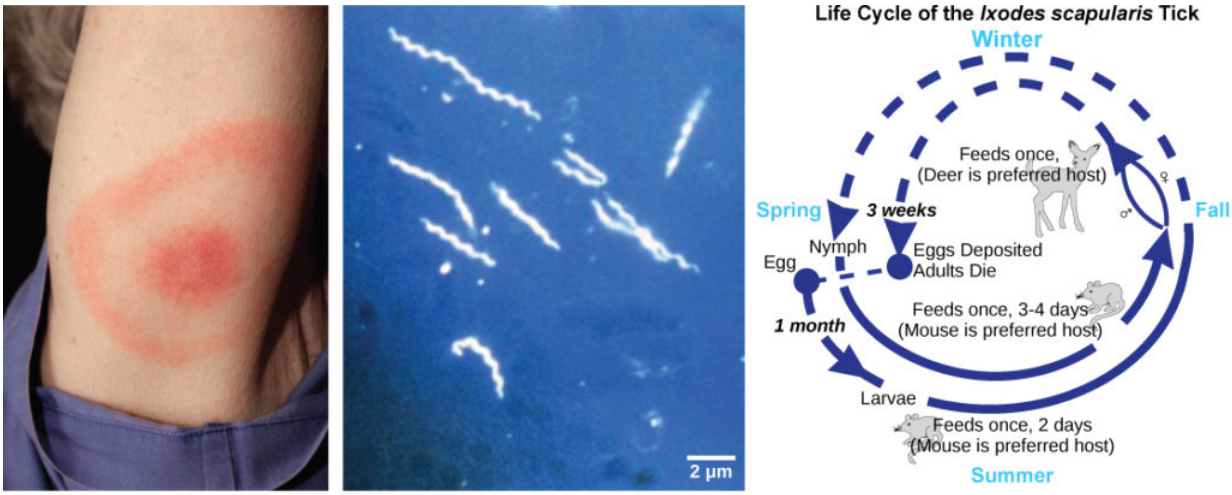


Figure 4. Lyme disease often, but not always, results in (a) a characteristic bullseye rash. The disease is caused by a (b) Gram-negative spirochete bacterium of the genus *Borrelia*. The bacteria (c) infect ticks, which in turns infect mice. Deer are the preferred secondary host, but the ticks also 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)

1. Papagrigorakis MJ, Synodinos PN, and Yapijakis C. Ancient typhoid epidemic reveals possible ancestral strain of Salmonella enterica serovar Typhi. *Infect Genet Evol* 7 (2007): 126–7, Epub 2006 Jun. ↵

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7.16: Biofilms and Foodborne Diseases

Prokaryotes are everywhere: they readily colonize the surface of any type of material, and food is not an exception. Most of the time, prokaryotes colonize food and food-processing equipment in the form of a biofilm.

Biofilms

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.

Foodborne Diseases

Outbreaks of bacterial infection related to food consumption are common. A **foodborne disease** (colloquially called "food poisoning") is an illness resulting from the consumption the pathogenic bacteria, viruses, or other parasites that contaminate food. Although the United States has one of the safest food supplies in the world, the U.S. Centers for Disease Control and Prevention (CDC) has reported that "76 million people get sick, more than 300,000 are hospitalized, and 5,000 Americans die each year from foodborne illness."

The characteristics of foodborne illnesses have changed over time. In the past, it was relatively common to hear about sporadic cases of **botulism**, the potentially fatal disease produced by a toxin from the anaerobic bacterium *Clostridium botulinum*. Some of the most common sources for this bacterium were non-acidic canned foods, homemade pickles, and processed meat and sausages. The can, jar, or package created a suitable anaerobic environment where *Clostridium* could grow. Proper sterilization and canning procedures have reduced the incidence of this disease.

While people may tend to think of foodborne illnesses as associated with animal-based foods, most cases are now linked to produce. There have been serious, produce-related outbreaks associated with raw spinach in the United States and with vegetable sprouts in Germany, and these types of outbreaks have become more common. The raw spinach outbreak in 2006 was produced by the bacterium *E. coli* serotype O157:H7. A **serotype** is a strain of bacteria that carries a set of similar antigens on its cell surface, and there are often many different serotypes of a bacterial species. Most *E. coli* are not particularly dangerous to humans, but serotype O157:H7 can cause bloody diarrhea and is potentially fatal.

All types of food can potentially be contaminated with bacteria. Recent outbreaks of *Salmonella* reported by the CDC occurred in foods as diverse as peanut butter, alfalfa sprouts, and eggs. A deadly outbreak in Germany in 2010 was caused by *E. coli* contamination of vegetable sprouts (Figure 1). The strain that caused the outbreak was found to be a new serotype not previously involved in other outbreaks, which indicates that *E. coli* is continuously evolving.

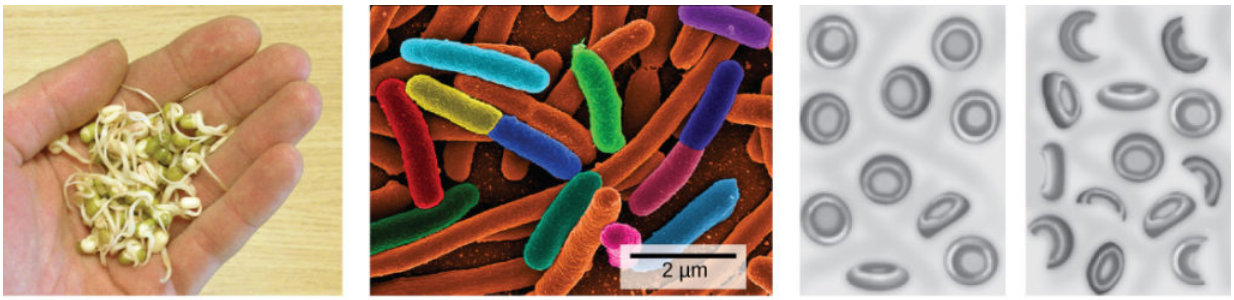


Figure 1. (a) Vegetable sprouts grown at an organic farm were the cause of an (b) *E. coli* outbreak that killed 32 people and sickened 3,800 in Germany in 2011. The strain responsible, *E. coli* O104:H4, produces Shiga toxin, a substance that inhibits protein synthesis in the host cell. The toxin (c) destroys red blood cells resulting in bloody diarrhea. Deformed red blood cells clog the capillaries of the kidney, which can lead to kidney failure, as happened to 845 patients in the 2011 outbreak. Kidney failure is usually reversible, but some patients experience kidney problems years later. (credit c: NIDDK, NIH)

? Try It

Epidemiology is the study of the occurrence, distribution, and determinants of health and disease in a population. It is, therefore, part of public health. An epidemiologist studies the frequency and distribution of diseases within human populations and environments.



Figure 2. Vaccinations can slow the spread of communicable diseases. (credit: modification of work by Daniel Paquet)

Epidemiologists collect data about a particular disease and track its spread to identify the original mode of transmission. They sometimes work in close collaboration with historians to try to understand the way a disease evolved geographically and over time, tracking the natural history of pathogens. They gather information from clinical records, patient interviews, surveillance, and any other available means. That information is used to develop strategies, such as vaccinations (Figure 2), and design public health policies to reduce the incidence of a disease or to prevent its spread. Epidemiologists also conduct rapid investigations in case of an outbreak to recommend immediate measures to control it.

An epidemiologist has a bachelor's degree, plus a master's degree in public health (MPH). Many epidemiologists are also physicians (have an M.D.), or they have a Ph.D. in an associated field, such as biology or microbiology.

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7.17: Antibiotic Resistance

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 because these illnesses are caused by viruses, not bacteria. 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 maximize the probability of resistance developing, and these resistant bacteria are readily transferred to humans.

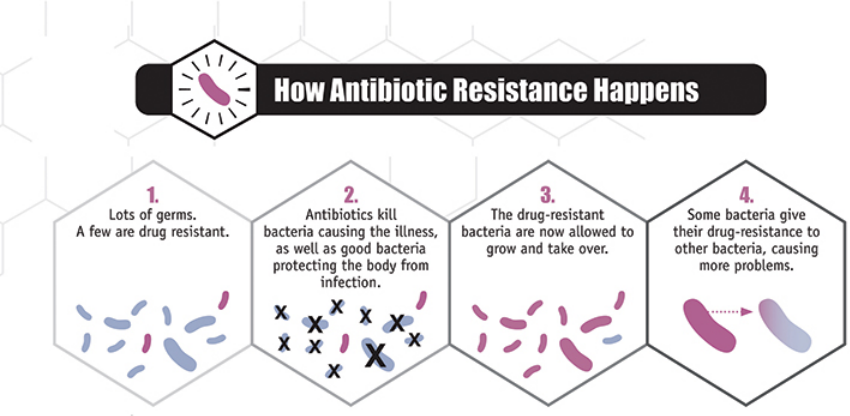
Watch a recent news report on the problem of routine antibiotic administration to livestock and antibiotic-resistant bacteria.

Drug Resistance

Antimicrobial resistance is not a new phenomenon. In nature, microbes are constantly evolving in order to overcome the antimicrobial compounds produced by other microorganisms. Human development of antimicrobial drugs and their widespread clinical use has simply provided another selective pressure that promotes further evolution. Several important factors can accelerate the evolution of **drug resistance**. These include the overuse and misuse of antimicrobials, inappropriate use of antimicrobials, subtherapeutic dosing, and patient noncompliance with the recommended course of treatment.

Exposure of a pathogen to an antimicrobial compound can select for chromosomal mutations conferring resistance, which can be transferred vertically to subsequent microbial generations and eventually become predominant in a microbial population that is repeatedly exposed to the antimicrobial. Alternatively, many genes responsible for drug resistance are found on **plasmids** or in **transposons** that can be transferred easily between microbes through **horizontal gene transfer**. Transposons also have the ability to move resistance genes between plasmids and chromosomes to further promote the spread of resistance.

How Resistance Happens



How Resistance Spreads

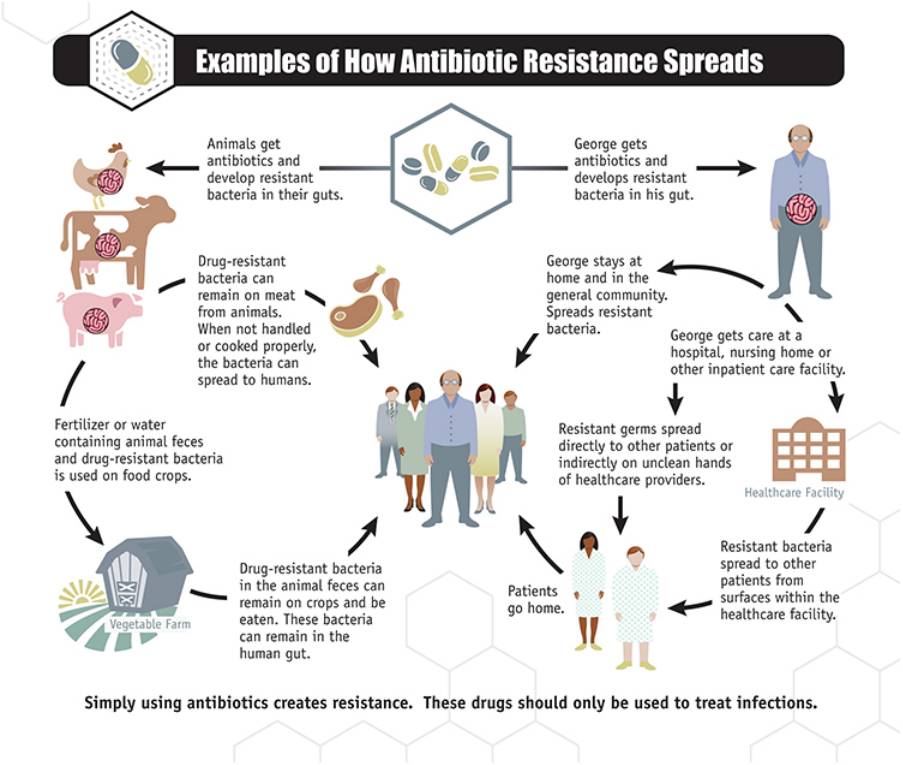
All animals carry bacteria in their intestines. Giving antibiotics will kill many bacteria, but resistant bacteria can survive and multiply.

- When food animals are slaughtered and processed, these resistant bacteria can contaminate the meat or other animal products.

- These bacteria can also get into the environment when an animal poops and may spread to produce that is irrigated with contaminated water.

There are several direct routes by which people can get antibiotic-resistant bacteria that develop in industrial food animal production:

- Improperly handling or consuming inadequately cooked contaminated meat.
- Contact with infected farm workers or meat processors, or perhaps their families, doctors and others with whom they interact.
- Drinking contaminated surface or ground water and eating contaminated crops.
- Contacting air that is vented from concentrated animal housing or is released during animal transport.



Due to increasing drug-resistance, physicians often have to recommend second- or third-choice drugs for treatment when the bacteria that cause infections are resistant to the drug of choice and this drug doesn't work. But the alternative drugs might be less effective, more toxic, and more expensive. Preserving the effectiveness of antibiotics is vital to protecting human and animal health.

To learn more about the top 18 drug-resistant threats to the US, visit the CDC's website.

Try It

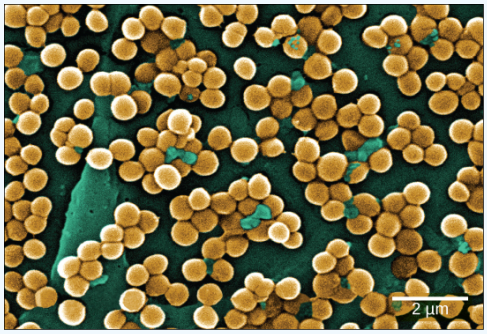


Figure 1. This scanning electron micrograph shows methicillin-resistant *Staphylococcus aureus* bacteria, commonly known as MRSA. *S. aureus* is not always pathogenic, but can cause diseases such as food poisoning and skin and respiratory infections. (credit: modification of work by Janice Haney Carr; scale-bar data from Matt Russell)

The imprudent use of antibiotics has paved the way for bacteria to expand populations of resistant forms. For example, *Staphylococcus aureus*, often called "staph," is a common bacterium that can live in the human body and is usually easily treated with antibiotics. A very dangerous strain, however, **methicillin-resistant *Staphylococcus aureus* (MRSA)** has made the news over the past few years (Figure 1). This strain is resistant to many commonly used antibiotics, including methicillin, amoxicillin, penicillin, and oxacillin. MRSA can cause infections of the skin, but it can also infect the bloodstream, lungs, urinary tract, or sites of injury. While MRSA infections are common among people in healthcare facilities, they have also appeared in healthy people who haven't been hospitalized but who live or work in tight populations (like military personnel and prisoners). Researchers have expressed concern about the way this latter source of MRSA targets a much younger population than those residing in care facilities. *The Journal of the American Medical Association* reported that, among MRSA-afflicted persons in healthcare facilities, the average age is 68, whereas people with "community-associated MRSA" (**CA-MRSA**) have an average age of 23.[1]

Learning Objectives

The medical community is facing an antibiotic crisis. Some scientists believe that after years of being protected from bacterial infections by antibiotics, we may be returning to a time in which a simple bacterial infection could again devastate the human population. Researchers are developing new antibiotics, but it takes many years to of research and clinical trials, plus financial investments in the millions of dollars, to generate an effective and approved drug.

1. Naimi, TS, LeDell, KH, Como-Sabetti, K, et al. Comparison of community- and health care-associated methicillin-resistant *Staphylococcus aureus* infection. JAMA 290 (2003): 2976–84, doi: 10.1001/jama.290.22.2976. ↵

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7.18: Introduction to Beneficial Prokaryotes

Identify common prokaryotes that are beneficial to humans

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.

What You'll Learn to Do

- Explain the need for nitrogen fixation and how it is accomplished
- Identify foods in which prokaryotes are used in the processing
- Describe the use of prokaryotes in bioremediation
- Describe the beneficial effects of bacteria that colonize our skin and digestive tracts

Learning Activities

The learning activities for this section include the following:

- Nitrogen Fixation
- Food from Bacteria
- Bioremediation
- Microbes and the Human Body
- Self Check: Beneficial Prokaryotes

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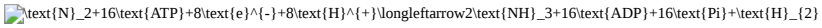
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7.19: Nitrogen Fixation

Nitrogen is a very important element to living things, because it is part of nucleotides and amino acids that are the building blocks of nucleic acids and proteins, respectively. Nitrogen is usually the most limiting element in terrestrial ecosystems, with atmospheric nitrogen, N_2, providing the largest pool of available nitrogen. However, eukaryotes cannot use atmospheric, gaseous nitrogen to synthesize macromolecules. Fortunately, nitrogen can be "fixed," meaning it is converted into ammonia (NH_3) either biologically or abiotically. Abiotic nitrogen fixation occurs as a result of lightning or by industrial processes.

Biological nitrogen fixation (BNF) is exclusively carried out by prokaryotes: soil bacteria, cyanobacteria, and *Frankia* spp. (filamentous bacteria interacting with actinorhizal plants such as alder, bayberry, and sweet fern). After photosynthesis, BNF is the second most important biological process on Earth. The equation representing the process is as follows



where Pi stands for inorganic phosphate. The total fixed nitrogen through BNF is about 100 to 180 million metric tons per year. Biological processes contribute 65 percent of the nitrogen used in agriculture.

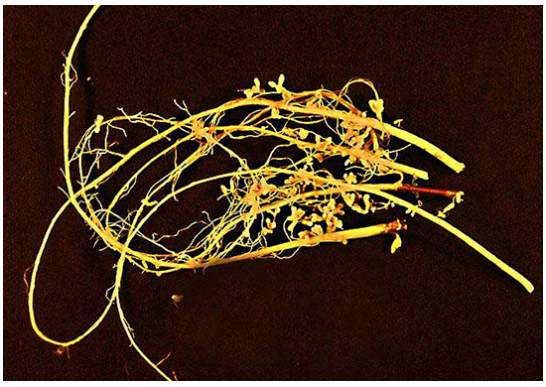


Figure 1. Soybean (*Glycine max)* is a legume that interacts symbiotically with the soil bacterium *Bradyrhizobium japonicum* to form specialized structures on the roots called nodules where nitrogen fixation occurs. (credit: USDA)

Cyanobacteria are the most important nitrogen fixers in aquatic environments. In soil, members of the genus *Clostridium* are examples of free-living, nitrogen-fixing bacteria. Other bacteria live symbiotically with legume plants, providing the most important source of BNF. Symbionts may fix more nitrogen in soils than free-living organisms by a factor of 10. Soil bacteria, collectively called rhizobia, are able to symbiotically interact with legumes to form **nodules**, specialized structures where nitrogen fixation occurs (Figure 1).

Nitrogenase, the enzyme that fixes nitrogen, is inactivated by oxygen, so the nodule provides an oxygen-free area for nitrogen fixation to take place. This process provides a natural and inexpensive plant fertilizer, as it reduces atmospheric nitrogen to ammonia, which is easily usable by plants. The use of legumes is an excellent alternative to chemical fertilization and is of special interest to sustainable agriculture, which seeks to minimize the use of chemicals and conserve natural resources. Through symbiotic nitrogen fixation, the plant benefits from using an endless source of nitrogen: the atmosphere. Bacteria benefit from using photosynthates (carbohydrates produced during photosynthesis) from the plant and having a protected niche. Additionally, the soil benefits from being naturally fertilized. Therefore, the use of rhizobia as biofertilizers is a sustainable practice.

Why are legumes so important? Some, like soybeans, are key sources of agricultural protein. Some of the most important grain legumes are soybean, peanuts, peas, chickpeas, and beans. Other legumes, such as alfalfa, are used to feed cattle.

This article provides nice look at how the role of microbes is expanding in agriculture.

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7.20: Food from Bacteria

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 1).

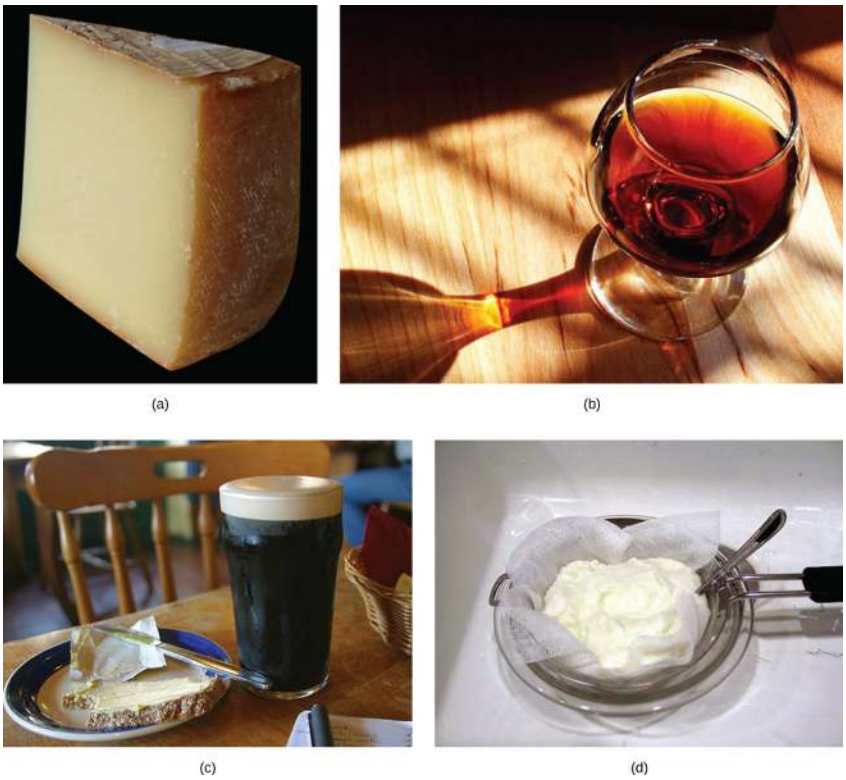


Figure 1. Some of the products derived from the use of prokaryotes in early biotechnology include (a) cheese, (b) wine, (c) beer and bread, and (d) yogurt. (credit bread: modification of work by F. Rodrigo/Wikimedia Commons; credit wine: modification of work by Jon Sullivan; credit beer and bread: modification 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.

1. http://www.cbd.int/convention/articles/?a=cbd-02, United Nations Convention on Biological Diversity: Article 2: Use of Terms. ↵

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7.21: 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 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 1), 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).



(a) (b)

Figure 1. (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)

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.

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7.22: Microbes and the Human Body

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

The 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.

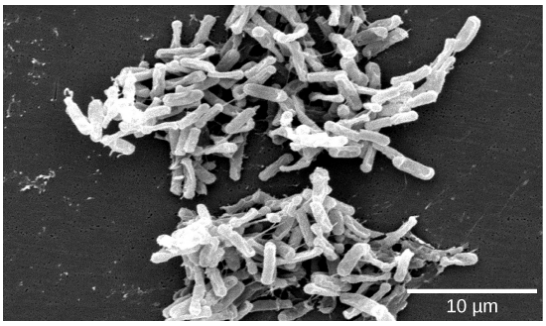


Figure 1. This scanning electron micrograph shows *Clostridium difficile*, a Gram-positive, rod-shaped bacterium that causes severe diarrhea. Infection commonly occurs after the normal gut fauna is eradicated by antibiotics. (credit: modification of work by CDC, HHS; scale-bar data from Matt Russell)

A particularly fascinating example of our normal flora relates to our digestive systems. People who take high doses of antibiotics tend to lose many of their normal gut bacteria, allowing a naturally antibiotic-resistant species called *Clostridium difficile* to overgrow and cause severe gastric problems, especially chronic diarrhea (Figure 1). Obviously, trying to treat this problem with antibiotics only makes it worse. However, it has been successfully treated by giving the patients fecal transplants from healthy donors to reestablish the normal intestinal microbial community. Clinical trials are underway to ensure the safety and effectiveness of this technique.

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

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7.23: Putting It Together- Prokaryotes

At the beginning of this lesson, we talked about a recent case of a superbug: a strain of *Klebsiella* that was resistant to all twenty-six of the available antibiotics.

Think about It

Can you guess how this strain of *Klebsiella* became so resistant?

[practice-area rows="4"][/practice-area]
[reveal-answer q="863404"]Show Our Thoughts[/reveal-answer]
[hidden-answer a="863404"]These resistant bacteria are known as "superbugs": they result from the overuse of antibiotics. As more and more antibiotics are used, only the bacteria who can survive the antibiotics survive, and they pass this resistance on to later generations. With this knowledge, we can guess that the bacteria originated from an area with particularly high antibiotic overuse. Bacteria can also share resistance genes across species lines, so antibiotic resistance in general increases, even if an antibiotic is only used on one or two species.[/hidden-answer]

Remember, prokaryotes represent a broad spectrum of organisms. This video teaches us about the (mostly) single-celled organisms that make up two of the three taxonomic domains of life, and one of the four kingdoms: Archaea, Bacteria, and Protists (which we'll learn about in the next module). They are by far the most abundant organisms on Earth, and are our oldest, oddest relatives.



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7.24: Cerego- Prokaryotes

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for Prokaryotes. You'll need to create a free log-in to practice these items, if you haven't already.

https://cerego.com/sets/796508/learn

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CHAPTER OVERVIEW

8: Module 5- Protists

8.1: Why It Matters- Protists
8.2: Introduction to the Characteristics of Protists
8.3: Cell Structure and Motility
8.4: Metabolism
8.5: Life Cycles and Habitats
8.6: Introduction to Groups of Protists
8.7: Excavata
8.8: Chromalveolata
8.9: Rhizaria
8.10: Archaeplastida
8.11: Amoebozoa
8.12: Opisthokonta
8.13: Introduction to the Ecology of Protists
8.14: Primary Producers
8.15: Protists as Decomposers
8.16: Pathogenic Protists
8.17: Putting It Together- Protists
8.18: Cerego- Protists

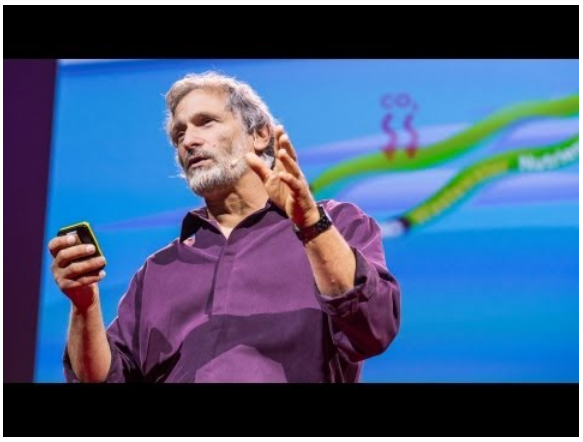
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8.1: Why It Matters- Protists

Why discuss the organisms in Kingdom Protista?

Protists exist as a kind of “grey area” in biology. The organisms found in this kingdom are varied, and often seem like they might be more closely related to organisms in another kingdom: some protists resemble bacteria, some resemble fungi, and some resemble plants.

One group of these plant-like protists are the micro-algae. Watch this video to learn how these microscopic organisms could serve as a future fuel source:



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Learning Outcomes

- Identify the common characteristics of protists
- Classify protists into unique categories
- Describe the role that protists play in the ecosystem

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- Energy from floating algae pods. **Authored by**: Jonathan Trent. **Provided by**: TED. **Located at**: https://youtu.be/X-HE4Hfa-OY. **License**: *All Rights Reserved*. **License Terms**: Standard YouTube License

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8.2: Introduction to the Characteristics of Protists

Identify the common 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.

What You'll Learn to Do

- Describe the cell structure of protists
- Describe the motility of protists
- Describe the metabolic diversity of protists
- Describe the life cycle and habitat diversity of protists

Learning Activities

The learning activities for this section include the following:

- Cell Structure and Motility
- Metabolism
- Life Cycles and Habitats
- Self Check: Characteristics of Protists

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8.3: Cell Structure and Motility

Cell Structure

The cells of protists are among the most elaborate of all cells. Most protists are microscopic and unicellular, but some true multicellular forms exist. A few protists live as colonies that behave in some ways as a group of free-living cells and in other ways as a multicellular organism. Still other protists are composed of enormous, multinucleate, single cells that look like amorphous blobs of slime, or in other cases, like ferns. 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 (a single hectare is nearly 2.5 acres in size). 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. The pellicle functions like a flexible coat of armor, preventing the protist from being torn or pierced without compromising its range of motion.

Motility

The majority of protists are motile, but different types of protists have evolved varied modes of movement (Figure 1). Some protists have one or more flagella, which they rotate or whip: these are typically **euglena**. Others are covered in rows or tufts of tiny cilia that they coordinately beat to swim—typically **paramecium**. Still others form cytoplasmic extensions called pseudopodia anywhere on the cell, anchor the pseudopodia to a substrate, and pull themselves forward in an "oozing" movement: these are typically **amoeba**.

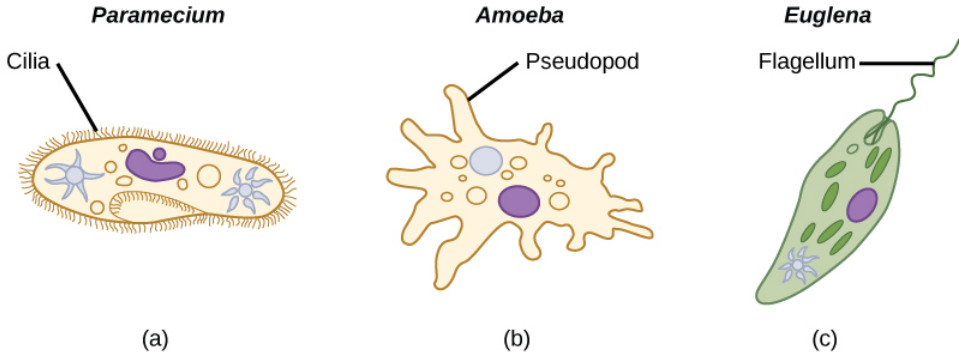


Figure 1. Protists use various methods for transportation. (a) *Paramecium* waves hair-like appendages called cilia to propel itself. (b) *Amoeba* uses lobe-like pseudopodia to anchor itself to a solid surface and pull itself forward. (c) *Euglena* uses a whip-like tail called a flagellum to propel itself.

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.

? Practice Questions

Protists that have a pellicle are surrounded by _____.

a. silica dioxide
b. calcium carbonate
c. carbohydrates
d. proteins

[reveal-answer q="368573"]Show Answer[/reveal-answer]
[hidden-answer a="368573"]Answer d. Protists that have a pellicle are surrounded by **proteins**.

[/hidden-answer]

Which of these locomotor organs would likely be the shortest?

a. a flagellum

b. a cilium
c. an extended pseudopod
d. a pellicle

[reveal-answer q="166771"]Show Answer[/reveal-answer]
[hidden-answer a="166771"]Answer b. A **cilium** would likely be the shortest locomotor organs.[/hidden-answer]

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8.4: 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 1). The vesicle containing the ingested particle, the phagosome, then fuses with a lysosome containing hydrolytic enzymes to produce a **phagolysosome**, and the food particle is broken down into small molecules that can diffuse into the cytoplasm and be used in cellular metabolism. Undigested remains ultimately are expelled from the cell via exocytosis.

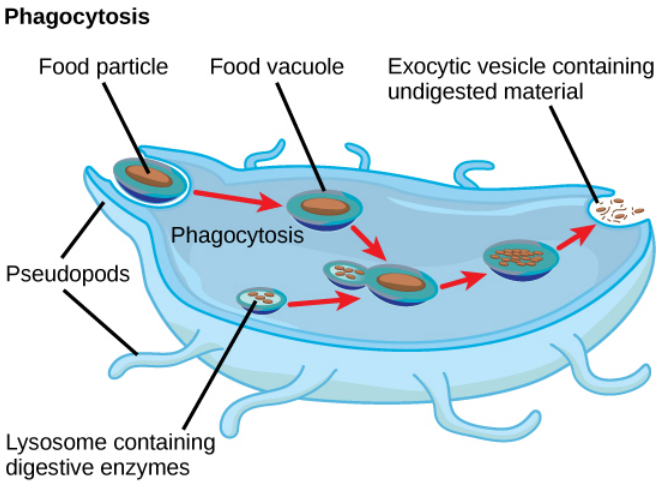


Figure 1. The stages of phagocytosis include the engulfment of a food particle, the digestion of the particle using hydrolytic enzymes contained within a lysosome, and the expulsion of undigested materials from the cell.

Subtypes of heterotrophs, called saprobes, absorb nutrients from dead organisms or their organic wastes. Some protists, like, euglena, can function as **mixotrophs**, obtaining nutrition by photoautotrophic or heterotrophic routes, depending on whether sunlight or organic nutrients are available.

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8.5: Life Cycles and Habitats

Life Cycles

Protists reproduce by a variety of mechanisms. Most undergo some form of asexual reproduction, such as binary fission, to produce two daughter cells. In protists, binary fission can be divided into transverse or longitudinal, depending on the axis of orientation; sometimes *Paramecium* exhibits this method. 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 common among protists, and many protist species can switch from asexual to sexual reproduction when necessary. Sexual reproduction is often associated with periods when nutrients are depleted or environmental changes occur. Sexual reproduction may allow the protist to recombine genes and produce new variations of progeny that may be better suited to surviving in the new environment. However, sexual reproduction is often associated with resistant cysts that are a protective, resting stage. 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 virtually no cellular metabolism.

Protist life cycles range from simple to extremely elaborate. 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. Other protists have multicellular stages in both haploid and diploid forms, a strategy called alternation of generations that is also used by plants.

Habitats

Nearly all protists exist in some type of aquatic environment, including freshwater and marine environments, damp soil, and even snow. 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.

? Practice Questions

Explain in your own words why sexual reproduction can be useful if a protist's environment changes.

[practice-area rows="2"][/practice-area]
[reveal-answer q="347707"]Show Answer[/reveal-answer]
[hidden-answer a="347707"]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.

[/hidden-answer]

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?

[practice-area rows="2"][/practice-area]
[reveal-answer q="155458"]Show Answer[/reveal-answer]
[hidden-answer a="155458"]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.[/hidden-answer]

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8.6: Introduction to Groups of Protists

Classify protists into unique categories

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. The emerging classification scheme groups the entire domain Eukaryota into six "supergroups" that contain all of the protists as well as animals, plants, and fungi that evolved from a common ancestor (Figure 1). 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.

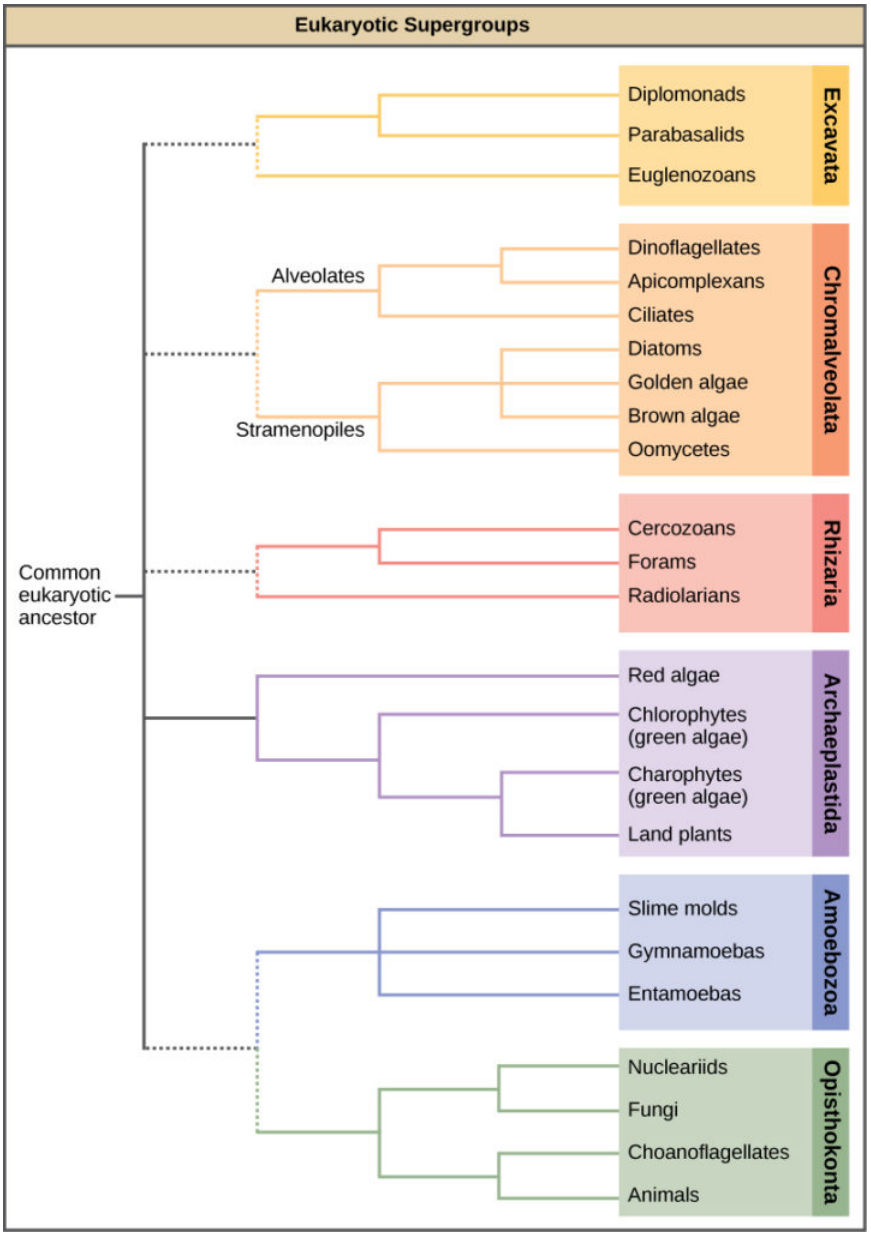


Figure 1. This diagram shows a proposed classification of the domain Eukara. Currently, the domain Eukarya is divided into six supergroups. Within each supergroup are multiple kingdoms. Dotted lines indicate suggested evolutionary relationships that remain under debate.

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. When learning about protists, it is helpful to focus less on the nomenclature and more on the commonalities and differences that define the groups themselves.

What You'll Learn to Do

- Identify characteristics and examples of protists in the supergroup Excavata
- Identify characteristics and examples of protists in the supergroup Chromalveolata
- Identify characteristics and examples of protists in the supergroup Rhizaria
- Identify characteristics and examples of protists in the supergroup Archaeplastida
- Identify characteristics and examples of protists in the supergroup Amoebozoa
- Identify characteristics and examples of protists in the supergroup Opisthokonta

Learning Activities

The learning activities for this section include the following:

- Excavata
- Chromalveolata
- Rhizaria
- Archaeplastida
- Amoebozoa
- Opisthokonta
- Self Check: Groups of Protists

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8.7: 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



Figure 1. The mammalian intestinal parasite *Giardia lamblia*, visualized here using scanning electron microscopy, is a waterborne protist that causes severe diarrhea when ingested. (credit: modification of work by Janice Carr, CDC; scale-bar data from Matt Russell)

Among the Excavata are the diplomonads, which include the intestinal parasite, *Giardia lamblia* (Figure 1). Until recently, these protists were believed to lack mitochondria. Mitochondrial remnant organelles, called **mitosomes**, have since been identified in diplomonads, but these mitosomes are essentially nonfunctional. 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

A second Excavata subgroup, the parabasalids, also exhibits semi-functional mitochondria. In parabasalids, these structures function anaerobically and are called **hydrogenosomes** because they produce hydrogen gas as a byproduct. 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. Whereas men rarely exhibit symptoms during an infection with this protist, infected women may become more susceptible to secondary infection with human immunodeficiency virus (HIV) and may be more likely to develop cervical cancer. Pregnant women infected with *T. vaginalis* are at an increased risk of serious complications, such as pre-term delivery.

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.

The human parasite, *Trypanosoma brucei*, belongs to a different 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. 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. *T. brucei* is common in central Africa and is the

causative agent of African sleeping sickness, a disease associated with severe chronic fatigue, coma, and can be fatal if left untreated.

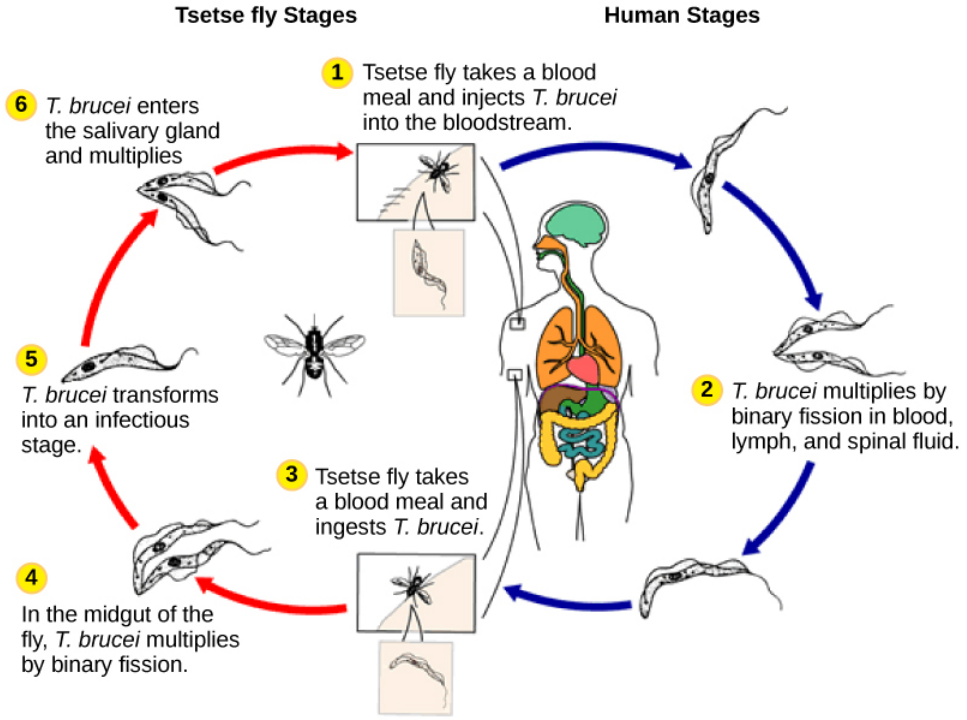


Figure 2. *Trypanosoma brucei*, the causative agent of sleeping sickness, spends part of its life cycle in the tsetse fly and part in humans. (credit: modification of work by CDC)

Watch this video to see *T. brucei* swimming. Note that there is no audio in this video.



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- Trypanosoma brucei bloodstream form. **Authored by**: TheOtonII. **Located at**: https://youtu.be/EnsydwITLYk. **License**: *All Rights Reserved*. **License Terms**: Standard YouTube License

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8.8: 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.

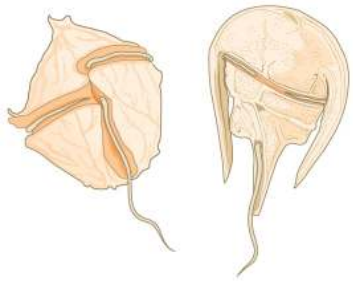


Figure 1. The dinoflagellates exhibit great diversity in shape. Many are encased in cellulose armor and have two flagella that fit in grooves between the plates. Movement of these two perpendicular flagella causes a spinning motion.

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 (Figure 1). 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.

Some dinoflagellates generate light, called **bioluminescence**, when they are jarred or stressed. Large numbers of marine dinoflagellates (billions or trillions of cells per wave) can emit light and cause an entire breaking wave to twinkle or take on a brilliant blue color (Figure 2). For approximately 20 species of marine dinoflagellates, population explosions (also called blooms) during the summer months can tint the ocean with a muddy red color. This phenomenon is called a red tide, and it results from the abundant red pigments present in dinoflagellate plastids. In large quantities, these dinoflagellate species secrete an asphyxiating toxin that can kill fish, birds, and marine mammals. Red tides can be massively detrimental to commercial fisheries, and humans who consume these protists may become poisoned.



Figure 2. Bioluminescence is emitted from dinoflagellates in a breaking wave, as seen from the New Jersey coast. (credit: “catalano82”/Flickr)

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 3). 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. Apicomplexan life cycles are complex, involving multiple hosts and stages of sexual and asexual reproduction.

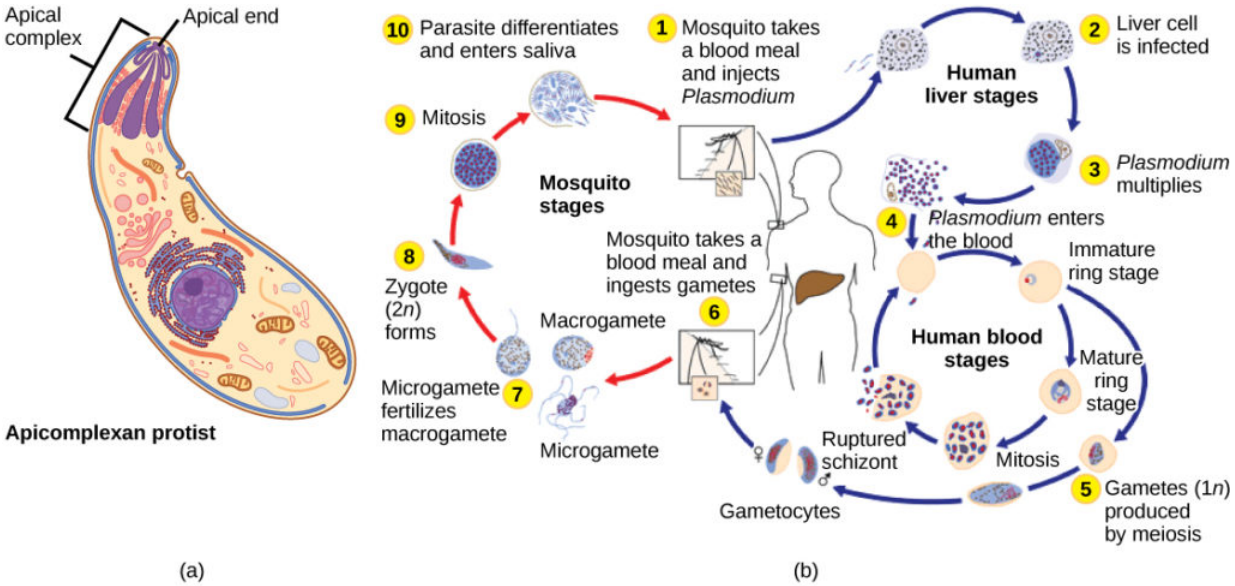


Figure 3. (a) Apicomplexans are parasitic protists. They have a characteristic apical complex that enables them to infect host cells. (b) Plasmodium, the causative agent of malaria, has a complex life cycle typical of apicomplexans. (credit b: modification of work by CDC)

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 (Figure 4). Food captured in the oral groove enters a food vacuole, where it combines with digestive enzymes. Waste particles are expelled by an exocytic vesicle that fuses at a specific region on the cell membrane, called the anal pore. In addition to a vacuole-based digestive system, *Paramecium* also uses **contractile vacuoles**, which are osmoregulatory vesicles that fill with water as it enters the cell by osmosis and then contract to squeeze water from the cell.

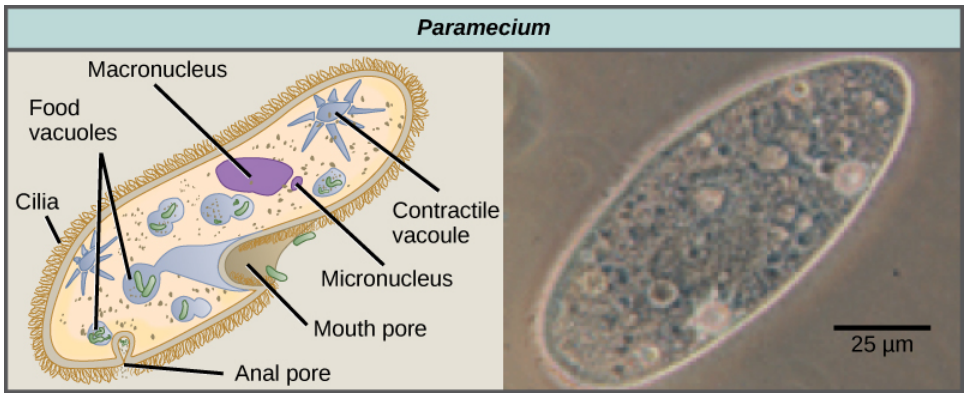


Figure 4. *Paramecium* has a primitive mouth (called an oral groove) to ingest food, and an anal pore to excrete it. Contractile vacuoles allow the organism to excrete excess water. Cilia enable the organism to move. (credit "paramecium micrograph": modification of work by NIH; scale-bar data from Matt Russell)

Watch the video of the contractile vacuole of *Paramecium* expelling water to keep the cell osmotically balanced.

A link to an interactive elements can be found at the bottom of this page.

Paramecium has two nuclei, a macronucleus and a micronucleus, in each cell. The micronucleus is essential for sexual reproduction, whereas the macronucleus directs asexual binary fission and all other biological functions. The process of sexual reproduction in *Paramecium* underscores the importance of the micronucleus to these protists. *Paramecium* and most other ciliates reproduce sexually by conjugation. This process begins when two different mating types of *Paramecium* make physical contact and join with a cytoplasmic bridge (Figure 5). The diploid micronucleus in each cell then undergoes meiosis to produce four haploid micronuclei. Three of these degenerate in each cell, leaving one micronucleus that then undergoes mitosis, generating two haploid micronuclei. The cells each exchange one of these haploid nuclei and move away from each other. A similar process occurs in bacteria that have plasmids. Fusion of the haploid micronuclei generates a completely novel diploid pre-micronucleus in each conjugative cell. This pre-micronucleus undergoes three rounds of mitosis to produce eight copies, and the original macronucleus disintegrates. Four of the eight pre-micronuclei become full-fledged micronuclei, whereas the other four perform multiple rounds of DNA replication and go on to become new macronuclei. Two cell divisions then yield four new *Paramecia* from each original conjugative cell.

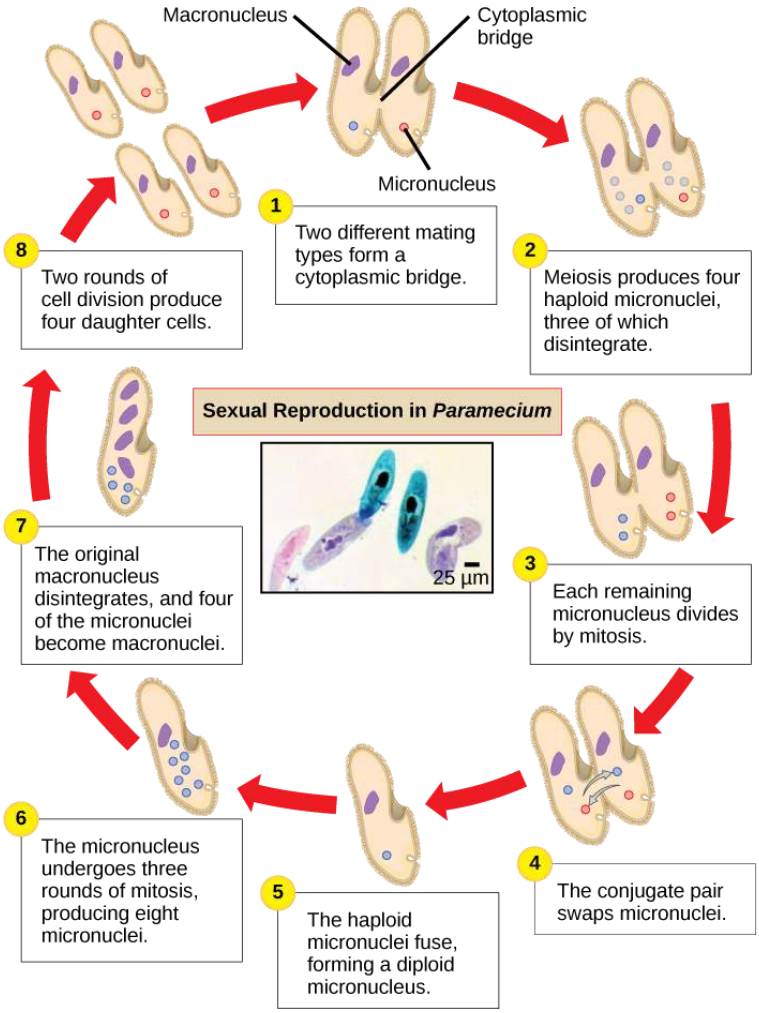


Figure 5. The complex process of sexual reproduction in *Paramecium* creates eight daughter cells from two original cells. Each cell has a macronucleus and a micronucleus. During sexual reproduction, the macronucleus dissolves and is replaced by a micronucleus. (credit "micrograph": modification of work by Ian Sutton; scale-bar data from Matt Russell)

Practice Question

Which of the following statements about *Paramecium* sexual reproduction is false?

a. The macronuclei are derived from micronuclei.
b. Both mitosis and meiosis occur during sexual reproduction.
c. The conjugate pair swaps macronucleii.
d. Each parent produces four daughter cells.

[reveal-answer q="294017"]Show Answer[/reveal-answer]
[hidden-answer a="294017"]Statement c is false.[/hidden-answer]

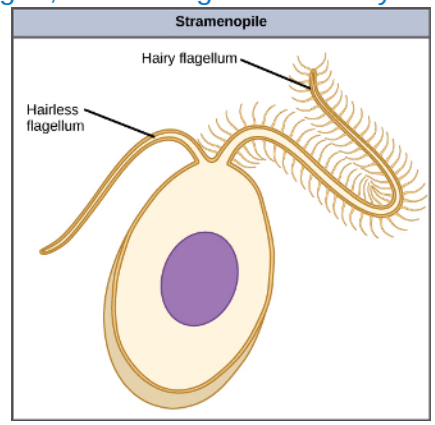


Figure 6. This stramenopile cell has a single hairy flagellum and a secondary smooth flagellum.

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 (Figure 6). 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 (Figure 7). 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. Some diatoms exhibit a slit in their silica shell, called a **raphe**. By expelling a stream of mucopolysaccharides from the raphe, the diatom can attach to surfaces or propel itself in one direction.

During periods of nutrient availability, diatom populations bloom to numbers greater than can be consumed by aquatic organisms. The excess diatoms die and sink to the sea floor where they are not easily reached by saprobes that feed on dead organisms. As a result, the carbon dioxide that the diatoms had consumed and incorporated into their cells during photosynthesis is not returned to the atmosphere. In general, this process by which carbon is transported deep into the ocean is described as the **biological carbon pump**, because carbon is "pumped" to the ocean depths where it is inaccessible to the atmosphere as carbon dioxide. The biological carbon pump is a crucial component of the carbon cycle that maintains lower atmospheric carbon dioxide levels.

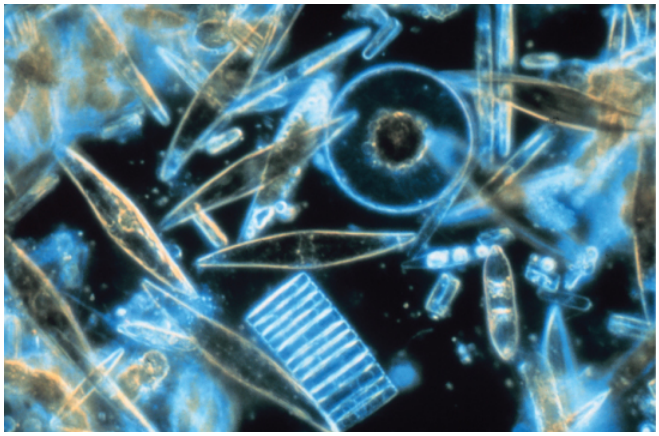


Figure 7. Assorted diatoms, visualized here using light microscopy, live among annual sea ice in McMurdo Sound, Antarctica. Diatoms range in size from 2 to 200 µm. (credit: Prof. Gordon T. Taylor, Stony Brook University, NSF, NOAA)

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. Compare this life cycle to that of humans, for instance. Haploid gametes produced by meiosis (sperm and egg) combine in fertilization to generate a diploid zygote that undergoes many rounds of mitosis to produce a multicellular embryo and then a fetus. However, the individual sperm and egg themselves never become multicellular beings. Terrestrial plants also have evolved alternation of generations. In the brown algae genus *Laminaria*, haploid spores develop into multicellular gametophytes, which produce haploid gametes that combine to produce diploid organisms that then become multicellular organisms with a different structure from the haploid form (Figure 8). Certain other organisms perform alternation of generations in which both the haploid and diploid forms look the same.

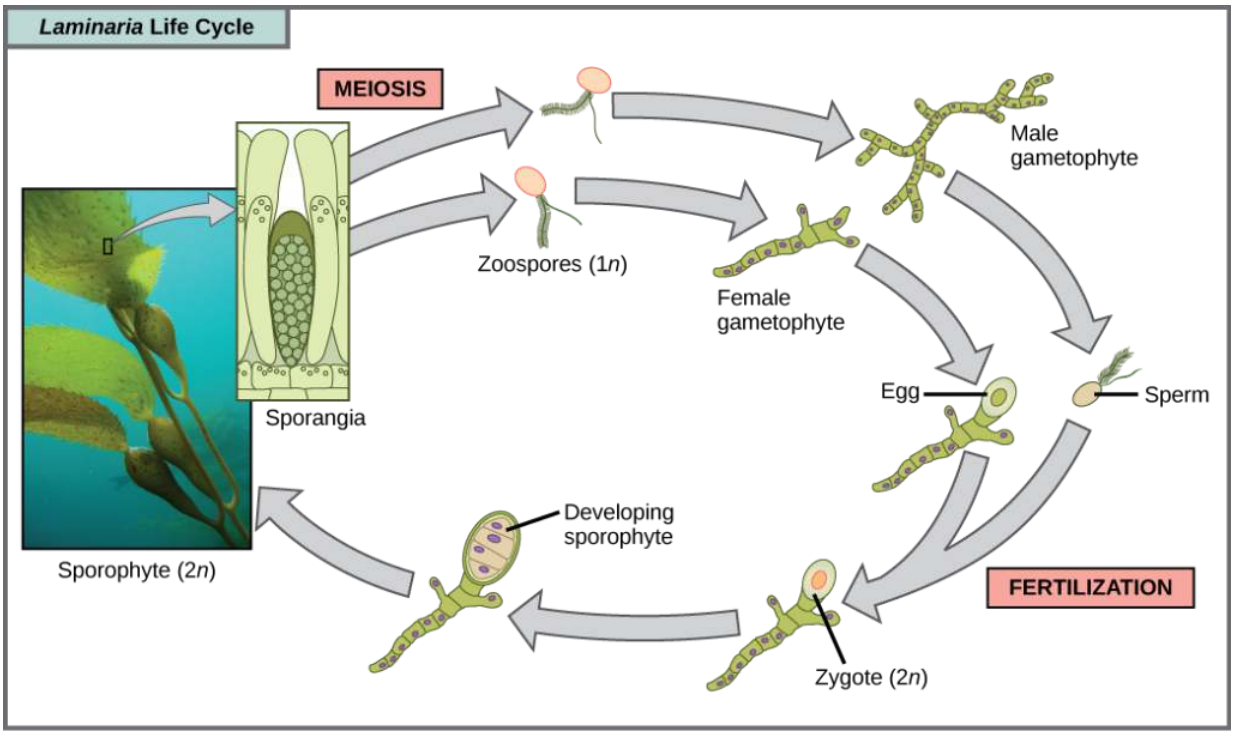


Figure 8. Several species of brown algae, such as the Laminaria shown here, have evolved life cycles in which both the haploid (gametophyte) and diploid (sporophyte) forms are multicellular. The gametophyte is different in structure than the sporophyte. (credit “laminaria photograph”: modification of work by Claire Fackler, CINMS, NOAA Photo Library)

? Practice Question

Which of the following statements about the *Laminaria* life cycle is false?

a. 1*n* zoospores form in the sporangia.
b. The sporophyte is the 2*n* plant.
c. The gametophyte is diploid.
d. Both the gametophyte and sporophyte stages are multicellular.

[reveal-answer q=”65382″]Show Answer[/reveal-answer]
[hidden-answer a=”65382″]Statement c is false.[/hidden-answer]



Figure 9. A saprobic oomycete engulfs a dead insect. (credit: modification of work by Thomas Bresson)

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. The oomycetes are nonphotosynthetic and include many saprobes and parasites. The saprobes appear as white fluffy growths on dead organisms (Figure 9).

Most oomycetes are aquatic, but some parasitize terrestrial plants. One plant pathogen is *Phytophthora infestans*, the causative agent of late blight of potatoes, such as occurred in the nineteenth century Irish potato famine.

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8.9: Rhizaria

The Rhizaria supergroup includes many of the amoebas, most of which have threadlike or needle-like pseudopodia (ammonia tepida, a Rhizaria species, can be seen in Figure 1).

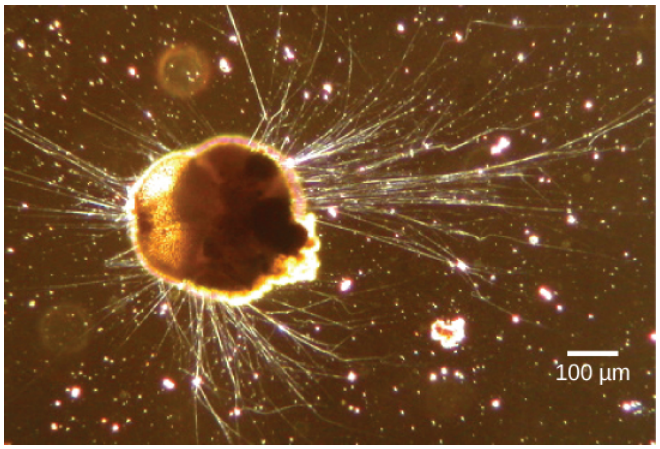
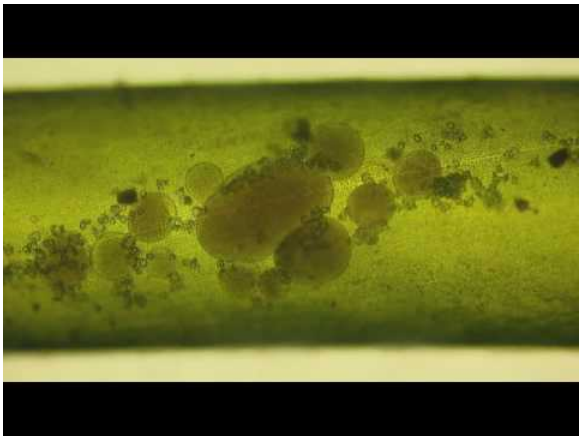


Figure 1. Ammonia Tepida, under a phase contrasty light microscope (credit: modification of work by Scott Fay, UC Berkeley; scale-bar data from Matt Russell)

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.

Take a look at this video to see cytoplasmic streaming in a green alga. Note that there is no audio in this video.



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Forams

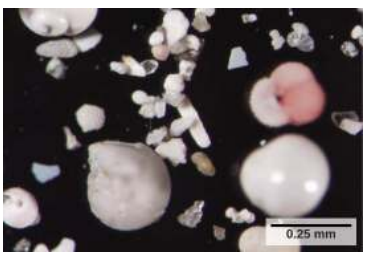


Figure 2. These shells from foraminifera sank to the sea floor. (credit: Deep East 2001, NOAA/OER)

Foraminiferans, or forams, are unicellular heterotrophic protists, ranging from approximately 20 micrometers to several centimeters in length, and occasionally resembling tiny snails (Figure 2).

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.

Radiolarians

A second subtype of Rhizaria, the radiolarians, exhibit intricate exteriors of glassy silica with radial or bilateral symmetry (Figure 3). 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.

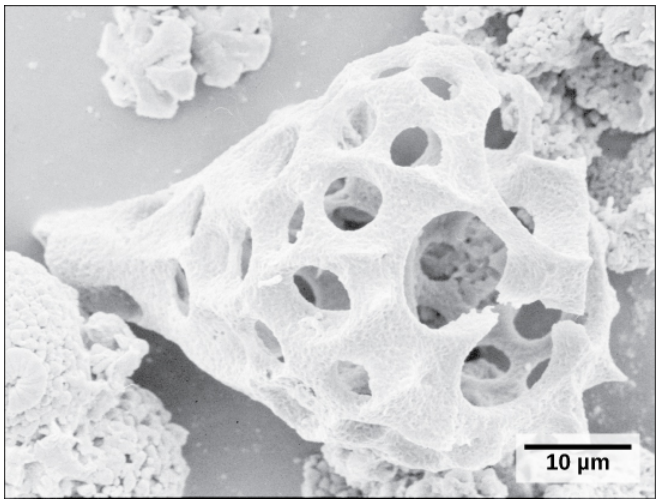


Figure 3. This fossilized radiolarian shell was imaged using a scanning electron microscope. (credit: modification of work by Hannes Grobe, Alfred Wegener Institute; scale-bar data from Matt Russell)

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8.10: 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 lack flagella, and are primarily multicellular, although they range in size from microscopic, unicellular protists to large, multicellular forms grouped into the informal seaweed category. Red algae have a second cell wall outside an inner cellulose cell wall. Carbohydrates in this wall are the source of agarose used for electrophoresis gels and agar for solidifying bacterial media. The “red” in the red algae comes from phycoerythrins, accessory photopigments that are red in color and obscure the green tint of chlorophyll in some species. Other protists classified as red algae lack phycoerythrins and are parasites. Both the red algae and the glaucophytes store carbohydrates in the cytoplasm rather than in the plastid. 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. The red algae life cycle is an unusual alternation of generations that includes two sporophyte phases, with meiosis occurring only in the second sporophyte.

Green Algae: Chlorophytes and Charophytes

The most abundant group of algae is the green algae. The green algae exhibit features similar to those of the land plants, particularly in terms of chloroplast structure. In both green algae and plants, carbohydrates are stored in the plastid. 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. The familiar *Spirogyra* is a charophyte. 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*.

The chlorophyte *Volvox* is one of only a few examples of a colonial organism, which behaves in some ways like a collection of individual cells, but in other ways like the specialized cells of a multicellular organism (Figure 1). *Volvox* colonies contain 500 to 60,000 cells, each with two flagella, contained within a hollow, spherical matrix composed of a gelatinous glycoprotein secretion. Individual cells in a *Volvox* colony move in a coordinated fashion and are interconnected by cytoplasmic bridges. Only a few of the cells reproduce to create daughter colonies, an example of basic cell specialization in this organism. Daughter colonies are produced with their flagella on the inside and have to evert as they are released.



Figure 1. *Volvox aureus* is a green alga in the supergroup Archaeplastida. This species exists as a colony, consisting of cells immersed in a gel-like matrix and intertwined with each other via hair-like cytoplasmic extensions. (credit: Dr. Ralf Wagner)

True multicellular organisms, such as the sea lettuce, *Ulva*, are also 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 (Figure 2). *Caulerpa* species undergo nuclear division, but their cells do not complete cytokinesis, remaining instead as massive and elaborate single cells.



Figure 2. *Caulerpa taxifolia* is a chlorophyte consisting of a single cell containing potentially thousands of nuclei. (credit: NOAA)

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8.11: Amoebozoa

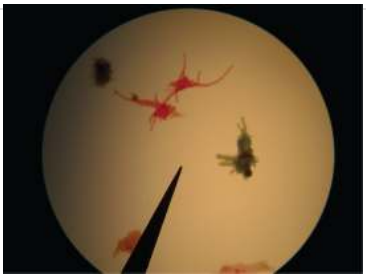


Figure 1. Amoebae with tubular and lobe-shaped pseudopodia are seen under a microscope. These isolates would be morphologically classified as amoebozoans.

The amoebozoans characteristically exhibit pseudopodia that extend like tubes or flat lobes, rather than the hair-like pseudopodia of rhizarian amoeba (Figure 1). 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 2). 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.

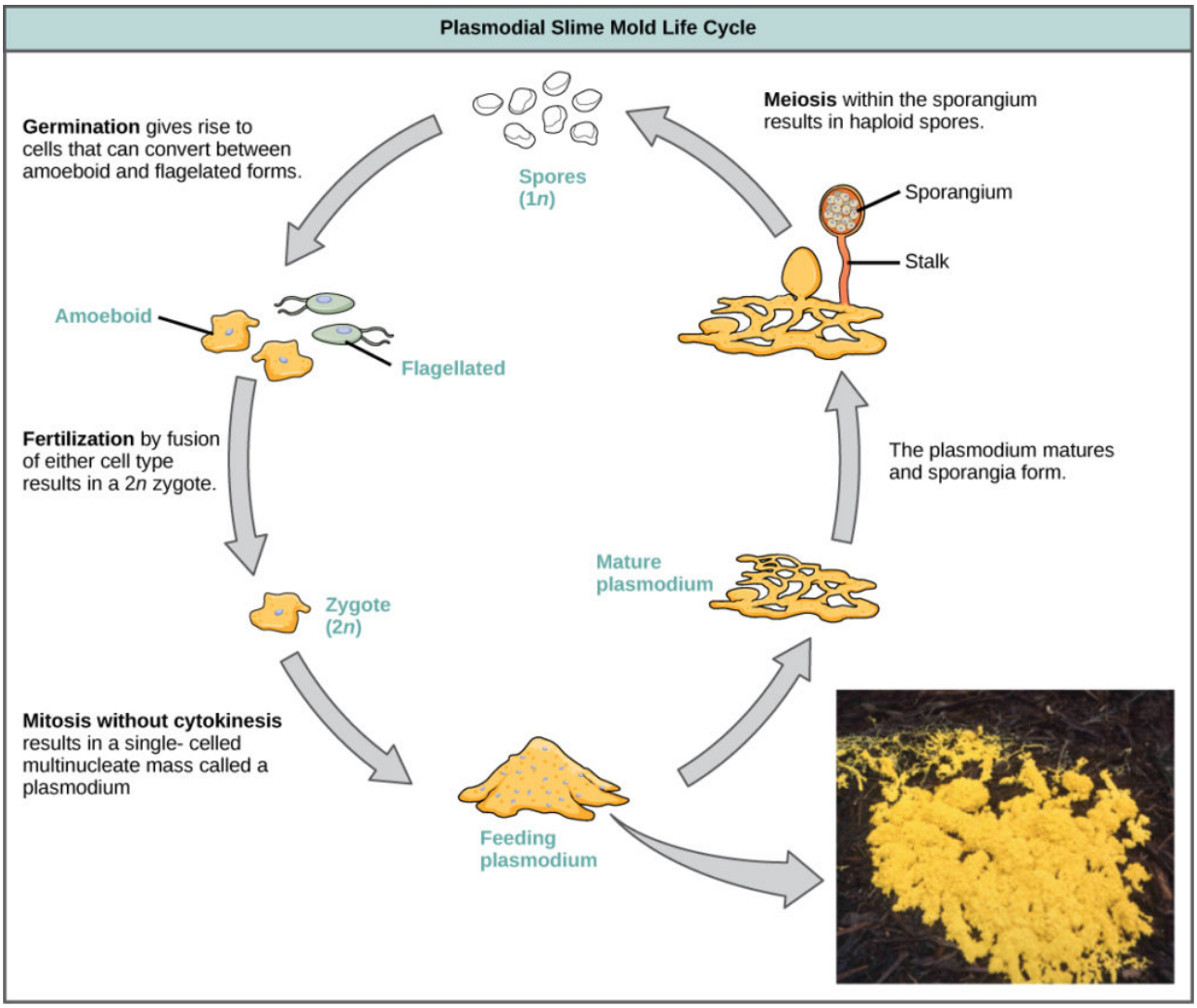


Figure 2. The life cycle of the plasmodial slime mold is shown. The brightly colored plasmodium in the inset photo is a single-celled, multinucleate mass. (credit: modification of work by Dr. Jonatha Gott and the Center for RNA Molecular Biology, Case Western Reserve University)

The cellular slime molds function as independent amoeboid cells when nutrients are abundant (Figure 3). When food is depleted, cellular slime molds pile onto each other into a mass of cells that behaves as a single unit, called a slug. Some cells in the slug contribute to a 2–3-millimeter stalk, drying up and dying in the process. Cells atop the stalk form an asexual fruiting body that contains haploid spores. As with plasmodial slime molds, the spores are disseminated and can germinate if they land in a moist environment. One representative genus of the cellular slime molds is *Dictyostelium*, which commonly exists in the damp soil of forests.

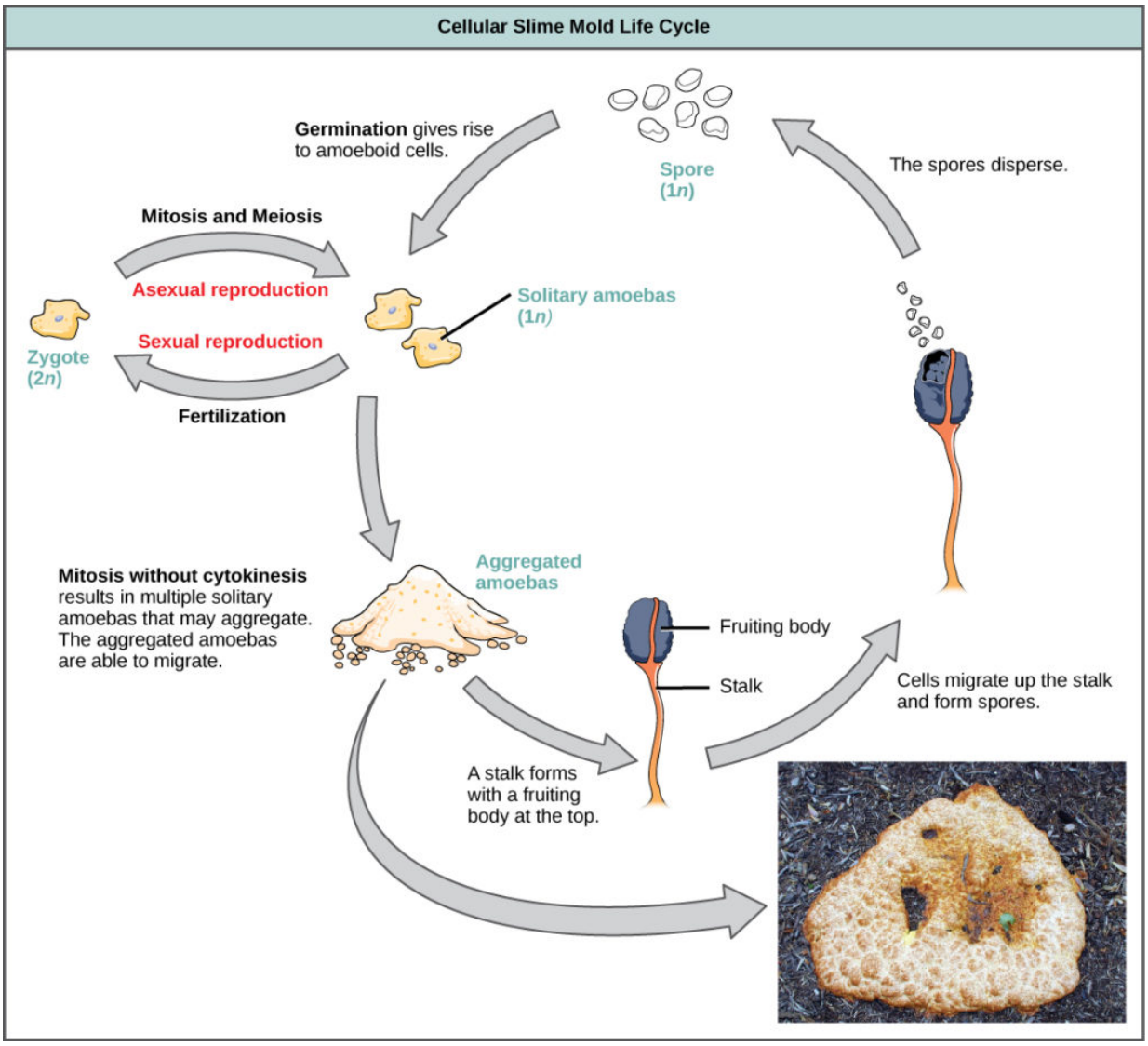
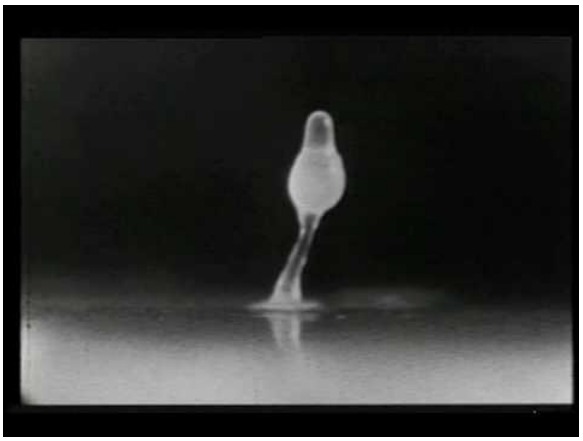


Figure 3. Cellular slime molds may exist as solitary or aggregated amoebas. (credit: modification of work by "thatredhead4"/Flickr)

Watch this video to see the formation of a fruiting body by a cellular slime mold. Note that there isn't any narration in the video.



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8.12: Opisthokonta



Figure 1. Sphaeroeca, a colony of choanoflagellates (aproximately 230 individuals)

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. The **Mesomycetozoa** form a small group of parasites, primarily of fish, and at least one form that can parasitize humans. Their life cycles are poorly understood.

These organisms are of special interest, because they appear to be so closely related to animals. In the past, they were grouped with fungi and other protists based on their morphology. Some phylogenetic trees still group animals and fungi into the Opisthokonta supergroup though this is also considered a protist specific group in other phylogenies.

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8.13: Introduction to the Ecology of Protists

Describe the role that protists play in the ecosystem

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.

What You'll Learn to Do

- Identify protists that act as primary producers
- Provide examples of the protists' important roles in decomposition
- Describe important pathogenic species of protists

Learning Activities

The learning activities for this section include the following:

- Primary Producers
- Protists as Decomposers
- Pathogenic Protists
- Self Check: Ecology of Protists

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8.14: Primary Producers



Figure 1. Coral polyps obtain nutrition through a symbiotic relationship with dinoflagellates.

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. For instance, photosynthetic dinoflagellates called zooxanthellae use sunlight to fix inorganic carbon. In this symbiotic relationship, these protists provide nutrients for coral polyps (Figure 1) that house them, giving corals a boost of energy to secrete a calcium carbonate skeleton. In turn, the corals provide the protist with a protected environment and the compounds needed for photosynthesis. This type of symbiotic relationship is important in nutrient-poor environments. Without dinoflagellate symbionts, corals lose algal pigments in a process called coral bleaching, and they eventually die. This explains why reef-building corals do not reside in waters deeper than 20 meters: insufficient light reaches those depths for dinoflagellates to photosynthesize.

The protists themselves and their products of photosynthesis are essential—directly or indirectly—to the survival of organisms ranging from bacteria to mammals (Figure 2). 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.



Figure 2. Virtually all aquatic organisms depend directly or indirectly on protists for food.

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.

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8.15: Protists as Decomposers

Various organisms with a protist-level organization were originally treated as fungi, because they produce sporangia, structures producing and containing spores. These include chytrids, slime molds, water molds, and Labyrinthulomycetes. Many of these organisms were also treated as fungi due to a similar environmental role: that of a decomposer.

These fungus-like protist saprobes are specialized to absorb nutrients from nonliving organic matter, such as dead organisms or their wastes. For instance, many types of oomycetes grow on dead animals or algae. Saprobic protists have the essential function of returning inorganic nutrients to the soil and water. This process allows for new plant growth, which in turn generates sustenance for other organisms along the food chain. Indeed, without saprobe species, such as protists, fungi, and bacteria, life would cease to exist as all organic carbon became “tied up” in dead organisms.

Chytrids can be single or multi-cellular. There are about one thousand species, most living in water or soil. Most are decomposers. Some are parasites and can cause diseases in plants, including corn, alfalfa, and potatoes. One species, *Batrachochytrium dendrobatidis*, seems to be the cause of chytridiomycosis, a disease of frogs that is seriously affecting many wild frog populations around the world.



Figure 1. Slime mold on lawn, U.S.A

Slime molds are notable for their unusual life cycle. In some species, individual single-celled organisms come together and fuse to form a giant cell with thousands of nuclei. This body, called a plasmodium, can move around consuming bacteria, fungi, and decaying plant matter. (This is a different usage of the word plasmoidium from that used previously for the genus of parasitic protozoa.) Slime molds are found worldwide.

Water molds thrive in water and wet soil. They are considered to be more closely related to plants than fungi since they have cellulose cell walls. They are single-celled. Many are parasites and can cause diseases in plants, fungi, and animals. One species *Phytophthora infestans* causes the potato blight, which led to the Irish potato famine.

Labyrinthulomycetes form a network of tubes or filaments over which the single-celled organisms slide to gather food. They are mostly marine and are decomposers of dead plant material or parasites on plants and algae or some animals.

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8.16: Pathogenic Protists

Human Pathogens

A pathogen is anything that causes disease. Parasites live in or on an organism and harm the organism. A significant number of protists are pathogenic parasites that must infect other organisms to survive and propagate. Protist parasites include the causative agents of malaria, African sleeping sickness, and waterborne gastroenteritis in humans. Other protist pathogens prey on plants, effecting massive destruction of food crops.

Plasmodium Species

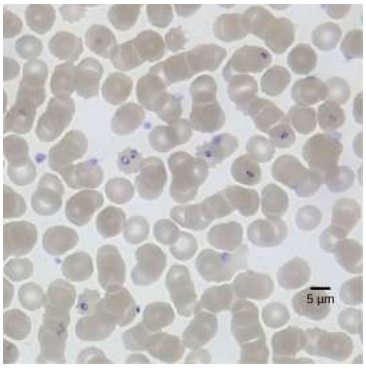


Figure 1. Red blood cells are shown to be infected with *P. falciparum.* In this light microscopic image, the ring-shaped *P. falciparum* stains purple. (credit: modification of work by Michael Zahniser; scale-bar data from Matt Russell)

Members of the genus *Plasmodium* must colonize both a mosquito and a vertebrate to complete their life cycle. In vertebrates, the parasite develops in liver cells and goes on to infect red blood cells, bursting from and destroying the blood cells with each asexual replication cycle (Figure 1).

Of the four *Plasmodium* species known to infect humans, *P. falciparum* accounts for 50 percent of all malaria cases and is the primary cause of disease-related fatalities in tropical regions of the world. In 2010, it was estimated that malaria caused between one-half and one million deaths, mostly in African children.

During the course of malaria, *P. falciparum* can infect and destroy more than one-half of a human's circulating blood cells, leading to severe anemia. In response to waste products released as the parasites burst from infected blood cells, the host immune system mounts a massive inflammatory response with episodes of delirium-inducing fever as parasites lyse red blood cells, spilling parasite waste into the bloodstream. *P. falciparum* is transmitted to humans by the African malaria mosquito, *Anopheles gambiae*. Techniques to kill, sterilize, or avoid exposure to this highly aggressive mosquito species are crucial to malaria control.

This movie depicts the pathogenesis of *Plasmodium falciparum*, the causative agent of malaria:

A link to an interactive elements can be found at the bottom of this page.

Trypanosomes

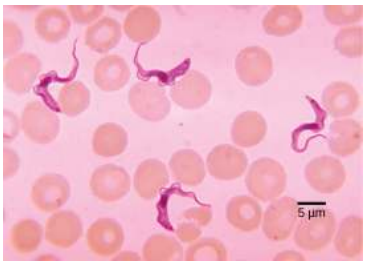


Figure 2. Trypanosomes are shown among red blood cells. (credit: modification of work by Dr. Myron G. Shultz; scale-bar data from Matt Russell)

Trypanosoma brucei, the parasite that is responsible for African sleeping sickness, confounds the human immune system by changing its thick layer of surface glycoproteins with each infectious cycle (Figure 2). 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. Without treatment, *T. brucei* attacks red blood cells, causing the patient to lapse into a coma and eventually die. 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.

This movie discusses the pathogenesis of *Trypanosoma brucei*, the causative agent of African sleeping sickness:

A link to an interactive elements can be found at the bottom of this page.

In Latin America, another species, *T. cruzi*, is responsible for Chagas disease. *T. cruzi* infections are mainly caused by a blood-sucking bug. The parasite inhabits heart and digestive system tissues in the chronic phase of infection, leading to malnutrition and heart failure due to abnormal heart rhythms. An estimated 10 million people are infected with Chagas disease, and it caused 10,000 deaths in 2008.

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 3). 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.

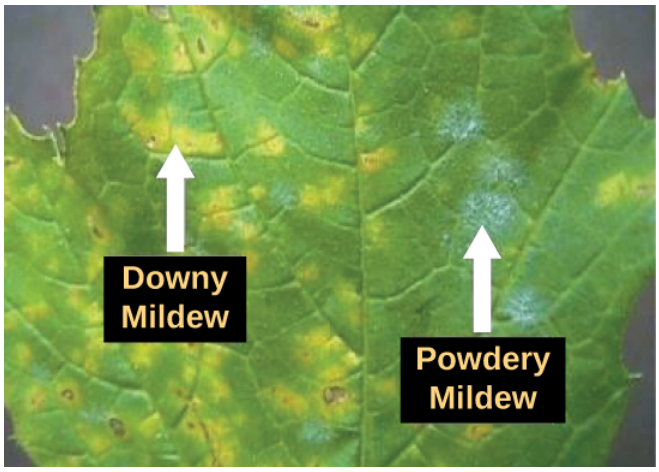


Figure 3. Both downy and powdery mildews on this grape leaf are caused by an infection of *P. viticola*. (credit: modification of work by USDA)



Figure 4. These unappetizing remnants result from an infection with *P. infestans*, the causative agent of potato late blight. (credit: USDA)

Phytophthora infestans is an oomycete responsible for potato late blight, which causes potato stalks and stems to decay into black slime (Figure 4). 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.

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8.17: Putting It Together- Protists

As we've just seen, perhaps the easiest way to determine if a eukaryotic organism is a protist is to first determine if it's an animal, a plant, a or fungus. If the organism isn't any of those, then it's a protist. Unlike the other kingdoms, which are grouped together based on shared characteristics, protists are grouped together out of convenience.

At the beginning of this chapter, we talked about the potential to use micro-algae, a type of protist, as a sustainable energy source. However, as we've learned, not all protists are benign.

Researchers at the Agricultural Research Service (ARS) have assembled and maintained collections that allow them to explore the diversity, evolution, and distribution of parasites and pathogens. This collection was established in 1892 and is among the largest parasite collections in the world. It holds more than 20 million catalogued specimens representing nematodes, tapeworms, flukes, protists, and some parasitic arthropods, such as fleas, ticks, and lice. Such archives provide a foundation to identify shifting geographic and host ranges for parasites and diseases that may emerge with accelerated global climate change.



Figure 1. Paratype specimen of *S. invicta* collected from Brazil.

At the Center for Medical, Agricultural and Veterinary Entomology (CMAVE), in Gainesville, Fla., researchers are using a collection of microsporidia to act as soldiers of biological warfare at the tiniest level against red imported fire ants. CMAVE entomologist David Oi is using species of spore-producing insect pathogens, such as *Kneallhazia solenopsae*, to bring about declines in red imported fire ant (*Solenopsis invicta*) populations. In Argentina, these infectious soldiers are associated with localized declines of 53 percent to 100 percent in fire ant populations, according to Oi.

In addition, Oi and CMAVE colleagues Sanford Porter and Steven Valles were able to get *K. solenopsae* to infect phorid flies without harming them. This is important because phorid flies may serve as vectors to infect red imported fire ants with the microsporidia—perhaps facilitating the spread of infection to other colonies.

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8.18: Cerego- Protists

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for Protists. You'll need to create a free log-in to practice these items, if you haven't already.

https://cerego.com/sets/796510/learn

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CHAPTER OVERVIEW

9: Module 6- Fungi

9.1: Why It Matters- Fungi
9.2: Introduction to the Characteristics of Fungi
9.3: Fungal Structure and Habitats
9.4: Nutrition and Growth
9.5: Reproduction
9.6: Introduction to the Classifications of Fungi
9.7: Chytridiomycota- The Chytrids
9.8: Zygomycota- The Conjugated Fungi
9.9: Ascomycota- The Sac Fungi
9.10: Basidiomycota- The Club Fungi
9.11: Glomeromycota
9.12: Deuteromycota- The Imperfect Fungi
9.13: Introduction to the Ecology of Fungi
9.14: Decomposers and Recyclers
9.15: Mutualistic Relationships
9.16: Introduction to Fungal Parasites and Pathogens
9.17: Infections in Plants
9.18: Infections in Humans
9.19: Antifungal Therapy
9.20: Putting It Together- Fungi
9.21: Cerego- Fungi

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9.1: Why It Matters- Fungi

Why discuss the organisms in Kingdom Fungi?



Figure 1. These wood-decay fungi play an important role in a forest's ecosystem. Without the removal of old trees, there would be no room for new growth.

Perhaps the most recognizable fungi are mushrooms and yeasts, which can be found in everyday cuisine. However, fungi play other roles in the daily lives of human beings: they act as medicines, serve as pesticides, and play an important role as decomposers in the ecosystem. Decomposers are organisms that break down dead or decaying organisms, and in doing so, they carry out the natural process of decomposition. Like herbivores and predators, decomposers are heterotrophic: they use organic substrates to get their energy, carbon and nutrients for growth and development. Without decomposers, dead organisms would not decay and make room for new life. In this module, we'll learn more about just how fungi decompose and recycle nutrients.

In addition to their roles as food and decomposers, fungi can serve in a variety of other functions. Yeast is often used to aid in the fermentation of wines and beers, and penicillin is an important antibiotic with broad usage.

Learning Outcomes

- Identify the common characteristics of fungi
- Classify fungi into unique categories
- Describe the role that fungi play in the ecosystem
- Identify common fungal parasites and pathogens

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9.2: Introduction to the Characteristics of Fungi

Identify the common characteristics of fungi

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 don't produce mushrooms at all. Being eukaryotes, a typical fungal cell contains a true nucleus and many membrane-bound organelles. The kingdom Fungi includes an enormous 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.

Fungi, once considered plant-like organisms, are more closely related to animals than plants. Fungi are not capable of photosynthesis: they are heterotrophic because they use complex organic compounds as sources of energy and carbon. Some fungal organisms multiply only asexually, whereas others undergo both asexual reproduction and sexual reproduction with alternation of generations. Most fungi produce a large number of spores, which are haploid cells that can undergo mitosis to form multicellular, haploid individuals. Like bacteria, fungi play an essential role in ecosystems because they are decomposers and participate in the cycling of nutrients by breaking down organic materials to simple molecules.

What You'll Learn to Do

- Describe the common structures of fungi
- Identify common habitats of fungi
- Describe the mode of nutrition and growth in fungi
- Explain sexual and asexual reproduction in fungi

Learning Activities

The learning activities for this section include the following:

- Fungal Structure and Habitats
- Nutrition and Growth
- Reproduction
- Self Check: Characteristics of Fungi

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9.3: Fungal Structure and Habitats

Cell Structure and Function

Fungi are eukaryotes, and as such, have a complex cellular organization. As eukaryotes, fungal cells contain a membrane-bound nucleus. The DNA in the nucleus is wrapped around histone proteins, as is observed in other eukaryotic cells. A few types of fungi have structures comparable to bacterial plasmids (loops of DNA); however, the horizontal transfer of genetic information from one mature bacterium to another rarely occurs in fungi. Fungal cells also contain mitochondria and a complex system of internal membranes, including the endoplasmic reticulum and Golgi apparatus.



Figure 1. The poisonous Amanita muscaria is native to temperate and boreal regions of North America. (credit: Christine Majul)

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 1). Pigments in fungi are associated with the cell wall and play a protective role against ultraviolet radiation. Some fungal pigments are toxic.

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 similar to 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.

Habitats

Although fungi are primarily associated with humid and cool environments that provide a supply of organic matter, they colonize a surprising diversity of habitats, from seawater to human skin and mucous membranes. Chytrids are found primarily in aquatic environments. Other fungi, such as *Coccidioides immitis*, which causes pneumonia when its spores are inhaled, thrive in the dry and sandy soil of the southwestern United States. Fungi that parasitize coral reefs live in the ocean. However, most members of the Kingdom Fungi grow on the forest floor, where the dark and damp environment is rich in decaying debris from plants and animals. In these environments, fungi play a major role as decomposers and recyclers, making it possible for members of the other kingdoms to be supplied with nutrients and live.

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9.4: Nutrition and Growth

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. 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** (also known as *saprophytes*): organisms that derive nutrients from decaying organic matter. They obtain their nutrients from dead or decomposing organic matter: mainly plant material. Fungal exoenzymes are able to 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). 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. In environments poor in nitrogen, some fungi resort to predation of nematodes (small non-segmented roundworms). Species of *Arthrobotrys* fungi have a number of mechanisms to trap nematodes. One mechanism involves constricting rings within the network of hyphae. The rings swell when they touch the nematode, gripping it in a tight hold. The fungus penetrates the tissue of the worm by extending specialized hyphae called **haustoria**. Many parasitic fungi possess haustoria, as these structures penetrate the tissues of the host, release digestive enzymes within the host's body, and absorb the digested nutrients.

Growth

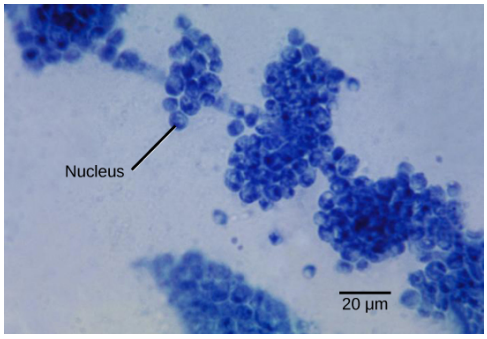


Figure 1. *Candida albicans*. (credit: modification of work by Dr. Godon Roberstad, CDC; scale-bar data from Matt Russell)

The vegetative body of a fungus is a unicellular or multicellular **thallus**. Dimorphic fungi can change from the unicellular to multicellular state depending on environmental conditions. Unicellular fungi are generally referred to as **yeasts**. *Saccharomyces cerevisiae* (baker's yeast) and *Candida* species (the agents of thrush, a common fungal infection) are examples of unicellular fungi (Figure 1). Canadida albicans is a yeast cell and the agent of candidiasis and thrush and has a similar morphology to coccus bacteria; however, yeast is a eukaryotic organism (note the nucleus).

Most fungi are multicellular organisms. They display two distinct morphological stages: the 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. The mass of hyphae is a **mycelium** (Figure 2).

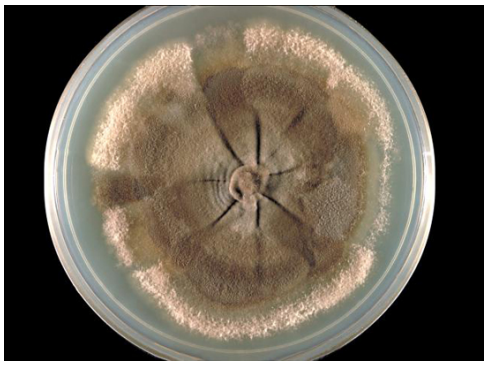


Figure 2. The mycelium of the fungus *Neotestudina rosati* can be pathogenic to humans. The fungus enters through a cut or scrape and develops a mycetoma, a chronic subcutaneous infection. (credit: CDC)

It can grow on a surface, in soil or decaying material, in a liquid, or even on living tissue. Although individual hyphae must be observed under a microscope, the mycelium of a fungus can be very large, with some species truly being "the fungus humongous." 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.

Most fungal hyphae are divided into separate cells by endwalls called **septa** (singular, **septum**) (Figure 3a, c). 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 3b).

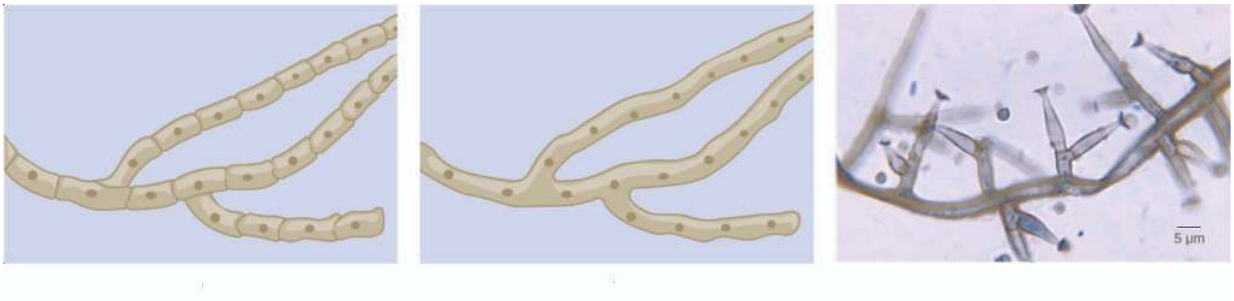


Figure 3. Fungal hyphae may be (a) septated or (b) coenocytic (coeno- = "common"; -cytic = "cell") with many nuclei present in a single hypha. A bright field light micrograph of (c) *Phialophora richardsiae* shows septa that divide the hyphae. (credit c: modification of work by Dr. Lucille Georg, CDC; 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 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.

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9.5: Reproduction

Fungi reproduce sexually and/or asexually. Perfect fungi reproduce both sexually and asexually, while 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 or hitching a ride on 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 1).



Figure 1. The (a) giant puff ball mushroom releases (b) 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

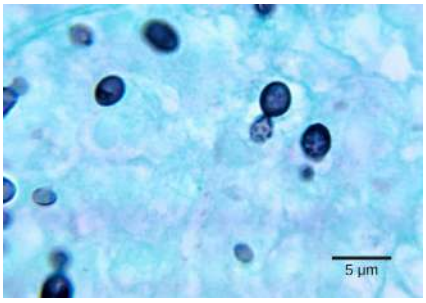


Figure 2. The dark cells in this bright field light micrograph are the pathogenic yeast *Histoplasma capsulatum*, seen against a backdrop of light blue tissue. (credit: modification of work by Dr. Libero Ajello, CDC; scale-bar data from Matt Russell)

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. Histoplasma (Figure 2) primarily infects lungs but can spread to other tissues, causing histoplasmosis, a potentially fatal disease.

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 3). 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.

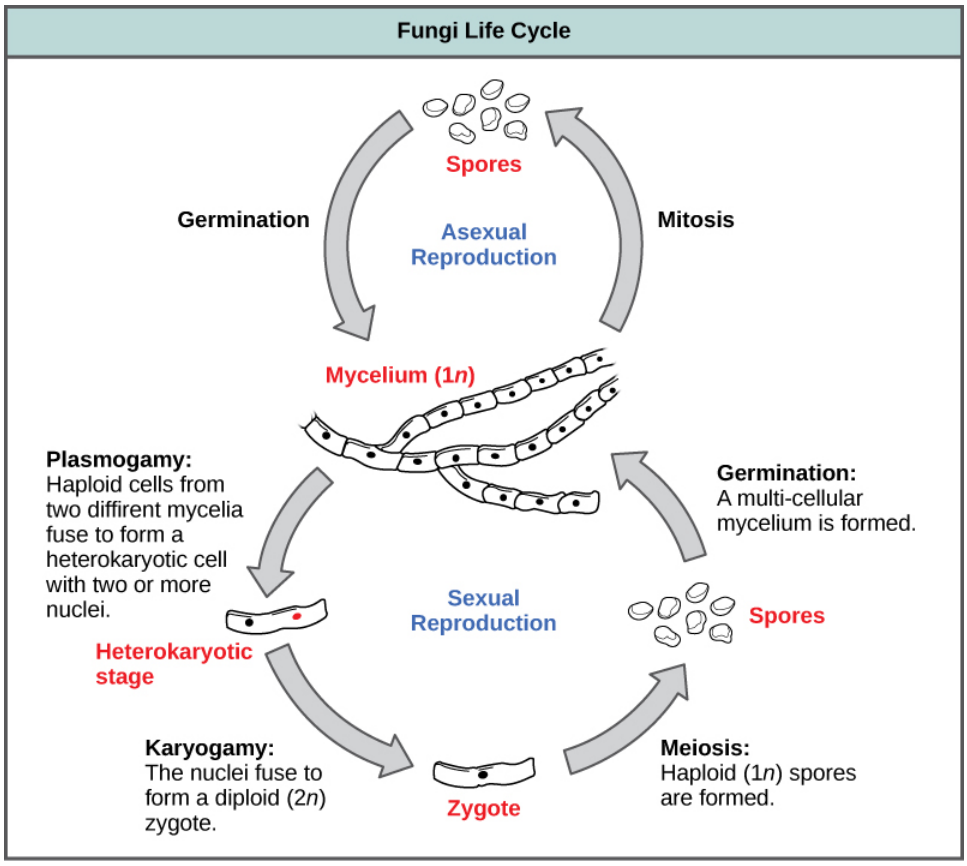


Figure 3. Fungi may have both asexual and sexual stages of reproduction.

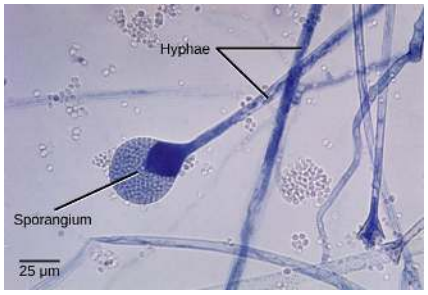


Figure 4. This bright field light micrograph shows the release of spores from a sporangium at the end of a hypha called a sporangiophore. The organism is a *Mucor sp.* fungus, a mold often found indoors. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

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 4).

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 3). 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.

Fungivores

Animal dispersal is important for some fungi because an animal may carry spores considerable distances from the source. Fungal spores are rarely completely degraded in the gastrointestinal tract of an animal, and many are able to germinate when they are passed in the feces. Some dung fungi actually require passage through the digestive system of herbivores to complete their lifecycle. The black truffle—a prized gourmet delicacy—is the fruiting body of an underground mushroom. Almost all truffles are ectomycorrhizal, and are usually found in close association with trees. Animals eat truffles and disperse the spores. In Italy and France, truffle hunters use female pigs to sniff out truffles. Female pigs are attracted to truffles because the fungus releases a volatile compound closely related to a pheromone produced by male pigs.

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9.6: Introduction to the Classifications of Fungi

Classify fungi into unique categories

The kingdom Fungi contains five major phyla that were established according to their mode of sexual reproduction or using molecular data. Polyphyletic, unrelated fungi that reproduce without a sexual cycle are placed for convenience in a sixth group called a “form phylum.” Not all mycologists agree with this scheme. Rapid advances in molecular biology and the sequencing of 18S rRNA (a part of RNA) continue to show new and different relationships between the various categories of fungi.

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. The Deuteromycota is an informal group of unrelated fungi that all share a common character – they use strictly asexual reproduction.

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.

What You’ll Learn to Do

- Identify characteristics and examples of fungi in the phylum Chytridiomycota
- Identify characteristics and examples of fungi in the phylum Zygomycota
- Identify characteristics and examples of fungi in the phylum Ascomycota
- Identify characteristics and examples of fungi in the phylum Basidiomycota
- Identify characteristics and examples of fungi in the phylum Glomeromycota
- Identify characteristics and examples of fungi in the informal group Deuteromycota

Learning Activities

The learning activities for this section include the following:

- Chytridiomycota: The Chytrids
- Zygomycota: The Conjugated Fungi
- Ascomycota: The Sac Fungi
- Basidiomycota: The Club Fungi
- Glomeromycota
- Deuteromycota: The Imperfect Fungi
- Self Check: Classifications of Fungi

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9.7: Chytridiomycota- The Chytrids

The only class in the Phylum Chytridiomycota is the **Chytridiomycetes**. The chytrids are the simplest and most primitive Eumycota, or true fungi. 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 produce gametes and diploid zoospores that swim with the help of a single flagellum.

The ecological habitat and cell structure of chytrids have much in common with protists. Chytrids usually live in aquatic environments, although some species live on land. Some species thrive as parasites on plants, insects, or amphibians (Figure 1), while others are saprobes. The chytrid species *Allomyces* is well characterized as an experimental organism. Its reproductive cycle includes both asexual and sexual phases. *Allomyces* produces diploid or haploid flagellated zoospores in a sporangium.

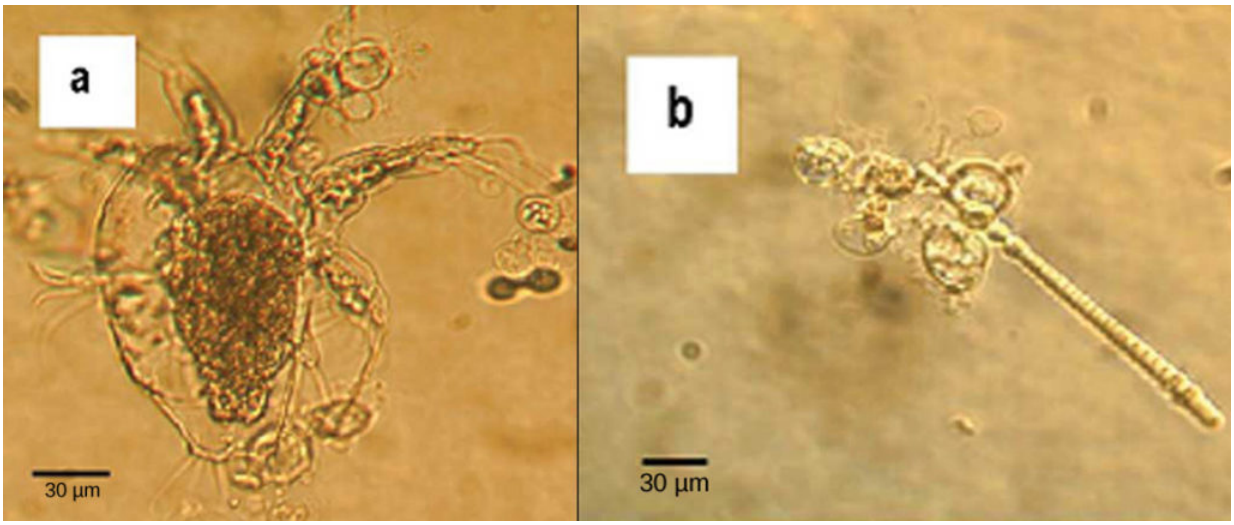


Figure 1. The chytrid *Batrachochytrium dendrobatidis* is seen in these light micrographs as transparent spheres growing on (a) a freshwater arthropod and (b) algae. This chytrid causes skin diseases in many species of amphibians, resulting in species decline and extinction. (credit: modification of work by Johnson ML, Speare R., CDC)

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9.8: Zygomycota- The Conjugated Fungi

The zygomycetes are a relatively small group of fungi belonging to the Phylum **Zygomycota**. 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.

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 1).

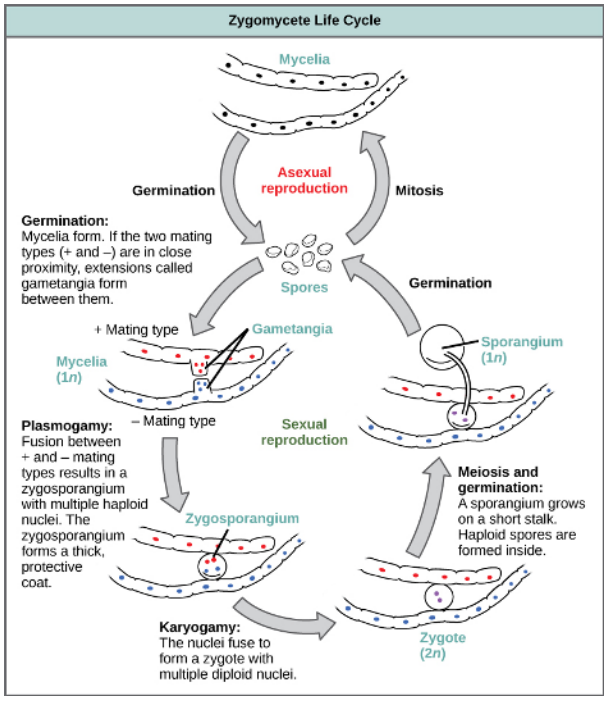
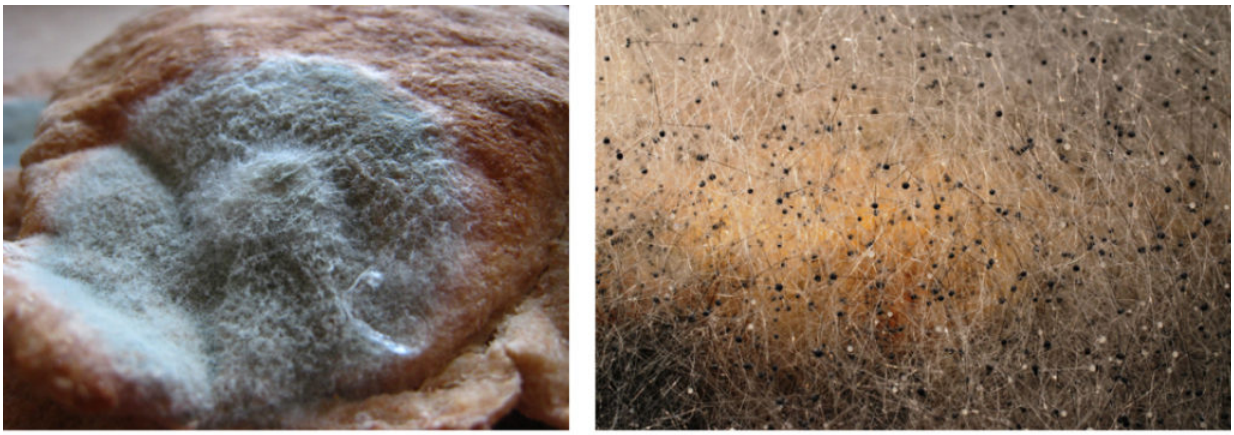


Figure 1. Zygomycetes have asexual and asexual life cycles. In the sexual life cycle, plus and minus mating types conjugate to form a zygosporangium.

The black tips of bread mold are the swollen sporangia packed with black spores (Figure 2). When spores land on a suitable substrate, they germinate and produce a new mycelium. Sexual reproduction starts when conditions become unfavorable. Two opposing mating strains (type + and type –) must be in close proximity for gametangia from the hyphae to be produced and fuse, leading to karyogamy. The developing diploid **zygospores** have thick coats that protect them from desiccation and other hazards. They may remain dormant until environmental conditions are favorable. When the zygospore germinates, it undergoes meiosis and produces haploid spores, which will, in turn, grow into a new organism. This form of sexual reproduction in fungi is called conjugation (although it differs markedly from conjugation in bacteria and protists), giving rise to the name “conjugated fungi.”



(a) (b)

Figure 2. 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)

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9.9: 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.

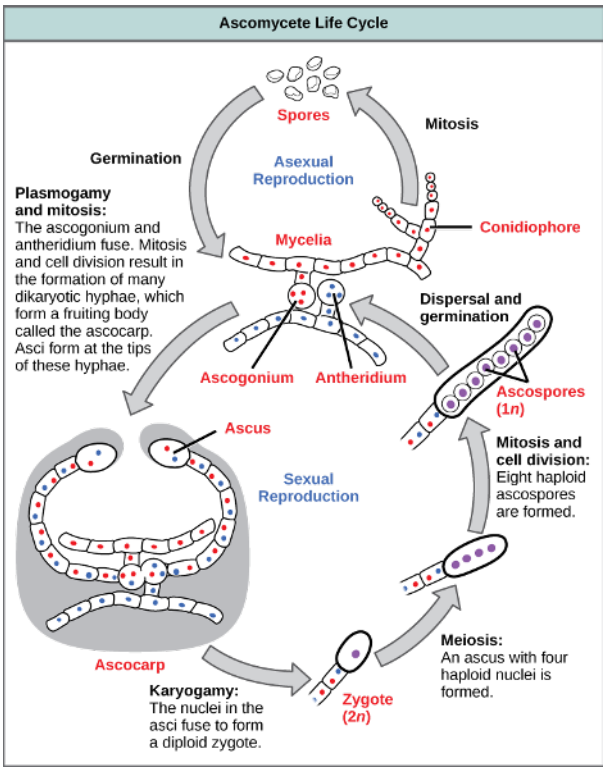


Figure 1. Click for a larger image. The lifecycle of an ascomycete is characterized by the production of asci during the sexual phase. The haploid phase is the predominant phase of the life cycle.

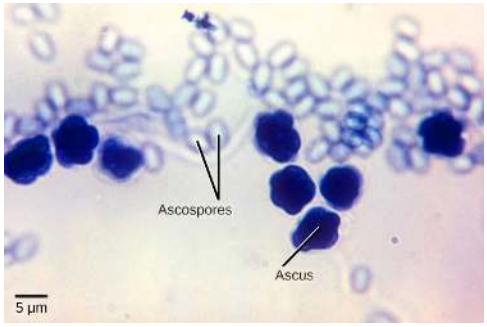


Figure 2. The bright field light micrograph shows ascospores being released from asci in the fungus *Talaromyces flavus* var. *flavus*. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Asexual reproduction is frequent and involves the production of conidiophores that release haploid conidiospores. Sexual reproduction starts with the development of special hyphae from either one of two types of mating strains (Figure 1).

The “male” strain produces an antheridium and the “female” strain develops an ascogonium. At fertilization, the antheridium and the ascogonium combine in plasmogamy without nuclear fusion. Special ascogenous hyphae arise, in which pairs of nuclei migrate: one from the “male” strain and one from the “female” strain. In each ascus, two or more haploid ascospores fuse their nuclei in karyogamy.

During sexual reproduction, thousands of asci fill a fruiting body called the **ascocarp**. The diploid nucleus gives rise to haploid nuclei by meiosis. The ascospores are then released, germinate, and form hyphae that are disseminated in the environment and start new mycelia (Figure 2).

Practice Question

Which of the following statements is true?

a. A dikaryotic ascus that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
b. A diploid ascus that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
c. A haploid zygote that forms in the ascocarp undergoes karyogamy, meiosis, and mitosis to form eight ascospores.
d. A dikaryotic ascus that forms in the ascocarp undergoes plasmogamy, meiosis, and mitosis to form eight ascospores.

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9.10: Basidiomycota- The Club Fungi



Figure 1. The fruiting bodies of a basidiomycete form a ring in a meadow, commonly called “fairy ring.” (Credit: “Cropcircles”/Wikipedia Commons)]

The fungi in the Phylum **Basidiomycota** are easily recognizable under a light microscope by their club-shaped fruiting bodies called **basidia** (singular, **basidium**), which are the swollen terminal cell of a hypha. The basidia, which are the reproductive organs of these fungi, are often contained within the familiar mushroom, commonly seen in fields after rain, on the supermarket shelves, and growing on your lawn. The fruiting bodies of a basidiomycete form a ring in a meadow, commonly called “fairy ring” (Figure 1). The best-known fairy ring fungus has the scientific name *Marasmius oreades*. The body of this fungus, its mycelium, is underground and grows outward in a circle. As it grows, the mycelium depletes the soil of nitrogen, causing the mycelia to grow away from the center and leading to the “fairy ring” of fruiting bodies where there is adequate soil nitrogen.

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. 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, and toadstools. 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 2). 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.

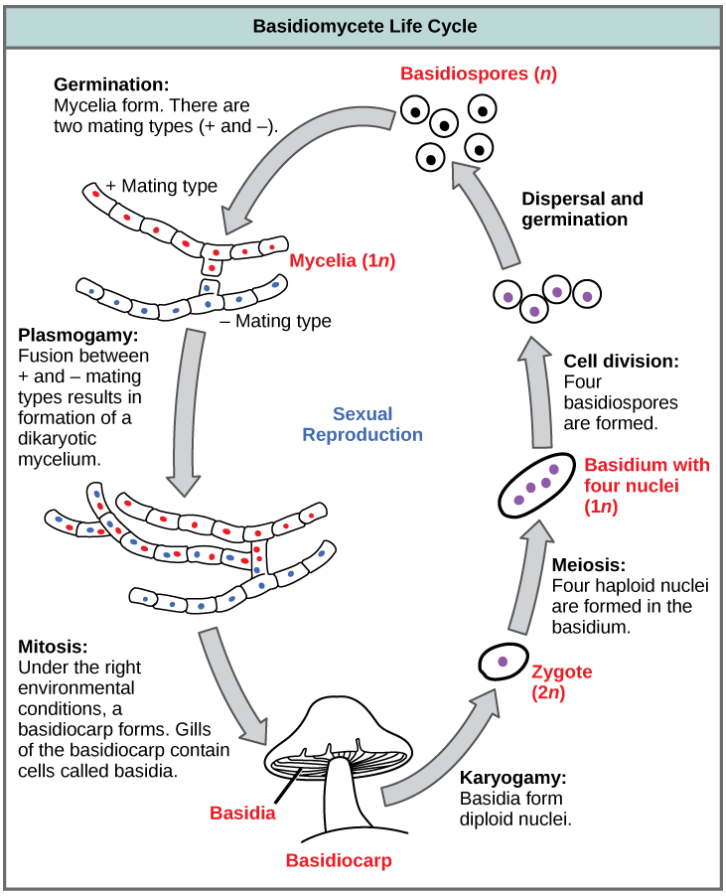


Figure 2. The lifecycle of a basidiomycete alternates generation with a prolonged stage in which two nuclei (dikaryon) are present in the hyphae.

Practice Question

Which of the following statements is true?

a. A basidium is the fruiting body of a mushroom-producing fungus, and it forms four basidiocarps.
b. The result of the plasmogamy step is four basidiospores.
c. Karyogamy results directly in the formation of mycelia.
d. A basidiocarp is the fruiting body of a mushroom-producing fungus.

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9.11: Glomeromycota

The **Glomeromycota** is a newly established phylum which comprises about 230 species that all live in close association with the roots of trees. 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.

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9.12: Deuteromycota- The Imperfect Fungi

Imperfect fungi—those that do not display a sexual phase—are classified in the form phylum **Deuteromycota**. Deuteromycota is a polyphyletic group where many species are more closely related to organisms in other phyla than to each other; hence it cannot be called a true phylum and must, instead, be given the name form phylum. Since they do not possess the sexual structures that are used to classify other fungi, they are less well described in comparison to other divisions. Most members live on land, with a few aquatic exceptions. They form visible mycelia with a fuzzy appearance and are commonly known as **mold**. Molecular analysis shows that the closest group to the deuteromycetes is the ascomycetes. In fact, some species, such as some *Aspergillus*, which were once classified as imperfect fungi, are now classified as ascomycetes.

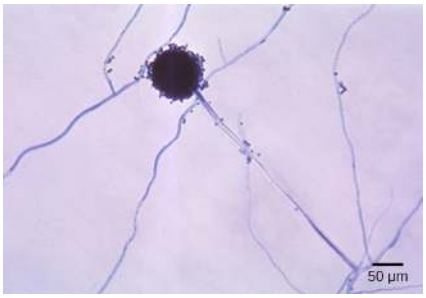


Figure 1. *Aspergillus niger* is an imperfect fungus commonly found as a food contaminant. The spherical structure in this light micrograph is a conidiophore. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Reproduction of Deuteromycota is strictly asexual and occurs mostly by production of asexual conidiospores (Figure 1). Some hyphae may recombine and form heterokaryotic hyphae.

Genetic recombination is known to take place between the different nuclei. Imperfect fungi have a large impact on everyday human life. The food industry relies on them for ripening some cheeses. The blue veins in Roquefort cheese and the white crust on Camembert are the result of fungal growth. The antibiotic penicillin was originally discovered on an overgrown Petri plate, on which a colony of *Penicillium* fungi killed the bacterial growth surrounding it. Many imperfect fungi cause serious diseases, either directly as parasites (which infect both plants and humans), or as producers of potent toxic compounds, as seen in the aflatoxins released by fungi of the genus *Aspergillus*.

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9.13: Introduction to the Ecology of Fungi

Describe the role that fungi play in the ecosystem

Fungi play a crucial role in the balance of ecosystems. They colonize most habitats on Earth, preferring dark, moist conditions. They can thrive in seemingly hostile environments, such as the tundra, thanks to a most successful symbiosis with photosynthetic organisms like algae to produce lichens. Fungi are not obvious in the way large animals or tall trees appear. Yet, like bacteria, they are the major decomposers of nature. With their versatile metabolism, fungi break down organic matter, which would not otherwise be recycled.

Fungi are important to everyday human life. Fungi are important decomposers in most ecosystems. Mycorrhizal fungi are essential for the growth of most plants. Fungi, as food, play a role in human nutrition in the form of mushrooms, and also as agents of fermentation in the production of bread, cheeses, alcoholic beverages, and numerous other food preparations. Secondary metabolites of fungi are used as medicines, such as antibiotics and anticoagulants. Fungi are model organisms for the study of eukaryotic genetics and metabolism.

What You'll Learn to Do

- Describe the importance of fungi to the balance of the environment
- Identify some mutualistic relationships of fungi with other organisms

Learning Activities

The learning activities for this section include the following:

- Decomposers and Recyclers
- Mutualistic Relationships
- Self Check: Ecology of Fungi

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9.14: Decomposers and Recyclers



Figure 1. 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 food web would be incomplete without organisms that decompose organic matter (Figure 1). 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.

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 2).



Figure 2. 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)



Figure 3. The emerald ash borer is an insect that attacks ash trees. It is in turn parasitized by a pathogenic fungus that holds promise as a biological insecticide. The parasitic fungus appears as white fuzz on the body of the insect. (credit: Houping Liu, USDA Agricultural Research Service)

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. It has been released in Michigan, Illinois, Indiana, Ohio, West Virginia and Maryland (Figure 3).

The mycorrhizal relationship between fungi and plant roots is essential for the productivity of farm land. Without the fungal partner in root systems, 80–90 percent of trees and grasses would not survive. Mycorrhizal fungal inoculants are available as soil amendments from gardening supply stores and are promoted by supporters of organic agriculture.



Figure 4. The morel mushroom is an ascomycete much appreciated for its delicate taste. (credit: Jason Hollinger)

We also eat some types of fungi. Mushrooms figure prominently in the human diet. Morels, shiitake mushrooms, chanterelles, and truffles are considered delicacies (Figure 4). The humble meadow mushroom, *Agaricus campestris*, appears in many dishes. Molds of the genus *Penicillium* ripen many cheeses. They originate in the natural environment such as the caves of Roquefort, France, where wheels of sheep milk cheese are stacked in order to capture the molds responsible for the blue veins and pungent taste of the cheese.

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.

As simple eukaryotic organisms, fungi are important model research organisms. Many advances in modern genetics were achieved by the use of the red bread mold *Neurospora crassa*. Additionally, many important genes originally discovered in *S. cerevisiae* served as a starting point in discovering analogous human genes. As a eukaryotic organism, the yeast cell produces and modifies proteins in a manner similar to human cells, as opposed to the bacterium *Escherichia coli*, which lacks the internal membrane structures and enzymes to tag proteins for export. This makes yeast a much better organism for use in recombinant DNA technology experiments. Like bacteria, yeasts grow easily in culture, have a short generation time, and are amenable to genetic modification.

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9.15: 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.

Fungus-Plant Mutualism

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.

There are a number of types of mycorrhizae. **Ectomycorrhizae** ("outside" mycorrhiza) depend on fungi enveloping the roots in a sheath (called a mantle) and a Hartig net of hyphae that extends into the roots between cells (Figure 1).

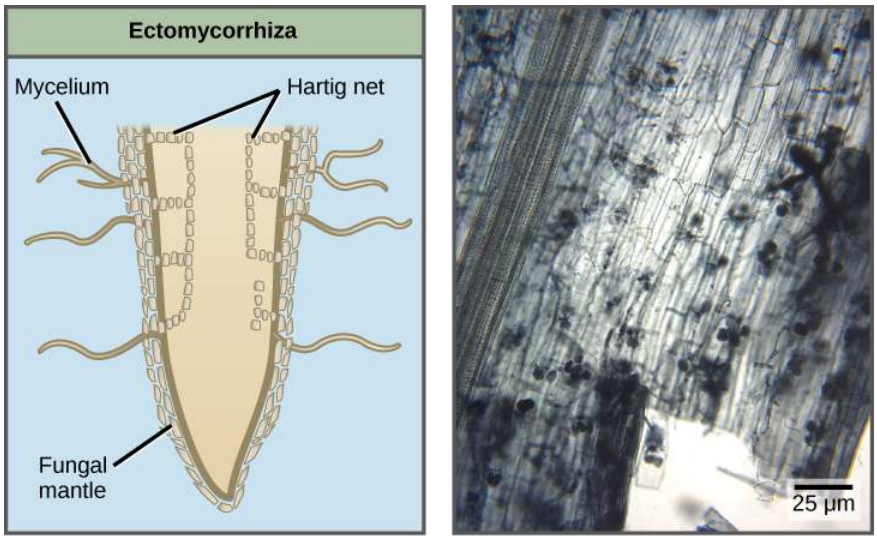
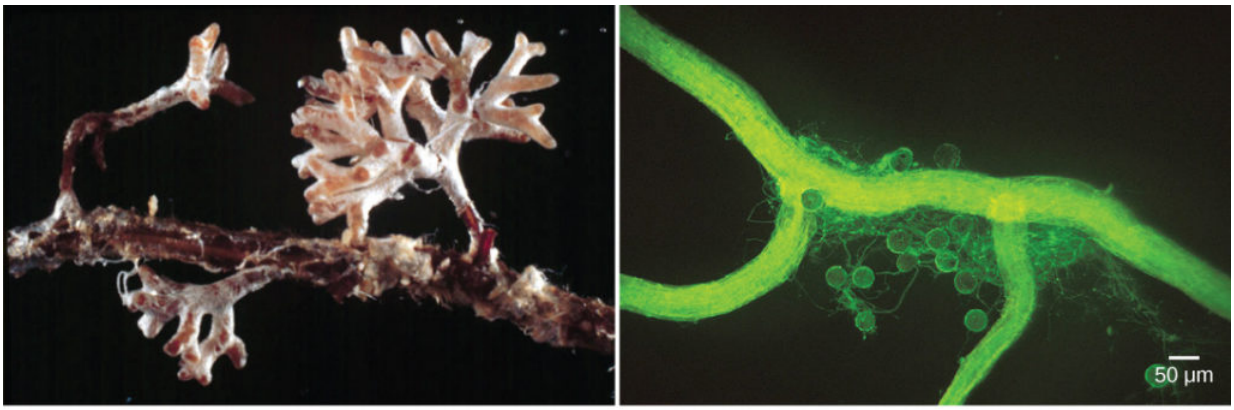


Figure 1. (a) Ectomycorrhiza and (b) arbuscular mycorrhiza have different mechanisms for interacting with the roots of plants. (credit b: MS Turmel, University of Manitoba, Plant Science Department)

The fungal partner can belong to the Ascomycota, Basidiomycota or Zygomycota. In a second type, the Glomeromycete fungi form vesicular–arbuscular interactions with **arbuscular mycorrhiza** (sometimes called endomycorrhizae). In these mycorrhiza, the fungi form arbuscules that penetrate root cells and are the site of the metabolic exchanges between the fungus and the host plant (Figure 1 and Figure 2). The arbuscules (from the Latin for little trees) have a shrub-like appearance. Orchids rely on a third type of mycorrhiza. Orchids are epiphytes that form small seeds without much storage to sustain germination and growth. Their seeds will not germinate without a mycorrhizal partner (usually a Basidiomycete). After nutrients in the seed are depleted, fungal symbionts support the growth of the orchid by providing necessary carbohydrates and minerals. Some orchids continue to be mycorrhizal throughout their lifecycle.



(a) (b)

Figure 2. The (a) infection of *Pinus radiata* (Monterey pine) roots by the hyphae of *Amanita muscaria* (fly amanita) causes the pine tree to produce many small, branched rootlets. The Amanita hyphae cover these small roots with a white mantle. (b) Spores (round bodies) and hyphae (thread-like structures) are evident in this light micrograph of an arbuscular mycorrhiza between a fungus and the root of a corn plant. (credit a: modification of work by Randy Molina, USDA; credit b: modification of work by Sara Wright, USDA-ARS; scale-bar data from Matt Russell)

? Practice Question

If symbiotic fungi are absent from the soil, what impact do you think this would have on plant growth?

[practice-area rows="2"][/practice-area]
[reveal-answer q="130749"]Show Answer[/reveal-answer]
[hidden-answer a="130749"]Without mycorrhiza, plants cannot absorb adequate nutrients, which stunts their growth. Addition of fungal spores to sterile soil can alleviate this problem.[/hidden-answer]

Other examples of fungus–plant mutualism include the endophytes: fungi that live inside tissue without damaging the host plant. Endophytes release toxins that repel herbivores, or confer resistance to environmental stress factors, such as infection by microorganisms, drought, or heavy metals in soil.

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 vesicular–arbuscular 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.

Lichens

Lichens display a range of colors and textures (Figure 3) and can survive in the most unusual and hostile habitats. They cover rocks, gravestones, tree bark, and the ground in the tundra where plant roots cannot penetrate. Lichens can survive extended periods of drought, when they become completely desiccated, and then rapidly become active once water is available again.



(a) (b) (c)

Figure 3. 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)

Explore the world of lichens using this site from Oregon State University.

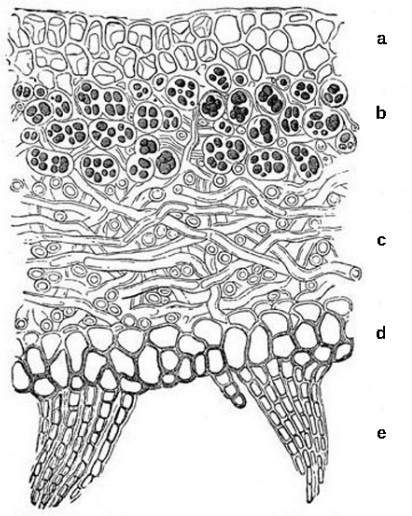


Figure 4. This cross-section of a lichen thallus shows the (a) upper cortex of fungal hyphae, which provides protection; the (b) algal zone where photosynthesis occurs, the (c) medulla of fungal hyphae, and the (d) lower cortex, which also provides protection and may have (e) rhizines to anchor the thallus to the substrate.

Lichens are not a single organism, but rather an example of a 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 4). Generally, neither the fungus nor the photosynthetic organism can survive alone outside of the symbiotic relationship. The body of a lichen, referred to as a thallus, is formed of hyphae wrapped around the photosynthetic partner. The photosynthetic organism provides carbon and energy in the form of carbohydrates. Some cyanobacteria fix nitrogen from the atmosphere, contributing nitrogenous compounds to the association. In return, the fungus supplies minerals and protection from dryness and excessive light by encasing the algae in its mycelium. The fungus also attaches the symbiotic organism to the substrate.

The thallus of lichens grows very slowly, expanding its diameter a few millimeters per year. Both the fungus and the alga participate in the formation of dispersal units for reproduction. Lichens produce **soredia**, clusters of algal cells surrounded by mycelia. Soredia are dispersed by wind and water and form new lichens.

Lichens are extremely sensitive to air pollution, especially to abnormal levels of nitrogen and sulfur. The U.S. Forest Service and National Park Service can monitor air quality by measuring the relative abundance and health of the lichen population in an area. Lichens fulfill many ecological roles. Caribou and reindeer eat lichens, and they provide cover for small invertebrates that hide in the mycelium. In the production of textiles, weavers used lichens to dye wool for many centuries until the advent of synthetic dyes.

Lichens are used to monitor the quality of air. Read more on this site from the United States Forest Service.

Fungus-Animal Mutualism



Figure 5. A leaf cutting ant transports a leaf that will feed a farmed fungus. (credit: Scott Bauer, USDA-ARS)

Fungi have evolved mutualisms with numerous insects in Phylum Arthropoda: jointed, legged invertebrates. Arthropods depend on the fungus for protection from predators and pathogens, while the fungus obtains nutrients and a way to disseminate spores into new environments. The association between species of Basidiomycota and scale insects is one example. The fungal mycelium covers and protects the insect colonies. The scale insects foster a flow of nutrients from the parasitized plant to the fungus. In a second example, leaf-cutting ants of Central and South America literally farm fungi. They cut disks of leaves from plants and pile them up in gardens (Figure 5). Fungi are cultivated in these disk gardens, digesting the cellulose in the leaves that the ants cannot break down. Once smaller sugar molecules are produced and consumed by the fungi, the fungi in turn become a meal for the ants. The insects also patrol their garden, preying on competing fungi. Both ants and fungi benefit from the association. The fungus receives a steady supply of leaves and freedom from competition, while the ants feed on the fungi they cultivate.

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9.16: Introduction to Fungal Parasites and Pathogens

Identify common fungal parasites and pathogens

Parasitism describes a symbiotic relationship in which one member of the association benefits at the expense of the other. Both parasites and pathogens harm the host; however, the pathogen causes a disease, whereas the parasite usually does not. **Commensalism** occurs when one member benefits without affecting the other. Fungi engage in both these types of relationships with other organisms, but as parasites are responsible for economic and environmental damage, as well as some human diseases.

What You'll Learn to Do

- Describe fungal parasites and pathogens of plants
- Describe the different types of fungal infections in humans
- Explain why antifungal therapy is becoming less successful in public health

Learning Activities

The learning activities for this section include the following:

- Infections in Plants
- Infections in Humans
- Antifungal Therapy
- Self Check: Fungal Parasites and Pathogens

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9.17: Infections in Plants

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 1). 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 the 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.

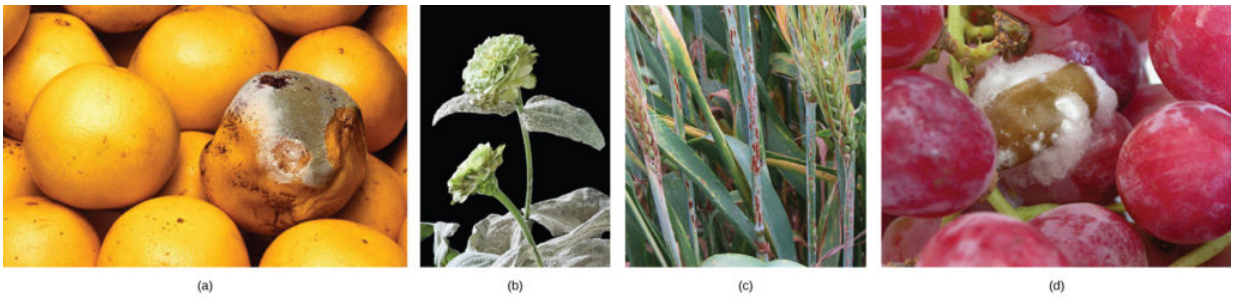


Figure 1. Some fungal pathogens include (a) green mold on grapefruit, (b) powdery mildew on a zinnia, (c) stem rust on a sheaf of barley, and (d) grey rot on grapes. In wet conditions *Botrytis cinerea*, the fungus that causes grey rot, can destroy a grape crop. However, controlled infection of grapes 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)

Aflatoxins are toxic, carcinogenic compounds released by fungi of the genus *Aspergillus*. Periodically, harvests of nuts and grains are tainted by aflatoxins, leading to massive recall of produce. This sometimes ruins producers and causes food shortages in developing countries.

Dutch Elm Disease

Question: Do trees resistant to Dutch elm disease secrete antifungal compounds?

Hypothesis: Construct a hypothesis that addresses this question.

Background: Dutch elm disease is a fungal infestation that affects many species of elm (*Ulmus*) in North America. The fungus infects the vascular system of the tree, which blocks water flow within the plant and mimics drought stress. Accidently introduced to the United States in the early 1930s, it decimated shade trees across the continent. It is caused by the fungus *Ophiostoma ulmi*. The elm bark beetle acts as a vector and transmits the disease from tree to tree. Many European and Asiatic elms are less susceptible to the disease than are American elms.

Test the hypothesis: A researcher testing this hypothesis might do the following. Inoculate several Petri plates containing a medium that supports the growth of fungi with fragments of *Ophiostoma* mycelium. Cut (with a metal punch) several disks from the vascular tissue of susceptible varieties of American elms and resistant European and Asiatic elms. Include control Petri plates inoculated with mycelia without plant tissue to verify that the medium and incubation conditions do not interfere with fungal growth. As a positive control, add paper disks impregnated with a known fungicide to Petri plates inoculated with the mycelium.

Incubate the plates for a set number of days to allow fungal growth and spreading of the mycelium over the surface of the plate. Record the diameter of the zone of clearing, if any, around the tissue samples and the fungicide control disk.

Record your observations in the following table.

Results of Antifungal Testing of Vascular Tissue from Different Species of Elm	
Disk	Zone of Inhibition (mm)
Distilled Water	
Fungicide	
Tissue from Susceptible Elm #1	
Tissue from Susceptible Elm #2	
Tissue from Resistant Elm #1	
Tissue from Resistant Elm #2	

Analyze the data and report the results. Compare the effect of distilled water to the fungicide. These are negative and positive controls that validate the experimental set up. The fungicide should be surrounded by a clear zone where the fungus growth was inhibited. Is there a difference among different species of elm?

Draw a conclusion: Was there antifungal activity as expected from the fungicide? Did the results support the hypothesis? If not, how can this be explained? There are several possible explanations for resistance to a pathogen. Active deterrence of infection is only one of them.

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9.18: Infections in Humans

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 *Pseudogymnoascus destructans*, which disseminates its deadly spores in caves where bats hibernate. Mycologists are researching the transmission, mechanism, and control of *P. destructans* to stop its spread.

Fungi that cause the superficial mycoses of the epidermis, hair, and nails rarely spread to the underlying tissue (Figure 1). These fungi are often misnamed "dermatophytes," from the Greek words *dermis* meaning skin and *phyte* meaning plant, although they are not plants. Dermatophytes are also called "ringworms" because of the red ring they cause on skin. They secrete extracellular enzymes that break down keratin (a protein found in hair, skin, and nails), causing conditions such as athlete's foot and jock itch. These conditions are usually treated with over-the-counter topical creams and powders, and are easily cleared. More persistent superficial mycoses may require prescription oral medications.

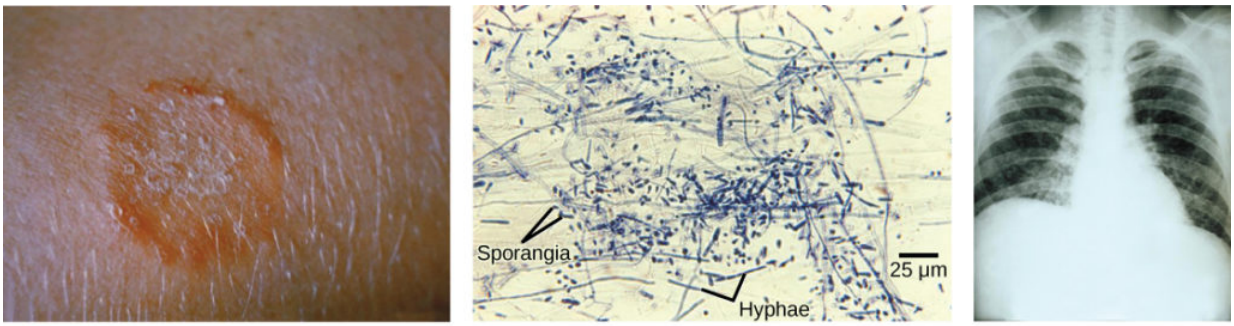


Figure 1. (a) Ringworm presents as a red ring on skin; (b) *Trichophyton violaceum*, shown in this bright field light micrograph, causes superficial mycoses on the scalp; (c) *Histoplasma capsulatum* is an ascomycete that infects airways and causes symptoms similar to influenza. (credit a: modification of work by Dr. Lucille K. Georg, CDC; credit b: modification of work by Dr. Lucille K. Georg, CDC; credit c: modification of work by M. Renz, CDC; scale-bar data from Matt Russell)

Systemic mycoses spread to internal organs, most commonly entering the body through the respiratory system. For example, coccidioidomycosis (valley fever) is commonly found in the southwestern United States, where the fungus resides in the dust. Once inhaled, the spores develop in the lungs and cause symptoms similar to those of tuberculosis. Histoplasmosis is caused by the dimorphic fungus *Histoplasma capsulatum*. It also causes pulmonary infections, and in rarer cases, swelling of the membranes of the brain and spinal cord. Treatment of these and many other fungal diseases requires the use of antifungal medications that have serious side effects.

Opportunistic mycoses are fungal infections that are either common in all environments, or part of the normal biota. They mainly affect individuals who have a compromised immune system. Patients in the late stages of AIDS suffer from opportunistic mycoses that can be life threatening. The yeast *Candida* sp., a common member of the natural biota, can grow unchecked and infect the vagina or mouth (oral thrush) if the pH of the surrounding environment, the person's immune defenses, or the normal population of bacteria are altered.

Mycetismus can occur when poisonous mushrooms are eaten. It causes a number of human fatalities during mushroom-picking season. Many edible fruiting bodies of fungi resemble highly poisonous relatives, and amateur mushroom hunters are cautioned to

carefully inspect their harvest and avoid eating mushrooms of doubtful origin. The adage “there are bold mushroom pickers and old mushroom pickers, but are there no old, bold mushroom pickers” is unfortunately true.

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9.19: Antifungal Therapy

Just like antibiotics cure bacterial infections, antifungal medications save lives by curing dangerous fungal infections. And just like some bacterial infections are resistant to antibiotics, some fungi no longer respond to the antifungal medications that are designed to cure them. This emerging phenomenon is known as antifungal resistance, and it's primarily a concern for invasive infections with the fungus *Candida*.

Although antibiotic-resistant bacterial infections are a widely-recognized public health threat, less is known about the effects of antifungal resistance and the burden of drug-resistant fungal infections. This highlights the need for an improved understanding of the reasons for their emergence, heightened awareness among medical and public health communities about these infections, and greater attention to methods that can be used to prevent and control them.

The Problem

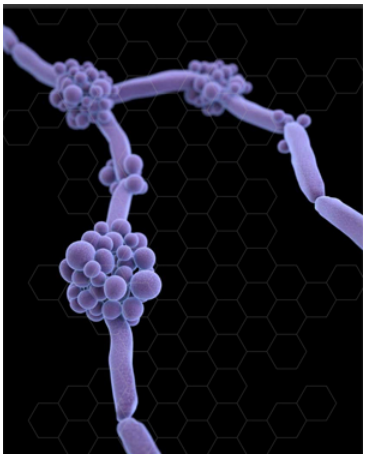


Figure 1. Medical illustration of fluconazole-resistant *Candida*

Invasive fungal infections cause substantial morbidity and mortality and are a costly, common problem in healthcare settings. The fungus *Candida* is the most common cause of healthcare-associated bloodstream infections in the United States.[1] Each case of *Candida* bloodstream infection (also known as candidemia) is estimated to result in an additional 3 to 13 days of hospitalization and $6,000 to $29,000 in healthcare costs.[2]

What's also concerning is that some types of *Candida* are becoming increasingly resistant to first-line and second-line antifungal medications, namely, fluconazole and echinocandins (anidulafungin, caspofungin, and micafungin). Approximately 7% of all *Candida* bloodstream isolates tested at CDC are resistant to fluconazole, most of which are *Candida glabrata*.[3],[4] CDC's surveillance data indicate that the proportion of *Candida* isolates that are resistant to fluconazole has remained fairly constant over the past twenty years.[5],[6],[7] Echinocandin resistance, however, appears to be on the rise, especially among *Candida glabrata*. CDC's surveillance data indicate that up to 8% of *Candida glabrata* isolates in 2014 may not be susceptible to echinocandins; this proportion nearly doubled from 4% in 2008. This is especially concerning as echinocandins are the mainstay of treatment for *Candida glabrata*, which already has high levels of resistance to fluconazole.[8]

The stable yet substantial rates of fluconazole resistance and the emergence of echinocandin resistance are concerning because echinocandins are typically used to treat infections caused by *C. glabrata*, the species that's most often associated with fluconazole resistance. For multi-drug resistant *Candida* infections (those that are resistant to both fluconazole and an echinocandin), the few remaining treatment options are expensive and can be toxic for patients who are already very sick. Not surprisingly, there is growing evidence to suggest that patients who have drug-resistant candidemia have poorer outcomes than patients who have candidemia that's susceptible to antifungal medications.[9],[10] Overall, antifungal resistance is still relatively uncommon, but the problem will likely continue to evolve unless more is done to prevent further resistance from developing and prevent the spread of these infections.

The Cause

Some species of fungi are naturally resistant to certain types of antifungal medications. Other species may be normally susceptible to a particular type of medication, but develop resistance over time as a result of improper antifungal use—for example, dosages that are too low or treatment courses that aren't long enough.[11],[12] Some studies have indicated that antibacterial medications may also contribute to antifungal resistance; this could occur for a variety of reasons, one of which is that antibacterials reduce bacteria in the gut and create favorable conditions for *Candida* growth.[13] It's not yet known if decreasing the use of all or certain antimicrobial agents can reduce *Candida* infections, but appropriate use of antibacterial and antifungal agents is one of the most important factors in fighting drug resistance.

What can be done

Antifungal resistance is becoming increasingly recognized, particularly for *Candida*. Everyone has a role in preventing *Candida* infections and reducing antifungal resistance.

- CDC is:
  - Tracking trends in antifungal resistance through the Emerging Infections Program by conducting multi-center candidemia surveillance and performing species confirmation and antifungal susceptibility testing on *Candida* bloodstream isolates.[14],[15]
  - Using genetic sequencing and developing new laboratory tests to identify and understand specific mutations associated with antifungal resistance in *Candida*.
- Hospital executives and infection control staff can:
  - Assess antifungal use as part of their antibiotic stewardship programs.
  - Ensure adherence to guidelines for hand hygiene, prevention of catheter-associated infections, and environmental infection control.
- Doctors and other hospital staff can:
  - Prescribe antifungal medications appropriately.
  - Document the dose, duration, and indication for every antifungal prescription.
  - Stay aware of local antifungal resistance patterns.
  - Participate in and lead efforts within your hospital to improve antifungal prescribing practices.
  - Follow hand hygiene and other infection control measures with every patient.
- Hospital patients can:
  - Be sure everyone cleans their hands before entering your room.
  - If you have a catheter, ask each day if it is necessary.

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9.20: Putting It Together- Fungi

Although humans have used yeasts and mushrooms since prehistoric times, the biology of fungi was poorly understood until recently. Up until the mid-twentieth century, many scientists classified fungi as plants. Fungi, like plants, arose seemingly rooted in place. They possess a stem-like structure similar to plants, as well as having a root-like fungal mycelium in the soil. In addition, their mode of nutrition was poorly understood.

Progress in the field of fungal biology was the result of mycology: the scientific study of fungi. Based on fossil evidence, fungi appeared in the pre-Cambrian era, about 450 million years ago. Molecular biology analysis of the fungal genome demonstrates 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.

Career Connection: Mycologist



Figure 1. Paul Stamets, an American mycologist, holding an Agarikon mushroom

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 is decimating bats in the Eastern United States.

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 wine making, relies not only on the knowledge of grape varietals and soil composition, but also on a solid understanding of the characteristics of the wild yeasts that thrive in different wine-making 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.

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- Paul Stamets with Agarikon. **Authored by**: Dusty Yao-Stamets. **Located at**: https://commons.wikimedia.org/wiki/File:Paul_Stamets_with_Agarikon.jpg. **License**: *CC BY: Attribution*

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9.21: Cerego- Fungi

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for Fungi. You'll need to create a free log-in to practice these items, if you haven't already.

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CHAPTER OVERVIEW

10: Module 7- Plant Diversity

10.1: Why It Matters- Plant Diversity
10.2: Introduction to Seedless Plants
10.3: Early Plant Life
10.4: Green Algae- Precursors of Land Plants
10.5: Bryophytes
10.6: Seedless Vascular Plants
10.7: Introduction to Seed Plants
10.8: Evolution of Seed Plants
10.9: Gymnosperms
10.10: Angiosperms
10.11: The Role of Seed Plants
10.12: Putting It Together- Plant Diversity
10.13: Cerego- Plant Diversity

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10.1: Why It Matters- Plant Diversity

Why differentiate between different types of plants?



Figure 1. Plant life on earth is diverse

Land plants evolved from a group of green algae, perhaps as early as 510 million years ago. The evolution of plants has resulted in widely varying levels of complexity, from the earliest algal mats, to bryophytes, lycopods, and ferns, to the complex gymnosperms and angiosperms of today. While many of the groups which appeared earlier continue to thrive, as exemplified by algal dominance in marine environments, more recently derived groups have also displaced previously ecologically dominant ones (for example, the ascendance of flowering plants over gymnosperms in terrestrial environments).

The establishment of a land-based flora caused increased accumulation of oxygen in the atmosphere, as the plants produced oxygen as a waste product. This rise in oxygen likely contributed to the evolution of life as we now know it.

Plants make our lives possible. Without the glucose they create through photosynthesis, and the oxygen they release into the air, it would be impossible for human life to continue on.

Learning Outcomes

- Classify seedless plants
- Classify seed plants

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10.2: Introduction to Seedless Plants

Classify seedless plants



Figure 1. 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)

An incredible variety of seedless plants populates the terrestrial landscape. Mosses may grow on a tree trunk, and horsetails may display their jointed stems and spindly leaves across the forest floor. 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.

Current evolutionary thought holds that all plants—green algae as well as land dwellers—are monophyletic; that is, they are descendants of a single common ancestor. The evolutionary transition from water to land imposed severe constraints on plants. They had to develop strategies to avoid drying out, to disperse reproductive cells in air, for structural support, and for capturing and filtering sunlight. While seed plants developed adaptations that allowed them to populate even the most arid habitats on Earth, full independence from water did not happen in all plants. Most seedless plants still require a moist environment.

What You'll Learn to Do

- Describe the timeline of plant evolution and the impact of land plants on other living things
- Describe the traits shared by green algae and land plants
- Identify the main characteristics of bryophytes
- Differentiate between vascular and non-vascular plants
- Identify the main characteristics of seedless vascular plants

Learning Activities

The learning activities for this section include the following:

- Early Plant Life
- Green Algae: Precursors of Land Plants
- Bryophytes
- Seedless Vascular Plants
- Self Check: Plant Structures

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10.3: Early Plant Life

The kingdom Plantae constitutes large and varied groups of organisms. There are more than 300,000 species of catalogued plants. Of these, more than 260,000 are seed plants. Mosses, ferns, conifers, and flowering plants are all members of the plant kingdom. Land plants arose within the Archaeplastida, which includes the red algae (Rhodophyta) and two groups of green algae, **Chlorophyta** and **Charaphyta**. Most biologists also consider at least some green algae to be plants, although others exclude all algae from the plant kingdom. The reason for this disagreement stems from the fact that only green algae, the Chlorophytes and Charophytes, share common characteristics with land plants (such as using chlorophyll *a* and *b* plus carotene in the same proportion as plants). These characteristics are absent from other types of algae.

? Try It

Some scientists consider all algae to be plants, while others assert that only the green algae belong in the kingdom Plantae. Still others include only the Charophytes among the plants. 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 didn't all become photosynthetic via the same path.

The ancestors to the Archaeplastida became photosynthetic by forming an endosymbiotic relationship with a green, photosynthetic bacterium about 1.65 billion years ago. That algal line evolved into the red and green algae, and eventually into the modern mosses, ferns, gymnosperms, and angiosperms. Their evolutionary trajectory was relatively straight and monophyletic. In contrast, algae outside of the Archaeplastida, e.g., the brown and golden algae of the stramenopiles, and so on—all became photosynthetic by secondary, or even tertiary, endosymbiotic events; that is, they engulfed cells that already contained an endosymbiotic cyanobacterium. These latecomers to photosynthesis are parallels to the Archaeplastida in terms of autotrophy, but they did not expand to the same extent as the Archaeplastida, nor did they colonize the land.

Scientists who solely track evolutionary straight lines (that is, monophyly), consider only the Charophytes as plants. The common ancestor of Charophytes and land plants excludes the other members of the Archaeplastida. Charophytes also share other features with the land plants.

Go to this interactive website to get a more in-depth view of the Charophytes.

Plant Adaptations to Life on Land

As organisms adapted to life on land, they had to contend with several challenges in the terrestrial environment. Water has been described as "the stuff of life." The cell's interior is a thick 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 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. On land, plants need to develop structural support in a medium that does not give the same lift as water. The organism is also subject to bombardment by mutagenic radiation, because air does not filter out ultraviolet rays of sunlight. 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 acts as a filter, altering the spectral quality of light absorbed by the photosynthetic pigment chlorophyll. Second, carbon dioxide is more readily available in air than in water, since it diffuses faster in air. Third, land plants evolved before land animals; therefore, until dry land was colonized by animals, no predators threatened plant life. This situation changed as animals emerged from the water and fed on the abundant sources of nutrients in the established flora. In turn, 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 solution was the development of new structures that gave plants the advantage when colonizing new and dry environments. Four major adaptations contribute to the success of terrestrial plants. The first adaptation is that the life cycle in all land plants exhibits the alternation of generations, a sporophyte in which the spores are formed and a gametophyte that produces gametes. Second is an apical meristem tissue in roots and shoots. Third is the evolution of a waxy cuticle to resist desiccation (absent from some mosses). Finally cell walls with lignin to support structures off the ground. These adaptations all contribute to the success of the land plants, but are noticeably lacking in the closely related green algae—another reason for the debate over their placement in the plant kingdom. They are also not all found in the mosses, which can be regarded as representing an intermediate stage in adaptation to land.

Alternation of Generations

All sexually reproducing organisms have both haploid and diploid cells in their life cycles. In organisms with **haplontic** life cycles, the haploid stage is dominant, while in organisms with a **diplontic** life cycle, the diploid stage is the dominant life stage. *Dominant* in this context means both the stage in which the organism spends most of its time, and the stage in which most mitotic cell reproduction occurs—the multicellular stage. In haplontic life cycles, the only diploid cell is the zygote, which undergoes immediate meiosis to restore the haploid state. In diplontic life cycles, the only haploid cells are the gametes, which combine to restore the diploid state at their earliest convenience. Humans, for example, are diplontic.

Alternation of generations describes a life cycle in which an organism has both haploid and diploid multicellular stages (Figure 1). This type of life cycle, which is found in all plants, is described as **haplodiplontic**.

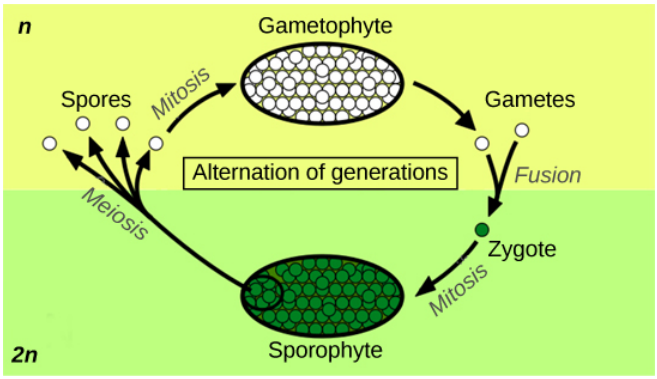


Figure 1. Alternation of generations between the 1*n* gametophyte and 2*n* sporophyte is shown. Mitosis occurs in both gametophyte and sporophyte generations. Diploid sporophytes produce haploid spores by meiosis, while haploid gametophytes produce gametes by mitosis. (credit: Peter Coxhead)

In alternation of generations, the multicellular haploid form, known as a gametophyte, is followed in the developmental sequence by a multicellular diploid form, the sporophyte. The gametophyte gives rise to the gametes (reproductive cells) by mitosis. This can be the most obvious phase of the life cycle of the plant, as in the mosses, or it can occur in a microscopic structure, such as a pollen grain, in the seed plants. The evolution of the land plants is marked by increasing prominence of the sporophyte generation. The sporophyte stage is barely noticeable in non-vascular plants (the collective term for the plants that include the liverworts and mosses). In the seed plants, the sporophyte phase can be a towering tree, as in sequoias and pines.

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 sporophyte. This distinguishing feature of land plants gave the group its alternate name of **embryophytes**.



Figure 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)

The sporophyte of seedless plants is diploid and results from syngamy (fusion) of two gametes. The sporophyte bears the sporangia (singular, sporangium). The term “sporangia” literally means “a vessel for spores,” as it is a reproductive sac in which spores are formed (Figure 2). Inside the multicellular sporangia, the diploid **sporocytes**, or mother cells, produce haploid spores by meiosis, during which the 2*n* chromosome number is reduced to 1*n* (note that in many plants, chromosome number is complicated by polyploidy: for example, durum wheat is tetraploid, bread wheat is hexaploid, and some ferns are 1000-ploid). The spores are later released by the sporangia and disperse in the environment. 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.

Plants that produce only one type of spore are called homosporous and the resultant gametophyte produces both male and female gametes, usually on the same individual. Non-vascular plants are homosporous, and the gametophyte is the dominant generation in the life cycle. Plants that produce two types of spores are called heterosporous. 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. A few seedless vascular plants and all seed plants are heterosporous, and the sporophyte is the dominant generation.

The spores of seedless plants are surrounded by thick cell walls containing a tough polymer known as sporopollenin. As the name suggests, it is also found in the walls of pollen grains. This complex substance is characterized by long chains of organic molecules related to fatty acids and carotenoids: hence the yellow color of most pollen. Sporopollenin is unusually resistant to chemical and biological degradation. In seed plants, in which pollen is the male gametophyte, the toughness of sporopollenin explains the existence of well-preserved pollen fossils. Sporopollenin was once thought to be an innovation of land plants; however, the charophyte *Coleochaetes* also forms spores that contain **sporopollenin**.

Gametangia in Seedless Plants

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.

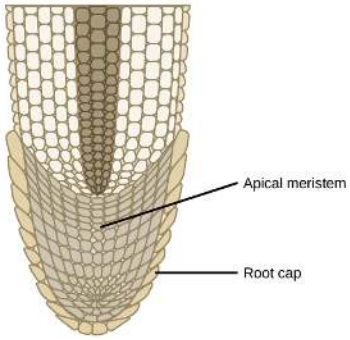


Figure 3. Addition of new cells in a root occurs at the apical meristem. Subsequent enlargement of these cells causes the organ to grow and elongate. The root cap protects the fragile apical meristem as the root tip is pushed through the soil by cell elongation.

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 3). The apical meristem is made of undifferentiated cells that continue to proliferate throughout the life of the plant. Meristematic cells give rise to all the specialized tissues of the organism. 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.

Additional Land Plant Adaptations

As plants adapted to dry land and became independent from the constant presence of water in damp habitats, 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.

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 traffic of gases and water vapor appeared in plants as they moved away from moist environments into drier habitats.

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.

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.

Evolution of Land Plants

No discussion of the evolution of plants on land can be undertaken without a brief review of the timeline of the geological eras. The early era, known as the Paleozoic, is divided into six periods. It starts with the Cambrian period, followed by the Ordovician, Silurian, Devonian, Carboniferous, and Permian. The major event to mark the Ordovician, more than 500 million years ago, 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 (Figure 4), where embedded fossils of some of the earliest vascular plants have been identified.

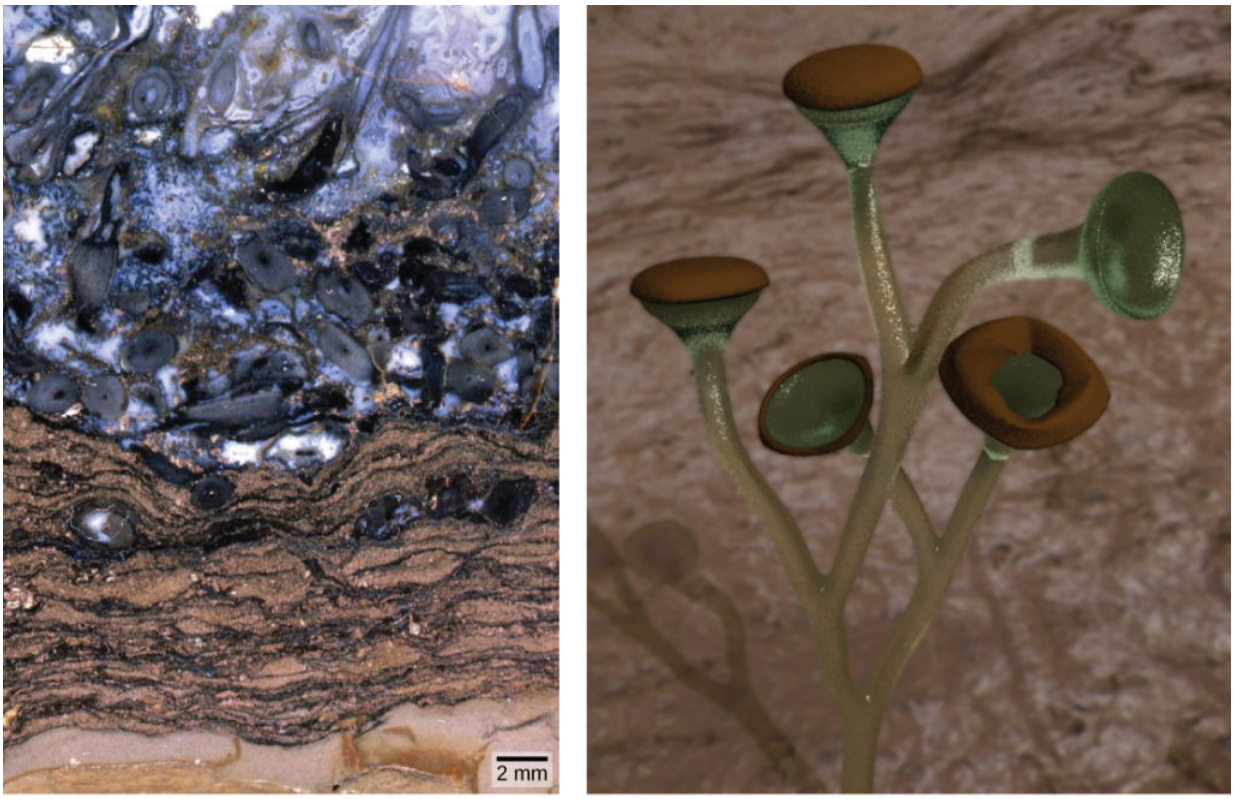


Figure 4. This Rhynie chert contains fossilized material from vascular plants. The area inside the circle contains bulbous underground stems called corms, and root-like structures called rhizoids. (credit b: modification of work by Peter Coxhead based on original image by "Smith609"/Wikimedia Commons; scale-bar data from Matt Russell)

Paleobotanists distinguish between **extinct** species, as fossils, and **extant** species, which are still living. The extinct vascular plants, classified as zosterophylls and trimerophytes, most probably lacked true leaves and roots and formed low vegetation mats similar in size to modern-day mosses, although some trimetophytes could reach one meter in height. The later genus *Cooksonia*, which flourished during the Silurian, has been extensively studied from well-preserved examples. Imprints of *Cooksonia* show slender branching stems ending in what appear to be sporangia. From the recovered specimens, it is not possible to establish for certain whether *Cooksonia* possessed vascular tissues. Fossils indicate that by the end of the Devonian period, ferns, horsetails, and seed plants populated the landscape, giving rising to trees and forests. This luxuriant vegetation helped enrich the atmosphere in oxygen, making it easier for air-breathing animals to colonize dry land. Plants also established early symbiotic relationships with fungi, creating mycorrhizae: a relationship in which the fungal network of filaments increases the efficiency of the plant root system, and the plants provide the fungi with byproducts of photosynthesis.

? Try It

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.

The Major Divisions 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 according to the absence or presence of vascular tissue, as detailed in Figure 5. Plants that lack vascular tissue, 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 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 (Gymnosperms), which produce “naked seeds,” and the most successful of all plants, the flowering plants (Angiosperms). Angiosperms protect their seeds inside chambers at the center of a flower; the walls of the chamber later develop into a fruit.

<table>
<tr><th colspan="8">STREPTOPHYTES: THE GREEN PLANTS</th></tr>
<tr><td rowspan="6">Charophytes</td><td colspan="7">Embryophytes: The Land Plants</td></tr>
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Bryophytes</td><td colspan="2">Seedless Plants</td><td colspan="2" rowspan="2">Seed Plants
Spermatophytes</td></tr>
<tr><td>Lycophytes</td><td>Pterophytes</td></tr>
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<tr><td>Quillworts</td><td>Horsetails</td></tr>
<tr><td>Spike Mosses</td><td>Ferns</td></tr>
</table>

Figure 5. This table shows the major divisions of green plants.

? Practice Question

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.

[reveal-answer q="755202"]Show Answer[/reveal-answer]
[hidden-answer a="755202"]Statement b is false.[/hidden-answer]

Learning Objectives

Land plants acquired traits that made it possible to colonize land and survive out of the water. All land plants share the following characteristics: alternation of generations, with the haploid plant called a gametophyte, and the diploid plant called a sporophyte; protection of the embryo, formation of haploid spores in a sporangium, formation of gametes in a gametangium, and an apical meristem. Vascular tissues, roots, leaves, cuticle cover, and a tough outer layer that protects the spores contributed to the adaptation of plants to dry land. Land plants appeared about 500 million years ago in the Ordovician period.

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10.4: Green Algae- Precursors of Land Plants

Streptophytes

Until recently, all photosynthetic eukaryotes were considered members of the kingdom Plantae. The brown, red, and gold algae, however, have been reassigned to the Protista kingdom. This is because apart from their ability to capture light energy and fix CO_2, they lack many structural and biochemical traits that distinguish plants from protists. The position of green algae is more ambiguous. Green algae contain the same carotenoids and chlorophyll *a* and *b* as land plants, whereas other algae have different accessory pigments and types of chlorophyll molecules in addition to chlorophyll *a*. Both green algae and land plants also store carbohydrates as starch. Cells in green algae divide along cell plates called phragmoplasts, and their cell walls are layered in the same manner as the cell walls of embryophytes. Consequently, land plants and closely related green algae are now part of a new monophyletic group called Streptophyta.

The remaining green algae, which belong to a group called Chlorophyta, include more than 7000 different species that live in fresh or brackish water, in seawater, or in snow patches. A few green algae even survive on soil, provided it is covered by a thin film of moisture in which they can live. Periodic dry spells provide a selective advantage to algae that can survive water stress. Some green algae may already be familiar, in particular *Spirogyra* and desmids. Their cells contain chloroplasts that display a dizzying variety of shapes, and their cell walls contain cellulose, as do land plants. Some green algae are single cells, such as *Chlorella* and *Chlamydomonas*, which adds to the ambiguity of green algae classification, because plants are multicellular. Other algae, like *Ulva* (commonly called sea lettuce), form colonies (Figure 1).

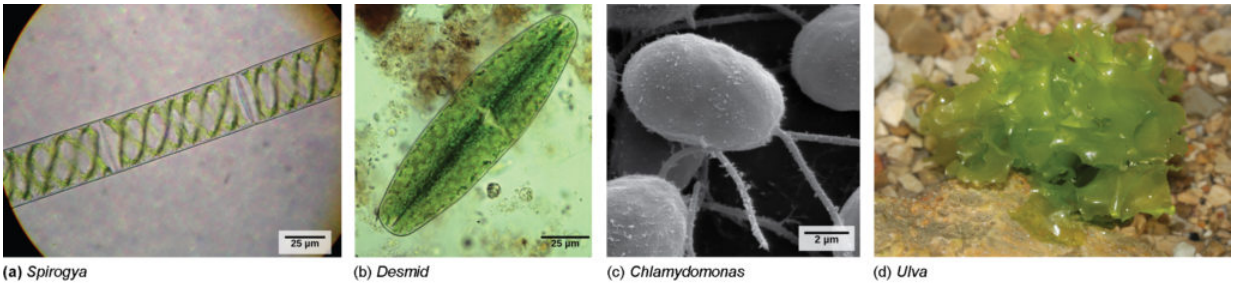


Figure 1. Chlorophyta include (a) *Spirogyra*, (b) desmids, (c) *Chlamydomonas*, and (d) *Ulva*. Desmids and *Chlamydomonas* are single-celled organisms, *Spirogyra* forms chains of cells, and *Ulva* forms colonies resembling leaves (credit b: modification of work by Derek Keats; credit c: modification of work by Dartmouth Electron Microscope Facility, Dartmouth College; credit d: modification of work by Holger Krisp; scale-bar data from Matt Russell)

Reproduction of Green Algae

Green algae reproduce both asexually, by fragmentation or dispersal of spores, or sexually, by producing gametes that fuse during fertilization. In a single-celled organism such as *Chlamydomonas*, there is no mitosis after fertilization. In the multicellular *Ulva*, a sporophyte grows by mitosis after fertilization (and thus exhibits alternation of generations). Both *Chlamydomonas* and *Ulva* produce flagellated gametes.

Charales



Figure 2. The representative alga, *Chara*, is a noxious weed in Florida, where it clogs waterways. (credit: South Florida Information Access, U.S. Geological Survey)

The charophytes include several different algal orders that have each been suggested to be the closest relatives of the land plants: the Charales, the Zygnematales, and the Coleochaetales. The Charales can be traced back 420 million years. They live in a range of freshwater habitats and vary in size from a few millimeters to a meter in length. The representative genus is *Chara* (Figure 25.8), often called muskgrass or skunkweed because of its unpleasant smell. Large cells form the *thallus*: the main stem of the alga. Branches arising from the nodes are made of smaller cells. Male and female reproductive structures are found on the nodes, and the sperm have flagella. Although *Chara* looks superficially like some land plants, a major difference is that the stem has no supportive tissue. However, the Charales exhibit a number of traits that are significant for adaptation to land life. They produce the compounds *lignin* and *sporopollenin*, and form plasmodesmata that connect the cytoplasm of adjacent cells. Although the life cycle of the Charales is haplontic (the main form is haploid, and diploid zygotes are formed but have a brief existence), the egg, and later, the zygote, form in a protected chamber on the haploid parent plant.

The Coleochaetes are branched or disclike multicellular forms. They can produce both sexually and asexually, but the life cycle is basically haplontic. Recent extensive DNA sequence analysis of charophytes indicates that the Zygnematales are more closely related to the embryophytes than the Charales or the Coleochaetales. The Zygnematales include the familiar genus *Spirogyra*, as well as the desmids. As techniques in DNA analysis improve and new information on comparative genomics arises, the phylogenetic connections between the charophytes and the land plants will continued to be examined to produce a satisfactory solution to the mystery of the origin of land plants.

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10.5: Bryophytes

Bryophytes are the group of plants that are the closest extant relative 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, the likelihood of bryophytes forming fossils is rather small. Some spores protected by sporopollenin have survived and are attributed to early bryophytes. 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.

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 actual tracheids (xylem cells specialized for water conduction). 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 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.

The bryophytes are divided into three phyla: the liverworts or Hepaticophyta, the hornworts or Anthocerotophyta, and the mosses or true Bryophyta.

Liverworts

Liverworts (Hepaticophyta) are viewed as the plants most closely related to the ancestor that moved to land. Liverworts have colonized every terrestrial habitat on Earth and diversified to more than 7000 existing species (Figure 1).



Figure 1. This 1904 drawing shows the variety of forms of Hepaticophyta.



Figure 2. A liverwort, *Lunularia cruciata*, displays its lobate, flat thallus. The organism in the photograph is in the gametophyte stage.

Some gametophytes form lobate green structures, as seen in Figure 2. The shape is similar to the lobes of the liver, and hence provides the origin of the name given to the phylum. Openings that allow the movement of gases may be observed in liverworts. However, these are not stomata, because they do not actively open and close. The plant takes up water over its entire surface and has no cuticle to prevent desiccation.

Figure 3 represents the lifecycle of a liverwort. The cycle starts with the release of haploid spores from the sporangium that developed on the sporophyte. Spores disseminated by wind or water germinate into flattened thalli attached to the substrate by thin, single-celled filaments. Male and female gametangia develop on separate, individual plants. Once released, male gametes swim with the aid of their flagella to the female gametangium (the archegonium), and fertilization ensues. The zygote grows into a small sporophyte still attached to the parent gametophyte. It will give rise, by meiosis, to the next generation of spores. Liverwort plants can also reproduce asexually, by the breaking of branches or the spreading of leaf fragments called gemmae. In this latter type of reproduction, the **gemmae**—small, intact, complete pieces of plant that are produced in a cup on the surface of the thallus (shown in Figure 3)—are splashed out of the cup by raindrops. The gemmae then land nearby and develop into gametophytes.

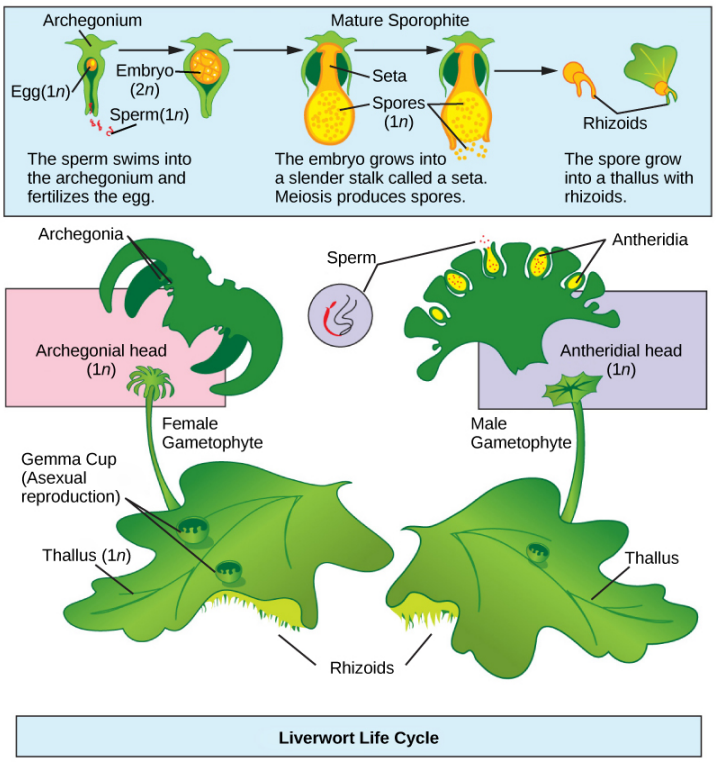


Figure 3. The life cycle of a typical liverwort is shown. (credit: modification of work by Mariana Ruiz Villareal)



Figure 4. Hornworts grow a tall and slender sporophyte. (credit: modification of work by Jason Hollinger)

The **hornworts** (*Anthocerotophyta*) belong to the broad bryophyte group. They have colonized a variety of habitats on land, although they are never far from a source of moisture. The short, blue-green gametophyte is the dominant phase of the lifecycle of a hornwort. The narrow, pipe-like sporophyte is the defining characteristic of the group. The sporophytes emerge from the parent gametophyte and continue to grow throughout the life of the plant (Figure 4).

Stomata appear in the hornworts and are abundant on the sporophyte. Photosynthetic cells in the thallus contain a single chloroplast. Meristem cells at the base of the plant keep dividing and adding to its height. Many hornworts establish symbiotic relationships with cyanobacteria that fix nitrogen from the environment.

The lifecycle of hornworts (Figure 5) follows the general pattern of alternation of generations. The gametophytes grow as flat thalli on the soil with embedded gametangia. Flagellated sperm swim to the archegonia and fertilize eggs. The zygote develops into a long and slender sporophyte that eventually splits open, releasing spores. Thin cells called pseudoelaters surround the spores and help propel them further in the environment. Unlike the elaters observed in horsetails, the hornwort pseudoelaters are single-celled structures. The haploid spores germinate and give rise to the next generation of gametophyte.

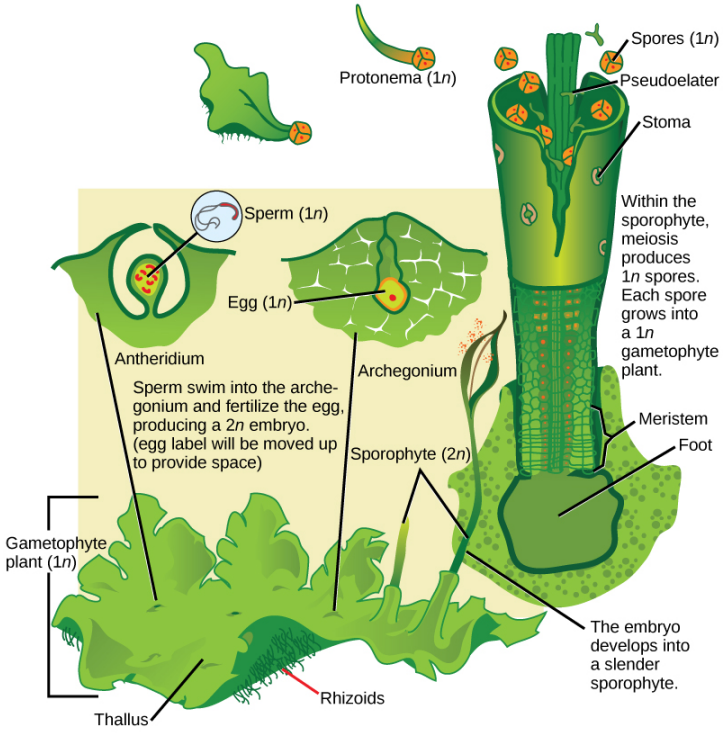


Figure 5. The alternation of generation in hornworts is shown. (credit: modification of work by “Smith609”/Wikimedia Commons based on original work by Mariana Ruiz Villareal)

Mosses

More than 10,000 species of **mosses** have been catalogued. Their habitats vary from the tundra, where they are the main vegetation, to the understory of tropical forests. In the tundra, the mosses' shallow rhizoids allow them to fasten to a substrate without penetrating the frozen soil. Mosses slow down erosion, store moisture and soil nutrients, and provide shelter for small animals as well as food for larger herbivores, such as the musk ox. Mosses are very sensitive to air pollution and are used to monitor air quality. They are also sensitive to copper salts, so these salts are a common ingredient of compounds marketed to eliminate mosses from lawns.

Mosses form diminutive gametophytes, which are the dominant phase of the lifecycle. Green, flat structures—resembling true leaves, but lacking vascular tissue—are attached in a spiral to a central stalk. The plants absorb water and nutrients directly through these leaf-like structures. Some mosses have small branches. Some primitive traits of green algae, such as flagellated sperm, are still present in mosses that are dependent on water for reproduction. Other features of mosses are clearly adaptations to dry land. For example, stomata are present on the stems of the sporophyte, and a primitive vascular system runs up the sporophyte's stalk. Additionally, mosses are anchored to the substrate—whether it is soil, rock, or roof tiles—by multicellular **rhizoids**. These structures are precursors of roots. They originate from the base of the gametophyte, but are not the major route for the absorption of water and minerals. The lack of a true root system explains why it is so easy to rip moss mats from a tree trunk. The moss lifecycle follows the pattern of alternation of generations as shown in Figure 6.

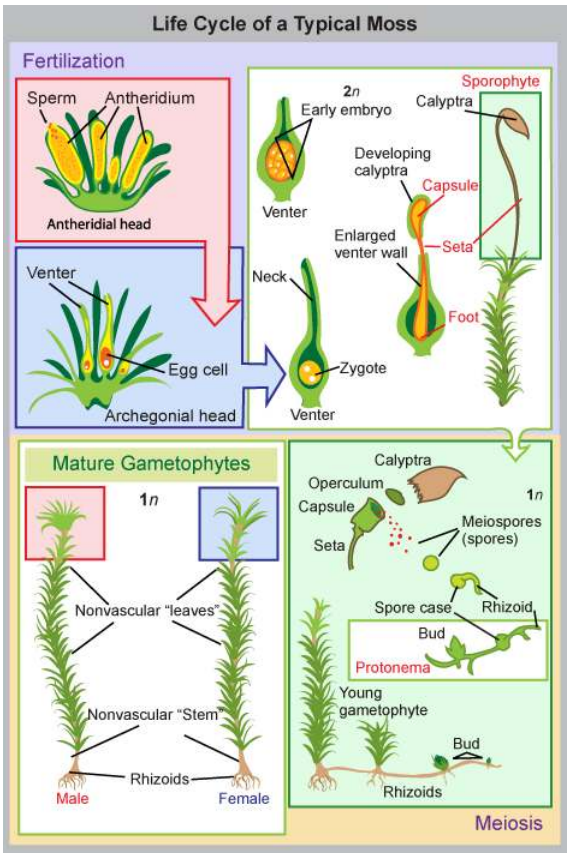


Figure 6. This illustration shows the life cycle of mosses. (credit: modification of work by Mariana Ruiz Villareal)



Figure 7. This photograph shows the long slender stems, called setae, connected to capsules of the moss *Thamnobryum alopecurum*. (credit: modification of work by Hermann Schachner)

The most familiar structure is the haploid gametophyte, which germinates from a haploid spore and forms first a **protonema**—usually, a tangle of single-celled filaments that hug the ground. Cells akin to an apical meristem actively divide and give rise to a gametophore, consisting of a photosynthetic stem and foliage-like structures. Rhizoids form at the base of the gametophore. Gametangia of both sexes develop on separate gametophores. The male organ (the antheridium) produces many sperm, whereas the archegonium (the female organ) forms a single egg. At fertilization, the sperm swims down the neck to the venter and unites with the egg inside the archegonium. The zygote, protected by the archegonium, divides and grows into a sporophyte, still attached by its foot to the gametophyte.

The slender **seta** (plural, setae), as seen in Figure 7, contains tubular cells that transfer nutrients from the base of the sporophyte (the foot) to the sporangium or **capsule**.

A structure called a **peristome** increases the spread of spores after the tip of the capsule falls off at dispersal. The concentric tissue around the mouth of the capsule is made of triangular, close-fitting units, a little like “teeth”; these open and close depending on moisture levels, and periodically release spores.

? Practice Question

Which of the following statements about the moss life cycle is false?

a. The mature gametophyte is haploid.
b. The sporophyte produces haploid spores.
c. The calyptra buds to form a mature gametophyte.
d. The zygote is housed in the venter.

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[hidden-answer a=”646233″]Statement c is false.[/hidden-answer]

Learning Objectives

Seedless nonvascular plants are small, having the gametophyte as the dominant stage of the lifecycle. Without a vascular system and roots, they absorb water and nutrients on all their exposed surfaces. Collectively known as bryophytes, the three main groups include the liverworts, the hornworts, and the mosses. Liverworts are the most primitive plants and are closely related to the first land plants. Hornworts developed stomata and possess a single chloroplast per cell. Mosses have simple conductive cells and are attached to the substrate by rhizoids. They colonize harsh habitats and can regain moisture after drying out. The moss sporangium is a complex structure that allows release of spores away from the parent plant.

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10.6: Seedless Vascular Plants

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.

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. Vascular plants, on the other hand, can achieve enormous heights, thus competing successfully for light. Photosynthetic organs become leaves, and pipe-like cells or vascular tissues transport water, minerals, and fixed carbon throughout the organism.

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. Seedless vascular plants still depend on water during fertilization, 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.

Vascular Tissue: Xylem and Phloem

The first fossils that show the presence of vascular tissue date to the Silurian period, about 430 million years ago. The simplest arrangement of conductive cells shows a pattern of xylem at the center surrounded by phloem. **Xylem** is the tissue responsible for the storage and long-distance transport of water and nutrients, as well as the transfer of water-soluble growth factors from the organs of synthesis to the target organs. The tissue consists of conducting cells, known as tracheids, and supportive filler tissue, called parenchyma. Xylem conductive cells incorporate the compound **lignin** into their walls, and are thus described as lignified. Lignin itself is a complex polymer that is impermeable to water and confers mechanical strength to vascular tissue. With their rigid cell walls, the xylem cells provide support to the plant and allow it to achieve impressive heights. Tall plants have a selective advantage by being able to reach unfiltered sunlight and disperse their spores or seeds further away, thus expanding their range. By growing higher than other plants, tall trees cast their shadow on shorter plants and limit competition for water and precious nutrients in the soil.

Phloem is the second type of vascular tissue; it transports sugars, proteins, and other solutes throughout the plant. Phloem cells are divided into sieve elements (conducting cells) and cells that support the sieve elements. Together, xylem and phloem tissues form the vascular system of plants.

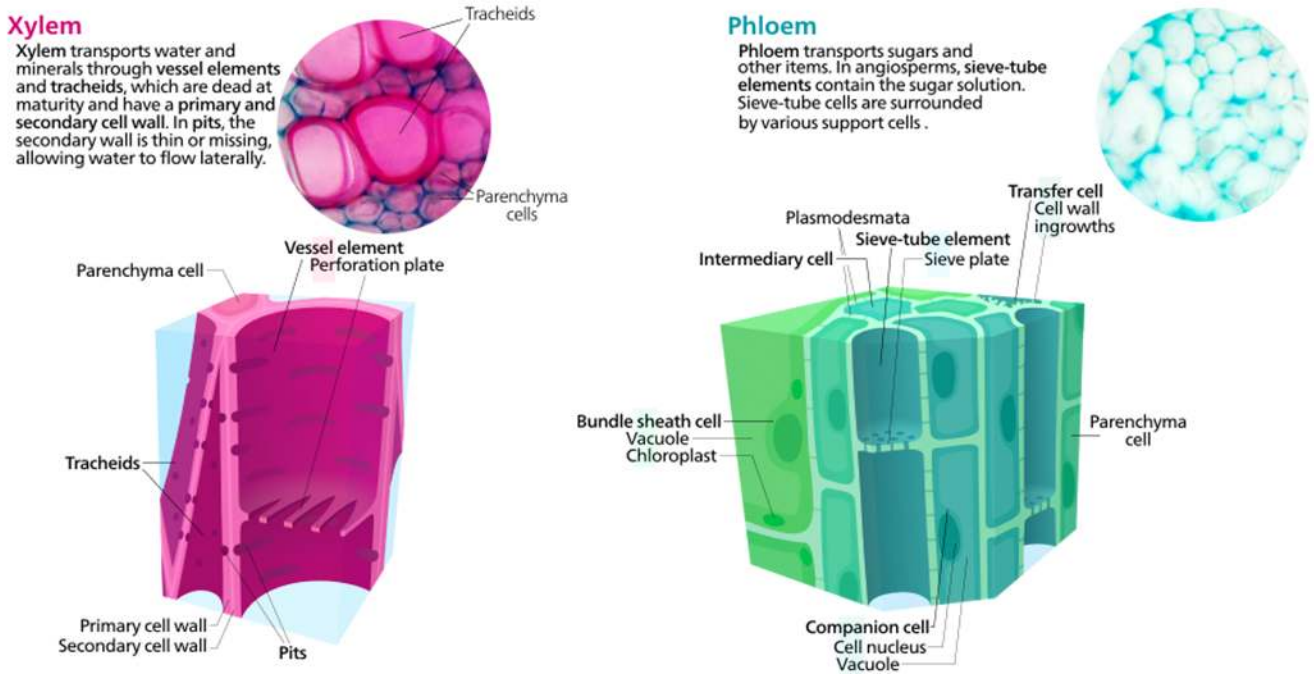


Figure 1. Diagrams of xylem and phloem tissues

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

A third innovation marks the seedless vascular plants. Accompanying the prominence of the sporophyte and the development of vascular tissue, the appearance of true leaves improved their 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.

The existence of two types of morphology suggests that leaves evolved independently in several groups of plants. The first type of leaf is the **microphyll**, or “little leaf,” which can be dated to 350 million years ago in the late Silurian. A microphyll is small and has a simple vascular system. A single unbranched **vein**—a bundle of vascular tissue made of xylem and phloem—runs through the center of the leaf. Microphylls may have originated from the flattening of lateral branches, or from sporangia that lost their reproductive capabilities. Microphylls are present in the club mosses and probably preceded the development of **megaphylls**, or “big leaves,” which are larger leaves with a pattern of branching veins. Megaphylls most likely appeared independently several times during the course of evolution. Their complex networks of veins suggest that several branches may have combined into a flattened organ, with the gaps between the branches being filled with photosynthetic tissue.

In addition to photosynthesis, leaves play another role in the life of the 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.

Ferns and Other Seedless Vascular Plants

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 and horsetails—some specimens reaching heights of more than 30 m (100 ft)—covered most of the land. These forests gave rise to the extensive coal deposits that gave the Carboniferous its name. In seedless vascular plants, the sporophyte became the dominant phase of the lifecycle.

Water is still required for fertilization of seedless vascular plants, and most favor a moist environment. Modern-day seedless tracheophytes include club mosses, horsetails, ferns, and whisk ferns.

Phylum Lycopodiophyta: Club Mosses



Figure 2. In the club mosses such as *Lycopodium clavatum*, sporangia are arranged in clusters called strobili. (credit: Cory Zanker)

The **club mosses**, or phylum **Lycopodiophyta**, are the earliest group of seedless vascular plants. They dominated the landscape of the Carboniferous, growing into tall trees and forming large swamp forests. Today's club mosses are diminutive, evergreen plants consisting of a stem (which may be branched) and microphylls (Figure 2). The phylum Lycopodiophyta consists of close to 1,200 species, including the quillworts (*Isoetales*), the club mosses (*Lycopodiales*), and spike mosses (*Selaginellales*), none of which are true mosses or bryophytes.

Lycophytes follow the pattern of alternation of generations seen in the bryophytes, except that the sporophyte is the major stage of the lifecycle. The gametophytes do not depend on the sporophyte for nutrients. Some gametophytes develop underground and form mycorrhizal associations with fungi. In club mosses, the sporophyte gives rise to sporophylls arranged in strobili, cone-like structures that give the class its name. Lycophytes can be homosporous or heterosporous.



Figure 3. Horsetails thrive in a marsh. (credit: Myriam Feldman)

Phylum Monilophyta: Class Equisetopsida (Horsetails)

Horsetails, whisk ferns and ferns belong to the phylum Monilophyta, with **horsetails** placed in the Class Equisetopsida. The single genus *Equisetum* is the survivor of a large group of plants, known as Arthrophyta, which produced large trees and entire swamp forests in the Carboniferous. The plants are usually found in damp environments and marshes (Figure 3).

The stem of a horsetail is characterized by the presence of joints or nodes, hence the name Arthrophyta (*arthro–* = "joint"; *–phyta* = "plant"). Leaves and branches come out as whorls from the evenly spaced joints. The needle-shaped leaves do not contribute greatly to photosynthesis, the majority of which takes place in the green stem (Figure 4).



Figure 4. Thin leaves originating at the joints are noticeable on the horsetail plant. Horsetails were once used as scrubbing brushes and were nicknamed scouring brushes. (credit: Myriam Feldman)

Silica collects in the epidermal cells, contributing to the stiffness of horsetail plants. Underground stems known as rhizomes anchor the plants to the ground. Modern-day horsetails are homosporous and produce bisexual gametophytes.

Phylum Monilophyta: Class Psilotopsida (Whisk Ferns)



Figure 5. The whisk fern *Psilotum nudum* has conspicuous green stems with knob-shaped sporangia. (credit: Forest & Kim Starr)

While most ferns form large leaves and branching roots, the **whisk ferns**, Class Psilotopsida, lack both roots and leaves, probably lost by reduction. Photosynthesis takes place in their green stems, and small yellow knobs form at the tip of the branch stem and contain the sporangia. Whisk ferns were considered an early pterophytes. However, recent comparative DNA analysis suggests that this group may have lost both vascular tissue and roots through evolution, and is more closely related to ferns.



Figure 6. Some specimens of this short tree-fern species can grow very tall. (credit: Adrian Pingstone)

Phylum Monilophyta: Class Polypodiopsida (True Ferns)

With their large fronds, the true **ferns** are perhaps the most readily recognizable seedless vascular plants. They are also considered to be the most advanced seedless vascular plants and display characteristics commonly observed in seed plants. More than 20,000 species of ferns live in environments ranging from the tropics to temperate forests. Although some species survive in dry environments, most ferns are restricted to moist, shaded places. Ferns made their appearance in the fossil record during the Devonian period (420 MYA) and expanded during the Carboniferous (360 to 300 MYA).

The dominant stage of the life cycle of a fern is the sporophyte, which consists of large compound leaves called fronds. Fronds may be either finely divided or broadly lobed. Fronds fulfill a double role; they are photosynthetic organs that also carry reproductive organs. The stem may be buried underground as a rhizome, from which adventitious roots grow to absorb water and nutrients from the soil; or, they may grow above ground as a trunk in tree ferns (Figure 25.21). **Adventitious** organs are those that grow in unusual places, such as roots growing from the side of a stem.

The tip of a developing fern frond is rolled into a crozier, or fiddlehead (Figure 7a and Figure 7b). Fiddleheads unroll as the frond develops.



Figure 7. Croziers, or fiddleheads, are the tips of fern fronds. (credit a: modification of work by Cory Zanker; credit b: modification of work by Myriam Feldman)

The lifecycle of a fern is depicted in Figure 8.

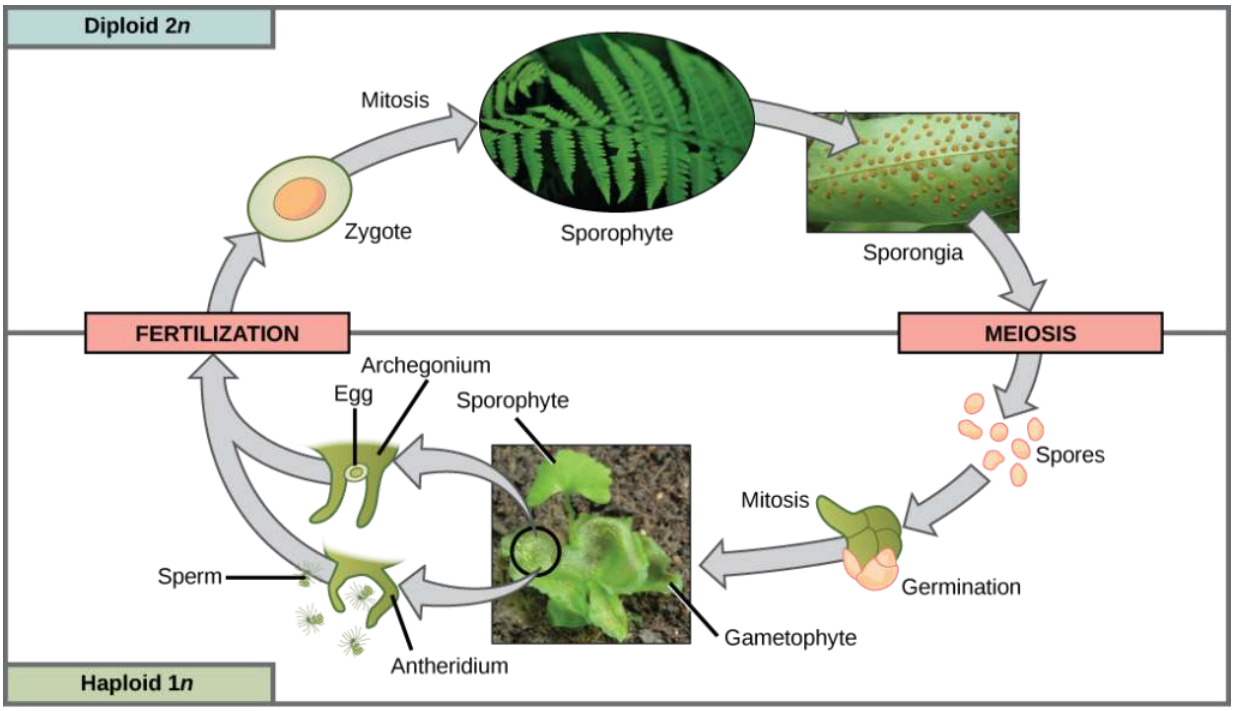


Figure 8. This life cycle of a fern shows alternation of generations with a dominant sporophyte stage. (credit “fern”: modification of work by Cory Zanker; credit “gametophyte”: modification of work by “Vlmastra”/Wikimedia Commons)

? Practice Question

Which of the following statements about the fern life cycle is false?

a. Sporangia produce haploid spores.
b. The sporophyte grows from a gametophyte.
c. The sporophyte is diploid and the gametophyte is haploid.
d. Sporangia form on the underside of the gametophyte.

[reveal-answer q=”184000″]Show Answer[/reveal-answer]
[hidden-answer a=”184000″]Statement d is false.[/hidden-answer]

To see an animation of the lifecycle of a fern and to test your knowledge, go to the website.



Figure 9. Sori appear as small bumps on the underside of a fern frond. (credit: Myriam Feldman)

Most ferns produce the same type of spores and are therefore homosporous. The diploid sporophyte is the most conspicuous stage of the lifecycle. On the underside of its mature fronds, sori (singular, sorus) form as small clusters where sporangia develop (Figure 9).

Inside the sori, spores are produced by meiosis and released into the air. Those that land on a suitable substrate germinate and form a heart-shaped gametophyte, which is attached to the ground by thin filamentous rhizoids (Figure 10).

The inconspicuous gametophyte harbors both sex gametangia. Flagellated sperm released from the antheridium swim on a wet surface to the archegonium, where the egg is fertilized. The newly formed zygote grows into a sporophyte that emerges from the gametophyte and grows by mitosis into the next generation sporophyte.

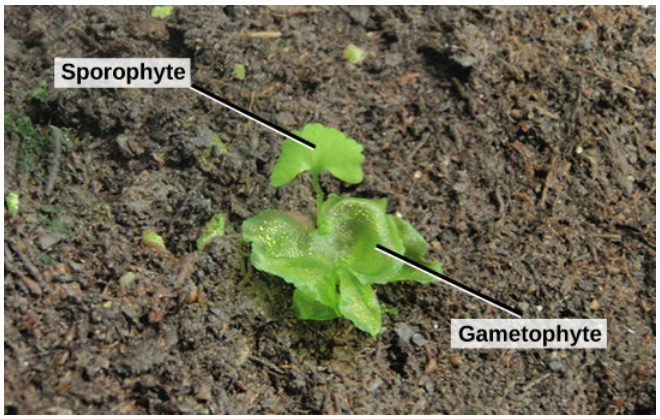


Figure 10. Shown here are a young sporophyte (upper part of image) and a heart-shaped gametophyte (bottom part of image). (credit: modification of work by “Vlmastra”/Wikimedia Commons)

? Try It

Looking at the well-laid parterres of flowers and fountains in the grounds of royal castles and historic houses of Europe, it’s clear that the gardens’ creators knew about more than art and design. They were also familiar with the biology of the plants they chose. Landscape design also has strong roots in the United States’ tradition. A prime example of early American classical design is Monticello: Thomas Jefferson’s private estate. Among his many interests, Jefferson maintained a strong passion for botany. Landscape layout can encompass a small private space, like a backyard garden; public gathering places, like Central Park in New York City; or an entire city plan, like Pierre L’Enfant’s design for Washington, DC.

A landscape designer will plan traditional public spaces—such as botanical gardens, parks, college campuses, gardens, and larger developments—as well as natural areas and private gardens. The restoration of natural places encroached on by human intervention, such as wetlands, also requires the expertise of a landscape designer.



Figure 11. This landscaped border at a college campus was designed by students in the horticulture and landscaping department of the college. (credit: Myriam Feldman)

With such an array of necessary skills, a landscape designer’s education includes a solid background in botany, soil science, plant pathology, entomology, and horticulture. Coursework in architecture and design software is also required for the completion of the degree. The successful design of a landscape rests on an extensive knowledge of plant growth requirements, such as light and shade, moisture levels, compatibility of different species, and susceptibility to pathogens and pests. Mosses and ferns will thrive in a shaded area, where fountains provide moisture; cacti, on the other hand, would not fare well in that environment. The future growth of individual plants must be taken into account, to avoid crowding and competition for light and nutrients. The appearance of the space over time is also of concern. Shapes, colors, and biology must be balanced for a well-maintained and sustainable green space. Art, architecture, and biology blend in a beautifully designed and implemented landscape.

The Importance of Seedless Vascular Plants

Mosses and liverworts are often the first macroscopic organisms to colonize an area, both in a primary succession—where bare land is settled for the first time by living organisms—or in a secondary succession, where soil remains intact after a catastrophic event wipes out many existing species. Their spores are carried by the wind, birds, or insects. Once mosses and liverworts are

established, they provide food and shelter for other species. In a hostile environment, like the tundra where the soil is frozen, bryophytes grow well because they do not have roots and can dry and rehydrate rapidly once water is again available. Mosses are at the base of the food chain in the tundra biome. Many species—from small insects to musk oxen and reindeer—depend on mosses for food. In turn, predators feed on the herbivores, which are the primary consumers. Some reports indicate that bryophytes make the soil more amenable to colonization by other plants. Because they establish symbiotic relationships with nitrogen-fixing cyanobacteria, mosses replenish the soil with nitrogen.

At the end of the nineteenth century, scientists observed that lichens and mosses were becoming increasingly rare in urban and suburban areas. Since bryophytes have neither a root system for absorption of water and nutrients, nor a cuticle layer that protects them from desiccation, pollutants in rainwater readily penetrate their tissues; they absorb moisture and nutrients through their entire exposed surfaces. Therefore, pollutants dissolved in rainwater penetrate plant tissues readily and have a larger impact on mosses than on other plants. The disappearance of mosses can be considered a bioindicator for the level of pollution in the environment.

Ferns contribute to the environment by promoting the weathering of rock, accelerating the formation of topsoil, and slowing down erosion by spreading rhizomes in the soil. The water ferns of the genus *Azolla* harbor nitrogen-fixing cyanobacteria and restore this important nutrient to aquatic habitats.



Figure 12. *Sphagnum acutifolium* is dried peat moss and can be used as fuel. (credit: Ken Goulding)

Seedless plants have historically played a role in human life through uses as tools, fuel, and medicine. Dried **peat moss**, *Sphagnum*, is commonly used as fuel in some parts of Europe and is considered a renewable resource. *Sphagnum* bogs (Figure 12) are cultivated with cranberry and blueberry bushes. The ability of *Sphagnum* to hold moisture makes the moss a common soil conditioner. Florists use blocks of *Sphagnum* to maintain moisture for floral arrangements.

The attractive fronds of ferns make them a favorite ornamental plant. Because they thrive in low light, they are well suited as house plants. More importantly, fiddleheads are a traditional spring food of Native Americans in the Pacific Northwest, and are popular as a side dish in French cuisine. The licorice fern, *Polypodium glycyrrhiza*, is part of the diet of the Pacific Northwest coastal tribes, owing in part to the sweetness of its rhizomes. It has a faint licorice taste and serves as a sweetener. The rhizome also figures in the pharmacopeia of Native Americans for its medicinal properties and is used as a remedy for sore throat.

Go to this website to learn how to identify fern species based upon their fiddleheads.

By far the greatest impact of seedless vascular plants on human life, however, comes from their extinct progenitors. The tall club mosses, horsetails, and tree-like ferns that flourished in the swampy forests of the Carboniferous period gave rise to large deposits of coal throughout the world. Coal provided an abundant source of energy during the Industrial Revolution, which had tremendous consequences on human societies, including rapid technological progress and growth of large cities, as well as the degradation of the environment. Coal is still a prime source of energy and also a major contributor to global warming.

Learning Objectives

Vascular systems consist of xylem tissue, which transports water and minerals, and phloem tissue, which transports sugars and proteins. With the development of the vascular system, there appeared leaves to act as large photosynthetic organs, and roots to access water from the ground. Small uncomplicated leaves are microphylls. Large leaves with vein patterns are megaphylls. Modified leaves that bear sporangia are sporophylls. Some sporophylls are arranged in cone structures called strobili.

The seedless vascular plants include club mosses, which are the most primitive; whisk ferns, which lost leaves and roots by reductive evolution; and horsetails and ferns. Ferns are the most advanced group of seedless vascular plants. They are

distinguished by large leaves called fronds and small sporangia-containing structures called sori, which are found on the underside of the fronds.

Mosses play an essential role in the balance of the ecosystems; they are pioneering species that colonize bare or devastated environments and make it possible for a succession to occur. They contribute to the enrichment of the soil and provide shelter and nutrients for animals in hostile environments. Mosses and ferns can be used as fuels and serve culinary, medical, and decorative purposes.

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10.7: Introduction to Seed Plants

Classify seed plants

The lush palms on tropical shorelines do not depend on water for the dispersal of their pollen, fertilization, or the survival of the zygote—unlike mosses, liverworts, and ferns of the terrain. Seed plants, such as palms, have broken free from the need to rely on water for their reproductive needs. 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. For millennia, human societies have depended on seed plants for nutrition and medicinal compounds: and more recently, for industrial by-products, such as timber and paper, dyes, and textiles. Palms provide materials including rattans, oils, and dates. Wheat is grown to feed both human and animal populations. The fruit of the cotton boll flower is harvested as a boll, with its fibers transformed into clothing or pulp for paper. The showy opium poppy is valued both as an ornamental flower and as a source of potent opiate compounds.



Figure 1. 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)

What You'll Learn to Do

- Describe the evolutionary history of seed plants
- Identify the main characteristics of gymnosperms
- Identify the main characteristics of angiosperms
- Discuss the roles that plants play in ecosystems

Learning Activities

The learning activities for this section include the following:

- Evolution of Seed Plants
- Gymnosperms
- Angiosperms
- The Role of Seed Plants
- Self Check: Seed Plants

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10.8: 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. The lifecycle of bryophytes and pterophytes is characterized by the alternation of generations, like gymnosperms and angiosperms; what sets bryophytes and pterophytes apart from gymnosperms and angiosperms is their reproductive requirement for water. The completion of the bryophyte and pterophyte life cycle requires water because the male gametophyte releases sperm, which must swim—propelled by their flagella—to reach and fertilize the female gamete or egg. After fertilization, the zygote matures and grows into a sporophyte, which in turn will form sporangia or "spore vessels." In the sporangia, mother cells undergo meiosis and produce the haploid spores. Release of spores in a suitable environment will lead to germination and a new generation of gametophytes.

In seed plants, the evolutionary trend led to a dominant sporophyte generation, and at the same time, a systematic reduction in the size of the gametophyte: from a conspicuous structure to a microscopic cluster of cells enclosed in the tissues of the sporophyte. Whereas lower vascular plants, such as club mosses and ferns, are mostly homosporous (produce only one type of spore), all seed plants, or **spermatophytes**, are heterosporous. They form two types of spores: megaspores (female) and microspores (male). Megaspores develop into female gametophytes that produce eggs, and microspores mature into male gametophytes that generate sperm. Because the gametophytes mature within the spores, they are not free-living, as are the gametophytes of other seedless vascular plants. Heterosporous seedless plants are seen as the evolutionary forerunners of seed plants.

Seeds and pollen—two critical adaptations to drought, and to reproduction that doesn't require water—distinguish seed plants from other (seedless) vascular plants. Both adaptations were required for the colonization of land begun by the bryophytes and their ancestors. Fossils place the earliest distinct seed plants at about 350 million years ago. The first reliable record of gymnosperms dates their appearance to the Pennsylvanian period, about 319 million years ago (Table 1). Gymnosperms were preceded by **progymnosperms**, the first naked seed plants, which arose about 380 million years ago. Progymnosperms were a transitional group of plants that superficially resembled conifers (cone bearers) because they produced wood from the secondary growth of the vascular tissues; however, they still reproduced like ferns, releasing spores into the environment. Gymnosperms dominated the landscape in the early (Triassic) and middle (Jurassic) Mesozoic era. Angiosperms surpassed gymnosperms by the middle of the Cretaceous (about 100 million years ago) in the late Mesozoic era, and today are the most abundant plant group in most terrestrial biomes.

Table 1. Geologic Timescale[1]

Eon	Era	Period	Start, MYA
Phanerozoic	Cenozoic	Quaternary	1.6
		Neogene	23
		Paleogene	66
	Mesozoic	Cretaceous	145
		Jurassic	201
		Triassic	252
	Paleozoic	Permian	298
		Carboniferous	360
		Devonian	419
		Silurian	444
		Ordovician	485
		Cambrian	540
Proterozoic	Late Proterozoic Middle Proterozoic Early Proterozoic		2500
Archean	Late Archean Middle Archean Early Archean		4000
Pre-Archean			~4600

Pollen and seed were innovative structures that allowed seed plants to break their dependence on water for reproduction and development of the embryo, and to conquer dry land. The **pollen grains** are the male gametophytes, which contain the sperm (gametes) of the plant. The small haploid (1*n*) cells are encased in a protective coat that prevents desiccation (drying out) and mechanical damage. Pollen grains can travel far from their original sporophyte, spreading the plant's genes. The **seed** offers the embryo protection, nourishment, and a mechanism to maintain dormancy for tens or even thousands of years, ensuring germination can occur when growth conditions are optimal. Seeds therefore allow plants to disperse the next generation through both space and time. With such evolutionary advantages, seed plants have become the most successful and familiar group of plants, in part because of their size and striking appearance.

Evolution of Gymnosperms



Figure 1. 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)

The fossil plant *Elkinsia polymorpha*, a “seed fern” from the Devonian period—about 400 million years ago—is considered the earliest seed plant known to date. Seed ferns (Figure 1) produced their seeds along their branches without specialized structures. What makes them the first true seed plants is that they developed structures called cupules to enclose and protect the **ovule**—the female gametophyte and associated tissues—which develops into a seed upon fertilization. Seed plants resembling modern tree ferns became more numerous and diverse in the coal swamps of the Carboniferous period.

Fossil records indicate the first gymnosperms (progymnosperms) most likely originated in the Paleozoic era, during the middle Devonian period: about 390 million years ago. 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.



Figure 2. This boreal forest (taiga) has low-lying plants and conifer trees. (credit: L.B. Brubaker, NOAA)

The Ginkgoales, a group of gymnosperms with only one surviving species—the *Gingko biloba*—were the first gymnosperms to appear during the lower Jurassic. Gymnosperms expanded in the Mesozoic era (about 240 million years ago), 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. 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) and the alpine forests at higher mountain elevations (Figure 2) because of their adaptation to cold and dry growth conditions.

Seeds and Pollen as an Evolutionary Adaptation to Dry Land

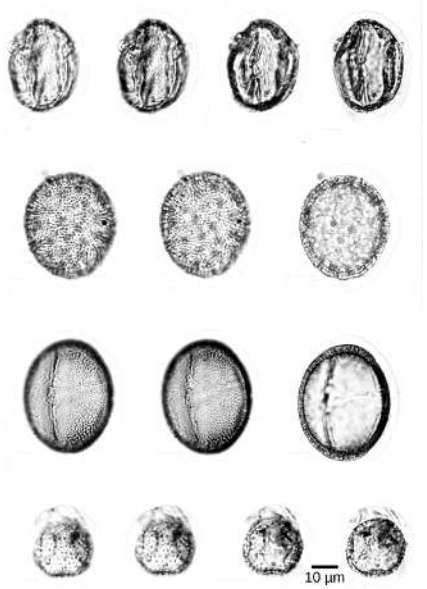


Figure 3. This fossilized pollen is from a Buckbean fen core found in Yellowstone National Park, Wyoming. The pollen is magnified 1,054 times. (credit: R.G. Baker, USGS; scale-bar data from Matt Russell)

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 (Figure 3) 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. 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.

Evolution of Angiosperms

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 (Figure 4) 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 million years ago. Earlier traces of angiosperms are scarce. Fossilized pollen recovered from Jurassic geological material has been attributed to 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 played a key role in ecology and the evolution of flowering plants.



Figure 4. This leaf imprint shows a *Ficus speciosissima*, an angiosperm that flourished during the Cretaceous period. (credit: W. T. Lee, USGS)

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 form a sister clade (a species and its descendents) 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.

The most primitive living angiosperm is considered to be *Amborella trichopoda*, a small plant native to the rainforest of New Caledonia, an island in the South Pacific. Analysis of the genome of *A. trichopoda* has shown that it is related to all existing flowering plants and belongs to the oldest confirmed branch of the angiosperm family tree. A few other angiosperm groups called basal angiosperms, are viewed as primitive because they branched off early from the phylogenetic tree. Most modern angiosperms are classified as either monocots or eudicots, based on the structure of their leaves and embryos. Basal angiosperms, such as water lilies, are considered more primitive because they share morphological traits with both monocots and eudicots.

Flowers and Fruits as an Evolutionary Adaptation

Angiosperms produce their gametes in separate organs, which are usually housed in a **flower**. Both fertilization and embryo development take place inside an 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.

Following fertilization of the egg, the ovule grows into a seed. The surrounding tissues of the ovary thicken, developing into a **fruit** that will protect the seed 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.

? Try It

All living organisms display patterns of relationships derived from their evolutionary history. Phylogeny is the science that describes the relative connections between organisms, in terms of ancestral and descendant species. Phylogenetic trees, such as the plant evolutionary history shown in Figure 5, are tree-like branching diagrams that depict these relationships. Species are found at the tips of the branches. Each branching point, called a node, is the point at which a single taxonomic group (taxon), such as a species, separates into two or more species.

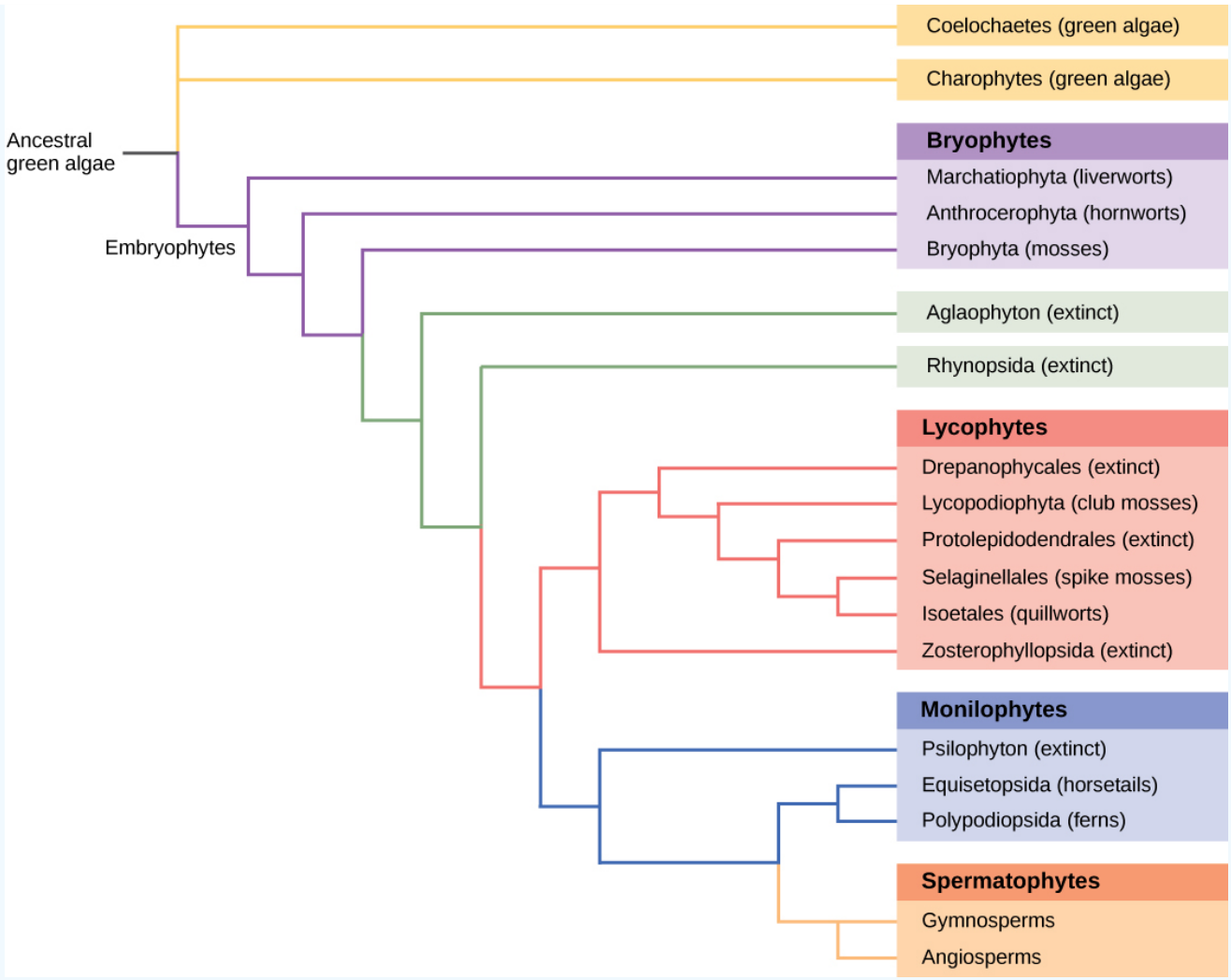


Figure 5. This phylogenetic tree shows the evolutionary relationships of plants.

Phylogenetic trees have been built to describe the relationships between species since Darwin's time. Traditional methods involve comparison of homologous anatomical structures and embryonic development, assuming that closely related organisms share anatomical features during embryo development. Some traits that disappear in the adult are present in the embryo; for example, a human fetus, at one point, has a tail. The study of fossil records shows the intermediate stages that link an ancestral form to its descendants. Most of these approaches are imprecise and lend themselves to multiple interpretations. As the tools of molecular biology and computational analysis have been developed and perfected in recent years, a new generation of tree-building methods has taken shape. The key assumption is that genes for essential proteins or RNA structures, such as the ribosomal RNA, are inherently conserved because mutations (changes in the DNA sequence) could compromise the survival of the organism. DNA from minute amounts of living organisms or fossils can be amplified by polymerase chain reaction (PCR) and sequenced, targeting the regions of the genome that are most likely to be conserved between species. The genes encoding the ribosomal RNA from the small 18S subunit and plastid genes are frequently chosen for DNA alignment analysis.

Once the sequences of interest are obtained, they are compared with existing sequences in databases such as GenBank, which is maintained by The National Center for Biotechnology Information. A number of computational tools are available to align and analyze sequences. Sophisticated computer analysis programs determine the percentage of sequence identity or homology. Sequence homology can be used to estimate the evolutionary distance between two DNA sequences and reflect the time elapsed since the genes separated from a common ancestor. Molecular analysis has revolutionized phylogenetic trees. In some cases, prior results from morphological studies have been confirmed: for example, confirming *Amborella trichopoda* as the most primitive angiosperm known. However, some groups and relationships have been rearranged as a result of DNA analysis.

Learning Objectives

Seed plants appeared about one million years ago, during the Carboniferous period. Two major innovations—seed and pollen—allowed seed plants to reproduce in the absence of water. The gametophytes of seed plants shrank, while the sporophytes became prominent structures and the diploid stage became the longest phase of the lifecycle. Gymnosperms became the dominant group during the Triassic. In these, pollen grains and seeds protect against desiccation. The seed, unlike a spore, is a diploid embryo surrounded by storage tissue and protective layers. It is equipped to delay germination until growth conditions are optimal. Angiosperms bear both flowers and fruit. The structures protect the gametes and the embryo during its development. Angiosperms appeared during the Mesozoic era and have become the dominant plant life in terrestrial habitats.

1. "Geologic time scale," *Wikipedia*. https://en.Wikipedia.org/wiki/Geologic_time_scale. ↵

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10.9: 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).

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** (plural = *strobili*) describes a tight arrangement of sporophylls around a central stalk, as seen in cones. Some seeds are enveloped by sporophyte tissues upon maturation. The layer of sporophyte tissue that surrounds the megasporangium, and later, the embryo, is called the **integument**.

Gymnosperms were the dominant phylum in Mesozoic era. They are adapted to live where fresh water is scarce during part of the year, or in the nitrogen-poor soil of a bog. Therefore, they are still the prominent phylum in the coniferous biome or taiga, where the evergreen conifers have a selective advantage in cold and dry weather. Evergreen conifers continue low levels of photosynthesis during the cold months, and are ready to take advantage of the first sunny days of spring. One disadvantage is that conifers are more susceptible than deciduous trees to infestations because conifers do not lose their leaves all at once. They cannot, therefore, shed parasites and restart with a fresh supply of leaves in spring.

The life cycle of a gymnosperm involves alternation of generations, with a dominant sporophyte in which the female gametophyte resides, and reduced gametophytes. 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) plants. The life cycle of a conifer will serve as our example of reproduction in gymnosperms.

Life Cycle of a Conifer

Pine trees are conifers (cone bearing) and carry both male and female sporophylls on the same mature sporophyte. Therefore, they are monoecious plants. Like all gymnosperms, pines are heterosporous and generate two different types of spores: male microspores and female megaspores. In the male cones, or staminate cones, the **microsporocytes** give rise to pollen grains by meiosis. In the spring, large amounts of yellow pollen are released and carried by the wind. Some gametophytes will land on a female cone. Pollination is defined as the initiation of pollen tube growth. The pollen tube develops slowly, and the generative cell in the pollen grain divides into two haploid sperm cells by mitosis. At fertilization, one of the sperm cells will finally unite its haploid nucleus with the haploid nucleus of a haploid egg cell.

Female cones, or **ovulate cones**, contain two ovules per scale. One megaspore mother cell, or **megasporocyte**, undergoes meiosis in each ovule. Three of the four cells break down; only a single surviving cell will develop into a female multicellular gametophyte, which encloses archegonia (an archegonium is a reproductive organ that contains a single large egg). Upon fertilization, the diploid egg will give rise to the embryo, which is enclosed in a seed coat of tissue from the parent plant. Fertilization and seed development is a long process in pine trees: it may take up to two years after pollination. The seed that is formed contains three generations of tissues: the seed coat that originates from the sporophyte tissue, the gametophyte that will provide nutrients, and the embryo itself.

Figure 1 illustrates the life cycle of a conifer. The sporophyte ($2n$) phase is the longest phase in the life of a gymnosperm. The gametophytes ($1n$)—microspores and megaspores—are reduced in size. It may take more than year between pollination and fertilization while the pollen tube grows towards the megasporocyte ($2n$), which undergoes meiosis into megaspores. The megaspores will mature into eggs ($1n$).

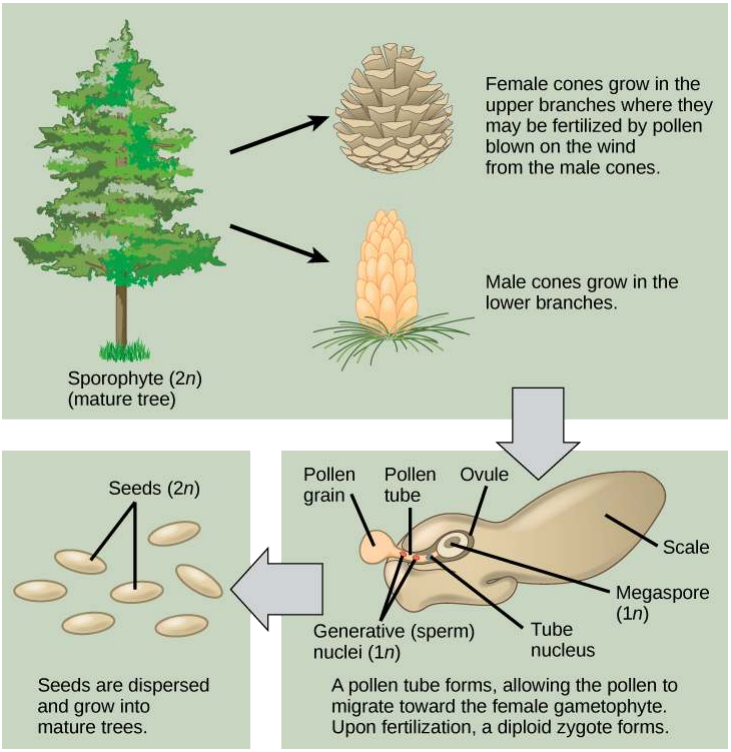


Figure 1. This image shows the life cycle of a conifer. Pollen from male cones blows up into upper branches, where it fertilizes female cones.

? Practice Question

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

[reveal-answer q="494399"]Show Answer[/reveal-answer]
[hidden-answer a="494399"]The diploid zygote forms after the pollen tube has finished forming, so that the male generative nuclei can fuse with the female gametophyte.[/hidden-answer]

Watch this video to see the process of seed production in gymnosperms.

A link to an interactive elements can be found at the bottom of this page.

Diversity of Gymnosperms

Modern gymnosperms are classified into four phyla. Coniferophyta, Cycadophyta, and Ginkgophyta 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 are considered the closest group to angiosperms because they produce true xylem tissue.

Conifers (Coniferophyta)

Conifers are the dominant phylum of gymnosperms, with the most variety of species (Figure 2). Most are typically tall trees that usually bear scale-like or needle-like leaves. Water evaporation from leaves is reduced by their thin shape and the thick cuticle. Snow slides easily off needle-shaped leaves, keeping the load light and decreasing breaking of branches. Adaptations to cold and dry weather explain the predominance of conifers at high altitudes and in cold climates. Conifers include familiar evergreen trees

such as pines, spruces, firs, cedars, sequoias, and yews. A few species are deciduous and lose their leaves in fall. The European larch and the tamarack are examples of deciduous conifers (Figure 2c). Many coniferous trees are harvested for paper pulp and timber. The wood of conifers is more primitive than the wood of angiosperms; it contains tracheids, but no vessel elements, and is therefore referred to as “soft wood.”



Figure 2. Conifers are the dominant form of vegetation in cold or arid environments and at high altitudes. Shown here are the (a) evergreen spruce *Picea sp*., (b) juniper *Juniperus sp*., (c) sequoia *Sequoia Semervirens*, which is a deciduous gymnosperm, and (d) the tamarack *Larix larcinia*. Notice the yellow leaves of the tamarack. (credit a: modification of work by Rosendahl; credit b: modification of work by Alan Levine; credit c: modification of work by Wendy McCormic; credit d: modification of work by NOAA)

Cycads



Figure 3. This *Encephalartos ferox* cycad has large cones and broad, fern-like leaves. (credit: Wendy Cutler)

Cycads thrive in mild climates, and are often mistaken for palms because of the shape of their large, compound leaves. Cycads bear large cones (Figure 3), and may be pollinated by beetles rather than wind: unusual for a gymnosperm. They dominated the landscape during the age of dinosaurs in the Mesozoic, but only a hundred or so species persisted to modern times. They face possible extinction, and several species are protected through international conventions. Because of their attractive shape, they are often used as ornamental plants in gardens in the tropics and subtropics.

Gingkophytes

The single surviving species of the **gingkophytes** group is the *Gingko biloba* (Figure 4). Its fan-shaped leaves—unique among seed plants because they feature a dichotomous venation pattern—turn yellow in autumn and fall from the tree. For centuries, *G. biloba*was cultivated by Chinese Buddhist monks in monasteries, which ensured its preservation. It is planted in public spaces because it is unusually resistant to pollution. Male and female organs are produced on separate plants. Typically, gardeners plant only male trees because the seeds produced by the female plant have an off-putting smell of rancid butter.



Figure 4. This plate from the 1870 book Flora Japonica, Sectio Prima (Tafelband) depicts the leaves and fruit of *Gingko biloba*, as drawn by Philipp Franz von Siebold and Joseph Gerhard Zuccarini.

Gnetophytes

Gnetophytes are the closest relative to modern angiosperms, and include three dissimilar genera of plants: *Ephedra*, *Gnetum*, and *Welwitschia* (Figure 5). Like angiosperms, they have broad leaves. In tropical and subtropical zones, gnetophytes are vines or small shrubs. *Ephedra* occurs in dry areas of the West Coast of the United States and Mexico. *Ephedra*'s small, scale-like leaves are the source of the compound ephedrine, which is used in medicine as a potent decongestant. Because ephedrine is similar to amphetamines, both in chemical structure and neurological effects, its use is restricted to prescription drugs. Like angiosperms, but unlike other gymnosperms, all gnetophytes possess vessel elements in their xylem.



(a) *Ephedra* (b) *Gnetum* (c) *Welwitschia*

Figure 5. (a) *Ephedra viridis*, known by the common name Mormon tea, grows on the West Coast of the United States and Mexico. (b)*Gnetum gnemon* grows in Malaysia. (c) The large *Welwitschia mirabilis* can be found in the Namibian desert. (credit a: modification of work by USDA; credit b: modification of work by Malcolm Manners; credit c: modification of work by Derek Keats)

Watch this video describing the amazing strangeness of Welwitschia.

A link to an interactive elements can be found at the bottom of this page.

Learning Objectives

Gymnosperms are heterosporous seed plants that produce naked seeds. They appeared in the Paleozoic period and were the dominant plant life during the Mesozoic. Modern-day gymnosperms belong to four phyla. The largest phylum, Coniferophyta, is represented by conifers, the predominant plants at high altitude and latitude. Cycads (phylum Cycadophyta) resemble palm trees and grow in tropical climates. *Gingko biloba* is the only representative of the phylum Gingkophyta. The last phylum, Gnetophyta, is a diverse group of shrubs that produce vessel elements in their wood.

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10.10: Angiosperms



Figure 1. These flowers grow in a botanical garden border in Bellevue, WA. Flowering plants dominate terrestrial landscapes. The vivid colors of flowers are an adaptation to pollination by animals such as insects and birds. (credit: Myriam Feldman)

From their humble and still obscure beginning during the early Jurassic period, the angiosperms—or flowering plants—have evolved to dominate most terrestrial ecosystems (Figure 1). 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. The function of the flower is to ensure pollination. 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. 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.

Flowers

Flowers are modified leaves, or sporophylls, organized around a central stalk. Although they vary greatly in appearance, all flowers contain the same structures: sepals, petals, carpels, and stamens. The peduncle attaches the flower to the plant. A whorl of **sepals** (collectively called the **calyx**) is located at the base of the peduncle and encloses the unopened floral bud. Sepals are usually photosynthetic organs, although there are some exceptions. For example, the corolla in lilies and tulips consists of three sepals and three petals that look virtually identical. **Petals**, collectively the **corolla**, are located inside the whorl of sepals and often display vivid colors to attract pollinators. Flowers pollinated by wind are usually small, feathery, and visually inconspicuous. Sepals and petals together form the **perianth**. The sexual organs (carpels and stamens) are located at the center of the flower.

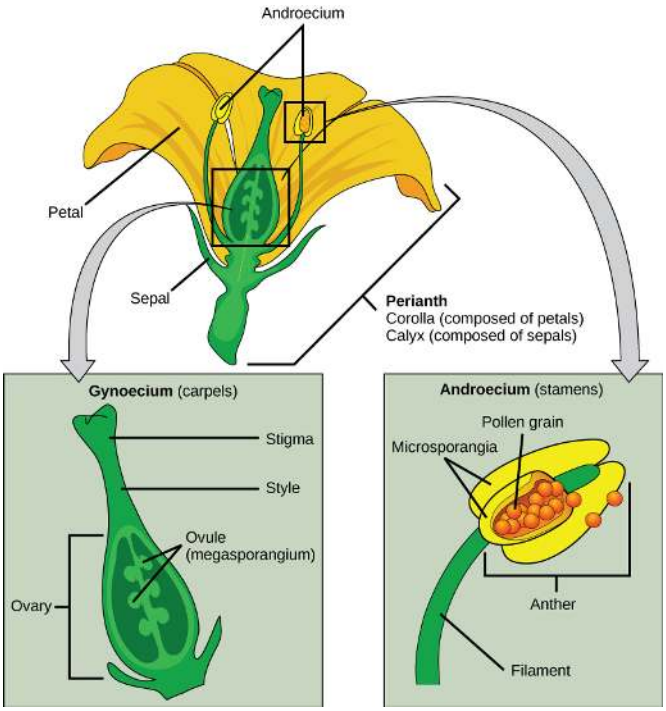


Figure 2. This image depicts the structure of a perfect flower. Perfect flowers produce both male and female floral organs. The flower shown has only one carpel, but some flowers have a cluster of carpels. Together, all the carpels make up the gynoecium. (credit: modification of work by Mariana Ruiz Villareal)

As illustrated in Figure 2, styles, stigmas, and ovules constitute the female organ: the **gynoecium** or **carpel**. Flower structure is very diverse, and carpels may be singular, multiple, or fused. Multiple fused carpels comprise a **pistil**. The megaspores and the female gametophytes are produced and protected by the thick tissues of the carpel. A long, thin structure called a **style** leads from the sticky **stigma**, where pollen is deposited, to the **ovary**, enclosed in the carpel. The ovary houses one or more ovules, each of which will develop into a seed upon fertilization. The male reproductive organs, the **stamens** (collectively called the androecium), surround the central carpel. Stamens are composed of a thin stalk called a **filament** and a sac-like structure called the anther. The filament supports the **anther**, where the microspores are produced by meiosis and develop into pollen grains.

Fruit

As the seed develops, the walls of the ovary thicken and form the fruit. The seed forms in an ovary, which also enlarges as the seeds grow. In botany, a fertilized and fully grown, ripened ovary is a fruit. Many foods commonly called vegetables are actually fruit. Eggplants, zucchini, string beans, and bell peppers are all technically fruit because they contain seeds and are derived from the thick ovary tissue. Acorns are nuts, and winged maple whirligigs (whose botanical name is samara) are also fruit. Botanists classify fruit into more than two dozen different categories, only a few of which are actually fleshy and sweet.

Mature fruit can be fleshy or dry. Fleshy fruit include the familiar berries, peaches, apples, grapes, and tomatoes. Rice, wheat, and nuts are examples of dry fruit. Another distinction is that not all fruits are derived from the ovary. For instance, strawberries are derived from the receptacle and apples from the pericarp, or hypanthium. Some fruits are derived from separate ovaries in a single flower, such as the raspberry. Other fruits, such as the pineapple, form from clusters of flowers. Additionally, some fruits, like watermelon and orange, have rinds. Regardless of how they are formed, fruits are an agent of seed dispersal. The variety of shapes and characteristics reflect the mode of dispersal. Wind carries the light dry fruit of trees and dandelions. Water transports floating coconuts. Some fruits attract herbivores with color or perfume, or as food. Once eaten, tough, undigested seeds are dispersed through the herbivore's feces. Other fruits have burs and hooks to cling to fur and hitch rides on animals.

The Life Cycle of an Angiosperm

The adult, or sporophyte, phase is the main phase of an angiosperm's life cycle (Figure 3). 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.

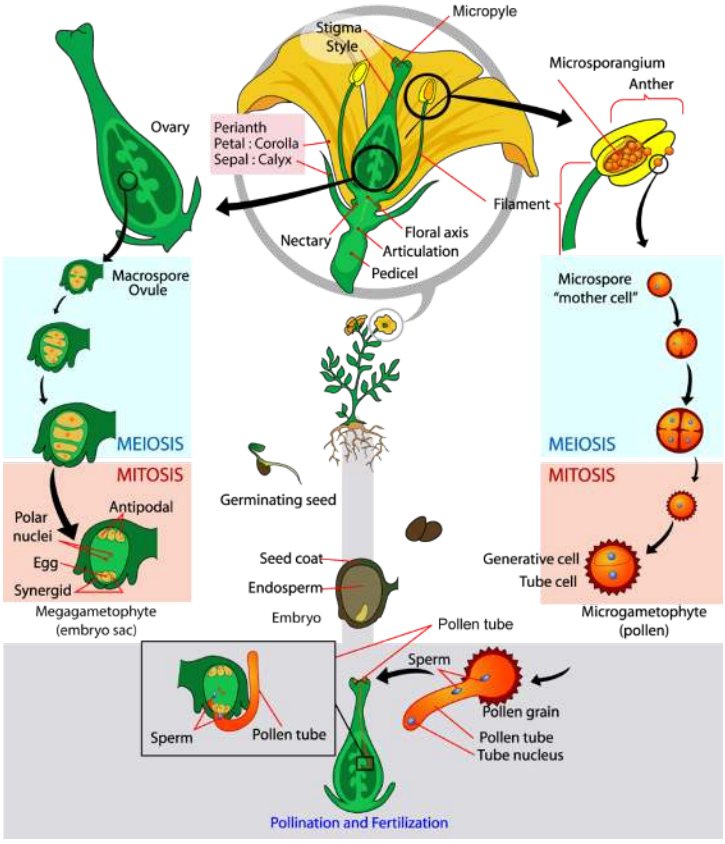


Figure 3. The life cycle of an angiosperm is shown. Anthers and carpels are structures that shelter the actual gametophytes: the pollen grain and embryo sac. Double fertilization is a process unique to angiosperms. (credit: modification of work by Mariana Ruiz Villareal)

? Practice Question

If a flower lacked a megasporangium, what type of gamete would not form?

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If the flower lacked a microsporangium, what type of gamete would not form?

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[hidden-answer a="773905"]Without a microsporangium, pollen would not form.[/hidden-answer]

The ovule, sheltered within the ovary of the carpel, contains the megasporangium protected by two layers of integuments and the ovary wall. Within each megasporangium, a megasporocyte undergoes meiosis, generating four megaspores—three small and one large. Only the large megaspore survives; it produces the female gametophyte, referred to as the embryo sac. The megaspore divides three times to form an eight-cell stage. Four of these cells migrate to each pole of the embryo sac; two come to the equator, and will eventually fuse to form a 2*n* polar nucleus; the three cells away from the egg form antipodals, and the two cells closest to the egg become the synergids.

The mature embryo sac contains one egg cell, two synergids or “helper” cells, three antipodal cells, and two polar nuclei in a central cell. When a pollen grain reaches the stigma, a pollen tube extends from the grain, grows down the style, and enters through the micropyle: an opening in the integuments of the ovule. The two sperm cells are deposited in the embryo sac.

A double fertilization event then occurs. One sperm and the egg combine, forming a diploid zygote—the future embryo. The other sperm fuses with the 2*n* polar nuclei, forming a triploid cell that will develop into the endosperm, which is tissue that serves as a food reserve. The zygote develops into an embryo with a radicle, or small root, and one (monocot) or two (dicot) leaf-like organs called **cotyledons**. This difference in the number of embryonic leaves is the basis for the two major groups of angiosperms: the monocots and the eudicots. Seed food reserves are stored outside the embryo, in the form of complex carbohydrates, lipids or proteins. The cotyledons serve as conduits to transmit the broken-down food reserves from their storage site inside the seed to the developing embryo. The seed consists of a toughened layer of integuments forming the coat, the endosperm with food reserves, and at the center, the well-protected embryo.

Most flowers are monoecious or bisexual, which means that they carry both stamens and carpels; only a few species self-pollinate. Monoecious flowers are also known as “perfect” flowers because they contain both types of sex organs (Figure 2). Both anatomical and environmental barriers promote cross-pollination mediated by a physical agent (wind or water), or an animal, such as an insect or bird. Cross-pollination increases genetic diversity in a species.

Diversity of Angiosperms

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, pollen grains, and other structures. **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.

Basal Angiosperms

The Magnoliidae are represented by the magnolias: tall trees bearing large, fragrant flowers that have many parts and are considered archaic (Figure 4d). Laurel trees produce fragrant leaves and small, inconspicuous flowers. The *Laurales* grow mostly in warmer climates and are small trees and shrubs. Familiar plants in this group include the bay laurel, cinnamon, spice bush (Figure 4a), and avocado tree. The *Nymphaeales* are comprised of the water lilies, lotus (Figure 4c), and similar plants; all species thrive in freshwater biomes, and have leaves that float on the water surface or grow underwater. Water lilies are particularly prized by gardeners, and have graced ponds and pools for thousands of years. The *Piperales* are a group of herbs, shrubs, and small trees that grow in the tropical climates. They have small flowers without petals that are tightly arranged in long spikes. Many species are the source of prized fragrance or spices, for example the berries of *Piper nigrum* (Figure 4b) are the familiar black peppercorns that are used to flavor many dishes.

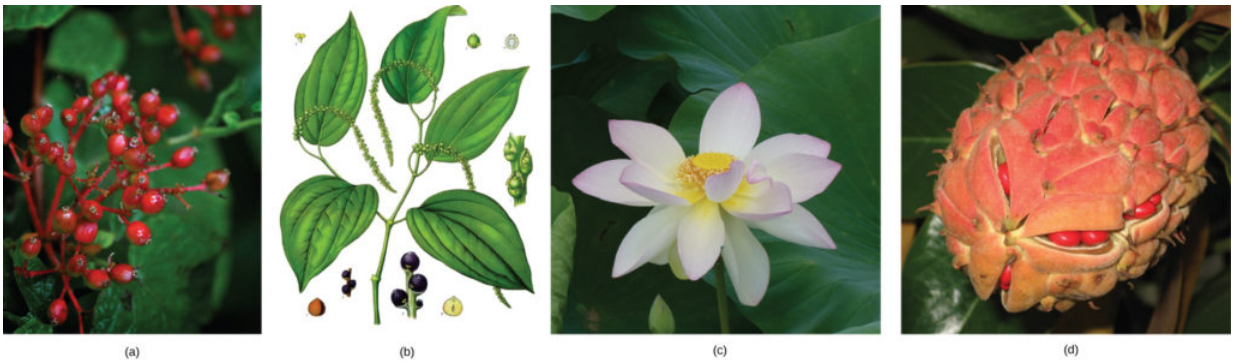


Figure 4. The (a) common spicebush belongs to the *Laurales*, the same family as cinnamon and bay laurel. The fruit of (b) the *Piper nigrumplant* is black pepper, the main product that was traded along spice routes. Notice the small, unobtrusive, clustered flowers. (c) Lotus flowers, *Nelumbo nucifera*, have been cultivated since ancient times for their ornamental value; the root of the lotus flower is eaten as a vegetable. The red seeds of (d) a magnolia tree, characteristic of the final stage, are just starting to appear. (credit a: modification of work by Cory Zanker; credit b: modification of work by Franz Eugen Köhler; credit c: modification of work by “berduchwal”/Flickr; credit d: modification of work by “Coastside2″/Wikimedia Commons).

Monocots

Plants in the monocot group are primarily identified as such by the presence of a single cotyledon in the seedling. Other anatomical features shared by monocots include veins that run parallel to the length of the leaves, and flower parts that are arranged in a three- or six-fold symmetry. True woody tissue is rarely found in monocots. In palm trees, vascular and parenchyma tissues produced by the primary and secondary thickening meristems form the trunk. The pollen from the first angiosperms was monosulcate, containing a single furrow or pore through the outer layer. This feature is still seen in the modern monocots. Vascular tissue of the stem is not arranged in any particular pattern. The root system is mostly adventitious and unusually positioned, with no major tap root. The monocots include familiar plants such as the true lilies (which are at the origin of their alternate name of Liliopsida), orchids, grasses, and palms. Many important crops are monocots, such as rice and other cereals, corn, sugar cane, and tropical fruits like bananas and pineapples (Figure 5).



Figure 5. The world's major crops are flowering plants. (a) Rice, (b) wheat, and (c) bananas are monocots, while (d) cabbage, (e) beans, and (f) peaches are dicots. (credit a: modification of work by David Nance, USDA ARS; credit b, c: modification of work by Rosendahl; credit d: modification of work by Bill Tarpenning, USDA; credit e: modification of work by Scott Bauer, USDA ARS; credit f: modification of work by Keith Weller, USDA)

Eudicots

Eudicots, or true dicots, are characterized by the presence of two cotyledons in the developing shoot. Veins form a network in leaves, and flower parts come in four, five, or many whorls. Vascular tissue forms a ring in the stem; in monocots, vascular tissue is scattered in the stem. Eudicots can be **herbaceous** (like grasses), or produce woody tissues. Most eudicots produce pollen that is trisulcate or triporate, with three furrows or pores. The root system is usually anchored by one main root developed from the embryonic radicle. Eudicots comprise two-thirds of all flowering plants. The major differences between monocots and eudicots are summarized in Table 1. Many species exhibit characteristics that belong to either group; as such, the classification of a plant as a monocot or a eudicot is not always clearly evident.

Table 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

Learning Objectives

Angiosperms are the dominant form of plant life in most terrestrial ecosystems, comprising about 90 percent of all plant species. Most crops and ornamental plants are angiosperms. Their success comes from two innovative structures that protect reproduction from variability in the environment: the flower and the fruit. Flowers were derived from modified leaves. The main parts of a flower are the sepals and petals, which protect the reproductive parts: the stamens and the carpels. The stamens produce the male gametes in pollen grains. The carpels contain the female gametes (the eggs inside the ovules), which are within the ovary of a carpel. The walls of the ovary thicken after fertilization, ripening into fruit that ensures dispersal by wind, water, or animals.

The angiosperm life cycle is dominated by the sporophyte stage. Double fertilization is an event unique to angiosperms. One sperm in the pollen fertilizes the egg, forming a diploid zygote, while the other combines with the two polar nuclei, forming a triploid cell that develops into a food storage tissue called the endosperm. Flowering plants are divided into two main groups, the monocots and eudicots, according to the number of cotyledons in the seedlings. Basal angiosperms belong to an older lineage than monocots and eudicots.

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10.11: 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.

Animals and Plants: Herbivory

Coevolution of flowering plants and insects is a hypothesis that has received much attention and support, especially because both angiosperms and insects diversified at about the same time in the middle Mesozoic. Many authors have attributed the diversity of plants and insects to pollination and herbivory, or consumption of plants by insects and other animals. This is believed to have been as much a driving force as pollination. Coevolution of herbivores and plant defenses is observed in nature. Unlike animals, most plants cannot outrun predators or use mimicry to hide from hungry animals. A sort of arms race exists between plants and herbivores. To “combat” herbivores, some plant seeds—such as acorn and unripened persimmon—are high in alkaloids and therefore unsavory to some animals. Other plants are protected by bark, although some animals developed specialized mouth pieces to tear and chew vegetal material. Spines and thorns (Figure 1) deter most animals, except for mammals with thick fur, and some birds have specialized beaks to get past such defenses.



(a) (b)

Figure 1. (a) Spines and (b) thorns are examples of plant defenses. (credit a: modification of work by Jon Sullivan; credit b: modification of work by I. Sáček, Sr.)

Herbivory has been used by seed plants for their own benefit in a display of mutualistic relationships. The dispersal of fruit by animals is the most striking example. The plant offers to the herbivore a nutritious source of food in return for spreading the plant’s genetic material to a wider area.

An extreme example of collaboration between an animal and a plant is the case of acacia trees and ants. The trees support the insects with shelter and food. In return, ants discourage herbivores, both invertebrates and vertebrates, by stinging and attacking leaf-eating insects.

Animals and Plants: Pollination

Grasses are a successful group of flowering plants that are wind pollinated. They produce large amounts of powdery pollen carried over large distances by the wind. The flowers are small and wisp-like. Large trees such as oaks, maples, and birches are also wind pollinated.

Explore this website for additional information on pollinators.



Figure 2. As a bee collects nectar from a flower, it is dusted by pollen, which it then disperses to other flowers. (credit: John Severns)

More than 80 percent of angiosperms depend on animals for pollination: the transfer of pollen from the anther to the stigma. Consequently, plants have developed many adaptations to attract pollinators. The specificity of specialized plant structures that target animals can be very surprising. It is possible, for example, to determine the type of pollinator favored by a plant just from the flower's characteristics. Many bird or insect-pollinated flowers secrete nectar, which is a sugary liquid.

They also produce both fertile pollen, for reproduction, and sterile pollen rich in nutrients for birds and insects. Butterflies and bees can detect ultraviolet light. Flowers that attract these pollinators usually display a pattern of low ultraviolet reflectance that helps them quickly locate the flower's center and collect nectar while being dusted with pollen (Figure 2). Large, red flowers with little smell and a long funnel shape are preferred by hummingbirds, who have good color perception, a poor sense of smell, and need a strong perch. White flowers opened at night attract moths. Other animals—such as bats, lemurs, and lizards—can also act as pollinating agents. Any disruption to these interactions, such as the disappearance of bees as a consequence of colony collapse disorders, can lead to disaster for agricultural industries that depend heavily on pollinated crops.

Testing Attraction of Flies by Rotting Flesh Smell

Question: Will flowers that offer cues to bees attract carrion flies if sprayed with compounds that smell like rotten flesh?

Background: Visitation of flowers by pollinating flies is a function mostly of smell. Flies are attracted by rotting flesh and carrions. The putrid odor seems to be the major attractant. The polyamines putrescine and cadaverine, which are the products of protein breakdown after animal death, are the source of the pungent smell of decaying meat. Some plants strategically attract flies by synthesizing polyamines similar to those generated by decaying flesh and thereby attract carrion flies.

Flies seek out dead animals because they normally lay their eggs on them and their maggots feed on the decaying flesh. Interestingly, time of death can be determined by a forensic entomologist based on the stages and type of maggots recovered from cadavers.

Hypothesis: Because flies are drawn to other organisms based on smell and not sight, a flower that is normally attractive to bees because of its colors will attract flies if it is sprayed with polyamines similar to those generated by decaying flesh.

Test the hypothesis:

1. Select flowers usually pollinated by bees. White petunia may be good choice.
2. Divide the flowers into two groups, and while wearing eye protection and gloves, spray one group with a solution of either putrescine or cadaverine. (Putrescine dihydrochloride is typically available in 98 percent concentration; this can be diluted to approximately 50 percent for this experiment.)
3. Place the flowers in a location where flies are present, keeping the sprayed and unsprayed flowers separated.
4. Observe the movement of the flies for one hour. Record the number of visits to the flowers using a table similar to Table 1. Given the rapid movement of flies, it may be beneficial to use a video camera to record the fly–flower interaction. Replay the video in slow motion to obtain an accurate record of the number of fly visits to the flowers.
5. Repeat the experiment four more times with the same species of flower, but using different specimens.
6. Repeat the entire experiment with a different type of flower that is normally pollinated by bees.

Table 1. Results of Number of Visits by Flies to Sprayed and Control/Unsprayed Flowers		
Trial #	Sprayed Flowers	Unsprayed Flowers
1		
2		
3		
4		
5		

Analyze your data: Review the data you have recorded. Average the number of visits that flies made to sprayed flowers over the course of the five trials (on the first flower type) and compare and contrast them to the average number of visits that flies made to the unsprayed/control flowers. Can you draw any conclusions regarding the attraction of the flies to the sprayed flowers?

For the second flower type used, average the number of visits that flies made to sprayed flowers over the course of the five trials and compare and contrast them to the average number of visits that flies made to the unsprayed/control flowers. Can you draw any conclusions regarding the attraction of the flies to the sprayed flowers?

Compare and contrast the average number of visits that flies made to the two flower types. Can you draw any conclusions about whether the appearance of the flower had any impact on the attraction of flies? Did smell override any appearance differences, or were the flies attracted to one flower type more than another?

Form a conclusion: Do the results support the hypothesis? If not, how can this be explained?

The Importance of Seed Plants in Human Life

Seed plants are the foundation of human diets across the world (Figure 3). Many societies eat almost exclusively vegetarian fare and depend solely on seed plants for their nutritional needs. A few crops (rice, wheat, and potatoes) dominate the agricultural landscape. Many crops were developed during the agricultural revolution, when human societies made the transition from nomadic hunter–gatherers to horticulture and agriculture. Cereals, rich in carbohydrates, provide the staple of many human diets. Beans and nuts supply proteins. Fats are derived from crushed seeds, as is the case for peanut and rapeseed (canola) oils, or fruits such as olives. Animal husbandry also consumes large amounts of crops.

Staple crops are not the only food derived from seed plants. Fruits and vegetables provide nutrients, vitamins, and fiber. Sugar, to sweeten dishes, is produced from the monocot sugarcane and the eudicot sugar beet. Drinks are made from infusions of tea leaves, chamomile flowers, crushed coffee beans, or powdered cocoa beans. Spices come from many different plant parts: saffron and cloves are stamens and buds, black pepper and vanilla are seeds, the bark of a bush in the *Laurales* family supplies cinnamon, and the herbs that flavor many dishes come from dried leaves and fruit, such as the pungent red chili pepper. The volatile oils of flowers and bark provide the scent of perfumes. Additionally, no discussion of seed plant contribution to human diet would be complete without the mention of alcohol. Fermentation of plant-derived sugars and starches is used to produce alcoholic beverages in all societies. In some cases, the beverages are derived from the fermentation of sugars from fruit, as with wines and, in other cases, from the fermentation of carbohydrates derived from seeds, as with beers.

Seed plants have many other uses, including providing wood as a source of timber for construction, fuel, and material to build furniture. Most paper is derived from the pulp of coniferous trees. Fibers of seed plants such as cotton, flax, and hemp are woven into cloth. Textile dyes, such as indigo, were mostly of plant origin until the advent of synthetic chemical dyes.

Lastly, it is more difficult to quantify the benefits of ornamental seed plants. These grace private and public spaces, adding beauty and serenity to human lives and inspiring painters and poets alike.



Figure 3. Humans rely on plants for a variety of reasons. (a) Cacao beans were introduced in Europe from the New World, where they were used by Mesoamerican civilizations. Combined with sugar, another plant product, chocolate is a popular food. (b) Flowers like the tulip are cultivated for their beauty. (c) Quinine, extracted from cinchona trees, is used to treat malaria, to reduce fever, and to alleviate pain. (d) This violin is made of wood. (credit a: modification of work by "Everjean"/Flickr; credit b: modification of work by Rosendahl; credit c: modification of work by Franz Eugen Köhler)

The medicinal properties of plants have been known to human societies since ancient times. There are references to the use of plants' curative properties in Egyptian, Babylonian, and Chinese writings from 5,000 years ago. Many modern synthetic therapeutic drugs are derived or synthesized de novo from plant secondary metabolites. It is important to note that the same plant extract can be a therapeutic remedy at low concentrations, become an addictive drug at higher doses, and can potentially kill at high concentrations. Table 2 presents a few drugs, their plants of origin, and their medicinal applications.

Table 2. Plant Origin of Medicinal Compounds and Medical Applications

Plant	Compound	Application
Deadly nightshade (*Atropa belladonna*)	Atropine	Dilate eye pupils for eye exams
Foxglove (*Digitalis purpurea*)	Digitalis	Heart disease, stimulates heart beat
Yam (*Dioscorea* spp.)	Steroids	Steroid hormones: contraceptive pill and cortisone
Ephedra (*Ephedra* spp.)	Ephedrine	Decongestant and bronchiole dilator
Pacific yew (*Taxus brevifolia*)	Taxol	Cancer chemotherapy; inhibits mitosis
Opium poppy (*Papaver somniferum*)	Opioids	Analgesic (reduces pain without loss of consciousness) and narcotic (reduces pain with drowsiness and loss of consciousness) in higher doses
Quinine tree (*Cinchona* spp.)	Quinine	Antipyretic (lowers body temperature) and antimalarial
Willow (*Salix* spp.)	Salicylic acid (aspirin)	Analgesic and antipyretic

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 catalogued, 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. Efforts to preserve biodiversity take several lines of action, from preserving heirloom seeds to barcoding species. Heirloom seeds come from plants that were traditionally grown in human populations, as opposed to the seeds used for large-scale agricultural production. Barcoding is a technique in which one or more short gene sequences, taken from a well-characterized portion of the genome, are used to identify a species through DNA analysis.

Learning Objectives

Angiosperm diversity is due in part to multiple interactions with animals. Herbivory has favored the development of defense mechanisms in plants, and avoidance of those defense mechanism in animals. Pollination (the transfer of pollen to a carpel) is mainly carried out by wind and animals, and angiosperms have evolved numerous adaptations to capture the wind or attract specific classes of animals.

Plants play a key role in ecosystems. They are a source of food and medicinal compounds, and provide raw materials for many industries. Rapid deforestation and industrialization, however, threaten plant biodiversity. In turn, this threatens the ecosystem.

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10.12: Putting It Together- Plant Diversity

As we learned at the beginning of this module, plants are essential to human life (as well as the lives of several other organisms): they act as food and release oxygen into the atmosphere. We've also learned that plants play a key role in the ecosystem by stabilizing soils, cycling carbon, and moderating the climate. With all these roles, it becomes clear that we must preserve plants and their diversity—or else we put ourselves and the biosphere at large at risk. As we continue on, we'll learn about how plants function and reproduce. As you learn, think about ways you can take this new knowledge and work to preserve your local plant diversity.

If plants and their interactions with humans interest you, you may want to look into the field of ethnobotany.

EthnobotanisT

The relatively new field of ethnobotany studies the interaction between a particular culture and the plants native to the region. Seed plants have a large influence on day-to-day human life. Not only are plants the major source of food and medicine, they also influence many other aspects of society, from clothing to industry. The medicinal properties of plants were recognized early on in human cultures. From the mid-1900s, synthetic chemicals began to supplant plant-based remedies.

Pharmacognosy is the branch of pharmacology that focuses on medicines derived from natural sources. With massive globalization and industrialization, there is a concern that much human knowledge of plants and their medicinal purposes will disappear with the cultures that fostered them. This is where ethnobotanists come in. To learn about and understand the use of plants in a particular culture, an ethnobotanist must bring in knowledge of plant life and an understanding and appreciation of diverse cultures and traditions. The Amazon forest is home to an incredible diversity of vegetation and is considered an untapped resource of medicinal plants; yet, both the ecosystem and its indigenous cultures are threatened with extinction.

To become an ethnobotanist, a person must acquire a broad knowledge of plant biology, ecology and sociology. Not only are the plant specimens studied and collected, but also the stories, recipes, and traditions that are linked to them. For ethnobotanists, plants are not viewed solely as biological organisms to be studied in a laboratory, but as an integral part of human culture. The convergence of molecular biology, anthropology, and ecology make the field of ethnobotany a truly multidisciplinary science.

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10.13: Cerego- Plant Diversity

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for Plant Diversity. You'll need to create a free log-in to practice these items, if you haven't already.

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CHAPTER OVERVIEW

11: Module 8- Plant Structure and Function

11.1: Why It Matters- Plant Structure and Function
11.2: Introduction to Plant Structures
11.3: Plant Cells
11.4: Plant Tissues and Organs
11.5: Stems
11.6: Leaves
11.7: Roots
11.8: Introduction to Transport of Water and Solutes in Plants
11.9: Water Potential
11.10: Transpiration
11.11: Photosynthates
11.12: Introduction to Plant Sensory Systems and Responses
11.13: Plant Responses to Light
11.14: Plant Responses to Gravity
11.15: Plant Responses to Wind and Touch
11.16: Defense Responses against Herbivores and Pathogens
11.17: Introduction to Plant Growth
11.18: How Plants Grow
11.19: Stem Growth
11.20: Growth Responses
11.21: Introduction to Plant Nutrition
11.22: Nutritional Requirements
11.23: Autotrophic Plants
11.24: Heterotrophic Plants
11.25: Putting It Together- Plant Structure and Function
11.26: Cerego- Plant Structure and Function

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11.1: Why It Matters- Plant Structure and Function

Why discuss the structure and function of plants?

We use plant-derived products every day in our lives, from paper to clothing to food. The different structures and components of plants allow them to form these different items we use.

The roots, stems, and leaves of plants are also structured to ensure that a plant can obtain the required sunlight, water, soil nutrients, and oxygen resources. Plants have developed some remarkable adaptations to thrive in less than ideal habitats, where one or more of these resources is in short supply.

In tropical rainforests, light is often scarce, since many trees and plants grow close together and block much of the sunlight from reaching the forest floor. Some plants have special adaptations that help them to survive in nutrient-poor environments. Many swamp plants have adaptations that enable them to thrive in wet areas, where their submerged roots have low access to oxygen. What type of adaptations do you think would help plants in these conditions?

Learning Outcomes

- Identify basic common structures of plants
- Describe how water and solutes are transported in plants
- Identify common sensory systems and responses in plants
- Identify the key elements and processes in plant growth
- Discuss the common nutritional needs of plants

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11.2: Introduction to Plant Structures

Identify basic common structures of plants

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

What You'll Learn to Do

- Discuss features of plant cells
- Identify the different tissue types and organ systems in plants
- Describe the main function and basic structure of stems
- Identify the structure and function of a typical leaf
- Identify the two types of root systems

Learning Activities

The learning activities for this section include the following:

- Plant Cells
- Plant Tissues and Organs
- Stems
- Leaves
- Roots
- Self Check: Plant Structures

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11.3: Plant Cells

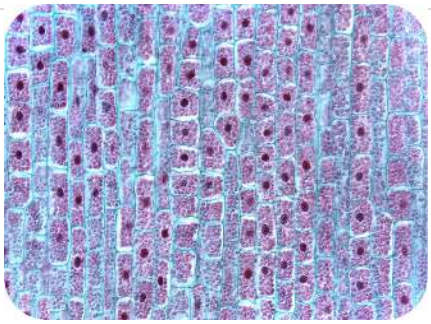


Figure 1. A section of a pine embryo.

Why do plant cells look like little rectangles? Look at Figure 1 and notice how all the cells seem to stack on each other, with no spaces in between. Might this allow the cells to form structures that can grow upright?

Organs in Plants?

Your body includes organ systems, such as the digestive system, made of individual organs, such as the stomach, liver, and pancreas, which work together to carry out a certain function (in this case, breaking down and absorbing food). These organs, in turn, are made of different kinds of tissues, which are groups of cells which work together to perform a specific job. For example, your stomach is made of muscle tissue to facilitate movement and glandular tissue to secrete enzymes for chemical breakdown of food molecules. These tissues, in turn, are made of cells specialized in shape, size, and component organelles, such as mitochondria for energy and microtubules for movement.

Plants, too, are made of organs, which in turn are made of tissues. Plant tissues, like ours, are constructed of specialized cells, which in turn contain specific organelles. It is these cells, tissues, and organs that carry out the dramatic lives of plants.

Plant Cells

Plant cells resemble other eukaryotic cells in many ways. For example, they are enclosed by a plasma membrane and have a nucleus and other membrane-bound organelles. A typical plant cell is represented by the diagram in Figure 2.

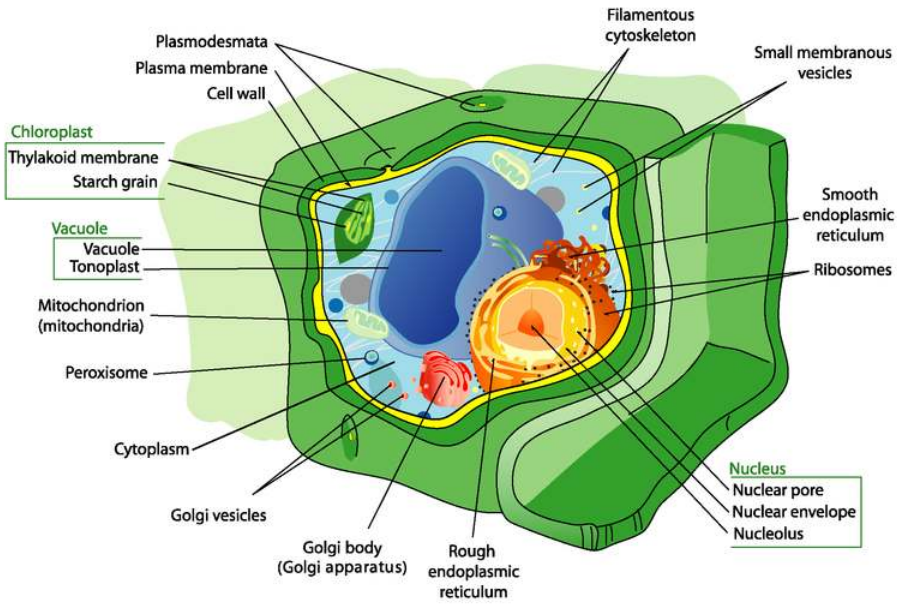


Figure 2. Plant cells have all the same structures as animal cells, plus some additional structures. Can you identify the unique plant structures in the diagram?

Plant Cell Structures

Structures found in plant cells but not animal cells include a large central vacuole, cell wall, and plastids such as chloroplasts.

- The large **central vacuole** is surrounded by its own membrane and contains water and dissolved substances. Its primary role is to maintain pressure against the inside of the cell wall, giving the cell shape and helping to support the plant.
- The **cell wall** is located outside the cell membrane. It consists mainly of **cellulose** and may also contain **lignin** , which makes it more rigid. The cell wall shapes, supports, and protects the cell. It prevents the cell from absorbing too much water and bursting. It also keeps large, damaging molecules out of the cell.
- **Plastids** are membrane-bound organelles with their own DNA. Examples are chloroplasts and chromoplasts. **Chloroplasts** contain the green pigment **chlorophyll** and carry out **photosynthesis**. Chromoplasts make and store other pigments. They give flower petals their bright colors.

Types of Plant Cells

There are three basic types of cells in most plants. These cells make up ground tissue, which will be discussed in another concept. The three types of cells are described in table below. The different types of plant cells have different structures and functions.

Type of Cell	Structure	Functions	Example
Parenchymal	cube-shaped loosely packed thin-walled relatively unspecialized contain chloroplasts	photosynthesis cellular respiration storage	food storage tissues of potatoes 
Collenchymal	elongated irregularly thickened walls	support wind resistance	*strings* running through a stalk of celery 
Sclerenchymal	very thick cell walls containing lignin	support strength	tough fibers in jute (used to make rope) 

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11.4: Plant Tissues and Organs

Plant Tissues

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

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

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

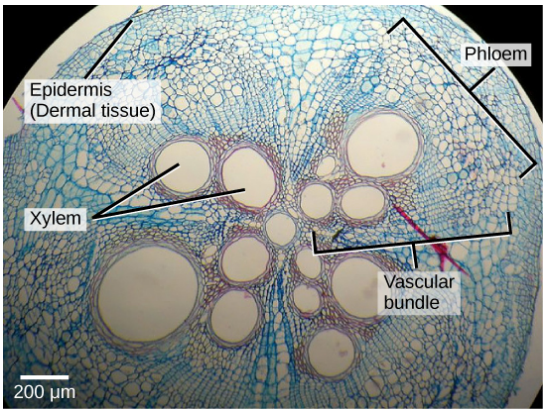


Figure 1. This light micrograph shows a cross section of a squash (*Curcurbita maxima*) stem. Each teardrop-shaped vascular bundle consists of large xylem vessels toward the inside and smaller phloem cells toward the outside. Xylem cells, which transport water and nutrients from the roots to the rest of the plant, are dead at functional maturity. Phloem cells, which transport sugars and other organic compounds from photosynthetic tissue to the rest of the plant, are living. The vascular bundles are encased in ground tissue and surrounded by dermal tissue. (credit: modification of work by “(biophotos)”/Flickr; scale-bar data from Matt Russell)

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

All animals are made of four types of tissue: epidermal, muscle, nerve, and connective tissues. Plants, too, are built of tissues, but not surprisingly, their very different lifestyles derive from different kinds of tissues. All three types of plant cells are found in most plant tissues. Three major types of plant tissues are dermal, ground, and vascular tissues.

Dermal Tissue

The dermal tissue of the stem consists primarily of **epidermis**, a single layer of cells covering and protecting the underlying tissue. Woody plants have a tough, waterproof outer layer of cork cells commonly known as **bark**, which further protects the plant from damage. Epidermal cells are the most numerous and least differentiated of the cells in the epidermis. The epidermis of a leaf also contains openings known as stomata, through which the exchange of gases takes place (Figure 2). Two cells, known as **guard cells**, surround each leaf stoma, controlling its opening and closing and thus regulating the uptake of carbon dioxide and the release of oxygen and water vapor. **Trichomes** are hair-like structures on the epidermal surface. They help to reduce **transpiration** (the loss of water by aboveground plant parts), increase solar reflectance, and store compounds that defend the leaves against predation by herbivores.

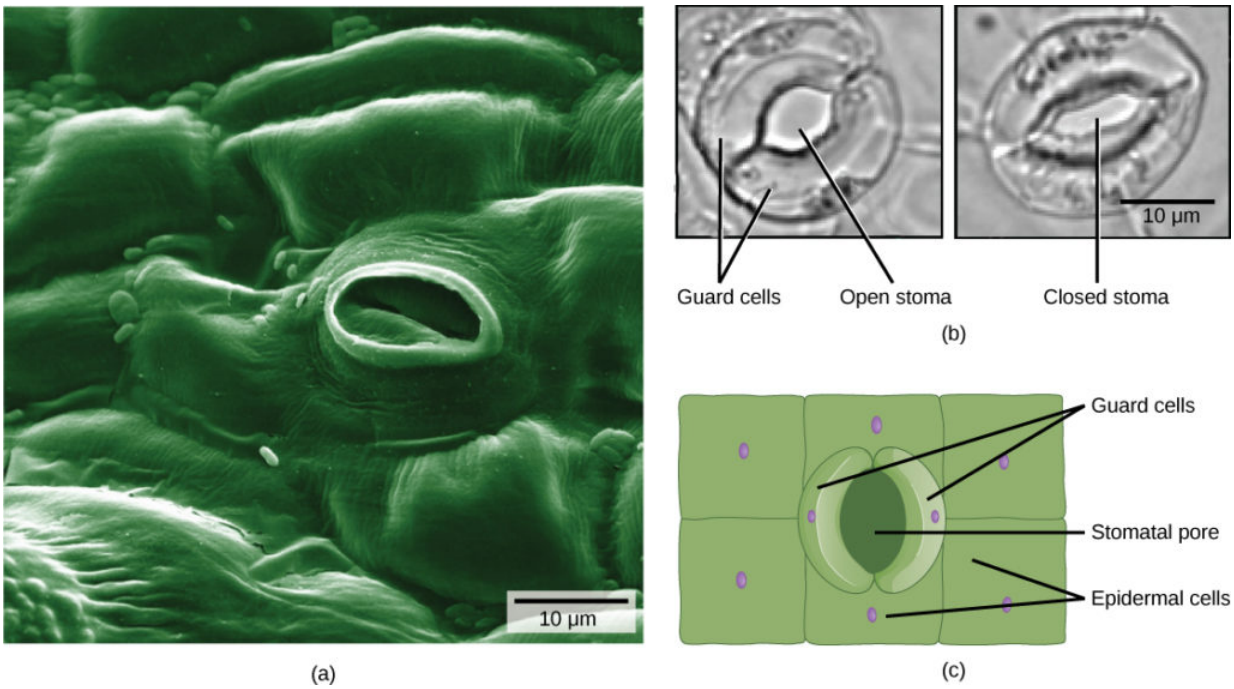


Figure 2. Openings called stomata (singular: stoma) allow a plant to take up carbon dioxide and release oxygen and water vapor. The (a) colorized scanning-electron micrograph shows a closed stoma of a dicot. Each stoma is flanked by two guard cells that regulate its (b) opening and closing. The (c) guard cells sit within the layer of epidermal cells (credit a: modification of work by Louisa Howard, Rippel Electron Microscope Facility, Dartmouth College; credit b: modification of work by June Kwak, University of Maryland; scale-bar data from Matt Russell)

Vascular Tissue

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

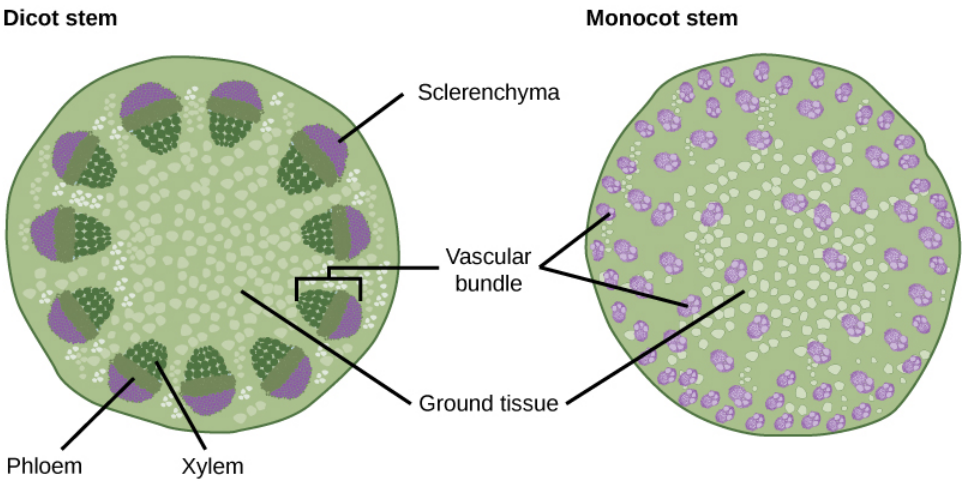


Figure 3. In (a) dicot stems, vascular bundles are arranged around the periphery of the ground tissue. The xylem tissue is located toward the interior of the vascular bundle, and phloem is located toward the exterior. Sclerenchyma fibers cap the vascular bundles. In (b) monocot stems, vascular bundles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

Xylem tissue has three types of cells: xylem parenchyma, tracheids, and vessel elements. The latter two types conduct water and are dead at maturity. **Tracheids** are xylem cells with thick secondary cell walls that are lignified. Water moves from one tracheid to another through regions on the side walls known as pits, where secondary walls are absent. **Vessel elements** are xylem cells with thinner walls; they are shorter than tracheids. Each vessel element is connected to the next by means of a perforation plate at the end walls of the element. Water moves through the perforation plates to travel up the plant.

Phloem tissue is composed of sieve-tube cells, companion cells, phloem parenchyma, and phloem fibers. A series of **sieve-tube cells** (also called sieve-tube elements) are arranged end to end to make up a long sieve tube, which transports organic substances such as sugars and amino acids. The sugars flow from one sieve-tube cell to the next through perforated sieve plates, which are found at the end junctions between two cells. Although still alive at maturity, the nucleus and other cell components of the sieve-tube cells have disintegrated. **Companion cells** are found alongside the sieve-tube cells, providing them with metabolic support. The companion cells contain more ribosomes and mitochondria than the sieve-tube cells, which lack some cellular organelles.

Ground Tissue

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

Plant Organs

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

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

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

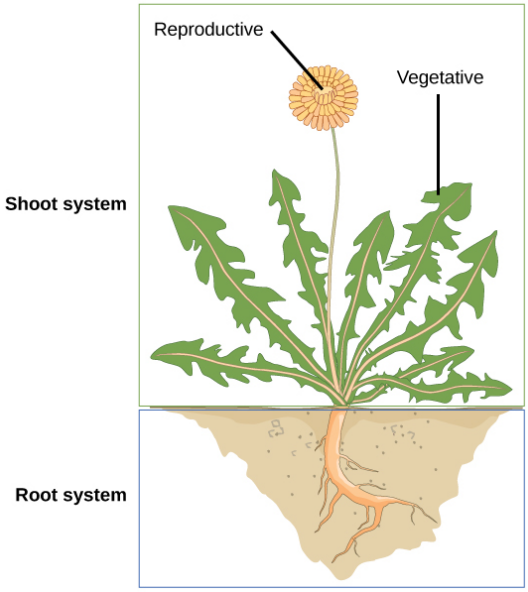


Figure 4. The shoot system of a plant consists of leaves, stems, flowers, and fruits. The root system anchors the plant while absorbing water and minerals from the soil.

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11.5: Stems

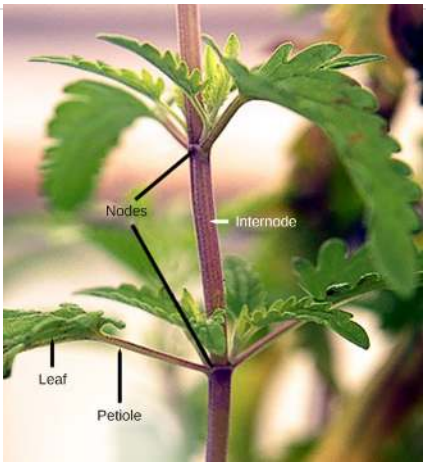


Figure 1. Leaves are attached to the plant stem at areas called nodes. An internode is the stem region between two nodes. The petiole is the stalk connecting the leaf to the stem. The leaves just above the nodes arose from axillary buds.

Stems are a part of the shoot system of a plant. They may range in length from a few millimeters to hundreds of meters, and also vary in diameter, depending on the plant type. Stems are usually above ground, although the stems of some plants, such as the potato, also grow underground. Stems may be herbaceous (soft) or woody in nature. Their main function is to provide support to the plant, holding leaves, flowers and buds; in some cases, stems also store food for the plant. A stem may be unbranched, like that of a palm tree, or it may be highly branched, like that of a magnolia tree. The stem of the plant connects the roots to the leaves, helping to transport absorbed water and minerals to different parts of the plant. It also helps to transport the products of photosynthesis, namely sugars, from the leaves to the rest of the plant.

Plant stems, whether above or below ground, are characterized by the presence of nodes and internodes (Figure 1). **Nodes** are points of attachment for leaves, aerial roots, and flowers. The stem region between two nodes is called an **internode**. The stalk that extends from the stem to the base of the leaf is the petiole. An **axillary bud** is usually found in the axil—the area between the base of a leaf and the stem—where it can give rise to a branch or a flower. The apex (tip) of the shoot contains the apical meristem within the **apical bud**.

Stem Anatomy

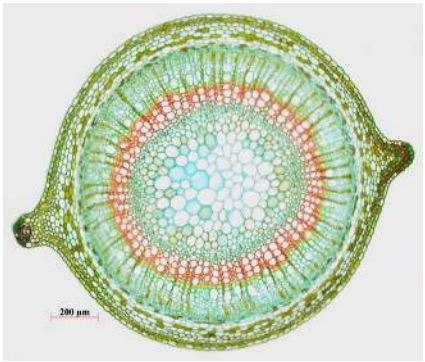


Figure 2. The stem of common St John's Wort (*Hypericum perforatum*) is shown in cross section in this light micrograph. (credit: Rolf-Dieter Mueller)

The stem and other plant organs arise from the ground tissue, and are primarily made up of simple tissues formed from three types of cells: parenchyma, collenchyma, and sclerenchyma cells.

Parenchyma cells are the most common plant cells (Figure 2). They are found in the stem, the root, the inside of the leaf, and the pulp of the fruit. Parenchyma cells are responsible for metabolic functions, such as photosynthesis, and they help repair and heal wounds. Some parenchyma cells also store starch. In Figure 2, we see the central pith (greenish-blue, in the center) and peripheral

cortex (narrow zone 3–5 cells thick just inside the epidermis); both are composed of parenchyma cells. Vascular tissue composed of xylem (red) and phloem tissue (green, between the xylem and cortex) surrounds the pith.

Collenchyma cells are elongated cells with unevenly thickened walls (Figure 3). They provide structural support, mainly to the stem and leaves. These cells are alive at maturity and are usually found below the epidermis. The “strings” of a celery stalk are an example of collenchyma cells.

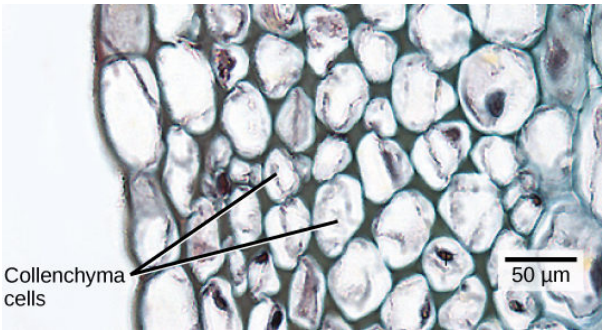


Figure 3. Collenchyma cell walls are uneven in thickness, as seen in this light micrograph. They provide support to plant structures. (credit: modification of work by Carl Szczerski; scale-bar data from Matt Russell)

Sclerenchyma cells also provide support to the plant, but unlike collenchyma cells, many of them are dead at maturity. There are two types of sclerenchyma cells: fibers and sclereids. Both types have secondary cell walls that are thickened with deposits of lignin, an organic compound that is a key component of wood. Fibers are long, slender cells; sclereids are smaller-sized. Sclereids give pears their gritty texture. Humans use sclerenchyma fibers to make linen and rope (Figure 4).

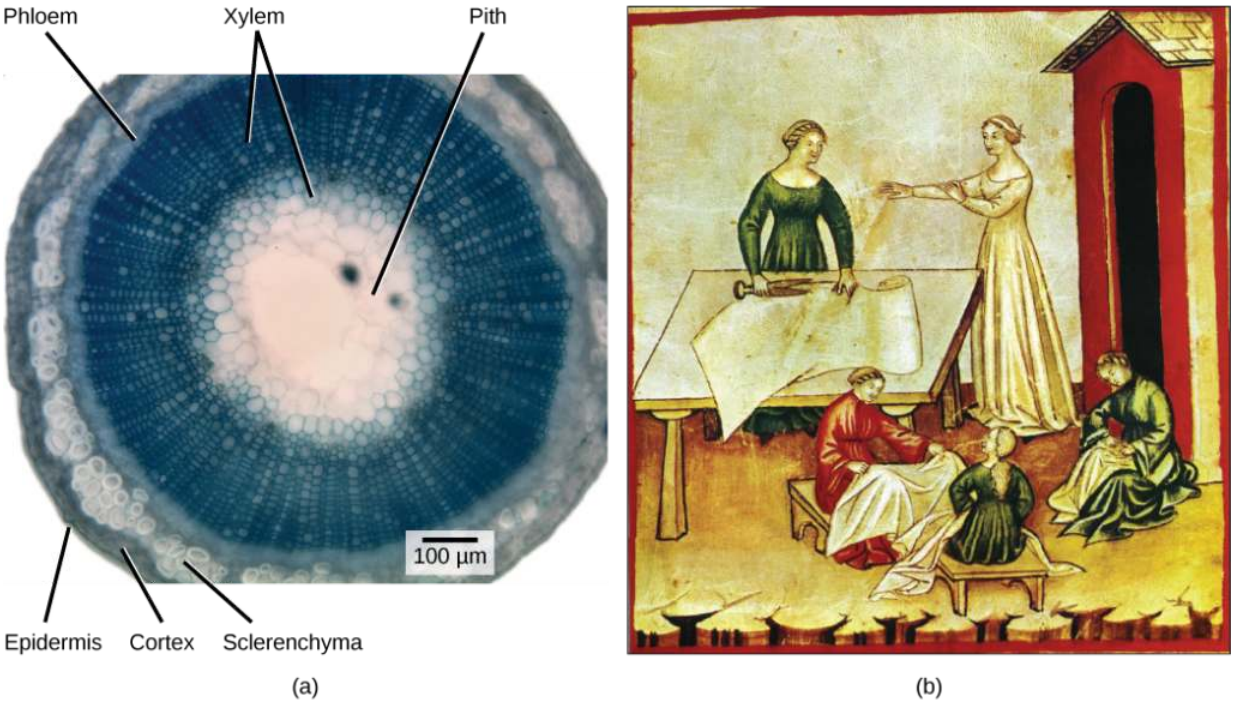


Figure 4. The central pith and outer cortex of the (a) flax stem are made up of parenchyma cells. Inside the cortex is a layer of sclerenchyma cells, which make up the fibers in flax rope and clothing. Humans have grown and harvested flax for thousands of years. In (b) this drawing, fourteenth-century women prepare linen. The (c) flax plant is grown and harvested for its fibers, which are used to weave linen, and for its seeds, which are the source of linseed oil. (credit a: modification of work by Emmanuel Boutet based on original work by Ryan R. MacKenzie; credit c: modification of work by Brian Dearth; scale-bar data from Matt Russell)

? Practice Question

Which layers of the stem are made of parenchyma cells?

a. cortex and pith
b. phloem
c. sclerenchyma
d. xylem

[reveal-answer q="700313"]Show Answer[/reveal-answer]
[hidden-answer a="700313"]Answer a and b. The cortex, pith, and epidermis are made of parenchyma cells.[/hidden-answer]

Stem Modifications

Some plant species have modified stems that are especially suited to a particular habitat and environment (Figure 5). A **rhizome** is a modified stem that grows horizontally underground and has nodes and internodes. Vertical shoots may arise from the buds on the rhizome of some plants, such as ginger and ferns. **Corms** are similar to rhizomes, except they are more rounded and fleshy (such as in gladiolus). Corms contain stored food that enables some plants to survive the winter. **Stolons** are stems that run almost parallel to the ground, or just below the surface, and can give rise to new plants at the nodes. **Runners** are a type of stolon that runs above the ground and produces new clone plants at nodes at varying intervals: strawberries are an example. **Tubers** are modified stems that may store starch, as seen in the potato (*Solanum* sp.). Tubers arise as swollen ends of stolons, and contain many adventitious or unusual buds (familiar to us as the "eyes" on potatoes). A **bulb**, which functions as an underground storage unit, is a modification of a stem that has the appearance of enlarged fleshy leaves emerging from the stem or surrounding the base of the stem, as seen in the iris.



Figure 5. Stem modifications enable plants to thrive in a variety of environments. Shown are (a) ginger (*Zingiber officinale*) rhizomes, (b) a carrion flower (*Amorphophallus titanum*) corm (c) Rhodes grass (*Chloris gayana*) stolons, (d) strawberry (*Fragaria ananassa*) runners, (e) potato (*Solanum tuberosum*) tubers, and (f) red onion (*Allium*) bulbs. (credit a: modification of work by Maja Dumat; credit c: modification of work by Harry Rose; credit d: modification of work by Rebecca Siegel; credit e: modification of work by Scott Bauer, USDA ARS; credit f: modification of work by Stephen Ausmus, USDA ARS)

Watch botanist Wendy Hodgson, of Desert Botanical Garden in Phoenix, Arizona, explain how agave plants were cultivated for food hundreds of years ago in the Arizona desert in this video: *Finding the Roots of an Ancient Crop*.

A link to an interactive elements can be found at the bottom of this page.

Some aerial modifications of stems are tendrils and thorns (Figure 6). Tendrils are slender, twining strands that enable a plant (like a vine or pumpkin) to seek support by climbing on other surfaces. Thorns are modified branches appearing as sharp outgrowths that protect the plant; common examples include roses, Osage orange and devil's walking stick.



(a) (b)

Figure 6. Found in southeastern United States, (a) buckwheat vine (Brunnichia ovata) is a weedy plant that climbs with the aid of tendrils. This one is shown climbing up a wooden stake. (b) Thorns are modified branches. (credit a: modification of work by Christopher Meloche, USDA ARS; credit b: modification of work by “macrophile”/Flickr)

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11.6: Leaves

Leaves are the main sites for photosynthesis: the process by which plants synthesize food. Most leaves are usually green, due to the presence of chlorophyll in the leaf cells. However, some leaves may have different colors, caused by other plant pigments that mask the green chlorophyll.

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

Structure of a Typical Leaf

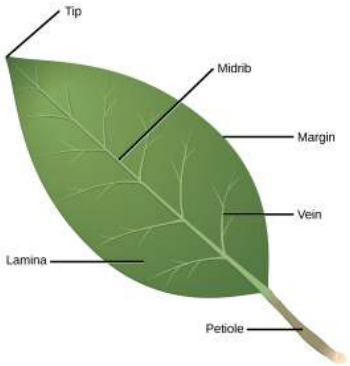


Figure 1. Deceptively simple in appearance, a leaf is a highly efficient structure.

Each leaf typically has a leaf blade called the **lamina**, which is also the widest part of the leaf. Some leaves are attached to the plant stem by a **petiole**. Leaves that do not have a petiole and are directly attached to the plant stem are called **sessile** leaves. Small green appendages usually found at the base of the petiole are known as **stipules**. Most leaves have a midrib, which travels the length of the leaf and branches to each side to produce veins of vascular tissue. The edge of the leaf is called the margin. Figure 1 shows the structure of a typical eudicot leaf.

Within each leaf, the vascular tissue forms veins. The arrangement of veins in a leaf is called the **venation** pattern. Monocots and dicots differ in their patterns of venation (Figure 2). Monocots have parallel venation; the veins run in straight lines across the length of the leaf without converging at a point. In dicots, however, the veins of the leaf have a net-like appearance, forming a pattern known as reticulate venation. One extant plant, the *Ginkgo biloba*, has dichotomous venation where the veins fork.

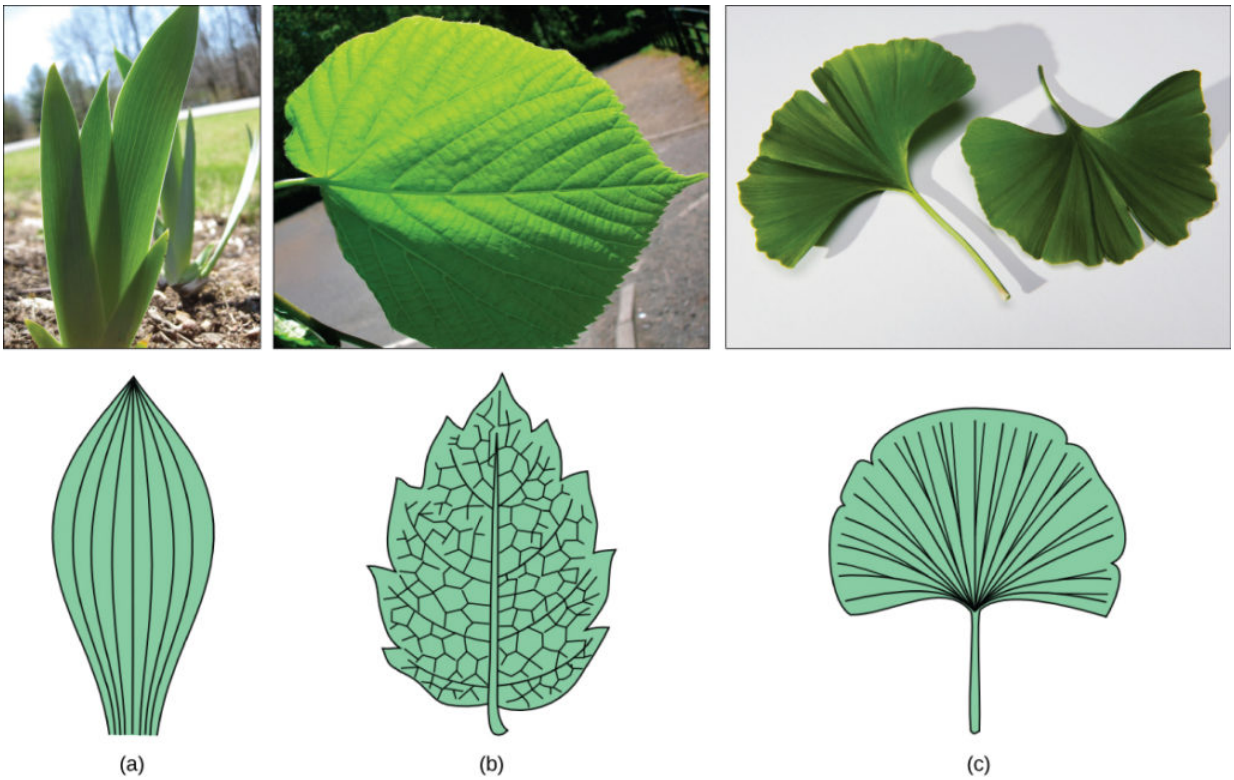


Figure 2. (a) Tulip (*Tulipa*), a monocot, has leaves with parallel venation. The netlike venation in this (b) linden (*Tilia cordata*) leaf distinguishes it as a dicot. The (c) *Ginkgo biloba* tree has dichotomous venation. (credit a photo: modification of work by "Drewboy64"/Wikimedia Commons; credit b photo: modification of work by Roger Griffith; credit c photo: modification of work by "geishaboy500"/Flickr; credit abc illustrations: modification of work by Agnieszka Kwiecień)

Leaf Arrangement

The arrangement of leaves on a stem is known as **phyllotaxy**. The number and placement of a plant's leaves will vary depending on the species, with each species exhibiting a characteristic leaf arrangement. Leaves are classified as either alternate, spiral, or opposite. Plants that have only one leaf per node have leaves that are said to be either alternate—meaning the leaves alternate on each side of the stem in a flat plane—or spiral, meaning the leaves are arrayed in a spiral along the stem. In an opposite leaf arrangement, two leaves arise at the same point, with the leaves connecting opposite each other along the branch. If there are three or more leaves connected at a node, the leaf arrangement is classified as **whorled**.

Leaf Form

Leaves may be simple or compound (Figure 3). In a **simple leaf**, the blade is either completely undivided—as in the banana leaf—or it has lobes, but the separation does not reach the midrib, as in the maple leaf. In a **compound leaf**, the leaf blade is completely divided, forming leaflets, as in the locust tree. Each leaflet may have its own stalk, but is attached to the rachis. A **palmately compound leaf** resembles the palm of a hand, with leaflets radiating outwards from one point Examples include the leaves of poison ivy, the buckeye tree, or the familiar houseplant *Schefflera* sp. (common name "umbrella plant"). **Pinnately compound leaves** take their name from their feather-like appearance; the leaflets are arranged along the midrib, as in rose leaves (*Rosa* sp.), or the leaves of hickory, pecan, ash, or walnut trees.

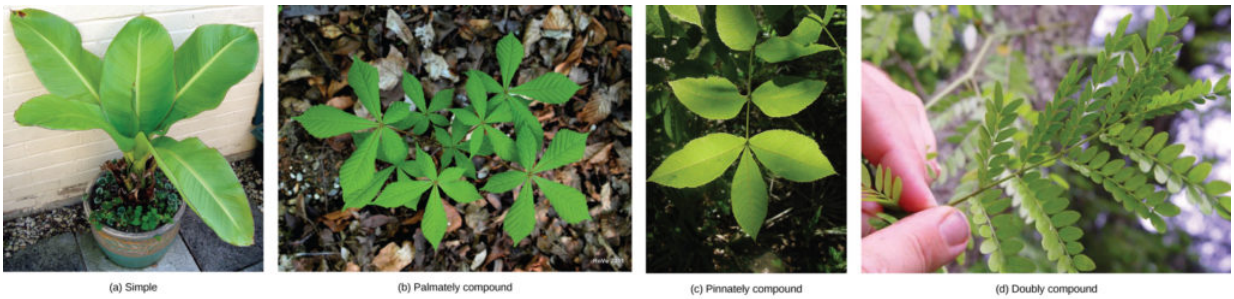


Figure 3. Leaves may be simple or compound. In simple leaves, the lamina is continuous. The (a) banana plant (*Musa* sp.) has simple leaves. In compound leaves, the lamina is separated into leaflets. Compound leaves may be palmate or pinnate. In (b) palmately compound leaves, such as those of the horse chestnut (*Aesculus hippocastanum*), the leaflets branch from the petiole. In (c) pinnately compound leaves, the leaflets branch from the midrib, as on a scrub hickory (*Carya floridana*). The (d) honey locust has double compound leaves, in which leaflets branch from the veins. (credit a: modification of work by "BazzaDaRambler"/Flickr; credit b: modification of work by Roberto Verzo; credit c: modification of work by Eric Dion; credit d: modification of work by Valerie Lykes)

Leaf Structure and Function

The outermost layer of the leaf is the epidermis; it is present on both sides of the leaf and is called the upper and lower epidermis, respectively. Botanists call the upper side the adaxial surface (or adaxis) and the lower side the abaxial surface (or abaxis). The epidermis helps in the regulation of gas exchange. It contains stomata (Figure 4): openings through which the exchange of gases takes place. Two guard cells surround each stoma, regulating its opening and closing.

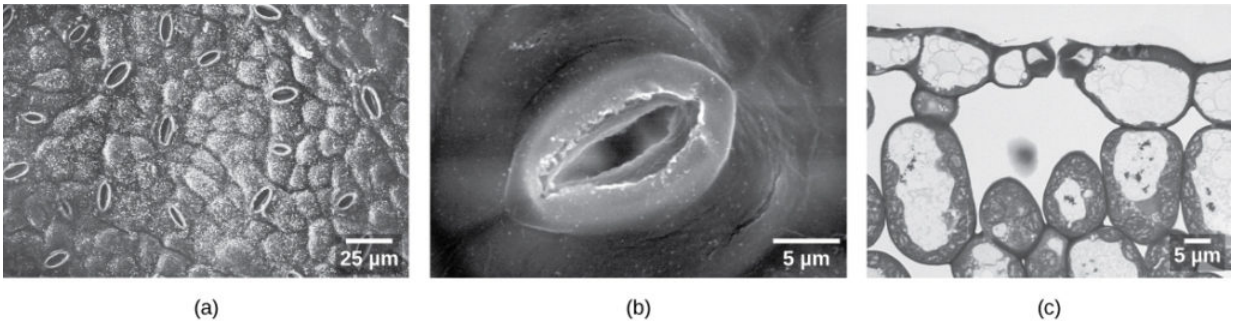


Figure 4. Visualized at 500x with a scanning electron microscope, several stomata are clearly visible on (a) the surface of this sumac (*Rhus glabra*) leaf. At 5,000x magnification, the guard cells of (b) a single stoma from lyre-leaved sand cress (*Arabidopsis lyrata)* have the appearance of lips that surround the opening. In this (c) light micrograph cross-section of an *A. lyrata* leaf, the guard cell pair is visible along with the large, sub-stomatal air space in the leaf. (credit: modification of work by Robert R. Wise; part c scale-bar data from Matt Russell)

The epidermis is usually one cell layer thick; however, in plants that grow in very hot or very cold conditions, the epidermis may be several layers thick to protect against excessive water loss from transpiration. A waxy layer known as the **cuticle** covers the leaves of all plant species. The cuticle reduces the rate of water loss from the leaf surface. Other leaves may have small hairs (trichomes) on the leaf surface. Trichomes help to deter herbivory by restricting insect movements, or by storing toxic or bad-tasting compounds; they can also reduce the rate of transpiration by blocking air flow across the leaf surface (Figure 5).

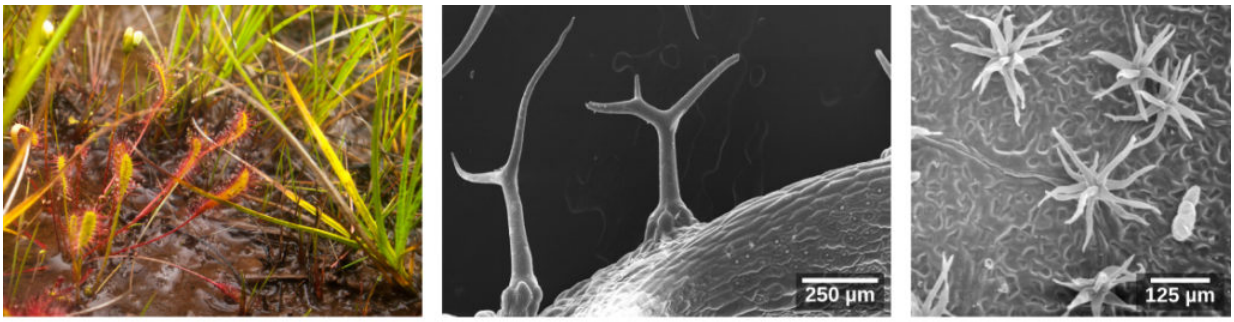


Figure 5. Trichomes give leaves a fuzzy appearance as in this (a) sundew (*Drosera* sp.). Leaf trichomes include (b) branched trichomes on the leaf of *Arabidopsis lyrata* and (c) multibranched trichomes on a mature *Quercus marilandica* leaf. (credit a: John Freeland; credit b, c: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Below the epidermis of dicot leaves are layers of cells known as the mesophyll, or "middle leaf." The mesophyll of most leaves typically contains two arrangements of parenchyma cells: the palisade parenchyma and spongy parenchyma (Figure 6). The palisade parenchyma (also called the palisade mesophyll) has column-shaped, tightly packed cells, and may be present in one, two, or three layers. Below the palisade parenchyma are loosely arranged cells of an irregular shape. These are the cells of the spongy parenchyma (or spongy mesophyll). The air space found between the spongy parenchyma cells allows gaseous exchange between the leaf and the outside atmosphere through the stomata. In aquatic plants, the intercellular spaces in the spongy parenchyma help the leaf float. Both layers of the mesophyll contain many chloroplasts. Guard cells are the only epidermal cells to contain chloroplasts.

In the leaf drawing (Figure 6a), the central mesophyll is sandwiched between an upper and lower epidermis. The mesophyll has two layers: an upper palisade layer comprised of tightly packed, columnar cells, and a lower spongy layer, comprised of loosely packed, irregularly shaped cells. Stomata on the leaf underside allow gas exchange. A waxy cuticle covers all aerial surfaces of land plants to minimize water loss. These leaf layers are clearly visible in the scanning electron micrograph (Figure 6b). The numerous small bumps in the palisade parenchyma cells are chloroplasts. Chloroplasts are also present in the spongy parenchyma, but are not as obvious. The bumps protruding from the lower surface of the leave are glandular trichomes, which differ in structure from the stalked trichomes in Figure 5.

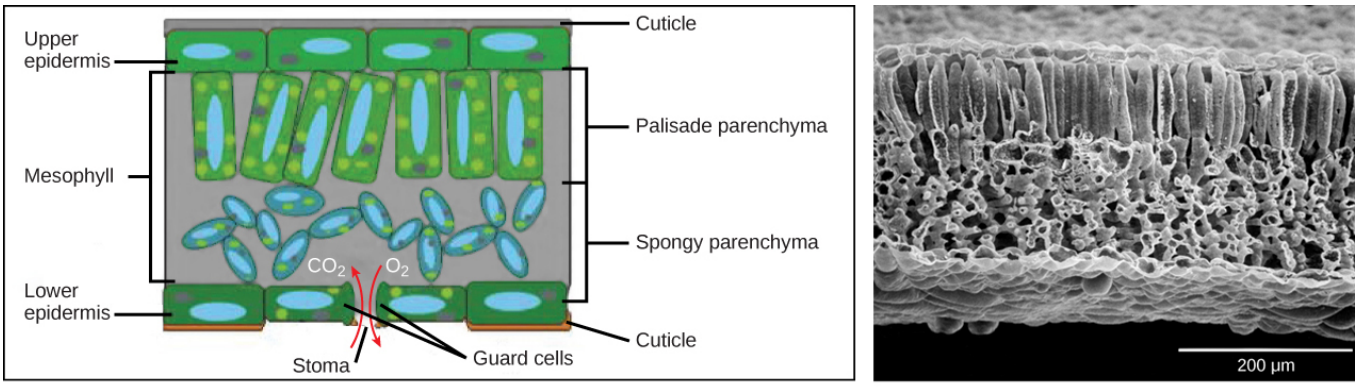


Figure 6. (a) Leaf drawing (b) Scanning electron micrograph of a leaf. (credit b: modification of work by Robert R. Wise)

Like the stem, the leaf contains vascular bundles composed of xylem and phloem (Figure 7). The xylem consists of tracheids and vessels, which transport water and minerals to the leaves. The phloem transports the photosynthetic products from the leaf to the other parts of the plant. A single vascular bundle, no matter how large or small, always contains both xylem and phloem tissues.

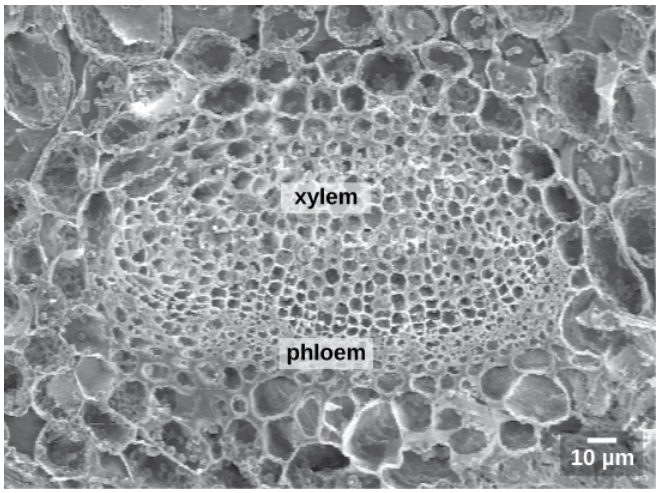


Figure 7. This scanning electron micrograph shows xylem and phloem in the leaf vascular bundle from the lyre-leaved sand cress (Arabidopsis lyrata). (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Leaf Adaptations

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

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

A link to an interactive elements can be found at the bottom of this page.

Learning Objectives

Leaves are the main site of photosynthesis. A typical leaf consists of a lamina (the broad part of the leaf, also called the blade) and a petiole (the stalk that attaches the leaf to a stem). The arrangement of leaves on a stem, known as phyllotaxy, enables maximum exposure to sunlight. Each plant species has a characteristic leaf arrangement and form. The pattern of leaf arrangement may be alternate, opposite, or spiral, while leaf form may be simple or compound. Leaf tissue consists of the epidermis, which forms the outermost cell layer, and mesophyll and vascular tissue, which make up the inner portion of the leaf. In some plant species, leaf form is modified to form structures such as tendrils, spines, bud scales, and needles.

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11.7: Roots

The roots of seed plants have three major functions: anchoring the plant to the soil, absorbing water and minerals and transporting them upwards, and storing the products of photosynthesis. Some roots are modified to absorb moisture and exchange gases. Most roots are underground. Some plants, however, also have **adventitious roots**, which emerge above the ground from the shoot.

Types of Root Systems

Root systems are mainly of two types (Figure 1). Dicots have a tap root system, while monocots have a fibrous root system. A **tap root system** has a main root that grows down vertically, and from which many smaller lateral roots arise. Dandelions are a good example; their tap roots usually break off when trying to pull these weeds, and they can regrow another shoot from the remaining root). A tap root system penetrates deep into the soil. In contrast, a **fibrous root system** is located closer to the soil surface, and forms a dense network of roots that also helps prevent soil erosion (lawn grasses are a good example, as are wheat, rice, and corn). Some plants have a combination of tap roots and fibrous roots. Plants that grow in dry areas often have deep root systems, whereas plants growing in areas with abundant water are likely to have shallower root systems.



Figure 1. (a) Tap root systems have a main root that grows down, while (b) fibrous root systems consist of many small roots. (credit b: modification of work by “Austen Squarepants”/Flickr)

Root Growth and Anatomy

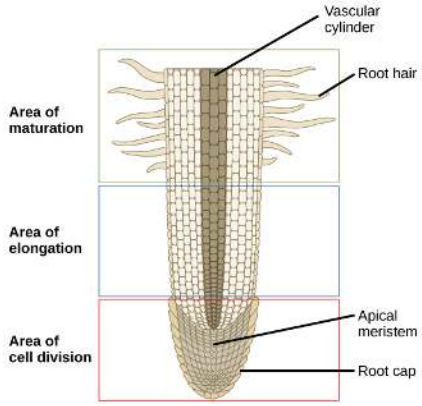


Figure 2. A longitudinal view of the root reveals the zones of cell division, elongation, and maturation. Cell division occurs in the apical meristem.

Root growth begins with seed germination. When the plant embryo emerges from the seed, the radicle of the embryo forms the root system. The tip of the root is protected by the **root cap**, a structure exclusive to roots and unlike any other plant structure. The root cap is continuously replaced because it gets damaged easily as the root pushes through soil. The root tip can be divided into three zones: a zone of cell division, a zone of elongation, and a zone of maturation and differentiation (Figure 2). The zone of cell division is closest to the root tip; it is made up of the actively dividing cells of the root meristem. The zone of elongation is where the newly formed cells increase in length, thereby lengthening the root. Beginning at the first root hair is the zone of cell maturation where the root cells begin to differentiate into special cell types. All three zones are in the first centimeter or so of the root tip.

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

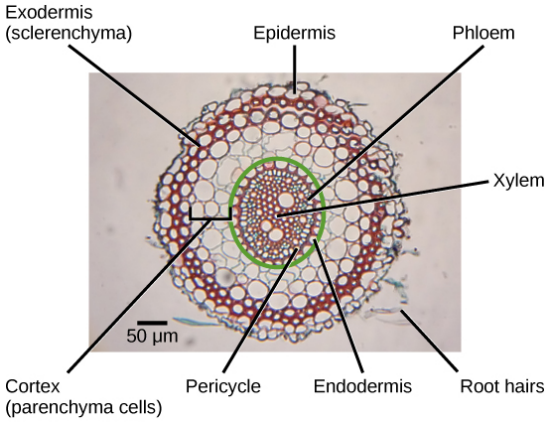


Figure 3. Staining reveals different cell types in this light micrograph of a wheat (*Triticum*) root cross section. Sclerenchyma cells of the exodermis and xylem cells stain red, and phloem cells stain blue. Other cell types stain black. The stele, or vascular tissue, is the area inside endodermis (indicated by a green ring). Root hairs are visible outside the epidermis. (credit: scale-bar data from Matt Russell)

Inside the root, the ground tissue forms two regions: the cortex and the pith (Figure 3). Compared to stems, roots have lots of cortex and little pith. Both regions include cells that store photosynthetic products. The cortex is between the epidermis and the vascular tissue, whereas the pith lies between the vascular tissue and the center of the root.

The vascular tissue in the root is arranged in the inner portion of the root, which is called the **stele** (Figure 4). A layer of cells known as the **endodermis** separates the stele from the ground tissue in the outer portion of the root. The endodermis is exclusive to roots, and serves as a checkpoint for materials entering the root's vascular system. A waxy substance called suberin is present on the walls of the endodermal cells. This waxy region, known as the **Casparian strip**, forces water and solutes to cross the plasma membranes of endodermal cells instead of slipping between the cells. This ensures that only materials required by the root pass through the endodermis, while toxic substances and pathogens are generally excluded. The outermost cell layer of the root's vascular tissue is the **pericycle**, an area that can give rise to lateral roots. In dicot roots, the xylem and phloem of the stele are arranged alternately in an X shape, whereas in monocot roots, the vascular tissue is arranged in a ring around the pith.

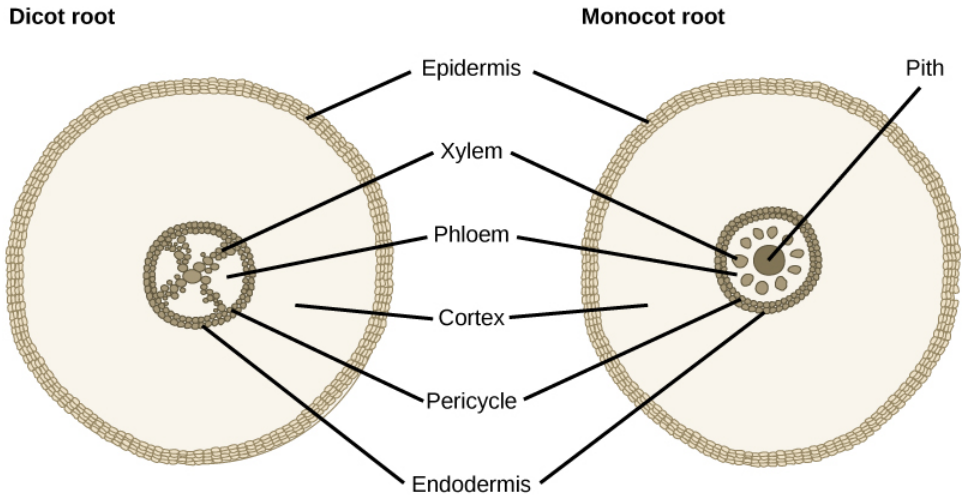


Figure 4. In (left) typical dicots, the vascular tissue forms an X shape in the center of the root. In (right) typical monocots, the phloem cells and the larger xylem cells form a characteristic ring around the central pith.

Root Modifications



Figure 5. Many vegetables are modified roots.

Root structures may be modified for specific purposes. For example, some roots are bulbous and store starch. Aerial roots and prop roots are two forms of aboveground roots that provide additional support to anchor the plant. Tap roots, such as carrots, turnips, and beets, are examples of roots that are modified for food storage (Figure 5).

Epiphytic roots enable a plant to grow on another plant. For example, the epiphytic roots of orchids develop a spongy tissue to absorb moisture. The banyan tree (*Ficus* sp.) begins as an epiphyte, germinating in the branches of a host tree; aerial roots develop from the branches and eventually reach the ground, providing additional support (Figure 6). In screwpine (*Pandanus* sp.), a palm-like tree that grows in sandy tropical soils, aboveground prop roots develop from the nodes to provide additional support.



(a) (b)

Figure 6. The (a) banyan tree, also known as the strangler fig, begins life as an epiphyte in a host tree. Aerial roots extend to the ground and support the growing plant, which eventually strangles the host tree. The (b) screwpine develops aboveground roots that help support the plant in sandy soils. (credit a: modification of work by “psyberartist”/Flickr; credit b: modification of work by David Eikhoff)

? Practice Questions

Compare a tap root system with a fibrous root system. For each type, name a plant that provides a food in the human diet. Which type of root system is found in monocots? Which type of root system is found in dicots?

[practice-area rows=”2″][/practice-area]
[reveal-answer q=”866090″]Show Answer[/reveal-answer]
[hidden-answer a=”866090″]A tap root system has a single main root that grows down. A fibrous root system forms a dense network of roots that is closer to the soil surface. An example of a tap root system is a carrot. Grasses such as wheat, rice, and corn are examples of fibrous root systems. Fibrous root systems are found in monocots; tap root systems are found in dicots.

[/hidden-answer]

What might happen to a root if the pericycle disappeared?

[practice-area rows=”2″][/practice-area]
[reveal-answer q=”755869″]Show Answer[/reveal-answer]
[hidden-answer a=”755869″]The root would not be able to produce lateral roots.[/hidden-answer]

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11.8: Introduction to Transport of Water and Solutes in Plants

Describe how water and solutes are transported in plants

The structure of plant roots, stems, and leaves facilitates the transport of water, nutrients, and photosynthates throughout the plant. The phloem and xylem are the main tissues responsible for this movement. Water potential, evapotranspiration, and stomatal regulation influence how water and nutrients are transported in plants. To understand how these processes work, we must first understand the energetics of water potential.

What You'll Learn to Do

- Describe how water potential influences how water is transported in plants
- Describe the process of transpiration
- Explain how photosynthates are transported in plants

Learning Activities

The learning activities for this section include the following:

- Water Potential
- Transpiration
- Photosynthates
- Self Check: Transport of Water and Solutes in Plants

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11.9: Water Potential

Plants are phenomenal hydraulic engineers. Using only the basic laws of physics and the simple manipulation of potential energy, plants can move water to the top of a 116-meter-tall tree (Figure 1a). Plants can also use hydraulics to generate enough force to split rocks and buckle sidewalks (Figure 1b). Plants achieve this because of water potential.



(a) (b)

Figure 1. With heights nearing 116 meters, (a) coastal redwoods (*Sequoia sempervirens*) are the tallest trees in the world. Plant roots can easily generate enough force to (b) buckle and break concrete sidewalks, much to the dismay of homeowners and city maintenance departments. (credit a: modification of work by Bernt Rostad; credit b: modification of work by Pedestrians Educating Drivers on Safety, Inc.)

Water potential is a measure of the potential energy in water. Plant physiologists are not interested in the energy in any one particular aqueous system, but are very interested in water movement between two systems. In practical terms, therefore, water potential is the difference in potential energy between a given water sample and pure water (at atmospheric pressure and ambient temperature). Water potential is denoted by the Greek letter ψ (psi) and is expressed in units of pressure (pressure is a form of energy) called **megapascals** (MPa). The potential of pure water ($\Psi_w^{\text{pure } H_2O}$) is, by convenience of definition, designated a value of zero (even though pure water contains plenty of potential energy, that energy is ignored). Water potential values for the water in a plant root, stem, or leaf are therefore expressed relative to $\Psi_w^{\text{pure } H_2O}$.

The water potential in plant solutions is influenced by solute concentration, pressure, gravity, and factors called matrix effects. Water potential can be broken down into its individual components using the following equation:

$$\Psi_{system} = \Psi_{total} = \Psi_s + \Psi_p + \Psi_g + \Psi_m$$

where Ψ_s, Ψ_p, Ψ_g, and Ψm refer to the solute, pressure, gravity, and matric potentials, respectively. “System” can refer to the water potential of the soil water (Ψ^{soil}), root water (Ψ^{root}), stem water (Ψ^{stem}), leaf water (Ψ^{leaf}) or the water in the atmosphere ($\Psi^{atmosphere}$): whichever aqueous system is under consideration. As the individual components change, they raise or lower the total water potential of a system. When this happens, water moves to equilibrate, moving from the system or compartment with a higher water potential to the system or compartment with a lower water potential. This brings the difference in water potential between the two systems (ΔΨ) back to zero (ΔΨ = 0). Therefore, for water to move through the plant from the soil to the air (a process called transpiration), Ψ^{soil} must be $>\Psi^{root} >\Psi^{stem} >\Psi^{leaf} >\Psi^{atmosphere}$.

Water only moves in response to ΔΨ, not in response to the individual components. However, because the individual components influence the totalΨ_{system}, by manipulating the individual components (especially Ψ_s), a plant can control water movement.

Solute Potential

Solute potential (Ψ_s), also called osmotic potential, is negative in a plant cell and zero in distilled water. Typical values for cell cytoplasm are –0.5 to –1.0 MPa. Solutes reduce water potential (resulting in a negative Ψ_w) by consuming some of the potential energy available in the water. Solute molecules can dissolve in water because water molecules can bind to them via hydrogen bonds; a hydrophobic molecule like oil, which cannot bind to water, cannot go into solution. The energy in the hydrogen bonds between solute molecules and water is no longer available to do work in the system because it is tied up in the bond. In other words, the amount of available potential energy is reduced when solutes are added to an aqueous system. Thus, Ψ_s decreases with increasing solute concentration. Because Ψ_s is one of the four components of Ψ_{system} or Ψ_{total}, a decrease in Ψ_s will cause a decrease in Ψ_{total}. The internal water potential of a plant cell is more negative than pure water because of the cytoplasm's high solute content (Figure 2). Because of this difference in water potential water will move from the soil into a plant's root cells via the process of osmosis. This is why solute potential is sometimes called osmotic potential.

Plant cells can metabolically manipulate Ψ_s (and by extension,Ψ_{total}) by adding or removing solute molecules. Therefore, plants have control over Ψ_{total} via their ability to exert metabolic control over Ψ_s.

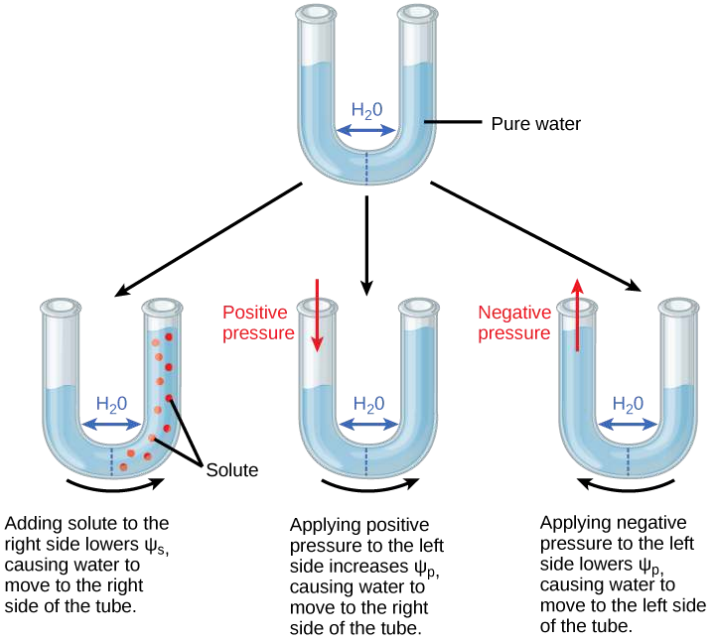


Figure 2. A semipermeable membrane between two aqueous systems

In Figure 2, water will move from a region of higher to lower water potential until equilibrium is reached. Solutes (Ψ_s), pressure (Ψ_p), and gravity (Ψ_g) influence total water potential for each side of the tube ($\Psi_{total}^{\text{right or left}}$), and therefore, the difference between Ψ_{total} on each side ($\Delta\Psi$). (Ψ_m, the potential due to interaction of water with solid substrates, is ignored in this example because glass is not especially hydrophilic). Water moves in response to the difference in water potential between two systems (the left and right sides of the tube).

? Practice Question

Positive water potential is placed on the left side of the tube by increasing Ψ_p such that the water level rises on the right side. Could you equalize the water level on each side of the tube by adding solute, and if so, how?

[practice-area rows="2"][/practice-area]
[reveal-answer q="229403"]Show Answer[/reveal-answer]
[hidden-answer a="229403"]Yes, you can equalize the water level by adding the solute to the left side of the tube such that water moves toward the left until the water levels are equal.[/hidden-answer]

Pressure Potential

Pressure potential (Ψ_p), also called turgor potential, may be positive or negative (Figure 2). Because pressure is an expression of energy, the higher the pressure, the more potential energy in a system, and vice versa. Therefore, a positive Ψ_p (compression) increases Ψ_{total}, and a negative Ψ_p (tension) decreases Ψ_{total}. Positive pressure inside cells is contained by the cell wall, producing turgor pressure. Pressure potentials are typically around 0.6–0.8 MPa, but can reach as high as 1.5 MPa in a well-watered plant. A Ψ_p of 1.5 MPa equates to 210 pounds per square inch (1.5 MPa x 140 lb in^{-2} MPa^{-1} = 210 lb/in^{-2}). As a comparison, most automobile tires are kept at a pressure of 30–34 psi. An example of the effect of turgor pressure is the wilting of leaves and their restoration after the plant has been watered (Figure 3). Water is lost from the leaves via transpiration (approaching Ψ_p = 0 MPa at the wilting point) and restored by uptake via the roots.

A plant can manipulate Ψ_p via its ability to manipulate Ψ_s and by the process of osmosis. If a plant cell increases the cytoplasmic solute concentration, Ψs will decline, Ψ_{total} will decline, the ΔΨ between the cell and the surrounding tissue will decline, water will move into the cell by osmosis, and Ψ_p will increase. Ψ_p is also under indirect plant control via the opening and closing of stomata. Stomatal openings allow water to evaporate from the leaf, reducing Ψ_p and Ψ_{total} of the leaf and increasing ii between the water in the leaf and the petiole, thereby allowing water to flow from the petiole into the leaf.



(a) (b)

Figure 3. When (a) total water potential (Ψtotal) is lower outside the cells than inside, water moves out of the cells and the plant wilts. When (b) the total water potential is higher outside the plant cells than inside, water moves into the cells, resulting in turgor pressure (Ψ_p) and keeping the plant erect. (credit: modification of work by Victor M. Vicente Selvas)

Gravity Potential

Gravity potential (Ψ_g) is always negative to zero in a plant with no height. It always removes or consumes potential energy from the system. The force of gravity pulls water downwards to the soil, reducing the total amount of potential energy in the water in the plant (Ψ_{total}). The taller the plant, the taller the water column, and the more influential Ψ_g becomes. On a cellular scale and in short plants, this effect is negligible and easily ignored. However, over the height of a tall tree like a giant coastal redwood, the gravitational pull of –0.1 MPa m^{-1} is equivalent to an extra 1 MPa of resistance that must be overcome for water to reach the leaves of the tallest trees. Plants are unable to manipulate Ψ_g.

Matric Potential

Matric potential (Ψ_m) is always negative to zero. In a dry system, it can be as low as –2 MPa in a dry seed, and it is zero in a water-saturated system. The binding of water to a matrix always removes or consumes potential energy from the system. Ψ_m is similar to solute potential because it involves tying up the energy in an aqueous system by forming hydrogen bonds between the water and some other component. However, in solute potential, the other components are soluble, hydrophilic solute molecules, whereas in Ψ_m, the other components are insoluble, hydrophilic molecules of the plant cell wall. Every plant cell has a cellulosic cell wall and the cellulose in the cell walls is hydrophilic, producing a matrix for adhesion of water: hence the name matric potential. Ψ_m is very large (negative) in dry tissues such as seeds or drought-affected soils. However, it quickly goes to zero as the seed takes up water or the soil hydrates. Ψ_m cannot be manipulated by the plant and is typically ignored in well-watered roots, stems, and leaves.

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11.10: Transpiration

Solutes, pressure, gravity, and matric potential are all important for the transport of water in plants. Water moves from an area of higher total water potential (higher Gibbs free energy) to an area of lower total water potential. Gibbs free energy is the energy associated with a chemical reaction that can be used to do work. This is expressed as $\Delta\Psi$.

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

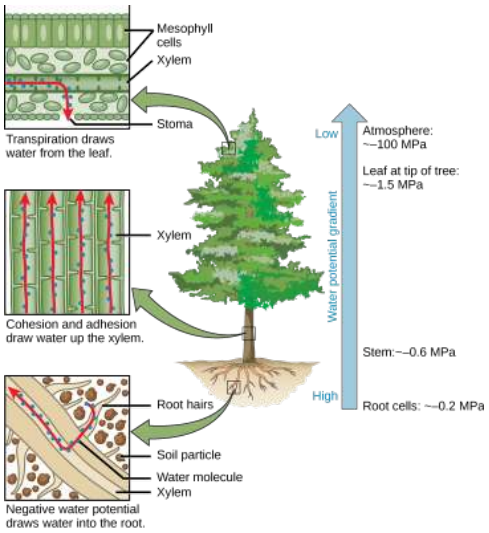


Figure 1. The cohesion–tension theory of sap ascent is shown. Evaporation from the mesophyll cells produces a negative water potential gradient that causes water to move upwards from the roots through the xylem.

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

This decrease creates a greater tension on the water in the mesophyll cells (Figure 1), thereby increasing the pull on the water in the xylem vessels. The xylem vessels and tracheids are structurally adapted to cope with large changes in pressure. Rings in the vessels maintain their tubular shape, much like the rings on a vacuum cleaner hose keep the hose open while it is under pressure. Small perforations between vessel elements reduce the number and size of gas bubbles that can form via a process called cavitation. The formation of gas bubbles in xylem interrupts the continuous stream of water from the base to the top of the plant, causing a break termed an embolism in the flow of xylem sap. The taller the tree, the greater the tension forces needed to pull water, and the more cavitation events. In larger trees, the resulting embolisms can plug xylem vessels, making them non-functional.

? Practice Question

Which of the following statements is false?

a. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the xylem. Transpiration draws water from the leaf.
b. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the phloem. Transpiration draws water from the leaf.
c. Water potential decreases from the roots to the top of the plant.

d. Water enters the plants through root hairs and exits through stoma.

[reveal-answer q="218046"]Show Answer[/reveal-answer]
[hidden-answer a="218046"]Statement b is false.[/hidden-answer]

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

Control of Transpiration

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

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

Plants have evolved over time to adapt to their local environment and reduce transpiration (Figure 2). Desert plant (xerophytes) and plants that grow on other plants (epiphytes) have limited access to water. Such plants usually have a much thicker waxy cuticle than those growing in more moderate, well-watered environments (mesophytes). Aquatic plants (hydrophytes) also have their own set of anatomical and morphological leaf adaptations.

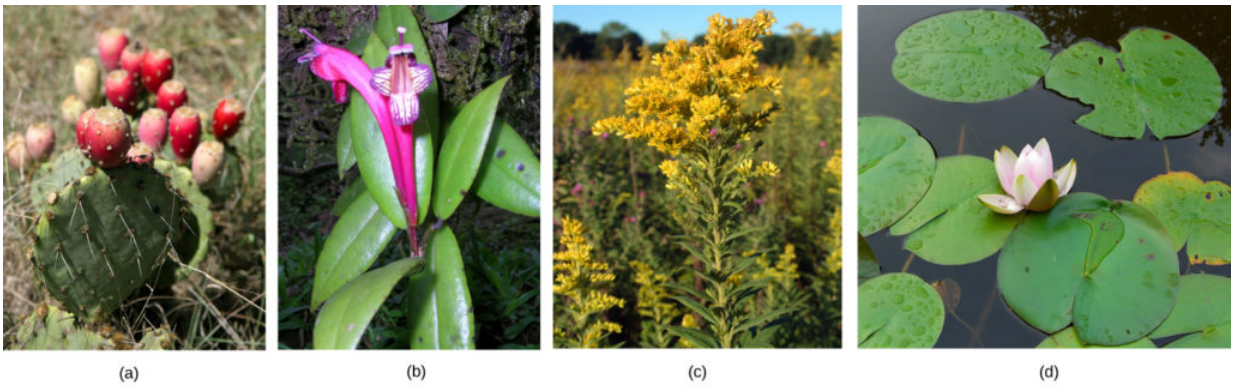


Figure 2. Plants are suited to their local environment. (a) Xerophytes, like this prickly pear cactus (*Opuntia sp*.) and (b) epiphytes such as this tropical *Aeschynanthus perrottetii* have adapted to very limited water resources. The leaves of a prickly pear are modified into spines, which lowers the surface-to-volume ratio and reduces water loss. Photosynthesis takes place in the stem, which also stores water. (b) *A. perottetii* leaves have a waxy cuticle that prevents water loss. (c) Goldenrod (*Solidago sp*.) is a mesophyte, well suited for moderate environments. (d) Hydrophytes, like this fragrant water lily (*Nymphaea odorata*), are adapted to thrive in aquatic environments. (credit a: modification of work by Jon Sullivan; credit b: modification of work by L. Shyamal/Wikimedia Commons; credit c: modification of work by Huw Williams; credit d: modification of work by Jason Hollinger)

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

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11.11: Photosynthates

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

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

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

Translocation: Transport from Source to Sink

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

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

Once in the phloem, the photosynthates are translocated to the closest sink. Phloem sap is an aqueous solution that contains up to 30 percent sugar, minerals, amino acids, and plant growth regulators. The high percentage of sugar decreases Ψs, which decreases the total water potential and causes water to move by osmosis from the adjacent xylem into the phloem tubes, thereby increasing pressure. This increase in total water potential causes the bulk flow of phloem from source to sink (Figure 1b). Sucrose concentration in the sink cells is lower than in the phloem STEs because the sink sucrose has been metabolized for growth, or converted to starch for storage or other polymers, such as cellulose, for structural integrity. Unloading at the sink end of the phloem tube occurs by either diffusion or active transport of sucrose molecules from an area of high concentration to one of low concentration. Water diffuses from the phloem by osmosis and is then transpired or recycled via the xylem back into the phloem sap.

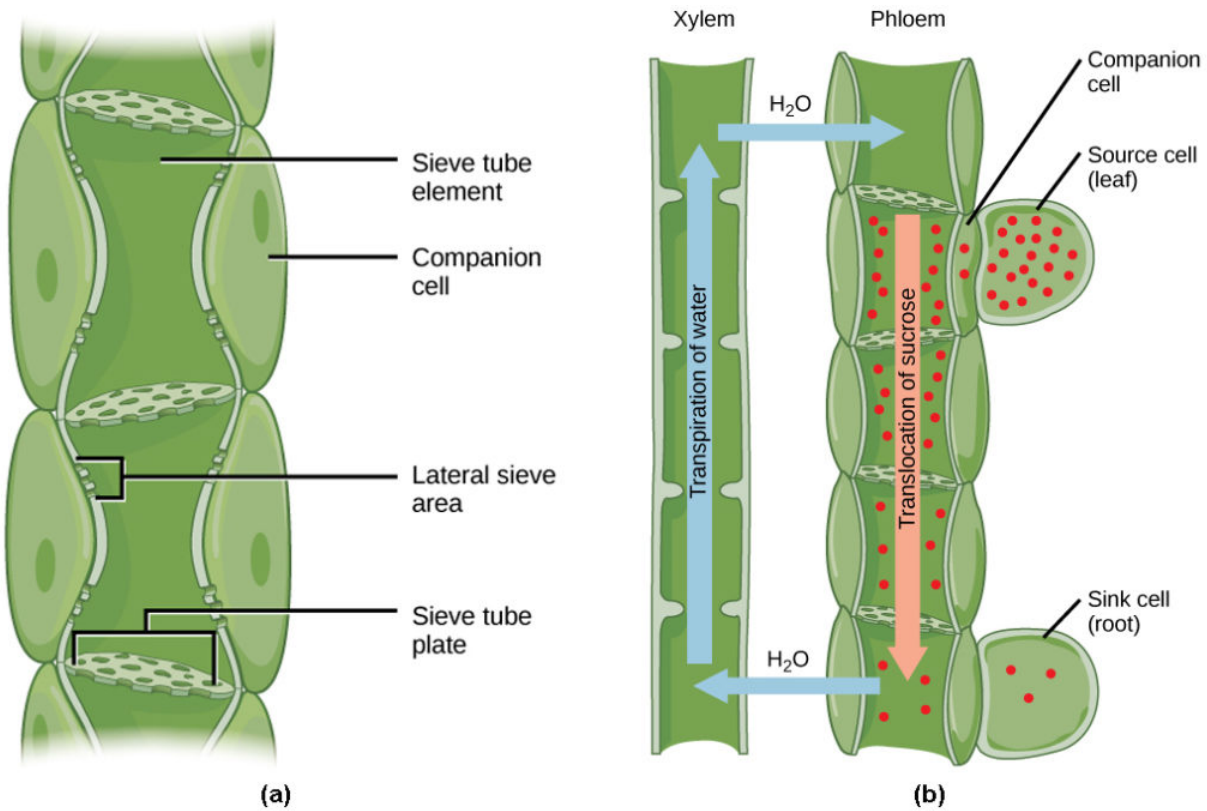


Figure 1. (a) Phloem is comprised of cells called sieve-tube elements. Phloem sap travels through perforations called sieve tube plates. Neighboring companion cells carry out metabolic functions for the sieve-tube elements and provide them with energy. Lateral sieve areas connect the sieve-tube elements to the companion cells. (b) Sucrose is actively transported from source cells into companion cells and then into the sieve-tube elements. This reduces the water potential, which causes water to enter the phloem from the xylem. The resulting positive pressure forces the sucrose-water mixture down toward the roots, where sucrose is unloaded. Transpiration causes water to return to the leaves through the xylem vessels.

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11.12: Introduction to Plant Sensory Systems and Responses

Identify common sensory systems and responses in plants

Animals can respond to environmental factors by moving to a new location. Plants, however, are rooted in place and must respond to the surrounding environmental factors. Plants have sophisticated systems to detect and respond to light, gravity, temperature, and physical touch. Receptors sense environmental factors and relay the information to effector systems—often through intermediate chemical messengers—to bring about plant responses.

What You'll Learn to Do

- Describe how red and blue light affect plant growth and metabolic activities
- Discuss gravitropism
- Describe thigmotropism, thigmonastism, and thigmogenesis
- Explain how plants defend themselves from predators and respond to wounds

Learning Activities

The learning activities for this section include the following:

- Plant Responses to Light
- Plant Responses to Gravity
- Plant Responses to Wind and Touch
- Defense Responses against Herbivores and Pathogens
- Self Check: Plant Sensory Systems and Responses

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11.13: Plant Responses to Light

Plants have a number of sophisticated uses for light that go far beyond their ability to photosynthesize low-molecular-weight sugars using only carbon dioxide, light, and water. **Photomorphogenesis** is the growth and development of plants in response to light. It allows plants to optimize their use of light and space. **Photoperiodism** is the ability to use light to track time. Plants can tell the time of day and time of year by sensing and using various wavelengths of sunlight. **Phototropism** is a directional response that allows plants to grow towards, or even away from, light.

The sensing of light in the environment is important to plants; it can be crucial for competition and survival. The response of plants to light is mediated by different photoreceptors, which are comprised of a protein covalently bonded to a light-absorbing pigment called a **chromophore**. Together, the two are called a chromoprotein.

The red/far-red and violet-blue regions of the visible light spectrum trigger structural development in plants. Sensory photoreceptors absorb light in these particular regions of the visible light spectrum because of the quality of light available in the daylight spectrum. In terrestrial habitats, light absorption by chlorophylls peaks in the blue and red regions of the spectrum. As light filters through the canopy and the blue and red wavelengths are absorbed, the spectrum shifts to the far-red end, shifting the plant community to those plants better adapted to respond to far-red light. Blue-light receptors allow plants to gauge the direction and abundance of sunlight, which is rich in blue–green emissions. Water absorbs red light, which makes the detection of blue light essential for algae and aquatic plants.

The Phytochrome System and the Red/Far-Red Response

The **phytochromes** are a family of chromoproteins with a linear tetrapyrrole chromophore, similar to the ringed tetrapyrrole light-absorbing head group of chlorophyll. Phytochromes have two photo-interconvertible forms: P_r and P_{fr}. P_r absorbs red light (~667 nm) and is immediately converted to P_{fr}. P_{fr} absorbs far-red light (~730 nm) and is quickly converted back to P_r. The minute difference between light defined as red or far-red is very important in this reaction. Absorption of red or far-red light causes a massive change to the shape of the chromophore, altering the conformation and activity of the phytochrome protein to which it is bound. P_{fr} is the physiologically active form of the protein; therefore, exposure to red light yields physiological activity. Exposure to far-red light inhibits phytochrome activity. Together, the two forms represent the phytochrome system (Figure 1).

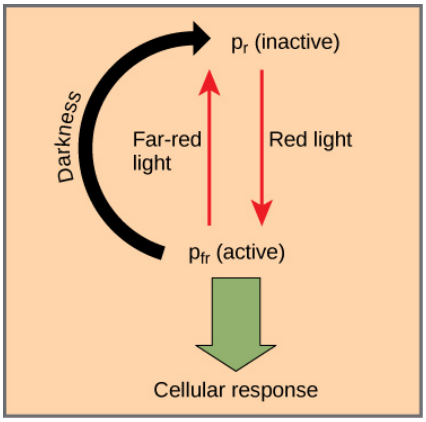


Figure 1. The biologically inactive form of phytochrome (Pr) is converted to the biologically active form Pfr under illumination with red light. Far-red light and darkness convert the molecule back to the inactive form.

The phytochrome system acts as a biological light switch. It monitors the level, intensity, duration, and color of environmental light. The effect of red light is reversible by immediately shining far-red light on the sample, which converts the chromoprotein to the inactive P_r form. Additionally, P_{fr} can slowly revert to P_r in the dark, or break down over time. In all instances, the physiological response induced by red light is reversed. The active form of phytochrome (P_{fr}) can directly activate other molecules in the cytoplasm, or it can be trafficked to the nucleus, where it directly activates or represses specific gene expression.

Once the phytochrome system evolved, plants adapted it to serve a variety of needs. Unfiltered, full sunlight contains much more red light than far-red light. Because chlorophyll absorbs strongly in the red region of the visible spectrum, but not in the far-red region, any plant in the shade of another plant on the forest floor will be exposed to red-depleted, far-red-enriched light. The

preponderance of far-red light converts phytochrome in the shaded leaves to the P_r (inactive) form, slowing growth. The nearest non-shaded (or even less-shaded) areas on the forest floor have more red light; leaves exposed to these areas sense the red light, which activates the P_{fr} form and induces growth. In short, plant shoots use the phytochrome system to grow away from shade and towards light. Because competition for light is so fierce in a dense plant community, the evolutionary advantages of the phytochrome system are obvious.

In seeds, the phytochrome system is not used to determine direction and quality of light (shaded versus unshaded). Instead, is it used merely to determine if there is any light at all. This is especially important in species with very small seeds, such as lettuce. Because of their size, lettuce seeds have few food reserves. Their seedlings cannot grow for long before they run out of fuel. If they germinated even a centimeter under the soil surface, the seedling would never make it into the sunlight and would die. In the dark, phytochrome is in the P_r (inactive form) and the seed will not germinate; it will only germinate if exposed to light at the surface of the soil. Upon exposure to light, P_r is converted to P_{fr} and germination proceeds.

Plants also use the phytochrome system to sense the change of season. Photoperiodism is a biological response to the timing and duration of day and night. It controls flowering, setting of winter buds, and vegetative growth. Detection of seasonal changes is crucial to plant survival. Although temperature and light intensity influence plant growth, they are not reliable indicators of season because they may vary from one year to the next. Day length is a better indicator of the time of year.

As stated above, unfiltered sunlight is rich in red light but deficient in far-red light. Therefore, at dawn, all the phytochrome molecules in a leaf quickly convert to the active P_{fr} form, and remain in that form until sunset. In the dark, the P_{fr} form takes hours to slowly revert back to the P_r form. If the night is long (as in winter), all of the P_{fr} form reverts. If the night is short (as in summer), a considerable amount of P_{fr} may remain at sunrise. By sensing the P_r/P_{fr} ratio at dawn, a plant can determine the length of the day/night cycle. In addition, leaves retain that information for several days, allowing a comparison between the length of the previous night and the preceding several nights. Shorter nights indicate springtime to the plant; when the nights become longer, autumn is approaching. This information, along with sensing temperature and water availability, allows plants to determine the time of the year and adjust their physiology accordingly. Short-day (long-night) plants use this information to flower in the late summer and early fall, when nights exceed a critical length (often eight or fewer hours). Long-day (short-night) plants flower during the spring, when darkness is less than a critical length (often eight to 15 hours). Not all plants use the phytochrome system in this way. Flowering in day-neutral plants is not regulated by day length.

? Try It

The word “horticulturist” comes from the Latin words for garden (*hortus*) and culture (*cultura*). This career has been revolutionized by progress made in the understanding of plant responses to environmental stimuli. Growers of crops, fruit, vegetables, and flowers were previously constrained by having to time their sowing and harvesting according to the season. Now, horticulturists can manipulate plants to increase leaf, flower, or fruit production by understanding how environmental factors affect plant growth and development.

Greenhouse management is an essential component of a horticulturist’s education. To lengthen the night, plants are covered with a blackout shade cloth. Long-day plants are irradiated with red light in winter to promote early flowering. For example, fluorescent (cool white) light high in blue wavelengths encourages leafy growth and is excellent for starting seedlings. Incandescent lamps (standard light bulbs) are rich in red light, and promote flowering in some plants. The timing of fruit ripening can be increased or delayed by applying plant hormones. Recently, considerable progress has been made in the development of plant breeds that are suited to different climates and resistant to pests and transportation damage. Both crop yield and quality have increased as a result of practical applications of the knowledge of plant responses to external stimuli and hormones.

Horticulturists find employment in private and governmental laboratories, greenhouses, botanical gardens, and in the production or research fields. They improve crops by applying their knowledge of genetics and plant physiology. To prepare for a horticulture career, students take classes in botany, plant physiology, plant pathology, landscape design, and plant breeding. To complement these traditional courses, horticulture majors add studies in economics, business, computer science, and communications.



Figure 2. Azure bluets (*Houstonia caerulea*) display a phototropic response by bending toward the light. (credit: Cory Zanker)

Phototropism—the directional bending of a plant toward or away from a light source—is a response to blue wavelengths of light. Positive phototropism is growth towards a light source (Figure 2), while negative phototropism (also called skototropism) is growth away from light.

The aptly-named **phototropins** are protein-based receptors responsible for mediating the phototropic response. Like all plant photoreceptors, phototropins consist of a protein portion and a light-absorbing portion, called the chromophore. In phototropins, the chromophore is a covalently-bound molecule of flavin; hence, phototropins belong to a class of proteins called flavoproteins.

Other responses under the control of phototropins are leaf opening and closing, chloroplast movement, and the opening of stomata. However, of all responses controlled by phototropins, phototropism has been studied the longest and is the best understood.

In their 1880 treatise *The Power of Movements in Plants*, Charles Darwin and his son Francis first described phototropism as the bending of seedlings toward light. Darwin observed that light was perceived by the tip of the plant (the apical meristem), but that the response (bending) took place in a different part of the plant. They concluded that the signal had to travel from the apical meristem to the base of the plant.

In 1913, Peter Boysen-Jensen demonstrated that a chemical signal produced in the plant tip was responsible for the bending at the base. He cut off the tip of a seedling, covered the cut section with a layer of gelatin, and then replaced the tip. The seedling bent toward the light when illuminated. However, when impermeable mica flakes were inserted between the tip and the cut base, the seedling did not bend. A refinement of the experiment showed that the signal traveled on the shaded side of the seedling. When the mica plate was inserted on the illuminated side, the plant did bend towards the light. Therefore, the chemical signal was a growth stimulant because the phototropic response involved faster cell elongation on the shaded side than on the illuminated side. We now know that as light passes through a plant stem, it is diffracted and generates phototropin activation across the stem. Most activation occurs on the lit side, causing the plant hormone indole acetic acid (IAA) to accumulate on the shaded side. Stem cells elongate under influence of IAA.

Cryptochromes are another class of blue-light absorbing photoreceptors that also contain a flavin-based chromophore. Cryptochromes set the plants 24-hour activity cycle, also know as its circadian rhythem, using blue light cues. There is some evidence that cryptochromes work together with phototropins to mediate the phototropic response.

Use the navigation menu in the left panel of this website to view images of plants in motion.

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11.14: Plant Responses to Gravity

Whether or not they germinate in the light or in total darkness, shoots usually sprout up from the ground, and roots grow downward into the ground. A plant laid on its side in the dark will send shoots upward when given enough time. Gravitropism ensures that roots grow into the soil and that shoots grow toward sunlight. Growth of the shoot apical tip upward is called **negative gravitropism**, whereas growth of the roots downward is called **positive gravitropism**.

Amyloplasts (also known as **statoliths**) are specialized plastids that contain starch granules and settle downward in response to gravity. Amyloplasts are found in shoots and in specialized cells of the root cap. When a plant is tilted, the statoliths drop to the new bottom cell wall. A few hours later, the shoot or root will show growth in the new vertical direction.

The mechanism that mediates gravitropism is reasonably well understood. When amyloplasts settle to the bottom of the gravity-sensing cells in the root or shoot, they physically contact the endoplasmic reticulum (ER), causing the release of calcium ions from inside the ER. This calcium signaling in the cells causes polar transport of the plant hormone IAA to the bottom of the cell. In roots, a high concentration of IAA inhibits cell elongation. The effect slows growth on the lower side of the root, while cells develop normally on the upper side. IAA has the opposite effect in shoots, where a higher concentration at the lower side of the shoot stimulates cell expansion, causing the shoot to grow up. After the shoot or root begin to grow vertically, the amyloplasts return to their normal position. Other hypotheses—involving the entire cell in the gravitropism effect—have been proposed to explain why some mutants that lack amyloplasts may still exhibit a weak gravitropic response.

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11.15: Plant Responses to Wind and Touch

The shoot of a pea plant winds around a trellis, while a tree grows on an angle in response to strong prevailing winds. These are examples of how plants respond to touch or wind.

The movement of a plant subjected to constant directional pressure is called **thigmotropism**, from the Greek words *thigma* meaning “touch,” and *tropism* implying “direction.” Tendrils are one example of this. The meristematic region of tendrils is very touch sensitive; light touch will evoke a quick coiling response. Cells in contact with a support surface contract, whereas cells on the opposite side of the support expand. Application of jasmonic acid is sufficient to trigger tendril coiling without a mechanical stimulus.

A **thigmonastic** response is a touch response independent of the direction of stimulus. In the Venus flytrap, two modified leaves are joined at a hinge and lined with thin fork-like tines along the outer edges. Tiny hairs are located inside the trap. When an insect brushes against these trigger hairs, touching two or more of them in succession, the leaves close quickly, trapping the prey. Glands on the leaf surface secrete enzymes that slowly digest the insect. The released nutrients are absorbed by the leaves, which reopen for the next meal.

Thigmomorphogenesis is a slow developmental change in the shape of a plant subjected to continuous mechanical stress. When trees bend in the wind, for example, growth is usually stunted and the trunk thickens. Strengthening tissue, especially xylem, is produced to add stiffness to resist the wind’s force. Researchers hypothesize that mechanical strain induces growth and differentiation to strengthen the tissues. Ethylene and jasmonate are likely involved in thigmomorphogenesis.

Use the menu at the left to navigate to three short movies: a Venus fly trap capturing prey, the progressive closing of sensitive plant leaflets, and the twining of tendrils.

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11.16: Defense Responses against Herbivores and Pathogens

Plants face two types of enemies: herbivores and pathogens. Herbivores both large and small use plants as food, and actively chew them. Pathogens are agents of disease. These infectious microorganisms, such as fungi, bacteria, and nematodes, live off of the plant and damage its tissues. Plants have developed a variety of strategies to discourage or kill attackers.

The first line of defense in plants is an intact and impenetrable barrier. Bark and the waxy cuticle can protect against predators. Other adaptations against herbivory include thorns, which are modified branches, and spines, which are modified leaves. They discourage animals by causing physical damage and inducing rashes and allergic reactions. A plant's exterior protection can be compromised by mechanical damage, which may provide an entry point for pathogens. If the first line of defense is breached, the plant must resort to a different set of defense mechanisms, such as toxins and enzymes.

Secondary metabolites are compounds that are not directly derived from photosynthesis and are not necessary for respiration or plant growth and development. Many metabolites are toxic, and can even be lethal to animals that ingest them. Some metabolites are alkaloids, which discourage predators with noxious odors (such as the volatile oils of mint and sage) or repellent tastes (like the bitterness of quinine). Other alkaloids affect herbivores by causing either excessive stimulation (caffeine is one example) or the lethargy associated with opioids. Some compounds become toxic after ingestion; for instance, glycol cyanide in the cassava root releases cyanide only upon ingestion by the herbivore.

Mechanical wounding and predator attacks activate defense and protection mechanisms both in the damaged tissue and at sites farther from the injury location. Some defense reactions occur within minutes: others over several hours. The infected and surrounding cells may die, thereby stopping the spread of infection.

Long-distance signaling elicits a systemic response aimed at deterring the predator. As tissue is damaged, jasmonates may promote the synthesis of compounds that are toxic to predators. Jasmonates also elicit the synthesis of volatile compounds that attract parasitoids, which are insects that spend their developing stages in or on another insect, and eventually kill their host. The plant may activate abscission of injured tissue if it is damaged beyond repair.

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11.17: Introduction to Plant Growth

Identify the key elements and processes in plant growth

Most plants continue to grow throughout their lives. Like other multicellular organisms, plants grow through a combination of cell growth and cell division. Cell growth increases cell size, while cell division (mitosis) increases the number of cells.

What You'll Learn to Do

- Describe the way that plants grow
- Distinguish between primary growth and secondary growth in stems
- Understand how hormones affect plant growth and development

Learning Activities

The learning activities for this section include the following:

- How Plants Grow
- Stem Growth
- Growth Responses
- Self Check: Plant Growth

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11.18: How Plants Grow

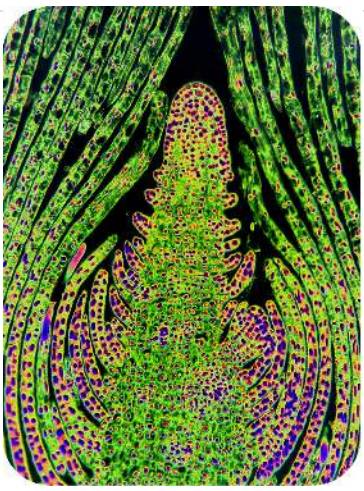


Figure 1. There must be an area of growth, similar to how the bones in your fingers, arms, and legs grow longer. There is, and it is called the apical meristem, which is shown here.

Most plants continue to grow throughout their lives. Like other multicellular organisms, plants grow through a combination of cell growth and cell division. Cell growth increases cell size, while cell division (mitosis) increases the number of cells. As plant cells grow, they also become specialized into different cell types through cellular differentiation. Once cells differentiate, they can no longer divide. How do plants grow or replace damaged cells after that?

The key to continued growth and repair of plant cells is **meristem**. Meristem is a type of plant tissue consisting of undifferentiated cells that can continue to divide and differentiate.

Apical meristems are found at the apex, or tip, of roots and buds, allowing roots and stems to grow in length and leaves and flowers to differentiate. Roots and stems grow in length because the meristem adds tissue "behind" it, constantly propelling itself further into the ground (for roots) or air (for stems). Often, the apical meristem of a single branch will become dominant, suppressing the growth of meristems on other branches and leading to the development of a single trunk. In grasses, meristems at the base of the leaf blades allow for regrowth after grazing by herbivores—or mowing by lawnmowers.

Apical meristems differentiate into the three basic types of meristem tissue which correspond to the three types of tissue: protoderm produces new epidermis, ground meristem produces ground tissue, and procambium produces new xylem and phloem. These three types of meristem are considered **primary meristem** because they allow growth in length or height, which is known as **primary growth**.

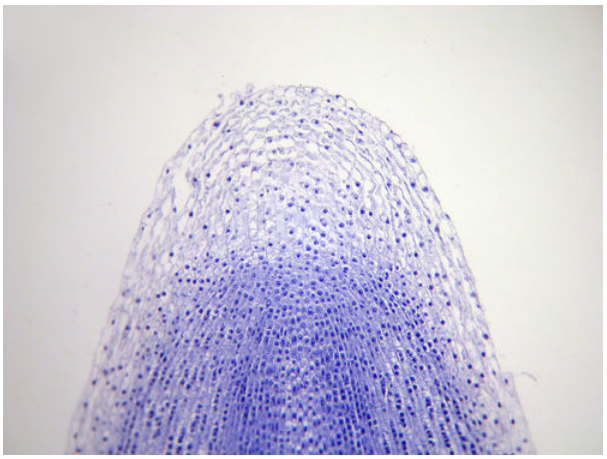


Figure 2. Microphotograph of the root tip of a broad bean show rapidly dividing apical meristem tissue just behind the root cap. Numerous cells in various stages of mitosis can be observed.

Secondary meristems allow growth in diameter (**secondary growth**) in woody plants. Herbaceous plants do not have secondary growth. The two types of **secondary meristem** are both named **cambium**, meaning "exchange" or "change." **Vascular cambium** produces secondary xylem (toward the center of the stem or root) and phloem (toward the outside of the stem or root), adding growth to the diameter of the plant. This process produces wood, and builds the sturdy trunks of trees. **Cork cambium** lies between the epidermis and the phloem, and replaces the epidermis of roots and stems with bark, one layer of which is cork.

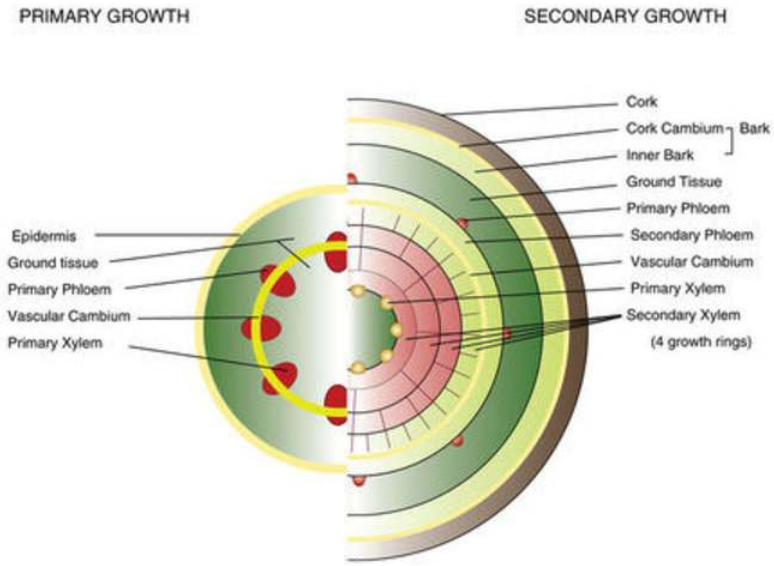


Figure 3. Primary and secondary growth

Woody plants grow in two ways. **Primary growth** adds length or height, mediated by apical meristem tissue at the tips of roots and shoots—which is difficult to show clearly in cross-sectional diagrams. **Secondary growth** adds to the diameter of a stem or root; vascular cambium adds xylem (inward) and phloem (outward), and cork cambium replaces epidermis with bark.

Watch this time-lapse video of plant growth. Note that there isn't any narration in the video.



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=388

In Summary: How Plants Grow

Most plants continue to grow as long as they live. They grow through a combination of cell growth and cell division (mitosis). The key to plant growth is meristem, a type of plant tissue consisting of undifferentiated cells that can continue to divide and differentiate. Meristem allows plant stems and roots to grow longer (primary growth) and wider (secondary growth).

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11.19: Stem Growth

Growth in plants occurs as the stems and roots lengthen. Some plants, especially those that are woody, also increase in thickness during their life span. The increase in length of the shoot and the root is referred to as **primary growth**, and is the result of cell division in the shoot apical meristem. **Secondary growth** is characterized by an increase in thickness or girth of the plant, and is caused by cell division in the lateral meristem. Figure 1 shows the areas of primary and secondary growth in a plant. Herbaceous plants mostly undergo primary growth, with hardly any secondary growth or increase in thickness. Secondary growth or "wood" is noticeable in woody plants; it occurs in some dicots, but occurs very rarely in monocots.

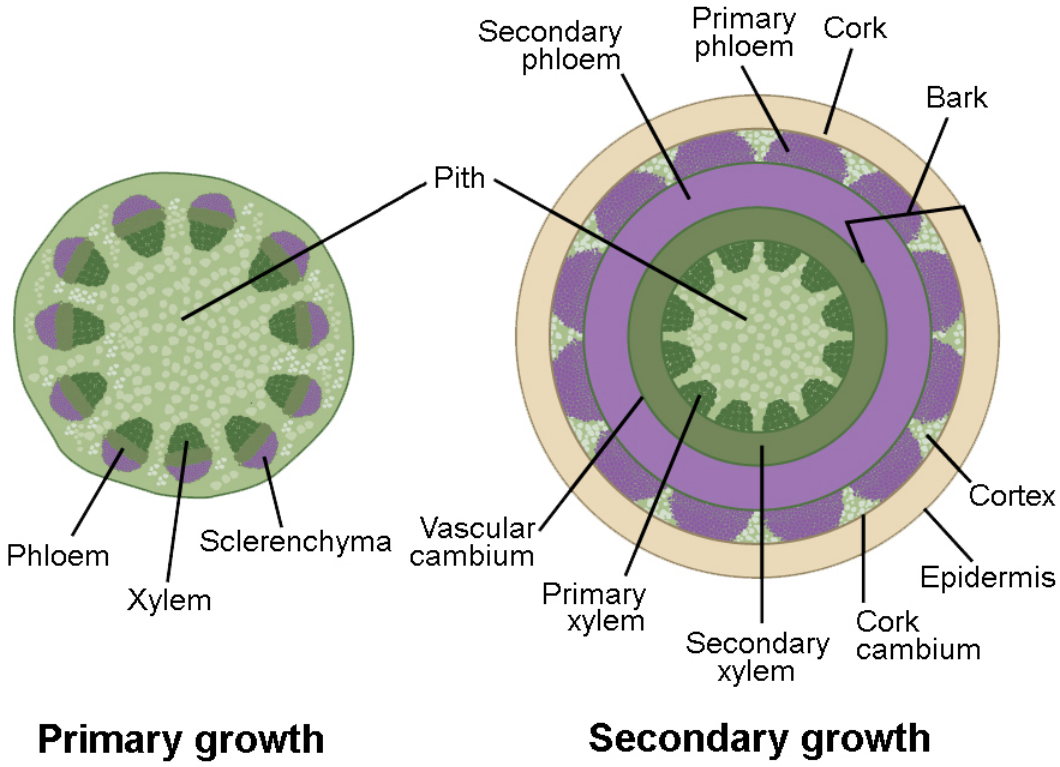


Figure 1. In woody plants, primary growth is followed by secondary growth, which allows the plant stem to increase in thickness or girth. Secondary vascular tissue is added as the plant grows, as well as a cork layer. The bark of a tree extends from the vascular cambium to the epidermis.

Some plant parts, such as stems and roots, continue to grow throughout a plant's life: a phenomenon called indeterminate growth. Other plant parts, such as leaves and flowers, exhibit determinate growth, which ceases when a plant part reaches a particular size.

Primary Growth

Most primary growth occurs at the apices, or tips, of stems and roots. Primary growth is a result of rapidly dividing cells in the apical meristems at the shoot tip and root tip. Subsequent cell elongation also contributes to primary growth. The growth of shoots and roots during primary growth enables plants to continuously seek water (roots) or sunlight (shoots).

The influence of the apical bud on overall plant growth is known as apical dominance, which diminishes the growth of axillary buds that form along the sides of branches and stems. Most coniferous trees exhibit strong apical dominance, thus producing the typical conical Christmas tree shape. If the apical bud is removed, then the axillary buds will start forming lateral branches. Gardeners make use of this fact when they prune plants by cutting off the tops of branches, thus encouraging the axillary buds to grow out, giving the plant a bushy shape.

Watch this BBC Nature video showing how time-lapse photography captures plant growth at high speed.

Secondary Growth

The increase in stem thickness that results from secondary growth is due to the activity of the lateral meristems, which are lacking in herbaceous plants. Lateral meristems include the vascular cambium and, in woody plants, the cork cambium (see Figure 1).



Figure 2. Lenticels on the bark of this cherry tree enable the woody stem to exchange gases with the surrounding atmosphere. (credit: Roger Griffith)

The vascular cambium is located just outside the primary xylem and to the interior of the primary phloem. The cells of the vascular cambium divide and form secondary xylem (tracheids and vessel elements) to the inside, and secondary phloem (sieve elements and companion cells) to the outside. The thickening of the stem that occurs in secondary growth is due to the formation of secondary phloem and secondary xylem by the vascular cambium, plus the action of cork cambium, which forms the tough outermost layer of the stem. The cells of the secondary xylem contain lignin, which provides hardiness and strength.

In woody plants, cork cambium is the outermost lateral meristem. It produces cork cells (bark) containing a waxy substance known as suberin that can repel water. The bark protects the plant against physical damage and helps reduce water loss. The cork cambium also produces a layer of cells known as phelloderm, which grows inward from the cambium. The cork cambium, cork cells, and phelloderm are collectively termed the **periderm**. The periderm substitutes for the epidermis in mature plants. In some plants, the periderm has many openings, known as **lenticels**, which allow the interior cells to exchange gases with the outside atmosphere (Figure 2). This supplies oxygen to the living and metabolically active cells of the cortex, xylem and phloem.

Annual Rings



Figure 3. The rate of wood growth increases in summer and decreases in winter, producing a characteristic ring for each year of growth. Seasonal changes in weather patterns can also affect the growth rate—note how the rings vary in thickness. (credit: Adrian Pingstone)

The activity of the vascular cambium gives rise to annual growth rings. During the spring growing season, cells of the secondary xylem have a large internal diameter and their primary cell walls are not extensively thickened. This is known as early wood, or spring wood. During the fall season, the secondary xylem develops thickened cell walls, forming late wood, or autumn wood, which is denser than early wood. This alternation of early and late wood is due largely to a seasonal decrease in the number of vessel elements and a seasonal increase in the number of tracheids. It results in the formation of an annual ring, which can be seen as a circular ring in the cross section of the stem (Figure 3). An examination of the number of annual rings and their nature (such as their size and cell wall thickness) can reveal the age of the tree and the prevailing climatic conditions during each season.

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11.20: Growth Responses

A plant's sensory response to external stimuli relies on chemical messengers (hormones). Plant hormones affect all aspects of plant life, from flowering to fruit setting and maturation, and from phototropism to leaf fall. Potentially every cell in a plant can produce plant hormones. They can act in their cell of origin or be transported to other portions of the plant body, with many plant responses involving the synergistic or antagonistic interaction of two or more hormones. In contrast, animal hormones are produced in specific glands and transported to a distant site for action, and they act alone.

Plant hormones are a group of unrelated chemical substances that affect plant morphogenesis. Five major plant hormones are traditionally described: auxins (particularly IAA), cytokinins, gibberellins, ethylene, and abscisic acid. In addition, other nutrients and environmental conditions can be characterized as growth factors.

Auxins

The term auxin is derived from the Greek word *auxein*, which means "to grow." **Auxins** are the main hormones responsible for cell elongation in phototropism and gravitropism. They also control the differentiation of meristem into vascular tissue, and promote leaf development and arrangement. While many synthetic auxins are used as herbicides, IAA is the only naturally occurring auxin that shows physiological activity. Apical dominance—the inhibition of lateral bud formation—is triggered by auxins produced in the apical meristem. Flowering, fruit setting and ripening, and inhibition of **abscission** (leaf falling) are other plant responses under the direct or indirect control of auxins. Auxins also act as a relay for the effects of the blue light and red/far-red responses.

Commercial use of auxins is widespread in plant nurseries and for crop production. IAA is used as a rooting hormone to promote growth of adventitious roots on cuttings and detached leaves. Applying synthetic auxins to tomato plants in greenhouses promotes normal fruit development. Outdoor application of auxin promotes synchronization of fruit setting and dropping to coordinate the harvesting season. Fruits such as seedless cucumbers can be induced to set fruit by treating unfertilized plant flowers with auxins.

Cytokinins

The effect of cytokinins was first reported when it was found that adding the liquid endosperm of coconuts to developing plant embryos in culture stimulated their growth. The stimulating growth factor was found to be **cytokinin**, a hormone that promotes cytokinesis (cell division). Almost 200 naturally occurring or synthetic cytokinins are known to date. Cytokinins are most abundant in growing tissues, such as roots, embryos, and fruits, where cell division is occurring. Cytokinins are known to delay senescence in leaf tissues, promote mitosis, and stimulate differentiation of the meristem in shoots and roots. Many effects on plant development are under the influence of cytokinins, either in conjunction with auxin or another hormone. For example, apical dominance seems to result from a balance between auxins that inhibit lateral buds, and cytokinins that promote bushier growth.

Gibberellins



Figure 1. In grapes, application of gibberellic acid increases the size of fruit and loosens clustering. (credit: Bob Nichols, USDA)

Gibberellins (GAs) are a group of about 125 closely related plant hormones that stimulate shoot elongation, seed germination, and fruit and flower maturation. GAs are synthesized in the root and stem apical meristems, young leaves, and seed embryos. In urban areas, GA antagonists are sometimes applied to trees under power lines to control growth and reduce the frequency of pruning.

GAs break dormancy (a state of inhibited growth and development) in the seeds of plants that require exposure to cold or light to germinate. Abscisic acid is a strong antagonist of GA action. Other effects of GAs include gender expression, seedless fruit development, and the delay of senescence in leaves and fruit. Seedless grapes are obtained through standard breeding methods and contain inconspicuous seeds that fail to develop. Because GAs are produced by the seeds, and because fruit development and stem elongation are under GA control, these varieties of grapes would normally produce small fruit in compact clusters. Maturing grapes are routinely treated with GA to promote larger fruit size, as well as looser bunches (longer stems), which reduces the instance of mildew infection (Figure 1).

Abscisic Acid

The plant hormone **abscisic acid** (ABA) was first discovered as the agent that causes the abscission or dropping of cotton bolls. However, more recent studies indicate that ABA plays only a minor role in the abscission process. ABA accumulates as a response to stressful environmental conditions, such as dehydration, cold temperatures, or shortened day lengths. Its activity counters many of the growth-promoting effects of GAs and auxins. ABA inhibits stem elongation and induces dormancy in lateral buds.

ABA induces dormancy in seeds by blocking germination and promoting the synthesis of storage proteins. Plants adapted to temperate climates require a long period of cold temperature before seeds germinate. This mechanism protects young plants from sprouting too early during unseasonably warm weather in winter. As the hormone gradually breaks down over winter, the seed is released from dormancy and germinates when conditions are favorable in spring. Another effect of ABA is to promote the development of winter buds; it mediates the conversion of the apical meristem into a dormant bud. Low soil moisture causes an increase in ABA, which causes stomata to close, reducing water loss in winter buds.

Ethylene

Ethylene is associated with fruit ripening, flower wilting, and leaf fall. Ethylene is unusual because it is a volatile gas (C_2H_4). Hundreds of years ago, when gas street lamps were installed in city streets, trees that grew close to lamp posts developed twisted, thickened trunks and shed their leaves earlier than expected. These effects were caused by ethylene volatilizing from the lamps.

Aging tissues (especially senescing leaves) and nodes of stems produce ethylene. The best-known effect of the hormone, however, is the promotion of fruit ripening. Ethylene stimulates the conversion of starch and acids to sugars. Some people store unripe fruit, such as avocadoes, in a sealed paper bag to accelerate ripening; the gas released by the first fruit to mature will speed up the maturation of the remaining fruit. Ethylene also triggers leaf and fruit abscission, flower fading and dropping, and promotes germination in some cereals and sprouting of bulbs and potatoes.

Ethylene is widely used in agriculture. Commercial fruit growers control the timing of fruit ripening with application of the gas. Horticulturalists inhibit leaf dropping in ornamental plants by removing ethylene from greenhouses using fans and ventilation.

Nontraditional Hormones

Recent research has discovered a number of compounds that also influence plant development. Their roles are less understood than the effects of the major hormones described so far.

Jasmonates play a major role in defense responses to herbivory. Their levels increase when a plant is wounded by a predator, resulting in an increase in toxic secondary metabolites. They contribute to the production of volatile compounds that attract natural enemies of predators. For example, chewing of tomato plants by caterpillars leads to an increase in jasmonic acid levels, which in turn triggers the release of volatile compounds that attract predators of the pest.

Oligosaccharins also play a role in plant defense against bacterial and fungal infections. They act locally at the site of injury, and can also be transported to other tissues. **Strigolactones** promote seed germination in some species and inhibit lateral apical development in the absence of auxins. Strigolactones also play a role in the establishment of mycorrhizae, a mutualistic association of plant roots and fungi. Brassinosteroids are important to many developmental and physiological processes. Signals between these compounds and other hormones, notably auxin and GAs, amplifies their physiological effect. Apical dominance, seed germination,

gravitropism, and resistance to freezing are all positively influenced by hormones. Root growth and fruit dropping are inhibited by steroids.

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11.21: Introduction to Plant Nutrition

Discuss the common nutritional needs of plants

Plants obtain food in two different ways. Autotrophic plants can make their own food from inorganic raw materials, such as carbon dioxide and water, through photosynthesis in the presence of sunlight. Green plants are included in this group. Some plants, however, are heterotrophic: they are totally parasitic and lacking in chlorophyll. These plants, referred to as holo-parasitic plants, are unable to synthesize organic carbon and draw all of their nutrients from the host plant.

Plants may also enlist the help of microbial partners in nutrient acquisition. Particular species of bacteria and fungi have evolved along with certain plants to create a mutualistic symbiotic relationship with roots. This improves the nutrition of both the plant and the microbe. The formation of nodules in legume plants and mycorrhization can be considered among the nutritional adaptations of plants. However, these are not the only type of adaptations that we may find; many plants have other adaptations that allow them to thrive under specific conditions.

What You'll Learn to Do

- List the elements and compounds required for proper plant nutrition
- Describe how symbiotic relationships help autotrophic plants obtain nutrients
- Describe how heterotrophic plants obtain nutrients

Learning Activities

The learning activities for this section include the following:

- Nutritional Requirements
- Autotrophic Plants
- Heterotrophic Plants
- Self Check: Plant Nutrition

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11.22: Nutritional Requirements

Plants are unique organisms that can absorb nutrients and water through their root system, as well as carbon dioxide from the atmosphere. Soil quality and climate are the major determinants of plant distribution and growth. The combination of soil nutrients, water, and carbon dioxide, along with sunlight, allows plants to grow.

The Chemical Composition of Plants

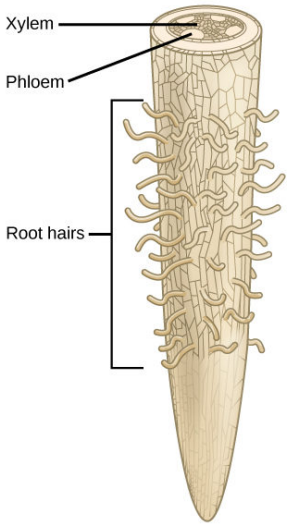


Figure 1. Water is absorbed through the root hairs and moves up the xylem to the leaves.

Since plants require nutrients in the form of elements such as carbon and potassium, it is important to understand the chemical composition of plants. The majority of volume in a plant cell is water; it typically comprises 80 to 90 percent of the plant's total weight. Soil is the water source for land plants, and can be an abundant source of water, even if it appears dry. Plant roots absorb water from the soil through root hairs and transport it up to the leaves through the xylem. As water vapor is lost from the leaves, the process of transpiration and the polarity of water molecules (which enables them to form hydrogen bonds) draws more water from the roots up through the plant to the leaves (Figure 1). Plants need water to support cell structure, for metabolic functions, to carry nutrients, and for photosynthesis.

Plant cells need essential substances, collectively called nutrients, to sustain life. Plant nutrients may be composed of either organic or inorganic compounds. An **organic compound** is a chemical compound that contains carbon, such as carbon dioxide obtained from the atmosphere. Carbon that was obtained from atmospheric CO_2 composes the majority of the dry mass within most plants. An **inorganic compound** does not contain carbon and is not part of, or produced by, a living organism. Inorganic substances, which form the majority of the soil solution, are commonly called minerals: those required by plants include nitrogen (N) and potassium (K) for structure and regulation.

Essential Nutrients

Plants require only light, water and about 20 elements to support all their biochemical needs: these 20 elements are called essential nutrients (Table 1). For an element to be regarded as **essential**, three criteria are required: 1) a plant cannot complete its life cycle without the element; 2) no other element can perform the function of the element; and 3) the element is directly involved in plant nutrition.

Table 1. Essential Elements for Plant Growth	
Macronutrients	Micronutrients
Carbon (C)	Iron (Fe)
Hydrogen (H)	Manganese (Mn)
Oxygen (O)	Boron (B)
Nitrogen (N)	Molybdenum (Mo)
Phosphorus (P)	Copper (Cu)
Potassium (K)	Zinc (Zn)
Calcium (Ca)	Chlorine (Cl)
Magnesium (Mg)	Nickel (Ni)
Sulfur (S)	Cobalt (Co)
	Sodium (Na)
	Silicon (Si)

Macronutrients and Micronutrients

The essential elements can be divided into two groups: macronutrients and micronutrients. Nutrients that plants require in larger amounts are called **macronutrients**. About half of the essential elements are considered macronutrients: carbon, hydrogen, oxygen, nitrogen, phosphorus, potassium, calcium, magnesium and sulfur. The first of these macronutrients, carbon (C), is required to form carbohydrates, proteins, nucleic acids, and many other compounds; it is therefore present in all macromolecules. On average, the dry weight (excluding water) of a cell is 50 percent carbon. As shown in Figure 2, carbon is a key part of plant biomolecules.

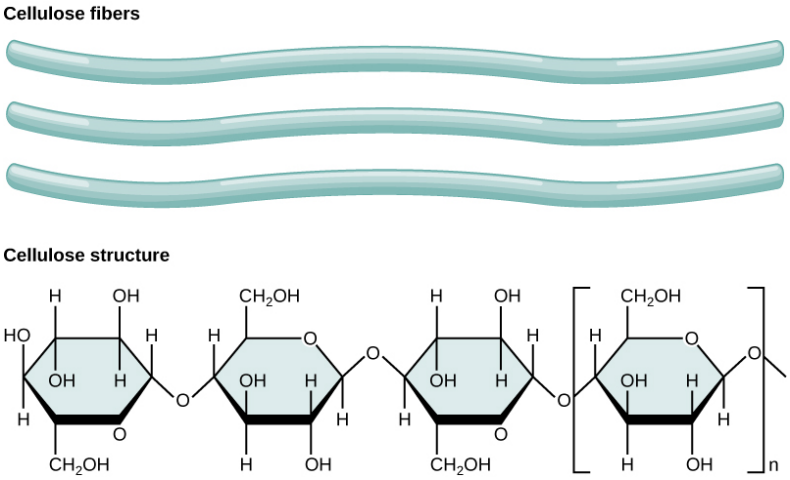


Figure 2. Cellulose, the main structural component of the plant cell wall, makes up over thirty percent of plant matter. It is the most abundant organic compound on earth.

The next most abundant element in plant cells is nitrogen (N); it is part of proteins and nucleic acids. Nitrogen is also used in the synthesis of some vitamins. Hydrogen and oxygen are macronutrients that are part of many organic compounds, and also form water. Oxygen is necessary for cellular respiration; plants use oxygen to store energy in the form of ATP. Phosphorus (P), another macromolecule, is necessary to synthesize nucleic acids and phospholipids. As part of ATP, phosphorus enables food energy to be converted into chemical energy through oxidative phosphorylation. Likewise, light energy is converted into chemical energy during photophosphorylation in photosynthesis, and into chemical energy to be extracted during respiration. Sulfur is part of certain amino acids, such as cysteine and methionine, and is present in several coenzymes. Sulfur also plays a role in photosynthesis as part of the electron transport chain, where hydrogen gradients play a key role in the conversion of light energy into ATP. Potassium (K) is

important because of its role in regulating stomatal opening and closing. As the openings for gas exchange, stomata help maintain a healthy water balance; a potassium ion pump supports this process.

Magnesium (Mg) and calcium (Ca) are also important macronutrients. The role of calcium is twofold: to regulate nutrient transport, and to support many enzyme functions. Magnesium is important to the photosynthetic process. These minerals, along with the micronutrients, which are described below, also contribute to the plant's ionic balance.

In addition to macronutrients, organisms require various elements in small amounts. These **micronutrients**, or trace elements, are present in very small quantities. They include boron (B), chlorine (Cl), manganese (Mn), iron (Fe), zinc (Zn), copper (Cu), molybdenum (Mo), nickel (Ni), silicon (Si), and sodium (Na).

Deficiencies in any of these nutrients—particularly the macronutrients—can adversely affect plant growth (Figure 3). Depending on the specific nutrient, a lack can cause stunted growth, slow growth, or chlorosis (yellowing of the leaves). Extreme deficiencies may result in leaves showing signs of cell death.



Figure 3. Nutrient deficiency is evident in the symptoms these plants show. This (a) grape tomato suffers from blossom end rot caused by calcium deficiency. The yellowing in this (b) Frangula alnus results from magnesium deficiency. Inadequate magnesium also leads to (c) intervenal chlorosis, seen here in a sweetgum leaf. This (d) palm is affected by potassium deficiency. (credit c: modification of work by Jim Conrad; credit d: modification of work by Malcolm Manners)

Visit this website to participate in an interactive experiment on plant nutrient deficiencies. You can adjust the amounts of N, P, K, Ca, Mg, and Fe that plants receive . . . and see what happens.

? Try It

Hydroponics is a method of growing plants in a water-nutrient solution instead of soil. Since its advent, hydroponics has developed into a growing process that researchers often use. Scientists who are interested in studying plant nutrient deficiencies can use hydroponics to study the effects of different nutrient combinations under strictly controlled conditions. Hydroponics has also developed as a way to grow flowers, vegetables, and other crops in greenhouse environments. You might find hydroponically grown produce at your local grocery store. Today, many lettuces and tomatoes in your market have been hydroponically grown.

Learning Objectives

Plants can absorb inorganic nutrients and water through their root system, and carbon dioxide from the environment. The combination of organic compounds, along with water, carbon dioxide, and sunlight, produce the energy that allows plants to grow. Inorganic compounds form the majority of the soil solution. Plants access water though the soil. Water is absorbed by the plant root, transports nutrients throughout the plant, and maintains the structure of the plant. Essential elements are indispensable elements for plant growth. They are divided into macronutrients and micronutrients. The macronutrients plants require are carbon, nitrogen, hydrogen, oxygen, phosphorus, potassium, calcium, magnesium, and sulfur. Important micronutrients include iron, manganese, boron, molybdenum, copper, zinc, chlorine, nickel, cobalt, silicon and sodium.

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11.23: Autotrophic Plants

Nitrogen Fixation: Root and Bacteria Interactions

Nitrogen is an important macronutrient because it is part of nucleic acids and proteins. Atmospheric nitrogen, which is the diatomic molecule N_2, or dinitrogen, is the largest pool of nitrogen in terrestrial ecosystems. However, plants cannot take advantage of this nitrogen because they do not have the necessary enzymes to convert it into biologically useful forms. However, nitrogen can be "fixed," which means that it can be converted to ammonia (NH_3) through biological, physical, or chemical processes. As you have learned, biological nitrogen fixation (BNF) is the conversion of atmospheric nitrogen (N_2) into ammonia (NH_3), exclusively carried out by prokaryotes such as soil bacteria or cyanobacteria. Biological processes contribute 65 percent of the nitrogen used in agriculture. The following equation represents the process:



The most important source of BNF is the symbiotic interaction between soil bacteria and legume plants, including many crops important to humans (Figure 1). The NH3 resulting from fixation can be transported into plant tissue and incorporated into amino acids, which are then made into plant proteins. Some legume seeds, such as soybeans and peanuts, contain high levels of protein, and serve among the most important agricultural sources of protein in the world.



Figure 1. Some common edible legumes—like (a) peanuts, (b) beans, and (c) chickpeas—are able to interact symbiotically with soil bacteria that fix nitrogen. (credit a: modification of work by Jules Clancy; credit b: modification of work by USDA)

? Practice Question

Farmers often rotate corn (a cereal crop) and soy beans (a legume), planting a field with each crop in alternate seasons. What advantage might this crop rotation confer?

[practice-area rows="2"][/practice-area]
[reveal-answer q="890921"]Show Answer[/reveal-answer]
[hidden-answer a="890921"]Soybeans are able to fix nitrogen in their roots, which are not harvested at the end of the growing season. The belowground nitrogen can be used in the next season by the corn.[/hidden-answer]

Soil bacteria, collectively called **rhizobia**, symbiotically interact with legume roots to form specialized structures called **nodules**, in which nitrogen fixation takes place. This process entails the reduction of atmospheric nitrogen to ammonia, by means of the enzyme **nitrogenase**. Therefore, using rhizobia is a natural and environmentally friendly way to fertilize plants, as opposed to chemical fertilization that uses a nonrenewable resource, such as natural gas. Through symbiotic nitrogen fixation, the plant benefits from using an endless source of nitrogen from the atmosphere. The process simultaneously contributes to soil fertility because the plant root system leaves behind some of the biologically available nitrogen. As in any symbiosis, both organisms benefit from the interaction: the plant obtains ammonia, and bacteria obtain carbon compounds generated through photosynthesis, as well as a protected niche in which to grow (Figure 2).



Figure 2. Soybean roots contain (a) nitrogen-fixing nodules. Cells within the nodules are infected with *Bradyrhyzobium japonicum*, a rhizobia or "root-loving" bacterium. The bacteria are encased in (b) vesicles inside the cell, as can be seen in this transmission electron micrograph. (credit a: modification of work by USDA; credit b: modification of work by Louisa Howard, Dartmouth Electron Microscope Facility; scale-bar data from Matt Russell)

Mycorrhizae: The Symbiotic Relationship between Fungi and Roots

A nutrient depletion zone can develop when there is rapid soil solution uptake, low nutrient concentration, low diffusion rate, or low soil moisture. These conditions are very common; therefore, most plants rely on fungi to facilitate the uptake of minerals from the soil. Fungi form symbiotic associations called mycorrhizae with plant roots, in which the fungi actually are integrated into the physical structure of the root. The fungi colonize the living root tissue during active plant growth.



Figure 3. Root tips proliferate in the presence of mycorrhizal infection, which appears as off-white fuzz in this image. (credit: modification of work by Nilsson et al., BMC Bioinformatics 2005)

Through mycorrhization, the plant obtains mainly phosphate and other minerals, such as zinc and copper, from the soil. The fungus obtains nutrients, such as sugars, from the plant root (Figure 3). Mycorrhizae help increase the surface area of the plant root system because hyphae, which are narrow, can spread beyond the nutrient depletion zone. Hyphae can grow into small soil pores that allow access to phosphorus that would otherwise be unavailable to the plant. The beneficial effect on the plant is best observed in poor soils. The benefit to fungi is that they can obtain up to 20 percent of the total carbon accessed by plants. Mycorrhizae functions as a physical barrier to pathogens. It also provides an induction of generalized host defense mechanisms, and sometimes involves production of antibiotic compounds by the fungi.

There are two types of mycorrhizae: ectomycorrhizae and endomycorrhizae. Ectomycorrhizae form an extensive dense sheath around the roots, called a mantle. Hyphae from the fungi extend from the mantle into the soil, which increases the surface area for water and mineral absorption. This type of mycorrhizae is found in forest trees, especially conifers, birches, and oaks. Endomycorrhizae, also called arbuscular mycorrhizae, do not form a dense sheath over the root. Instead, the fungal mycelium is embedded within the root tissue. Endomycorrhizae are found in the roots of more than 80 percent of terrestrial plants.

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11.24: Heterotrophic Plants

Some plants cannot produce their own food and must obtain their nutrition from outside sources—these plants are heterotrophic. This may occur with plants that are parasitic or saprophytic. Some plants are mutualistic symbionts, epiphytes, or insectivorous.

Plant Parasites

A **parasitic plant** depends on its host for survival. Some parasitic plants have no leaves. An example of this is the dodder (Figure 1a), which has a weak, cylindrical stem that coils around the host and forms suckers. From these suckers, cells invade the host stem and grow to connect with the vascular bundles of the host. The parasitic plant obtains water and nutrients through these connections. The plant is a total parasite (a holoparasite) because it is completely dependent on its host. Other parasitic plants (hemiparasites) are fully photosynthetic and only use the host for water and minerals. There are about 4,100 species of parasitic plants.

Saprophytes

A **saprophyte** is a plant that does not have chlorophyll and gets its food from dead matter, similar to bacteria and fungi (note that fungi are often called saprophytes, which is incorrect, because fungi are not plants). Plants like these use enzymes to convert organic food materials into simpler forms from which they can absorb nutrients (Figure 1b). Most saprophytes do not directly digest dead matter: instead, they parasitize fungi that digest dead matter, or are mycorrhizal, ultimately obtaining photosynthate from a fungus that derived photosynthate from its host. Saprophytic plants are uncommon; only a few species are described.



Figure 1. (a) The dodder is a holoparasite that penetrates the host's vascular tissue and diverts nutrients for its own growth. Note that the vines of the dodder, which has white flowers, are beige. The dodder has no chlorophyll and cannot produce its own food. (b) Saprophytes, like this Dutchmen's pipe (*Monotropa hypopitys*), obtain their food from dead matter and do not have chlorophyll. (a credit: "Lalithamba"/Flickr; b credit: modification of work by Iwona Erskine-Kellie)

Symbionts

A **symbiont** is a plant in a symbiotic relationship, with special adaptations such as mycorrhizae or nodule formation. Fungi also form symbiotic associations with cyanobacteria and green algae (called lichens). Lichens can sometimes be seen as colorful growths on the surface of rocks and trees (Figure 2a). The algal partner (phycobiont) makes food autotrophically, some of which it shares with the fungus; the fungal partner (mycobiont) absorbs water and minerals from the environment, which are made available to the green alga. If one partner was separated from the other, they would both die.

Epiphytes

An **epiphyte** is a plant that grows on other plants, but is not dependent upon the other plant for nutrition (Figure 2b). Epiphytes have two types of roots: clinging aerial roots, which absorb nutrients from humus that accumulates in the crevices of trees; and aerial roots, which absorb moisture from the atmosphere.



Figure 2. (a) Lichens, which often have symbiotic relationships with other plants, can sometimes be found growing on trees. (b) These epiphyte plants grow in the main greenhouse of the *Jardin des Plantes* in Paris. (credit: a "benketaro"/Flickr)

Insectivorous Plants



Figure 3. A Venus flytrap has specialized leaves to trap insects. (credit: "Selena N. B. H."/Flickr)

An **insectivorous** plant has specialized leaves to attract and digest insects. The Venus flytrap is popularly known for its insectivorous mode of nutrition, and has leaves that work as traps (Figure 3).

The minerals it obtains from prey compensate for those lacking in the boggy (low pH) soil of its native North Carolina coastal plains. There are three sensitive hairs in the center of each half of each leaf. The edges of each leaf are covered with long spines. Nectar secreted by the plant attracts flies to the leaf. When a fly touches the sensory hairs, the leaf immediately closes. Next, fluids and enzymes break down the prey and minerals are absorbed by the leaf. Since this plant is popular in the horticultural trade, it is threatened in its original habitat.

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11.25: Putting It Together- Plant Structure and Function

think about It

Let’s think back to the beginning of the module: we mentioned that many plants have evolved to thrive in conditions that limit their access to light, nutrients, and oxygen. Can you think of any adaptations that would help plants in these situations?

Before you move on to the examples of adaptations, take some time to record your thoughts here:

[practice-area rows=”4″][/practice-area]

In tropical rainforests, light is often scarce, since many trees and plants grow close together and block much of the sunlight from reaching the forest floor. Many tropical plant species have exceptionally broad leaves to maximize the capture of sunlight. Other species are epiphytes: plants that grow on other plants that serve as a physical support. Such plants are able to grow high up in the canopy atop the branches of other trees, where sunlight is more plentiful. Epiphytes live on rain and minerals collected in the branches and leaves of the supporting plant. Bromeliads (members of the pineapple family), ferns, and orchids are examples of tropical epiphytes (Figure 1). Many epiphytes have specialized tissues that enable them to efficiently capture and store water.



Figure 1. One of the most well known bromeliads is Spanish moss (*Tillandsia usneoides*), seen here in an oak tree. (credit: Kristine Paulus)

Some plants have special adaptations that help them to survive in nutrient-poor environments. Carnivorous plants, such as the Venus flytrap and the pitcher plant (Figure 2), grow in bogs where the soil is low in nitrogen. In these plants, leaves are modified to capture insects. The insect-capturing leaves may have evolved to provide these plants with a supplementary source of much-needed nitrogen.



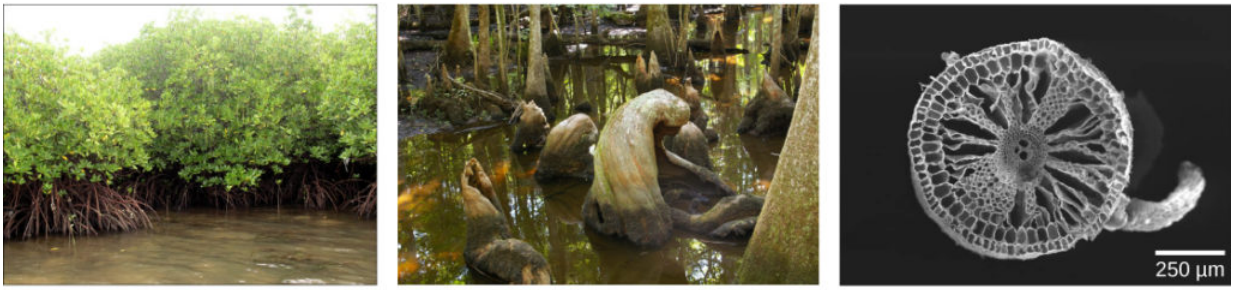
(a) (b)

Figure 2. The (a) Venus flytrap has modified leaves that can capture insects. When an unlucky insect touches the trigger hairs inside the leaf, the trap suddenly closes. The opening of the (b) pitcher plant is lined with a slippery wax. Insects crawling on the lip slip and fall into a pool of water in the bottom of the pitcher, where they are digested by bacteria. The plant then absorbs the smaller molecules. (credit a: modification of work by Peter Shanks; credit b: modification of work by Tim Mansfield)

Watch *Venus Flytraps: Jaws of Death*, an extraordinary BBC close-up of the Venus flytrap in action.

A link to an interactive elements can be found at the bottom of this page.

Many swamp plants have adaptations that enable them to thrive in wet areas, where their roots grow submerged underwater. In these aquatic areas, the soil is unstable and little oxygen is available to reach the roots. Trees such as mangroves (*Rhizophora* sp.) growing in coastal waters produce aboveground roots that help support the tree (Figure 3). Some species of mangroves, as well as cypress trees, have pneumatophores: upward-growing roots containing pores and pockets of tissue specialized for gas exchange. Wild rice is an aquatic plant with large air spaces in the root cortex. The air-filled tissue—called aerenchyma—provides a path for oxygen to diffuse down to the root tips, which are embedded in oxygen-poor bottom sediments.



(a) (b) (c)

Figure 3. The branches of (a) mangrove trees develop aerial roots, which descend to the ground and help to anchor the trees. (b) Cypress trees and some mangrove species have upward-growing roots called pneumatophores that are involved in gas exchange. Aquatic plants such as (c) wild rice have large spaces in the root cortex called aerenchyma, visualized here using scanning electron microscopy. (credit a: modification of work by Roberto Verzo; credit b: modification of work by Duane Burdick; credit c: modification of work by Robert R. Wise)

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11.26: Cerego- Plant Structure and Function

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for Plant Structure and Function. You'll need to create a free log-in to practice these items, if you haven't already.

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CHAPTER OVERVIEW

12: Module 9- Plant Reproduction

12.1: Why It Matters- Plant Reproduction
12.2: Introduction to Reproductive Development and Structure
12.3: Stages of a Plant’s Life Cycle
12.4: Flower Structure
12.5: Sexual Reproduction in Angiosperms
12.6: Sexual Reproduction in Gymnosperms
12.7: Angiosperms versus Gymnosperms
12.8: Introduction to Asexual Reproduction in Plants
12.9: Asexual Plants
12.10: Natural and Artificial Asexual Reproduction
12.11: Plant Life Spans
12.12: Introduction to Sexual Reproduction in Plants
12.13: Self-Pollination and Cross-Pollination
12.14: Methods of Pollination
12.15: Double Fertilization
12.16: Development Seeds and Fruit
12.17: Fruit and Seed Dispersal
12.18: Putting It Together- Plant Reproduction
12.19: Cerego- Plant Reproduction

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12.1: Why It Matters- Plant Reproduction

Why discuss the methods and structures of plant reproduction?

Over 50 million Americans suffer from seasonal allergies every year. Each spring, summer, and fall, trees, weeds, and grasses release tiny pollen grains into the air. Some of the pollen ends up in your nose and throat. This can trigger a type of allergy called hay fever.

Symptoms can include

- Sneezing, often with a runny or clogged nose
- Coughing and postnasal drip
- Itching eyes, nose and throat
- Red and watery eyes
- Dark circles under the eyes

The pollen that causes these allergies is an essential part of plant reproduction (at least, sexual reproduction in plants). Let's learn what role these irksome particles play in the plant lifecycle.

Learning Outcomes

- Discuss the reproductive development and structure of plants
- Describe how plants reproduce asexually
- Describe how plants reproduce sexually

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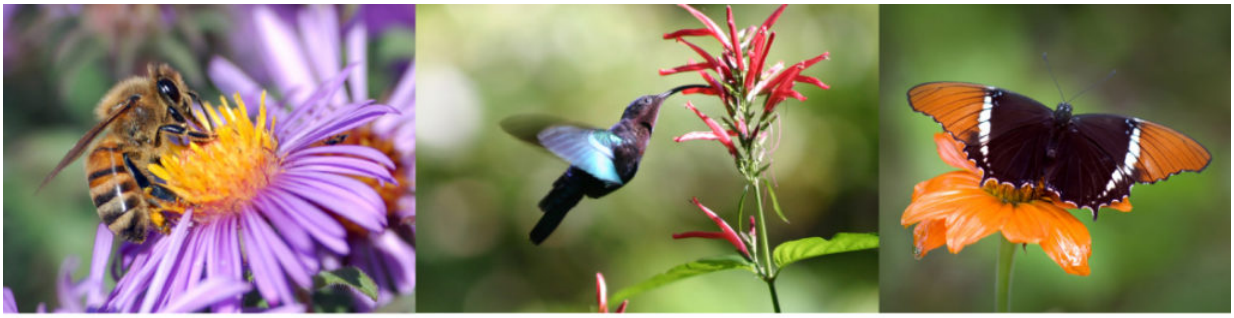
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12.2: Introduction to Reproductive Development and Structure

Discuss the reproductive development and structure of plants

Plants have evolved different reproductive strategies for the continuation of their species. Some plants reproduce sexually, and others asexually, in contrast to animal species, which rely almost exclusively on sexual reproduction. Plant sexual reproduction usually depends on pollinating agents, while asexual reproduction is independent of these agents. Flowers are often the showiest or most strongly scented part of plants. With their bright colors, fragrances, and interesting shapes and sizes, flowers attract insects, birds, and animals to serve their pollination needs. Other plants pollinate via wind or water; still others self-pollinate.



(a) (b) (c)

Figure 1. Plants that reproduce sexually often achieve fertilization with the help of pollinators such as (a) bees, (b) birds, and (c) butterflies. (credit a: modification of work by John Severns; credit b: modification of work by Charles J. Sharp; credit c: modification of work by “Galawebdesign”/Flickr)

What You’ll Learn to Do

- Describe the two stages of a plant’s lifecycle
- Describe the components of a complete flower
- Identify the structures involved in reproduction of angiosperms
- Identify the structures involved in reproduction of gymnosperms

Learning Activities

The learning activities for this section include the following:

- Stages of a Plant’s Life Cycle
- Flower Structure
- Sexual Reproduction in Angiosperms
- Sexual Reproduction in Gymnosperms
- Angiosperms versus Gymnosperms
- Self Check: Reproductive Development and Structure

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12.3: Stages of a Plant's Life Cycle

Sexual reproduction takes place with slight variations in different groups of plants. Plants have two distinct stages in their lifecycle: the gametophyte stage and the sporophyte stage. The haploid **gametophyte** produces the male and female gametes by mitosis in distinct multicellular structures. Fusion of the male and females gametes forms the diploid zygote, which develops into the **sporophyte**. After reaching maturity, the diploid sporophyte produces spores by meiosis, which in turn divide by mitosis to produce the haploid gametophyte. The new gametophyte produces gametes, and the cycle continues. This is the alternation of generations, and is typical of plant reproduction (Figure 1).

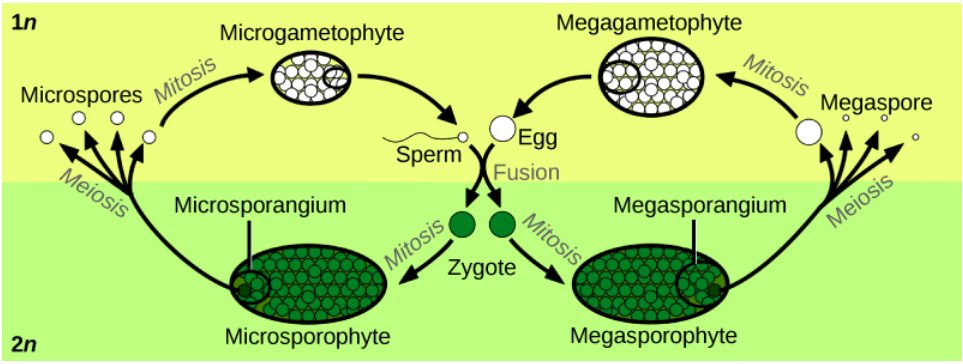


Figure 1. The alternation of generations in angiosperms is depicted in this diagram. (credit: modification of work by Peter Coxhead)

The life cycle of higher plants is dominated by the sporophyte stage, with the gametophyte borne on the sporophyte. In ferns, the gametophyte is free-living and very distinct in structure from the diploid sporophyte. In bryophytes, such as mosses, the haploid gametophyte is more developed than the sporophyte.

During the vegetative phase of growth, plants increase in size and produce a shoot system and a root system. As they enter the reproductive phase, some of the branches start to bear flowers. Many flowers are borne singly, whereas some are borne in clusters. The flower is borne on a stalk known as a receptacle. Flower shape, color, and size are unique to each species, and are often used by taxonomists to classify plants.

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12.4: Flower Structure

Flowers contain the plant's reproductive structures. A typical flower has four main parts—or whorls—known as the calyx, corolla, androecium, and gynoecium (Figure 1).

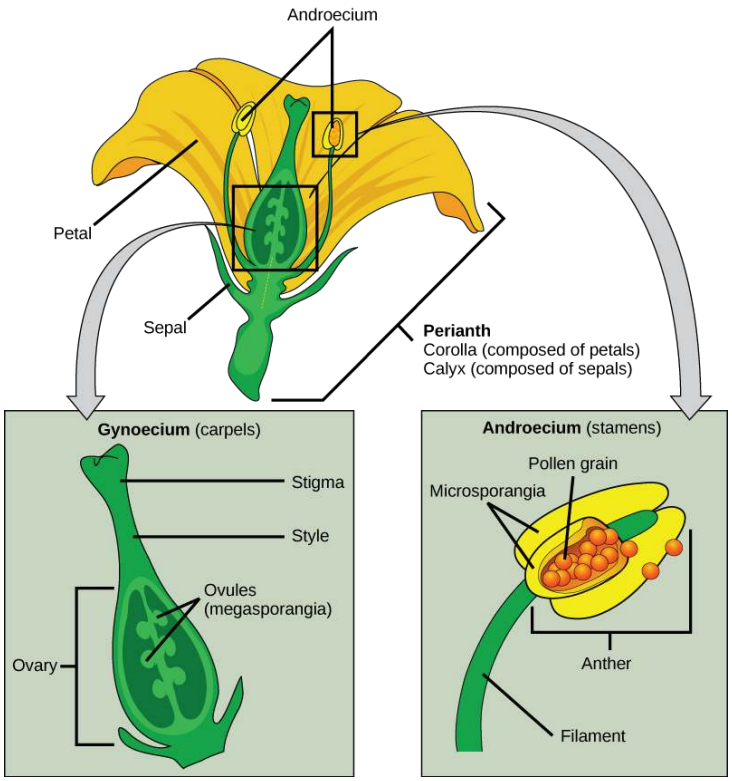


Figure 1. The four main parts of the flower are the calyx, corolla, androecium, and gynoecium. The androecium is the sum of all the male reproductive organs, and the gynoecium is the sum of the female reproductive organs. (credit: modification of work by Mariana Ruiz Villareal)

The outermost whorl of the flower has green, leafy structures known as sepals. The sepals, collectively called the calyx, help to protect the unopened bud. The second whorl is comprised of petals—usually, brightly colored—collectively called the corolla. The number of sepals and petals varies depending on whether the plant is a monocot or dicot. In monocots, petals usually number three or multiples of three; in dicots, the number of petals is four or five, or multiples of four and five. Together, the calyx and corolla are known as the **perianth**. The third whorl contains the male reproductive structures and is known as the androecium. The **androecium** has stamens with anthers that contain the microsporangia. The innermost group of structures in the flower is the **gynoecium**, or the female reproductive component(s). The carpel is the individual unit of the gynoecium and has a stigma, style, and ovary. A flower may have one or multiple carpels.

If all four whorls (the calyx, corolla, androecium, and gynoecium) are present, the flower is described as complete. If any of the four parts is missing, the flower is known as incomplete. Flowers that contain both an androecium and a gynoecium are called perfect, androgynous or hermaphrodites. There are two types of incomplete flowers: staminate flowers contain only an androecium, and carpellate flowers have only a gynoecium (Figure 2).



Figure 2. The corn plant has both staminate (male) and carpellate (female) flowers. Staminate flowers, which are clustered in the tassel at the tip of the stem, produce pollen grains. Carpellate flower are clustered in the immature ears. Each strand of silk is a stigma. The corn kernels are seeds that develop on the ear after fertilization. Also shown is the lower stem and root.

Practice Question

If the anther is missing, what type of reproductive structure will the flower be unable to produce?

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[reveal-answer q="261989"]Show Answer[/reveal-answer]
[hidden-answer a="261989"]Pollen (or sperm)

[/hidden-answer]

What term is used to describe an incomplete flower lacking the androecium?

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[reveal-answer q="261988"]Show Answer[/reveal-answer]
[hidden-answer a="261988"]Carpellate

[/hidden-answer]

What term describes an incomplete flower lacking a gynoecium?

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[reveal-answer q="261987"]Show Answer[/reveal-answer]
[hidden-answer a="261987"]Staminate[/hidden-answer]

If both male and female flowers are borne on the same plant, the species is called monoecious (meaning "one home"): examples are corn and pea. Species with male and female flowers borne on separate plants are termed dioecious, or "two homes," examples of which are *C. papaya* and *Cannabis*. The ovary, which may contain one or multiple ovules, may be placed above other flower parts, which is referred to as superior; or, it may be placed below the other flower parts, referred to as inferior (Figure 3).

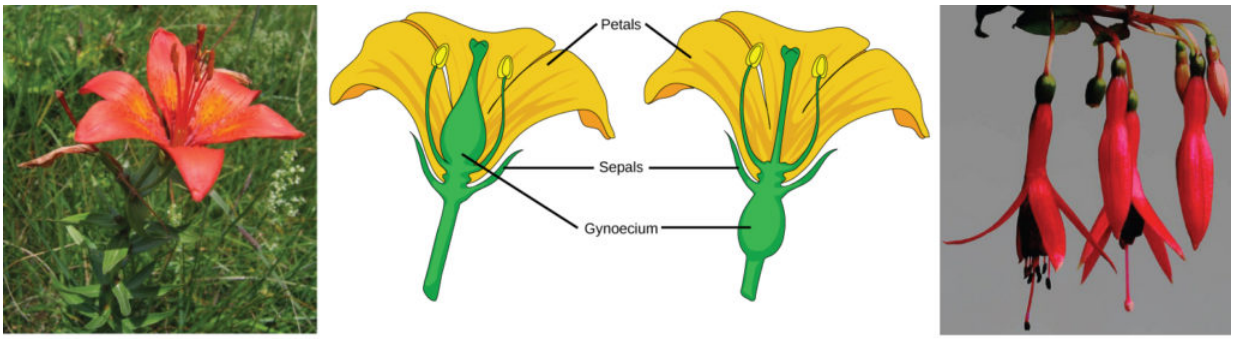


Figure 3. The (a) lily is a superior flower, which has the ovary above the other flower parts. (b) Fuchsia is an inferior flower, which has the ovary beneath other flower parts. (credit a photo: modification of work by Benjamin Zwittnig; credit b photo: modification of work by “Koshy Koshy”/Flickr)

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12.5: Sexual Reproduction in Angiosperms

The lifecycle of angiosperms follows the alternation of generations explained previously. The haploid gametophyte alternates with the diploid sporophyte during the sexual reproduction process of angiosperms.

Male Gametophyte: The Pollen Grain

The male gametophyte develops and reaches maturity in an immature anther. In a plant's male reproductive organs, development of pollen takes place in a structure known as the **microsporangium** (Figure 1). The microsporangia, which are usually bi-lobed, are pollen sacs in which the microspores develop into pollen grains. These are found in the anther, which is at the end of the stamen—the long filament that supports the anther.

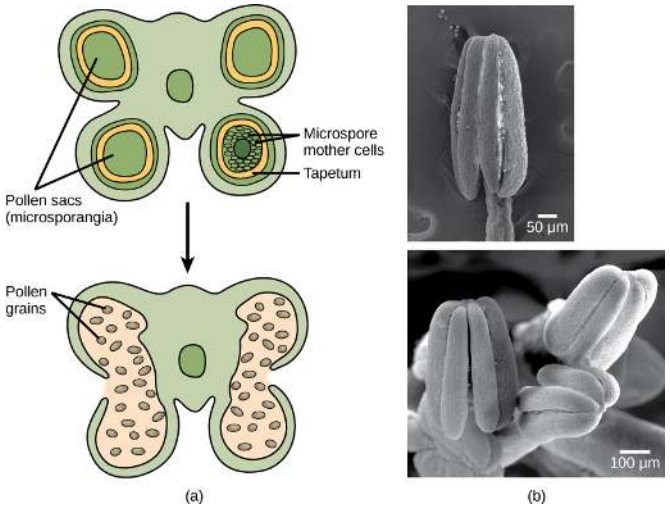


Figure 1. Shown is (a) a cross section of an anther at two developmental stages. The immature anther (top) contains four microsporangia, or pollen sacs. Each microsporangium contains hundreds of microspore mother cells that will each give rise to four pollen grains. The tapetum supports the development and maturation of the pollen grains. Upon maturation of the pollen (bottom), the pollen sac walls split open and the pollen grains (male gametophytes) are released. (b) In these scanning electron micrographs, pollen sacs are ready to burst, releasing their grains. (credit b: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Within the microsporangium, the microspore mother cell divides by meiosis to give rise to four microspores, each of which will ultimately form a pollen grain (Figure 2). An inner layer of cells, known as the tapetum, provides nutrition to the developing microspores and contributes key components to the pollen wall. Mature pollen grains contain two cells: a generative cell and a pollen tube cell. The generative cell is contained within the larger pollen tube cell. Upon germination, the tube cell forms the pollen tube through which the generative cell migrates to enter the ovary. During its transit inside the pollen tube, the generative cell divides to form two male gametes (sperm cells). Upon maturity, the microsporangia burst, releasing the pollen grains from the anther.

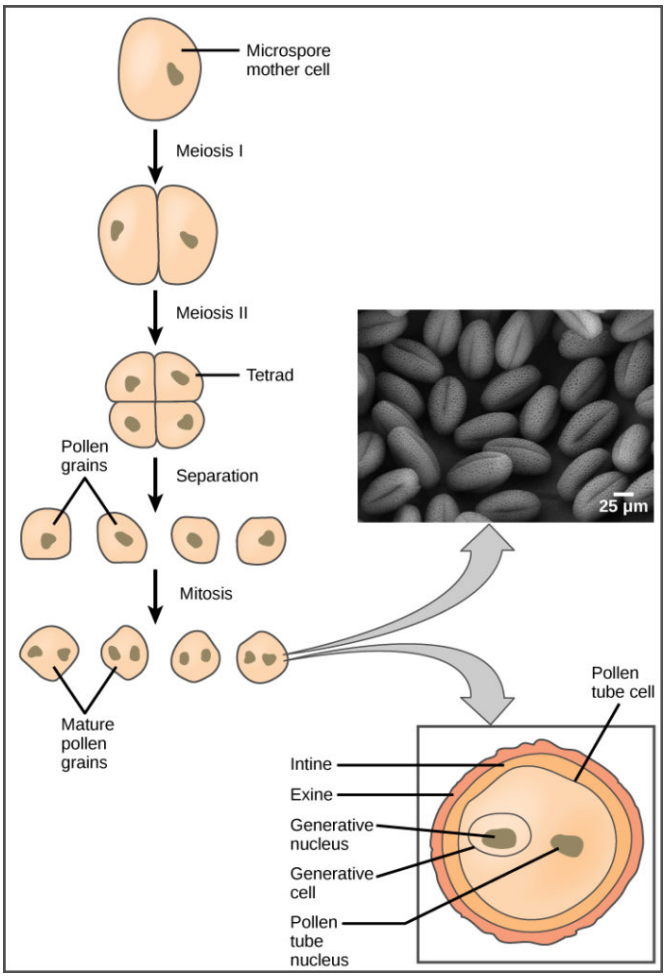


Figure 2. Pollen develops from the microspore mother cells. The mature pollen grain is composed of two cells: the pollen tube cell and the generative cell, which is inside the tube cell. The pollen grain has two coverings: an inner layer (intine) and an outer layer (exine). The inset scanning electron micrograph shows *Arabidopsis lyrata* pollen grains. (credit "pollen micrograph": modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Female Gametophyte: The Embryo Sac

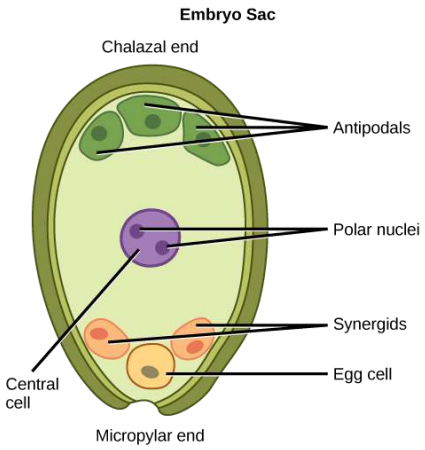


Figure 3. As shown in this diagram of the embryo sac in angiosperms, the ovule is covered by integuments and has an opening called a micropyle. Inside the embryo sac are three antipodal cells, two synergids, a central cell, and the egg cell.

While the details may vary between species, the overall development of the female gametophyte has two distinct phases. First, in the process of **megasporogenesis**, a single cell in the diploid **megasporangium**—an area of tissue in the ovules—undergoes meiosis to produce four megaspores, only one of which survives. During the second phase, **megagametogenesis**, the surviving

haploid megaspore undergoes mitosis to produce an eight-nucleate, seven-cell female gametophyte, also known as the megagametophyte or embryo sac. Two of the nuclei—the **polar nuclei**—move to the equator and fuse, forming a single, diploid central cell. This central cell later fuses with a sperm to form the triploid endosperm. Three nuclei position themselves on the end of the embryo sac opposite the micropyle and develop into the **antipodal** cells, which later degenerate. The nucleus closest to the micropyle becomes the female gamete, or egg cell, and the two adjacent nuclei develop into **synergid** cells (Figure 3). The synergids help guide the pollen tube for successful fertilization, after which they disintegrate. Once fertilization is complete, the resulting diploid zygote develops into the embryo, and the fertilized ovule forms the other tissues of the seed.

A double-layered integument protects the megasporangium and, later, the embryo sac. The integument will develop into the seed coat after fertilization and protect the entire seed. The ovule wall will become part of the fruit. The integuments, while protecting the megasporangium, do not enclose it completely, but leave an opening called the **micropyle**. The micropyle allows the pollen tube to enter the female gametophyte for fertilization.

? Practice Question

An embryo sac is missing the synergids. What specific impact would you expect this to have on fertilization?

a. The pollen tube will be unable to form.
b. The pollen tube will form but will not be guided toward the egg.
c. Fertilization will not occur because the synergid is the egg.
d. Fertilization will occur but the embryo will not be able to grow.

[reveal-answer q="673553"]Show Answer[/reveal-answer]
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12.6: Sexual Reproduction in Gymnosperms

As with angiosperms, the lifecycle of a gymnosperm is also characterized by alternation of generations. In conifers such as pines, the green leafy part of the plant is the sporophyte, and the cones contain the male and female gametophytes (Figure 1). The female cones are larger than the male cones and are positioned towards the top of the tree; the small, male cones are located in the lower region of the tree. Because the pollen is shed and blown by the wind, this arrangement makes it difficult for a gymnosperm to self-pollinate.

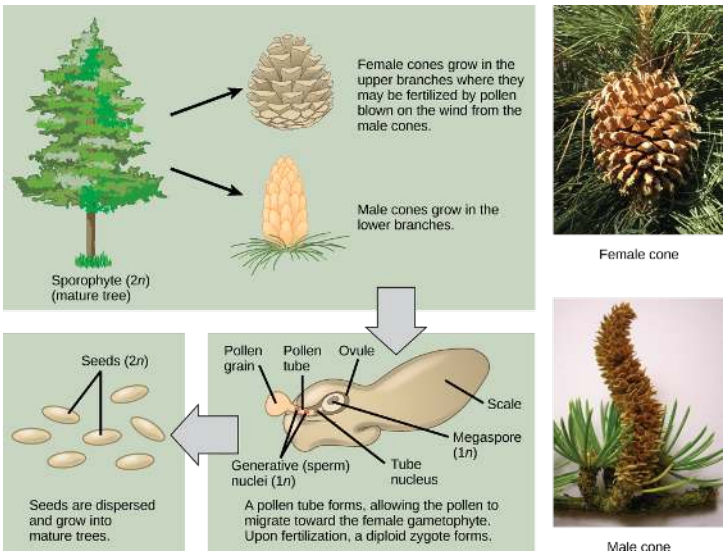


Figure 1. This image shows the life cycle of a conifer. Pollen from male cones blows up into upper branches, where it fertilizes female cones. Examples are shown of female and male cones. (credit “female”: modification of work by “Geographer”/Wikimedia Commons; credit “male”: modification of work by Roger Griffith)

Male Gametophyte

A male cone has a central axis on which bracts, a type of modified leaf, are attached. The bracts are known as **microsporophylls** (Figure 2) and are the sites where microspores will develop. The microspores develop inside the microsporangium. Within the microsporangium, cells known as microsporocytes divide by meiosis to produce four haploid microspores. Further mitosis of the microspore produces two nuclei: the generative nucleus, and the tube nucleus. Upon maturity, the male gametophyte (pollen) is released from the male cones and is carried by the wind to land on the female cone.

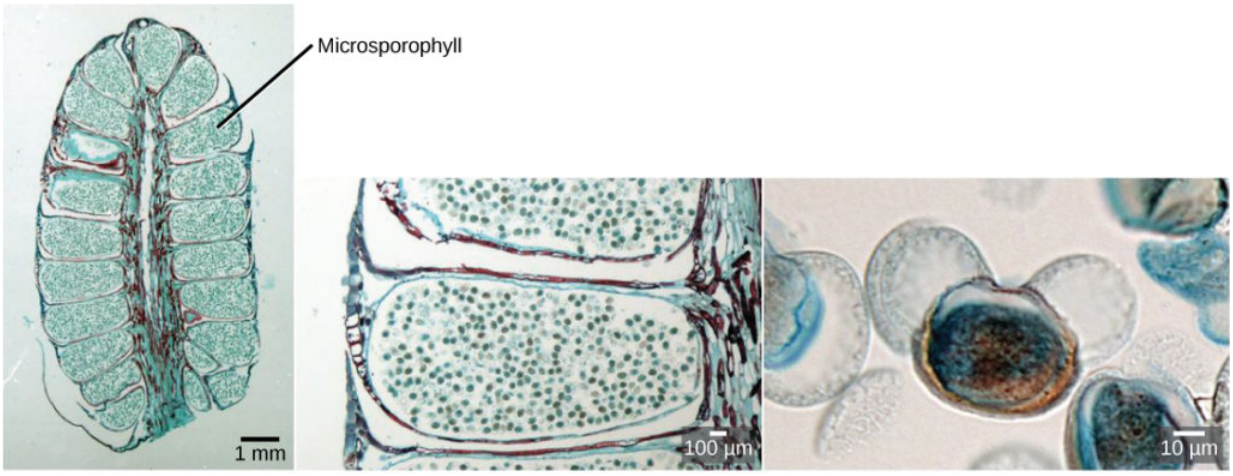


Figure 2. These series of micrographs shows a male gymnosperm gametophyte. (a) This male cone, shown in cross section, has approximately 20 microsporophylls, each of which produces hundreds of male gametophytes (pollen grains). (b) Pollen grains are visible in this single microsporophyll. (c) This micrograph shows an individual pollen grain. (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Watch this video to see a cedar releasing its pollen in the wind. Note that there isn't any narration in the video.



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=418

Female Gametophyte

The female cone also has a central axis on which bracts known as **megasporophylls** (Figure 3) are present. In the female cone, megaspore mother cells are present in the megasporangium. The megaspore mother cell divides by meiosis to produce four haploid megaspores. One of the megaspores divides to form the multicellular female gametophyte, while the others divide to form the rest of the structure. The female gametophyte is contained within a structure called the archegonium.

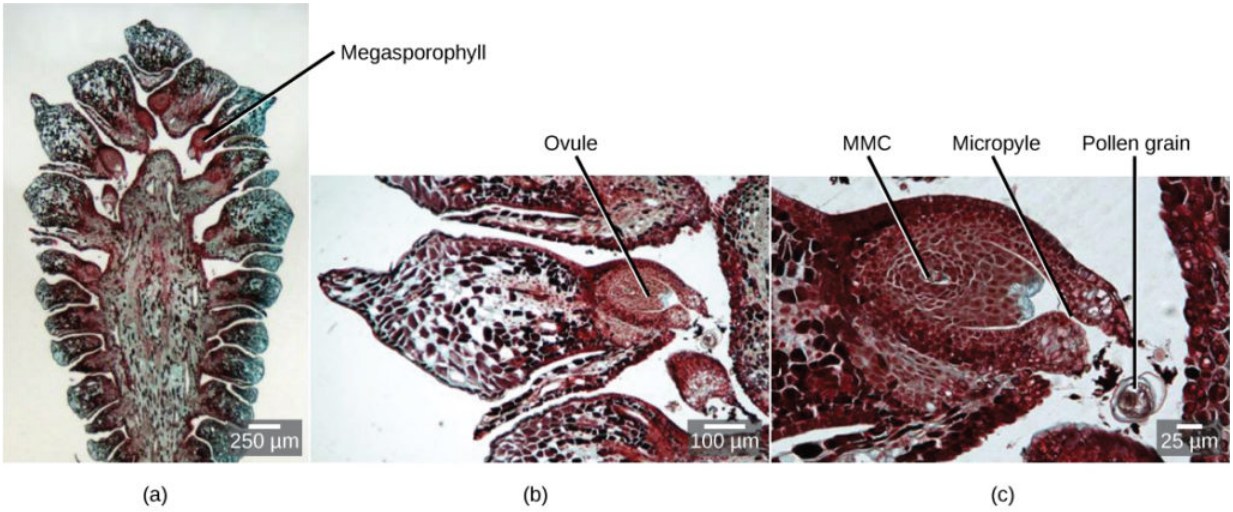


Figure 3. These series of micrographs shows a female gymnosperm gametophyte. (a) This cross section of a female cone shows portions of about 15 megasporophylls. (b) The ovule can be seen in this single megasporophyll. (c) Within this single ovule are the megaspore mother cell (MMC), micropyle, and a pollen grain. (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Reproductive Process

Upon landing on the female cone, the tube cell of the pollen forms the pollen tube, through which the generative cell migrates towards the female gametophyte through the micropyle. It takes approximately one year for the pollen tube to grow and migrate towards the female gametophyte. The male gametophyte containing the generative cell splits into two sperm nuclei, one of which fuses with the egg, while the other degenerates. After fertilization of the egg, the diploid zygote is formed, which divides by mitosis to form the embryo. The scales of the cones are closed during development of the seed. The seed is covered by a seed coat, which is derived from the female sporophyte. Seed development takes another one to two years. Once the seed is ready to be dispersed, the bracts of the female cones open to allow the dispersal of seed; no fruit formation takes place because gymnosperm seeds have no covering.

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12.7: Angiosperms versus Gymnosperms



(a) (b)

Figure 1. (a) Angiosperms are flowering plants, and include grasses, herbs, shrubs and most deciduous trees, while (b) gymnosperms are conifers. Both produce seeds but have different reproductive strategies. (credit a: modification of work by Wendy Cutler; credit b: modification of work by Lews Castle UHI)

Gymnosperm reproduction differs from that of angiosperms in several ways (Figure 1). In angiosperms, the female gametophyte exists in an enclosed structure—the ovule—which is within the ovary; in gymnosperms, the female gametophyte is present on exposed bracts of the female cone. Double fertilization is a key event in the lifecycle of angiosperms, but is completely absent in gymnosperms. The male and female gametophyte structures are present on separate male and female cones in gymnosperms, whereas in angiosperms, they are a part of the flower. Lastly, wind plays an important role in pollination in gymnosperms because pollen is blown by the wind to land on the female cones. Although many angiosperms are also wind-pollinated, animal pollination is more common.

Watch this video to see an animation of the double fertilization process of angiosperms.

A link to an interactive elements can be found at the bottom of this page.

In Summary: Angiosperms versus Gymnosperms

The flower contains the reproductive structures of a plant. All complete flowers contain four whorls: the calyx, corolla, androecium, and gynoecium. The stamens are made up of anthers, in which pollen grains are produced, and a supportive strand called the filament. The pollen contains two cells— a generative cell and a tube cell—and is covered by two layers called the intine and the exine. The carpels, which are the female reproductive structures, consist of the stigma, style, and ovary. The female gametophyte is formed from mitotic divisions of the megaspore, forming an eight-nuclei ovule sac. This is covered by a layer known as the integument. The integument contains an opening called the micropyle, through which the pollen tube enters the embryo sac.

The diploid sporophyte of angiosperms and gymnosperms is the conspicuous and long-lived stage of the life cycle. The sporophytes differentiate specialized reproductive structures called sporangia, which are dedicated to the production of spores. The microsporangium contains microspore mother cells, which divide by meiosis to produce haploid microspores. The microspores develop into male gametophytes that are released as pollen. The megasporangium contains megaspore mother cells, which divide by meiosis to produce haploid megaspores. A megaspore develops into a female gametophyte containing a haploid egg. A new diploid sporophyte is formed when a male gamete from a pollen grain enters the ovule sac and fertilizes this egg.

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12.8: Introduction to Asexual Reproduction in Plants

Describe plants that reproduce asexually

Many plants reproduce asexually as well as sexually. In asexual reproduction, part of the parent plant is used to generate a new plant. Grafting, layering, and micropropagation are some methods used for artificial asexual reproduction. The new plant is genetically identical to the parent plant from which the stock has been taken. Asexually reproducing plants thrive well in stable environments.

What You'll Learn to Do

- Describe characteristics of plants that reproduce asexually
- Discuss the mechanisms, advantages, and disadvantages of natural and artificial asexual reproduction
- Discuss plant life spans

Learning Activities

The learning activities for this section include the following:

- Asexual Plants
- Natural and Artificial Asexual Reproduction
- Plant Life Spans
- Self Check: Asexual Reproduction in Plants

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12.9: Asexual Plants

Many plants are able to propagate themselves using asexual reproduction. This method does not require the investment required to produce a flower, attract pollinators, or find a means of seed dispersal. Asexual reproduction produces plants that are genetically identical to the parent plant because no mixing of male and female gametes takes place. Traditionally, these plants survive well under stable environmental conditions when compared with plants produced from sexual reproduction because they carry genes identical to those of their parents.

Many different types of roots exhibit asexual reproduction Figure 1. The corm is used by gladiolus and garlic. Bulbs, such as a scaly bulb in lilies and a tunicate bulb in daffodils, are other common examples. A potato is a stem tuber, while parsnip propagates from a taproot. Ginger and iris produce rhizomes, while ivy uses an adventitious root (a root arising from a plant part other than the main or primary root), and the strawberry plant has a stolon, which is also called a runner.

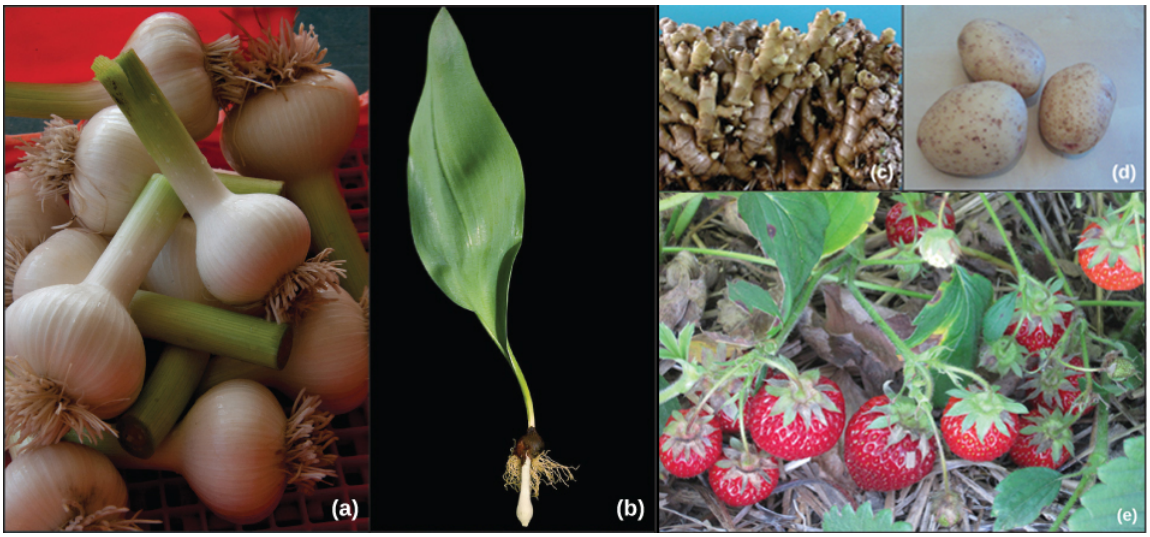


Figure 1. Different types of stems allow for asexual reproduction. (a) The corm of a garlic plant looks similar to (b) a tulip bulb, but the corm is solid tissue, while the bulb consists of layers of modified leaves that surround an underground stem. Both corms and bulbs can self-propagate, giving rise to new plants. (c) Ginger forms masses of stems called rhizomes that can give rise to multiple plants. (d) Potato plants form fleshy stem tubers. Each eye in the stem tuber can give rise to a new plant. (e) Strawberry plants form stolons: stems that grow at the soil surface or just below ground and can give rise to new plants. (credit a: modification of work by Dwight Sipler; credit c: modification of work by Albert Cahalan, USDA ARS; credit d: modification of work by Richard North; credit e: modification of work by Julie Magro)

Some plants can produce seeds without fertilization. Either the ovule or part of the ovary, which is diploid in nature, gives rise to a new seed. This method of reproduction is known as **apomixis**.

An advantage of asexual reproduction is that the resulting plant will reach maturity faster. Since the new plant is arising from an adult plant or plant parts, it will also be sturdier than a seedling. Asexual reproduction can take place by natural or artificial (assisted by humans) means.

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12.10: Natural and Artificial Asexual Reproduction

Natural Methods of Asexual Reproduction

Natural methods of asexual reproduction include strategies that plants have developed to self-propagate. Many plants—like ginger, onion, gladioli, and dahlia—continue to grow from buds that are present on the surface of the stem. In some plants, such as the sweet potato, adventitious roots or runners can give rise to new plants (Figure 1). In *Bryophyllum* and kalanchoe, the leaves have small buds on their margins. When these are detached from the plant, they grow into independent plants; or, they may start growing into independent plants if the leaf touches the soil. Some plants can be propagated through cuttings alone.

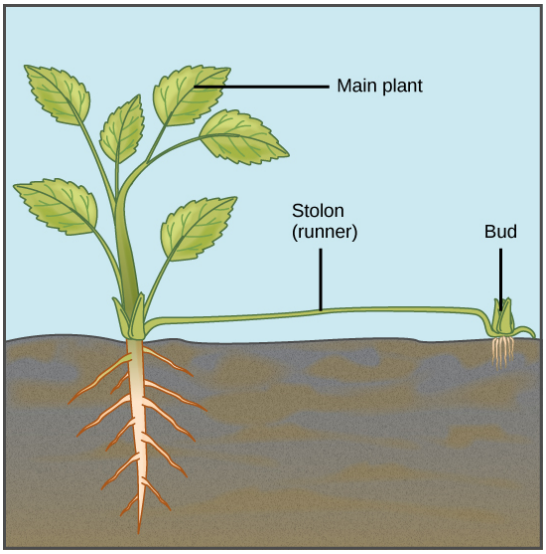


Figure 1. A stolon, or runner, is a stem that runs along the ground. At the nodes, it forms adventitious roots and buds that grow into a new plant.

Artificial Methods of Asexual Reproduction

These methods are frequently employed to give rise to new, and sometimes novel, plants. They include grafting, cutting, layering, and micropropagation.

Grafting

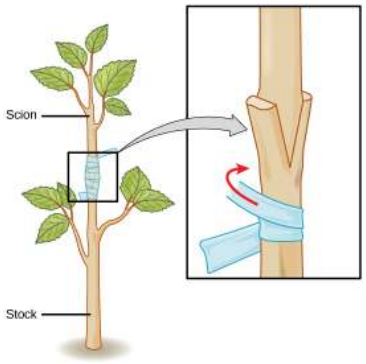


Figure 2. Grafting is an artificial method of asexual reproduction used to produce plants combining favorable stem characteristics with favorable root characteristics. The stem of the plant to be grafted is known as the scion, and the root is called the stock.

Grafting has long been used to produce novel varieties of roses, citrus species, and other plants. In **grafting**, two plant species are used; part of the stem of the desirable plant is grafted onto a rooted plant called the stock. The part that is grafted or attached is called the **scion**. Both are cut at an oblique angle (any angle other than a right angle), placed in close contact with each other, and are then held together Figure 2. Matching up these two surfaces as closely as possible is extremely important because these will be holding the plant together. The vascular systems of the two plants grow and fuse, forming a graft. After a period of time, the scion starts producing shoots, and eventually starts bearing flowers and fruits. Grafting is widely used in viticulture (grape growing) and

the citrus industry. Scions capable of producing a particular fruit variety are grated onto root stock with specific resistance to disease.

Cutting

Plants such as coleus and money plant are propagated through stem **cuttings**, where a portion of the stem containing nodes and internodes is placed in moist soil and allowed to root. In some species, stems can start producing a root even when placed only in water. For example, leaves of the African violet will root if kept in water undisturbed for several weeks.

Layering

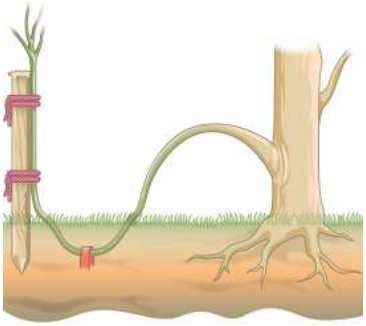


Figure 3. In layering, a part of the stem is buried so that it forms a new plant.

Layering is a method in which a stem attached to the plant is bent and covered with soil. Young stems that can be bent easily without any injury are preferred. Jasmine and bougainvillea (paper flower) can be propagated this way Figure 3.

In some plants, a modified form of layering known as air layering is employed. A portion of the bark or outermost covering of the stem is removed and covered with moss, which is then taped. Some gardeners also apply rooting hormone. After some time, roots will appear, and this portion of the plant can be removed and transplanted into a separate pot.

Micropropagation

Micropropagation (also called plant tissue culture) is a method of propagating a large number of plants from a single plant in a short time under laboratory conditions (Figure 4). This method allows propagation of rare, endangered species that may be difficult to grow under natural conditions, are economically important, or are in demand as disease-free plants.



Figure 4. Micropropagation is used to propagate plants in sterile conditions. (credit: Nikhilesh Sanyal)

To start plant tissue culture, a part of the plant such as a stem, leaf, embryo, anther, or seed can be used. The plant material is thoroughly sterilized using a combination of chemical treatments standardized for that species. Under sterile conditions, the plant material is placed on a plant tissue culture medium that contains all the minerals, vitamins, and hormones required by the plant. The plant part often gives rise to an undifferentiated mass known as callus, from which individual plantlets begin to grow after a period of time. These can be separated and are first grown under greenhouse conditions before they are moved to field conditions.

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12.11: Plant Life Spans



Figure 1. The bristlecone pine, shown here in the Ancient Bristlecone Pine Forest in the White Mountains of eastern California, has been known to live for 4,500 years. (credit: Rick Goldwaser)

The length of time from the beginning of development to the death of a plant is called its life span. The life cycle, on the other hand, is the sequence of stages a plant goes through from seed germination to seed production of the mature plant. Some plants, such as annuals, only need a few weeks to grow, produce seeds and die. Other plants, such as the bristlecone pine, live for thousands of years. Some bristlecone pines have a documented age of 4,500 years (Figure 1). Even as some parts of a plant, such as regions containing meristematic tissue—the area of active plant growth consisting of undifferentiated cells capable of cell division—continue to grow, some parts undergo programmed cell death (apoptosis). The cork found on stems, and the water-conducting tissue of the xylem, for example, are composed of dead cells.

Plant species that complete their lifecycle in one season are known as annuals, an example of which is *Arabidopsis*, or mouse-ear cress. Biennials such as carrots complete their lifecycle in two seasons. In a biennial's first season, the plant has a vegetative phase, whereas in the next season, it completes its reproductive phase. Commercial growers harvest the carrot roots after the first year of growth, and do not allow the plants to flower. Perennials, such as the magnolia, complete their lifecycle in two years or more.

In another classification based on flowering frequency, **monocarpic** plants flower only once in their lifetime; examples include bamboo and yucca. During the vegetative period of their life cycle (which may be as long as 120 years in some bamboo species), these plants may reproduce asexually and accumulate a great deal of food material that will be required during their once-in-a-lifetime flowering and setting of seed after fertilization. Soon after flowering, these plants die. **Polycarpic** plants form flowers many times during their lifetime. Fruit trees, such as apple and orange trees, are polycarpic; they flower every year. Other polycarpic species, such as perennials, flower several times during their life span, but not each year. By this means, the plant does not require all its nutrients to be channelled towards flowering each year.

As is the case with all living organisms, genetics and environmental conditions have a role to play in determining how long a plant will live. Susceptibility to disease, changing environmental conditions, drought, cold, and competition for nutrients are some of the factors that determine the survival of a plant. Plants continue to grow, despite the presence of dead tissue such as cork. Individual parts of plants, such as flowers and leaves, have different rates of survival. In many trees, the older leaves turn yellow and eventually fall from the tree. Leaf fall is triggered by factors such as a decrease in photosynthetic efficiency, due to shading by upper leaves, or oxidative damage incurred as a result of photosynthetic reactions. The components of the part to be shed are recycled by the plant for use in other processes, such as development of seed and storage. This process is known as nutrient recycling.

The aging of a plant and all the associated processes is known as **senescence**, which is marked by several complex biochemical changes. One of the characteristics of senescence is the breakdown of chloroplasts, which is characterized by the yellowing of leaves. The chloroplasts contain components of photosynthetic machinery such as membranes and proteins. Chloroplasts also contain DNA. The proteins, lipids, and nucleic acids are broken down by specific enzymes into smaller molecules and salvaged by the plant to support the growth of other plant tissues.

The complex pathways of nutrient recycling within a plant are not well understood. Hormones are known to play a role in senescence. Applications of cytokinins and ethylene delay or prevent senescence; in contrast, abscissic acid causes premature onset of senescence.

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12.12: Introduction to Sexual Reproduction in Plants

Describe how plants reproduce sexually

There are several different methods and processes involved in the sexual reproduction of plants. Many of the structures associated with sexual reproduction in plants are valuable commodities for humans (think fruits, berries, and vegetables). An equal number of them are “baneful” (think seasonal allergies). In this section, we’ll learn just how the process of sexual reproduction in plants occurs.

What You’ll Learn to Do

- Describe the process of self-pollination and cross-pollination
- Identify several common methods of pollination
- Define double fertilization
- Describe the process that leads to the development of a seed
- Describe the process that leads to the development of a fruit
- Identify different methods of fruit and seed dispersal

Learning Activities

The learning activities for this section include the following:

- Self-Pollination and Cross-Pollination
- Methods of Pollination
- Double Fertilization
- Development Seeds and Fruit
- Fruit and Seed Dispersal
- Self Check: Sexual Reproduction in Plants

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12.13: Self-Pollination and Cross-Pollination

In angiosperms, **pollination** is defined as the placement or transfer of pollen from the anther to the stigma of the same flower or another flower. In gymnosperms, pollination involves pollen transfer from the male cone to the female cone. Upon transfer, the pollen germinates to form the pollen tube and the sperm for fertilizing the egg. Pollination has been well studied since the time of Gregor Mendel. Mendel successfully carried out self- as well as cross-pollination in garden peas while studying how characteristics were passed on from one generation to the next. Today's crops are a result of plant breeding, which employs artificial selection to produce the present-day cultivars. A case in point is today's corn, which is a result of years of breeding that started with its ancestor, teosinte. The teosinte that the ancient Mayans originally began cultivating had tiny seeds—vastly different from today's relatively giant ears of corn. Interestingly, though these two plants appear to be entirely different, the genetic difference between them is miniscule.

Pollination takes two forms: self-pollination and cross-pollination. **Self-pollination** occurs when the pollen from the anther is deposited on the stigma of the same flower, or another flower on the same plant. **Cross-pollination** is the transfer of pollen from the anther of one flower to the stigma of another flower on a different individual of the same species. Self-pollination occurs in flowers where the stamen and carpel mature at the same time, and are positioned so that the pollen can land on the flower's stigma. This method of pollination does not require an investment from the plant to provide nectar and pollen as food for pollinators.

Explore this interactive website to review self-pollination and cross-pollination.

Living species are designed to ensure survival of their progeny; those that fail become extinct. Genetic diversity is therefore required so that in changing environmental or stress conditions, some of the progeny can survive. Self-pollination leads to the production of plants with less genetic diversity, since genetic material from the same plant is used to form gametes, and eventually, the zygote. In contrast, cross-pollination—or out-crossing—leads to greater genetic diversity because the microgametophyte and megagametophyte are derived from different plants.

Because cross-pollination allows for more genetic diversity, plants have developed many ways to avoid self-pollination. In some species, the pollen and the ovary mature at different times. These flowers make self-pollination nearly impossible. By the time pollen matures and has been shed, the stigma of this flower is mature and can only be pollinated by pollen from another flower. Some flowers have developed physical features that prevent self-pollination. The primrose is one such flower. Primroses have evolved two flower types with differences in anther and stigma length: the pin-eyed flower has anthers positioned at the pollen tube's halfway point, and the thrum-eyed flower's stigma is likewise located at the halfway point. Insects easily cross-pollinate while seeking the nectar at the bottom of the pollen tube. This phenomenon is also known as heterostyly. Many plants, such as cucumber, have male and female flowers located on different parts of the plant, thus making self-pollination difficult. In yet other species, the male and female flowers are borne on different plants (dioecious). All of these are barriers to self-pollination; therefore, the plants depend on pollinators to transfer pollen. The majority of pollinators are biotic agents such as insects (like bees, flies, and butterflies), bats, birds, and other animals. Other plant species are pollinated by abiotic agents, such as wind and water.

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12.14: Methods of Pollination

Pollination by Insects



Figure 1. Insects, such as bees, are important agents of pollination. (credit: modification of work by Jon Sullivan)

Bees are perhaps the most important pollinator of many garden plants and most commercial fruit trees (Figure 1). The most common species of bees are bumblebees and honeybees. Since bees cannot see the color red, bee-pollinated flowers usually have shades of blue, yellow, or other colors. Bees collect energy-rich pollen or nectar for their survival and energy needs. They visit flowers that are open during the day, are brightly colored, have a strong aroma or scent, and have a tubular shape, typically with the presence of a nectar guide. A **nectar guide** includes regions on the flower petals that are visible only to bees, and not to humans; it helps to guide bees to the center of the flower, thus making the pollination process more efficient. The pollen sticks to the bees' fuzzy hair, and when the bee visits another flower, some of the pollen is transferred to the second flower. Recently, there have been many reports about the declining population of honeybees. Many flowers will remain unpollinated and not bear seed if honeybees disappear. The impact on commercial fruit growers could be devastating.

Many flies are attracted to flowers that have a decaying smell or an odor of rotting flesh. These flowers, which produce nectar, usually have dull colors, such as brown or purple. They are found on the corpse flower or voodoo lily (*Amorphophallus*), dragon arum (*Dracunculus*), and carrion flower (*Stapleia*, *Rafflesia*). The nectar provides energy, whereas the pollen provides protein. Wasps are also important insect pollinators, and pollinate many species of figs.



Figure 2. A corn earworm sips nectar from a night-blooming Gaura plant. (credit: Juan Lopez, USDA ARS)

Butterflies, such as the monarch, pollinate many garden flowers and wildflowers, which usually occur in clusters. These flowers are brightly colored, have a strong fragrance, are open during the day, and have nectar guides to make access to nectar easier. The pollen is picked up and carried on the butterfly's limbs. Moths, on the other hand, pollinate flowers during the late afternoon and night. The flowers pollinated by moths are pale or white and are flat, enabling the moths to land. One well-studied example of a moth-pollinated plant is the yucca plant, which is pollinated by the yucca moth. The shape of the flower and moth have adapted in such a way as to allow successful pollination. The moth deposits pollen on the sticky stigma for fertilization to occur later. The female moth also deposits eggs into the ovary. As the eggs develop into larvae, they obtain food from the flower and developing seeds. Thus, both the insect and flower benefit from each other in this symbiotic relationship. The corn earworm moth and Gaura plant have a similar relationship (Figure 2).

Pollination by Bats

In the tropics and deserts, bats are often the pollinators of nocturnal flowers such as agave, guava, and morning glory. The flowers are usually large and white or pale-colored; thus, they can be distinguished from the dark surroundings at night. The flowers have a

strong, fruity, or musky fragrance and produce large amounts of nectar. They are naturally large and wide-mouthed to accommodate the head of the bat. As the bats seek the nectar, their faces and heads become covered with pollen, which is then transferred to the next flower.

Pollination by Birds



Figure 3. Hummingbirds have adaptations that allow them to reach the nectar of certain tubular flowers. (credit: Lori Branham)

Many species of small birds, such as the hummingbird (Figure 3) and sun birds, are pollinators for plants such as orchids and other wildflowers. Flowers visited by birds are usually sturdy and are oriented in such a way as to allow the birds to stay near the flower without getting their wings entangled in the nearby flowers. The flower typically has a curved, tubular shape, which allows access for the bird's beak. Brightly colored, odorless flowers that are open during the day are pollinated by birds. As a bird seeks energy-rich nectar, pollen is deposited on the bird's head and neck and is then transferred to the next flower it visits. Botanists have been known to determine the range of extinct plants by collecting and identifying pollen from 200-year-old bird specimens from the same site.

Pollination by Wind



Figure 4. A person knocks pollen from a pine tree.

Most species of conifers, and many angiosperms, such as grasses, maples and oaks, are pollinated by wind. Pine cones are brown and unscented, while the flowers of wind-pollinated angiosperm species are usually green, small, may have small or no petals, and produce large amounts of pollen. Unlike the typical insect-pollinated flowers, flowers adapted to pollination by wind do not produce nectar or scent. In wind-pollinated species, the microsporangia hang out of the flower, and, as the wind blows, the lightweight pollen is carried with it (Figure 4).

The flowers usually emerge early in the spring, before the leaves, so that the leaves do not block the movement of the wind. The pollen is deposited on the exposed feathery stigma of the flower (Figure 5).



Figure 5. These male (a) and female (b) catkins are from the goat willow tree (Salix caprea). Note how both structures are light and feathery to better disperse and catch the wind-blown pollen.

Pollination by Water

Some weeds, such as Australian sea grass and pond weeds, are pollinated by water. The pollen floats on water, and when it comes into contact with the flower, it is deposited inside the flower.

Pollination by Deception



Figure 6. Certain orchids use food deception or sexual deception to attract pollinators. Shown here is a bee orchid (*Ophrys apifera*). (credit: David Evans)

Orchids are highly valued flowers, with many rare varieties (Figure 6). They grow in a range of specific habitats, mainly in the tropics of Asia, South America, and Central America. At least 25,000 species of orchids have been identified.

Flowers often attract pollinators with food rewards, in the form of nectar. However, some species of orchid are an exception to this standard: they have evolved different ways to attract the desired pollinators. They use a method known as food deception, in which bright colors and perfumes are offered, but no food. *Anacamptis morio*, commonly known as the green-winged orchid, bears bright purple flowers and emits a strong scent. The bumblebee, its main pollinator, is attracted to the flower because of the strong scent—which usually indicates food for a bee—and in the process, picks up the pollen to be transported to another flower.

Other orchids use sexual deception. *Chiloglottis trapeziformis* emits a compound that smells the same as the pheromone emitted by a female wasp to attract male wasps. The male wasp is attracted to the scent, lands on the orchid flower, and in the process, transfers pollen. Some orchids, like the Australian hammer orchid, use scent as well as visual trickery in yet another sexual deception strategy to attract wasps. The flower of this orchid mimics the appearance of a female wasp and emits a pheromone. The male wasp tries to mate with what appears to be a female wasp, and in the process, picks up pollen, which it then transfers to the next counterfeit mate.

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12.15: Double Fertilization

After pollen is deposited on the stigma, it must germinate and grow through the style to reach the ovule. The microspores, or the pollen, contain two cells: the pollen tube cell and the generative cell. The pollen tube cell grows into a pollen tube through which the generative cell travels. The germination of the pollen tube requires water, oxygen, and certain chemical signals. As it travels through the style to reach the embryo sac, the pollen tube's growth is supported by the tissues of the style. In the meantime, if the generative cell has not already split into two cells, it now divides to form two sperm cells. The pollen tube is guided by the chemicals secreted by the synergids present in the embryo sac, and it enters the ovule sac through the micropyle. Of the two sperm cells, one sperm fertilizes the egg cell, forming a diploid zygote; the other sperm fuses with the two polar nuclei, forming a triploid cell that develops into the **endosperm**. Together, these two fertilization events in angiosperms are known as **double fertilization** (Figure 1). After fertilization is complete, no other sperm can enter. The fertilized ovule forms the seed, whereas the tissues of the ovary become the fruit, usually enveloping the seed.

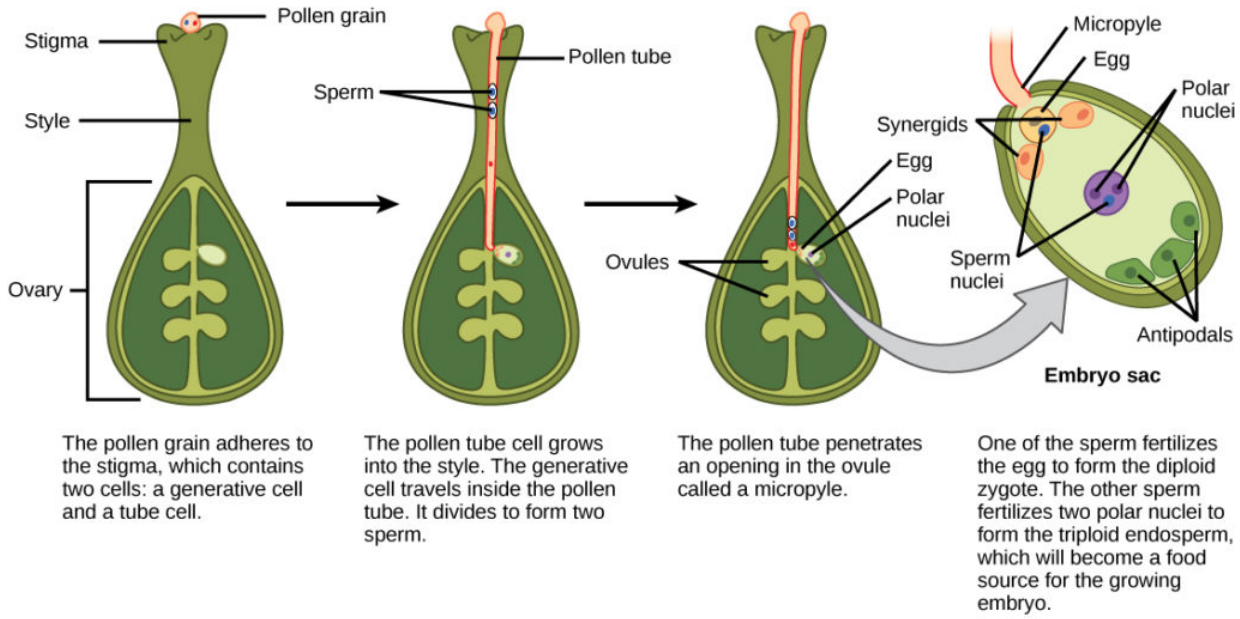


Figure 1. In angiosperms, one sperm fertilizes the egg to form the 2*n* zygote, and the other sperm fertilizes the central cell to form the 3*n* endosperm. This is called a double fertilization.

After fertilization, the zygote divides to form two cells: the upper cell, or terminal cell, and the lower, or basal, cell. The division of the basal cell gives rise to the **suspensor**, which eventually makes connection with the maternal tissue. The suspensor provides a route for nutrition to be transported from the mother plant to the growing embryo. The terminal cell also divides, giving rise to a globular-shaped proembryo (Figure 2a). In dicots (eudicots), the developing embryo has a heart shape, due to the presence of the two rudimentary **cotyledons** (Figure 2b). In non-endospermic dicots, such as *Capsella bursa*, the endosperm develops initially, but is then digested, and the food reserves are moved into the two cotyledons. As the embryo and cotyledons enlarge, they run out of room inside the developing seed, and are forced to bend (Figure 2c). Ultimately, the embryo and cotyledons fill the seed (Figure 2d), and the seed is ready for dispersal. Embryonic development is suspended after some time, and growth is resumed only when the seed germinates. The developing seedling will rely on the food reserves stored in the cotyledons until the first set of leaves begin photosynthesis.

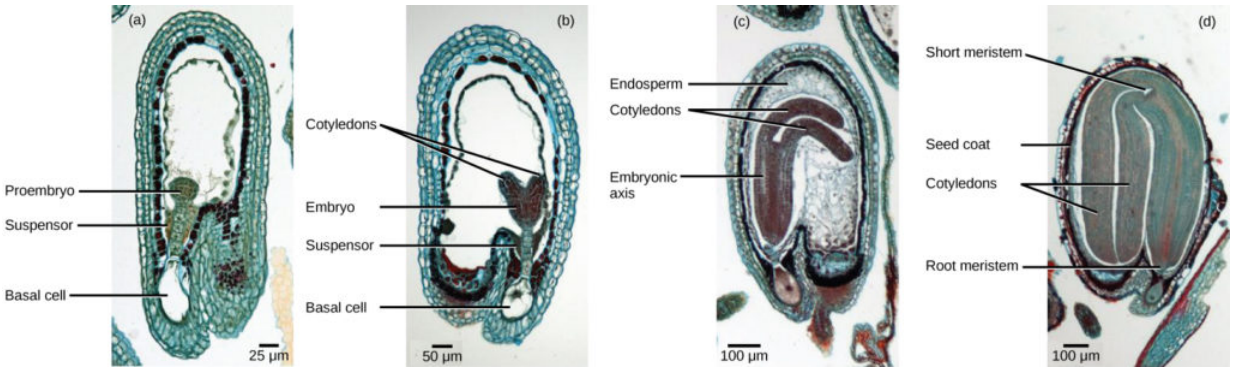


Figure 2. Shown are the stages of embryo development in the ovule of a shepherd's purse (Capsella bursa). After fertilization, the zygote divides to form an upper terminal cell and a lower basal cell. (a) In the first stage of development, the terminal cell divides, forming a globular pro-embryo. The basal cell also divides, giving rise to the suspensor. (b) In the second stage, the developing embryo has a heart shape due to the presence of cotyledons. (c) In the third stage, the growing embryo runs out of room and starts to bend. (d) Eventually, it completely fills the seed. (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

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12.16: Development Seeds and Fruit

Development of a Seed

The mature ovule develops into the seed. A typical seed contains a seed coat, cotyledons, endosperm, and a single embryo (Figure 1).

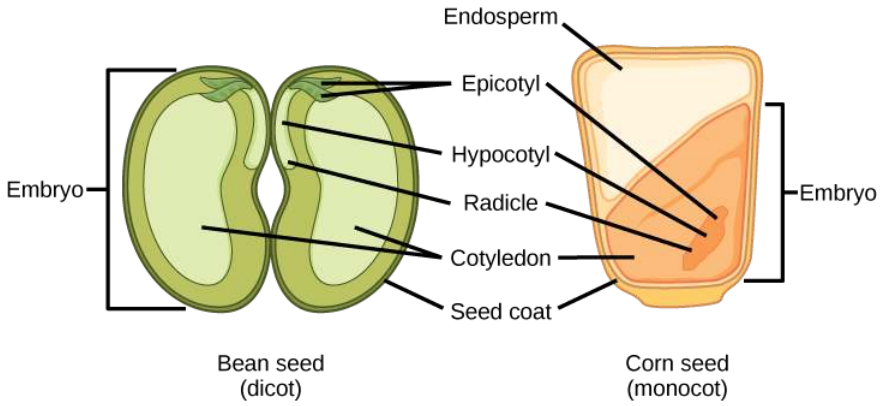


Figure 1. The structures of dicot and monocot seeds are shown. Dicots (left) have two cotyledons. Monocots, such as corn (right), have one cotyledon, called the scutellum; it channels nutrition to the growing embryo. Both monocot and dicot embryos have a plumule that forms the leaves, a hypocotyl that forms the stem, and a radicle that forms the root. The embryonic axis comprises everything between the plumule and the radicle, not including the cotyledon(s).

? Practice Question

What is of the following statements is true?

a. Both monocots and dicots have an endosperm.
b. The radicle develops into the root.
c. The plumule is part of the epicotyl
d. The endosperm is part of the embryo.

[reveal-answer q="763494"]Show Answer[/reveal-answer]
[hidden-answer a="763494"]Statement b is true.[/hidden-answer]

The storage of food reserves in angiosperm seeds differs between monocots and dicots. In monocots, such as corn and wheat, the single cotyledon is called a **scutellum**; the scutellum is connected directly to the embryo via vascular tissue (xylem and phloem). Food reserves are stored in the large endosperm. Upon germination, enzymes are secreted by the **aleurone**, a single layer of cells just inside the seed coat that surrounds the endosperm and embryo. The enzymes degrade the stored carbohydrates, proteins and lipids, the products of which are absorbed by the scutellum and transported via a vasculature strand to the developing embryo. Therefore, the scutellum can be seen to be an absorptive organ, not a storage organ.

The two cotyledons in the dicot seed also have vascular connections to the embryo. In **endospermic dicots**, the food reserves are stored in the endosperm. During germination, the two cotyledons therefore act as absorptive organs to take up the enzymatically released food reserves, much like in monocots (monocots, by definition, also have endospermic seeds). Tobacco (*Nicotiana tabaccum*), tomato (*Solanum lycopersicum*), and pepper (*Capsicum annuum*) are examples of endospermic dicots. In **non-endospermic dicots**, the triploid endosperm develops normally following double fertilization, but the endosperm food reserves are quickly remobilized and moved into the developing cotyledon for storage. The two halves of a peanut seed (*Arachis hypogaea*) and the split peas (*Pisum sativum*) of split pea soup are individual cotyledons loaded with food reserves.

The seed, along with the ovule, is protected by a seed coat that is formed from the integuments of the ovule sac. In dicots, the seed coat is further divided into an outer coat known as the **testa** and inner coat known as the **tegmen**.

The embryonic axis consists of three parts: the plumule, the radicle, and the hypocotyl. The portion of the embryo between the cotyledon attachment point and the radicle is known as the **hypocotyl** (hypocotyl means “below the cotyledons”). The embryonic

axis terminates in a **radicle** (the embryonic root), which is the region from which the root will develop. In dicots, the hypocotyls extend above ground, giving rise to the stem of the plant. In monocots, the hypocotyl does not show above ground because monocots do not exhibit stem elongation. The part of the embryonic axis that projects above the cotyledons is known as the **epicotyl**. The **plumule** is composed of the epicotyl, young leaves, and the shoot apical meristem.

Upon germination in dicot seeds, the epicotyl is shaped like a hook with the plumule pointing downwards. This shape is called the plumule hook, and it persists as long as germination proceeds in the dark. Therefore, as the epicotyl pushes through the tough and abrasive soil, the plumule is protected from damage. Upon exposure to light, the hypocotyl hook straightens out, the young foliage leaves face the sun and expand, and the epicotyl continues to elongate. During this time, the radicle is also growing and producing the primary root. As it grows downward to form the tap root, lateral roots branch off to all sides, producing the typical dicot tap root system.

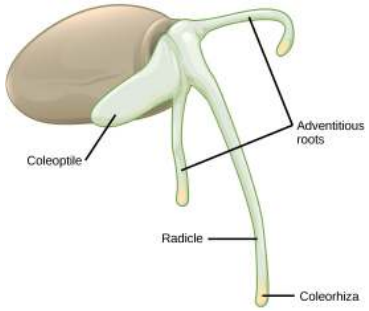


Figure 2. As this monocot grass seed germinates, the primary root, or radicle, emerges first, followed by the primary shoot, or coleoptile, and the adventitious roots.

In monocot seeds (Figure 2), the testa and tegmen of the seed coat are fused. As the seed germinates, the primary root emerges, protected by the root-tip covering: the **coleorhiza**. Next, the primary shoot emerges, protected by the **coleoptile**: the covering of the shoot tip. Upon exposure to light (i.e. when the plumule has exited the soil and the protective coleoptile is no longer needed), elongation of the coleoptile ceases and the leaves expand and unfold. At the other end of the embryonic axis, the primary root soon dies, while other, adventitious roots (roots that do not arise from the usual place – i.e. the root) emerge from the base of the stem. This gives the monocot a fibrous root system.

Seed Germination

Many mature seeds enter a period of inactivity, or extremely low metabolic activity: a process known as **dormancy**, which may last for months, years or even centuries. Dormancy helps keep seeds viable during unfavorable conditions. Upon a return to favorable conditions, seed germination takes place. Favorable conditions could be as diverse as moisture, light, cold, fire, or chemical treatments. After heavy rains, many new seedlings emerge. Forest fires also lead to the emergence of new seedlings. Some seeds require **vernalization** (cold treatment) before they can germinate. This guarantees that seeds produced by plants in temperate climates will not germinate until the spring. Plants growing in hot climates may have seeds that need a heat treatment in order to germinate, to avoid germination in the hot, dry summers. In many seeds, the presence of a thick seed coat retards the ability to germinate. **Scarification**, which includes mechanical or chemical processes to soften the seed coat, is often employed before germination. Presoaking in hot water, or passing through an acid environment, such as an animal's digestive tract, may also be employed.

Depending on seed size, the time taken for a seedling to emerge may vary. Species with large seeds have enough food reserves to germinate deep below ground, and still extend their epicotyl all the way to the soil surface. Seeds of small-seeded species usually require light as a germination cue. This ensures the seeds only germinate at or near the soil surface (where the light is greatest). If they were to germinate too far underneath the surface, the developing seedling would not have enough food reserves to reach the sunlight.

Development of Fruit and Fruit Types

After fertilization, the ovary of the flower usually develops into the fruit. Fruits are usually associated with having a sweet taste; however, not all fruits are sweet. Botanically, the term "fruit" is used for a ripened ovary. In most cases, flowers in which fertilization has taken place will develop into fruits, and flowers in which fertilization has not taken place will not. Some fruits

develop from the ovary and are known as true fruits, whereas others develop from other parts of the female gametophyte and are known as accessory fruits. The fruit encloses the seeds and the developing embryo, thereby providing it with protection. Fruits are of many types, depending on their origin and texture. The sweet tissue of the blackberry, the red flesh of the tomato, the shell of the peanut, and the hull of corn (the tough, thin part that gets stuck in your teeth when you eat popcorn) are all fruits. As the fruit matures, the seeds also mature.

Fruits may be classified as simple, aggregate, multiple, or accessory, depending on their origin (Figure 3). If the fruit develops from a single carpel or fused carpels of a single ovary, it is known as a **simple fruit**, as seen in nuts and beans. An **aggregate fruit** is one that develops from more than one carpel, but all are in the same flower: the mature carpels fuse together to form the entire fruit, as seen in the raspberry. **Multiple fruit** develops from an inflorescence or a cluster of flowers. An example is the pineapple, where the flowers fuse together to form the fruit. **Accessory fruits** (sometimes called false fruits) are not derived from the ovary, but from another part of the flower, such as the receptacle (strawberry) or the hypanthium (apples and pears).

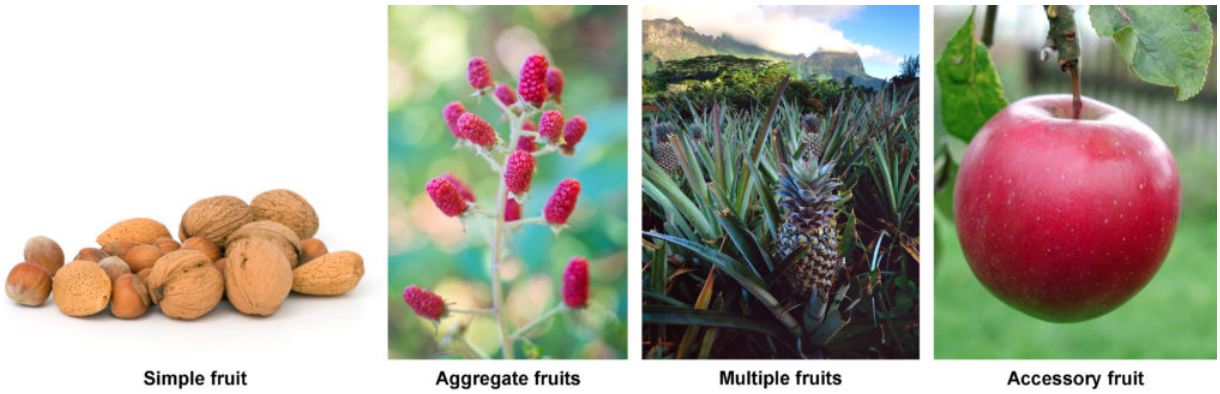


Figure 3. There are four main types of fruits. Simple fruits, such as these nuts, are derived from a single ovary. Aggregate fruits, like raspberries, form from many carpels that fuse together. Multiple fruits, such as pineapple, form from a cluster of flowers called an inflorescence. Accessory fruit, like the apple, are formed from a part of the plant other than the ovary. (credit “nuts”: modification of work by Petr Kratochvil; credit “raspberries”: modification of work by jill111; credit “pineapple”: modification of work by psaudio; credit “apple”: modification of work by Paolo Neo)

Fruits generally have three parts: the **exocarp** (the outermost skin or covering), the **mesocarp** (middle part of the fruit), and the **endocarp** (the inner part of the fruit). Together, all three are known as the **pericarp**. The mesocarp is usually the fleshy, edible part of the fruit; however, in some fruits, such as the almond, the endocarp is the edible part. In many fruits, two or all three of the layers are fused, and are indistinguishable at maturity. Fruits can be dry or fleshy. Furthermore, fruits can be divided into dehiscent or indehiscent types. Dehiscent fruits, such as peas, readily release their seeds, while indehiscent fruits, like peaches, rely on decay to release their seeds.

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12.17: Fruit and Seed Dispersal

The fruit has a single purpose: seed dispersal. Seeds contained within fruits need to be dispersed far from the mother plant, so they may find favorable and less competitive conditions in which to germinate and grow.

Some fruit have built-in mechanisms so they can disperse by themselves, whereas others require the help of agents like wind, water, and animals (Figure 1). Modifications in seed structure, composition, and size help in dispersal. Wind-dispersed fruit are lightweight and may have wing-like appendages that allow them to be carried by the wind. Some have a parachute-like structure to keep them afloat. Some fruits—for example, the dandelion—have hairy, weightless structures that are suited to dispersal by wind.



Figure 1. Fruits and seeds are dispersed by various means. (a) Dandelion seeds are dispersed by wind, the (b) coconut seed is dispersed by water, and the (c) acorn is dispersed by animals that cache and then forget it. (credit a: modification of work by "Rosendahl"/Flickr; credit b: modification of work by Shine Oa; credit c: modification of work by Paolo Neo)

Seeds dispersed by water are contained in light and buoyant fruit, giving them the ability to float. Coconuts are well known for their ability to float on water to reach land where they can germinate. Similarly, willow and silver birches produce lightweight fruit that can float on water.

Animals and birds eat fruits, and the seeds that are not digested are excreted in their droppings some distance away. Some animals, like squirrels, bury seed-containing fruits for later use; if the squirrel does not find its stash of fruit, and if conditions are favorable, the seeds germinate. Some fruits, like the cocklebur, have hooks or sticky structures that stick to an animal's coat and are then transported to another place. Humans also play a big role in dispersing seeds when they carry fruits to new places and throw away the inedible part that contains the seeds.

All of the above mechanisms allow for seeds to be dispersed through space, much like an animal's offspring can move to a new location. Seed dormancy, which was described earlier, allows plants to disperse their progeny through time: something animals cannot do. Dormant seeds can wait months, years, or even decades for the proper conditions for germination and propagation of the species.

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12.18: Putting It Together- Plant Reproduction

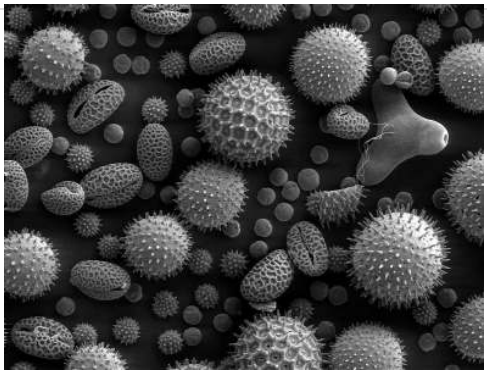


Figure 1. A micrograph of miscellaneous pollen

As we discussed at the beginning of this module, pollen in the air can cause problems for a lot of people (over 50 million Americans per year, in fact). However, without pollen, a large number of plants wouldn't be able to reproduce.

For allergy sufferers, the best treatment is to avoid the offending allergens altogether. This may be possible if the allergen is a specific food, like peanuts, which can be cut out of the diet, but not when the very air we breathe is loaded with allergens, such as ragweed pollen. Air purifiers, filters, humidifiers, and conditioners provide varying degrees of relief, but none is 100 percent effective. Various over-the-counter or prescription medications offer relief, too.

- Antihistamines counter the effects of histamine, the substance that makes eyes water and noses itch and causes sneezing during allergic reactions. Sleepiness was a problem with the first generation of antihistamines, but the newest drugs do not cause such a problem.
- Nasal steroids are give as anti-inflammatory sprays. They help decrease inflammation, swelling, and mucus production. They work well in combination with antihistamines and, in low doses for brief periods of time, are relatively free of side effects.
- A nasal spray, cromolyn sodium can help stop hay fever, perhaps by blocking release of histamine and other symptom-producing chemicals. It has few side effects.
- Available in capsule and spray form, decongestants thin nasal secretions and can reduce swelling and sinus discomfort. Intended for short-term use, they are usually used in combination with antihistamines. Long-term usage of spray decongestants can actually make symptoms worse, while decongestant pills do not have this problem.
- Immunotherapy (allergy shots) might provide relief for patients who don't find relief with antihistamines or nasal steroids. They alter the body's immune response to allergens, thereby helping to prevent allergic reactions. Current immunotherapy treatments are limited because of potential side effects.

Many complementary health approaches have been studied for seasonal allergies. There's some evidence that a few may be helpful.

- A 2007 evaluation of six studies of the herb butterbur for seasonal allergies, involving a total of 720 participants, indicated that butterbur may be helpful.
- Researchers have been investigating probiotics (live microorganisms that may have health benefits) for diseases of the immune system, including allergies. Although some studies have had promising results, the overall evidence on probiotics and seasonal allergies is inconsistent. It's possible that some types of probiotics might be helpful but that others are not.
- It's been thought that eating honey might help to relieve pollen allergies because honey contains small amounts of pollen and might help people build up a tolerance to it. Another possibility is that honey could act as an antihistamine or anti-inflammatory agent. Only a few studies have examined the effects of honey in people with seasonal allergies, and their results have been inconsistent.

Many other natural products have been studied for seasonal allergies, including astragalus, capsaicin, grape seed extract, omega-3 fatty acids, Pycnogenol (French maritime pine bark extract), quercetin, spirulina, stinging nettle, and an herb used in Ayurvedic medicine called tinospora or guduchi. In all instances, the evidence is either inconsistent or too limited to show whether these products are helpful.

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12.19: Cerego- Plant Reproduction

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for Plant Reproduction. You'll need to create a free log-in to practice these items, if you haven't already.

https://cerego.com/sets/796519/learn

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CHAPTER OVERVIEW

13: Module 10- Animal Diversity

13.1: Why It Matters- Animal Diversity
13.2: Introduction to the Evolutionary History of the Animal Kingdom
13.3: Pre-Cambrian Animal Life
13.4: The Cambrian Explosion
13.5: Post-Cambrian Evolution
13.6: Introduction to Animal Phylogeny
13.7: Classifying Animals
13.8: Constructing an Animal Phylogenetic Tree
13.9: Modern Revisions of Phylogeny
13.10: Introduction to Animal Form and Function
13.11: Body Plans
13.12: Limits on Animal Size and Shape
13.13: Animal Bioenergetics
13.14: Introduction to Animal Primary Tissues
13.15: Complex Tissue Structure
13.16: Epithelial Tissues
13.17: Connective Tissues
13.18: Muscle and Nervous Tissues
13.19: Introduction to Animal Reproduction
13.20: Processes of Animal Reproduction and Development
13.21: Embryological Development
13.22: Hox Genes
13.23: Introduction to Homeostasis
13.24: What is Homeostasis?
13.25: Control of Homeostasis
13.26: Thermoregulation
13.27: Putting It Together- Animal Diversity
13.28: Cerego- Animal Diversity

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13.1: Why It Matters- Animal Diversity

Why discuss the importance of animal diversity?



Figure 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.

Learning Outcomes

- Discuss the evolutionary history of the animal kingdom
- Chart animal phylogeny
- Describe the various types of body plans that occur in animals
- Discuss the tissue structures found in animals
- Discuss methods and features of animal reproduction
- Discuss the importance of homeostasis in animals

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13.2: Introduction to the Evolutionary History of the Animal Kingdom

Discuss the evolutionary history of the animal kingdom



Figure 1. An artist's rendition depicts some organisms from the Cambrian period.

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.

What You'll Learn to Do

- 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
- Discuss the implications of mass animal extinctions that have occurred in evolutionary history

Learning Activities

The learning activities for this section include the following:

- Pre-Cambrian Animal Life
- The Cambrian Explosion
- Post-Cambrian Evolution
- Self Check: The Evolutionary History of the Animal Kingdom

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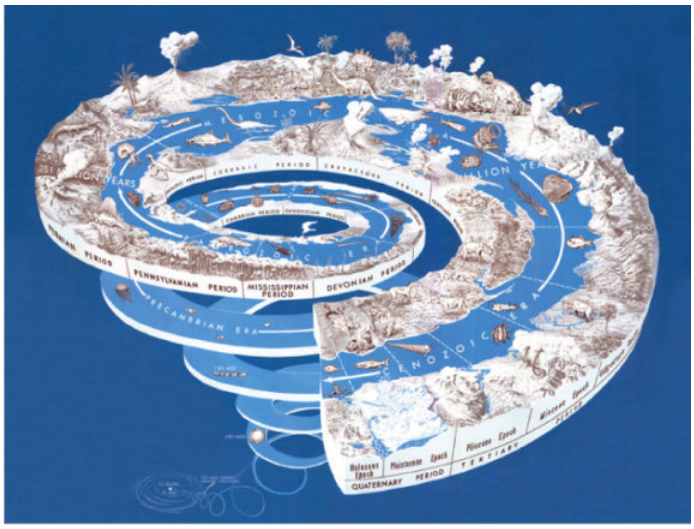
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13.3: Pre-Cambrian Animal Life

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 1). It is believed that early animal life, termed Ediacaran biota, evolved from protists at this time. Some protist 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 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 2.



(a) (b)

Figure 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.

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13.4: The Cambrian Explosion

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. 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 1).

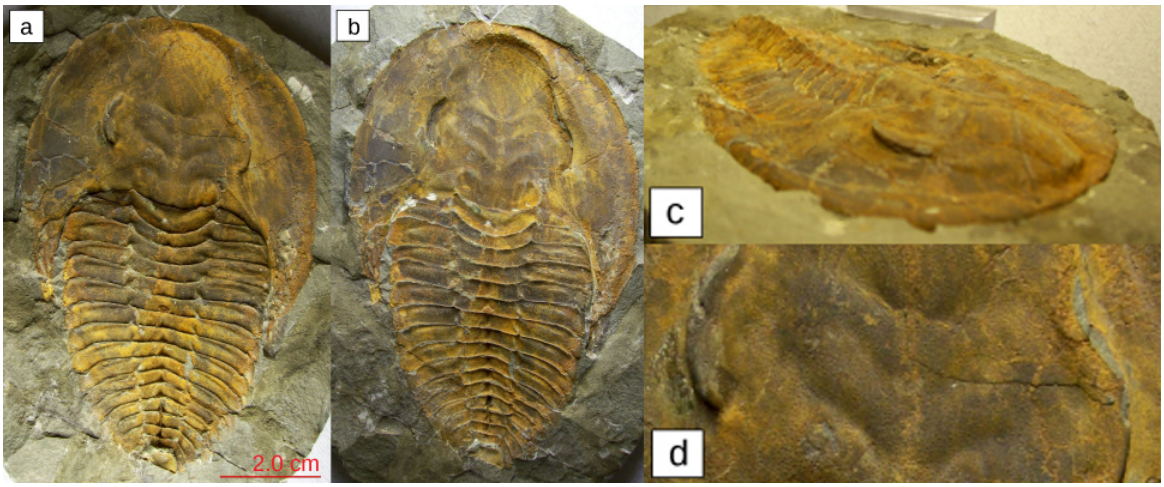


Figure 1. These fossils (a–d) belong to trilobites, extinct arthropods that appeared in the early Cambrian period, 525 million years ago, and disappeared from the fossil record during a mass extinction at the end of the Permian period, about 250 million years ago.

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 2).

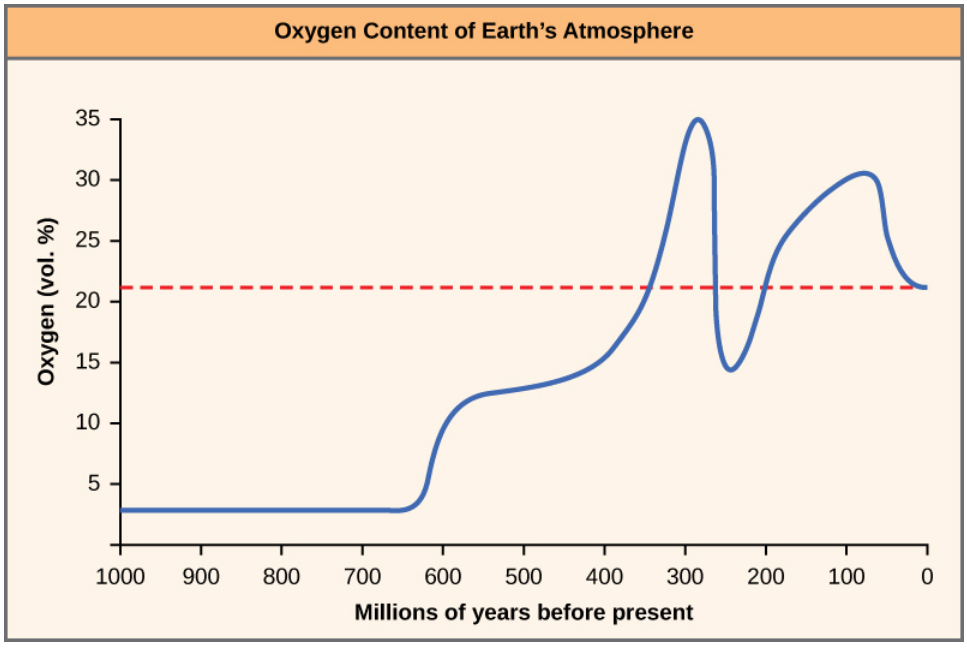


Figure 2. The oxygen concentration in Earth's atmosphere rose sharply around 300 million years ago.

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.

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.

View an animation of what ocean life may have been like during the Cambrian explosion. Note that there isn't any narration in the video.



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=454

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13.5: Post-Cambrian Evolution

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 1) 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.

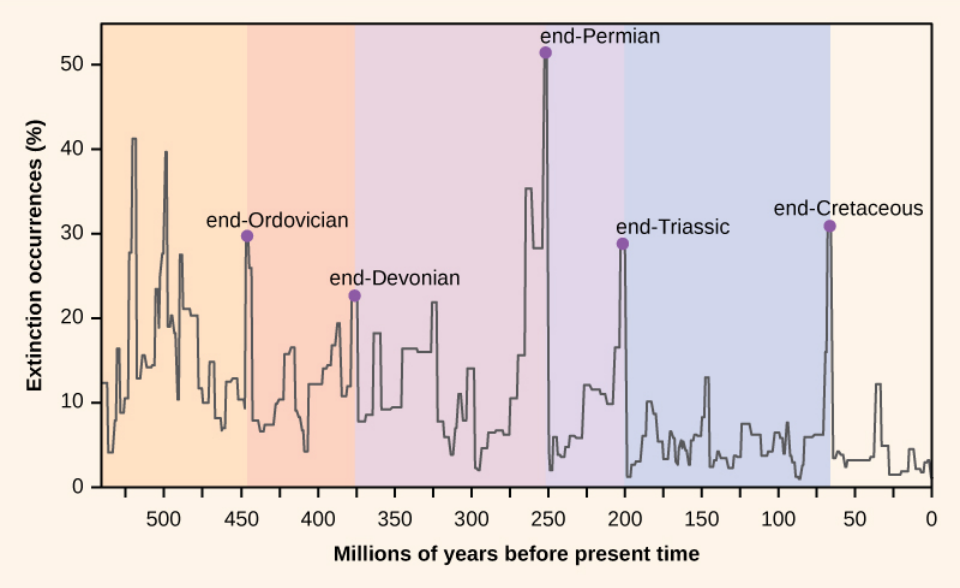


Figure 1. Mass extinctions have occurred repeatedly over geological time.

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.

Watch the following video to learn more about the mass extinctions.

A link to an interactive elements can be found at the bottom of this page.

Paleontologist

Natural history museums contain the fossil casts of extinct animals and information about how these animals evolved, lived, and died. Paleontologists 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.

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13.6: Introduction to Animal Phylogeny

Chart animal phylogeny

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.

What You'll Learn to Do

- Identify key features scientists use to classify animals
- Interpret the metazoan phylogenetic tree
- List some of the relationships within the modern phylogenetic tree that have been discovered as a result of modern molecular data

Learning Activities

The learning activities for this section include the following:

- Classifying Animals
- Constructing an Animal Phylogenetic Tree
- Modern Revisions of Phylogeny
- Self Check: Animal Phylogeny

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13.7: Classifying Animals

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 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.

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.

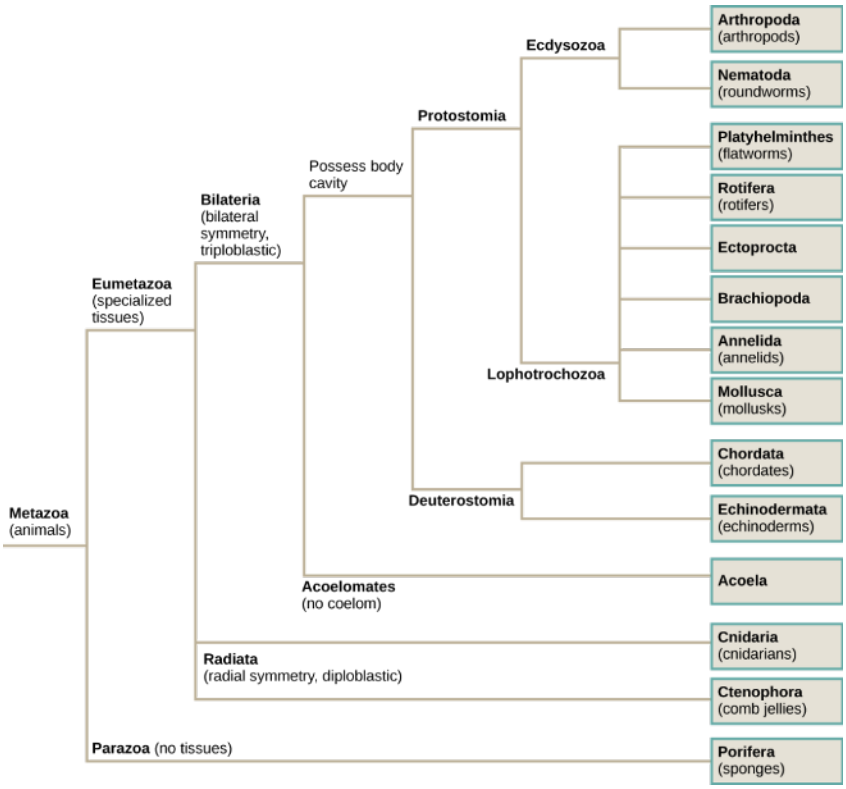


Figure 1. The phylogenetic tree of animals is based on morphological, fossil, and genetic evidence.

Practice Question

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.

[reveal-answer q=”692101″]Show Answer[/reveal-answer]
[hidden-answer a=”692101″]Statement c is false.[/hidden-answer]

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13.8: 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 1).

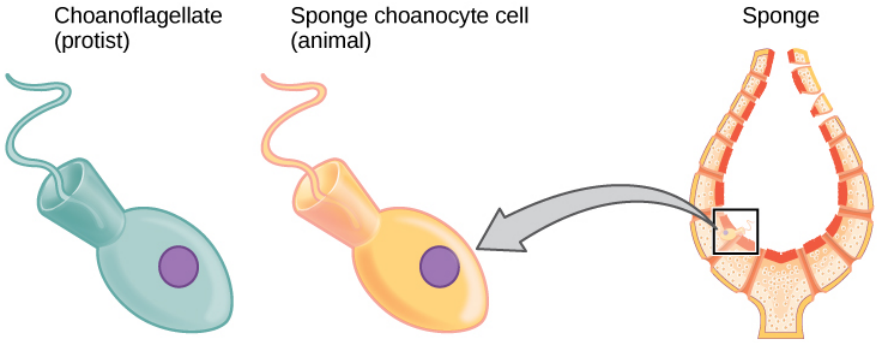


Figure 1. Cells of the protist choanoflagellate resemble sponge choanocyte cells. Beating of choanocyte flagella draws water through the sponge so that nutrients can be extracted and waste removed.

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 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.



Figure 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)

Explore an interactive tree of life here. Zoom and click to learn more about the organisms and their evolutionary relationships.

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13.9: Modern Revisions of Phylogeny

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.

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.

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13.10: Introduction to Animal Form and Function

Describe common forms and functions in the animal kingdom

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 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 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)

What You'll Learn to Do

- Describe the various types of body plans that occur in animals
- Describe limits on animal size and shape
- Relate bioenergetics to body size, levels of activity, and the environment

Learning Activities

The learning activities for this section include the following:

- Body Plans
- Animal Size and Shape
- Bioenergetics
- Self Check: Animal Form and Function

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13.11: Body Plans

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. All types of symmetry are well suited to meet the unique demands of a particular animal's lifestyle.



Figure 1. The sponge is asymmetrical. (credit: modification of work by Andrew Turner)

Asymmetry is a unique feature of Parazoa (Figure 1).

Radial symmetry is the arrangement of body parts around a central axis, as is seen in a drinking glass or pie. Only a few animal groups display radial symmetry. 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 2a and 2b). 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.



(a) (b)

Figure 2. The (a) jellyfish and (b) anemone are radially symmetrical. (credit a: modification of work by Robert Freiburger; credit b: modification of work by Samuel Chow)



Figure 3. The butterfly is bilaterally symmetrical. (credit: 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 3), 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 4). 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.

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.

Watch this video to see a quick sketch of the different types of body symmetry.

A link to an interactive elements can be found at the bottom of this page.

Animal Body Planes and Cavities

A standing vertebrate animal can be divided by several planes. A **sagittal plane** divides the body into right and left portions. A **midsagittal plane** divides the body exactly in the middle, making two equal right and left halves. A **frontal plane** (also called a coronal plane) separates the front from the back. A **transverse plane** (or, horizontal plane) divides the animal into upper and lower portions. This is sometimes called a cross section, and, if the transverse cut is at an angle, it is called an oblique plane. Figure 4 illustrates these planes on a goat (a four-legged animal) and a human being.

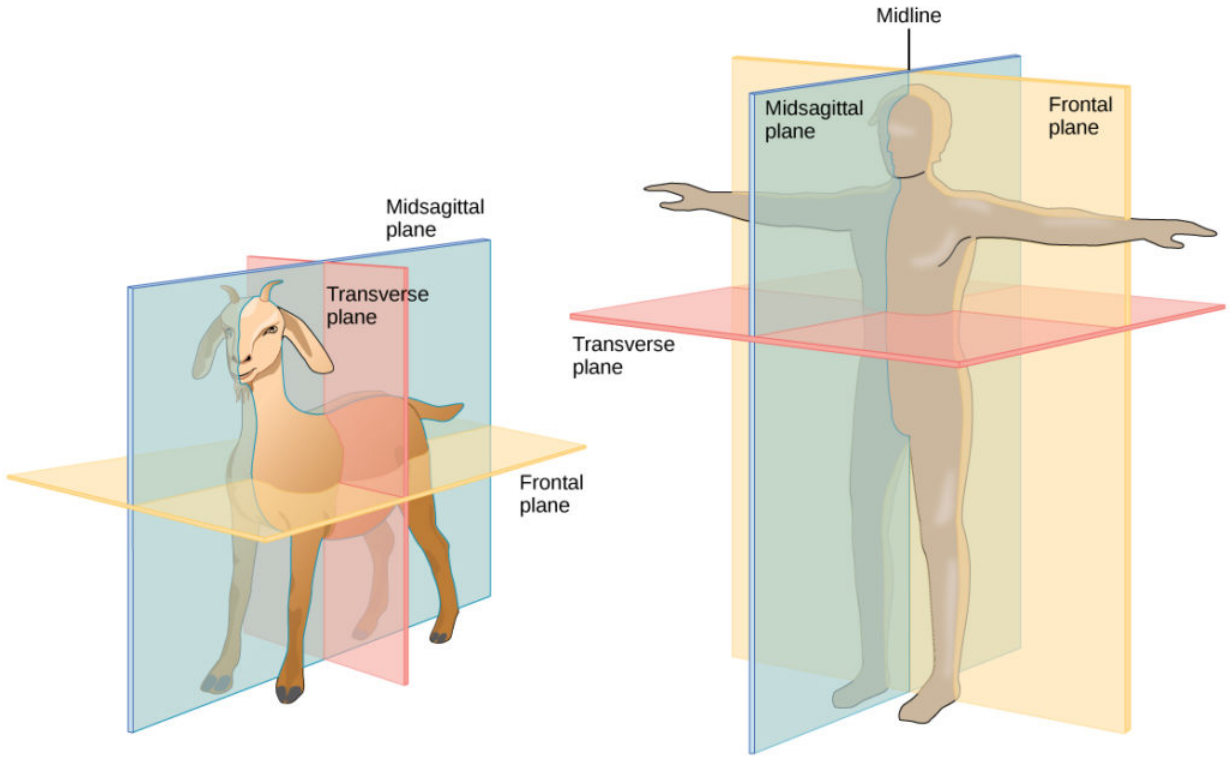


Figure 4. Shown are the planes of a quadruped goat and a bipedal human. The midsagittal plane divides the body exactly in half, into right and left portions. The frontal plane divides the front and back, and the transverse plane divides the body into upper and lower portions.

Vertebrate animals have a number of defined body cavities, as illustrated in Figure 5. Two of these are major cavities that contain smaller cavities within them. The **dorsal cavity** contains the cranial and the vertebral (or spinal) cavities. The **ventral cavity** contains the thoracic cavity, which in turn contains the pleural cavity around the lungs and the pericardial cavity, which surrounds

the heart. The ventral cavity also contains the abdominopelvic cavity, which can be separated into the abdominal and the pelvic cavities.

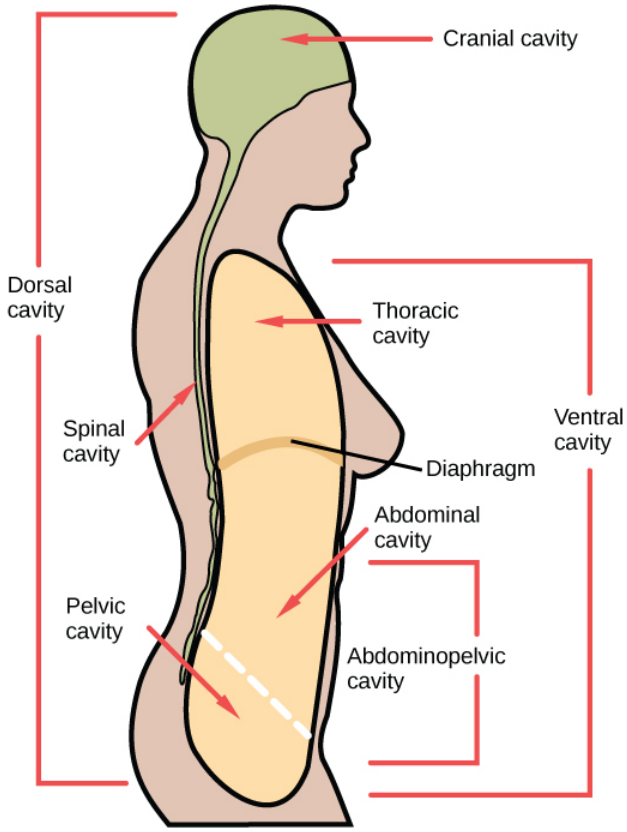


Figure 5. Vertebrate animals have two major body cavities. The dorsal cavity, indicated in green, contains the cranial and the spinal cavity. The ventral cavity, indicated in yellow, contains the thoracic cavity and the abdominopelvic cavity. The thoracic cavity is separated from the abdominopelvic cavity by the diaphragm. The thoracic cavity is separated into the abdominal cavity and the pelvic cavity by an imaginary line parallel to the pelvis bones. (credit: modification of work by NCI)

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13.12: Limits on Animal Size and Shape

Animals with bilateral symmetry that live in water tend to have a **fusiform** shape: this is a tubular shaped body that is tapered at both ends. This shape decreases the drag on the body as it moves through water and allows the animal to swim at high speeds. Table 1 lists the maximum speed of various animals. Certain types of sharks can swim at fifty kilometers an hour and some dolphins at 32 to 40 kilometers per hour. Land animals frequently travel faster, although the tortoise and snail are significantly slower than cheetahs. Another difference in the adaptations of aquatic and land-dwelling organisms is that aquatic organisms are constrained in shape by the forces of drag in the water since water has higher viscosity than air. On the other hand, land-dwelling organisms are constrained mainly by gravity, and drag is relatively unimportant. For example, most adaptations in birds are for gravity not for drag.

Table 1. Maximum Speed of Assorted Land Marine Animals

Animal	Speed (kmh)	Speed (mph)
Cheetah	113	70
Quarter horse	77	48
Fox	68	42
Shortfin mako shark	50	31
Domestic house cat	48	30
Human	45	28
Dolphin	32–40	20–25
Mouse	13	8
Snail	0.05	0.03

Most animals have an exoskeleton, including insects, spiders, scorpions, horseshoe crabs, centipedes, and crustaceans. Scientists estimate that, of insects alone, there are over 30 million species on our planet. The exoskeleton is a hard covering or shell that provides benefits to the animal, such as protection against damage from predators and from water loss (for land animals); it also provides for the attachments of muscles.

As the tough and resistant outer cover of an arthropod, the exoskeleton may be constructed of a tough polymer such as chitin and is often biomineralized with materials such as calcium carbonate. This is fused to the animal's epidermis. Ingrowths of the exoskeleton, called **apodemes**, function as attachment sites for muscles, similar to tendons in more advanced animals (Figure 1).

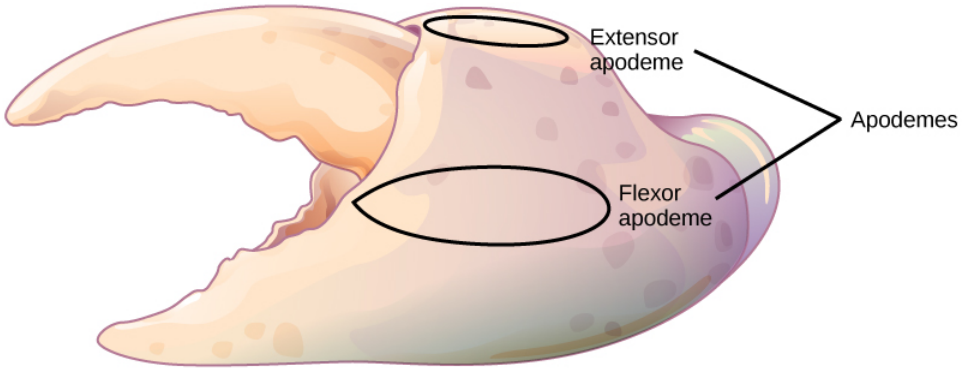


Figure 1. Apodemes are ingrowths on arthropod exoskeletons to which muscles attach. The apodemes on this crab leg are located above and below the fulcrum of the claw. Contraction of muscles attached to the apodemes pulls the claw closed.

In order to grow, the animal must first synthesize a new exoskeleton underneath the old one and then shed or molt the original covering. This limits the animal's ability to grow continually, and may limit the individual's ability to mature if molting does not

occur at the proper time. The thickness of the exoskeleton must be increased significantly to accommodate any increase in weight. It is estimated that a doubling of body size increases body weight by a factor of eight. The increasing thickness of the chitin necessary to support this weight limits most animals with an exoskeleton to a relatively small size. The same principles apply to endoskeletons, but they are more efficient because muscles are attached on the outside, making it easier to compensate for increased mass.

An animal with an endoskeleton has its size determined by the amount of skeletal system it needs in order to support the other tissues and the amount of muscle it needs for movement. As the body size increases, both bone and muscle mass increase. The speed achievable by the animal is a balance between its overall size and the bone and muscle that provide support and movement.

Limiting Effects of Diffusion on Size and Development

The exchange of nutrients and wastes between a cell and its watery environment occurs through the process of diffusion. All living cells are bathed in liquid, whether they are in a single-celled organism or a multicellular one. Diffusion is effective over a specific distance and limits the size that an individual cell can attain. If a cell is a single-celled microorganism, such as an amoeba, it can satisfy all of its nutrient and waste needs through diffusion. If the cell is too large, then diffusion is ineffective and the center of the cell does not receive adequate nutrients nor is it able to effectively dispel its waste.

An important concept in understanding how efficient diffusion is as a means of transport is the surface to volume ratio. Recall that any three-dimensional object has a surface area and volume; the ratio of these two quantities is the surface-to-volume ratio. Consider a cell shaped like a perfect sphere: it has a surface area of $4\pi r^2$, and a volume of $(4/3)\pi r^3$. The surface-to-volume ratio of a sphere is 3/r; as the cell gets bigger, its surface to volume ratio decreases, making diffusion less efficient. The larger the size of the sphere, or animal, the less surface area for diffusion it possesses.

The solution to producing larger organisms is for them to become multicellular. Specialization occurs in complex organisms, allowing cells to become more efficient at doing fewer tasks. For example, circulatory systems bring nutrients and remove waste, while respiratory systems provide oxygen for the cells and remove carbon dioxide from them. Other organ systems have developed further specialization of cells and tissues and efficiently control body functions. Moreover, surface-to-volume ratio applies to other areas of animal development, such as the relationship between muscle mass and cross-sectional surface area in supporting skeletons, and in the relationship between muscle mass and the generation of dissipation of heat.

Visit this interactive site to see an entire animal (a zebrafish embryo) at the cellular and sub-cellular level. Use the zoom and navigation functions for a virtual nanoscopy exploration.

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13.13: Animal Bioenergetics

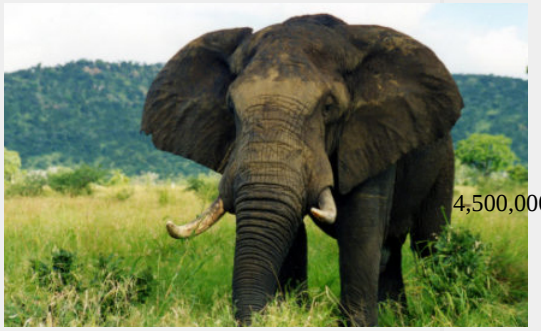
All animals must obtain their energy from food they ingest or absorb. These nutrients are converted to adenosine triphosphate (ATP) for short-term storage and use by all cells. Some animals store energy for slightly longer times as glycogen, and others store energy for much longer times in the form of triglycerides housed in specialized adipose tissues. No energy system is one hundred percent efficient, and an animal's metabolism produces waste energy in the form of heat. If an animal can conserve that heat and maintain a relatively constant body temperature, it is classified as a warm-blooded animal and called an **endotherm**. The insulation used to conserve the body heat comes in the forms of fur, fat, or feathers. The absence of insulation in **ectothermic** animals increases their dependence on the environment for body heat.

The amount of energy expended by an animal over a specific time is called its metabolic rate. The rate is measured variously in joules, calories, or kilocalories (1000 calories). Carbohydrates and proteins contain about 4.5 to 5 kcal/g, and fat contains about 9 kcal/g. Metabolic rate is estimated as the **basal metabolic rate (BMR)** in endothermic animals at rest and as the **standard metabolic rate (SMR)** in ectotherms. Human males have a BMR of 1600 to 1800 kcal/day, and human females have a BMR of 1300 to 1500 kcal/day. Even with insulation, endothermal animals require extensive amounts of energy to maintain a constant body temperature. An ectotherm such as an alligator has an SMR of 60 kcal/day.

Energy Requirements Related to Body Size

Smaller endothermic animals have a greater surface area for their mass than larger ones (Table 1). Therefore, smaller animals lose heat at a faster rate than larger animals and require more energy to maintain a constant internal temperature. This results in a smaller endothermic animal having a higher BMR, per body weight, than a larger endothermic animal.

Table 1. Relative Metabolic Rates

Species	Mass	Metabolic Rate
 A mouse	35 g	890 mm^3 0_2/g body mass/hr
 An elephant	4,500,000 g	75 mm^3 0_2/g body mass/hr

Energy Requirements Related to Levels of Activity

The more active an animal is, the more energy is needed to maintain that activity, and the higher its BMR or SMR. The average daily rate of energy consumption is about two to four times an animal's BMR or SMR. Humans are more sedentary than most animals and have an average daily rate of only 1.5 times the BMR. The diet of an endothermic animal is determined by its BMR. For example: the type of grasses, leaves, or shrubs that an herbivore eats affects the number of calories that it takes in. The relative caloric content of herbivore foods, in descending order, is tall grasses > legumes > short grasses > forbs (any broad-leaved plant, not a grass) > subshrubs > annuals/biennials.

Energy Requirements Related to Environment

Animals adapt to extremes of temperature or food availability through torpor. **Torpor** is a process that leads to a decrease in activity and metabolism and allows animals to survive adverse conditions. Torpor can be used by animals for long periods, such as entering a state of **hibernation** during the winter months, in which case it enables them to maintain a reduced body temperature. During hibernation, ground squirrels can achieve an abdominal temperature of 0° C (32° F), while a bear's internal temperature is maintained higher at about 37° C (99° F).

If torpor occurs during the summer months with high temperatures and little water, it is called **estivation**. Some desert animals use this to survive the harshest months of the year. Torpor can occur on a daily basis; this is seen in bats and hummingbirds. While endothermy is limited in smaller animals by surface to volume ratio, some organisms can be smaller and still be endotherms because they employ daily torpor during the part of the day that is coldest. This allows them to conserve energy during the colder parts of the day, when they consume more energy to maintain their body temperature.

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13.15: 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.

Watch a presentation by biologist E.O. Wilson on the importance of diversity.



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13.16: Epithelial Tissues

Epithelial tissues cover the outside of organs and structures in the body and line the lumens of organs in a single layer or multiple layers of cells. The types of epithelia are classified by the shapes of cells present and the number of layers of cells. Epithelia composed of a single layer of cells is called **simple epithelia**; epithelial tissue composed of multiple layers is called **stratified epithelia**. Table 1 summarizes the different types of epithelial tissues.

Table 1. Different Types of Epithelial Tissues

Cell shape	Description	Location
squamous	flat, irregular round shape	simple: lung alveoli, capillaries stratified: skin, mouth, vagina
cuboidal	cube shaped, central nucleus	glands, renal tubules
columnar	tall, narrow, nucleus toward base tall, narrow, nucleus along cell	simple: digestive tract pseudostratified: respiratory tract
transitional	round, simple but appear stratified	urinary bladder

Squamous Epithelia

Squamous epithelial cells are generally round, flat, and have a small, centrally located nucleus. The cell outline is slightly irregular, and cells fit together to form a covering or lining. When the cells are arranged in a single layer (simple epithelia), they facilitate diffusion in tissues, such as the areas of gas exchange in the lungs and the exchange of nutrients and waste at blood capillaries.

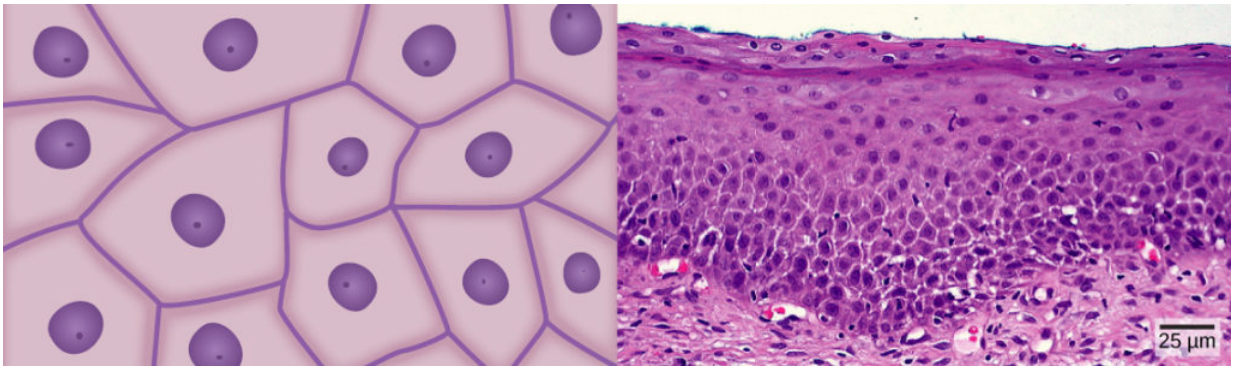


Figure 1. Squamous epithelia cells (a) have a slightly irregular shape, and a small, centrally located nucleus. These cells can be stratified into layers, as in (b) this human cervix specimen. (credit b: modification of work by Ed Uthman; scale-bar data from Matt Russell)

Figure 1a illustrates a layer of squamous cells with their membranes joined together to form an epithelium. Image Figure 1b illustrates squamous epithelial cells arranged in stratified layers, where protection is needed on the body from outside abrasion and damage. This is called a stratified squamous epithelium and occurs in the skin and in tissues lining the mouth and vagina.

Cuboidal Epithelia

Cuboidal epithelial cells, shown in Figure 2, are cube-shaped with a single, central nucleus. They are most commonly found in a single layer representing a simple epithelia in glandular tissues throughout the body where they prepare and secrete glandular material. They are also found in the walls of tubules and in the ducts of the kidney and liver.

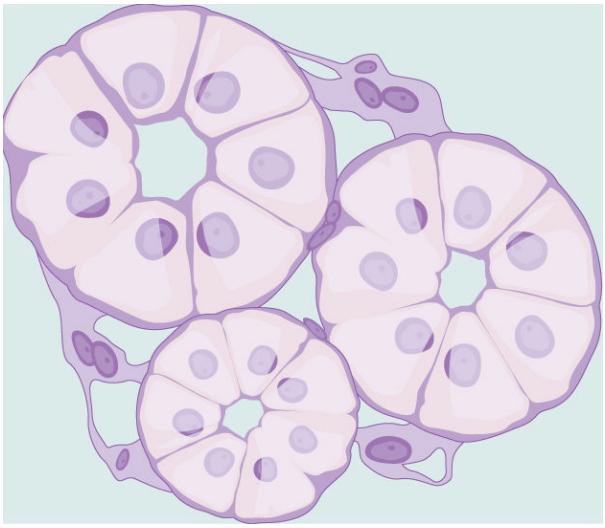


Figure 2. Simple cuboidal epithelial cells line tubules in the mammalian kidney, where they are involved in filtering the blood.

Columnar Epithelia

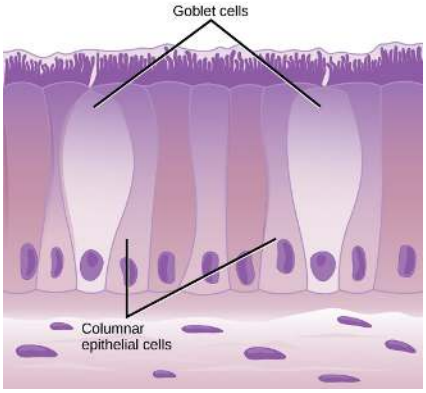


Figure 3. Simple columnar epithelial cells absorb material from the digestive tract. Goblet cells secret mucous into the digestive tract lumen.

Columnar epithelial cells are taller than they are wide: they resemble a stack of columns in an epithelial layer, and are most commonly found in a single-layer arrangement. The nuclei of columnar epithelial cells in the digestive tract appear to be lined up at the base of the cells, as illustrated in Figure 3. These cells absorb material from the lumen of the digestive tract and prepare it for entry into the body through the circulatory and lymphatic systems.

Columnar epithelial cells lining the respiratory tract appear to be stratified. However, each cell is attached to the base membrane of the tissue and, therefore, they are simple tissues. The nuclei are arranged at different levels in the layer of cells, making it appear as though there is more than one layer, as seen in Figure 4. This is called **pseudostratified**, columnar epithelia. This cellular covering has cilia at the apical, or free, surface of the cells. The cilia enhance the movement of mucous and trapped particles out of the respiratory tract, helping to protect the system from invasive microorganisms and harmful material that has been breathed into the body. Goblet cells are interspersed in some tissues (such as the lining of the trachea). The goblet cells contain mucous that traps irritants, which in the case of the trachea keep these irritants from getting into the lungs.

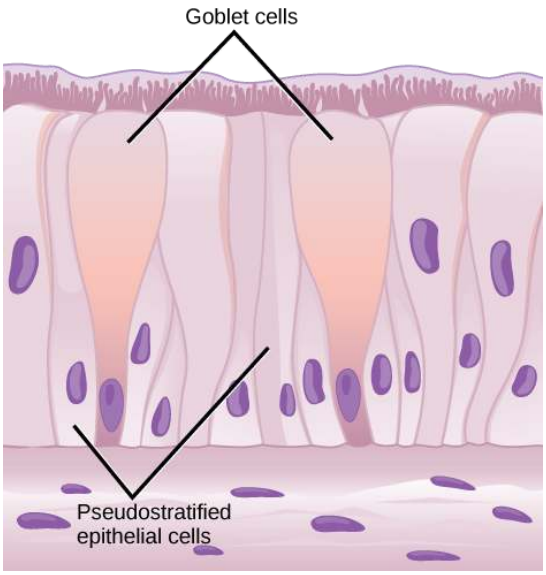


Figure 4. Pseudostratified columnar epithelia line the respiratory tract. They exist in one layer, but the arrangement of nuclei at different levels makes it appear that there is more than one layer. Goblet cells interspersed between the columnar epithelial cells secrete mucous into the respiratory tract.

Transitional Epithelia

Transitional or uroepithelial cells appear only in the urinary system, primarily in the bladder and ureter. These cells are arranged in a stratified layer, but they have the capability of appearing to pile up on top of each other in a relaxed, empty bladder, as illustrated in Figure 5. As the urinary bladder fills, the epithelial layer unfolds and expands to hold the volume of urine introduced into it. As the bladder fills, it expands and the lining becomes thinner. In other words, the tissue transitions from thick to thin.

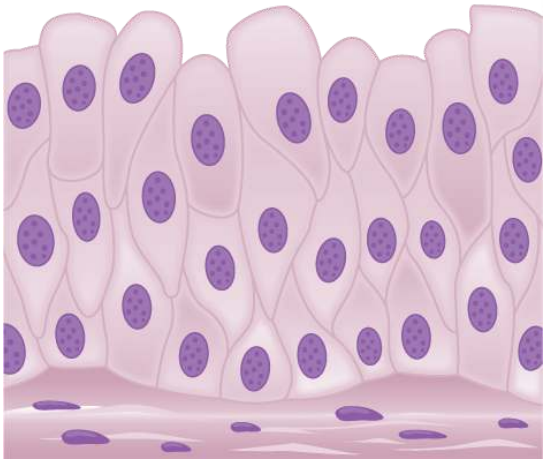


Figure 5. Transitional epithelia of the urinary bladder undergo changes in thickness depending on how full the bladder is.

? Practice Question

Which of the following statements about types of epithelial cells is false?

a. Simple columnar epithelial cells line the tissue of the lung.
b. Simple cuboidal epithelial cells are involved in the filtering of blood in the kidney.
c. Pseudostratisfied columnar epithilia occur in a single layer, but the arrangement of nuclei makes it appear that more than one layer is present.
d. Transitional epithelia change in thickness depending on how full the bladder is.

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[hidden-answer a="277616"]Statement d is false.[/hidden-answer]

Click through the interactive review to learn more about epithelial tissues.

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13.17: Connective Tissues

Connective tissues are made up of a matrix consisting of living cells and a non-living substance, called the ground substance. The ground substance is made of an organic substance (usually a protein) and an inorganic substance (usually a mineral or water). The principal cell of connective tissues is the fibroblast. This cell makes the fibers found in nearly all of the connective tissues. Fibroblasts are motile, able to carry out mitosis, and can synthesize whichever connective tissue is needed. Macrophages, lymphocytes, and, occasionally, leukocytes can be found in some of the tissues. Some tissues have specialized cells that are not found in the others. The **matrix** in connective tissues gives the tissue its density. When a connective tissue has a high concentration of cells or fibers, it has proportionally a less dense matrix.

The organic portion or protein fibers found in connective tissues are either collagen, elastic, or reticular fibers. Collagen fibers provide strength to the tissue, preventing it from being torn or separated from the surrounding tissues. Elastic fibers are made of the protein elastin; this fiber can stretch to one and one half of its length and return to its original size and shape. Elastic fibers provide flexibility to the tissues. Reticular fibers are the third type of protein fiber found in connective tissues. This fiber consists of thin strands of collagen that form a network of fibers to support the tissue and other organs to which it is connected. The various types of connective tissues, the types of cells and fibers they are made of, and sample locations of the tissues is summarized in Table 1.

Table 1. Connective Tissues

Tissue	Cells	Fibers	Location
loose/areolar	fibroblasts, macrophages, some lymphocytes, some neutrophils	few: collagen, elastic, reticular	around blood vessels; anchors epithelia
dense, fibrous connective tissue	fibroblasts, macrophages,	mostly collagen	irregular: skin regular: tendons, ligaments
cartilage	chondrocytes, chondroblasts	hyaline: few collagen fibrocartilage: large amount of collagen	shark skeleton, fetal bones, human ears, intervertebral discs
bone	osteoblasts, osteocytes, osteoclasts	some: collagen, elastic	vertebrate skeletons
adipose	adipocytes	few	adipose (fat)
blood	red blood cells, white blood cells	none	blood

Loose/Areolar Connective Tissue

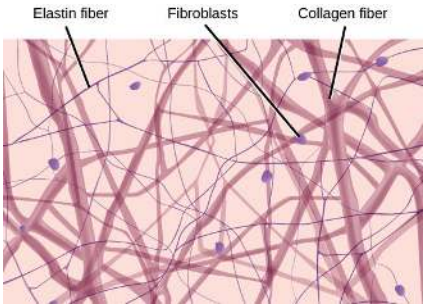


Figure 1. Loose connective tissue is composed of loosely woven collagen and elastic fibers. The fibers and other components of the connective tissue matrix are secreted by fibroblasts.

Loose connective tissue, also called areolar connective tissue, has a sampling of all of the components of a connective tissue. As illustrated in Figure 1, loose connective tissue has some fibroblasts; macrophages are present as well. Collagen fibers are relatively wide and stain a light pink, while elastic fibers are thin and stain dark blue to black. The space between the formed elements of the tissue is filled with the matrix. The material in the connective tissue gives it a loose consistency similar to a cotton ball that has

been pulled apart. Loose connective tissue is found around every blood vessel and helps to keep the vessel in place. The tissue is also found around and between most body organs. In summary, areolar tissue is tough, yet flexible, and comprises membranes.

Fibrous Connective Tissue

Fibrous connective tissues contain large amounts of collagen fibers and few cells or matrix material. The fibers can be arranged irregularly or regularly with the strands lined up in parallel. Irregularly arranged fibrous connective tissues are found in areas of the body where stress occurs from all directions, such as the dermis of the skin. Regular fibrous connective tissue, shown in Figure 2, is found in tendons (which connect muscles to bones) and ligaments (which connect bones to bones).

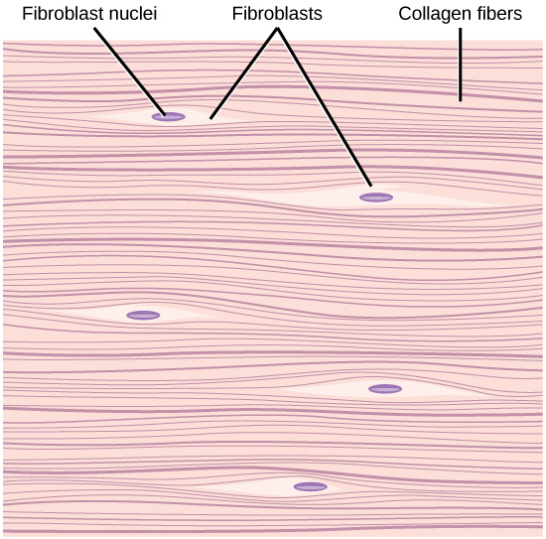


Figure 2. Fibrous connective tissue from the tendon has strands of collagen fibers lined up in parallel.

Cartilage

Cartilage is a connective tissue with a large amount of the matrix and variable amounts of fibers. The cells, called **chondrocytes**, make the matrix and fibers of the tissue. Chondrocytes are found in spaces within the tissue called **lacunae**.

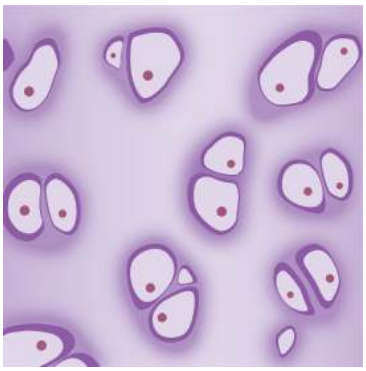


Figure 3. Hyaline cartilage consists of a matrix with cells called chondrocytes embedded in it. The chondrocytes exist in cavities in the matrix called lacunae.

A cartilage with few collagen and elastic fibers is hyaline cartilage, illustrated in Figure 3. The lacunae are randomly scattered throughout the tissue and the matrix takes on a milky or scrubbed appearance with routine histological stains. Sharks have cartilaginous skeletons, as does nearly the entire human skeleton during a specific pre-birth developmental stage. A remnant of this cartilage persists in the outer portion of the human nose. Hyaline cartilage is also found at the ends of long bones, reducing friction and cushioning the articulations of these bones.

Elastic cartilage has a large amount of elastic fibers, giving it tremendous flexibility. The ears of most vertebrate animals contain this cartilage as do portions of the larynx, or voice box. Fibrocartilage contains a large amount of collagen fibers, giving the tissue tremendous strength. Fibrocartilage comprises the intervertebral discs in vertebrate animals. Hyaline cartilage found in movable

joints such as the knee and shoulder becomes damaged as a result of age or trauma. Damaged hyaline cartilage is replaced by fibrocartilage and results in the joints becoming “stiff.”

Bone

Bone, or osseous tissue, is a connective tissue that has a large amount of two different types of matrix material. The organic matrix is similar to the matrix material found in other connective tissues, including some amount of collagen and elastic fibers. This gives strength and flexibility to the tissue. The inorganic matrix consists of mineral salts—mostly calcium salts—that give the tissue hardness. Without adequate organic material in the matrix, the tissue breaks; without adequate inorganic material in the matrix, the tissue bends.

There are three types of cells in bone: osteoblasts, osteocytes, and osteoclasts. Osteoblasts are active in making bone for growth and remodeling. Osteoblasts deposit bone material into the matrix and, after the matrix surrounds them, they continue to live, but in a reduced metabolic state as osteocytes. Osteocytes are found in lacunae of the bone. Osteoclasts are active in breaking down bone for bone remodeling, and they provide access to calcium stored in tissues. Osteoclasts are usually found on the surface of the tissue.

Bone can be divided into two types: compact and spongy. Compact bone is found in the shaft (or diaphysis) of a long bone and the surface of the flat bones, while spongy bone is found in the end (or epiphysis) of a long bone. Compact bone is organized into subunits called **osteons**, as illustrated in Figure 4. A blood vessel and a nerve are found in the center of the structure within the Haversian canal, with radiating circles of lacunae around it known as lamellae. The wavy lines seen between the lacunae are microchannels called **canaliculi**; they connect the lacunae to aid diffusion between the cells. Spongy bone is made of tiny plates called **trabeculae** these plates serve as struts to give the spongy bone strength. Over time, these plates can break causing the bone to become less resilient. Bone tissue forms the internal skeleton of vertebrate animals, providing structure to the animal and points of attachment for tendons.

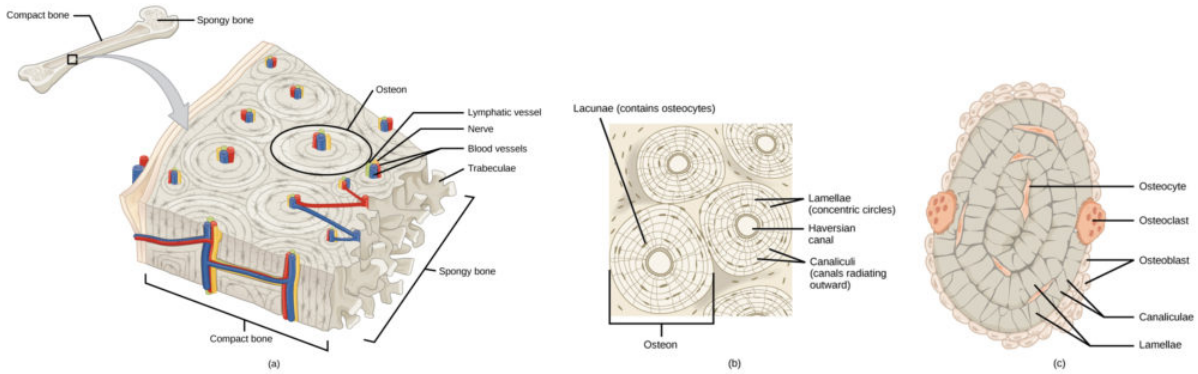


Figure 4. (a) Compact bone is a dense matrix on the outer surface of bone. Spongy bone, inside the compact bone, is porous with web-like trabeculae. (b) Compact bone is organized into rings called osteons. Blood vessels, nerves, and lymphatic vessels are found in the central Haversian canal. Rings of lamellae surround the Haversian canal. Between the lamellae are cavities called lacunae. Canaliculi are microchannels connecting the lacunae together. (c) Osteoblasts surround the exterior of the bone. Osteoclasts bore tunnels into the bone and osteocytes are found in the lacunae.

Adipose Tissue

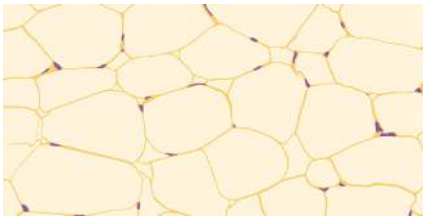


Figure 5. Adipose is a connective tissue is made up of cells called adipocytes. Adipocytes have small nuclei localized at the cell edge.

Adipose tissue, or fat tissue, is considered a connective tissue even though it does not have fibroblasts or a real matrix and only has a few fibers. Adipose tissue is made up of cells called adipocytes that collect and store fat in the form of triglycerides, for energy metabolism. Adipose tissues additionally serve as insulation to help maintain body temperatures, allowing animals to be

endothermic, and they function as cushioning against damage to body organs. Under a microscope, adipose tissue cells appear empty due to the extraction of fat during the processing of the material for viewing, as seen in Figure 5. The thin lines in the image are the cell membranes, and the nuclei are the small, black dots at the edges of the cells.

Blood

Blood is considered a connective tissue because it has a matrix, as shown in Figure 6. The living cell types are red blood cells (RBC), also called erythrocytes, and white blood cells (WBC), also called leukocytes. The fluid portion of whole blood, its matrix, is commonly called plasma.

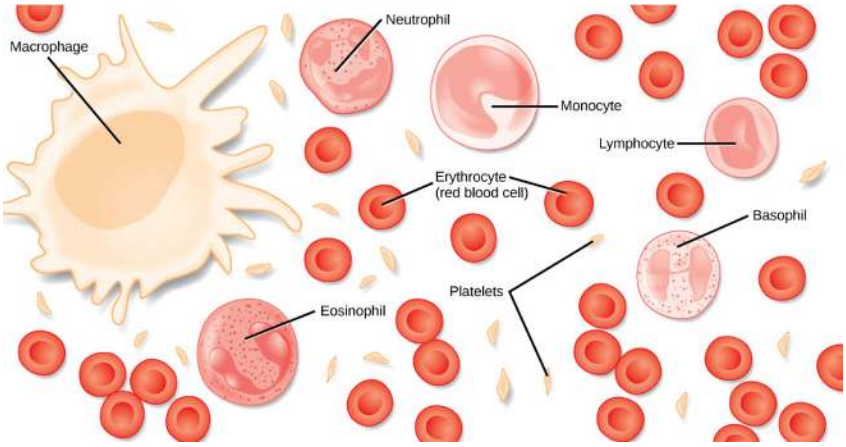


Figure 6. Blood is a connective tissue that has a fluid matrix, called plasma, and no fibers. Erythrocytes (red blood cells), the predominant cell type, are involved in the transport of oxygen and carbon dioxide. Also present are various leukocytes (white blood cells) involved in immune response.

The cell found in greatest abundance in blood is the erythrocyte. Erythrocytes are counted in millions in a blood sample: the average number of red blood cells in primates is 4.7 to 5.5 million cells per microliter. Erythrocytes are consistently the same size in a species, but vary in size between species. For example, the average diameter of a primate red blood cell is 7.5 µl, a dog is close at 7.0 µl, but a cat's RBC diameter is 5.9 µl. Sheep erythrocytes are even smaller at 4.6 µl. Mammalian erythrocytes lose their nuclei and mitochondria when they are released from the bone marrow where they are made. Fish, amphibian, and avian red blood cells maintain their nuclei and mitochondria throughout the cell's life. The principal job of an erythrocyte is to carry and deliver oxygen to the tissues.

Leukocytes are the predominant white blood cells found in the peripheral blood. Leukocytes are counted in the thousands in the blood with measurements expressed as ranges: primate counts range from 4,800 to 10,800 cells per µl, dogs from 5,600 to 19,200 cells per µl, cats from 8,000 to 25,000 cells per µl, cattle from 4,000 to 12,000 cells per µl, and pigs from 11,000 to 22,000 cells per µl.

Lymphocytes function primarily in the immune response to foreign antigens or material. Different types of lymphocytes make antibodies tailored to the foreign antigens and control the production of those antibodies. Neutrophils are phagocytic cells and they participate in one of the early lines of defense against microbial invaders, aiding in the removal of bacteria that has entered the body. Another leukocyte that is found in the peripheral blood is the monocyte. Monocytes give rise to phagocytic macrophages that clean up dead and damaged cells in the body, whether they are foreign or from the host animal. Two additional leukocytes in the blood are eosinophils and basophils—both help to facilitate the inflammatory response.

The slightly granular material among the cells is a cytoplasmic fragment of a cell in the bone marrow. This is called a platelet or thrombocyte. Platelets participate in the stages leading up to coagulation of the blood to stop bleeding through damaged blood vessels. Blood has a number of functions, but primarily it transports material through the body to bring nutrients to cells and remove waste material from them.

? Try It

A pathologist is a medical doctor or veterinarian who has specialized in the laboratory detection of disease in animals, including humans. These professionals complete medical school education and follow it with an extensive post-graduate residency at a medical center. A pathologist may oversee clinical laboratories for the evaluation of body tissue and blood samples for the detection of disease or infection. They examine tissue specimens through a microscope to identify cancers and other diseases. Some pathologists perform autopsies to determine the cause of death and the progression of disease.

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13.18: Muscle and Nervous Tissues

Muscle Tissues

There are three types of muscle in animal bodies: smooth, skeletal, and cardiac. They differ by the presence or absence of striations or bands, the number and location of nuclei, whether they are voluntarily or involuntarily controlled, and their location within the body. Table 1 summarizes these differences.

Table 1. Types of Muscles

Type of Muscle	Striations	Nuclei	Control	Location
smooth	no	single, in center	involuntary	visceral organs
skeletal	yes	many, at periphery	voluntary	skeletal muscles
cardiac	yes	single, in center	involuntary	heart

Smooth Muscle

Smooth muscle does not have striations in its cells. It has a single, centrally located nucleus, as shown in Figure 1. Constriction of smooth muscle occurs under involuntary, autonomic nervous control and in response to local conditions in the tissues. Smooth muscle tissue is also called non-striated as it lacks the banded appearance of skeletal and cardiac muscle. The walls of blood vessels, the tubes of the digestive system, and the tubes of the reproductive systems are composed of mostly smooth muscle.

Skeletal Muscle

Skeletal muscle has striations across its cells caused by the arrangement of the contractile proteins actin and myosin. These muscle cells are relatively long and have multiple nuclei along the edge of the cell. Skeletal muscle is under voluntary, somatic nervous system control and is found in the muscles that move bones. Figure 1 illustrates the histology of skeletal muscle.

Cardiac Muscle

Cardiac muscle, shown in Figure 1, is found only in the heart. Like skeletal muscle, it has cross striations in its cells, but cardiac muscle has a single, centrally located nucleus. Cardiac muscle is not under voluntary control but can be influenced by the autonomic nervous system to speed up or slow down. An added feature to cardiac muscle cells is a line than extends along the end of the cell as it abuts the next cardiac cell in the row. This line is called an intercalated disc: it assists in passing electrical impulse efficiently from one cell to the next and maintains the strong connection between neighboring cardiac cells.

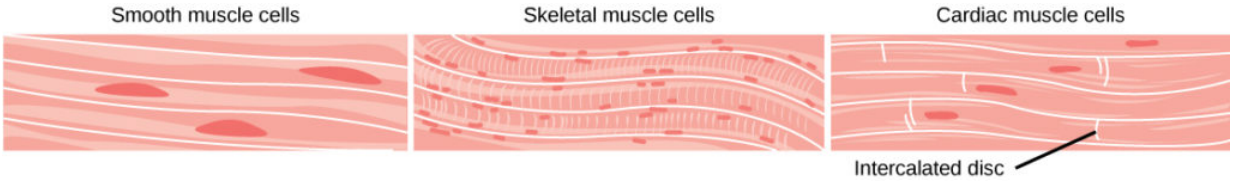


Figure 1. Smooth muscle cells do not have striations, while skeletal muscle cells do. Cardiac muscle cells have striations, but, unlike the multinucleate skeletal cells, they have only one nucleus. Cardiac muscle tissue also has intercalated discs, specialized regions running along the plasma membrane that join adjacent cardiac muscle cells and assist in passing an electrical impulse from cell to cell.

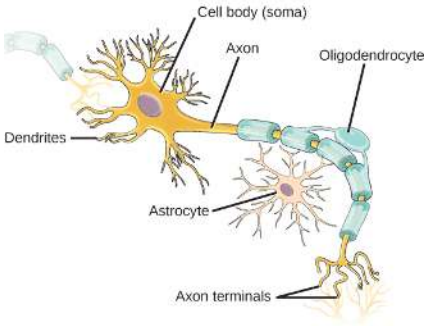


Figure 2. Diagram of a neuron

Nervous tissues are made of cells specialized to receive and transmit electrical impulses from specific areas of the body and to send them to specific locations in the body. The main cell of the nervous system is the neuron, illustrated in Figure 2.

The large structure with a central nucleus is the cell body of the neuron. Projections from the cell body are either dendrites specialized in receiving input or a single axon specialized in transmitting impulses. Some glial cells are also shown. Astrocytes regulate the chemical environment of the nerve cell, and oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently. Other glial cells that are not shown support the nutritional and waste requirements of the neuron. Some of the glial cells are phagocytic and remove debris or damaged cells from the tissue. A nerve consists of neurons and glial cells.

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13.19: Introduction to Animal Reproduction

Discuss methods and features of animal reproduction

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.

What You'll Learn to Do

- Explain the processes of animal reproduction and embryonic development
- Compare and contrast the embryonic development of protostomes and deuterostomes
- Describe the roles that Hox genes play in development

Learning Activities

The learning activities for this section include the following:

- Animal Reproduction and Development
- Embryological Development
- Hox Genes
- Self Check: Animal Reproduction

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13.20: Processes of Animal Reproduction and 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.

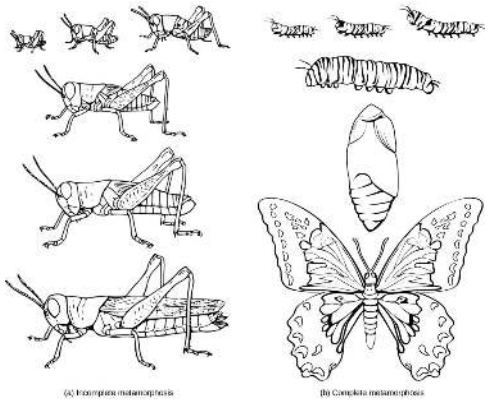


Figure 1. (a) The grasshopper undergoes incomplete metamorphosis. (b) The butterfly undergoes complete metamorphosis. (credit: S.E. Snodgrass, USDA)

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 1). 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.

The process of animal development begins with the **cleavage**, or series of mitotic cell divisions, of the zygote (Figure 2). 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**.

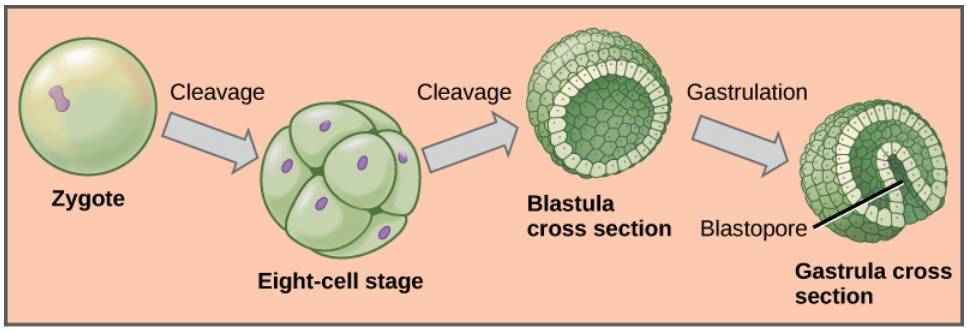


Figure 2. During embryonic development, the zygote undergoes a series of mitotic cell divisions, or cleavages, to form an eight-cell stage, then a hollow blastula. During a process called gastrulation, the blastula folds inward to form a cavity in the gastrula.

Watch the following video to see how human embryonic development (after the blastula and gastrula stages of development) reflects evolution:

A link to an interactive elements can be found at the bottom of this page.

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13.21: 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 1). 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**.

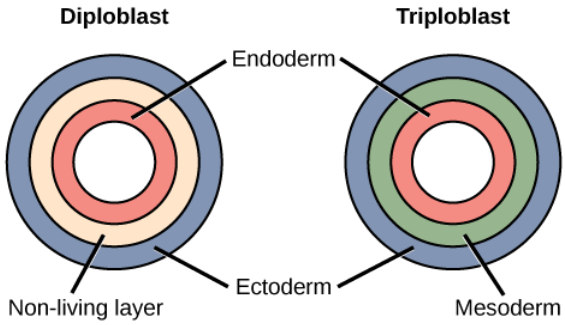


Figure 1. During embryogenesis, diploblasts develop two embryonic germ layers: an ectoderm and an endoderm. Triploblasts develop a third layer—the mesoderm—between the endoderm and ectoderm.

? Practice Question

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.

[reveal-answer q="815922"]Show Answer[/reveal-answer]
[hidden-answer a="815922"]Statement d is false.[/hidden-answer]

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 2). 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.

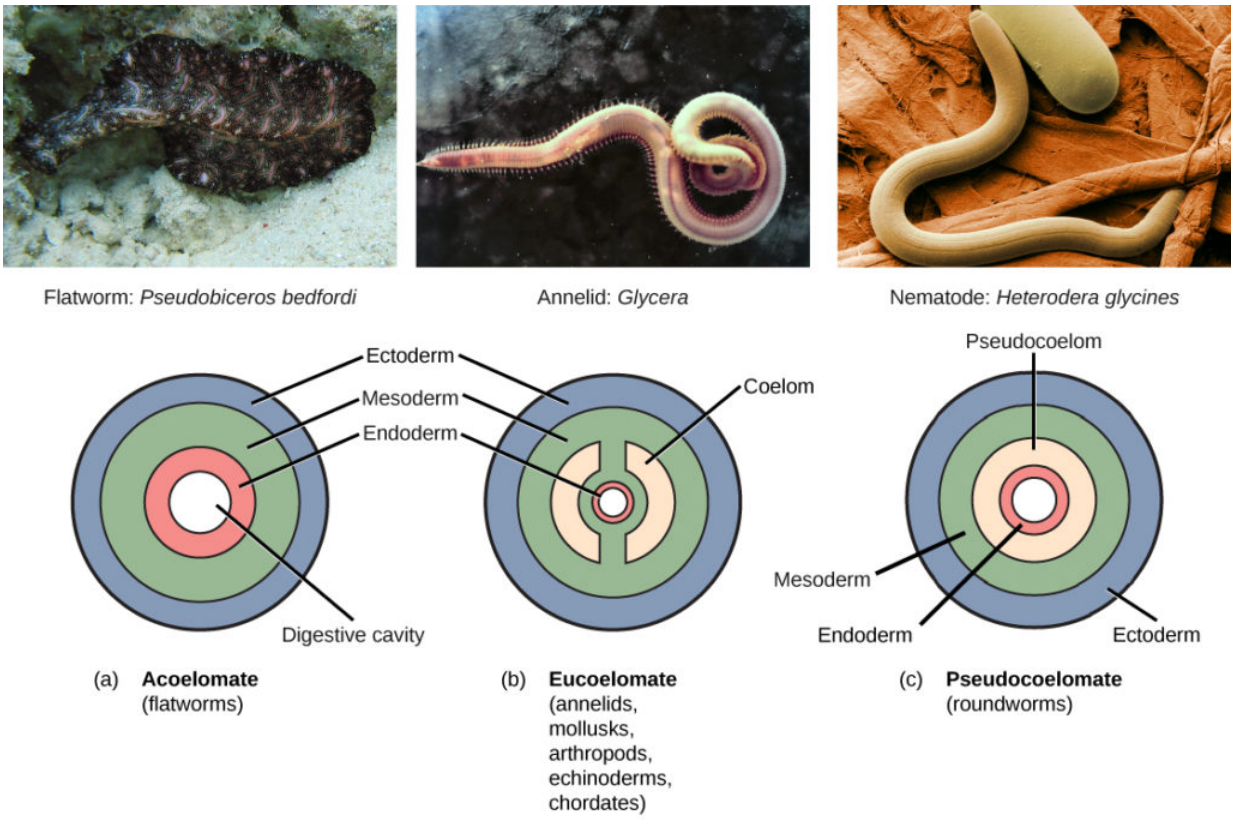


Figure 2. Triploblasts may be (a) acoelomates, (b) eucoelomates, or (c) pseudocoelomates. Acoelomates have no body cavity. Eucoelomates have a body cavity within the mesoderm, called a coelom, which is lined with mesoderm. Pseudocoelomates also have a body cavity, but it is sandwiched between the endoderm 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)

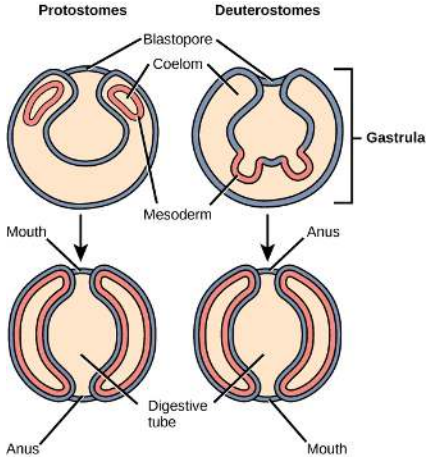


Figure 3. Eucoelomates can be divided into two groups based on their early embryonic development. In protostomes, part of the mesoderm separates to form the coelom in a process called schizocoely. In deuterostomes, the mesoderm pinches off to form the coelom in a process called enterocoely. It was long believed that the blastopore developed into the mouth in protostomes and into the anus in deuterostomes, but recent evidence challenges this belief.

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 3).

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 3). 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.

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.

Try It

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.

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13.22: Hox Genes

Since the early nineteenth 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 twentieth 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.

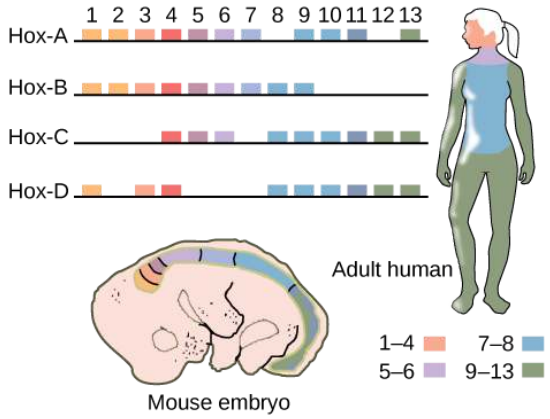


Figure 1. Shown here is the homology between *Hox* genes in mice and humans. Note how *Hox* gene expression, as indicated with orange, pink, blue and green shading, occurs in the same body segments in both the mouse and the human.

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 1).

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.

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.

Practice Question

If a *Hox 13* gene in a mouse was replaced with a *Hox 1* gene, how might this alter animal development?

[practice-area rows=”2″][/practice-area]
[reveal-answer q=”319959″]Show Answer[/reveal-answer]
[hidden-answer a=”319959″]The animal might develop two heads and no tail.[/hidden-answer]

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13.23: Introduction to Homeostasis

Discuss the importance of homeostasis in animals

Animal organs and organ systems constantly adjust to internal and external changes through a process called homeostasis (“steady state”). These changes might be in the level of glucose or calcium in blood or in external temperatures. Homeostasis means to maintain dynamic equilibrium in the body. It is dynamic because it is constantly adjusting to the changes that the body’s systems encounter. It is equilibrium because body functions are kept within specific ranges. Even an animal that is apparently inactive is maintaining this homeostatic equilibrium.

What You’ll Learn to Do

- Define homeostasis
- Describe the factors affecting homeostasis
- Describe the process of thermoregulation
- Describe thermoregulation of endothermic and ectothermic animals

Learning Activities

The learning activities for this section include the following:

- What is Homeostasis?
- Control of Homeostasis
- Thermoregulation
- Self Check: Homeostasis

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13.24: What is Homeostasis?

Homeostasis, in a general sense, refers to stability, balance, or equilibrium. Physiologically, it is the body's attempt to maintain a constant and balanced internal environment, which requires persistent monitoring and adjustments as conditions change. Adjustment of physiological systems within the body is called homeostatic regulation, which involves three parts or mechanisms:

1. the receptor
2. the control center
3. the effector

The **receptor** receives information that something in the environment is changing. The **control center** or integration center receives and processes information from the receptor. The **effector** responds to the commands of the control center by either opposing or enhancing the stimulus. This ongoing process continually works to restore and maintain homeostasis. For example, during body temperature regulation, temperature receptors in the skin communicate information to the brain (the control center) which signals the effectors: blood vessels and sweat glands in the skin. As the internal and external environment of the body are constantly changing, adjustments must be made continuously to stay at or near a specific value: the **set point**.

The goal of homeostasis is the maintenance of equilibrium around a specific value of some aspect of the body or its cells called a set point. While there are normal fluctuations from the set point, the body's systems will usually attempt to go back to this point. A change in the internal or external environment is called a stimulus and is detected by a receptor; the response of the system is to adjust the activities of the system so the value moves back toward the set point. For instance, if the body becomes too warm, adjustments are made to cool the animal. If glucose levels in the blood rise after a meal, adjustments are made to lower them and to get the nutrient into tissues that need it or to store it for later use.

When a change occurs in an animal's environment, an adjustment must be made so that the internal environment of the body and cells remains stable. The receptor that senses the change in the environment is part of a feedback mechanism. The stimulus—temperature, glucose, or calcium levels—is detected by the receptor. The receptor sends information to a control center, often the brain, which relays appropriate signals to an effector organ that is able to cause an appropriate change, either up or down, depending on the information the sensor was sending.

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13.25: Control of Homeostasis

When a change occurs in an animal's environment, an adjustment must be made. The receptor senses the change in the environment, then sends a signal to the control center (in most cases, the brain) which in turn generates a response that is signaled to an effector. The effector is a muscle (that contracts or relaxes) or a gland that secretes. Homeostatsis is maintained by negative feedback loops. Positive feedback loops actually push the organism further out of homeostasis, but may be necessary for life to occur. Homeostasis is controlled by the nervous and endocrine system of mammals.

Negative Feedback Mechanisms

Any homeostatic process that changes the direction of the stimulus is a **negative feedback loop**. It may either increase or decrease the stimulus, but the stimulus is not allowed to continue as it did before the receptor sensed it. In other words, if a level is too high, the body does something to bring it down, and conversely, if a level is too low, the body does something to make it go up. Hence the term negative feedback. An example is animal maintenance of blood glucose levels. When an animal has eaten, blood glucose levels rise. This is sensed by the nervous system. Specialized cells in the pancreas sense this, and the hormone insulin is released by the endocrine system. Insulin causes blood glucose levels to decrease, as would be expected in a negative feedback system, as illustrated in Figure 1. However, if an animal has not eaten and blood glucose levels decrease, this is sensed in another group of cells in the pancreas, and the hormone glucagon is released causing glucose levels to increase. This is still a negative feedback loop, but not in the direction expected by the use of the term "negative." Another example of an increase as a result of the feedback loop is the control of blood calcium. If calcium levels decrease, specialized cells in the parathyroid gland sense this and release parathyroid hormone (PTH), causing an increased absorption of calcium through the intestines and kidneys and, possibly, the breakdown of bone in order to liberate calcium. The effects of PTH are to raise blood levels of the element. Negative feedback loops are the predominant mechanism used in homeostasis.

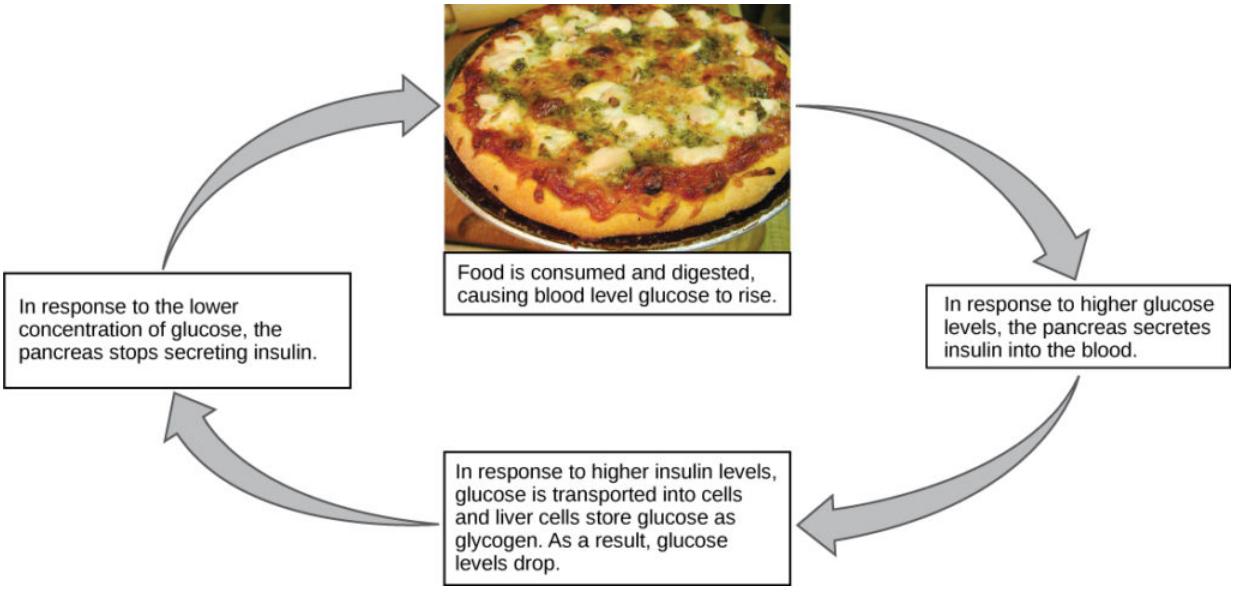


Figure 1. Blood sugar levels are controlled by a negative feedback loop. (credit: modification of work by Jon Sullivan)

Positive Feedback Loop

A **positive feedback loop** maintains the direction of the stimulus, possibly accelerating it. Few examples of positive feedback loops exist in animal bodies, but one is found in the cascade of chemical reactions that result in blood clotting, or coagulation. As one clotting factor is activated, it activates the next factor in sequence until a fibrin clot is achieved. The direction is maintained, not changed, so this is positive feedback. Another example of positive feedback is uterine contractions during childbirth, as illustrated in Figure 2. The hormone oxytocin, made by the endocrine system, stimulates the contraction of the uterus. This produces pain sensed by the nervous system. Instead of lowering the oxytocin and causing the pain to subside, more oxytocin is produced until the contractions are powerful enough to produce childbirth.

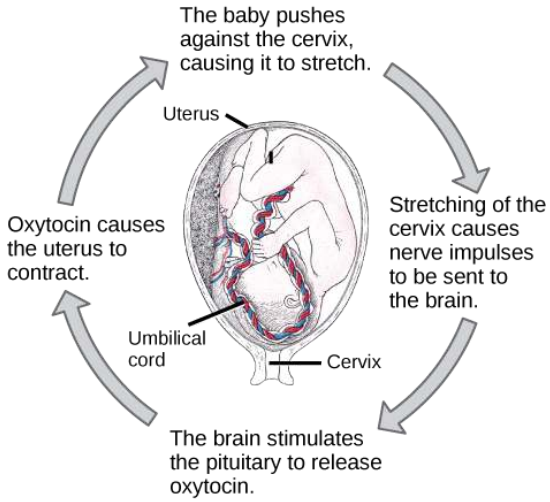


Figure 2. The birth of a human infant is the result of positive feedback.

? Practice Question

State whether each of the following processes is regulated by a positive feedback loop or a negative feedback loop.

a. A person feels satiated after eating a large meal.
b. The blood has plenty of red blood cells. As a result, erythropoietin, a hormone that stimulates the production of new red blood cells, is no longer released from the kidney.

[practice-area rows="2"][/practice-area]
[reveal-answer q="82193"]Show Answer[/reveal-answer]
[hidden-answer a="82193"]Both processes are the result of negative feedback loops. Negative feedback loops, which tend to keep a system at equilibrium, are more common than positive feedback loops.[/hidden-answer]

Set Point

It is possible to adjust a system's set point. When this happens, the feedback loop works to maintain the new setting. An example of this is blood pressure: over time, the normal or set point for blood pressure can increase as a result of continued increases in blood pressure. The body no longer recognizes the elevation as abnormal and no attempt is made to return to the lower set point. The result is the maintenance of an elevated blood pressure that can have harmful effects on the body. Medication can lower blood pressure and lower the set point in the system to a more healthy level. This is called a process of **alteration** of the set point in a feedback loop.

Changes can be made in a group of body organ systems in order to maintain a set point in another system. This is called **acclimatization**. This occurs, for instance, when an animal migrates to a higher altitude than it is accustomed to. In order to adjust to the lower oxygen levels at the new altitude, the body increases the number of red blood cells circulating in the blood to ensure adequate oxygen delivery to the tissues. Another example of acclimatization is animals that have seasonal changes in their coats: a heavier coat in the winter ensures adequate heat retention, and a light coat in summer assists in keeping body temperature from rising to harmful levels.

Feedback mechanisms can be understood in terms of driving a race car along a track: watch a short video lesson on positive and negative feedback loops.

A link to an interactive elements can be found at the bottom of this page.

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13.26: Thermoregulation

Body temperature affects body activities. Generally, as body temperature rises, enzyme activity rises as well. For every ten degree centigrade rise in temperature, enzyme activity doubles, up to a point. Body proteins, including enzymes, begin to denature and lose their function with high heat (around 50º C for mammals). Enzyme activity will decrease by half for every ten degree centigrade drop in temperature, to the point of freezing, with a few exceptions. Some fish can withstand freezing solid and return to normal with thawing.

Watch this Discovery Channel video on thermoregulation to see illustrations of this process in a variety of animals.

A link to an interactive elements can be found at the bottom of this page.

Neural Control of Thermoregulation

The nervous system is important to **thermoregulation**. The processes of homeostasis and temperature control are centered in the hypothalamus of the advanced animal brain.

? Practice Question

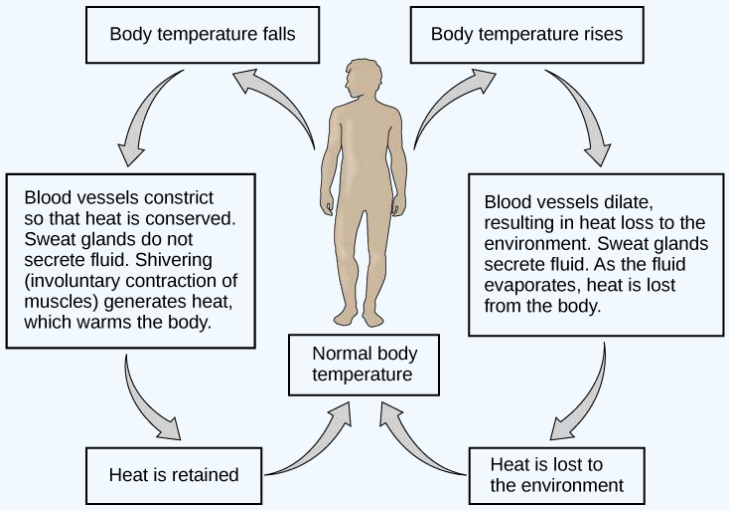


Figure 1. The body is able to regulate temperature in response to signals from the nervous system.

When bacteria are destroyed by leuckocytes, pyrogens are released into the blood. Pyrogens reset the body's thermostat to a higher temperature, resulting in fever. How might pyrogens cause the body temperature to rise?

[practice-area rows="2"][/practice-area]
[reveal-answer q="104188"]Show Answer[/reveal-answer]
[hidden-answer a="104188"]Pyrogens increase body temperature by causing the blood vessels to constrict, inducing shivering, and stopping sweat glands from secreting fluid.[/hidden-answer]

The hypothalamus maintains the set point for body temperature through reflexes that cause vasodilation and sweating when the body is too warm, or vasoconstriction and shivering when the body is too cold. It responds to chemicals from the body. When a bacterium is destroyed by phagocytic leukocytes, chemicals called endogenous pyrogens are released into the blood. These pyrogens circulate to the hypothalamus and reset the thermostat. This allows the body's temperature to increase in what is commonly called a fever. An increase in body temperature causes iron to be conserved, which reduces a nutrient needed by bacteria. An increase in body heat also increases the activity of the animal's enzymes and protective cells while inhibiting the enzymes and activity of the invading microorganisms. Finally, heat itself may also kill the pathogen. A fever that was once thought to be a complication of an infection is now understood to be a normal defense mechanism.

Endotherms and Ectotherms

Animals can be divided into two groups: some maintain a constant body temperature in the face of differing environmental temperatures, while others have a body temperature that is the same as their environment and thus varies with the environment. Animals that do not control their body temperature are ectotherms; instead they rely on external energy to dictate their body temperature. This group has been called cold-blooded, but the term may not apply to an animal in the desert with a very warm body temperature. Endotherms are animals that rely on internal sources for body temperature but which can exhibit extremes in temperature. These animals are able to maintain a level of activity at cooler temperature, which an ectotherm cannot due to differing enzyme levels of activity. Poikilotherms are animals with constantly varying internal temperatures, while an animal that maintains a constant body temperature in the face of environmental changes is called a homeotherm.

Heat can be exchanged between an animal and its environment through four mechanisms: radiation, evaporation, convection, and conduction (Figure 2). Radiation is the emission of electromagnetic "heat" waves. Heat comes from the sun in this manner and radiates from dry skin the same way. Heat can be removed with liquid from a surface during evaporation. This occurs when a mammal sweats. Convection currents of air remove heat from the surface of dry skin as the air passes over it. Heat will be conducted from one surface to another during direct contact with the surfaces, such as an animal resting on a warm rock.

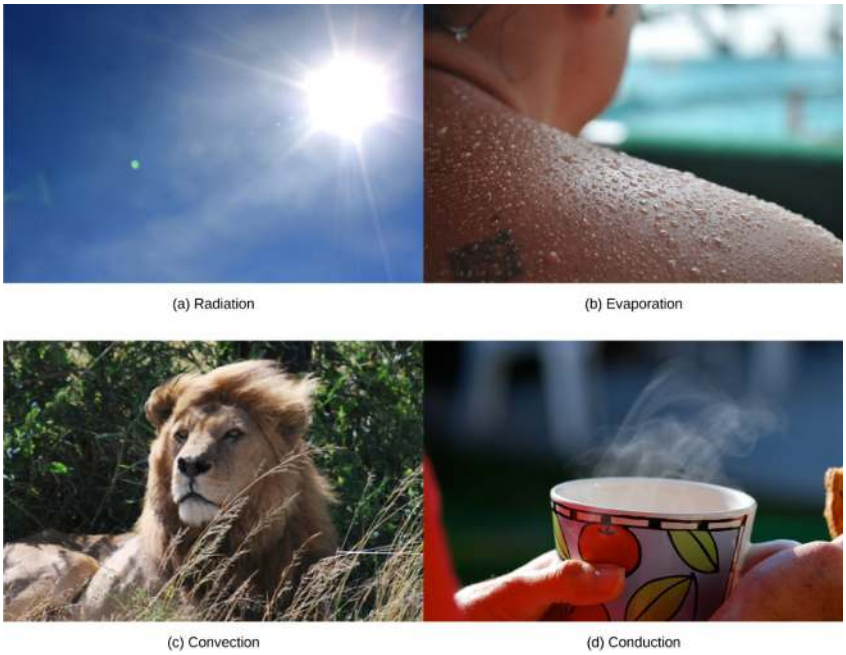


Figure 2. Heat can be exchanged by four mechanisms: (a) radiation, (b) evaporation, (c) convection, or (d) conduction. (credit b: modification of work by "Kullez"/Flickr; credit c: modification of work by Chad Rosenthal; credit d: modification of work by "stacey.d"/Flickr)

Heat Conservation and Dissipation

Animals conserve or dissipate heat in a variety of ways. In certain climates, endothermic animals have some form of insulation, such as fur, fat, feathers, or some combination thereof. Animals with thick fur or feathers create an insulating layer of air between their skin and internal organs. Polar bears and seals live and swim in a subfreezing environment and yet maintain a constant, warm, body temperature. The arctic fox, for example, uses its fluffy tail as extra insulation when it curls up to sleep in cold weather. Mammals have a residual effect from shivering and increased muscle activity: arrector pili muscles cause "goose bumps," causing small hairs to stand up when the individual is cold; this has the intended effect of increasing body temperature. Mammals use layers of fat to achieve the same end. Loss of significant amounts of body fat will compromise an individual's ability to conserve heat.

Endotherms use their circulatory systems to help maintain body temperature. Vasodilation brings more blood and heat to the body surface, facilitating radiation and evaporative heat loss, which helps to cool the body. Vasoconstriction reduces blood flow in peripheral blood vessels, forcing blood toward the core and the vital organs found there, and conserving heat. Some animals have adaptions to their circulatory system that enable them to transfer heat from arteries to veins, warming blood returning to the heart. This is called a countercurrent heat exchange; it prevents the cold venous blood from cooling the heart and other internal organs.

This adaption can be shut down in some animals to prevent overheating the internal organs. The countercurrent adaption is found in many animals, including dolphins, sharks, bony fish, bees, and hummingbirds. In contrast, similar adaptations can help cool endotherms when needed, such as dolphin flukes and elephant ears.

Some ectothermic animals use changes in their behavior to help regulate body temperature. For example, a desert ectothermic animal may simply seek cooler areas during the hottest part of the day in the desert to keep from getting too warm. The same animals may climb onto rocks to capture heat during a cold desert night. Some animals seek water to aid evaporation in cooling them, as seen with reptiles. Other ectotherms use group activity such as the activity of bees to warm a hive to survive winter.

Many animals, especially mammals, use metabolic waste heat as a heat source. When muscles are contracted, most of the energy from the ATP used in muscle actions is wasted energy that translates into heat. Severe cold elicits a shivering reflex that generates heat for the body. Many species also have a type of adipose tissue called brown fat that specializes in generating heat.

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13.27: Putting It Together- Animal Diversity

Animals vary in form and function. From a sponge to a worm to a goat, an organism has a distinct body plan that limits its size and shape. Animals' bodies are also designed to interact with their environments, whether in the deep sea, a rainforest canopy, or the desert. Therefore, a large amount of information about the structure of an organism's body (anatomy) and the function of its cells, tissues and organs (physiology) can be learned by studying that organism's environment.

Physical Anthropologist

Physical anthropologists study the adaption, variability, and evolution of human beings, plus their living and fossil relatives. They can work in a variety of settings, although most will have an academic appointment at a university, usually in an anthropology department or a biology, genetics, or zoology department.

Non-academic positions are available in the automotive and aerospace industries where the focus is on human size, shape, and anatomy. Research by these professionals might range from studies of how the human body reacts to car crashes to exploring how to make seats more comfortable. Other non-academic positions can be obtained in museums of natural history, anthropology, archaeology, or science and technology. These positions involve educating students from grade school through graduate school. Physical anthropologists serve as education coordinators, collection managers, writers for museum publications, and as administrators. Zoos employ these professionals, especially if they have an expertise in primate biology; they work in collection management and captive breeding programs for endangered species. Forensic science utilizes physical anthropology expertise in identifying human and animal remains, assisting in determining the cause of death, and for expert testimony in trials.

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13.28: Cerego- Animal Diversity

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for Animal Diversity. You'll need to create a free log-in to practice these items, if you haven't already.

https://cerego.com/sets/796514/learn

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CHAPTER OVERVIEW

14: Module 11- Invertebrates

14.1: Why It Matters- Invertebrates
14.2: Introduction to Phylum Porifera
14.3: Morphology of Sponges
14.4: Physiological Processes in Sponges
14.5: Introduction to Phylum Cnidaria
14.6: Characteristics of Phylum Cnidaria
14.7: Classes in the Phylum Cnidaria
14.8: Introduction to Superphylum Lophotrochozoa
14.9: Characteristics of Superphylum Lophotrochozoa
14.10: Phylum Platyhelminthes
14.11: Phylum Rotifera
14.12: Phylum Nemertea
14.13: Phylum Mollusca
14.14: Phylum Annelida
14.15: Introduction to Superphylum Ecdysozoa
14.16: Phylum Nematoda
14.17: Nematodes in Research
14.18: Phylum Arthropoda
14.19: Subphylums of Arthropoda
14.20: Introduction to Superphylum Deuterostomia
14.21: Characteristics of Superphylum Deuterostomia
14.22: Phylum Echinodermata
14.23: Putting It Together- Invertebrates
14.24: Cerego- Invertebrates

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14.1: Why It Matters- Invertebrates

Why classify different types of invertebrates?

Invertebrates make up the largest group of animals on earth. They're an incredibly diverse group, ranging from scorpions to octopuses to centipedes. Despite their vast diversity, some of their smallest members are the most interesting.

Animal owners often learn the hard way how difficult it can be to keep their pets flea-free and happy. One of the biggest concerns pet owners run into is the fact that outdoor treatments, while effective in killing fleas are also toxic to their pets or harmful to the plant life in their backyards. One solution to this problem is *Steinerma carpocapsae*, a type of nematode. *S. carpocapsae* is a natural predator of fleas. Applying a spray populated with *S. carpocapsae* in the outdoor areas your pet spends time in can have dramatic effects, without putting your animal at risk.[1]



Figure 1. *Ancylostoma caninum*, a type of hookworm, attached to the intestinal mucosa.

However, not all invertebrates are so beneficial. In fact, not even all nematodes are benign: hookworms, pinworms, and whipworms are all parasites that can infect a human host. Hookworms make their way into the small intestine and feed off of human blood. While infections are typically asymptomatic, a serious infection can result in anemia and cause complications in pregnancy. Pinworms use humans to distribute their eggs, and can cause itching and insomnia in their hosts. Whipworms also use their hosts to distribute eggs, and while small infections are asymptomatic, a person infected with many worms may experience abdominal pain, tiredness, and diarrhea.

Learning Outcomes

- Identify the common characteristics of phylum Porifera
- Identify the common characteristics of phylum Cnidaria
- Identify the common characteristics of superphylum Lophotrochozoa
- Identify the common characteristics of superphylum Ecdysozoa
- Identify the common characteristics of superphylum Deuterostomia

1. Olesen, Jacob. "Beneficial Nematodes for Fleas – How They Work," *Fleabites.net*. http://www.fleabites.net/beneficial-nematodes-for-fleas-how-they-work/. ↵

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14.2: Introduction to Phylum Porifera

Identify the common characteristics of phylum Porifera



Figure 1. Sponges are members of the Phylum Porifera, which contains the simplest invertebrates. (credit: Andrew Turner)

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 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.

What You’ll Learn to Do

- Describe the organizational features of the simplest multicellular organisms
- Explain the various body forms and bodily functions of sponges

Learning Activities

The learning activities for this section include the following:

- Morphology of Sponges
- Physiological Processes in Sponges
- Self Check: Phylum Porifera

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14.3: 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.

Watch this video to see the movement of water through the sponge body.



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=510

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 1.

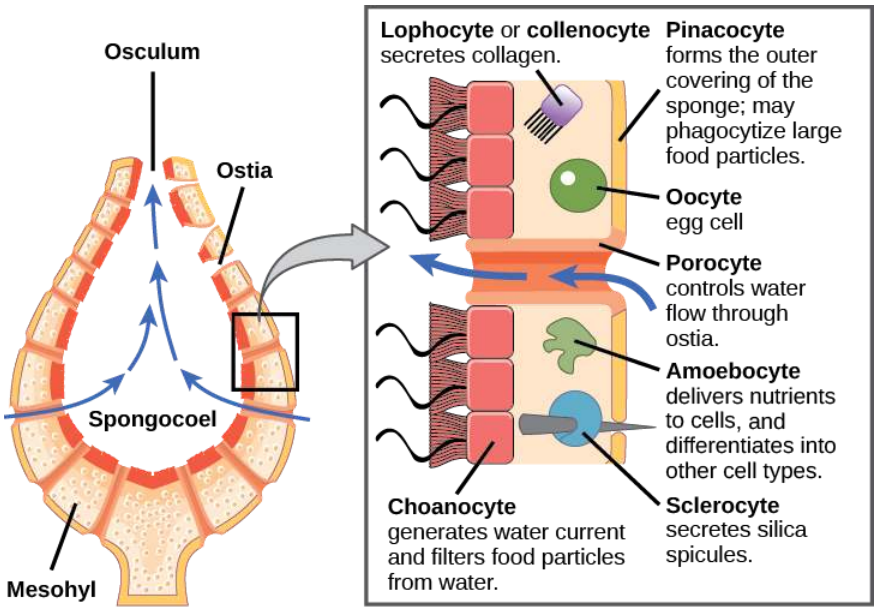


Figure 1. The sponge's (a) basic body plan and (b) some of the specialized cell types found in sponges are shown.

Practice Question

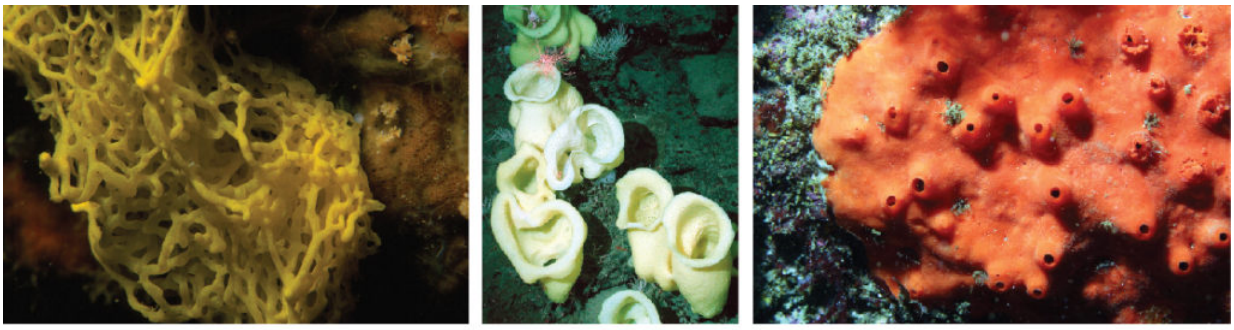
Which of the following statements is false?

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.

[reveal-answer q="651191"]Show Answer[/reveal-answer]
[hidden-answer a="651191"]Statement b is false.[/hidden-answer]

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 (shown in Figure 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 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)

Use the Interactive Sponge Guide to identify species of sponges based on their external form, mineral skeleton, fiber, and skeletal architecture.

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- Amazing footage of sponges pumping!. **Authored by**: BlueWorldTV. **Located at**: https://youtu.be/pTZ211cIjX8. **License**: *All Rights Reserved*. **License Terms**: Standard YouTube License

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14.4: 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.

Watch this BBC video showing the array of sponges seen along the Cayman Wall during a submersible dive.

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14.5: Introduction to Phylum Cnidaria

Identify the common characteristics of phylum Cnidaria

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.

What You'll Learn to Do

- Identify common structural and organization characteristics of the phylum Cnidaria
- Identify the features of animals classified in class Anthozoa
- Identify the features of animals classified in class Scyphozoa
- Identify the features of animals classified in class Cubozoa
- Identify the features of animals classified in class Hydrozoa

Learning Activities

The learning activities for this section include the following:

- Characteristics of Phylum Cnidaria
- Classes in the Phylum Cnidaria
- Self Check: Phylum Cnidaria

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14.6: Characteristics of 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. 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 1) or ensnare it. These coiled threads release toxins into the target and can often immobilize prey or scare away predators.

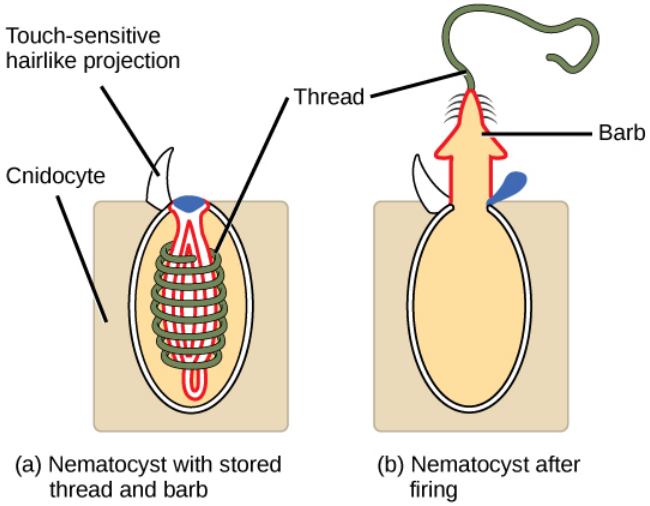


Figure 1. Animals from the phylum Cnidaria have stinging cells called cnidocytes. Cnidocytes contain large organelles called (a) nematocysts that store a coiled thread and barb. When hairlike projections on the cell surface are touched, (b) the thread, barb, and a toxin are fired from the organelle.

View this video animation showing two anemones engaged in a battle.



A Vimeo element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=516

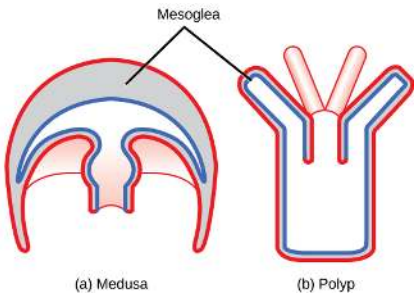


Figure 2. Cnidarians have two distinct body plans, the medusa (a) and the polyp (b). All cnidarians have two membrane layers, with a jelly-like mesoglea between them.

Animals in this phylum display two distinct morphological body plans: **polyp** or “stalk” and **medusa** or “bell” (Figure 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.

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 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.

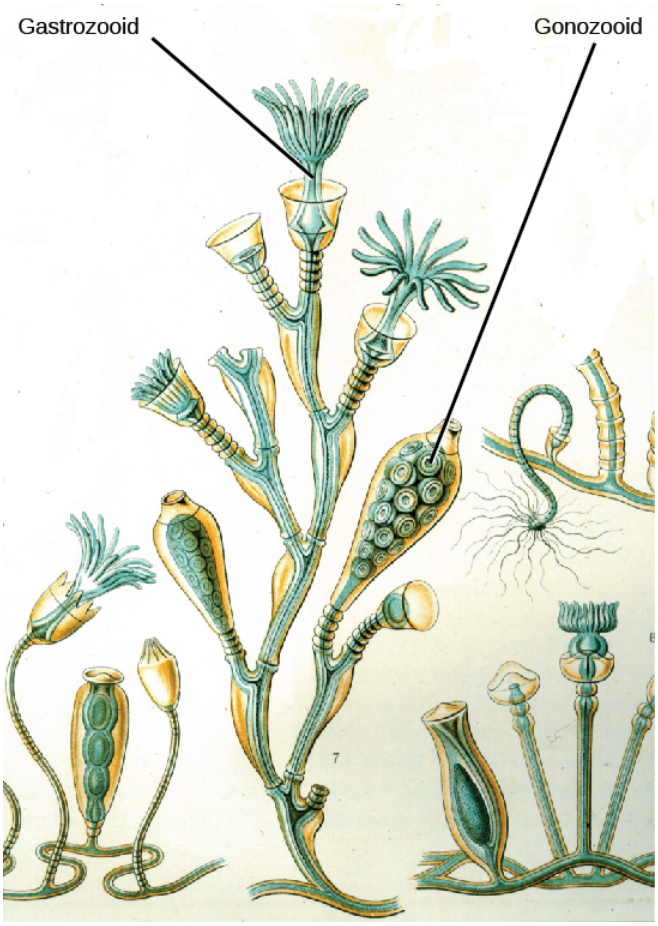


Figure 3. The sessile form of Obelia geniculate has two types of polyps: gastrozooids, which are adapted for capturing prey, and gonozooids, which bud to produce medusae asexually.

Click here to follow the life cycle of the *Obelia.*

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 **extracellulardigestion** in which the food is taken into the **gastrovascularcavity**, 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.

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14.7: Classes in the Phylum Cnidaria

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 1), 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.

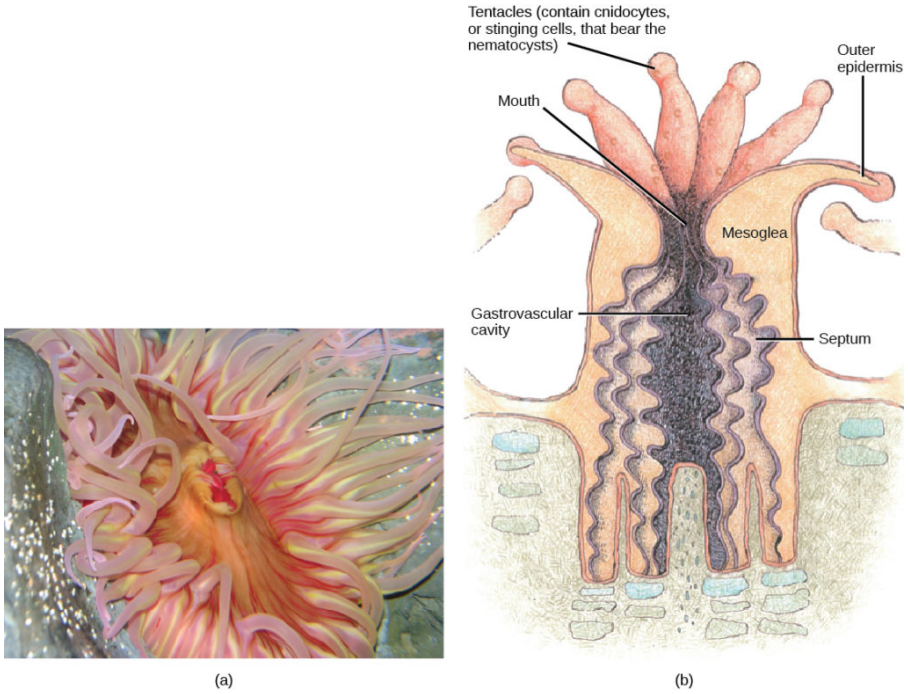


Figure 1. The sea anemone is shown (a) photographed and (b) in a diagram illustrating its morphology. (credit a: modification of work by “Dancing With Ghosts”/Flickr; credit b: modification of work by NOAA)

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 2).

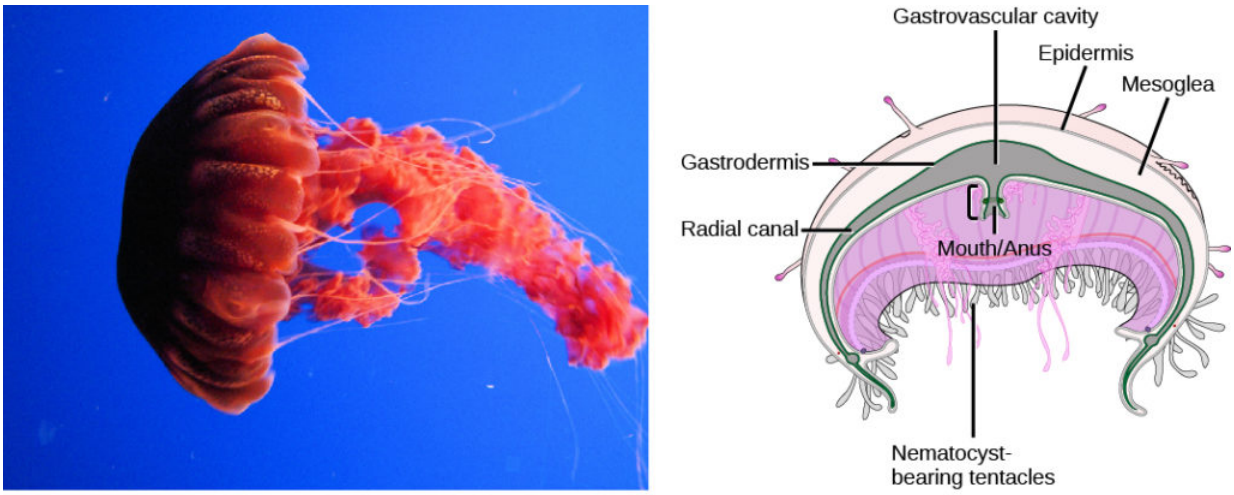


Figure 2. A jelly is shown (a) photographed and (b) in a diagram illustrating its morphology. (credit a: modification of work by "Jimg944"/Flickr; credit b: modification of work by Mariana Ruiz Villareal)

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 3) 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.

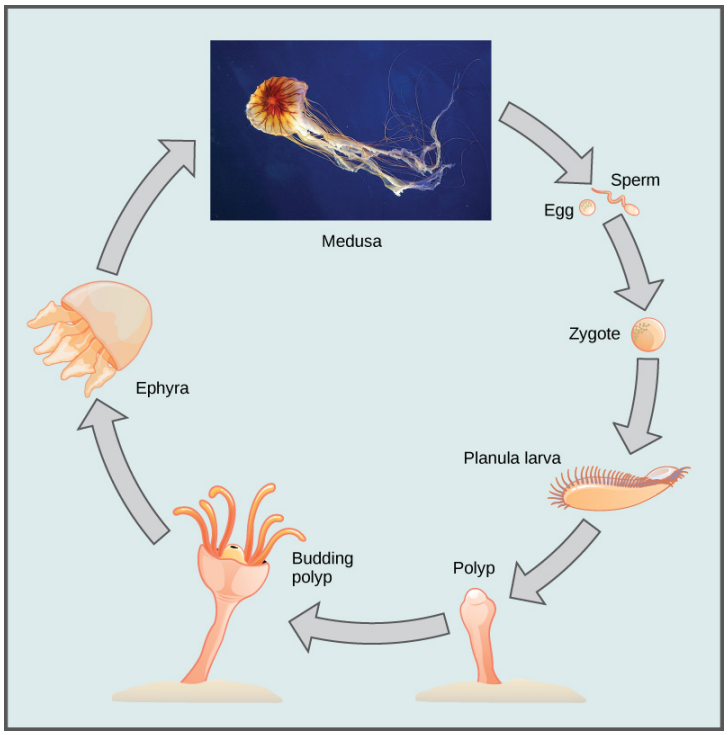


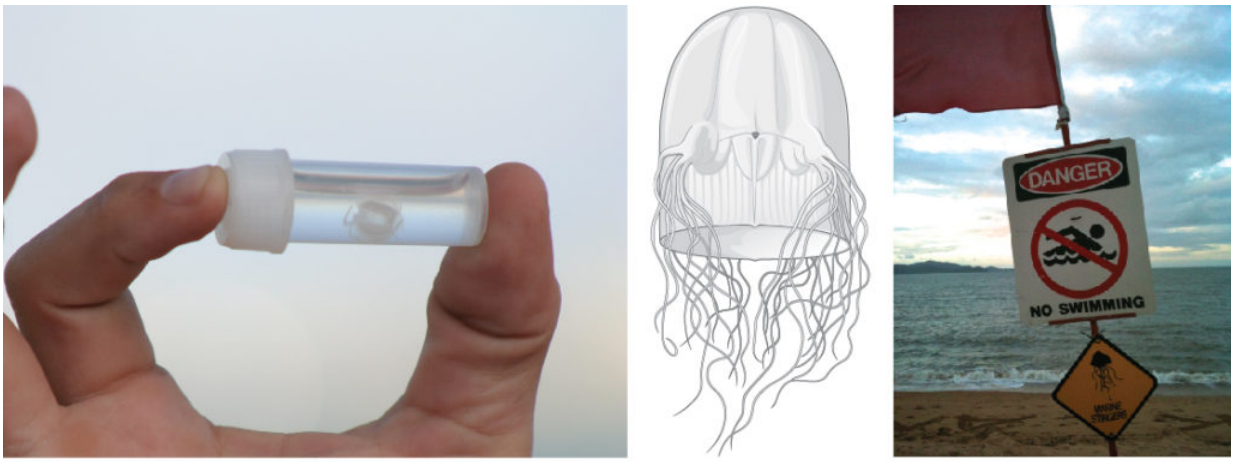
Figure 3. The lifecycle of a jellyfish includes two stages: the medusa stage and the polyp stage. The polyp reproduces asexually by budding, and the medusa reproduces sexually. (credit “medusa”: modification of work by Francesco Crippa)

Identify the life cycle stages of jellies using this video animation quiz from the New England Aquarium.

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 4).

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.



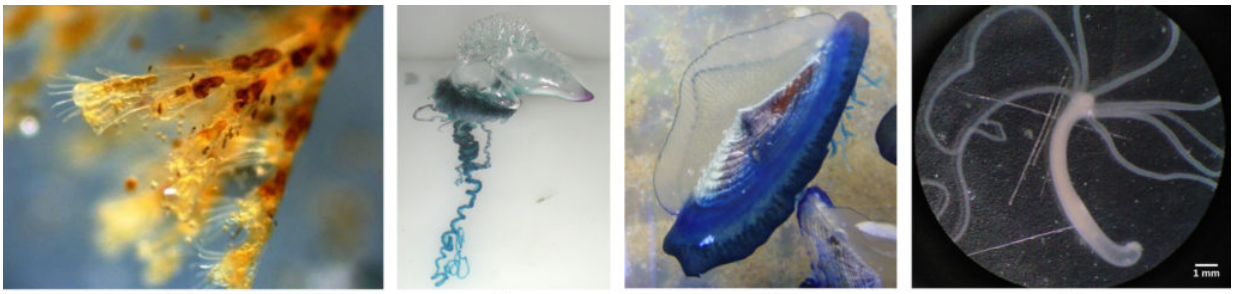
(a) (b) (c)

Figure 4. 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). 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) (b) (c) (d)

Figure 5. (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)

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14.8: Introduction to Superphylum Lophotrochozoa

Identify the common characteristics of superphylum Lophotrochozoa

There are five phyla in the superphylum Lophotrochozoa (also known as the crest or wheel animals): Platyhelminthes, Rotifera, Nemertea, Mollusca, and Annelida. These phyla include animals from flatworms to squids. While these may seem like very different creatures, they share characteristics that place them together in the tree of life. Let's figure out just what makes these animals part of the same superphylum.

What You'll Learn to Do

- Identify common structural and organization characteristics of the superphylum Lophotrochozoa
- Describe the unique anatomical and morphological features of flatworms
- Describe the unique anatomical and morphological features of rotifers
- Describe the unique anatomical and morphological features of Nemertea
- Describe the unique anatomical and morphological features of mollusks
- Describe the features of animals classified in phylum Annelida

Learning Activities

The learning activities for this section include the following:

- Characteristics of Superphylum Lophotrochozoa
- Phylum Platyhelminthes
- Phylum Rotifera
- Phylum Nemertea
- Phylum Mollusca
- Phylum Annelida
- Self Check: Superphylum Lophotrochozoa

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14.9: Characteristics of Superphylum Lophotrochozoa

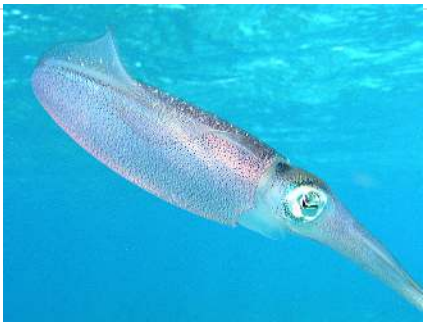


Figure 1. The Caribbean reef squid (*Sepioteuthis sepioidea*) is a complex lophotrochozoan.

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.

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14.10: 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 detach from the parents and therefore 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 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.

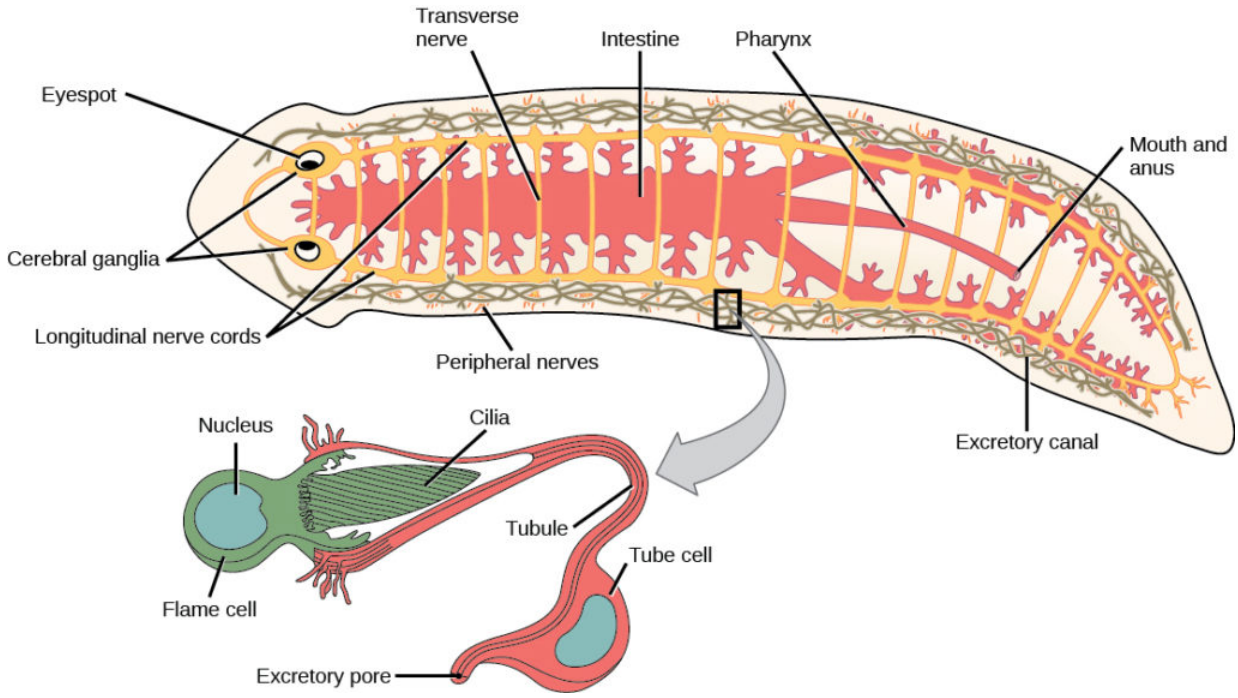


Figure 1. The planarian is a flatworm that has a gastrovascular cavity with one opening that serves as both mouth and anus. The excretory system is made up of tubules connected to excretory pores on both sides of the body. The nervous system is composed of two interconnected nerve cords running the length of the body, with cerebral ganglia and eyespots at the anterior end.

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.

Diversity of Flatworms

Platyhelminthes are traditionally divided into four classes: Turbellaria, Monogenea, Trematoda, and Cestoda (Figure 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.

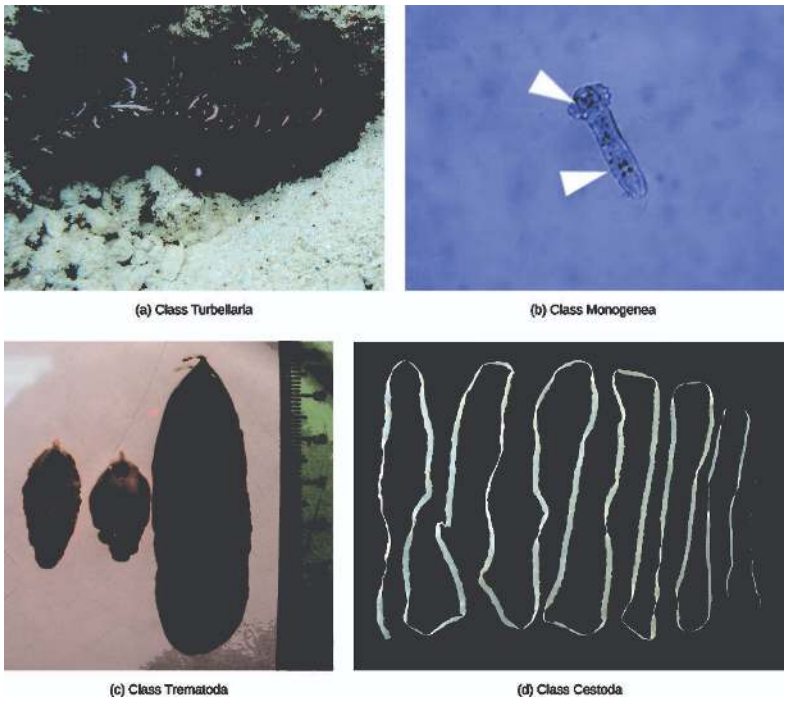


Figure 2. Phylum Platyhelminthes is divided into four classes. (a) Class Turbellaria includes the Bedford's flatworm (*Pseudobiceros bedfordi*), which is about 8–10 cm in length. (b) The parasitic class Monogenea includes *Dactylogyrus spp. Dactylogyrus*, commonly called a gill fluke, is about 0.2 mm 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 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.

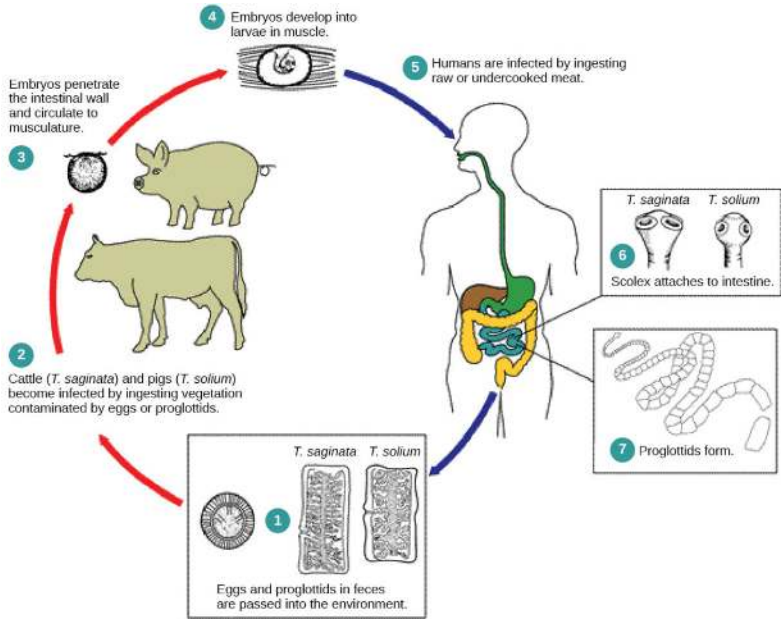


Figure 3. Tapeworm (*Taenia spp.*) infections occur when humans consume raw or undercooked infected meat. (credit: modification of work by CDC)

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.

Learning Objectives

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.

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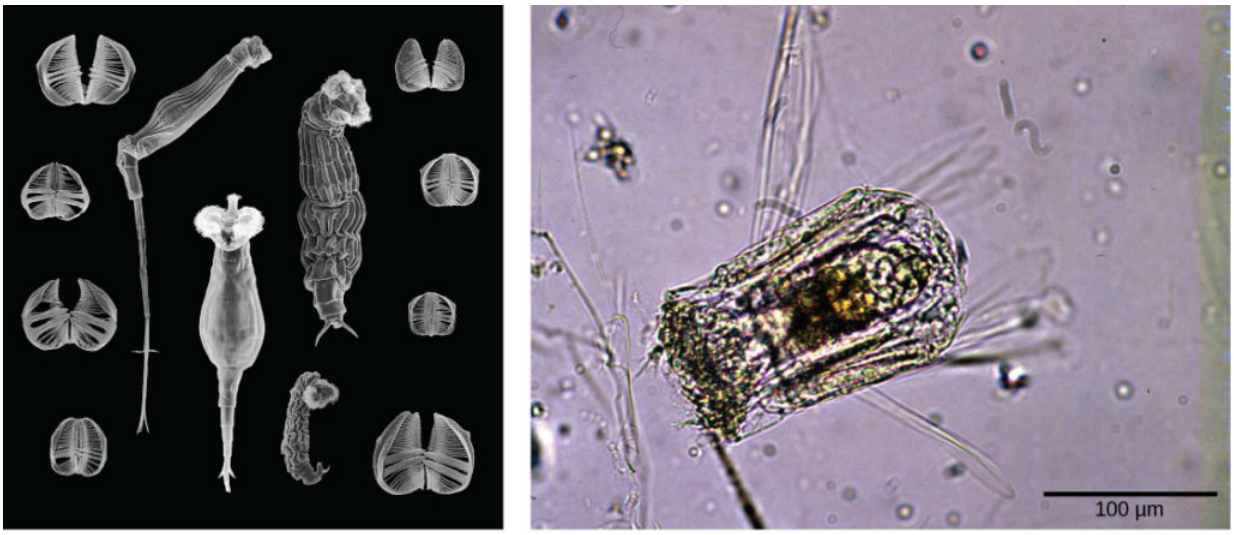
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14.11: Phylum Rotifera

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 1). 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.

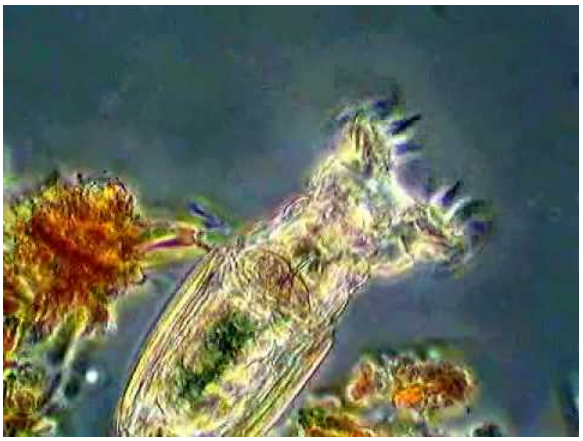


(a) Bdelloidea (a) Monogonota

Figure 1. 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.

Watch the video below to see rotifers feeding. Note that this video has no audio.



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=527

Rotifers are pseudocoelomates commonly found in fresh water and some salt water environments throughout the world. Figure 2 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.

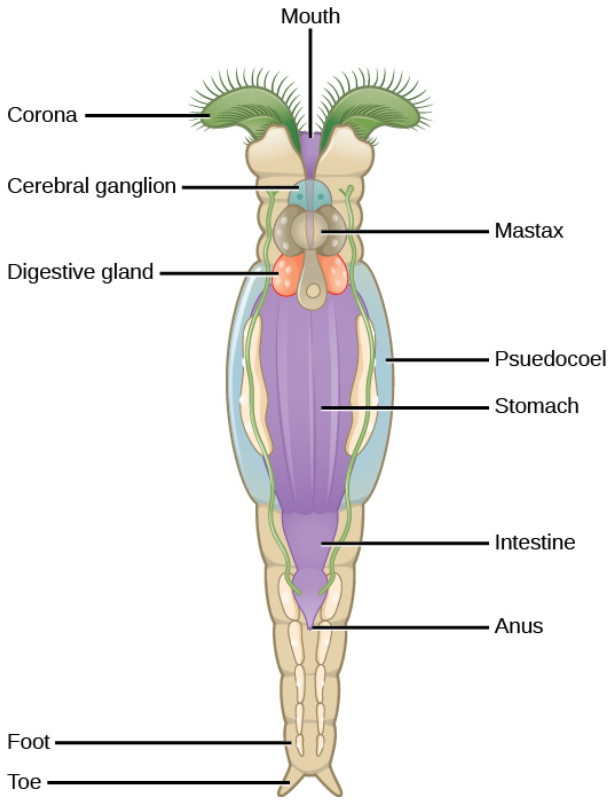


Figure 2. This illustration shows the anatomy of a bdelloid rotifer.

In Summary: Phylum Rotifera

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.

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14.12: 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

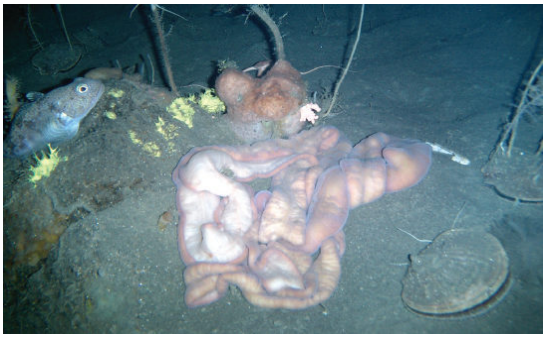


Figure 1. The proboscis worm (*Parborlasia corrugatus*) is a scavenger that combs the sea floor for food. The species is a member of the phylum Nemertea. The specimen shown here was photographed in the Ross Sea, Antarctica. (credit: Henry Kaiser, National Science Foundation)

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 1).

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 2). The proboscis may be extended or retracted by the retractor muscle attached to the wall of the rhynchocoel.

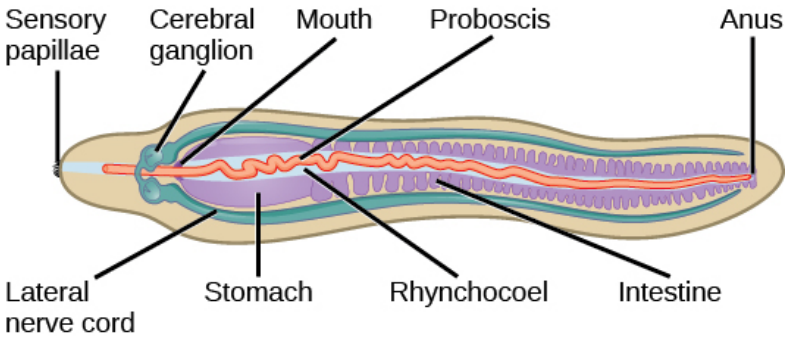


Figure 2. The anatomy of a Nemertean is shown.

Watch the video below to see a nemertean attack a polychaete with its proboscis.

A link to an interactive elements can be found at the bottom of this page.

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.

Learning Objectives

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.

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14.13: 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 1).

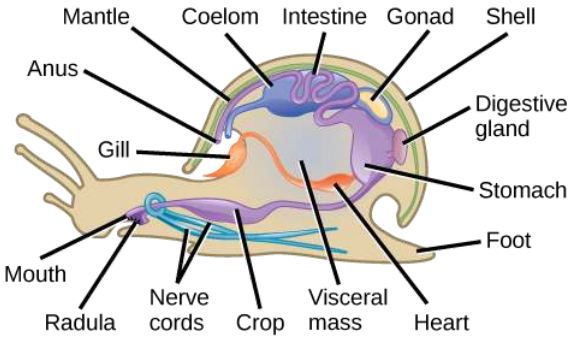


Figure 1. There are many species and variations of mollusks; this illustration shows the anatomy of an aquatic gastropod.

? Practice Questions

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.

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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.



Figure 2. This chiton from the class Polyplacaphora has the eight-plated shell that is indicative of its class. (credit: Jerry Kirkhart)

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 2). 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 3. These mussels, found in the intertidal zone in Cornwall, England, are bivalves. (credit: Mark A. Wilson)

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 3). The overall morphology is laterally flattened, and the head region is poorly developed. Eyespots and statocysts may be absent in some species. These animals are suspension feeders—they eat material, such as plankton, that is suspended in the water around them. Due to their diet, this class of mollusks lacks a radula. 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.

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.

Watch this animation of mussels feeding.

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 4). 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.



Figure 4. (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). 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.

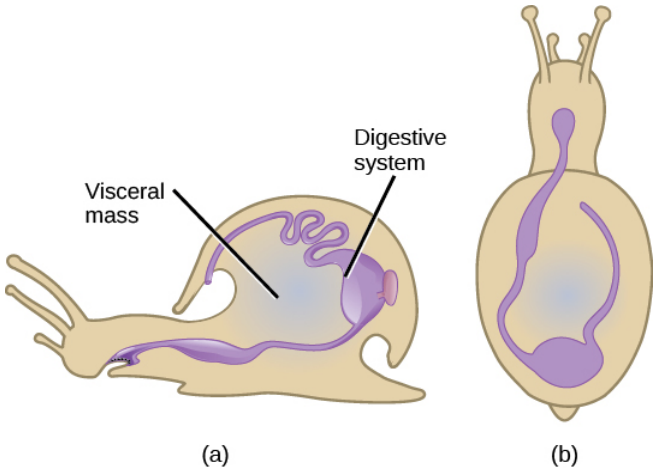


Figure 5. During embryonic development of gastropods, the visceral mass undergoes torsion, or counterclockwise rotation of anatomical features. As a result, the anus of the adult animal is located over the head. Torsion is an independent process from coiling of the shell.

? Try It



Figure 6. Members of the genus Conus produce neurotoxins that may one day have medical uses. (credit: David Burdick, NOAA)

Marine snails of the genus *Conus* (Figure 6) 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.

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 7.

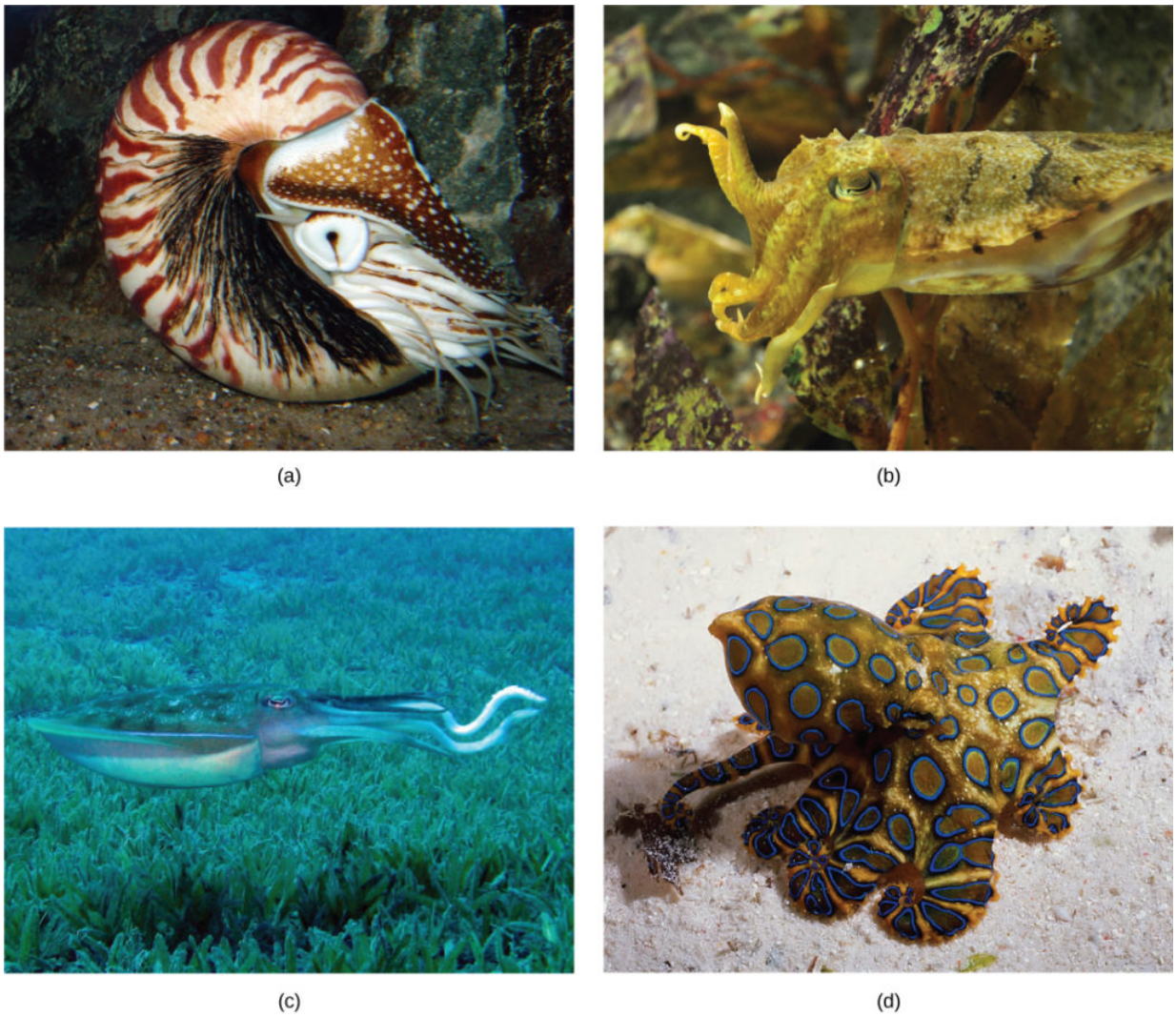


Figure 7. The (a) nautilus, (b) giant cuttlefish, (c) reef squid, and (d) blue-ring octopus are all members of the class Cephalopoda. (credit a: modification of work by J. Baecker; credit b: modification of work by Adrian Mohedano; credit c: modification of work by Silke Baron; credit d: modification of work by Angell Williams)



Figure 8. *Antalis vulgaris* shows the classic Dentaliidae shape that gives these animals their common name of "tusk shell." (credit: Georges Jansoone)

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 8).

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.

Learning Objectives

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

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14.14: 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



Figure 1. 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)

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 1).

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 2; each segment is limited by a membranous septum that divides the coelomic cavity into a series of compartments.

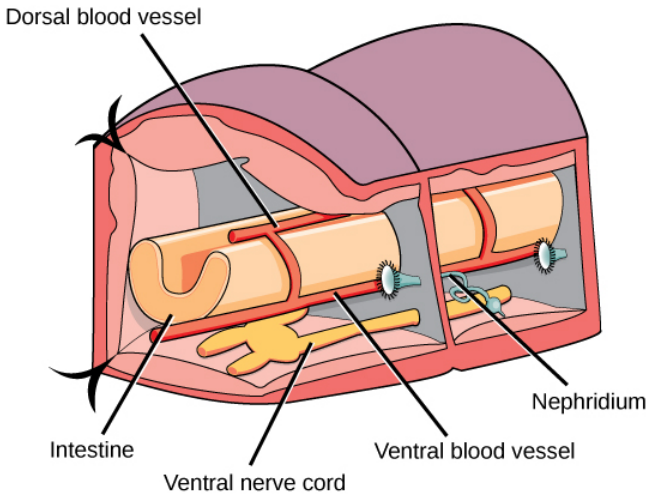


Figure 2. This schematic drawing shows the basic anatomy of annelids in a cross-sectional view.

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.

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.

This combination video and animation provides a closeup look at annelid anatomy.

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 3. 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)

Learning Objectives

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.

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14.15: Introduction to Superphylum Ecdysozoa

Identify the common characteristics of 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. 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.

What You'll Learn to Do

- Describe the features of animals classified in phylum Nematoda
- Understand the importance of nematodes like *Caenorhabditis elegans* in research
- Describe the features of animals classified in phylum Arthropoda
- Identify the different subphylums in phylum Arthropoda

Learning Activities

The learning activities for this section include the following:

- Phylum Nematoda
- Nematodes in Research
- Phylum Arthropoda
- Subphylums of Arthropoda
- Self Check: Superphylum Ecdysozoa

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14.16: 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 flatworms, 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 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.

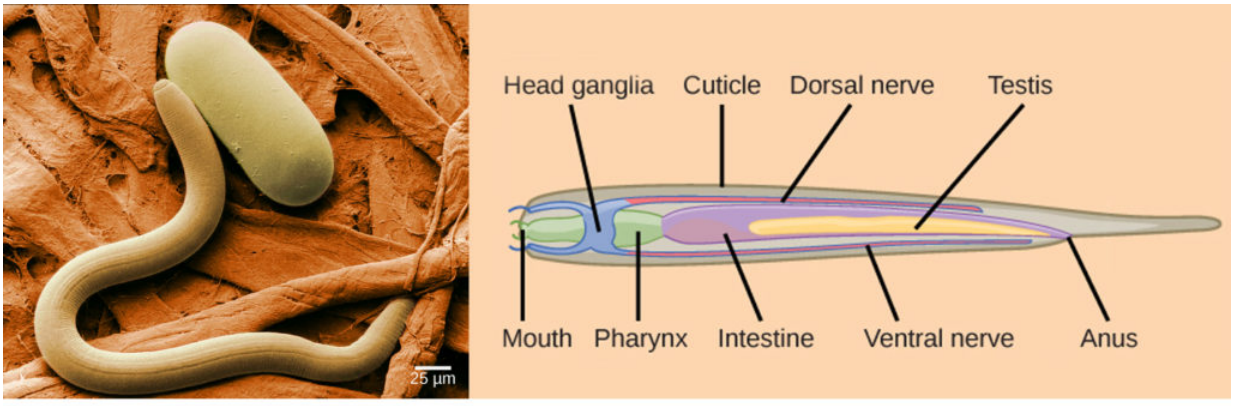


Figure 1. Scanning electron micrograph shows (a) the soybean cyst nematode (*Heterodera glycines*) and a nematode egg. (b) A schematic representation shows the anatomy of a typical nematode. (credit a: modification of work by USDA ARS; scale-bar data from Matt Russell)

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.

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1. Stoll, N. R., "This wormy world. 1947," *Journal of Parasitology* 85(3) (1999): 392–96. ↵

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14.17: Nematodes in Research

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). 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 1). 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.

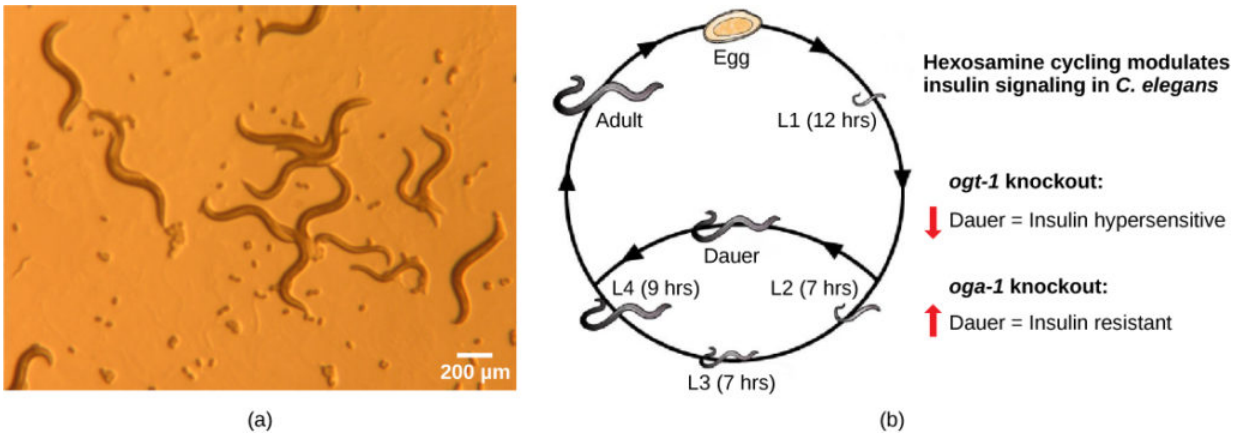


Figure 1. (a) This light micrograph shows *Caenorhabditis elegans*. Its transparent adult stage consists of exactly 959 cells. (b) The life cycle of *C. elegans* has four juvenile stages (L1 through L4) and an adult stage. Under ideal conditions, the nematode spends a set amount of time at each juvenile 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 2). 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.

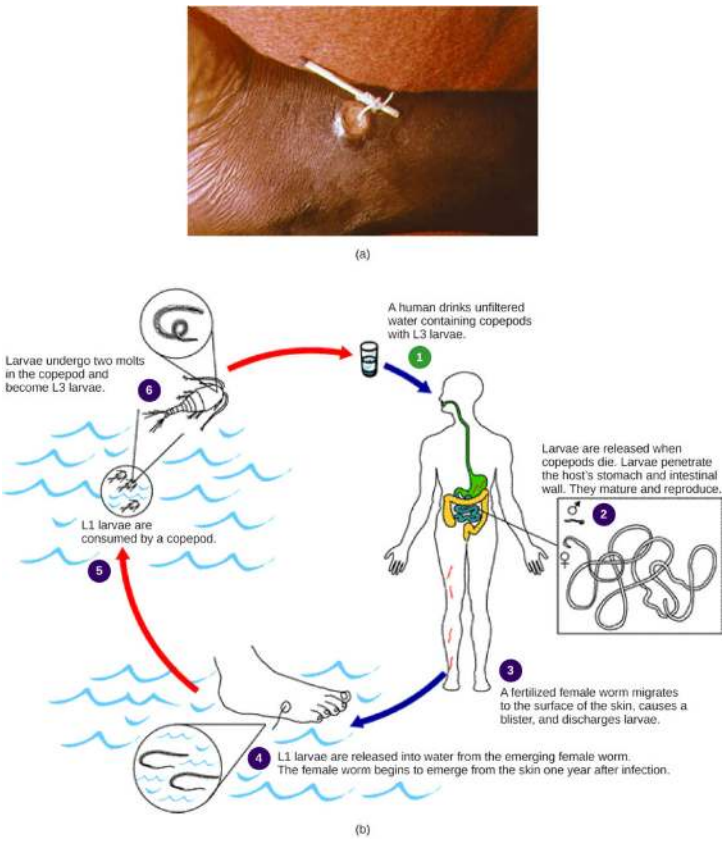


Figure 2. Click for a larger image. The guinea worm *Dracunculus medinensis* infects about 3.5 million people annually, mostly in Africa. (a) Here, the worm is wrapped around a stick so it can be extracted. (b) Infection occurs when people consume water contaminated by infected copepods, but this can easily be prevented by simple filtration systems. (credit: modification of work by CDC)

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14.18: 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.



Figure 1. Trilobites, like the one in this fossil, are an extinct group of arthropods. (credit: Kevin Walsh)

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 1).

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 2).

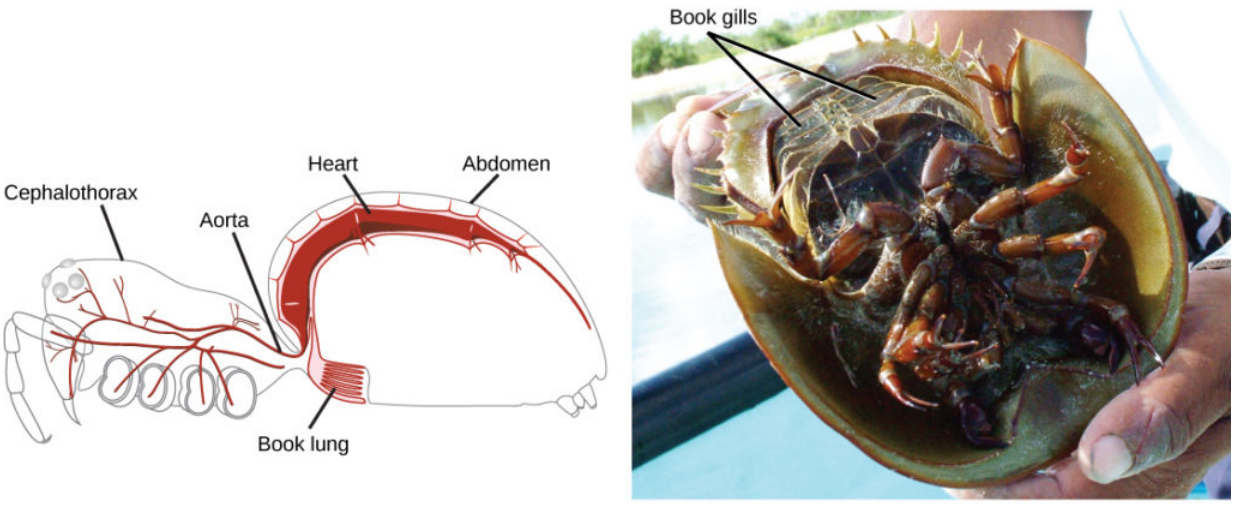


Figure 2. The book lungs of (a) arachnids are made up of alternating air pockets and hemocoel tissue shaped like a stack of books. The book gills of (b) crustaceans are similar to book lungs but are external so that gas exchange can occur with the surrounding water. (credit a: modification of work by Ryan Wilson based on original work by John Henry Comstock; credit b: modification of work by Angel Schatz)

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.

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14.19: Subphylums of Arthropoda

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.

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 1) 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).

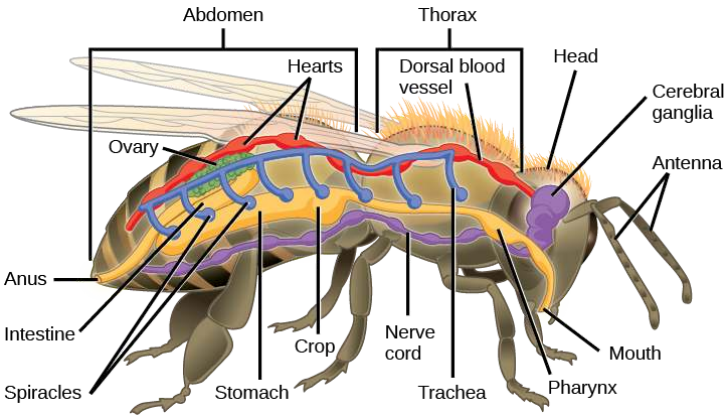


Figure 1. In this basic anatomy of a hexapod insect, note that insects have a developed digestive system (yellow), a respiratory system (blue), a circulatory system (red), and a nervous system (red).

? Practice Question

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.

[reveal-answer q="4825"]Show Answer[/reveal-answer]
[hidden-answer a="4825"]Statement c is false.[/hidden-answer]

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 2a) 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 2b).



Figure 2. (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)

Subphylum Crustacea

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 3). 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.



(a) (b)

Figure 3. 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 4).

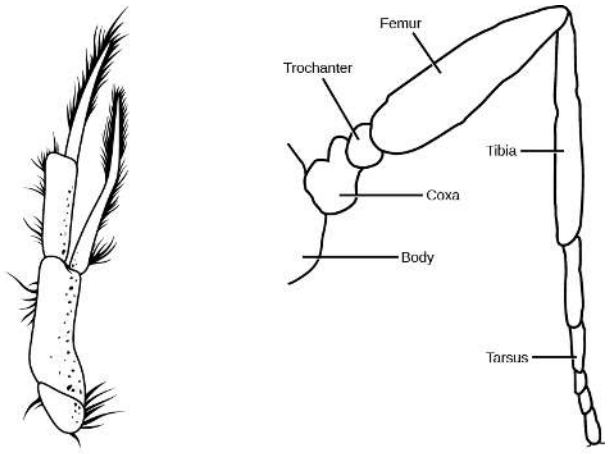


Figure 4. Arthropods may have (a) biramous (two-branched) appendages or (b) uniramous (one-branched) appendages. (credit b: modification of work by Nicholas W. Beeson)

Unlike that of the Hexapoda, the head and thorax of most crustaceans is fused to form a **cephalothorax** (Figure 5), 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.

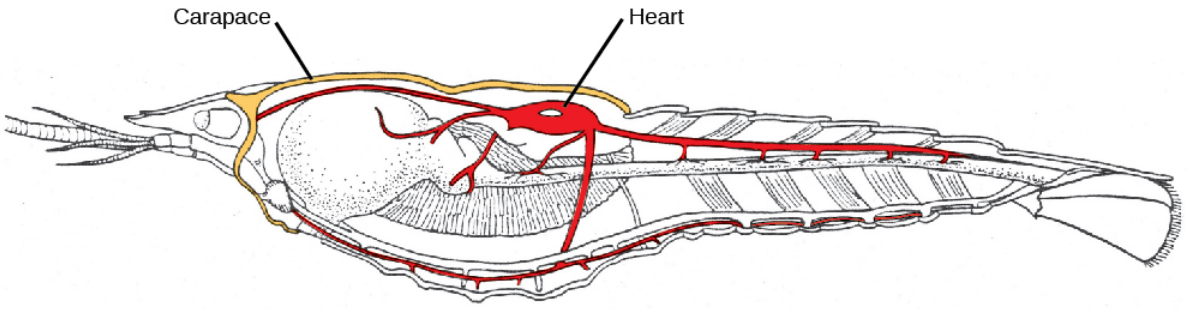
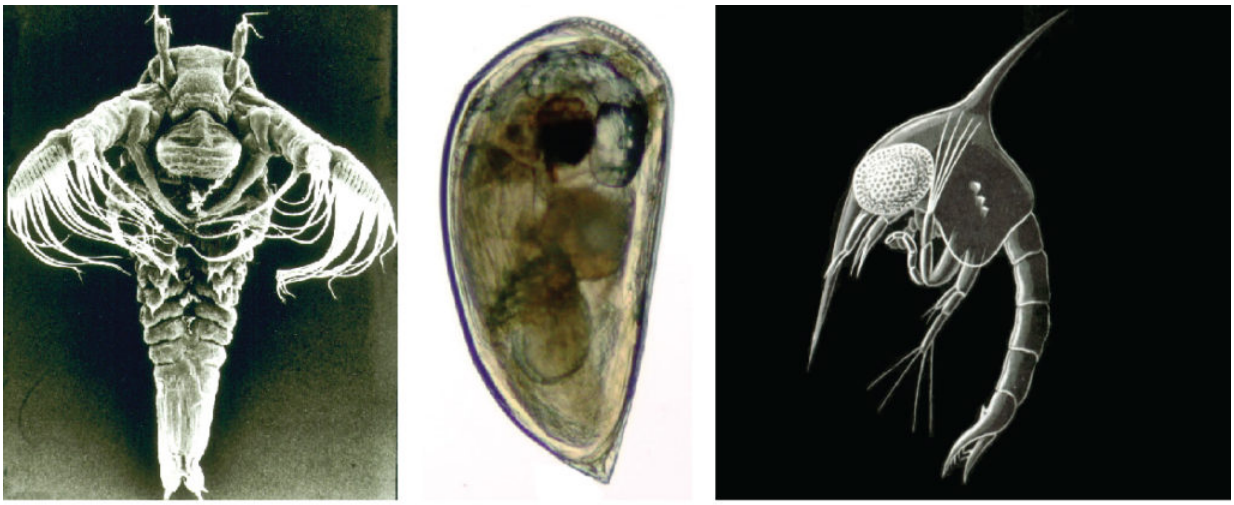


Figure 5. The crayfish is an example of a crustacean. It has a carapace around the cephalothorax and the heart in the dorsal thorax area. (credit: Jane Whitney)

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 6). 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.



(a) Nauplius larva of a tadpole shrimp (b) Cypris larva of a barnacle (c) Zoea larva of a green crab

Figure 6. 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)

Subphylum Chelicerata



Figure 7. The chelicerae (first set of appendages) are well developed in the scorpion. (credit: Kevin Walsh)

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 7), 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 8. The trapdoor spider, like all spiders, is a member of the subphylum Chelicerata. (credit: Marshal Hedin)

Chelicerae are mostly used for feeding, but in spiders, these are often modified into fangs that inject venom into their prey before feeding (Figure 8). 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.

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.

Visit this site to click through a lesson on arthropods, including interactive habitat maps, and more.

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14.20: Introduction to Superphylum Deuterostomia

Identify the common characteristics of superphylum Deuterostomia

Deuterostomia is a major subgroup of animals. It is comprised of two lineages, the **Chordata** and **Ambulacraria** (Edgecombe et al. 2011, Swalla & Smith 2008). Chordata consists of two exclusively marine groups, the fish-like lancelets (Cephalocordata) and the sea squirts, salps and relatives (Tunicata) as well as the vertebrates which include fishes, amphibians, reptiles, birds, and mammals. Ambulacraria contains the exclusively marine **echinoderms** (sea stars, brittle stars, sea urchins, sand dollars, sea cucumbers, and sea lilies) and **hemichordates** (soft-bodied benthic worm-like animals).

What You'll Learn to Do

- Identify the common characteristics of superphylum Deuterostomia
- Describe the distinguishing characteristics of chordates
- Describe the distinguishing characteristics of echinoderms
- Identify the different classes in phylum Echinodermata

Learning Activities

The learning activities for this section include the following:

- Characteristics of Superphylum Deuterostomia
- Phylum Echinodermata
- Self Check: Superphylum Deuterostomia

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14.21: Characteristics of 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. 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 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.

We will discuss the chordates in greater detail in a later module. For now, simply remember that most deuterostomes are chordates.

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14.22: Phylum Echinodermata

Characteristics of Echinoderms

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 1), sea cucumbers, sea urchins, sand dollars, and brittle stars are all examples of echinoderms. To date, no freshwater or terrestrial echinoderms are known.

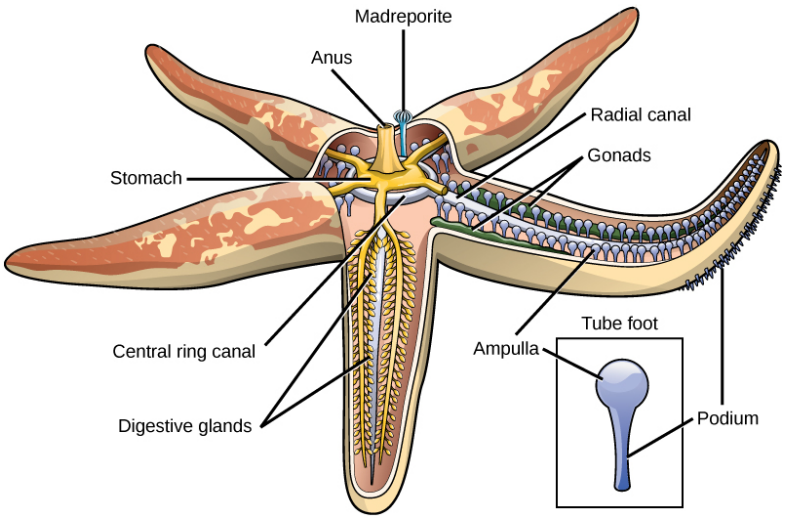


Figure 1. This diagram shows the anatomy of a sea star.

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.

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.

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 2).

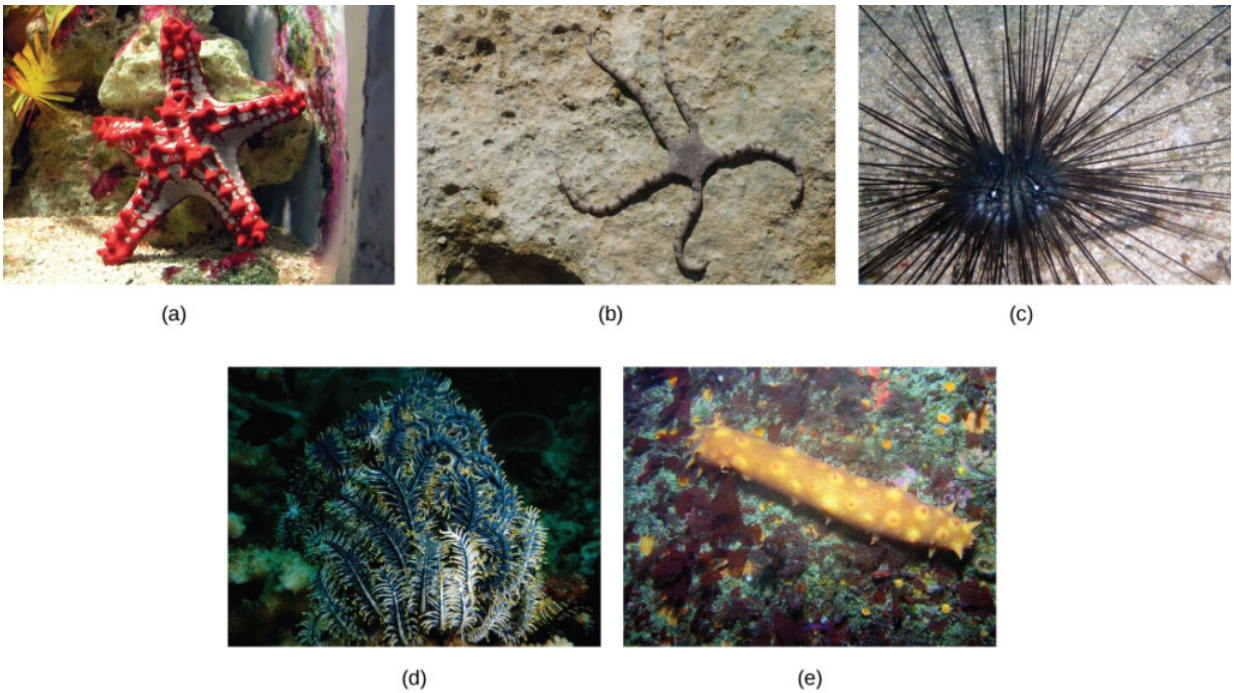


Figure 2. Different members of Echinodermata include the (a) sea star of class Asteroidea, (b) the brittle star of class Ophiuroidea, (c) the sea urchins of class Echinoidea, (d) the sea lilies belonging to class Crinoidea, and (d) sea cucumbers, representing class Holothuroidea. (credit a: modification 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)

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.

Explore the sea star's body plan up close, watch one move across the sea floor, and see it devour a mussel.

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.

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14.23: Putting It Together- Invertebrates

As we've seen, invertebrates include a broad scope of animals, from the simplest of animals—the sponges—to the complex arthropods and annelids. As you review the phyla we've discussed in this lesson, remember the characteristics that set apart each phyla. Remember: animals are grouped together based on their structure and appearance.

Simple Animals

This video introduces us to the "simplest" of the animals. We differentiate animals by the number of tissue layers they have, and by the complexity of those layers.



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Complex Animals

This video continues our exploration of invertebrates. We discuss the more complex annelids and arthropods.



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14.24: Cerego- Invertebrates

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for Invertebrates. You'll need to create a free log-in to practice these items, if you haven't already.

https://cerego.com/sets/796515/learn

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CHAPTER OVERVIEW

15: Module 12- Vertebrates

15.1: Why It Matters- Vertebrates
15.2: Introduction to Chordates
15.3: Characteristics of Chordates
15.4: Invertebrate Chordates
15.5: Craniates
15.6: Introduction to Fishes
15.7: Jawless Fishes
15.8: Jawed Fishes
15.9: Introduction to Amphibians
15.10: Amphibians
15.11: The Life Cycle of Amphibians
15.12: Clades of Amphibians
15.13: Introduction to Amniotes
15.14: Amniotic Animals
15.15: Evolution of Amniotes
15.16: Introduction to Reptiles
15.17: Characteristics of Reptiles
15.18: Classes of Reptiles
15.19: Evolutionary History of Reptiles
15.20: Introduction to Birds
15.21: Characteristics of Birds
15.22: Evolutionary History of Birds
15.23: Introduction to Mammals
15.24: Mammals
15.25: Primates
15.26: Evolution of Humans
15.27: Putting It Together- Vertebrates
15.28: Cerego- Vertebrates

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15.1: Why It Matters- Vertebrates

Why classify different types of 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.

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.

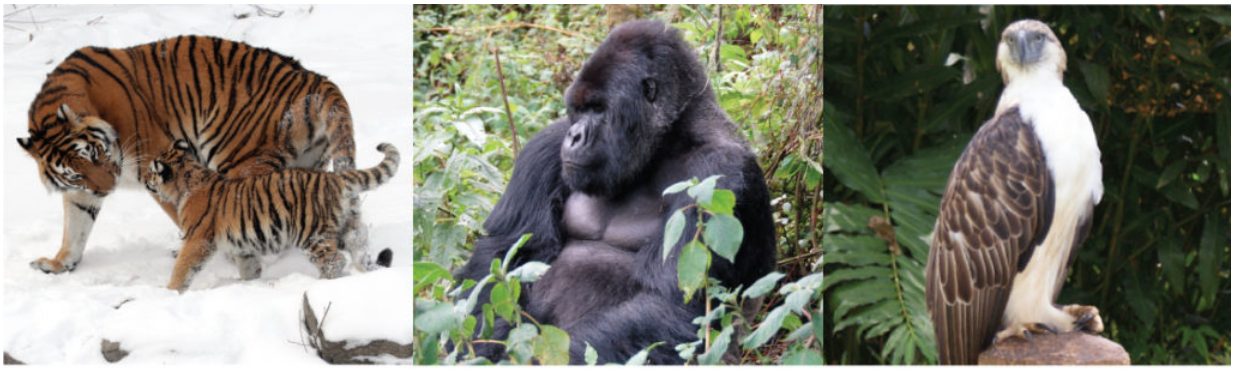


Figure 1. Examples of critically endangered vertebrate species include (a) the Siberian tiger (*Panthera tigris*), (b) the mountain gorilla (*Gorilla beringei*), and (c) the Philippine eagle (*Pithecophega jefferyi*). (credit a: modification of work by Dave Pape; credit b: modification of work by Dave Proffer; credit c: modification of work by "cuatrok77″/Flickr)

Additionally, most of our pets are vertebrates: birds, snakes, cats, dogs, etc. Human beings love their animal companions, and it's important to understand them and their needs.

Learning Outcomes

- Identify the common characteristics of chordates
- Identify characteristics of fishes
- Identify characteristics of amphibians
- Identify characteristics of amniotes
- Identify characteristics of reptiles
- Identify characteristics of birds
- Identify characteristics of mammals

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15.2: Introduction to Chordates

Identify the common characteristics of chordates

Vertebrates are members of the kingdom Animalia and the phylum Chordata. 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.

What You’ll Learn to Do

- Describe the distinguishing characteristics of chordates
- Discuss the invertebrate chordate lineages
- Identify the derived character of craniates that sets them apart from other chordates

Learning Activities

The learning activities for this section include the following:

- Characteristics of Chordates
- Invertebrate Chordates
- Craniates
- Self Check: Chordates

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15.3: Characteristics of Chordates

Vertebrates are members of the kingdom Animalia and the phylum Chordata (Figure 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.

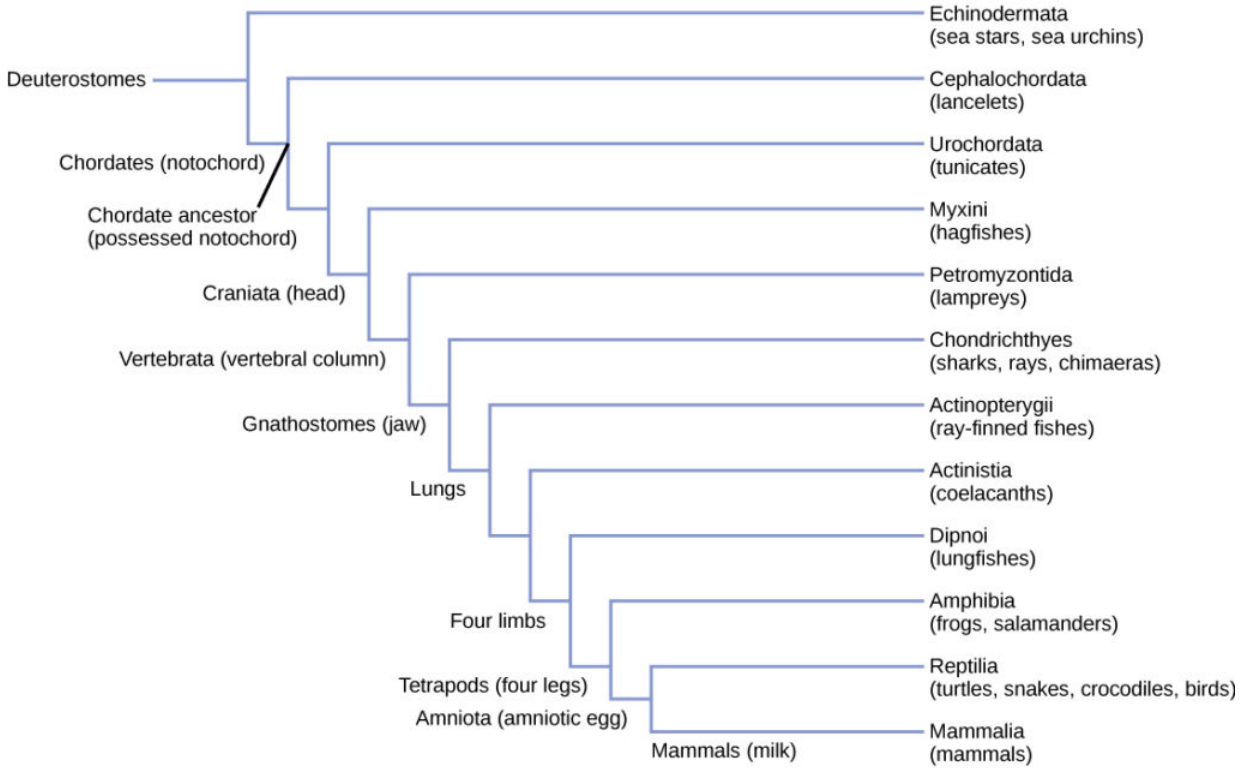


Figure 1. All chordates are deuterostomes possessing a notochord.

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 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).

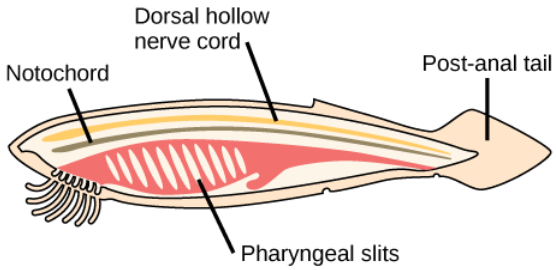


Figure 2. In chordates, four common features appear at some point during development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail.

? Practice Question

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.

[reveal-answer q="97577"]Show Answer[/reveal-answer]
[hidden-answer a="97577"]Statement a is true.[/hidden-answer]

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.

Watch this video discussing the evolution of chordates and five characteristics that they share.

A link to an interactive elements can be found at the bottom of this page.

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15.4: Invertebrate Chordates

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 1). 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.

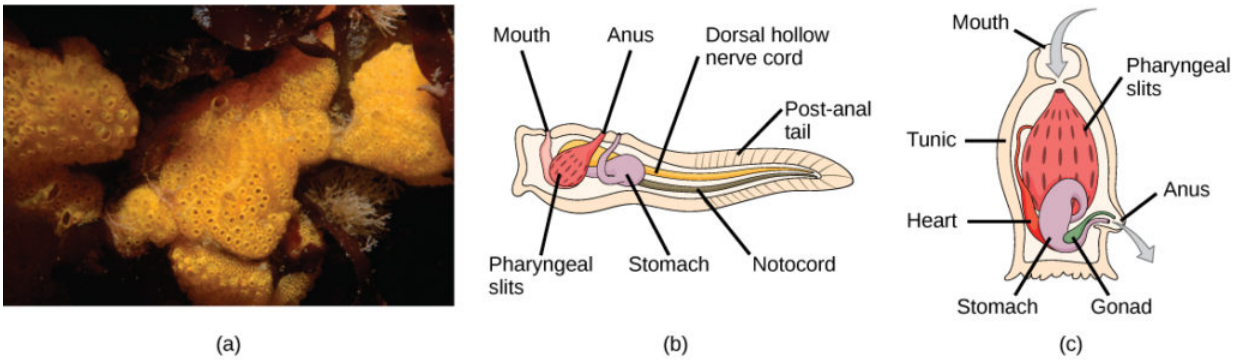


Figure 1. (a) This photograph shows a colony of the tunicate *Botrylloides violaceus*. (b) The larval stage of the tunicate possesses all of the features characteristic of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. (c) In the adult stage, the notochord, 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 2). 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.

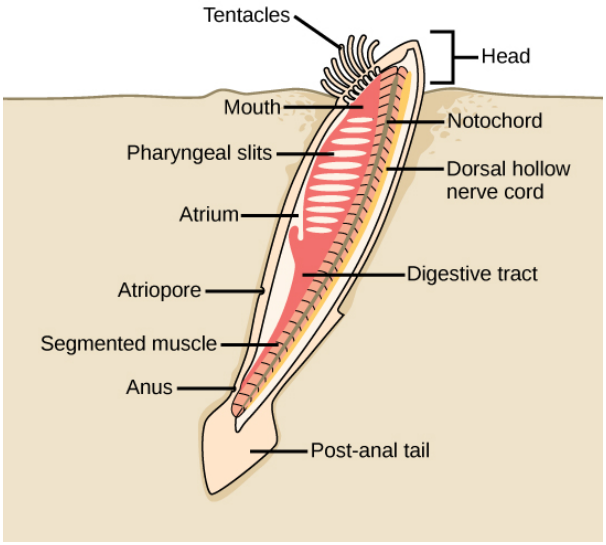


Figure 2. The lancelet, like all cephalochordates, has a head. Adult lancelets retain the four key features of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Water from the mouth enters the pharyngeal slits, which filter out food particles. The filtered water then collects in the atrium and exits through the atriopore.

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15.5: Craniates

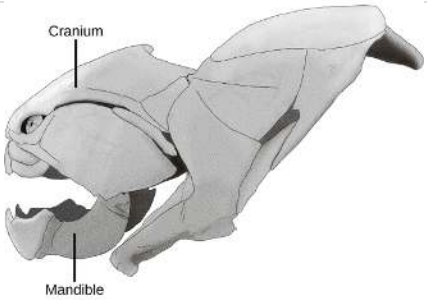


Figure 1. Craniata, including this fish (*Dunkleosteus sp.*), are characterized by the presence of a cranium, mandible, and other facial bones. (credit: “Steveoc 86”/Wikimedia Commons)

A **cranium** is a bony, cartilaginous, or fibrous structure surrounding the brain, jaw, and facial bones (Figure 1). 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.”

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 2). In adult vertebrates, the vertebral column replaces the notochord, which is only seen in the embryonic stage.

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.

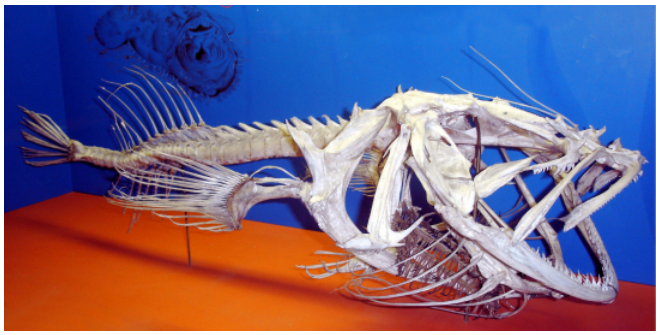


Figure 2. Vertebrata are characterized by the presence of a backbone, such as the one that runs through the middle of this fish. All vertebrates are in the Craniata clade and have a cranium. (credit: Ernest V. More; taken at Smithsonian Museum of Natural History, Washington, D.C.)

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.

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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. ↵

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15.6: Introduction to Fishes

Identify characteristics of 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.

What You'll Learn to Do

- Identify the common characteristics of jawless fishes
- Identify the common characteristics of jawed fishes

Learning Activities

The learning activities for this section include the following:

- Jawless Fishes
- Jawed Fishes
- Self Check: Fishes

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15.7: 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



Figure 1. Pacific hagfish are scavengers that live on the ocean floor. (credit: Linda Snook, NOAA/CBNMS)

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 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.

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



Figure 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)

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 2).

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.

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15.8: 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.



Figure 1. 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)

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 1), which arose in the late Silurian period and are now extinct. Most modern fishes are gnathostomes that belong to the clades Chondrichthyes and Osteichthyes.

Chondrichthyes: Cartilaginous Fishes

The clade **Chondrichthyes** is diverse, consisting of sharks (Figure 2), 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.



Figure 2. Hammerhead sharks tend to school during the day and hunt prey at night. (credit: Masashi Sugawara)

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.

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.



Figure 3. Shark embryos are clearly visible through these transparent egg cases. The round structure is the yolk that nourishes the growing embryo. (credit: Jek Bacarisas)

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 3) 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 4. This stingray blends into the sandy bottom of the ocean floor. (credit: "Sailn1"/Flickr)

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 4). Like sharks, rays and skates have a cartilaginous skeleton. Most species are marine and live on the sea floor, with nearly a worldwide distribution.

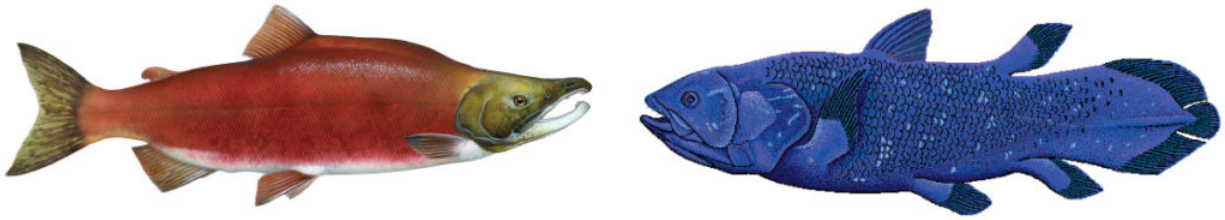
Osteichthyes: Bony Fishes

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 5a), 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 5b). Living members of this clade include the less-familiar lungfishes and coelacanths.



(a) (b)

Figure 5. 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)

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15.9: Introduction to Amphibians

Identify characteristics 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.

What You’ll Learn to Do

- Identify characteristics of amphibians
- Describe the evolutionary history of amphibians
- 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

Learning Activities

The learning activities for this section include the following:

- Amphibians
- The Life Cycle of Amphibians
- Clades of Amphibians
- Self Check: Amphibians

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15.10: Amphibians

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.

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. 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.

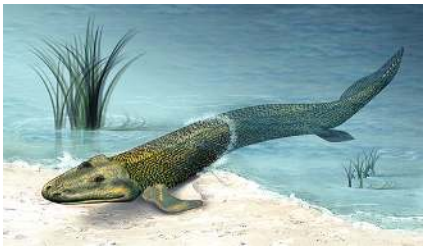


Figure 1. The recent fossil discovery of *Tiktaalik roseae* suggests evidence for an animal intermediate to finned fish and legged tetrapods. (credit: Zina Deretsky, National Science Foundation)

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 1). *Tiktaalik* likely lived in a shallow water environment about 375 million years ago.

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.

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 2). 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.

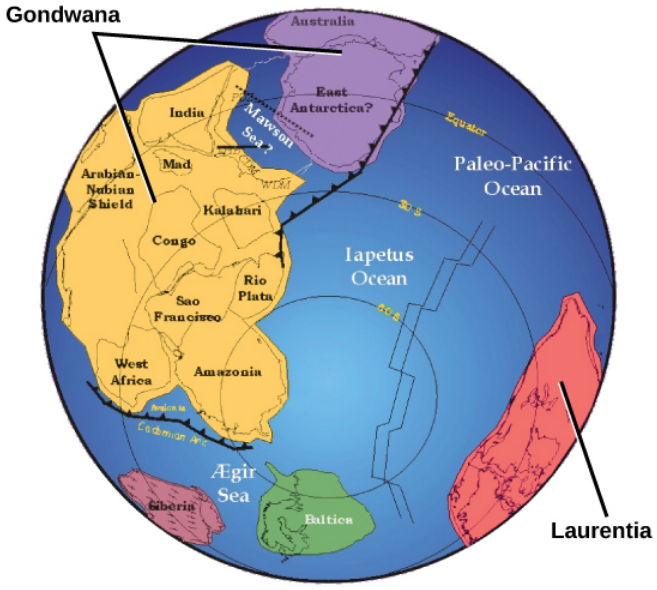


Figure 2. During the Paleozoic Era, around 550 million years ago, the continent Gondwana formed. Both Gondwana and the continent Laurentia were located near the equator.

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.

View Earth's Paleogeography: Continental Movements Through Time to see changes in Earth as life evolved.

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15.11: The Life Cycle of Amphibians

Metamorphosis is a biological process by which an animal physically develops after birth or hatching, involving a conspicuous and relatively abrupt change in the animal's body structure through cell growth and differentiation (Figure 1). Metamorphosis is iodothyronine-induced and an ancestral feature of all chordates.[1] Some insects, fishes, amphibians, mollusks, crustaceans, cnidarians, echinoderms and tunicates undergo metamorphosis, which is often accompanied by a change of nutrition source or behavior. Animals that goes through metamorphosis are called **metamorphoses**. Very few vertebrates undergo metamorphosis, but all the amphibians do to some extent.

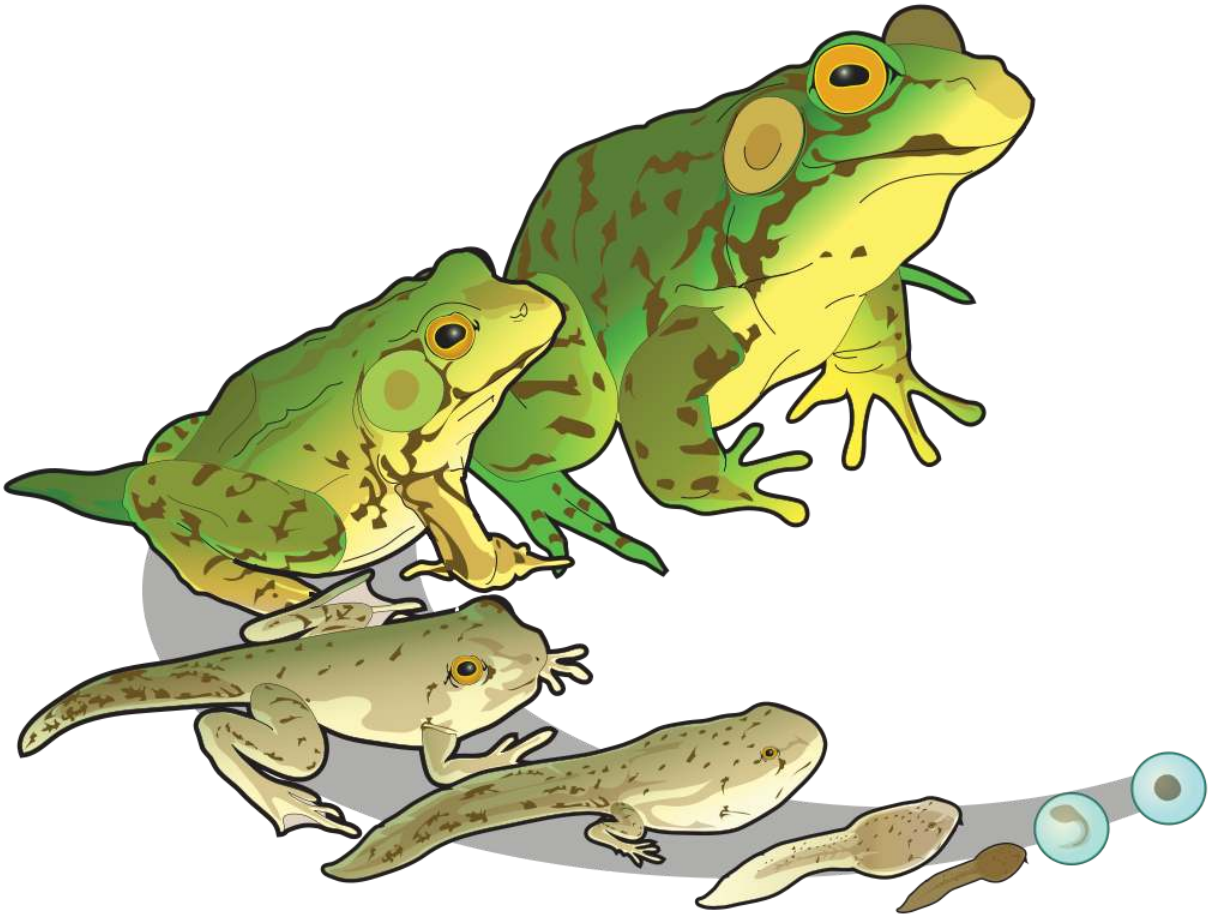


Figure 1. The life cycle of a green frog.

Amphibians

In typical amphibian development, eggs are laid in water and larvae are adapted to an aquatic lifestyle. Frogs, toads, and newts all hatch from the eggs as larvae with external gills but it will take some time for the amphibians to interact outside with pulmonary respiration. Afterwards, newt larvae start a predatory lifestyle, while tadpoles mostly scrape food off surfaces with their horny tooth ridges.

Metamorphosis in amphibians is regulated by thyroxin concentration in the blood, which stimulates metamorphosis, and prolactin, which counteracts its effect. Specific events are dependent on threshold values for different tissues. Because most embryonic development is outside the parental body, development is subject to many adaptations due to specific ecological circumstances. For this reason tadpoles can have horny ridges for teeth, whiskers, and fins. They also make use of the lateral line organ. After metamorphosis, these organs become redundant and will be resorbed by controlled cell death, called apoptosis. The amount of adaptation to specific ecological circumstances is remarkable, with many discoveries still being made.

Frogs and toads

With frogs and toads, the external gills of the newly hatched tadpole are covered with a gill sac after a few days, and lungs are quickly formed. Front legs are formed under the gill sac, and hindlegs are visible a few days later. Following that there is usually a longer stage during which the tadpole lives off a vegetarian diet. Tadpoles use a relatively long, spiral-shaped gut to digest that diet.

Rapid changes in the body can then be observed as the lifestyle of the frog changes completely. The spiral-shaped mouth with horny tooth ridges is resorbed together with the spiral gut. The animal develops a big jaw, and its gills disappear along with its gill sac. Eyes and legs grow quickly, a tongue is formed, and all this is accompanied by associated changes in the neural networks (development of stereoscopic vision, loss of the lateral line system, etc.) All this can happen in about a day, so it is truly a metamorphosis (Figure 2). It is not until a few days later that the tail is reabsorbed, due to the higher thyroxin concentrations required for tail resorption.

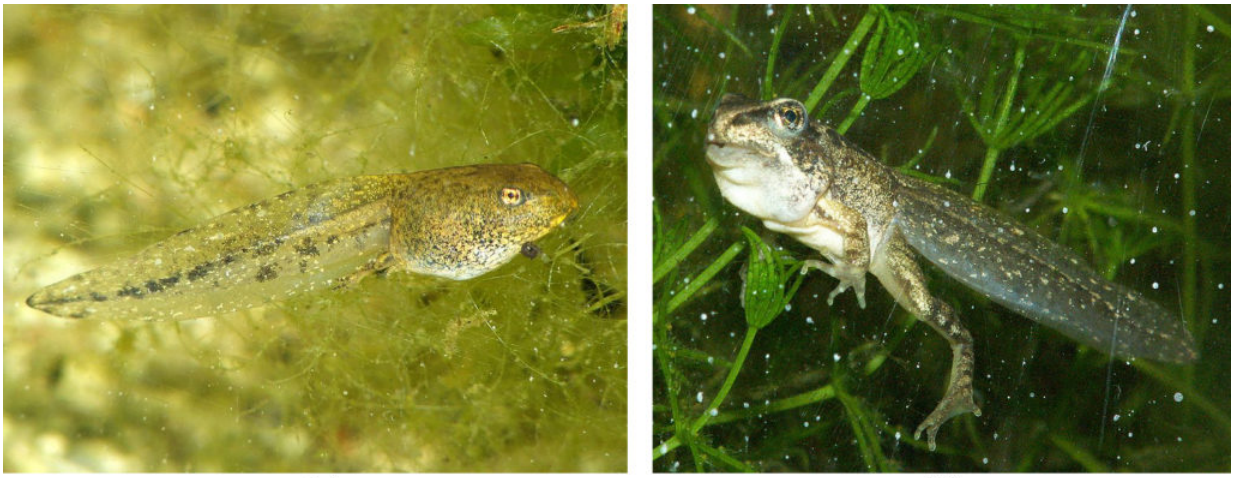


Figure 2. (a) Just before metamorphosis, only 24 hours are needed to reach the stage in part b. (b) Almost functional common frog with some remains of the gill sac and a not fully developed jaw

Salamanders

Salamander development is highly diverse; some species go through a dramatic reorganization when transitioning from aquatic larvae to terrestrial adults, while others, such as the Axolotl, display paedomorphosis and never develop into terrestrial adults. Within the genus Ambystoma, species have evolved to be paedomorphic several times, and paedomorphosis and complete development can both occur in some species.[2]

Newts



Figure 3. The large external gills of the crested newt

In newts, there is no true metamorphosis because newt larvae already feed as predators and continue doing so as adults. Newts' gills are never covered by a gill sac (Figure 3) and will be resorbed only just before the animal leaves the water. Just as in tadpoles, their lungs are functional early, but newts use them less frequently than tadpoles. Newts often have an aquatic phase in spring and summer, and a land phase in winter. For adaptation to a water phase, prolactin is the required hormone, and for adaptation to the land phase, thyroxin. External gills do not return in subsequent aquatic phases because these are completely absorbed upon leaving the water for the first time.

Caecilians

Basal caecilians such as Ichthyophis go through a metamorphosis in which aquatic larva transition into fossorial adults, which involves a loss of the lateral line.[3] More recently diverged caecilians (the Teresomata) do not undergo an ontogenetic niche shift of this sort and are in general fossorial throughout their lives. Thus, most caecilians do not undergo an anuran-like metamorphosis.[4]

1. Robert J. Denver. Chordate Metamorphosis: Ancient Control by Iodothyronines. *Current Biology*, 2008, Vol 18 No 13, R567-9. DOI: 10.1016/j.cub.2008.05.024 ↵
2. Laudet, Vincent. 2011. “The Origins and Evolution of Vertebrate Metamorphosis.” *Current Biology* 21: R726–R737 ↵
3. Dunker, Nicole, Marvalee H. Wake, Wendy M. Olson. 2000. “Embryonic and Larval Development in the Caecilian Ichthyophis kohtaoensis (Amphibia, Gymnophiona): A Staging Table” *Journal of Morphology* 243: 3–34 ↵
4. San Mauro, D., Gower, D. J., Oommen, O. V., Wilkinson, M. & Zardoya, R. 2004. "Phylogeny of caecilian amphibians (Gymnophiona) based on complete mitochondrial genomes and nuclear RAG1." *Molecular Phylogenetics and Evolution* 33: 413–427. ↵

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15.12: Clades of 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



Figure 1. Most salamanders have legs and a tail, but respiration varies among species. (credit: Valentina Storti)

Salamanders are amphibians that belong to the order Urodela. Living salamanders (Figure 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.

View River Monsters: Fish With Arms and Hands? to see a video about an unusually large salamander species.

Anura: Frogs

Frogs are amphibians that belong to the order Anura (Figure 2a). 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.



(a) (b)

Figure 2. (a) The Australian green tree frog is a nocturnal predator that lives in the canopies of trees near a water source. (b) A juvenile frog metamorphoses into a frog. Here, the frog has started to develop limbs, but its tadpole tail is still evident.

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 2b). 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.

Apoda: Caecilians



Figure 3. The Boettger's caecilian, *Siphonops paulensis*, is a species of caecilian.

An estimated 185 species comprise **caecilians** (Figure 3), 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.

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- Siphonops paulensis. **Authored by**: Ariovaldo Giaretta. **Located at**: https://commons.wikimedia.org/wiki/File:Siphonops_paulensis02.jpg. **License**: *CC BY-SA: Attribution-ShareAlike*

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15.13: Introduction to Amniotes

Identify characteristics of amniotes

Amniotes are a clade of tetrapod vertebrates comprising the reptiles, birds, and mammals. Amniotes are characterized by having an egg equipped with an amnion, an adaptation to lay eggs on land or retain the fertilized egg within the mother.

Amniote embryos, whether laid as eggs or carried by the female, are protected and aided by several extensive membranes. In eutherian mammals (such as humans), these membranes include the amniotic sac that surrounds the fetus. These embryonic membranes and the lack of a larval stage distinguish amniotes from tetrapod amphibians.

What You'll Learn to Do

- Identify the classes of animals that are amniotes
- Describe the main characteristics of amniotes
- Discuss the evolution of amniotes

Learning Activities

The learning activities for this section include the following:

- Amniotic Animals
- Evolution of Amniotes
- Self Check: Amniotes

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15.14: Amniotic Animals

In the past, the most common division of amniotes has been into the classes Mammalia, Reptilia, and Aves. Birds are directly 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. Instead, modern phylogenetics places birds and reptiles into a larger clade together, though birds (not reptiles) are the true descendants of dinosaurs.

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

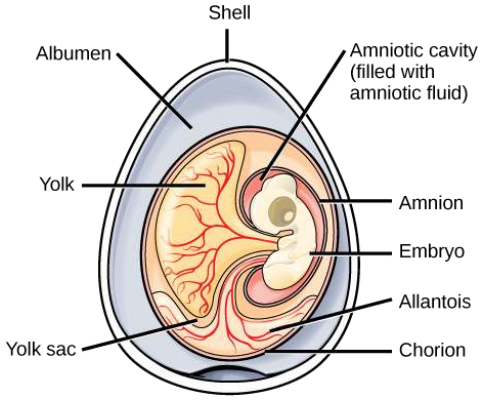


Figure 1. The key features of an amniotic egg are shown.

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 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.

Additional derived characteristics of amniotes include waterproof skin, due to the presence of lipids, and costal (rib) ventilation of the lungs.

? Practice Question

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.

[reveal-answer q="428004"]Show Answer[/reveal-answer]
[hidden-answer a="428004"]Statement d is false.[/hidden-answer]

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15.15: 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 1).

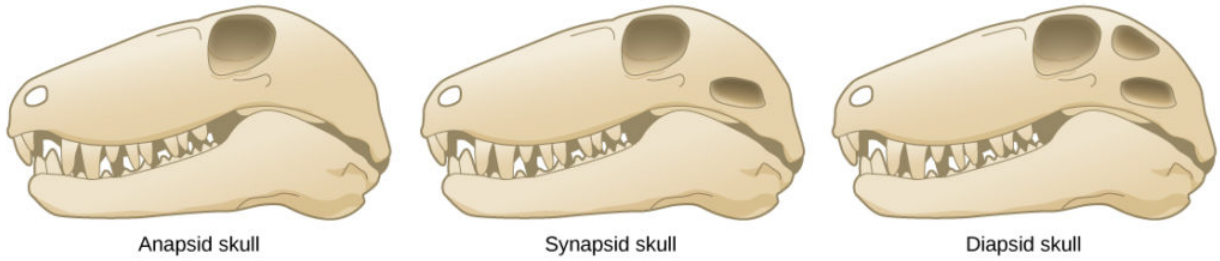


Figure 1. Compare the skulls and temporal fenestrae of anapsids, synapsids, and diapsids. Anapsids have no openings, synapsids have one opening, and diapsids have two openings.

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.

The diapsids diverged into two groups, the Archosauromorpha ("ancient lizard form") and the Lepidosauromorpha ("scaly lizard form") during the Mesozoic period (Figure 2). 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.

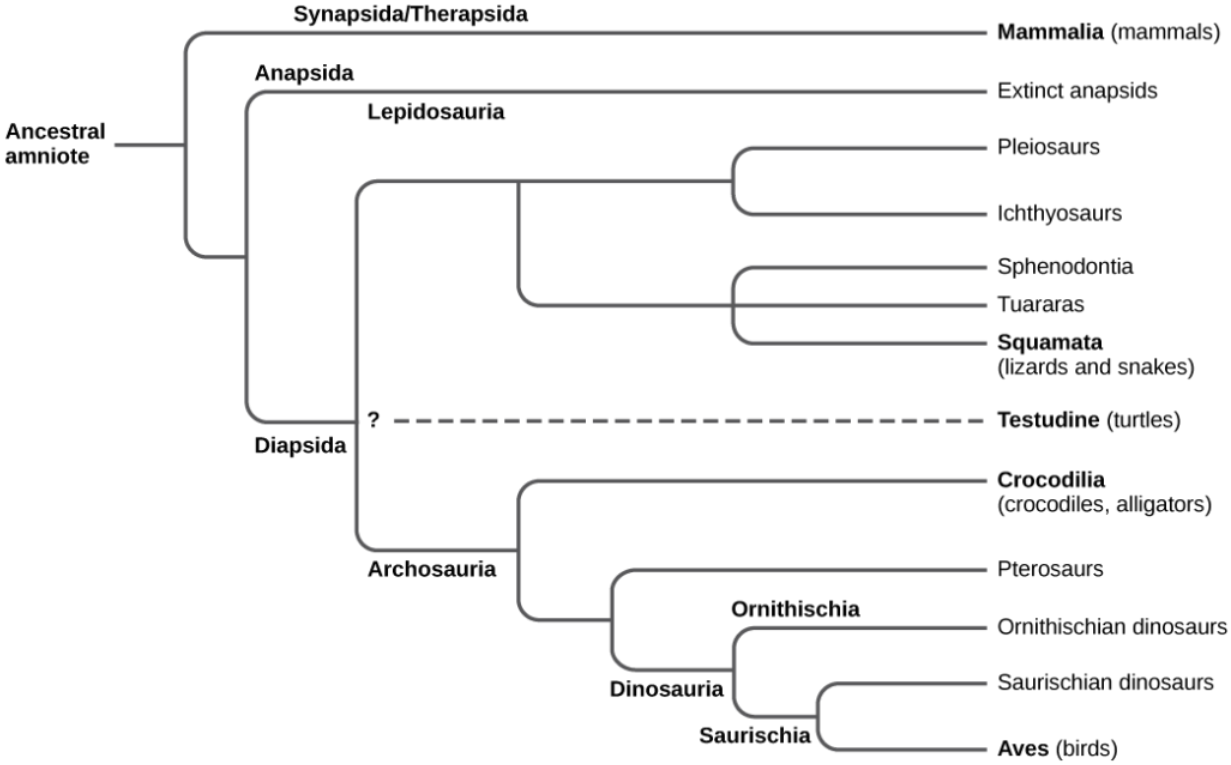


Figure 2. This chart shows the evolution of amniotes. The placement of Testudines (turtles) is currently still debated.

Practice Question

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?

[practice-area rows="2"][/practice-area]
[reveal-answer q="540837"]Show Answer[/reveal-answer]
[hidden-answer a="540837"]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.[/hidden-answer]

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15.16: Introduction to Reptiles

Identify characteristics of reptiles

Reptiles are tetrapod animals in the class Reptilia. This class includes today's turtles, crocodilians, snakes, amphisbaenians, lizards, tuatara, and their extinct relatives. The study of these traditional reptile orders, historically combined with that of modern amphibians, is called herpetology.

In more recent years, scientists have discovered that some reptiles are more closely related to birds than they are to other reptiles (e.g., crocodiles are more closely related to birds than they are to lizards). For this reason, many modern scientists prefer to consider the birds part of Reptilia as well.

What You'll Learn to Do

- Identify the characteristics of reptiles
- Explain the difference between the clades of reptiles
- Discuss the evolution of reptiles

Learning Activities

The learning activities for this section include the following:

- Characteristics of Reptiles
- Classes of Reptiles
- Evolutionary History of Reptiles
- Self Check: Reptiles

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15.17: 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.



Figure 1. This horned lizard belongs to the class reptila

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.

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15.18: Classes of Reptiles

Class Reptilia includes many diverse species that are classified into four living clades.Reptilia includes four living clades: Crocodilia (crocodiles and alligators), Sphenodontia (tuataras), Squamata (lizards and snakes), and Testudines (turtles). These are the 25 species of Crocodilia, 2 species of Sphenodontia, approximately 9,200 Squamata species, and the Testudines, with about 325 species.

Crocodilia



Figure 1. Crocodilians, such as this Siamese crocodile (*Crocodylus siamensis*), provide parental care for their offspring. (credit: Keshav Mukund Kandhadai)

Crocodilia (“small lizard”) arose with a distinct lineage by the middle Triassic; extant species include alligators, crocodiles, and caimans. Crocodilians (Figure 1) 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.

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 2). 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 2. This tuatara from New Zealand may resemble a lizard but belongs to a distinct lineage, the Sphenodontidae family. (credit: Sid Mosdell)

Squamata



Figure 3. This Jackson’s chameleon (*Trioceros jacksonii*) blends in with its surroundings.

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 3).

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 4. The garter snake belongs to the genus Thamnophis, the most widely distributed reptile genus in North America. (credit: Steve Jurvetson)

Snakes are thought to have descended from either burrowing lizards or aquatic lizards over 100 million years ago (Figure 4). 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.

Testudines



Figure 5. 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)

Turtles are members of the clade **Testudines** (“having a shell”) (Figure 5). 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.

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15.19: Evolutionary History 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.

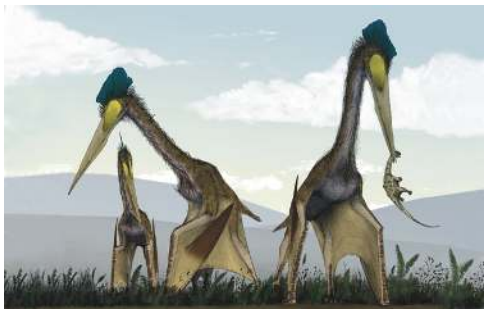


Figure 1. Pterosaurs, which existed from the late Triassic to the Cretaceous period (210 to 65.5 million years ago), possessed wings but are not believed to have been capable of powered flight. Instead, they may have been able to soar after launching from cliffs. (credit: Mark Witton, Darren Naish)

The 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 1). 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.

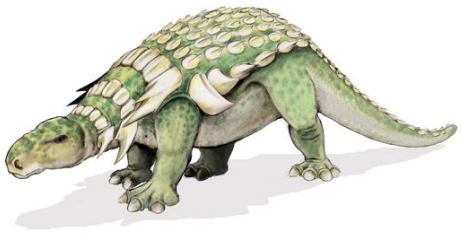


Figure 2. Edmontonia was an armored dinosaur that lived in the late Cretaceous period, 145.5 to 65.6 million years ago. (credit: Mariana Ruiz Villareal)

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 2); 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.

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.

Visit this site to see a video discussing the hypothesis that an asteroid caused the Cretaceous-Triassic (KT) extinction.

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15.20: Introduction to Birds

Identify characteristics of birds

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.

What You'll Learn to Do

- Identify characteristics of birds
- Describe the derived characteristics in birds that facilitate flight
- Describe the evolutionary history of birds

Learning Activities

The learning activities for this section include the following:

- Characteristics of Birds
- Evolutionary History of Birds
- Self Check: Birds

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15.21: 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.

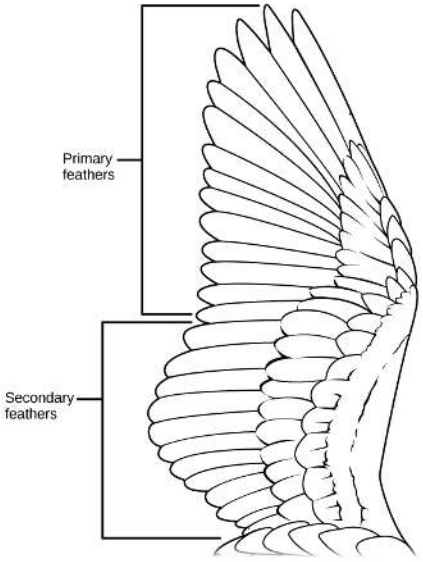


Figure 1. Primary feathers are located at the wing tip and provide thrust; secondary feathers are located close to the body and provide lift.

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 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.

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 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 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 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.

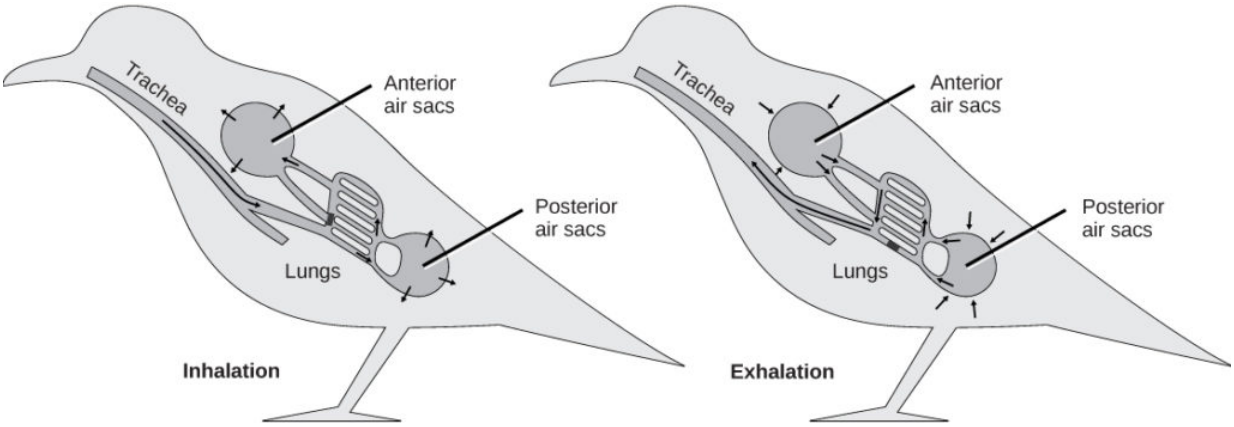


Figure 3. Avian respiration is an efficient system of gas exchange with air flowing unidirectionally. During inhalation, air passes from the trachea into posterior air sacs, then through the lungs to anterior air sacs. The air sacs are connected to the hollow interior of bones. During exhalation, air from air sacs passes into the lungs and out the trachea. (credit: modification of work by L. Shyamal)

In Summary: Characteristics of Birds

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.

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15.22: Evolutionary History 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 1). *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.



Figure 1. (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.



Figure 2. *Shanweiniao cooperorum* was a species of Enantiornithes that did not survive past the Cretaceous period. (credit: Nobu Tamura)

During the Cretaceous period, a group known as the **Enantiornithes** was the dominant bird type (Figure 2). 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.

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15.23: Introduction to Mammals

Identify characteristics of mammals

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).

What You'll Learn to Do

- Identify characteristics of mammals
- Name and describe the distinguishing features of the three main groups of mammals
- Describe the evolutionary history of mammals
- Identify characteristics of primates
- Describe the evolutionary history of primates
- Describe the evolutionary history of humans

Learning Activities

The learning activities for this section include the following:

- Mammals
- Primates
- Evolution of Humans
- Self Check: Mammals

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15.24: 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.

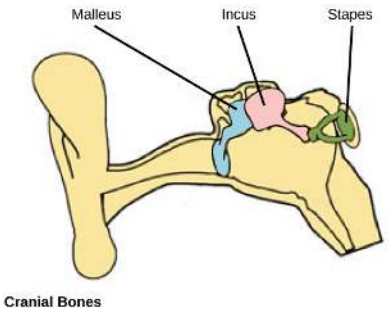


Figure 1. Bones of the mammalian inner ear are modified from bones of the jaw and skull. (credit: NCI)

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 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.

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.

Groups of Mammals

There are three groups of mammals: the **eutherians**, or placental mammals, the **marsupials**, and the **monotremes**, or metatherians. These groups are divided into two clades: the eutherians and marsupials comprise the clade of therian mammals, and monotremes form their sister clade.

Marsupials



Figure 2. The Tasmanian devil is one of several marsupials native to Australia. (credit: Wayne McLean)

Marsupials are found primarily in Australia, though the opossum is found in North America. Australian marsupials include the kangaroo, koala, bandicoot, Tasmanian devil (Figure 2), 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.

Eutherians

Eutherians (placentals) are the most widespread and numerous of the mammals, occurring throughout the world. Eutherian mammals are sometimes called “placental mammals” because all species possess a complex chorioallantoic placenta that connects a fetus to the mother, allowing for gas, fluid, and nutrient exchange. There are about 4,000 species of placental mammals in 18 to 20 orders with various adaptations for burrowing, flying, swimming, hunting, running, and climbing. In the evolutionary sense, they have been incredibly successful in form, diversity, and abundance. The eutherian mammals are classified in two major clades, the Atlantogenata and the Boreoeutheria. The Atlantogeneta include the Afrotheria (e.g., elephants, hyraxes, and manatees) and the Xenarthra (anteaters, armadillos, and sloths). The Boreoeutheria contain two large groups, the Euarchontoglires and the Laurasiatheria. Familiar orders in the Euarchontoglires are the Scandentia (tree shrews), Rodentia (rats, mice, squirrels, porcupines), Lagomorpha (rabbits and hares), and the Primates (including humans). Major Laurasiatherian orders include the Perissodactyla (e.g., horses and rhinos), the Cetartiodactyla (e.g., cows, giraffes, pigs, hippos, and whales), the Carnivora (e.g., cats, dogs, and bears), and the Chiroptera (bats and flying foxes). The two largest orders are the rodents (2,000 species) and bats (about 1,000 species), which together constitute approximately 60 percent of all eutherian species.

Monotremes

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 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 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)

Evolution of Mammals



Figure 4. 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)

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 4).

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.

Learning Objectives

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.

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15.25: Primates

Characteristics of Primates

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.

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.



Figure 1. The howler monkey is native to Central and South America. It makes a call that sounds like a lion roaring. (credit: Xavi Talleda)

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 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.

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 2a), ***Gorilla*** (gorillas), ***Pongo*** (orangutans), and ***Homo*** (humans) (Figure 2b). The very arboreal gibbons are smaller than the great apes; they have low sexual dimorphism (that is, the sexes are not markedly different in size); and they have relatively longer arms used for swinging through trees.

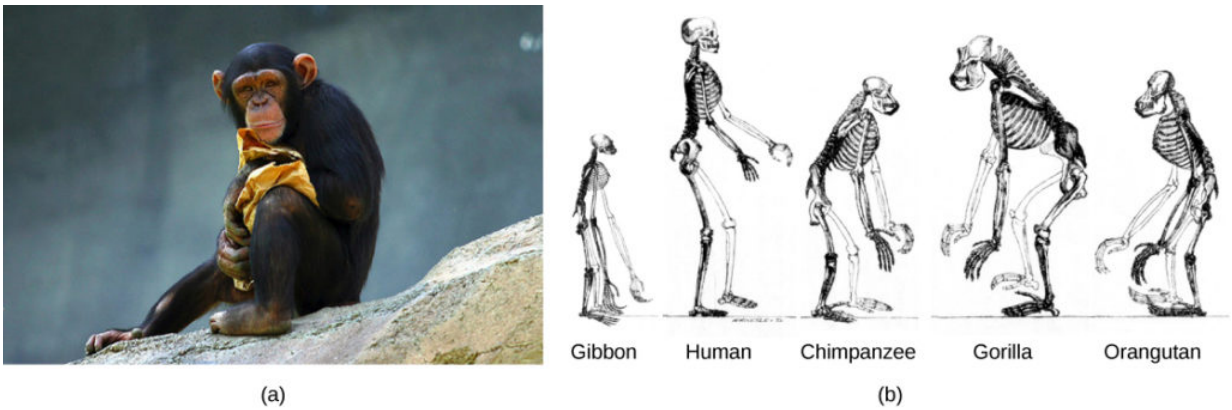


Figure 2. The (a) chimpanzee is one of the great apes. It possesses a relatively large brain and has no tail. (b) All great apes have a similar skeletal structure. (credit a: modification of work by Aaron Logan; credit b: modification of work by Tim Vickers)

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15.26: Evolution of Humans

The family Hominidae of order Primates includes the **hominoids**: the great apes (Figure 1). 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.

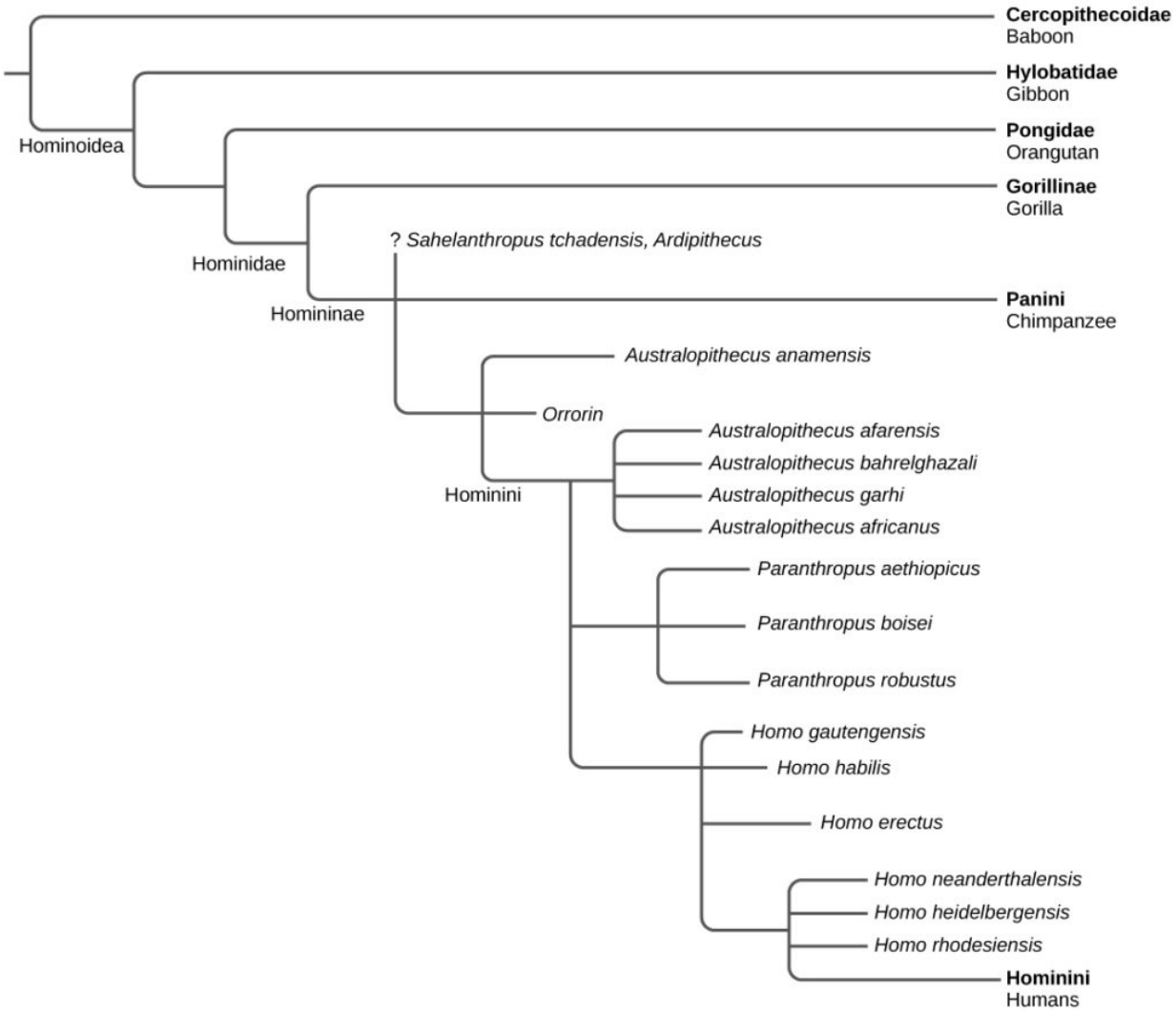


Figure 1. This chart shows the evolution of modern humans.

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 2) had smaller canines and molars compared to apes, but these were larger than those of modern humans.



Figure 2. 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.

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 3). 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.



Figure 3. 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 *Paranthropusrobustus* of South Africa, and *Paranthropusaethiopicus* and *Paranthropusboisei* 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.

Watch this video about Smithsonian paleontologist Briana Pobiner explaining the link between hominin eating of meat and evolutionary trends.



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Figure 4. *Homo erectus* had a prominent brow and a nose that pointed downward rather than forward.

H. erectus appeared approximately 1.8 million years ago (Figure 4). 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. The *Homo neanderthalensis* used tools and may have worn clothing.

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).

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.

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15.27: Putting It Together- Vertebrates

As we learned at the beginning of this lesson, vertebrates are perhaps the most recognizable animals on earth, from the endangered Siberian tiger to the domestic cat. Vertebrates are complex animals with unique features and needs.

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.

Perhaps more importantly, human beings are vertebrates! The more we can understand our own bodies, the better we can navigate through life. This video introduces us to ourselves by taking us on a journey through the fascinatingly diverse phyla known as chordata. And the next time someone asks you who you are, you can give them the facts: you're a mammalian amniotic tetrapodal sarcopterygian osteichthyen gnathostomal vertebrate cranial chordate.



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15.28: Cerego- Vertebrates

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for Vertebrates. You'll need to create a free log-in to practice these items, if you haven't already.

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CHAPTER OVERVIEW

16: Module 13- Overview of Body Systems

16.1: Why It Matters- Overview of Body Systems
16.2: Introduction to Integration of Systems
16.3: How Bodies Work
16.4: Maintaining Homeostasis
16.5: Blood Calcium and Glucose Levels
16.6: Introduction to Control Systems
16.7: Nervous System
16.8: Endocrine System
16.9: Reproductive System
16.10: Sensory Systems
16.11: Introduction to Cell Maintenance Systems
16.12: Circulatory System
16.13: Respiratory System
16.14: Immune System
16.15: Digestive System
16.16: Introduction to Support Systems
16.17: The Muscular System
16.18: The Skeletal System
16.19: Integumentary System
16.20: Putting It Together- Overview of Body Systems
16.21: Cerego- Overview of Body Systems

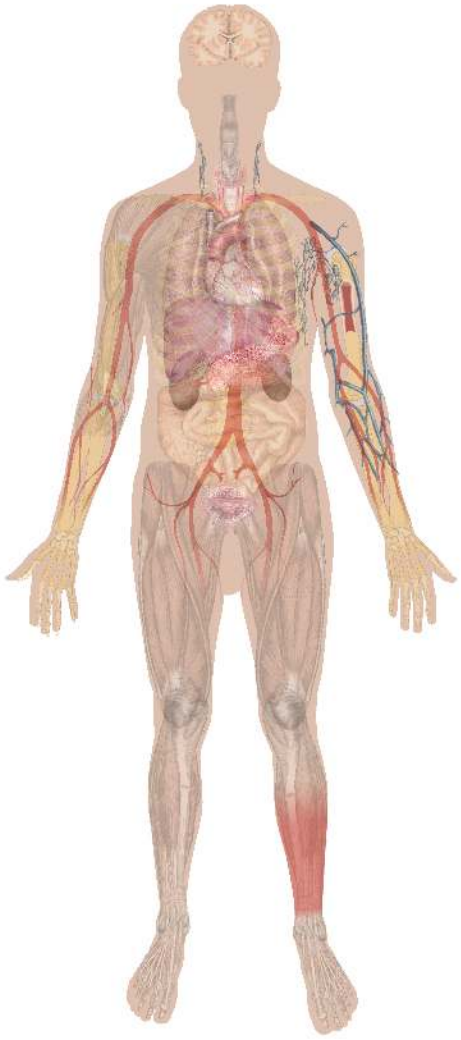
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16.1: Why It Matters- Overview of Body Systems

Why describe different body systems?

An understanding of the body can benefit your own health as you go through life. Familiarity with the human body can help you make healthful choices and prompt you to take appropriate action when signs of illness arise. Your knowledge in this field will help you understand news about nutrition, medications, medical devices, and procedures and help you understand genetic or infectious diseases. At some point, everyone will have a problem with some aspect of his or her body and your knowledge can help you to be a better parent, spouse, partner, friend, colleague, or caregiver.

This module will provide you with an introduction to the different body systems that enable human life:



Learning Outcomes

- Discuss how different body systems interact with one another
- Describe the nervous, endocrine, reproductive, and sensory systems
- Describe the circulatory, immune, respiratory, and digestive systems
- Describe the muscular, skeletal, and integumentary systems

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16.2: Introduction to Integration of Systems

Discuss how different body systems interact with one another

As we've learned our bodies are complicated systems made up of cells, tissues, organs, and organ systems. In order for life to function properly, however, these systems must work together. Organs often perform roles in multiple systems, due to their unique functions. In this section, we'll learn how systems work together, and we'll learn about a few essential life functions that require work from multiple body systems.

What You'll Learn to Do

- Discuss how different body systems interact with one another
- Explain how different organ systems relate to one another to maintain homeostasis
- Explain how different organ systems work together to maintain blood solute levels

Learning Activities

The learning activities for this section include the following:

- How Bodies Work
- Maintaining Homeostasis
- Blood Calcium and Glucose Levels
- Self Check: Integration of Systems

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16.3: How Bodies Work

The organ level of organization in the body may be the most familiar to us from our everyday experiences. Many of the common ailments we hear about—an upset stomach, a broken bone, lung disease, skin cancer—are named for the organs they affect.

An organ is made up of tissues that work together to perform a specific function for the body as a whole. Groups of organs that perform related functions are organized into organ systems, which perform more general functions. Table 1 describes the structures and functions of some common organs.

Table 1. Structure and Function of Organs

Organ	Primary function(s)	Tissues it contains	Organ system(s) it is a part of
brain	control of body systems and behavior; cognition	nervous, connective, epithelial	nervous system; endocrine system
skin	protection; support and containment; temperature and fluid regulation	epithelial, nervous, connective, muscular	integumentary system
stomach	chemical and mechanical digestion of food	epithelial, connective, muscular, nervous	digestive system
sternum (breastbone)	support; protection; blood cell production	epithelial, connective, nervous	skeletal system; immune system; cardiovascular system
kidney	waste removal; fluid regulation	epithelial, connective, nervous	urinary system

Organ Systems, The Whole Body, and Populations

Organ systems are made up of organs that work together to perform a specific function for the body as a whole. Table 2 describes the organ systems and their primary organs and physiological functions that we will cover in subsequent pages.

Note that we have opted to organize the rest of this module into three basic groups: systems involved in “control,” systems of “cell maintenance,” and systems of “support.” It is important to remember just as organs and systems work together that these categories are not mutually exclusive. For example, we have placed the reproductive system in the control category since it is involved in controlling the process and events of reproduction. However, the reproductive system is also a cell maintenance system, as it produces and maintains the actual cells used in reproduction. Just keep in mind these are groupings to help you mentally organize your learning more than they hard rules of anatomy and physiology.

Table 2. Organ Systems

Organ system	Key Organ(s)	Primary function(s)
nervous	brain, spinal cord	control of behavior and body systems; cognition
endocrine	glands	control of the body systems and development
reproductive	penis, testes, prostate (male); uterus, ovaries, vagina (female)	reproduction
sensory	nerves and receptors associated with tongue, ears, skin, eyes, nose	detect external stimuli and chemicals
cardiovascular	heart, blood vessels	transport of materials through the body; regulation of temperature
respiratory	trachea, lungs	gas exchange; regulation of temperature
immune	thymus, tonsils, spleen	defense agains infection
digestive	tongue, esophagus, stomach, small intestine, large intestine, gallbladder, rectum	digestion of food; waste removal
muscular	muscles, tendons	support; movement
skeletal	bones, cartilage	support; protection; movement; blood cell production
integumentary	skin	support; protection; regulation of fluid levels

The Whole Body

The organ systems of the body all work together to maintain proper physiological functions. Many times in the arena of anatomy and physiology, including in this course, we closely examine the molecules, cells, tissues and organs of the body to learn their forms and functions. However, it is important to consider that every molecule works as part of the entire system. Endocrine disorders such as diabetes affect glucose levels in the body. Altered blood glucose levels can affect many organ systems. For example, the immune system may not heal as well, the urinary system may experience kidney damage, and the cardiovascular system can experience vascular damage, even to the point of causing blindness. In the body, everything is interconnected.

Assigning organs to organ systems can be imprecise since organs that “belong” to one system can also have functions integral to another system. In fact, most organs contribute to more than one system.

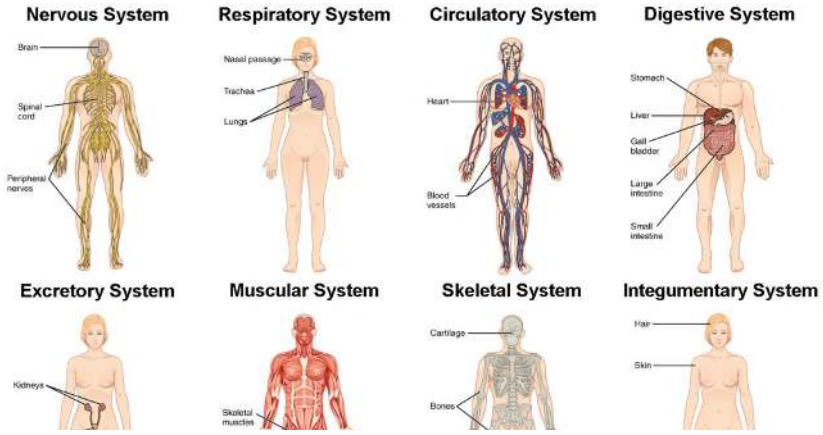


Figure 1. Click for a larger image. Organs that work together are grouped into organ systems.

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16.4: Maintaining Homeostasis

Each organ system performs specific functions for the body, and each organ system is typically studied independently. However, the organ systems also work together to help the body maintain homeostasis.

Water Levels

For example, the cardiovascular, urinary, and lymphatic systems all help the body control water balance. The cardiovascular and lymphatic systems transport fluids throughout the body and help sense both solute and water levels and regulate pressure. If the water level gets too high, the urinary system produces more dilute urine (urine with a higher water content) to help eliminate the excess water. If the water level gets too low, more concentrated urine is produced so that water is conserved.

Internal Temperatures

Similarly, the cardiovascular, integumentary (skin and associated structures), respiratory, and muscular systems work together to help the body maintain a stable internal temperature. If body temperature rises, blood vessels in the skin dilate, allowing more blood to flow near the skin's surface. This allows heat to dissipate through the skin and into the surrounding air. The skin may also produce sweat if the body gets too hot; when the sweat evaporates, it helps to cool the body. Rapid breathing can also help the body eliminate excess heat. Together, these responses to increased body temperature explain why you sweat, pant, and become red in the face when you exercise hard. (Heavy breathing during exercise is also one way the body gets more oxygen to your muscles, and gets rid of the extra carbon dioxide produced by the muscles.)

Conversely, if your body is too cold, blood vessels in the skin contract, and blood flow to the extremities (arms and legs) slows. Muscles contract and relax rapidly, which generates heat to keep you warm. The hair on your skin rises, trapping more air, which is a good insulator, near your skin. These responses to decreased body temperature explain why you shiver, get "goose bumps," and have cold, pale extremities when you are cold.

Case Study: Fevers

So what happens when you have a fever? Does this mean your body is unable to maintain its homeostasis, in the same way your house will get too hot if your air conditioner is broken?

In extreme cases, a fever can be a medical emergency; but fever is an adaptive physiological response of our body to certain infectious agents. Certain chemicals called pyrogens will trigger your hypothalamus to shift the set point to a higher value. This is more like you programming the thermostat in your house to a higher temperature to save energy on a hot day when you are not going to be home during the day. These pyrogens can come from microorganisms that infect you, or they can be produced by your body cells in response to an infection of some sort.

Practice Questions

1. [reveal-answer q="163634″]Show Answer[/reveal-answer]
   [hidden-answer a="163634″] Option b is correct. The increase in pyrogen chemicals in the blood is stimulating the receptors that reset the upper temperature limit for a febrile response. Temperature is the variable during normal body temperature regulation, but not in this scenario. The blood carries the chemical that is stimulating the febrile response, but the heart rate won't directly stimulate this receptor. The blood carries the chemical that is stimulating the febrile response, but the blood pressure won't directly stimulate this receptor.[/hidden-answer]
2. [reveal-answer q="542016″]Show Answer[/reveal-answer]
   [hidden-answer a="542016″]Answer d is correct. The hypothalamus is the control center for both normal body temperature homeostasis and febrile response.The skeletal muscle, sweat glands, and blood vessels are are all effectors.[/hidden-answer]
3. [reveal-answer q="277548″]Show Answer[/reveal-answer]
   [hidden-answer a="277548″]Option b is correct. This would increase the body temperature. Option a would decrease the body temperature.

   [/hidden-answer]

Although the evidence is only indirect, fever is believed to enhance the body's immune response. The increased temperature may actually impair the replication of infecting bacteria and viruses that are adapted to survive best at your normal homeostatic body temperature range. This can give your immune cells a chance to destroy the microorganisms before they can rapidly multiply and spread in the body. There is also some indirect evidence that increased body temperature slightly modifies several metabolic reactions in ways that also allow the immune system to function more efficiently.

Practice Questions

1. [reveal-answer q="413091"]Show Answer[/reveal-answer]
   [hidden-answer a="413091"]Option d is correct. The hypothalamus is the control center for both normal body temperature homeostasis and febrile response. Muscles, sweat glands, and blood vessels are effectors; they do not serve as a control center.

   [/hidden-answer]

2. [reveal-answer q="81873"]Show Answer[/reveal-answer]
   [hidden-answer a="81873"]Option a is correct. This will cool the body. Option b would warm the body.

   [/hidden-answer]

Unfortunately during some infections, pyrogen levels come in "waves." This adjusts your temperature set point up and down. When pyrogen levels dip, you get the other part of the fever experience: "the sweats" and feeling flushed. As long as the pyrogen levels continue to increase and decrease you will feel like you are swinging back and forth.

Practice Question

1. [reveal-answer q="873207"]Show Answer[/reveal-answer]
   [hidden-answer a="873207"]Option c is correct. The hypothalamus is still the control center that responds to a stimulus from some type of receptor. Thermoreceptors and chemoreceptors stimulate the control center in response to a change in the variable they monitor, in this case body temperature.[/hidden-answer]

Your body will continue to swing back and forth between the body's normal upper and lower temperature limits, but because it is now within your "normal" temperature range, you probably won't even notice that your body is still at work, maintaining the homoeostasis of this variable.

Practice Question

1. [reveal-answer q="523682"]Show Answer[/reveal-answer]
   [hidden-answer a="523682"]Option c is correct. Thermoreceptors are located throughout the body, so it is unlikely an operation would directly damage all the receptors. All other options could be a cause of post-operative fever.[/hidden-answer]

Homeostasis of Ions

Body functions such as regulation of the heartbeat, contraction of muscles, activation of enzymes, and cellular communication require tightly regulated calcium levels. Normally, we get a lot of calcium from our diet. The small intestine absorbs calcium from digested food.

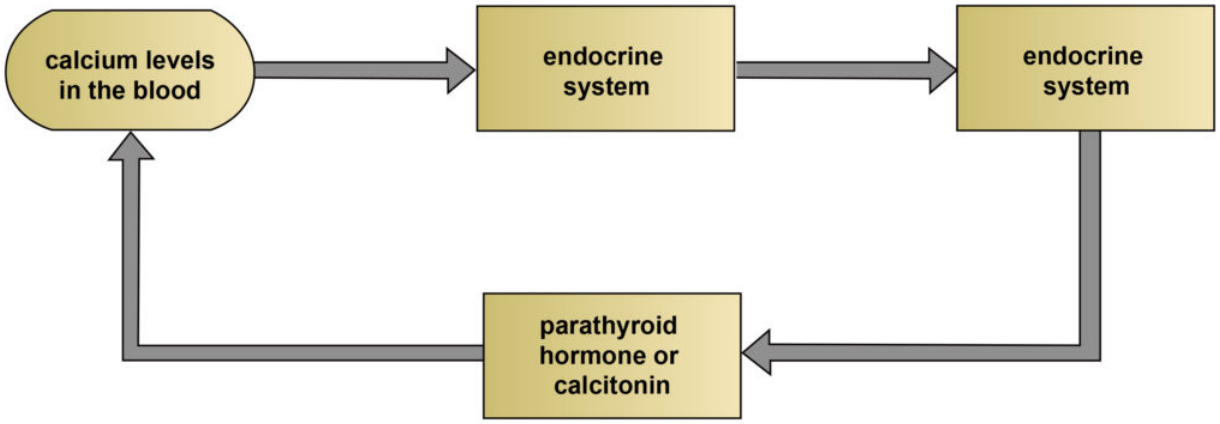
The endocrine system is the control center for regulating blood calcium homeostasis. The parathyroid and thyroid glands contain receptors that respond to levels of calcium in the blood. In this feedback system, blood calcium level is the variable, because it changes in response to the environment. Changes in blood calcium level have the following effects:

- When blood calcium is low, the parathyroid gland secretes **parathyroid hormone**. This hormone causes effector organs (the kidneys and bones) to respond to increase calcium levels. The kidneys prevent calcium from being excreted in the urine. Osteoclasts in bones reabsorb bone tissue and release calcium.
- When blood calcium levels are high, the thyroid gland releases **calcitonin**. Calcitonin causes the kidneys to reabsorb less calcium from the filtrate, allowing excess calcium to be removed from the body in urine. Calcitonin also suppresses the formation of active vitamin D in the kidneys; without vitamin D the small intestines don't absorb as much dietary calcium. Osteoblasts, stimulated by calcitonin, use calcium in the blood to add to bone tissue.

Practice Questions

Based on the above description of calcium homeostasis, try to answer these questions:

1. [reveal-answer q="688637"]Show Hint[/reveal-answer]
   [hidden-answer a="688637"]Here is the completed feedback loop:



   [/hidden-answer]
   [reveal-answer q="31679"]Show Answers[/reveal-answer]
   [hidden-answer a="31679"]
   1. Option d is correct: calcium is the variable. Proper calcium levels are important for many body functions.
   2. Option b is correct: the endocrine system is the receptor. The endocrine system regulates many things.
   3. Option b is correct: the endocrine system is the control center. The endocrine system can both sense and modulate calcium levels. The parathyroid hormone and calcitonin is the effector.
   4. Option c is correct: the parathyroid hormone and calcitonin are the effectors; they alter the function of the kidneys and bones to maintain calcium homeostasis. [/hidden-answer]

Calcium imbalance in the blood can lead to disease or even death. **Hypocalcemia** refers to low blood calcium levels. Signs of hypocalcemia include muscle spasms and heart malfunctions. **Hypercalcemia** occurs when blood calcium levels are higher than normal. Hypercalcemia can also cause heart malfunction as well as muscle weakness and kidney stones.

Practice Question

What problem(s) is/are associated with calcium homeostasis dysfunction?

a. heart disease
b. bone disease
c. both
d. neither

[reveal-answer q="477121"]Show Answer[/reveal-answer]
[hidden-answer a="477121"]Option c is correct. The heart is often affected by large short-term calcium changes, and bones are often affected by small long-term calcium changes. Calcium homeostasis dysfunction can also affect muscle function and can result in the formation of kidney stones.[/hidden-answer]

Watch this video for another discussion on homeostasis and organ systems:

A link to an interactive elements can be found at the bottom of this page.

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16.5: Blood Calcium and Glucose Levels

Blood Calcium Levels

As you have learned, proper calcium levels are important to maintain whole body homeostasis. Calcium ions are used for the heartbeat, the contraction of muscles, the activation of enzymes, and cellular communication. The parathyroid and thyroid glands of the endocrine system detect changes in blood calcium levels. When the parathyroid glands detect low blood calcium levels, several organ systems alter their function to restore blood calcium levels back to normal. The skeletal, urinary, and digestive systems all act as effectors to achieve this goal through negative feedback.

The release of parathyroid hormone from the endocrine system triggers osteoclasts of the skeletal system to resorb bone and release calcium into the blood. Similarly, this hormone causes the kidneys of the urinary system to reabsorb calcium and return it to the blood instead of excreting calcium into the urine. Through altered function of the kidneys to form active vitamin D, the small intestine of the digestive system increases the absorption of calcium.

When the thyroid gland detects elevated blood calcium levels, the skeletal, urinary, and digestive systems contribute to lower blood calcium levels back to normal. Release of the hormone calcitonin from the thyroid gland of the endocrine system triggers a series of responses. The osteoblasts of the skeletal system use excess calcium in the blood to deposit new bone. The kidneys of the urinary system excrete excess calcium into the urine instead of reclaiming calcium through reabsorption. Lastly, the kidneys stop forming active vitamin D, which causes decreased intestinal absorption of calcium through the digestive system.

? Practice Question

Graves' disease is an autoimmune disease in which the thyroid is overactive, producing an excessive amount of thyroid hormones. Some of the symptoms are heart palpitations and hand tremors.

Which system is impacted by the altered calcium levels in Graves' disease, according to the symptoms listed above?

1. skeletal
2. muscular
3. urinary
4. digestive

[reveal-answer q="114559"]Show Answer[/reveal-answer]
[hidden-answer a="114559"]Option b is correct. Skeletal muscles and the heart are impacted by altered calcium levels. The skeletal, urinary, and urinary systems are involved in calcium homeostasis, but they are not involved with the symptoms described here.[/hidden-answer]

Blood Glucose Levels

The endocrine functions of the pancreas and liver coordinate efforts to maintain normal blood glucose levels. When pancreatic cells detect low blood glucose levels, the pancreas synthesizes and secretes the hormone glucagon. Glucagon causes the liver to convert the polymerized sugar glycogen into glucose through a process known as glycogenolysis. Glucose then travels through the blood to allow all cells of the body to use it.

If pancreatic cells detect high blood glucose levels, the pancreas synthesizes and release the hormone insulin. Insulin causes polymerization of glucose into glycogen, which is then stored in the liver through a process known as glycogenesis.

The nervous and digestive systems also play a role in maintaining blood glucose levels. When the stomach is empty and blood glucose levels are low, the digestive system and the brain respond by making you feel hungry—your stomach may "growl," and you may feel pain or discomfort in your midsection. These sensations prompt you to eat, which raises blood glucose levels.

? PRactice Question

The liver and pancreas are part of both the endocrine system and the digestive system. What is the utility of having integrated digestion and regulation?

[practice-area rows=”2″][/practice-area]
[reveal-answer q=”641147″]Show Answer[/reveal-answer]
[hidden-answer a=”641147″]Both the liver and pancreas can sense and help process nutrients to maintain glucose homeostasis. This allows closer regulation.[/hidden-answer]

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16.6: Introduction to Control Systems

Describe the nervous, endocrine, reproductive, and sensory systems

The first set of body systems we'll learn about have been grouped together as the "control systems." It is important to remember that this isn't a hard-and-fast categorization: we've simply grouped these systems together to help you organize your learning. These control systems all function in roles that control the signals that direct your body's actions.

What You'll Learn to Do

- Identify the structure and function of the nervous system
- Identify the structure and function of the endocrine system
- Identify the structure and function of the reproductive system
- Identify the structure and function of the sensory systems

Learning Activities

The learning activities for this section include the following:

- Nervous System
- Endocrine System
- Reproductive System
- Sensory Systems
- Self Check: Control Systems

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16.7: Nervous System

The **central nervous system** includes the **brain** and **spinal cord**. The brain and spinal cord are protected by bony structures, membranes, and fluid. The brain is held in the cranial cavity of the skull and it consists of the **cerebrum**, **cerebellum**, and the **brain stem**. The nerves involved are cranial nerves and spinal nerves.

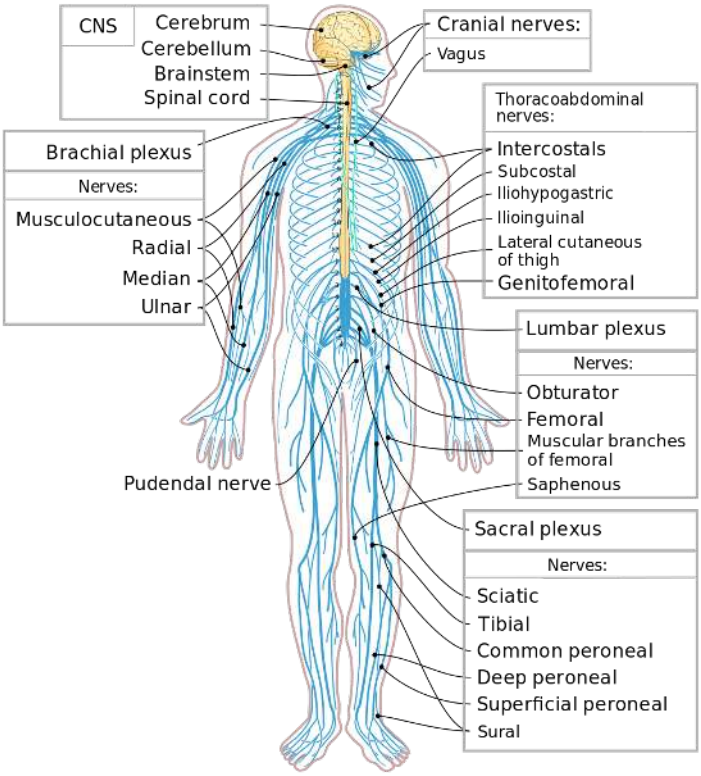


Figure 1. The nervous system.

The nervous system has three main functions: sensory input, integration of data and motor output. Sensory input is when the body gathers information or data, by way of neurons, glia and synapses. The nervous system is composed of excitable nerve cells (neurons) and synapses that form between the neurons and connect them to centers throughout the body or to other neurons. These neurons operate on excitation or inhibition, and although nerve cells can vary in size and location, their communication with one another determines their function. These nerves conduct impulses from sensory receptors to the brain and spinal cord. The data is then processed by way of integration of data, which occurs only in the brain. After the brain has processed the information, impulses are then conducted from the brain and spinal cord to muscles and glands, which is called motor output. Glia cells are found within tissues and are not excitable but help with myelination, ionic regulation and extracellular fluid.

The nervous system is comprised of two major parts, or subdivisions, the central nervous system (CNS) and the peripheral nervous system (PNS). The CNS includes the brain and spinal cord. The brain is the body's "control center." The CNS has various centers located within it that carry out the sensory, motor and integration of data. These centers can be subdivided to Lower Centers (including the spinal cord and brain stem) and Higher centers communicating with the brain via effectors.

The PNS is a vast network of spinal and cranial nerves that are linked to the brain and the spinal cord. It contains sensory receptors which help in processing changes in the internal and external environment. This information is sent to the CNS via afferent sensory nerves. The PNS is then subdivided into the autonomic nervous system and the somatic nervous system. The autonomic has involuntary control of internal organs, blood vessels, smooth and cardiac muscles. The somatic has voluntary control of skin, bones, joints, and skeletal muscle. The two systems function together, by way of nerves from the PNS entering and becoming part of the CNS, and vice versa.

General functions of the CNS

The central nervous system (CNS) represents the largest part of the nervous system, including the brain and the spinal cord. Together with the peripheral nervous system (PNS), it has a fundamental role in the control of behavior.

When the central nervous system becomes damaged or peripheral nerves become trapped, a variety of impacts are possible. It can increase or decrease your internal organs functionality, it can even affect your facial expressions, i.e. make you frown a lot, your smile may become lop sided, your lungs can overwork, or underwork, lung capacity may increase or decrease, your bladder can fill, but you become unable to urinate, your bowels become lapsed and you are unable to completely clear them upon each bowel movement, the muscles in your arms, legs and torso can become weaker and more fatty, not from lack of use, but from the nerves that run from your spine into them being restricted from working properly, you can suffer headaches, earaches, sore throats, blocked sinuses. Even your ability to orgasm can be affected.

The CNS is conceived as a system devoted to information processing, where an appropriate motor output is computed as a response to a sensory input. Many threads of research suggest that motor activity exists well before the maturation of the sensory systems, and senses only influence behavior without dictating it. This has brought the conception of the CNS as an autonomous system.

Neurons

Structure

Neurons are highly specialized for the processing and transmission of cellular signals. Given the diversity of functions performed by neurons in different parts of the nervous system, there is, as expected, a wide variety in the shape, size, and electrochemical properties of neurons. For instance, the soma of a neuron can vary in size from 4 to 100 micrometers in diameter.

The soma (cell body) is the central part of the neuron. It contains the nucleus of the cell, and therefore is where most protein synthesis occurs. The nucleus ranges from 3 to 18 micrometers in diameter. The dendrites of a neuron are cellular extensions with many branches, and metaphorically this overall shape and structure is referred to as a dendritic tree. This is where the majority of input to the neuron occurs. However, information outflow (i.e., from dendrites to other neurons) can also occur—except in chemical synapse in which backflow of impulse is inhibited by the fact that axon do not possess chemoreceptors and dendrites cannot secrete neurotransmitter chemical. This explains one way conduction of nerve impulse.

The axon is a finer, cable-like projection which can extend tens, hundreds, or even tens of thousands of times the diameter of the soma in length. The axon carries nerve signals away from the soma (and also carry some types of information back to it). Many neurons have only one axon, but this axon may—and usually will—undergo extensive branching, enabling communication with many target cells.

The part of the axon where it emerges from the soma is called the **axon hillock**. Besides being an anatomical structure, the axon hillock is also the part of the neuron that has the greatest density of voltage-dependent sodium channels. This makes it the most easily-excited part of the neuron and the spike initiation zone for the axon: in neurological terms it has the greatest hyperpolarized action potential threshold. While the axon and axon hillock are generally involved in information outflow, this region can also receive input from other neurons as well.

The axon terminal is a specialized structure at the end of the axon that is used to release neurotransmitter chemicals and communicate with target neurons. Although the canonical view of the neuron attributes dedicated functions to its various anatomical components, dendrites and axons often act in ways contrary to their so-called main function.

Axons and dendrites in the central nervous system are typically only about a micrometer thick, while some in the peripheral nervous system are much thicker. The soma is usually about 10–25 micrometers in diameter and often is not much larger than the cell nucleus it contains. The longest axon of a human motor neuron can be over a meter long, reaching from the base of the spine to the toes. Sensory neurons have axons that run from the toes to the dorsal columns, over 1.5 meters in adults. Giraffes have single axons several meters in length running along the entire length of their necks. Much of what is known about axonal function comes from studying the squids giant axon, an ideal experimental preparation because of its relatively immense size (0.5–1 millimeters thick, several centimeters long).

Function

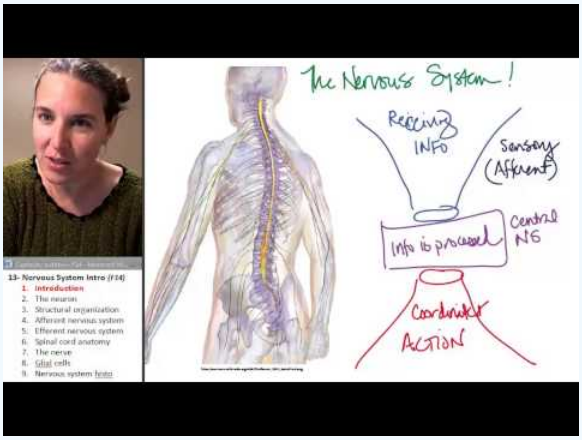
Sensory afferent neurons convey information from tissues and organs into the central nervous system. Efferent neurons transmit signals from the central nervous system to the effector cells and are sometimes called motor neurons. Interneurons connect neurons within specific regions of the central nervous system. Afferent and efferent can also refer generally to neurons which, respectively, bring information to or send information from brain region.

Classification

Excitatory neurons excite their target postsynaptic neurons or target cells causing it to function. Motor neurons and somatic neurons are all excitatory neurons. Excitatory neurons in the brain are often glutamatergic. Spinal motor neurons, which synapse on muscle cells, use acetylcholine as their neurotransmitter. Inhibitory neurons inhibit their target neurons. Inhibitory neurons are also known as short axon neurons, interneurons or microneurons. The output of some brain structures (neostriatum, globus pallidus, cerebellum) are inhibitory. The primary inhibitory neurotransmitters are GABA and glycine. Modulatory neurons evoke more complex effects termed neuromodulation. These neurons use such neurotransmitters as dopamine, acetylcholine, serotonin and others. Each synapses can receive both excitatory and inhibitory signals and the outcome is determined by the adding up of summation.

Learning Objectives

Watch this video for another introduction to the nervous system. This is the first in a series of nine videos. While you may enjoy all the videos in this series, you are only required to watch the first video.



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16.8: Endocrine System

The endocrine system is a control system of ductless glands that secrete hormones within specific organs. Hormones act as “messengers,” and are carried by the bloodstream to different cells in the body, which interpret these messages and act on them.

It seems like a far fetched idea that a small chemical can enter the bloodstream and cause an action at a distant location in the body. Yet this occurs in our bodies everyday of our lives. The ability to maintain homeostasis and respond to stimuli is largely due to hormones secreted within the body. Without hormones, you could not grow, maintain a constant temperature, produce offspring, or perform the basic actions and functions that are essential for life.

The endocrine system provides an electrochemical connection from the hypothalamus of the brain to all the organs that control the body metabolism, growth and development, and reproduction.

There are two types of hormones secreted in the endocrine system: Steroidal (or lipid based) and non-steroidal, (or protein based) hormones.

The endocrine system regulates its hormones through negative feedback, except in very specific cases like childbirth. Increases in hormone activity decrease the production of that hormone. The immune system and other factors contribute as control factors also, altogether maintaining constant levels of hormones.

Types of Glands

Exocrine Glands are those which release their cellular secretions through a duct which empties to the outside or into the lumen (empty internal space) of an organ. These include certain sweat glands, salivary and pancreatic glands, and mammary glands. They are not considered a part of the endocrine system.

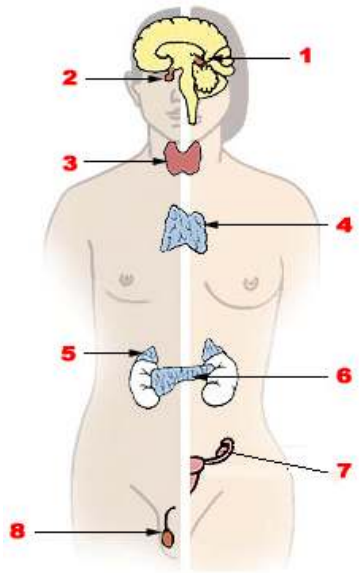


Figure 1. Major endocrine glands. (Male left, female on the right.) 1. Pineal gland 2. Pituitary gland 3. Thyroid gland 4. Thymus 5. Adrenal gland 6. Pancreas 7. Ovary 8. Testis

Endocrine Glands are those glands which have no duct and release their secretions directly into the intercellular fluid or into the blood. The collection of endocrine glands makes up the endocrine system.

1. The main endocrine glands are the pituitary (anterior and posterior lobes), thyroid, parathyroid, adrenal (cortex and medulla), pancreas and gonads.
2. The pituitary gland is attached to the hypothalamus of the lower forebrain.
3. The thyroid gland consists of two lateral masses, connected by a cross bridge, that are attached to the trachea. They are slightly inferior to the larynx.
4. The parathyroid glands are four masses of tissue, two embedded posterior in each lateral mass of the thyroid gland.

5. One adrenal gland is located on top of each kidney. The cortex is the outer layer of the adrenal gland. The medulla is the inner core.
6. The pancreas is along the lower curvature of the stomach, close to where it meets the first region of the small intestine, the duodenum.
7. The gonads (ovaries and testes) are found in the pelvic cavity.

Hormones and Types

A **hormone** is a type of chemical signal. They are a means of communication between cells.

The endocrine system produces hormones that are instrumental in maintaining homeostasis and regulating reproduction and development. A hormone is a chemical messenger produced by a cell that effects specific change in the cellular activity of other cells (target cells). Unlike exocrine glands (which produce substances such as saliva, milk, stomach acid and digestive enzymes), endocrine glands do not secrete substances into ducts (tubes). Instead, endocrine glands secrete their hormones directly into the surrounding extra cellular space. The hormones then diffuse into nearby capillaries and are transported throughout the body in the blood.

The endocrine and nervous systems often work toward the same goal. Both influence other cells with chemicals (hormones and neurotransmitters). However, they attain their goals differently. Neurotransmitters act immediately (within milliseconds) on adjacent muscle, gland, or other nervous cells, and their effect is short-lived. In contrast, hormones take longer to produce their intended effect (seconds to days), may affect any cell, nearby or distant, and produce effects that last as long as they remain in the blood, which could be up to several hours.

Table 1 shows the major hormones, their target and their function once in the target cell.

Table 1. Major Horomes

Endocrine Gland	Hormone Released	Chemical Class	Target Tissue/Organ	Major Function of Hormone
Hypothalamus	Hypothalamic releasing and inhibiting hormones	Peptide	Anterior pituitary	Regulate anterior pituitary hormone
Posterior Pituitary	Antidiuretic (ADH)	Peptide	Kidneys	Stimulates water reabsorption by kidneys
	Oxytocin	Peptide	Uterus, mammary glands	Stimulates uterine muscle contractions and release of milk by mammary glands
Anterior Pituitary	Thyroid stimulating (TSH)	Glycoprotein	Thyroid	Stimulates thyroid
	Adrenocorticotropic (ACTH)	Peptide	Adrenal cortex	Stimulates adrenal cortex
	Gonadotropic (FSH, LH)	Glycoprotein	Gonads	Egg and sperm production, sex hormone production
	Prolactin (PRL)	Protein	Mammary glands	Milk production
	Growth (GH)	Protein	Soft tissue, bones	Cell division, protein synthesis and bone growth
Thyroid	Thyroxine (T4) and Triiodothyronie (T3)	Iodinated amino acid	All tissue	Increase metabolic rate, regulates growth and development
	Calcitonin	Peptide	Bones, kidneys and intestine	Lowers blood calcium level
Parathyroids	Parathyroid (PTH)	Peptide	Bones, kidneys and intestine	Raises blood calcium level
Adrenal Cortex	Glucocorticoids (cortisol)	Steroid	All tissue	Raise blood glucose level, stimulates breakdown of protein
	Mineralocorticoids (aldosterone)	Steroid	Kidneys	Reabsorb sodium and excrete potassium
	Sex Hormones	Steroid	Gonads, skin, muscles and bones	Stimulates reproductive organs and brings on sex characteristics
Adrenal Medulla	Epinephrine and norepinephrine	Modified amino acid	Cardiac and other muscles	Released in emergency situations, raises blood glucose level, “fight or flight” response
Pancreas	Insulin	Protein	Liver, muscles, adipose tissue	Lowers blood glucose levels, promotes formation of glycogen

Table 1. Major Horomes

Endocrine Gland	Hormone Released	Chemical Class	Target Tissue/Organ	Major Function of Hormone
	Glucagon	Protein	Liver, muscles, adipose tissue	Raises blood glucose levels
Testes	Androgens (testosterone)	Steroid	Gonads, skin, muscles and bone	Stimulates male sex characteristics
Ovaries	Estrogen and progesterone	Steroid	Gonads, skin, muscles and bones	Stimulates female sex characteristics
Thymus	Thymosins	Peptide	T lymphocytes	Stimulates production and maturation of T lymphocytes
Pineal Gland	Melatonin	Modified amino acid	Brain	Controls circadian and circannual rhythms, possibly involved in maturation of sexual organs

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16.9: Reproductive System

In simple terms, reproduction is the process by which organisms create descendants. This miracle is a characteristic that all living things have in common and sets them apart from nonliving things. But even though the reproductive system is essential to keeping a species alive, it is not essential to keeping an individual alive.

In human reproduction, two kinds of sex cells or gametes are involved. Sperm, the male gamete, and a secondary oocyte (along with first polar body and corona radiata), the female gamete must meet in the female reproductive system to create a new individual. For reproduction to occur, both the female and male reproductive systems are essential. It is a common misnomer to refer to a woman's gametic cell as an egg or ovum, but this is impossible. A secondary oocyte must be fertilized by the male gamete before it becomes an "ovum" or "egg."

While both the female and male reproductive systems are involved with producing, nourishing and transporting either the oocyte or sperm, they are different in shape and structure. The male has reproductive organs, or genitals, that are both inside and outside the pelvis, while the female has reproductive organs entirely within the pelvis.

The Male Reproductive System

The male reproductive system consists of the testes and a series of ducts and glands. Sperm are produced in the testes and are transported through the reproductive ducts. These ducts include the epididymis, vas deferens, ejaculatory duct and urethra. The reproductive glands produce secretions that become part of semen, the fluid that is ejaculated from the urethra. These glands include the seminal vesicles, prostate gland, and bulbourethral glands.

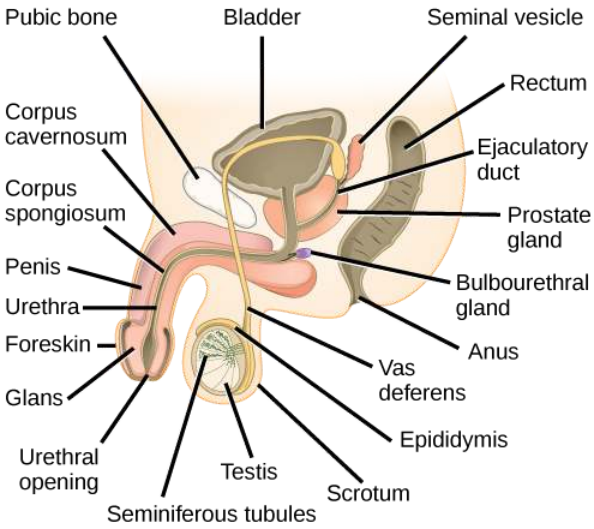


Figure 1. The reproductive structures of the human male are shown.

Table 1 describes the major components of the male reproductive system.

Table 1. Components of the Male Reproductive System

Structure	Location & Description	Function
Bulbourethral glands (2)	Pea sized organs posterior to the prostate on either side of the urethra.	Secretion of gelatinous seminal fluid called pre-ejaculate. This fluid helps to lubricate the urethra for spermatozoa to pass through, and to help flush out any residual urine or foreign matter. (< 1% of semen)
Epididymis	Tightly coiled duct lying just outside each testis connecting efferent ducts to vas deferens.	Storage and maturation of sperm.
Penis	Three columns of erectile tissue: two corpora cavernosa and one corpus spongiosum. Urethra passes through penis.	Male reproductive organ and also male organ of urination.
Prostate gland	Surrounds the urethra just below the urinary bladder and can be felt during a rectal exam.	Stores and secretes a clear, slightly alkaline fluid constituting up to one-third of the volume of semen. Raise vaginal pH.(25-30% of semen)
Seminal vesicles (2)	Convoluted structure attached to vas deferens near the base of the urinary bladder.	About 65-75% of the seminal fluid in humans originates from the seminal vesicles. Contain proteins, enzymes, fructose, mucus, vitamin C, flavins, phosphorylcholine and prostaglandins. High fructose concentrations provide nutrient energy for the spermatozoa as they travel through the female reproductive system.
Testes	Inside scrotum, outside of body.	Gonads that produce sperm and male sex hormones.Production of testosterone by cells of Leydig in the testicles.
Urethra	Connects bladder to outside body, about 8 inches long.	Tubular structure that receives urine from bladder and carries it to outside of the body. Also passage for sperm.
Vas deferens	Muscular tubes connecting the left and right epididymis to the ejaculatory ducts to move sperm. Each tube is about 30 cm long.	During ejaculation the smooth muscle in the vas deferens wall contracts, propelling sperm forward. Sperm are transferred from the vas deferens into the urethra, collecting fluids from accessory sex glands en route

The Female Reproductive System

Reproduction can be defined as the process by which an organism continues its species. As noted earlier, in the human reproductive process, two kinds of gametes are involved: the male gamete (sperm) and the female gamete (egg or ovum). These two gametes meet within the female's uterine tubes located one on each side of the upper pelvic cavity, and begin to create a new individual. The female needs a male to fertilize her egg; she then carries offspring through pregnancy and childbirth.

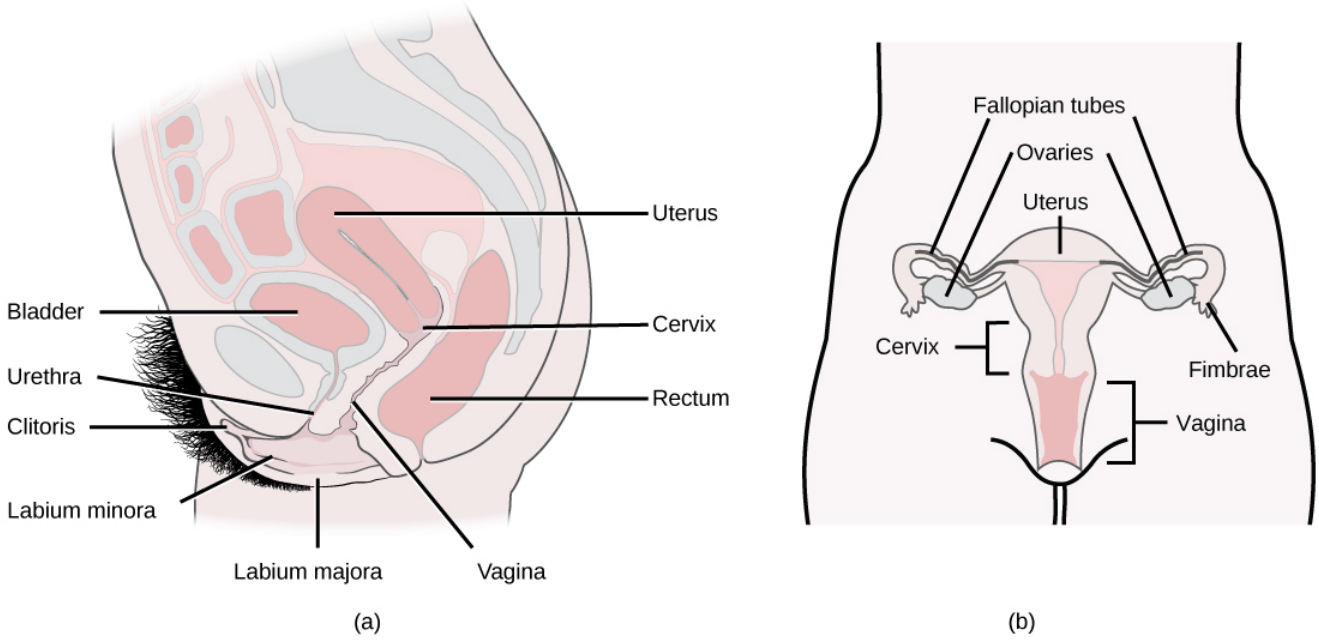


Figure 2. The reproductive structures of the human female are shown. (credit a: modification of work by Gray's Anatomy; credit b: modification of work by CDC)

Female Reproductive System

- Produces eggs (ova)
- Secretes sex hormones
- Receives the male spermatazoa during
- Protects and nourishes the fertilized egg until it is fully developed
- Delivers fetus through birth canal
- Provides nourishment to the baby through milk secreted by mammary glands in the breast

The major components of the female reproductive system are shown in Table 2.

Table 2. Components of the Male Reproductive System

Structure	Location & Description	Function
Ovaries (2)	Ovoid structures on either side of the uterus in the pelvic cavity	Primary sex organs of female; contain ovarian follicles that contain the oocytes. Oocytes are released during the ovulation stage of the menstrual cycle.
Fallopian Tubes (2)	Extend from lateral ares of uterus to near the ovaries	Transport oocyte to uterus after fertilization and are the sites where fertilization by sperm actually occurs
Uterus	Pear shaped structure divided into the fundus and the cervix	Site of fetal development during gestation
Vagina	Located between rectum and urethra; smooth muscle lined with an epithelial mucous membrane	Path for menstrual blood and tissue to leave the body, as well as the fetus during childbirth. Produces a variety of secretions for lubrication and receives secretions that facilitate fertilization.
Vulva	Externally located: labia majora and minora, mons pubis, clithoris, vestibule, greater and lesser vestibular glands	Sexual function: heavily innervated and provide pleasure when properly stimulated.
Perineum	Area between vagina and anus	Helps form the muscular floor of pelvis; can be torn during vaginal childbirth
Mammary glands	Superficial to pectoral muscles	Provide nourishment to the baby through milk secretions

Comparing Male and Female Reproductive Systems

Similarities

The reproductive systems of the male and female have some basic similarities and some specialized differences. They are the same in that most of the reproductive organs of both sexes develop from similar embryonic tissue, meaning they are homologous. Both systems have gonads that produce (sperm and egg or ovum) and sex organs. And both systems experience maturation of their reproductive organs, which become functional during puberty as a result of the gonads secreting sex hormones.

Table 3.

Indifferent	Male	Female
Gonad	Testis	Ovary
Müllerian duct	Appendix testis	Fallopian tubes
Müllerian duct	Prostatic utricle	Uterus, proximal vagina
Wolffian duct	Rete testis	Rete ovarii
Mesonephric tubules	Efferent ducts	Epoophoron
Wolffian duct	Epididymis	Gartner’s duct
Wolffian duct	Vas deferens	
Wolffian duct	Seminal vesicle	
Wolffian duct	Prostate	Skene’s glands
Urogenital sinus	Bladder, urethra	Bladder, urethra, distal vagina
Urogenital sinus	Bulbourethral gland	Bartholin’s gland
Genital swelling	Scrotum	Labia majora
Urogenital folds	Distal urethra	Labia minora
Genital tubercle	Penis	Clitoris
Prepuce	Foreskin	Clitoral hood
	Bulb of penis	Vestibular bulbs
	Glans penis	Clitoral glans
	Crus of penis	Clitoral crura

Differences

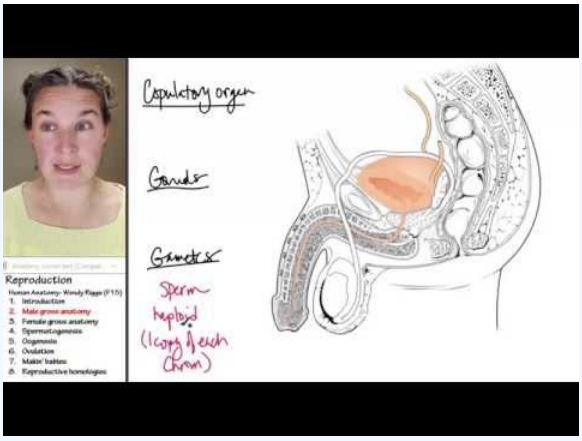
The differences between the female and male reproductive systems are based on the functions of each individual’s role in the reproduction cycle. A male who is healthy, and sexually mature, continuously produces sperm. The development of women’s “eggs” are arrested during fetal development. This means she is born with a predetermined number of oocytes and cannot produce new ones.

At about 5 months gestation, the ovaries contain approximately six to seven million oogonia, which initiate meiosis. The oogonia produce primary oocytes that are arrested in prophase I of meiosis from the time of birth until puberty. After puberty, during each menstrual cycle, one or several oocytes resume meiosis and undergo their first meiotic division during ovulation. This results in the production of a secondary oocyte and one polar body. The meiotic division is arrested in metaphase II. Fertilization triggers completion of the second meiotic division and the result is one ovum and an additional polar body.

The ovaries of a newborn baby girl contain about one million oocytes. This number declines to 400,000 to 500,000 by the time puberty is reached. On average, 500-1000 oocytes are ovulated during a woman’s reproductive lifetime. When a young woman reaches puberty around age 10 to 13, a promary oocyte is discharged from one of the ovaries every 28 days. This continues until the woman reaches menopause, usually around the age of 50 years. Occytes are present at birth, and age as a woman ages.

Learning Objectives

Watch the first three videos in this playlist for a review of the reproductive system:



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(click the list icon in the top right corner of the video frame to select more videos from the playlist)

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16.10: Sensory Systems

We experience reality through our senses. Senses are the physiological methods of perception, so a sense is a faculty by which outside stimuli are perceived. The senses and their operation, classification, and theory are overlapping topics studied by a variety of fields. Many neurologists disagree about how many senses there actually are due to a broad interpretation of the definition of a sense. Our senses are split into two different groups. Our **exteroceptors** detect stimulation from the outsides of our body: this includes smell, taste, and equilibrium. The **interoceptors** receive stimulation from the inside of our bodies: this includes blood pressure dropping, changes in the glucose, and pH levels. Children are generally taught that there are five senses (sight, hearing, touch, smell, taste). However, it is generally agreed that there are at least seven different senses in humans, and a minimum of two more observed in other organisms. Sense can also differ from one person to the next. Take taste for an example: what may taste great to one person will taste awful to someone else. This has to do with how the brain interprets the stimuli that are received.

Chemoreception

The senses of **gustation** (taste) and **olfaction** (smell) fall under the category of **chemoreception**. Specialized cells act as receptors for certain chemical compounds. As these compounds react with the receptors, an impulse is sent to the brain and is registered as a certain taste or smell. Gustation and olfaction are chemical senses because the receptors they contain are sensitive to the molecules in the food we eat, along with the air we breathe.

Gustatory System

In humans, the sense of **taste** is transduced by **taste buds** and is conveyed via three of the twelve cranial nerves. Cranial nerve VII, the facial nerve, carries taste sensations from the anterior two thirds of the tongue (excluding the circumvallate papillae, see lingual papilla) and soft palate. Cranial nerve IX the glossopharyngeal nerve carries taste sensations from the posterior one third of the tongue (including the circumvallate papillae). Also a branch of the vagus nerve carries some taste sensations from the back of the oral cavity (i.e., pharynx and epiglottis). Information from these cranial nerves is processed by the gustatory system. Though there are small differences in sensation, which can be measured with highly specific instruments, all taste buds can respond to all types of taste. Sensitivity to all tastes is distributed across the whole tongue and indeed to other regions of the mouth where there are taste buds (epiglottis, soft palate).

Papilla

Papilla are specialized epithelial cells. There are four types of papillae: **filiform** (thread-shape), **fungiform** (mushroom-shape), **foliate** (leaf-shape), and **circumvallate** (ringed-circle). All papillae except the filiform have taste buds on their surface. Some act directly by ion channels, others act indirectly.

- **Fungiform papillae:** as the name suggests, are slightly mushroom shaped if looked at in section. These are present mostly at the apex (tip) of the tongue.
- **Filiform papillae:** these are thin, longer papillae that don't contain taste buds but are the most numerous. These papillae are mechanical and not involved in gustation.
- **Foliate papillae:** these are ridges and grooves towards the posterior part of the tongue.
- **Circumvallate papillae:** there are only about 3–14 of these papillae on most people and they are present at the back of the oral part of the tongue. They are arranged in a circular-shaped row just in front of the sulcus terminalis of the tongue.

Olfactory System

Olfaction is the sense of smell. In humans the sense of **smell** is received in **nasopharynx**. Airborne molecules go into solution on moist epithelial surface of nasal passage. An olfactory receptors neuron sends an impulse via Cranial nerve I the olfactory nerve. Although 80–90 percent of what we think is "taste" actually is due to smell. This is why when we have a head cold or stuffed up nose we have a harder time tasting our foods.

Receptors

Humans have 347 functional odor receptor genes; the other genes have nonsense mutations. This number was determined by analyzing the genome in the Human Genome Project; the number may vary among ethnic groups, and does vary among individuals. For example, not all people can smell androstenone, a component of male sweat.

Each olfactory receptor neuron in the nose expresses only one functional odor receptor. Odor receptor nerve cells may function like a key-lock system: if the odor molecules can fit into the lock the nerve cell will respond. According to shape theory, each receptor detects a feature of the odor molecule. Weak-shape theory, known as odotope theory, suggests that different receptors detect only small pieces of molecules, and these minimal inputs are combined to create a larger olfactory perception (similar to the way visual perception is built up of smaller, information-poor sensations, combined and refined to create a detailed overall perception). An alternative theory, the vibration theory proposed by Luca Turin[1], posits that odor receptors detect the frequencies of vibrations of odor molecules in the infrared range by electron tunneling. However, the behavioral predictions of this theory have been found lacking[2].

An olfactory receptor neuron, also called an olfactory sensory neuron, is the primary transduction cell in the olfactory system. Humans have about 40 million olfactory receptor neurons. In vertebrates, olfactory receptor neurons reside on the olfactory epithelium in the nasal cavity. These cells are bipolar neurons with a dendrite facing the interior space of the nasal cavity and an axon that travels along the olfactory nerve to the olfactory bulb.

Many tiny hair-like cilia protrude from the olfactory receptor cell's dendrite and into the mucus covering the surface of the olfactory epithelium. These cilia contain olfactory receptors, a type of G protein-coupled receptor. Each olfactory receptor cell contains only one type of olfactory receptor, but many separate olfactory receptor cells contain the same type of olfactory receptor. The axons of olfactory receptor cells of the same type converge to form glomeruli in the olfactory bulb.

Olfactory receptors can bind to a variety of odor molecules. The activated olfactory receptor in turn activates the intracellular G-protein GOLF, and adenylate cyclase and production of Cyclic AMP opens ion channels in the cell membrane, resulting in an influx of sodium and calcium ions into the cell. This influx of positive ions causes the neuron to depolarize, generating an action potential.

Individual olfactory receptor neurons are replaced approximately every 40 days by neural stem cells residing in the olfactory epithelium. The regeneration of olfactory receptor cells, as one of the only few instances of adult neurogenesis in the central nervous system, has raised considerable interest in dissecting the pathways for neural development and differentiation in adult organisms.

In the Brain

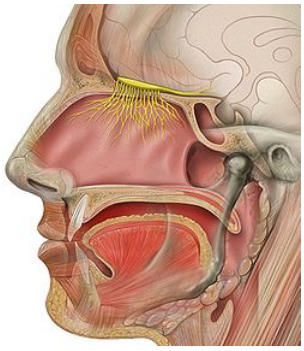


Figure 1. The Olfactory Nerve leading to the brain.

The axons from all the thousands of cells expressing the same odor receptor converge in the olfactory bulb (Figure 1). Mitral cells in the olfactory bulb send the information about the individual features to other parts of the olfactory system in the brain, which puts together the features into a representation of the odor. Since most odor molecules have many individual features, the combination of features gives the olfactory system a broad range of odors that it can detect.

Odor information is easily stored in long term memory and has strong connections to emotional memory. This is possibly due to the olfactory system's close anatomical ties to the limbic system and hippocampus, areas of the brain that have long been known to be involved in emotion and place memory, respectively.

Pheromonal Olfaction

Some pheromones are detected by the olfactory system, although in many vertebrates pheromones are also detected by the vomeronasal organ, located in the vomer, between the nose and the mouth. Snakes use it to smell prey, sticking their tongue out and touching it to the organ. Some mammals make a face called flehmen to direct air to this organ. In humans, it is unknown whether or not pheromones exist.

Olfaction and Gustation

Olfaction, taste and trigeminal receptors together contribute to flavor. It should be emphasized that there are no more than 5 distinctive tastes: salty, sour, sweet, bitter, and umami. The 10,000 different scents which humans usually recognize as “tastes” are often lost or severely diminished with the loss of olfaction. This is the reason why food has little flavor when your nose is blocked, as from a cold.

The key nutrition players in our taste is the olfactory function, 80–90 percent of what we consider taste is dependent on our senses of smell. With aging our olfactory function declines. In the elderly careful monitoring of appetite is necessary due to the alterations in the olfactory function.

The Sense of Vision

Vision needs to have the work of both the eyes and the brain to process any information. The majority of the stimuli is done in the eyes and then the information is sent to the brain by the way of nerve impulses. At least one-third of the information of what the eye sees is processed in the cerebral cortex of the brain.

Anatomy of the Eye

The human eye is a elongated ball about 1-inch (2.5 cm) in diameter and is protected by a bony socket in the skull. The eye has three layers or coats that make up the exterior wall of the eyeball, which are the sclera, choroid, and retina.

Sclera

The outer layer of the eye is the sclera, which is a tough white fibrous layer that maintains, protects and supports the shape of the eye. The front of the sclera is transparent and is called the cornea. The cornea refracts light rays and acts like the outer window of the eye.

Choroid

The middle thin layer of the eye is the choroid, also known as the choroidea or choroid coat, it is the vascular layer of the eye lying between the retina and the sclera. The choroid provides oxygen and nourishment to the outer layers of the retina. It also contains a nonreflective pigment that acts as a light shield and prevents light from scattering. Light enters the front of the eye through a hole in the choroid coat called the pupil. The iris contracts and dilates to compensate for the changes in light intensity. If the light is bright the iris then contracts making the pupil smaller, and if the light is dim, the iris dilates making the pupil bigger. Just posterior to the iris is the lens, which is composed mainly of proteins called crystallins. The lens is attached by the zonules to the ciliary body that contains the ciliary muscles that control the shape of the lens for accommodation. Along with the ciliary body and iris, the choroid forms the uveal tract. The uvea is the middle of the three concentric layers that make up an eye. The name is possibly a reference to its almost black color, wrinkled appearance and grape-like size and shape when stripped intact from a cadaveric eye.

Eye Movement

The visual system in the brain is too slow to process that information if the images are slipping across the retina at more than a few degrees per second, thus, for humans to be able to see while moving, the brain must compensate for the motion of the head by turning the eyes. To get a clear view of the world, the brain must turn the eyes so that the image of the object of regard falls on the fovea. Eye movements are thus very important for visual perception, and any failure to make them correctly can lead to serious visual disabilities. Having two eyes is an added complication, because the brain must point both of them accurately enough that the object of regard falls on corresponding points of the two retinas; otherwise, double vision would occur. The movements of different body parts are controlled by striated muscles acting around joints. The movements of the eye are no exception, but they have special advantages not shared by skeletal muscles and joints, and so are considerably different.

Try This Experiment

Hold your hand up, about one foot (30 cm) in front of your nose. Keep your head still, and shake your hand from side to side, slowly at first, and then faster and faster. At first you will be able to see your fingers quite clearly. But as the frequency of shaking passes about one hertz, the fingers will become a blur. Now, keep your hand still, and shake your head (up and down or left and right). No matter how fast you shake your head, the image of your fingers remains clear. This demonstrates that the

brain can move the eyes opposite to head motion much better than it can follow, or pursue, a hand movement. When your pursuit system fails to keep up with the moving hand, images slip on the retina and you see a blurred hand.

Depth Perception

Depth perception is the visual ability to perceive the world in three dimensions. It is a trait common to many higher animals. Depth perception allows the beholder to accurately gauge the distance to an object. Depth perception is often confused with binocular vision, also known as Stereopsis. Depth perception does rely on binocular vision, but it also uses many other monocular cues.

The Senses Of Hearing

The ear is the sense organ that collects and detects sound waves and plays a major role in the sense of balance and body position. The sensory receptors for both hearing and equilibrium are mechanoreceptors found in the inner ear; these receptors are hair cells that have stereocilia (long microvilli) that are extremely sensitive to mechanical stimulations.

Anatomy of the Ear

The ear has three divisions: the outer ear, the middle ear, and the inner ear (Figure 3).

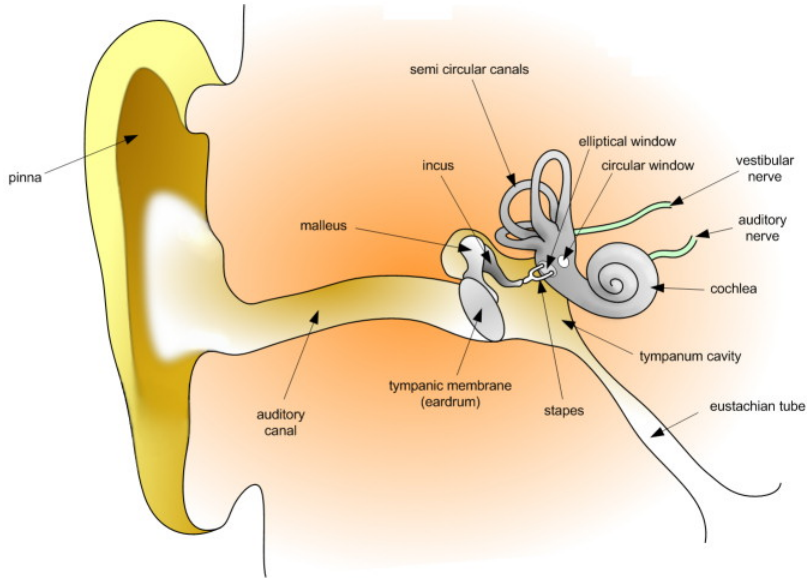


Figure 3. Anatomy of the human ear.

Outer Ear: Auricle, Ear Canal, Surface of Ear Drum

The outer ear is the most external portion of the ear. The outer ear includes the pinna (also called **auricle**), the ear canal, and the very most superficial layer of the ear drum (also called the **tympanic membrane**). Although the word “ear” may properly refer to the pinna (the flesh covered cartilage appendage on either side of the head), this portion of the ear is not vital for hearing. The complicated design of the human outer ear does help capture sound, but the most important functional aspect of the human outer ear is the ear canal itself. This outer ear canal skin is applied to cartilage; the thinner skin of the deep canal lies on the bone of the skull. If the ear canal is not open, hearing will be dampened. Ear wax (medical name: **cerumen**) is produced by glands in the skin of the outer portion of the ear canal. Only the thicker cerumen-producing ear canal skin has hairs. The outer ear ends at the most superficial layer of the tympanic membrane. The tympanic membrane is commonly called the ear drum.

Middle Ear: Air Filled Cavity behind the Ear Drum, includes most of the Ear Drum, and Ear Bones

The middle ear includes most of the ear drum (tympanic membrane) and the 3 ear bones ossicles: malleus (or hammer), incus (or anvil), and stapes (or stirrup). The opening of the Eustachian tube is also within the middle ear. The malleus has a long process (the handle) that is attached to the mobile portion of the ear drum. The incus is the bridge between the malleus and stapes. The stapes is the smallest named bone in the human body. The stapes transfers the vibrations of the incus to the **oval window**, a portion of the inner ear to which it is connected. It is the final bone in the chain to transfer vibrations from the eardrum to the inner ear. The

arrangement of these 3 bones is a sort of Rube Goldberg device: movement of the tympanic membrane causes movement of the first bone, which causes movement of the second, which causes movement of the third. When this third bone pushes down, it causes movement of fluid within the cochlea (a portion of the inner ear). This particular fluid only moves when the stapes footplate is depressed into the inner ear. Unlike the open ear canal, however, the air of the middle ear is not in direct contact with the atmosphere outside the body. The Eustachian tube connects from the chamber of the middle ear to the back of the pharynx. The middle ear in humans is very much like a specialized paranasal sinus, called the tympanic cavity, it, like the paranasal sinuses, is a hollow mucosa lined cavity in the skull that is ventilated through the nose. The mastoid portion of the temporal bone, which can be felt as a bump in the skull behind the pinna, also contains air, which ventilates through the middle ear.

Inner Ear: Cochlea, Vestibule, and Semi-Circular Canals

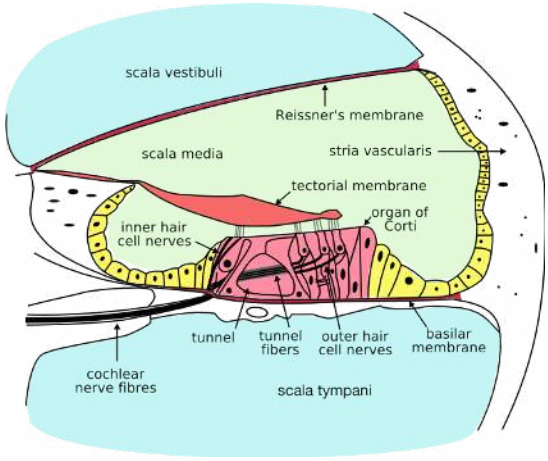


Figure 4. Cross section of the cochlea

The inner ear includes both the organ of hearing (the cochlea, Figure 4) and a sense organ (the labyrinth or vestibular apparatus) that is attuned to the effects of both gravity and motion. The balance portion of the inner ear consists of three semi-circular canals and the vestibule. The inner ear is encased in the hardest bone of the body. Within this ivory hard bone, there are fluid-filled hollows. Within the cochlea are three fluid filled spaces: the tympanic canal, the vestibular canal, and the middle canal. The eighth cranial nerve comes from the brain stem to enter the inner ear. When sound strikes the ear drum, the movement is transferred to the footplate of the stapes, which attaches to the oval window and presses into one of the fluid-filled ducts of the cochlea. The hair cells in the organ of Corti are stimulated by particular frequencies of sound, based on their location within the cochlea. High pitch sounds are at a higher frequency and, due to the shorter wavelength they “hit” the membrane “faster” (ie. close to the oval window). In contrast, low frequency sounds have large wavelengths, and will travel further through the scala vestibuli before “hitting” the tectorial membrane near the apex of the cochlea. The fluid inside the cochlea is moved, flowing against the receptor (hair) cells of the organ of Corti, which fire in a graded response based on the volume of the sound. The hair cells then stimulate the nerve cells in the Spiral Ganglion, which sends information through the auditory portion of the eighth cranial nerve to the brain. Humans are able to hear sounds between about 20 Hz and 20,000 Hz. Mammals that can hear lower frequency sounds, such as whales and elephants, have a longer cochlea. Humans tend to lose high-frequency hearing first, which has led some teenagers to using high-frequency ring tones (above 17,000 Hz) that may go undetected by their middle-aged teachers.

Hair Cell

Hair cells are columnar cells, each with a bundle of 100–200 specialized cilia at the top, for which they are named. These cilia are the mechanosensors for hearing. Lightly resting atop the longest cilia is the tectorial membrane, which moves back and forth with each cycle of sound, tilting the cilia and allowing electric current into the hair cell. Hair cells, like the photoreceptors of the eye, show a graded response, instead of the spikes typical of other neurons.

Immediately over the hair cells of the organ of Corti is an overhanging “tectorial membrane.” When the Bones of the Middle Ear vibrate the oval window, these vibrations are transmitted to the fluid within the cochlea and eventually cause the round window on the cochlea to bulge outward. These vibrations deflect the membrane on which the Organ of Corti is located, causing the three rows of outer hair cells to “rub” against the overhanging tectorial membrane. By their muscle-like activity they ampify the weakest

vibrations for the inner hair cells. The louder sounds are not amplified. The disturbed inner hair cells will then activate the cochlear nerve fibers.

The current model is that cilia are attached to one another by “tip links,” structures which link the tips of one cilium to another. Stretching and compressing the tip links may open an ion channel and produce the receptor potential in the hair cell. These graded potentials are not bound by the “all or none” properties of an action potential. There are far fewer hair cells than afferent (leading to the brain) nerve fibers in the cochlea. The nerve that innervates the cochlea is the cochlear nerve, and forms cranial nerve number VIII with the vestibular nerve from the balance organ. Neuronal dendrites innervate cochlear hair cells. The neurotransmitter itself is thought to be **glutamate**. At the presynaptic juncture, there is a distinct “presynaptic dense body” or ribbon. This dense body is surrounded by synaptic vesicles and is thought to aid in the fast release of neurotransmitter. Efferent projections from the brain to the cochlea also play a role in the perception of sound. Efferent synapses occur on outer hair cells and on afferent dendrites under inner hair cells.

Process of Hearing

Detection of sound motion is associated with the right posterior superior temporal gyrus. The superior temporal gyrus contains several important structures of the brain, including: marking the location of the primary auditory cortex, the cortical region responsible for the sensation of sound. Sections 41 and 42 are called the primary auditory area of the cerebrum, and processes the basic characteristics of sound such as pitch and rhythm. The auditory association area is located within the temporal lobe of the brain, in an area called the Wernicke’s area, or area 22. This area, near the lateral cerebral sulcus, is an important region for the processing of acoustic energy so that it can be distinguished as speech, music, or noise. It also interprets words that are heard into an associated thought pattern of understanding. The gnostic area of the cerebrum, (areas 5, 7, 39 and 40) helps to integrate all incoming sense patterns so that a common thought can be formed (correlated) using all arriving sensory information.

Hearing Under Water

Hearing threshold and the ability to localize sound sources are reduced underwater. in which the speed of sound is faster than in air. Underwater, hearing is by bone conduction and localization of sound appears to depend on differences in amplitude detected by bone conduction.

Localization of Sound by Humans

Humans are normally able to hear a variety of sound frequencies, from about 20Hz to 20kHz. Our ability to estimate just where the sound is coming from, sound localization, is dependent on both hearing ability of each of the two ears, and the exact quality of the sound. Since each ear lies on an opposite side of the head, a sound will reach the closest ear first, and its amplitide will be loudest in that ear. Much of the brain’s ability to localize sound depends on interaural (between ears) intensity differences and interaural temporal or phase differences.

Two mechanisms are known to be used. Bushy neurons can resolve time differences as small as the time it takes sound to pass one ear and reach the other (10 milliseconds). For high frequencies, frequencies with a wavelength shorter than the listener’s head, more sound reaches the nearer ear. Human echolocation is a technique involving echolocation used by some blind humans to navigate within their environment.

Process of Equilibrium

Equilibrioception or sense of balance is one of the physiological senses. It allows humans and animals to walk without falling. Some animals are better in this than humans, for example allowing a cat (as a quadruped using its inner ear and tail) to walk on a thin fence. All forms of equilibrioception can be described as the detection of acceleration.

It is determined by the level of fluid properly called endolymph in the labyrinth: a complex set of tubing in the inner ear.

When the sense of balance is interrupted it causes dizziness, disorientation and nausea.

You can temporarily disturb your sense of balance by closing your eyes and turning rapidly in circles five or six times. This starts the fluid swirling in circles inside your ear canal. When you stop turning it takes a few seconds for the fluid to lose momentum, and until then the sense from your inner ear conflicts with the information coming from your vision, causing dizziness and disorientation. Most astronauts find that their sense of balance is impaired when in orbit, because there is not enough gravity to keep the ear’s fluid in balance. This causes a form of motion sickness called space sickness.

Touch

Touch is the first sense developed in the womb and the last sense used before death. With 50 touch receptors for every square centimeter and about 5 million sensory cells overall, the skin is very sensitive and is the largest and one of the most complex organs in our bodies. These touch receptors are grouped by type and include mechanoreceptors (sensitive to pressure, vibration and slip), thermoreceptors (sensitive to changes in temperature), and nocioreceptors (responsible for pain).

Pacinian Corpuscles

Pacinian corpuscles detect gross pressure changes and vibrations. They are the largest of the receptors. Any deformation in the corpuscle causes action potentials to be generated, by opening pressure-sensitive sodium ion channels in the axon membrane. This allows sodium ions to influx in, creating a receptor potential. Pacinian corpuscles cause action potentials when the skin is rapidly indented but not when the pressure is steady, due to the layers of connective tissue that cover the nerve ending [3]. It is thought that they respond to high velocity changes in joint position.

Meissner's Corpuscle

Meissner's corpuscles are distributed throughout the skin, but concentrated in areas especially sensitive to light touch, such as the fingertips, palms, soles, lips, tongue, face, nipples and the external skin of the male and female genitals. They are primarily located just beneath the epidermis within the dermal papillae. Any physical deformation in the Meissner's corpuscle will cause an action potential in the nerve. Since they are rapidly adapting or phasic, the action potentials generated quickly decrease and eventually cease. If the stimulus is removed, the corpuscle regains its shape and while doing so (i.e., while physically reforming) causes another volley of action potentials to be generated. This is the reason one stops "feeling" one's clothes. This process is called **sensory adaption**. Because of their superficial location in the dermis, these corpuscles are particularly sensitive to touch and vibrations, but for the same reasons, they are limited in their detection because they can only signal that something is touching the skin. Meissner's corpuscles do not detect pain; this is signaled exclusively by free nerve endings.

Ruffini Corpuscles

Ruffini corpuscles are thermoreceptors, aiding in the detection of temperature changes. Named after Angelo Ruffini, the Ruffini ending is a class of slowly adapting mechanoreceptor thought to exist only in the glabrous dermis and subcutaneous tissue of humans. This spindle-shaped receptor is sensitive to skin stretch, and contributes to the kinesthetic sense of and control of finger position and movement.

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16.11: Introduction to Cell Maintenance Systems

Describe the circulatory, immune, respiratory, and digestive systems

This set of body systems has been grouped together as the “cell maintenance systems.” Remember, this isn’t a hard-and-fast categorization: these systems are grouped together to help you organize your learning. These body systems all function to maintain the cells in your body: the circulatory, respiratory, and digestive systems provide the nutrients and energy your cells need to live. The immune system protects these cells from pathogens.

What You’ll Learn to Do

- Identify the structure and function of the circulatory system
- Identify the structure and function of the respiratory system
- Identify the structure and function of the immune system
- Identify the structure and function of the digestive system

Learning Activities

The learning activities for this section include the following:

- Circulatory System
- Respiratory System
- Immune System
- Digestive System
- Self Check: Cell Maintenance Systems

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16.12: Circulatory System

The circulatory system is extremely important in sustaining life. It's proper functioning is responsible for the delivery of oxygen and nutrients to all cells, as well as the removal of carbon dioxide, waste products, maintenance of optimum pH, and the mobility of the elements, proteins and cells, of the immune system. In developed countries, the two leading causes of death, myocardial infarction and stroke are each direct results of an arterial system that has been slowly and progressively compromised by years of deterioration. The circulatory system includes the heart, blood vessels, blood, lymph and lymph vessels. But we often think of it as the vascular network that connects to the primary cardiac organ, the heart. More accurately the vascular network directly connected to the heart is just blood and blood vessels, but do not be surprised to see the terms *circulatory* and *cardiovascular* used interchangeably. Here we are focusing on the heart and vascular network that transports blood.

The Heart

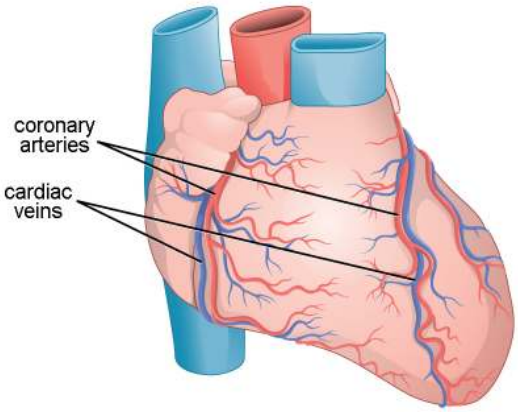


Figure 1. Blood vessels of the coronary system, including the coronary arteries and veins, keep the heart musculature oxygenated.

The heart is the life-giving, ever-beating muscle in your chest. From inside the womb until death, the thump goes on. The heart for the average human will contract about 3 billion times; never resting, never stopping to take a break except for a fraction of a second between beats. At 80 years of age, a person's heart will continue to beat an average of 100,000 times a day. Many believe that the heart is the first organ to become functional. Within weeks of conception the heart starts its mission of supplying the body with nutrients even though the embryo is no bigger than a capital letter on this page. The primary function of the heart is to pump blood through the arteries, capillaries, and veins. There are an estimated 60,000 miles of vessels throughout an adult body. Blood transports oxygen, nutrients, disease causing viruses, bacteria, hormones and has other important functions as well. The heart is the pump that keeps blood circulating properly. Americans today have many options to take care of their heart and circulatory system. Expanding medical technology has made it much easier to do so.

The heart is a hollow, muscular organ about the size of a fist. It is responsible for pumping blood through the blood vessels by repeated, rhythmic contractions. The heart is composed of cardiac muscle, an involuntary muscle tissue that is found only within this organ. The term "cardiac" (as in cardiology) means "related to the heart" and comes from the Greek word kardia, for "heart." It has a four-chambered, double pump and is located in the thoracic cavity between the lungs. The cardiac muscle is self-exciting, meaning it has its own conduction system. This is in contrast with skeletal muscle, which requires either conscious or reflex nervous stimuli. The heart's rhythmic contractions occur spontaneously, although the frequency or heart rate can be changed by nervous or hormonal influence such as exercise or the perception of danger.

The Cardiovascular System

Arteries

Arteries are muscular blood vessels that carry blood away from the heart, oxygenated and deoxygenated blood. The pulmonary arteries will carry deoxygenated blood to the lungs and the systemic arteries will carry oxygenated blood to the rest of the body. Arteries have a thick wall that consists of three layers. The inside layer is called the endothelium, the middle layer is mostly smooth muscle and the outside layer is connective tissue. The artery walls are thick so that when blood enters under pressure the walls can expand.

Arterioles

An arteriole is a small artery that extends and leads to capillaries. Arterioles have thick smooth muscular walls. These smooth muscles are able to contract (causing vessel constriction) and relax (causing vessel dilation). This contracting and relaxing affects blood pressure; the higher number of vessels dilated, the lower blood pressure will be. Arterioles are just visible to the naked eye.

Capillaries

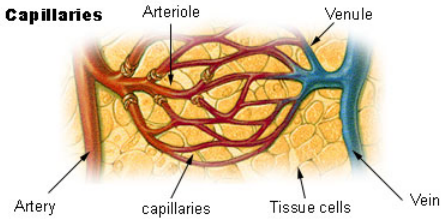


Figure 2. Capillaries

Capillaries are the smallest of a body's vessels; they connect arteries and veins, and most closely interact with tissues. They are very prevalent in the body; total surface area is about 6,300 square meters. Because of this, no cell is very far from a capillary, no more than 50 micrometers away. The walls of capillaries are composed of a single layer of cells, the endothelium, which is the inner lining of all the vessels. This layer is so thin that molecules such as oxygen, water and lipids can pass through them by diffusion and enter the tissues. Waste products such as carbon dioxide and urea can diffuse back into the blood to be carried away for removal from the body.

The "capillary bed" is the network of capillaries present throughout the body. These beds are able to be "opened" and "closed" at any given time, according to need. This process is called autoregulation and capillary beds usually carry no more than 25 percent of the amount of blood it could hold at any time. The more metabolically active the cells, the more capillaries it will require to supply nutrients.

Veins

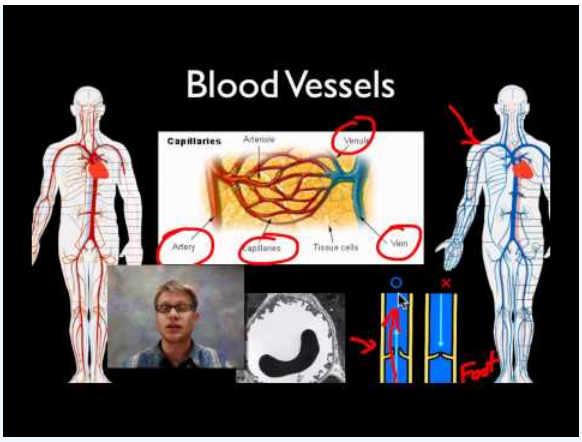
Veins carry blood to the heart. The pulmonary veins will carry oxygenated blood to the heart awhile the systemic veins will carry deoxygenated to the heart. Most of the blood volume is found in the venous system; about 70% at any given time. The veins outer walls have the same three layers as the arteries, differing only because there is a lack of smooth muscle in the inner layer and less connective tissue on the outer layer. Veins have low blood pressure compared to arteries and need the help of skeletal muscles to bring blood back to the heart. Most veins have one-way valves called venous valves to prevent backflow caused by gravity. They also have a thick collagen outer layer, which helps maintain blood pressure and stop blood pooling. If a person is standing still for long periods or is bedridden, blood can accumulate in veins and can cause varicose veins. The hollow internal cavity in which the blood flows is called the lumen. A muscular layer allows veins to contract, which puts more blood into circulation. Veins are used medically as points of access to the blood stream, permitting the withdrawal of blood specimens (venipuncture) for testing purposes, and enabling the infusion of fluid, electrolytes, nutrition, and medications (intravenous delivery).

Venules

A venule is a small vein that allows deoxygenated blood to return from the capillary beds to the larger blood veins, except in the pulmonary circuit were the blood is oxygenated. Venules have three layers; they have the same makeup as arteries with less smooth muscle, making them thinner.

Learning Objectives

Watch this video for a quick survey of the human circulatory system:



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16.13: Respiratory System

The **Respiratory System** is vital to every human being. Without it, we would cease to live outside of the womb. Let us begin by taking a look at the structure of the respiratory system and how vital it is to life. During inhalation or exhalation air is pulled towards or away from the lungs, by several cavities, tubes, and openings.

The organs of the respiratory system make sure that oxygen enters our bodies and carbon dioxide leaves our bodies.

The respiratory tract is the path of air from the nose to the lungs. It is divided into two sections: **Upper Respiratory Tract** and the **Lower Respiratory Tract**. Included in the upper respiratory tract are the **Nostrils**, **Nasal Cavities**, **Pharynx**, **Epiglottis**, and the **Larynx**. The lower respiratory tract consists of the **Trachea**, **Bronchi**, **Bronchioles**, and the **Lungs**.

As air moves along the respiratory tract it is warmed, moistened and filtered.

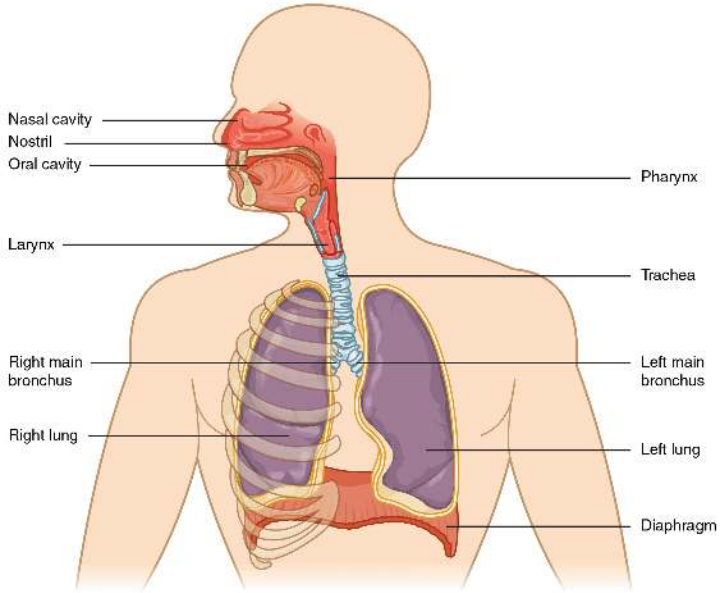


Figure 1. Click for a larger image. The major respiratory structures span the nasal cavity to the diaphragm.

Functions

There are four processes of respiration. They are:

1. **Breather** or ventilation
2. **External Respiration**, which is the exchange of gases (oxygen and carbon dioxide) between inhaled air and the blood.
3. **Internal Respiration**, which is the exchange of gases between the blood and tissue fluids.
4. **Cellular Respiration**

In addition to these main processes, the respiratory system serves for:

- **Regulation of Blood pH**, which occurs in coordination with the kidneys,
- **Defense against microbes**
- **Control of body temperature** due to loss of evaporate during expiration

Respiratory System: Upper and Lower Respiratory Tracts

For the sake of convenience, we will divide the respiratory system in to the upper and lower respiratory tracts:

Upper Respiratory Tract

The **upper respiratory tract**, can refer to the parts of the respiratory system lying above the sternal angle (outside of the thorax), above the vocal folds, or above the cricoid cartilage. The tract consists of the nasal cavity and paranasal sinuses, the pharynx

(nasopharynx, oropharynx and laryngopharynx) and sometimes includes the larynx. Its primary function is to receive the air from the external environment and filter, warm, and humidify it before it reaches the delicate lungs where gas exchange will occur.

Air enters through the nostrils of the nose and is partially filtered by the nose hairs, then flows into the nasal cavity. The nasal cavity is lined with epithelial tissue, containing blood vessels, which help warm the air; and secrete mucous, which further filters the air. The endothelial lining of the nasal cavity also contains tiny hairlike projections, called cilia. The *cilia* serve to transport dust and other foreign particles, trapped in mucous, to the back of the nasal cavity and to the pharynx. There the mucus is either coughed out, or swallowed and digested by powerful stomach acids. After passing through the nasal cavity, the air flows down the pharynx to the larynx.

Lower Respiratory Tract

The lower respiratory tract or lower airway is derived from the developing foregut and consists of the trachea, bronchi (primary, secondary and tertiary), bronchioles (including terminal and respiratory), and lungs (including alveoli). It also sometimes includes the larynx, which we have done here. This is where gas exchange actually takes place.

Larynx

The larynx (plural larynges), colloquially known as the voice box, is an organ in our neck involved in protection of the trachea and sound production. The larynx houses the vocal cords, and is situated just below where the tract of the pharynx splits into the trachea and the esophagus. The larynx contains two important structures: the epiglottis and the vocal cords.

The epiglottis is a flap of cartilage located at the opening to the larynx. During swallowing, the larynx (at the epiglottis and at the glottis) closes to prevent swallowed material from entering the lungs; the larynx is also pulled upwards to assist this process. Stimulation of the larynx by ingested matter produces a strong cough reflex to protect the lungs. Note: choking occurs when the epiglottis fails to cover the trachea, and food becomes lodged in our windpipe.

The vocal cords consist of two folds of connective tissue that stretch and vibrate when air passes through them, causing vocalization. The length the vocal cords are stretched determines what pitch the sound will have. The strength of expiration from the lungs also contributes to the loudness of the sound. Our ability to have some voluntary control over the respiratory system enables us to sing and to speak. In order for the larynx to function and produce sound, we need air. That is why we can’t talk when we’re swallowing.

Trachea

Air travels from the larynx to the trachea (Figure 1). The trachea is a tubular structure consisting of dense connective tissue and rings of hyaline cartilage. The trachea is lined with ciliated pseudostratified columnar epithelium with goblet cells. The epithelium moves substances toward the larynx and esophagus for swallowing. The cartilage rings do not completely encircle the trachea but are open posteriorly. The posterior section of the trachea contains a ligament and smooth muscle known as the trachealis muscle. The trachealis muscle can contract and constrict the trachea. The trachea usually ends at about the level of the fifth thoracic segment. The inferior end of the trachea divides into right and left bronchi at an area known as the carina. The carina is the last tracheal cartilage and forms a cartilage division between the two bronchi.

Bronchial Tree

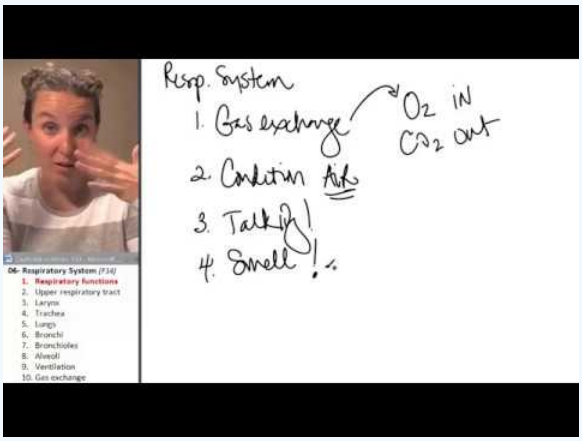
The trachea ends at the carina and divides into two tubular structures called the right and left primary bronchi. The bronchi then divide into smaller branches called secondary or lobar bronchi and then even smaller branches called tertiary or segmental bronchi. The structure of the bronchi is similar to the trachea with incomplete cartilage rings and smooth muscle. As the bronchi get smaller there is less cartilage and more smooth muscle until reaching the tertiary bronchi that consists entirely of smooth muscle. The smooth muscle can constrict the bronchi and impede air passage. The bronchi continue to branch and form small bronchioles which divide to form terminal bronchioles. The terminal bronchioles divide to form respiratory bronchioles that connect with alveolar ducts. The alveolar ducts give rise to alveoli. Alveoli are considered the functional unit of the lung and consist of Dr. Bruce Forciea Page 560 small hollow areas for gas exchange. The alveolar ducts and alveoli are lined with simple squamous epithelium that allows for gas exchange. The cells of the simple squamous epithelium are called Type I pneumocytes. The alveoli also contain other cells known as type II pneumocytes. These cells secrete a substance known as surfactant that helps to decrease the surface tension in the alveoli. The lungs contain about 300 million alveoli.

The Lungs

The lungs are two cone shaped structures residing in the thoracic cavity. The inferior portion of each lung reaches to the diaphragm. The superior portion extends about one inch above each clavicle. The right lung contains three lobes (superior, middle and inferior) and is larger than the left lung which contains two lobes (superior and inferior). The lobes are separated by fissures. The right lung includes a horizontal and oblique fissure while the left lung only contains an oblique fissure. The medial surface of each lung contains an area known as the hilum where vessels enter and exit. The left lung also contains the cardiac notch which is an indentation for the heart. The lungs are surrounded by two pleural membranes. The surface of each lung contains a visceral pleural membrane that closely adheres to the lung's surface. Lining the interior of the thoracic wall is the parietal pleural membrane. Both are serous membranes. A fluid known as pleural fluid is secreted by each membrane that reduces friction and helps to hold the membranes together.

Learning Objectives

Watch this video to learn more about the respiratory system:



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16.14: Immune System

Our immune systems offer us protection against a world full of pathogens. Our immune systems work by providing two types of immunity. In non-specific immunity our bodies present the same kinds of defense systems regardless of the type of pathogens. Non-specific immunity works much like a fence around your property. The fence does not differentiate between friend or foe. It keeps everyone out. The other type of immunity is known as specific immunity (defense). Specific defense produces an attack against a specific pathogen. This is much like having an attendant at the gate of the fence around your house. The attendant can identify potential foes and keep them out.

Before birth the body inventories all of the cells and tissues of the body and classifies them as “self” cells. The presentation of non-self cells can then trigger the immune system.

Table 1. Components of the immune system

Innate immune system	Adaptive immune system
Response is non-specific	Pathogen and antigen specific response
Exposure leads to immediate maximal response	Lag time between exposure and maximal response
Cell-mediated and humoral components	Cell-mediated and humoral components
No immunological memory	Exposure leads to immunological memory
Found in nearly all forms of life	Found only in jawed vertebrates

Non-Specific Defense

Non-specific defense (innate immunity) consists of mechanisms that either keep pathogens out or destroy them regardless of their type. Non-specific defense includes mechanical barriers, chemical substances, cells and inflammation.

Mechanical barriers include the skin and mucous membranes. Besides presenting a physical barrier that stops pathogens they also work to remove substances from the surface of membranes. Examples include the movement of mucous moving substances toward the digestive tract and tears washing substances from the eyes.

Chemical substances work to destroy pathogens. These include enzymes, cytokines, and the complement system. For example, mucous from the respiratory tract moves toward the pharynx and esophagus where it is swallowed. Upon reaching the digestive tract pathogens are destroyed by powerful digestive enzymes.

Cytokines are a series of protein substances secreted by cells that work to destroy pathogens. Interferons are cytokines that bind to cells causing them to produce substances that inhibit viral replication. One type of interferon can affect many types of viruses. Interferons can also activate other immune cells such as macrophages and natural killer cells. Some cytokines produce fever. Interleukin I (endogenous pyrogen) is a cytokine that acts as a pyrogen (raises body temperature). This cytokine is released in response to toxins or pathogens and causes an increase in body temperature.

The compliment system is a series of about 20 plasma proteins. They include proteins that are named C1-C9 and factors B, D, P. They act much like the clotting cascade in that activation of the first compliment protein causes the others to activate. Complement system responses include inflammation, phagocytosis from white blood cells attracted to the area, and attacking non-self cells.

Inflammation is characterized by swelling, redness, heat and pain (tumor, rubor, calor, dolor). Inflammation is produced by tissue destruction from trauma, cuts, temperature and chemicals. Inflammation causes an increased blood flow to the damaged area. Blood brings substances for repair and the stasis of blood in the area prevents further spread of pathogens. Inflammation is primarily caused by the release of histamine and heparin from mast cells (similar to basophils). Histamine promotes local vasodilation and capillary permeability while heparin inhibits clotting. Phagocytes are also attracted to the area and remove debris. Neutrophils release substances that activate fibroblasts to begin to repair the area. Substances released by cells stimulate pain receptors in the tissue causing the sensation of pain.

Specific Defense

Specific defense (sometimes called adaptive immunity) recognizes and coordinates attacks against specific pathogens. The system can also remember pathogens and produce a powerful response the next time a pathogen enters the body.

There are two types of specific defense. These include cell-mediated immunity and antibody-mediated immunity. Cell-mediated immunity occurs when T-lymphocytes (T-cells) become activated by exposure to pathogens. Activated T-cells then attack pathogens directly.

T-cells become activated when exposed to antigens on pathogens. T-cells react with portions of antigens called antigenic determinants (epitopes). T-cells contain antigen receptors on their surface that combine with antigenic determinants on pathogens. The antigen receptors are polypeptide chains that contain variable and constant regions. The variable region binds to the antigenic determinant. This is known as direct activation of T-cells.

Major Histocompatibility Complexes

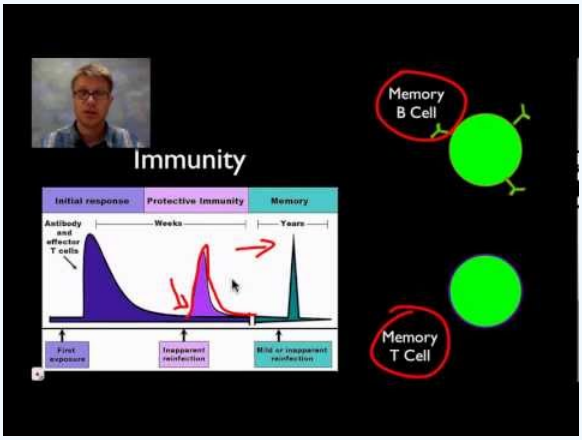
Specific glycoproteins can activate T-cells. These glycoproteins are called major histocompatibility complex molecules (MHC molecules). MHC molecules reside on cell membranes and contain a variable region. The variable region is the portion of the molecule that allows for binding to antigens.

MHC class I molecules display antigens on the surface of cells. The antigens are produced inside cells. One example is a cell infected with a virus. The virus replicates inside the cell producing proteins. These proteins combine with MHC class I molecules that move to the outer cell membrane for display. Once displayed on the surface of the cell the immune system can attack and destroy the cell.

MHC class II molecules are found on cells that present antigens. Antigens enter cells via endocytosis and combine with MHC class II molecules in vesicles. The antigen-MHC complex combination is then transported to the cell membrane and displayed on the surface. The response to MHC class II complexes differs from MHC class I in that the MHC class II presenting cells are not directly attacked. The MHC II complex acts more like a signal to other immune system cells to mobilize against the antigen.

Learning Objectives

Watch this video to learn more about your immune system:



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16.15: Digestive System

Which organ is the most important organ in the body? Most people would say the heart or the brain, completely overlooking the gastrointestinal tract (GI tract). Though definitely not the most attractive organs in the body, they are certainly among the most important. The 30 plus foot long tube that goes from the mouth to the anus is imperative for our well being and our lifelong health. A non-functioning or poorly functioning GI tract can be the source of many chronic health problems that can interfere with your quality of life. In many instances the death of a person begins in the intestines.

The old saying “you are what you eat” perhaps would be more accurate if worded “you are what you absorb and digest.” Here we will be looking at the importance of these two functions of the digestive system: digestion and absorption.

The **gastrointestinal system** is responsible for the breakdown and absorption of various foods and liquids needed to sustain life. Many different organs have essential roles in the digestion of food, from the mechanical disrupting by the teeth to the creation of bile (an emulsifier) by the liver. Bile production of the liver plays an important role in digestion: from being stored and concentrated in the gallbladder during fasting stages to being discharged to the small intestine.

The GI tract starts with the mouth and proceeds to the esophagus, stomach, small intestine (duodenum, jejunum, ileum), and then to the large intestine (colon), rectum, and terminates at the anus. You could probably say the human body is just like a big donut. The GI tract is the donut hole.

The Digestive System

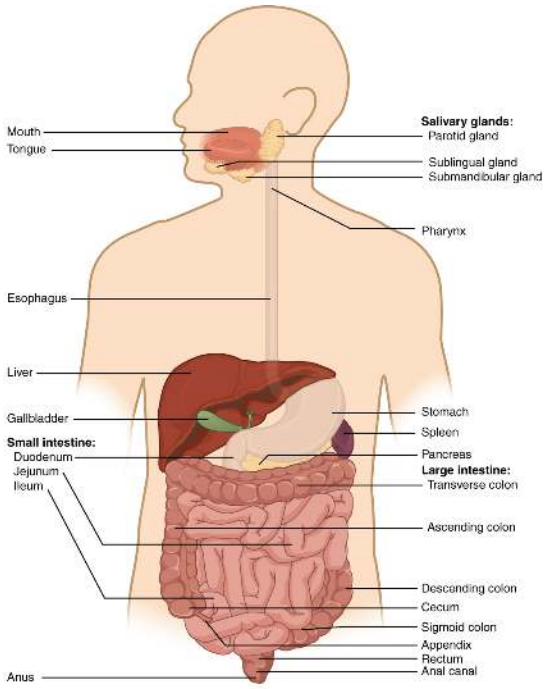


Figure 1. All digestive organs play integral roles in the life-sustaining process of digestion.

The first step in the digestive system can actually begin before the food is even in your mouth. When you smell or see something that you just have to eat, you start to salivate in anticipation of eating, thus beginning the digestive process.

Food is the body’s source of fuel. Nutrients in food give the body’s cells the energy they need to operate. Before food can be used it has to be broken down into tiny little pieces so it can be absorbed and used by the body. In humans, proteins need to be broken down into amino acids, starches into sugars, and fats into fatty acids and glycerol.

During digestion two main processes occur at the same time:

- **Mechanical Digestion**: larger pieces of food get broken down into smaller pieces while being prepared for chemical digestion. Mechanical digestion starts in the mouth and continues in to the stomach.

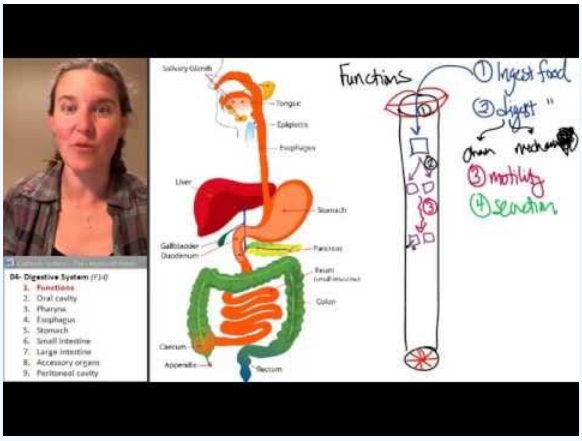
- **Chemical Digestion**: several different enzymes break down macromolecules into smaller molecules that can be more efficiently absorbed. Chemical digestion starts with saliva and continues into the intestines. The major enzymes involved in chemical digestion are shown in the table below.

The digestive system is made up by the alimentary canal, or the digestive tract, and other abdominal organs that play a part in digestion such as the liver and the pancreas. The alimentary canal is the long tube of organs that runs from the mouth (where the food enters) to the anus (where indigestible waste leaves). The organs in the alimentary canal include the mouth(for mastication),esophagus, stomach and the intestines. The average adult digestive tract is about thirty feet (30′) long. While in the digestive tract the food is really passing *through* the body rather than being *in* the body. The smooth muscles of the tubular digestive organs move the food efficiently along as it is broken down into absorb-able atoms and molecules. During absorption, the nutrients that come from food (such as proteins, fats, carbohydrates, vitamins, and minerals) pass through the wall of the small intestine and into the bloodstream and lymph. In this way nutrients can be distributed throughout the rest of the body. In the large intestine there is reabsorption of water and absorption of some minerals as feces are formed. The parts of the food that the body passes out through the anus is known as feces.

Enzyme	Produced In	Site of Release	pH Level
Carbohydrate Digestion			
Salivary amylase	Salivary glands	Mouth	Neutral
Pancreatic amylase	Pancreas	Small intestine	Basic
Maltase	Small intestine	Small intestine	Basic
Protein Digestion			
Pepsin	Gastric glands	Stomach	Acidic
Trypsin	Pancreas	Small intestine	Basic
Peptidases	Small intestine	Small intestine	Basic
Nucleic Acid Digestion			
Nuclease	Pancreas	Small intestine	Basic
Nucleosidases	Pancreas	Small intestine	Basic
Fat Digestion			
Lipase	Pancreas	Small intestine	Basic

Learning Objectives

Watch this video series introducing the digestive system:



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16.16: Introduction to Support Systems

Describe the muscular, skeletal, and integumentary systems

This set of body systems has been grouped together as the “support systems.” Remember, this isn’t a hard-and-fast categorization: these systems are grouped together to help you organize your learning. These support systems provide the structure (and support!) for your body: your muscles, skeleton, and skin.

What You’ll Learn to Do

- Identify the structure and function of the muscular system
- Identify the structure and function of the skeletal system
- Identify the structure and function of the integumentary system

Learning Activities

The learning activities for this section include the following:

- Muscular System
- Skeletal System
- Integumentary System
- Self Check: Support Systems

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16.17: The Muscular System

The **muscular system** is the biological system of humans that produces movement. The muscular system, in vertebrates, is controlled through the nervous system, although some muscles, like cardiac muscle, can be completely autonomous. **Muscle** is contractile tissue and is derived from the mesodermal layer of embryonic germ cells. Its function is to produce force and cause motion, either locomotion or movement within internal organs. Much of muscle contraction occurs without conscious thought and is necessary for survival, like the contraction of the heart or peristalsis, which pushes food through the digestive system. Voluntary muscle contraction is used to move the body and can be finely controlled, such as movements of the finger or gross movements like those of the biceps and triceps.

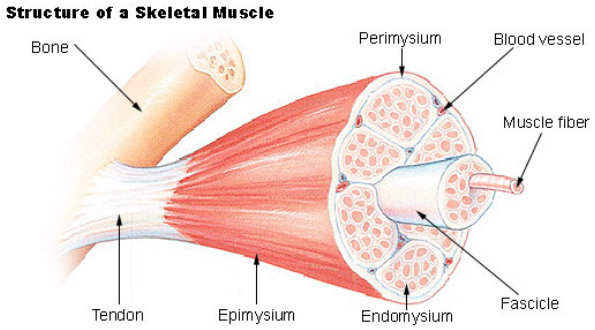


Figure 1. Muscle structure

Muscle is composed of muscle cells (sometimes known as “muscle fibers”). Within the cells are myofibrils; myofibrils contain sarcomeres which are composed of actin and myosin. Individual muscle cells are lined with endomysium. Muscle cells are bound together by perimysium into bundles called fascicles. These bundles are then grouped together to form muscle, and is lined by epimysium. Muscle spindles are distributed throughout the muscles, and provide sensory feedback information to the central nervous system.

Skeletal muscle, which involves muscles from the skeletal tissue, is arranged in discrete groups (Figure 1). An example is the biceps brachii. It is connected by tendons to processes of the skeleton. In contrast, smooth muscle occurs at various scales in almost every organ, from the skin (in which it controls erection of body hair) to the blood vessels and digestive tract (in which it controls the caliber of a lumen and peristalsis, respectively).

There are approximately 640 skeletal muscles in the human body. Contrary to popular belief, the number of muscle fibers cannot be increased through exercise; instead the muscle cells simply get bigger. It is however believed that myofibrils have a limited capacity for growth through hypertrophy and will split if subject to increased demand. There are three basic types of muscles in the body: smooth, cardiac, and skeletal (see Figure 2). While they differ in many regards, they all use actin sliding against myosin to create muscle contraction and relaxation. In skeletal muscle, contraction is stimulated at each cell by nervous impulses that releases acetylcholine at the neuromuscular junction, creating action potentials along the cell membrane. All skeletal muscle and many smooth muscle contractions are stimulated by the binding of the neurotransmitter acetylcholine. Muscular activity accounts for most of the body’s energy consumption. Muscles store energy for their own use in the form of glycogen, which represents about 1% of their mass. Glycogen can be rapidly converted to glucose when more energy is necessary.

Types

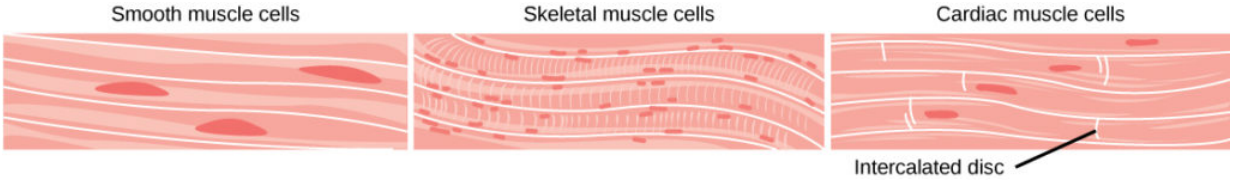


Figure 2. Smooth muscle cells do not have striations, while skeletal muscle cells do. Cardiac muscle cells have striations, but, unlike the multinucleate skeletal cells, they have only one nucleus. Cardiac muscle tissue also has intercalated discs, specialized regions running along the plasma membrane that join adjacent cardiac muscle cells and assist in passing an electrical impulse from cell to cell.

- **Smooth muscle** or “involuntary muscle” consists of spindle shaped muscle cells found within the walls of organs and structures such as the esophagus, stomach, intestines, bronchi, uterus, ureters, bladder, and blood vessels. Smooth muscle cells contain only one nucleus and no striations.
- **Cardiac muscle** is also an “involuntary muscle” but it is striated in structure and appearance. Like smooth muscle, cardiac muscle cells contain only one nucleus. Cardiac muscle is found only within the heart.
- **Skeletal muscle** or “voluntary muscle” is anchored by tendons to the bone and is used to effect skeletal movement such as locomotion. Skeletal muscle cells are multinucleated with the nuclei peripherally located. Skeletal muscle is called ‘striated’ because of the longitudinally striped appearance under light microscopy. Functions of the skeletal muscle include:
  - Support of the body
  - Aids in bone movement
  - Helps maintain a constant temperature throughout the body
  - Assists with the movement of cardiovascular and lymphatic vessels through contractions
  - Protection of internal organs and contributing to joint stability

Cardiac and skeletal muscle are striated in that they contain sarcomeres and are packed into highly-regular arrangements of bundles; smooth muscle has neither. Striated muscle is often used in short, intense bursts, whereas smooth muscle sustains longer or even near-permanent contractions.

Skeletal muscle is further divided into several subtypes:

1. Type I, slow oxidative, *slow twitch*, or “red” muscle is dense with capillaries and is rich in mitochondria and myoglobin, giving the muscle tissue its characteristic red color. It can carry more oxygen and sustain aerobic activity.
2. Type II, *fast twitch*, muscle has three major kinds that are, in order of increasing contractile speed:
   a. Type IIa, which, like slow muscle, is aerobic, rich in mitochondria and capillaries and appears red.
   b. Type IIx (also known as type IId), which is less dense in mitochondria and myoglobin. This is the fastest muscle type in humans. It can contract more quickly and with a greater amount of force than oxidative muscle, but can sustain only short, anaerobic bursts of activity before muscle contraction becomes painful (often attributed to a build-up of lactic acid). N.B. in some books and articles this muscle in humans was, confusingly, called type IIB
   c. Type IIb, which is anaerobic, glycolytic, “white” muscle that is even less dense in mitochondria and myoglobin. In small animals like rodents or rabbits this is the major fast muscle type, explaining the pale color of their meat.

For most skeletal muscles, contraction occurs as a result of conscious effort originating in the brain. The brain sends signals, in the form of action potentials, through the nervous system to the motor neuron that innervates the muscle fiber. However, some muscles (such as the heart) do not contract as a result of conscious effort. These are said to be autonomic. Also, it is not always necessary for the signals to originate from the brain. Reflexes are fast, unconscious muscular reactions that occur due to unexpected physical stimuli. The action potentials for reflexes originate in the spinal cord instead of the brain.

There are three general types of muscle contractions, matching the types of muscles: skeletal muscle contractions, heart muscle contractions, and smooth muscle contractions.

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16.18: The Skeletal System

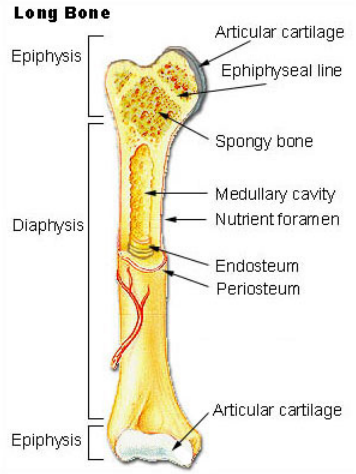


Figure 1. Parts of a long bone.

The skeletal system not only helps to provide movement and support but also serves as a storage area for calcium and inorganic salts and a source of blood cells. The adult human body has 206 bones in a variety of shapes and sizes. Basically there are 4 types of bones categorized according to shape:

- Long bones have a long longitudinal axis (Figure 1).
- Short bones have a short longitudinal axis and are more cube-like.
- Flat bones are thin and curved such as some of the bones of the skull.
- Irregular bones are often found in groups and have a variety of shapes and sizes.

Notice the long shaft or diaphysis in the middle of the bone. The diaphysis contains compact bone surrounding a medullary cavity containing bone marrow On either end is an epiphysis containing cancellous or spongy bone. The epiphyseal line is a remnant of the growth plate. The epiphyses also contain hyaline cartilage for forming joints with other bones. Surrounding the bone is a membrane called the periosteum. The periosteum contains blood vessels and cells that help to repair and restore bone.

There are also 2 types of bone tissue in different amounts in bones. Compact bone (sometimes called cortical bone) is very dense. Cancellous bone (sometimes called spongy bone) looks more like a trabeculated matrix (Figure 2). It is found in the central regions of some of the skull bones or at ends (epiphyses) of long bones. The bone forming cells (osteocytes) get their nutrients by diffusion.

Notice the spongy appearance of the trabeculated bone. The cortical bone is located near the margins of the bone and is more dense.



Figure 2.Trabecular and cortical bone of the femur. (Photo by Bruce Forciea).

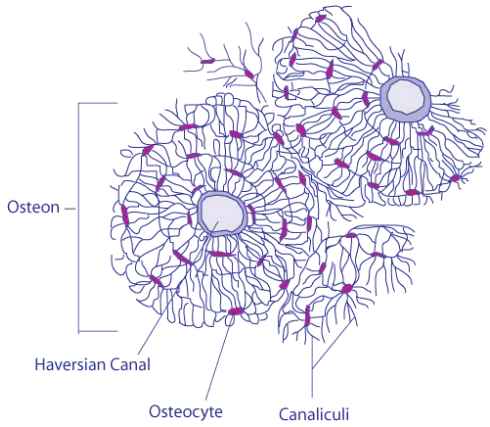


Figure 3. Haversian system.

Compact bone is organized according to structural units called Haversian systems or osteons (Figure 3). These are located along the lines of force and line up along the long axis of the bone. The Haversian systems are connected together and form an interconnected structure that provides support and strength to bones.

Haversian systems contain a central canal (Haversian canal) that serves as a pathway for blood vessels and nerves. The bone is deposited along concentric rings called lamellae. Along the lamellae are small openings called lacunae. The lacunae contain fluid and bone cells called osteocytes. Radiating out in all directions from lacunae are small canals called canaliculi. Haversian systems are interconnected by a series of larger canals called Volksmann's canals (perforating canals).

Bone Cells

There are 3 basic types of cells in bone. Osteoblasts undergo mitosis and secrete a substance that acts as the framework for bone. Once this substance (called osteoid) is secreted minerals can deposit and form hardened bone. Osteoblasts respond to certain bone forming hormones as well as from physical stress. Osteocytes are mature osteoblasts that cannot divide by mitosis (Figure 4).

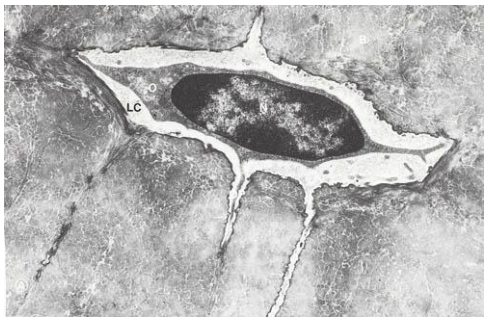


Figure 4. Osteocytes are mature osteoblasts that reside in a lacuna. They are surrounded by bony matrix.

Osteocytes reside in lacunae. Osteoclasts are capable of demineralizing bone. They free up calcium from bone to make it available to the body depending on the body's needs.

Bone Marrow

Bone marrow is located in the medullary (marrow) cavity of long bones and in some spongy bones. There are 2 kinds of marrow. Red marrow exists in the bones of infants and children. It is called red because it contains a large number of red blood cells. In adults the red marrow is replaced by yellow marrow. It is called yellow because it contains a large proportion of fat cells. Yellow marrow decreases its ability to form new red blood cells. However, not all adult bones contain yellow marrow. The following bones continue to contain red marrow and produce red blood cells:

- Proximal end of humerus
- Ribs
- Bodies of vertebrae
- Pelvis

- Femur

The Skeleton

The skeleton is divided into 2 sections: the axial and appendicular sections (Figure 5). The axial skeleton includes the skull, spine, ribcage, and sacrum and is indicated in blue in the figure below. The appendicular skeleton is indicated with red labels.

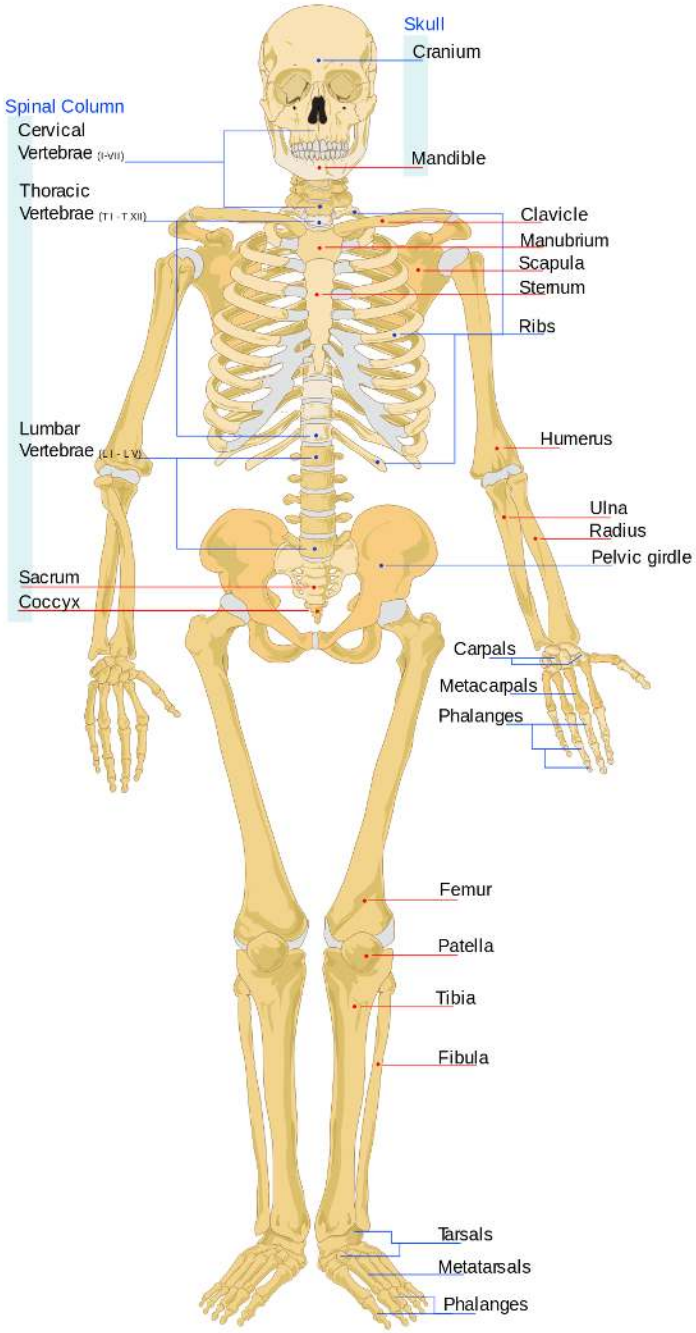


Figure 5. The skeleton.

Learning Objectives

This video provides another introduction to the skeletal system:



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16.19: Integumentary System

The **integumentary system** consists of the skin, hair, nails, the subcutaneous tissue below the skin, and assorted glands.The most obvious function of the integumentary system is the protection that the skin gives to underlying tissues. The skin not only keeps most harmful substances out, but also prevents the loss of fluids.

A major function of the subcutaneous tissue is to connect the skin to underlying tissues such as muscles. Hair on the scalp provides insulation from cold for the head. The hair of eyelashes and eyebrows helps keep dust and perspiration out of the eyes, and the hair in our nostrils helps keep dust out of the nasal cavities. Nails protect the tips of fingers and toes from mechanical injury. Fingernails give the fingers greater ability to pick up small objects.

There are four types of glands in the integumentary system: sudoriferous (sweat) glands, sebaceous glands, ceruminous glands, and mammary glands. These are all exocrine glands, secreting materials outside the cells and body. Sudoriferous glands are sweat producing glands. These are important to help maintain body temperature. Sebaceous glands are oil producing glands which help inhibit bacteria, keep us waterproof and prevent our hair and skin from drying out. Ceruminous glands produce earwax which keeps the outer surface of the eardrum pliable and prevents drying. Mammary glands produce milk.

Skin

In zoology and dermatology, skin is an organ of the integumentary system made up of a layer of tissues that guard underlying muscles and organs. As the interface with the surroundings, it plays the most important role in protecting against pathogens. Its other main functions are insulation and temperature regulation, sensation and vitamin D and B synthesis. Skin is considered one of the most important parts of the body.

Skin has pigmentation known as melanin that is provided by melanocytes. Melanin absorbs some of the potentially dangerous radiation in sunlight. It also contains DNA repair enzymes which reverse UV damage, and people who lack the genes for these enzymes suffer high rates of skin cancer. One form predominantly produced by UV light, malignant melanoma, is particularly invasive, causing it to spread quickly, and can often be deadly. Human skin pigmentation varies among populations in a striking manner. This has sometimes led to the classification of people(s) on the basis of skin color.

Damaged skin will try to heal by forming scar tissue, often giving rise to discoloration and depigmentation of the skin.

The skin is often known as “the largest organ in the human body.” This applies to exterior surface, as it covers the body, appearing to have the largest surface area of all the organs. Moreover, it applies to weight, as it weighs more than any single internal organ, accounting for about 15 percent of body weight. For the average adult human, the skin has a surface area of between 1.5-2.0 square meters, most of it is between 2–3 mm thick. The average square inch of skin holds 650 sweat glands, 20 blood vessels, 60,000 melanocytes, and more than a thousand nerve endings.

The use of natural or synthetic cosmetics to treat the appearance of the face and condition of the skin (such as pore control and black head cleansing) is common among many cultures.

Layers

The skin has two major layers which are made of different tissues and have very different functions.

Skin is composed of the *epidermis* and the *dermis*. Below these layers lies the *hypodermis or subcutaneous adipose layer*, which is not usually classified as a layer of skin.

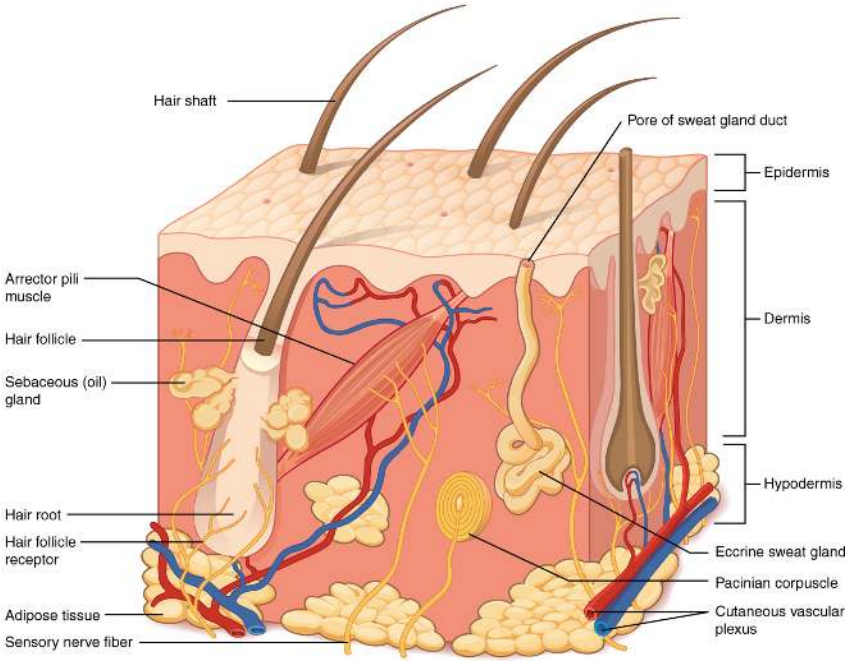


Figure 1. The skin is composed of two main layers: the epidermis, made of closely packed epithelial cells, and the dermis, made of dense, irregular connective tissue that houses blood vessels, hair follicles, sweat glands, and other structures. Beneath the dermis lies the hypodermis, which is composed mainly of loose connective and fatty tissues.

The outermost epidermis consists of stratified squamous keratinizing epithelium with an underlying basement membrane. It contains no blood vessels, and is nourished by diffusion from the dermis. The main type of cells which make up the epidermis are keratinocytes, with melanocytes and Langerhans cells also present. The epidermis can be further subdivided into the following *strata* (beginning with the outermost layer): corneum, lucidum, granulosum, spinosum, basale. Cells are formed through mitosis at the innermost layers. They move up the strata changing shape and composition as they differentiate, inducing expression of new types of keratin genes. They eventually reach the corneum and become sloughed off (desquamation). This process is called *keratinization* and takes place within about 30 days. This layer of skin is responsible for keeping water in the body and keeping other harmful chemicals and pathogens out.

Blood capillaries are found beneath the dermis, and are linked to an arteriole and a venule. Arterial shunt vessels may bypass the network in ears, the nose and fingertips.

The dermis lies below the epidermis and contains a number of structures including blood vessels, nerves, hair follicles, smooth muscle, glands and lymphatic tissue. It consists of loose connective tissue otherwise called areolar connective tissue – collagen, elastin and reticular fibers are present. Erector muscles, attached between the hair papilla and epidermis, can contract, resulting in the hair fiber pulled upright and consequentially goose bumps. The main cell types are fibroblasts, adipocytes (fat storage) and macrophages. Sebaceous glands are exocrine glands which produce, a mixture of lipids and waxy substances: lubrication, water-proofing, softening and antibactericidal actions are among the many functions of sebum. Sweat glands open up via a duct onto the skin by a pore.

The dermis is made of an irregular type of fibrous connective tissue consisting of collagen and elastin fibers. It can be split into the *papillary* and *reticular* layers. The papillary layer is outermost and extends into the epidermis to supply it with vessels. It is composed of loosely arranged fibers. Papillary ridges make up the lines of the hands giving us fingerprints. The reticular layer is more dense and is continuous with the hypodermis. It contains the bulk of the structures (such as sweat glands). The reticular layer is composed of irregularly arranged fibers and resists stretching.

The hypodermis is not part of the skin, and lies below the dermis. Its purpose is to attach the skin to underlying bone and muscle as well as supplying it with blood vessels and nerves. It consists of loose connective tissue and elastin. The main cell types are fibroblasts, macrophages and adipocytes (the hypodermis contains 95% of body fat). Fat serves as padding and insulation for the body.

Functions

1. Protection: Skin gives an anatomical barrier between the internal and external environment in bodily defense; Langerhans cells in the skin are part of the immune system
2. Sensation: Skin contains a variety of nerve endings that react to heat, cold, touch, pressure, vibration, and tissue injury
3. Heat regulation: The skin contains a blood supply far greater than its requirements which allows precise control of energy loss by radiation, convection and conduction. Dilated blood vessels increase perfusion and heat loss while constricted vessels greatly reduce cutaneous blood flow and conserve heat. Erector pili muscles are significant in animals.

Hair

Humans have three different types of hair:

- Lanugo, the fine, unpigmented hair that covers nearly the entire body of a fetus, although most has been replaced with vellus by the time of the baby's birth
- Vellus hair, the short, downy, "peach fuzz" body hair (also unpigmented) that grows in most places on the human body. While it occurs in both sexes, and makes up much of the hair in children, men have a much smaller percentage (around 10%) vellus whereas 2/3 of a female's hair is vellus.
- Terminal hair, the fully developed hair, which is generally longer, coarser, thicker, and darker than vellus hair, and often is found in regions such as the axillary, male beard, and pubic.

Nails



Figure 2. The parts of a finger nail

The fingernail is an important structure made of keratin. The fingernail generally serve two purposes. It serves as a protective plate and enhances sensation of the fingertip. The protection function of the fingernail is commonly known, but the sensation function is equally important. The fingertip has many nerve endings in it allowing us to receive volumes of information about objects we touch. The nail acts as a counterforce to the fingertip providing even more sensory input when an object is touched.

Nail Structure

The structure we know of as the nail is divided into six specific parts: the root, nail bed, nail plate, eponychium (cuticle), perionychium, and hyponychium.

Root The root of the fingernail is also known as the germinal matrix. This portion of the nail is actually beneath the skin behind the fingernail and extends several millimeters into the finger. The fingernail root produces most of the volume of the nail and the nail bed. This portion of the nail does not have any melanocytes, or melanin producing cells. The edge of the germinal matrix is seen as a white, crescent shaped structure called the lunula.

Nail Bed The nail bed is part of the nail matrix called the sterile matrix. It extends from the edge of the germinal matrix, or lunula, to the hyponychium. The nail bed contains the blood vessels, nerves, and melanocytes, or melanin-producing cells. As the nail is produced by the root, it streams down along the nail bed, which adds material to the undersurface of the nail making it thicker. It is important for normal nail growth that the nail bed be smooth. If it is not, the nail may split or develop grooves that can be cosmetically unappealing.

Nail Plate The nail plate is the actual fingernail, made of translucent keratin. The pink appearance of the nail comes from the blood vessels underneath the nail. The underneath surface of the nail plate has grooves along the length of the nail that help anchor it to the nail bed.

Eponychium The cuticle of the fingernail is also called the eponychium. The cuticle is situated between the skin of the finger and the nail plate fusing these structures together and providing a waterproof barrier.

Perionychium The perioncyhium is the skin that overlies the nail plate on its sides. It is also known as the paronychial edge. The perionychium is the site of hangnails, ingrown nails, and an infection of the skin called paronychia.

Hyponychium The hyponychium is the area between the nail plate and the fingertip. It is the junction between the free edge of the nail and the skin of the fingertip, also providing a waterproof barrier.

Glands

Sweat Glands

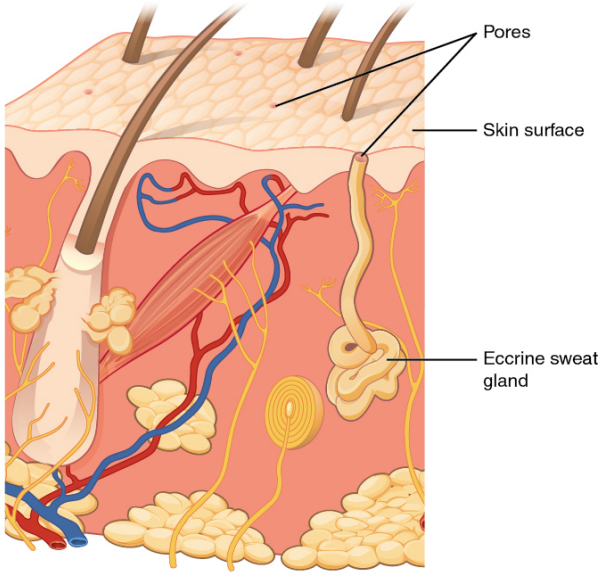


Figure 3. Eccrine glands are coiled glands in the dermis that release sweat that is mostly water.

In humans, there are two kinds of sweat glands which differ greatly in both the composition of the sweat and its purpose.

Eccrine (a.k.a. merocrine)

Eccrine sweat glands are exocrine glands distributed over the entire body surface but are particularly abundant on the palms of hands, soles of feet, and on the forehead. These produce sweat that is composed chiefly of water (99%) with various salts. The primary function is body temperature regulation.

Eccrine sweat glands are coiled tubular glands derived leading directly to the most superficial layer of the epidermis (out layer of skin) but extending into the inner layer of the skin (dermis layer). They are distributed over almost the entire surface of the body in humans and many other species, but are lacking in some marine and fur-bearing species. The sweat glands are controlled by sympathetic cholinergic nerves which are controlled by a center in the hypothalamus. The hypothalamus senses core temperature directly, and also has input from temperature receptors in the skin and modifies the sweat output, along with other thermoregulatory processes.

Human eccrine sweat is composed chiefly of water with various salts and organic compounds in solution. It contains minute amounts of fatty materials, urea, and other wastes. The concentration of sodium varies from 35–65 mmol/l and is lower in people acclimatised to a hot environment. The sweat of other species generally differ in composition.

Apocrine

Apocrine sweat glands only develop during early- to mid-puberty (approximately age 15) and release more than normal amounts of sweat for approximately a month and subsequently regulate and release normal amounts of sweat after a certain period of time. **Apocrine sweat glands** produce sweat that contains fatty materials. These glands are mainly present in the armpits and around the genital area and their activity is the main cause of sweat odor, due to the bacteria that break down the organic compounds in the

sweat from these glands. Emotional stress increases the production of sweat from the apocrine glands, or more precisely: the sweat already present in the tubule is squeezed out. Apocrine sweat glands essentially serve as scent glands.

Watch a short movie on sweat glands: How Our Body Sweats.

Sebaceous Glands

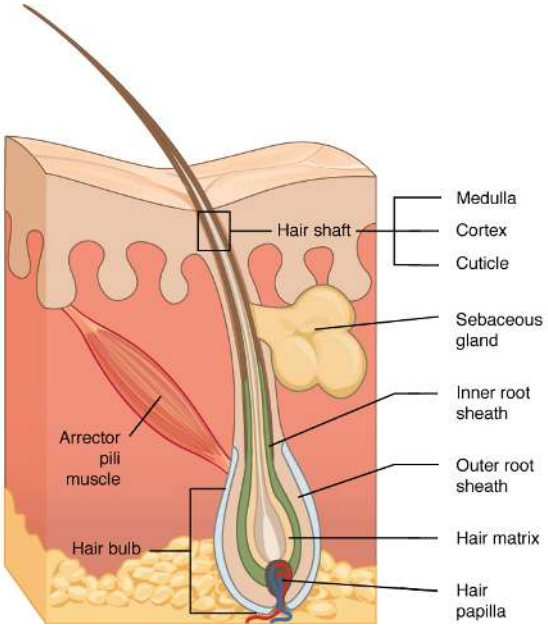


Figure 4. Hair follicles originate in the epidermis and have many different parts.

The **sebaceous glands** are glands found in the skin of mammals. They secrete an oily substance called **sebum** (Latin, meaning *fat* or *tallow*) that is made of fat (lipids) and the debris of dead fat-producing cells. These glands exist in humans throughout the skin except in the palms of the hands and soles of the feet. Sebum acts to protect and waterproof hair and skin, and keep them from becoming dry, brittle, and cracked. It can also inhibit the growth of microorganisms on skin.

Sebaceous glands can usually be found in hair-covered areas where they are connected to hair follicles to deposit sebum on the hairs, and bring it to the skin surface along the hair shaft. The structure consisting of hair, hair follicle and sebaceous gland is also known as **pilosebaceous unit**. Sebaceous glands are also found in non haired areas of lips, eyelids, penis, labia minora and nipples; here the sebum reaches the surface through ducts. In the glands, sebum is produced within specialized cells and is released as these cells burst; sebaceous glands are thus classified as holocrine glands.

Sebum is odorless, but its bacterial breakdown can produce odors. Sebum is the cause of some people experiencing “oily” hair if it is not washed for several days. Earwax is partly sebum, as is mucopurulent discharge, the dry substance accumulating in the corners of the eye after sleeping.

The composition of sebum varies from species to species; in humans, the lipid content consists of about 25% wax monoesters, 41% triglycerides, 16% free fatty acids, and 12% squalene.

The activity of the sebaceous glands increases during puberty because of heightened levels of androgens.

Sebaceous glands are involved in skin problems such as acne and keratosis pilaris. A blocked sebaceous gland can result in a sebaceous cyst. The prescription drug isotretinoin significantly reduces the amount of sebum produced by the sebaceous glands, and is used to treat acne. The extreme use (up to 10 times doctor prescribed amounts) of anabolic steroids by bodybuilders to prevent weight loss tend to stimulate the sebaceous glands which can cause acne.

The sebaceous glands of a human fetus *in utero* secrete a substance called vernix caseosa, a “waxy” or “cheesy” white substance coating the skin of newborns.

The preputial glands of mice and rats are large modified sebaceous glands that produce pheromones.

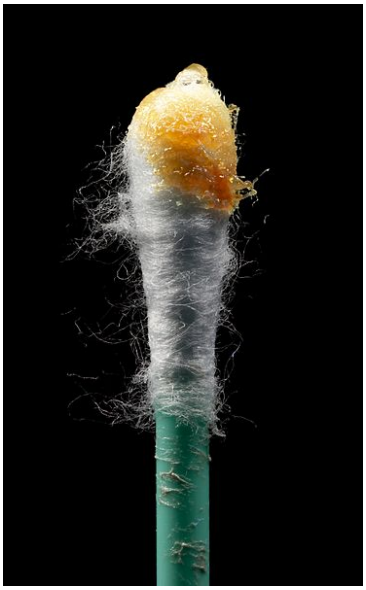


Figure 5. Wet-type human earwax on a cotton swab.

Earwax, also known by the medical term **cerumen**, is a yellowish, waxy substance secreted in the ear canal of humans and many other mammals. It plays a vital role in the human ear canal, assisting in cleaning and lubrication, and also provides some protection from bacteria, fungus, and insects. Excess or impacted cerumen can press against the eardrum and/or occlude the external auditory canal and impair hearing.

Production, composition, and different types

Cerumen is produced in the outer third of the cartilaginous portion of the human ear canal. It is a mixture of viscous secretions from sebaceous glands and less-viscous ones from modified apocrine sweat glands.

Two distinct genetically determined types of earwax are distinguished — the wet-type which is dominant, and the dry type which is recessive. Asians and Native Americans are more likely to have the dry type of cerumen (grey and flaky), whereas Caucasians and Africans are more likely to have the wet type (honey-brown to dark-brown and moist). Cerumen type has been used by anthropologists to track human migratory patterns, such as those of the Inuit.

The difference in cerumen type has been tracked to a single base change (an single nucleotide polymorphism) in a gene known as “ATP-binding cassette C11 gene”. In addition to affecting cerumen type, this mutation also reduces sweat production. The researchers conjecture that the reduction in sweat was beneficial to the ancestors of East Asians and Native Americans who are thought to have lived in cold climates.

Function

Cleaning. Cleaning of the ear canal occurs as a result of the “conveyor belt” process of epithelial migration, aided by jaw movement. Cells formed in the center of the tympanic membrane migrate outwards from the umbo (at a rate equivalent to that of fingernail growth) to the walls of the ear canal, and accelerate towards the entrance of the ear canal. The cerumen in the canal is also carried outwards, taking with it any dirt, dust, and particulate matter that may have gathered in the canal. Jaw movement assists this process by dislodging debris attached to the walls of the ear canal, increasing the likelihood of its extrusion.

Lubrication. Lubrication prevents desiccation and itching of the skin within the ear canal (known as *asteatosis*). The lubricative properties arise from the high lipid content of the sebum produced by the sebaceous glands. In wet-type cerumen at least, these lipids include cholesterol, squalene, and many long-chain fatty acids and alcohols.

Antibacterial and antifungal roles. While studies conducted up until the 1960s found little evidence supporting an antibacterial role for cerumen, more recent studies have found that cerumen provides some bactericidal protection against some strains of bacteria. Cerumen has been found to be effective in reducing the viability of a wide range of bacteria (sometimes by up to 99%), including *Haemophilus influenzae*, *Staphylococcus aureus*, and many variants of *Escherichia coli*. The growth of two fungi

commonly present in otomycosis was also significantly inhibited by human cerumen. These antimicrobial properties are due principally to the presence of saturated fatty acids, lysozyme and, especially, to the relatively low pH of cerumen (typically around 6.1 in normal individuals).

Mammary Glands

Mammary glands are the organs that, in the female mammal, produce milk for the sustenance of the young. These exocrine glands are enlarged and modified sweat glands and are the characteristic of mammals which gave the class its name.

Structure

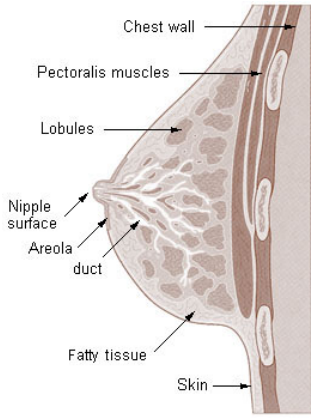


Figure 7. Cross section of the breast of a human female.

The basic components of the mammary gland are the *alveoli* (hollow cavities, a few millimetres large) lined with milk-secreting epithelial cells and surrounded by myoepithelial cells. These alveoli join up to form groups known as *lobules*, and each lobule has a *lactiferous duct* that drains into openings in the nipple. The myoepithelial cells can contract, similar to muscle cells, and thereby push the milk from the alveoli through the lactiferous ducts towards the nipple, where it collects in widenings (*sinuses*) of the ducts. A suckling baby essentially squeezes the milk out of these sinuses.

One distinguishes between a *simple mammary gland*, which consists of all the milk-secreting tissue leading to a single lactiferous duct, and a *complex mammary gland*, which consists of all the simple mammary glands serving one nipple.

Humans normally have two complex mammary glands, one in each breast, and each complex mammary gland consists of 10–20 simple glands. (The presence of more than two nipples is known as polythelia and the presence of more than two complex mammary glands as polymastia.)

Visit "Breast tissue" to see a movie visual of the breast.

Development and hormonal control

The development of mammary glands is controlled by hormones. The mammary glands exist in both sexes, but they are rudimentary until puberty when in response to ovarian hormones, they begin to develop in the female. Estrogen promotes formation, while testosterone inhibits it.

At the time of birth, the baby has lactiferous ducts but no alveoli. Little branching occurs before puberty when ovarian estrogens stimulate branching differentiation of the ducts into spherical masses of cells that will become alveoli. True secretory alveoli only develop in pregnancy, where rising levels of estrogen and progesterone cause further branching and differentiation of the duct cells, together with an increase in adipose tissue and a richer blood flow.

Colostrum is secreted in late pregnancy and for the first few days after giving birth. True milk secretion (lactation) begins a few days later due to a reduction in circulating progesterone and the presence of the hormone prolactin. The suckling of the baby causes the release of the hormone oxytocin which stimulates contraction of the myoepithelial cells.

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16.20: Putting It Together- Overview of Body Systems

If you found this introduction to the body interesting, you may want to consider learning more about anatomy and physiology. Human anatomy is the scientific study of the body's structures. Some of these structures are very small and can only be observed and analyzed with the assistance of a microscope. Other larger structures can readily be seen, manipulated, measured, and weighed. The word *anatomy* comes from a Greek root that means "to cut apart." Human anatomy was first studied by observing the exterior of the body and observing the wounds of soldiers and other injuries. Later, physicians were allowed to dissect bodies of the dead to augment their knowledge. When a body is dissected, its structures are cut apart in order to observe their physical attributes and their relationships to one another. Dissection is still used in medical schools, anatomy courses, and in pathology labs. In order to observe structures in living people, however, a number of imaging techniques have been developed. These techniques allow clinicians to visualize structures inside the living body such as a cancerous tumor or a fractured bone.

Whereas anatomy is about structure, physiology is about function. Human physiology is the scientific study of the chemistry and physics of the structures of the body and the ways in which they work together to support the functions of life. Much of the study of physiology centers on the body's tendency toward homeostasis. Homeostasis is the state of steady internal conditions maintained by living things. The study of physiology certainly includes observation, both with the naked eye and with microscopes, as well as manipulations and measurements. However, current advances in physiology usually depend on carefully designed laboratory experiments that reveal the functions of the many structures and chemical compounds that make up the human body.

At the beginning of the chapter, we discussed how an understanding of the body can help you monitor your own health. An understanding of the human body is also fundamental to becoming a doctor—of any kind.

Physicians and Surgeons

Physicians and surgeons diagnose and treat injuries or illnesses. Physicians examine patients; take medical histories; prescribe medications; and order, perform, and interpret diagnostic tests. They often counsel patients on diet, hygiene, and preventive healthcare. Surgeons operate on patients to treat injuries, such as broken bones; diseases, such as cancerous tumors; and deformities, such as cleft palates.

Physicians and surgeons work in one or more specialties. The following are examples of types of physicians and surgeons:

- **Anesthesiologists** focus on the care of surgical patients and on pain relief. They administer drugs (anesthetics) that reduce or eliminate the sensation of pain during an operation or another medical procedure. During surgery, they are responsible for adjusting the amount of anesthetic as needed and monitoring the patient's heart rate, body temperature, blood pressure, and breathing. They also work outside of the operating room, providing pain relief in the intensive care unit, during labor and delivery of babies, and for patients who suffer from chronic pain. Anesthesiologists work with other physicians and surgeons to decide on treatments and procedures before, during, and after surgery.
- **Family and general physicians** assess and treat a range of conditions that occur in everyday life. These conditions include anything from sinus and respiratory infections to broken bones. Family and general physicians typically have regular, long-term patients.
- **General pediatricians** provide care for infants, children, teenagers, and young adults. They specialize in diagnosing and treating problems specific to younger people. Most pediatricians treat common illnesses, minor injuries, and infectious diseases, and administer vaccinations. Some pediatricians specialize in pediatric surgery or serious medical conditions that commonly affect younger patients, such as autoimmune disorders or chronic ailments.
- **Surgeons** treat injuries, diseases, and deformities through operations. Using a variety of instruments, a surgeon corrects physical deformities, repairs bone and tissue after injuries, or performs preventive or elective surgeries on patients. Although a large number perform general surgery, many surgeons choose to specialize in a specific area. Specialties include orthopedic surgery (the treatment of the musculoskeletal system), neurological surgery (treatment of the brain and nervous system), cardiovascular surgery, and plastic or reconstructive surgery. Like other physicians, surgeons examine patients, perform and interpret diagnostic tests, and counsel patients on preventive healthcare. Some specialist physicians also perform surgery.

Physicians and surgeons may work in a number of other medical and surgical specialties and subspecialties. Physicians also work daily with other healthcare staff, such as registered nurses, other physicians, medical assistants, and medical records and health information technicians.

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16.21: Cerego- Overview of Body Systems

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for Overview of Body Systems. You'll need to create a free log-in to practice these items, if you haven't already.

https://cerego.com/sets/11042/learn

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CHAPTER OVERVIEW

17: Module 14- The Nervous System

17.1: Why It Matters- The Nervous System
17.2: Introduction to Components of the Nervous System
17.3: Diversity of Nervous Systems
17.4: The Central and Peripheral Nervous Systems
17.5: Neurons
17.6: Neurogenesis
17.7: Glial Cells
17.8: Introduction to Neuron Communication
17.9: Resting Membrane Potential
17.10: Action Potential
17.11: Chemical and Electrical Synapses
17.12: Signal Summation
17.13: Synaptic Plasticity
17.14: Introduction to the Central Nervous System
17.15: Components of the Central Nervous System
17.16: Brain
17.17: Spinal Cord
17.18: Introduction to the Peripheral Nervous System
17.19: Autonomic Nervous System
17.20: Sensory-Somatic Nervous System
17.21: Introduction to Nervous System Disorders
17.22: Neurodegenerative Disorders
17.23: Neurodevelopmental Disorders
17.24: Mental Illnesses
17.25: Other Neurological Disorders
17.26: Putting It Together- The Nervous System
17.27: Cerego- The Nervous System

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17.1: Why It Matters- The Nervous System

Why describe the components and role of the nervous system?

When you're reading this book, your nervous system is performing several functions simultaneously. The visual system is processing what is seen on the page; the motor system controls the turn of the pages (or click of the mouse); the prefrontal cortex maintains attention. Even fundamental functions, like breathing and regulation of body temperature, are controlled by the nervous system. A nervous system is an organism's control center: it processes sensory information from outside (and inside) the body and controls all behaviors—from eating to sleeping to finding a mate.



Figure 1. An athlete's nervous system is hard at work during the planning and execution of a movement as precise as a high jump. Parts of the nervous system are involved in determining how hard to push off and when to turn, as well as controlling the muscles throughout the body that make this complicated movement possible without knocking the bar down—all in just a few seconds. (credit: modification of work by Shane T. McCoy, U.S. Navy)

Learning Outcomes

- Identify the two primary parts of the nervous system and describe the function and structure of neurons and glial cells
- Explain the way neurons communicate
- Identify the components of the central nervous system
- Identify the components of the peripheral nervous system
- Describe the symptoms, potential causes, and treatment of several examples of nervous system disorders

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17.2: Introduction to Components of the Nervous System

Identify the two primary parts of the nervous system and describe the function and structure of neurons and glial cells

The nervous system is made up of neurons, specialized cells that can receive and transmit chemical or electrical signals, and glia, cells that provide support functions for the neurons by playing an information processing role that is complementary to neurons. A neuron can be compared to an electrical wire—it transmits a signal from one place to another. Glia can be compared to the workers at the electric company who make sure wires go to the right places, maintain the wires, and take down wires that are broken. Although glia have been compared to workers, recent evidence suggests that also usurp some of the signaling functions of neurons.

There is great diversity in the types of neurons and glia that are present in different parts of the nervous system. There are four major types of neurons, and they share several important cellular components.

What You'll Learn to Do

- Differentiate between the nervous systems of different animals
- Differentiate between the central and peripheral nervous systems
- List and describe the functions of the structural components of a neuron
- List and describe the four main types of neurons
- Describe the process of neurogenesis
- Compare the functions of different types of glial cells

Learning Activities

The learning activities for this section include the following:

- Diversity of Nervous Systems
- The Central and Peripheral Nervous Systems
- Neurons
- Neurogenesis
- Glial Cells
- Self Check: Neurons and Glial Cells

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17.3: Diversity of Nervous Systems

Nervous systems throughout the animal kingdom vary in structure and complexity, as illustrated by the variety of animals shown in Figure 1. Some organisms, like sea sponges, lack a true nervous system. Others, like jellyfish, lack a true brain and instead have a system of separate but connected nerve cells (neurons) called a “nerve net.” Echinoderms such as sea stars have nerve cells that are bundled into fibers called nerves.

Flatworms of the phylum Platyhelminthes have both a central nervous system (CNS), made up of a small “brain” and two nerve cords, and a peripheral nervous system (PNS) containing a system of nerves that extend throughout the body. The insect nervous system is more complex but also fairly decentralized. It contains a brain, ventral nerve cord, and ganglia (clusters of connected neurons). These ganglia can control movements and behaviors without input from the brain. Octopuses may have the most complicated of invertebrate nervous systems—they have neurons that are organized in specialized lobes and eyes that are structurally similar to vertebrate species.

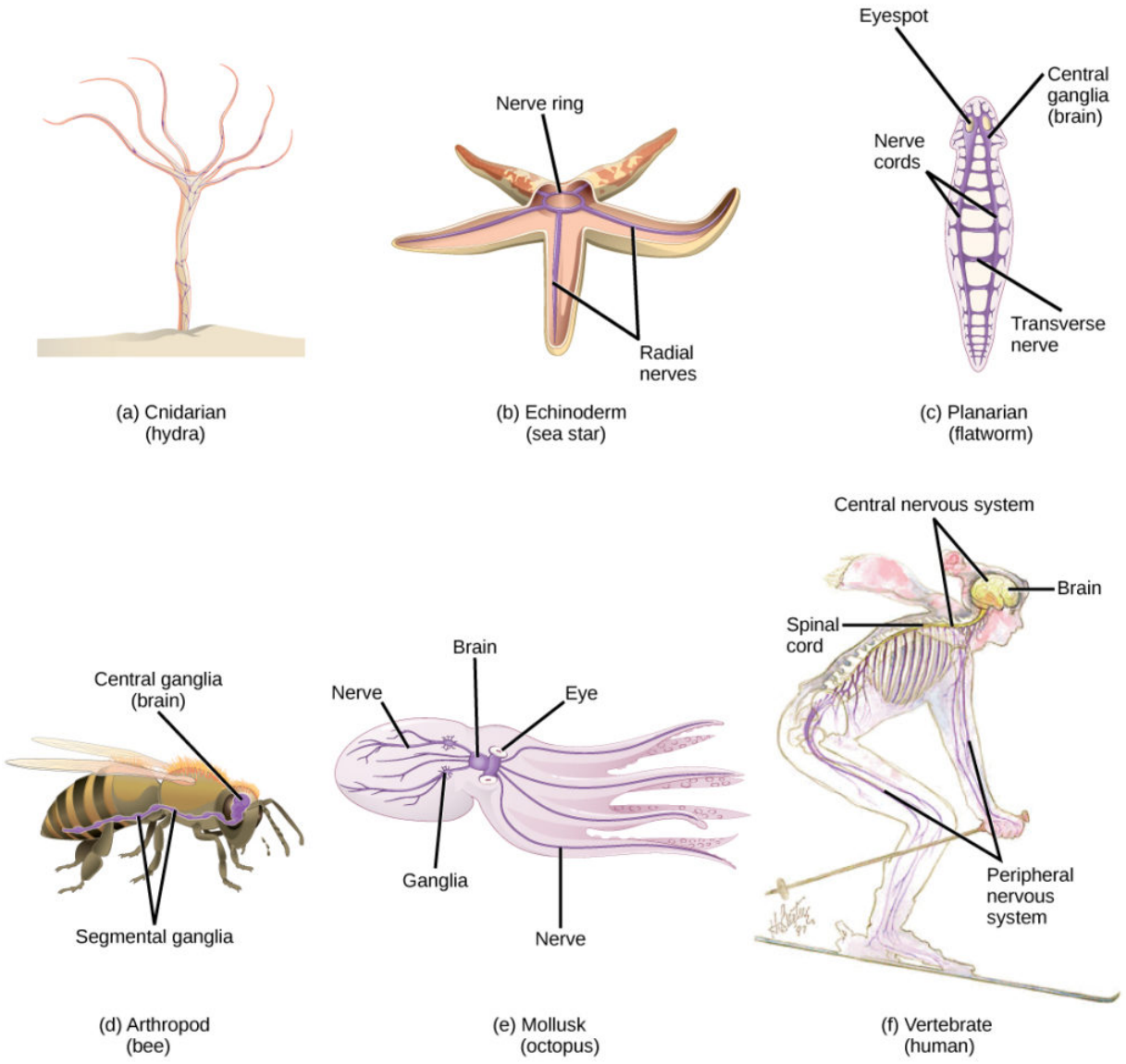
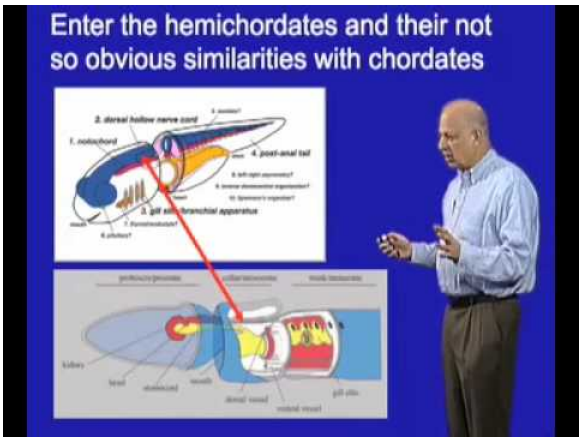


Figure 1. Nervous systems vary in structure and complexity. In (a) cnidarians, nerve cells form a decentralized nerve net. In (b) echinoderms, nerve cells are bundled into fibers called nerves. In animals exhibiting bilateral symmetry such as (c) planarians, neurons cluster into an anterior brain that processes information. In addition to a brain, (d) arthropods have clusters of nerve cell bodies, called peripheral ganglia, located along the ventral nerve cord. Mollusks such as squid and (e) octopuses, which must hunt to survive, have complex brains containing millions of neurons. In (f) vertebrates, the brain and spinal cord comprise the central nervous system, while neurons extending into the rest of the body comprise the peripheral nervous system. (credit e: modification of work by Michael Vecchione, Clyde F.E. Roper, and Michael J. Sweeney, NOAA; credit f: modification of work by NIH)

Compared to invertebrates, vertebrate nervous systems are more complex, centralized, and specialized. While there is great diversity among different vertebrate nervous systems, they all share a basic structure: a CNS that contains a brain and spinal cord and a PNS made up of peripheral sensory and motor nerves. One interesting difference between the nervous systems of invertebrates and vertebrates is that the nerve cords of many invertebrates are located ventrally whereas the vertebrate spinal cords are located dorsally. There is debate among evolutionary biologists as to whether these different nervous system plans evolved separately or whether the invertebrate body plan arrangement somehow “flipped” during the evolution of vertebrates.

Watch this video of biologist Mark Kirschner discussing the “flipping” phenomenon of vertebrate evolution.



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17.4: The Central and Peripheral Nervous Systems

The nervous system has three main functions: sensory input, integration of data and motor output. Sensory input is when the body gathers information or data, by way of neurons, glia and synapses. The nervous system is composed of excitable nerve cells (neurons) and synapses that form between the neurons and connect them to centers throughout the body or to other neurons. These neurons operate on excitation or inhibition, and although nerve cells can vary in size and location, their communication with one another determines their function. These nerves conduct impulses from sensory receptors to the brain and spinal cord. The data is then processed by way of integration of data, which occurs only in the brain. After the brain has processed the information, impulses are then conducted from the brain and spinal cord to muscles and glands, which is called motor output. Glia cells are found within tissues and are not excitable but help with myelination, ionic regulation and extracellular fluid.

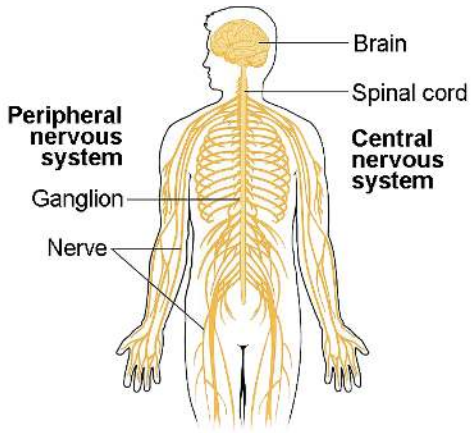


Figure 1. The central and peripheral nervous systems

The nervous system is comprised of two major parts, or subdivisions, the central nervous system (CNS) and the peripheral nervous system (PNS). The CNS includes the brain and spinal cord. The brain is the body's "control center." The CNS has various centers located within it that carry out the sensory, motor and integration of data. These centers can be subdivided to Lower Centers (including the spinal cord and brain stem) and Higher centers communicating with the brain via effectors.

The PNS is a vast network of spinal and cranial nerves that are linked to the brain and the spinal cord. It contains sensory receptors which help in processing changes in the internal and external environment. This information is sent to the CNS via afferent sensory nerves. The PNS is then subdivided into the autonomic nervous system and the somatic nervous system. The autonomic has involuntary control of internal organs, blood vessels, smooth and cardiac muscles. The somatic has voluntary control of skin, bones, joints, and skeletal muscle. The two systems function together, by way of nerves from the PNS entering and becoming part of the CNS, and vice versa.

We'll further discuss the components and roles of these systems later in this module.

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17.5: Neurons

The nervous system of the common laboratory fly, *Drosophila melanogaster*, contains around 100,000 neurons, the same number as a lobster. This number compares to 75 million in the mouse and 300 million in the octopus. A human brain contains around 86 billion neurons. Despite these very different numbers, the nervous systems of these animals control many of the same behaviors—from basic reflexes to more complicated behaviors like finding food and courting mates. The ability of neurons to communicate with each other as well as with other types of cells underlies all of these behaviors.

Most neurons share the same cellular components. But neurons are also highly specialized—different types of neurons have different sizes and shapes that relate to their functional roles.

Parts of a Neuron

Like other cells, each neuron has a cell body (or soma) that contains a nucleus, smooth and rough endoplasmic reticulum, Golgi apparatus, mitochondria, and other cellular components. Neurons also contain unique structures, illustrated in Figure 1 for receiving and sending the electrical signals that make neuronal communication possible. **Dendrites** are tree-like structures that extend away from the cell body to receive messages from other neurons at specialized junctions called **synapses**. Although some neurons do not have any dendrites, some types of neurons have multiple dendrites. Dendrites can have small protrusions called dendritic spines, which further increase surface area for possible synaptic connections.

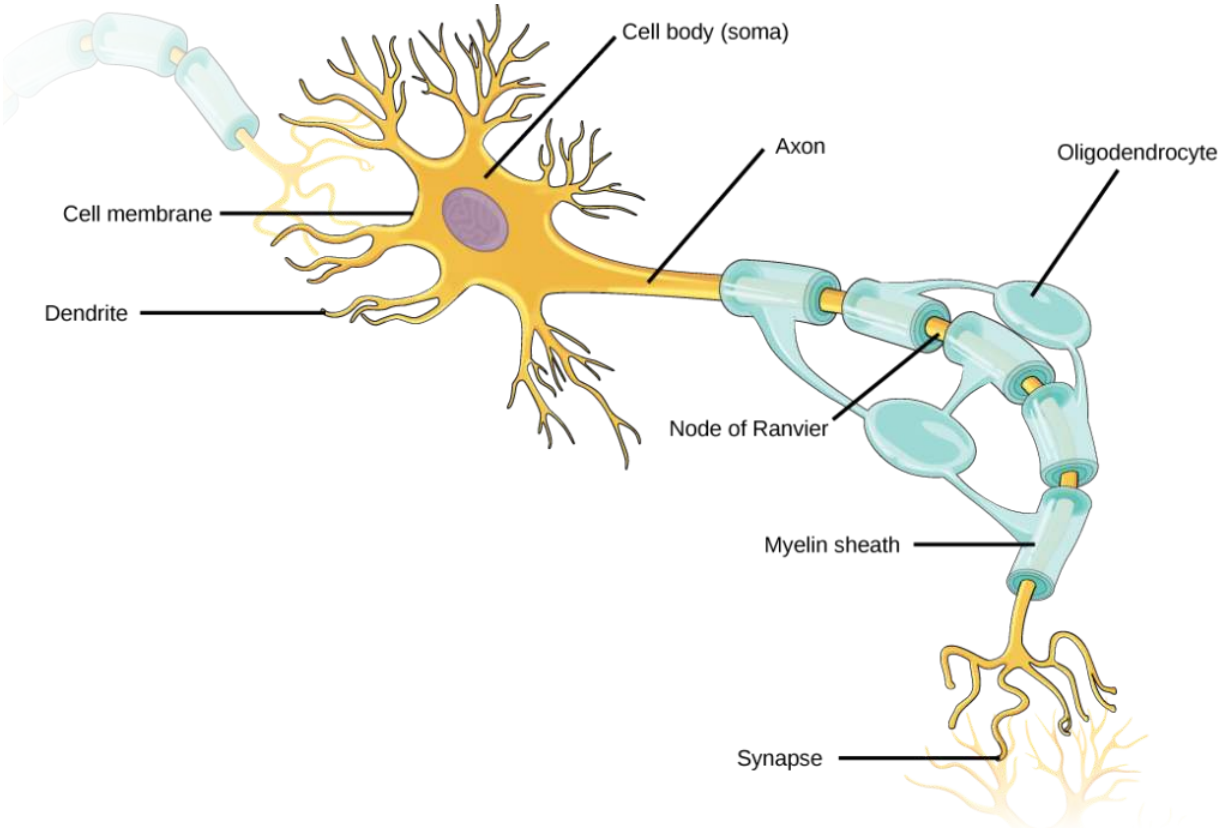


Figure 1. Neurons contain organelles common to many other cells, such as a nucleus and mitochondria. They also have more specialized structures, including dendrites and axons.

Once a signal is received by the dendrite, it then travels passively to the cell body. The cell body contains a specialized structure, the **axon hillock** that integrates signals from multiple synapses and serves as a junction between the cell body and an **axon**. An axon is a tube-like structure that propagates the integrated signal to specialized endings called **axon terminals**. These terminals in turn synapse on other neurons, muscle, or target organs. Chemicals released at axon terminals allow signals to be communicated to these other cells. Neurons usually have one or two axons, but some neurons, like amacrine cells in the retina, do not contain any axons. Some axons are covered with **myelin**, which acts as an insulator to minimize dissipation of the electrical signal as it travels down the axon, greatly increasing the speed on conduction. This insulation is important as the axon from a human motor neuron

can be as long as a meter—from the base of the spine to the toes. The myelin sheath is not actually part of the neuron. Myelin is produced by glial cells. Along the axon there are periodic gaps in the myelin sheath. These gaps are called **nodes of Ranvier** and are sites where the signal is "recharged" as it travels along the axon.

It is important to note that a single neuron does not act alone—neuronal communication depends on the connections that neurons make with one another (as well as with other cells, like muscle cells). Dendrites from a single neuron may receive synaptic contact from many other neurons. For example, dendrites from a Purkinje cell in the cerebellum are thought to receive contact from as many as 200,000 other neurons.

? Practice Question

Which of the following statements is false?

a. The soma is the cell body of a nerve cell.
b. Myelin sheath provides an insulating layer to the dendrites.
c. Axons carry the signal from the soma to the target.
d. Dendrites carry the signal to the soma.

[reveal-answer q="962754"]Show Answer[/reveal-answer]
[hidden-answer a="962754"]Statement b is false.[/hidden-answer]

Types of Neurons

There are different types of neurons, and the functional role of a given neuron is intimately dependent on its structure. There is an amazing diversity of neuron shapes and sizes found in different parts of the nervous system (and across species), as illustrated by the neurons shown in Figure 2.

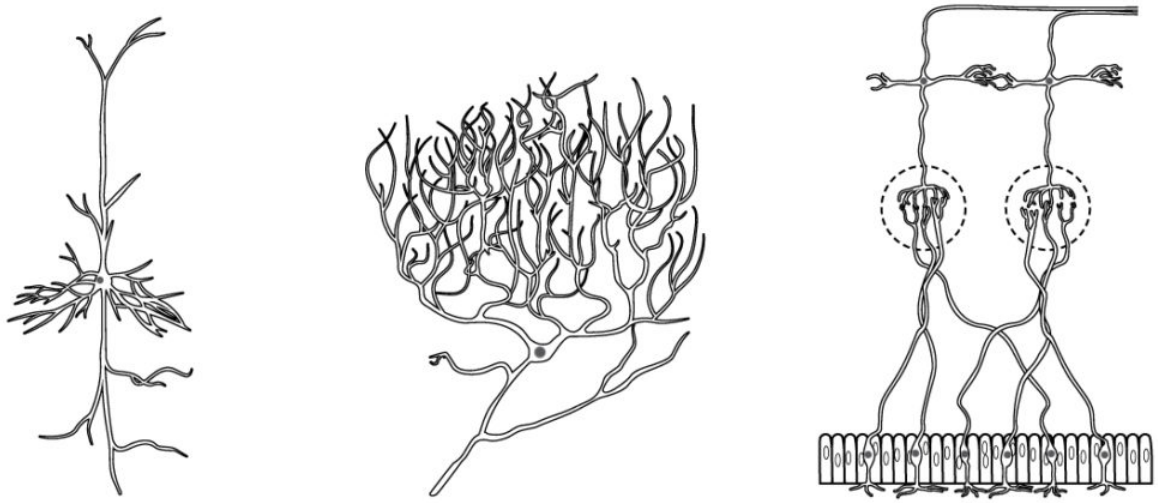


Figure 2. There is great diversity in the size and shape of neurons throughout the nervous system. Examples include (a) a pyramidal cell from the cerebral cortex, (b) a Purkinje cell from the cerebellar cortex, and (c) olfactory cells from the olfactory epithelium and olfactory bulb.

While there are many defined neuron cell subtypes, neurons are broadly divided into four basic types: unipolar, bipolar, multipolar, and pseudounipolar. Figure 3 illustrates these four basic neuron types. Unipolar neurons have only one structure that extends away from the soma. These neurons are not found in vertebrates but are found in insects where they stimulate muscles or glands. A bipolar neuron has one axon and one dendrite extending from the soma. An example of a bipolar neuron is a retinal bipolar cell, which receives signals from photoreceptor cells that are sensitive to light and transmits these signals to ganglion cells that carry the signal to the brain. Multipolar neurons are the most common type of neuron. Each multipolar neuron contains one axon and multiple dendrites. Multipolar neurons can be found in the central nervous system (brain and spinal cord). An example of a multipolar neuron is a Purkinje cell in the cerebellum, which has many branching dendrites but only one axon. Pseudounipolar cells

share characteristics with both unipolar and bipolar cells. A pseudounipolar cell has a single process that extends from the soma, like a unipolar cell, but this process later branches into two distinct structures, like a bipolar cell. Most sensory neurons are pseudounipolar and have an axon that branches into two extensions: one connected to dendrites that receive sensory information and another that transmits this information to the spinal cord.

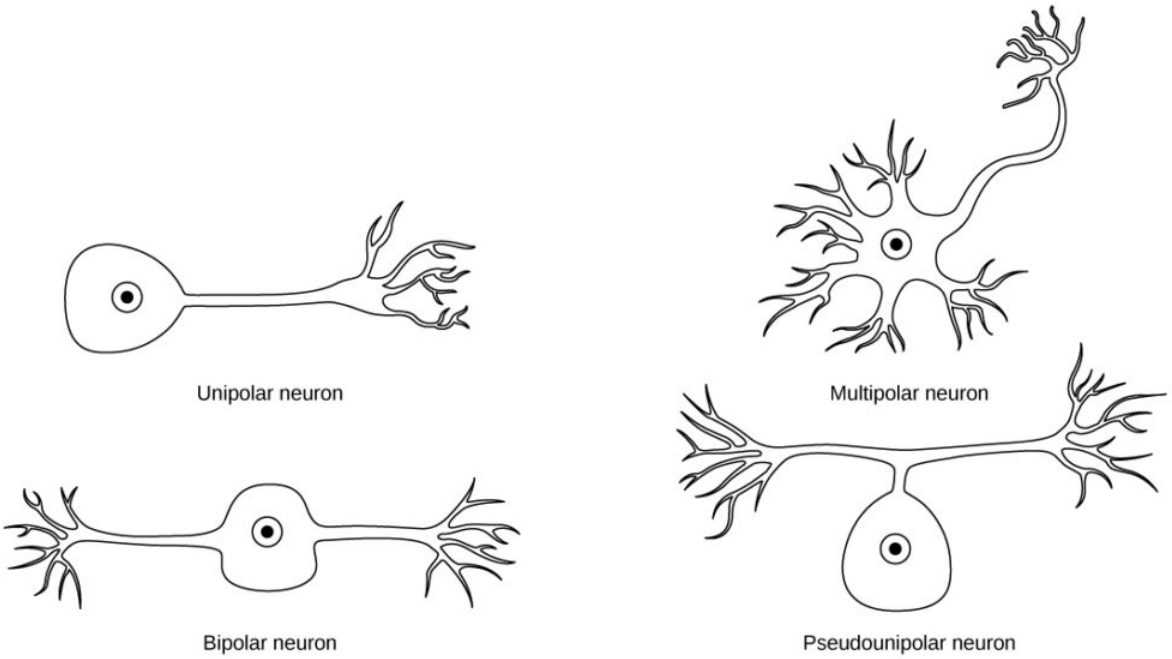


Figure 3. Neurons are broadly divided into four main types based on the number and placement of axons: (1) unipolar, (2) bipolar, (3) multipolar, and (4) pseudounipolar.

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17.6: Neurogenesis

At one time, scientists believed that people were born with all the neurons they would ever have. Research performed during the last few decades indicates that neurogenesis, the birth of new neurons, continues into adulthood. Neurogenesis was first discovered in songbirds that produce new neurons while learning songs. For mammals, new neurons also play an important role in learning: about 1000 new neurons develop in the hippocampus (a brain structure involved in learning and memory) each day. While most of the new neurons will die, researchers found that an increase in the number of surviving new neurons in the hippocampus correlated with how well rats learned a new task. Interestingly, both exercise and some antidepressant medications also promote neurogenesis in the hippocampus. Stress has the opposite effect. While neurogenesis is quite limited compared to regeneration in other tissues, research in this area may lead to new treatments for disorders such as Alzheimer's, stroke, and epilepsy.

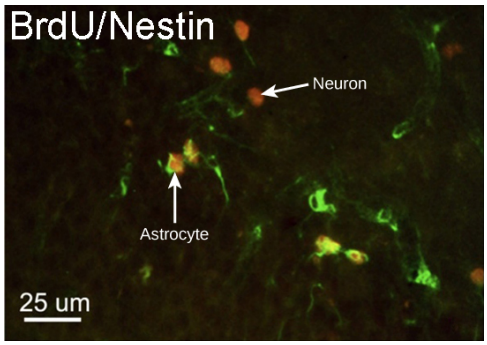


Figure 1. Micrograph which shows fluorescently labeled neurons in the hippocampus of a rat (credit: modification of work by Dr. Maryam Faiz, et. al., University of Barcelona; scale-bar data from Matt Russell)

How do scientists identify new neurons? A researcher can inject a compound called bromodeoxyuridine (BrdU) into the brain of an animal. While all cells will be exposed to BrdU, BrdU will only be incorporated into the DNA of newly generated cells that are in S phase. A technique called immunohistochemistry can be used to attach a fluorescent label to the incorporated BrdU, and a researcher can use fluorescent microscopy to visualize the presence of BrdU, and thus new neurons, in brain tissue.

Figure 1 shows fluorescently labeled new neurons in a rat hippocampus. Cells that are actively dividing have bromodoxyuridine (BrdU) incorporated into their DNA and are labeled in red. Cells that express glial fibrillary acidic protein (GFAP) are labeled in green. Astrocytes, but not neurons, express GFAP. Thus, cells that are labeled both red and green are actively dividing astrocytes, whereas cells labeled red only are actively dividing neurons.

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17.7: Glial Cells

While glia are often thought of as the supporting cast of the nervous system, the number of glial cells in the brain actually outnumbers the number of neurons by a factor of ten. Neurons would be unable to function without the vital roles that are fulfilled by these glial cells. Glia guide developing neurons to their destinations, buffer ions and chemicals that would otherwise harm neurons, and provide myelin sheaths around axons. Scientists have recently discovered that they also play a role in responding to nerve activity and modulating communication between nerve cells. When glia do not function properly, the result can be disastrous—most brain tumors are caused by mutations in glia.

Types of Glia

There are several different types of glia with different functions, two of which are shown in Figure 1.

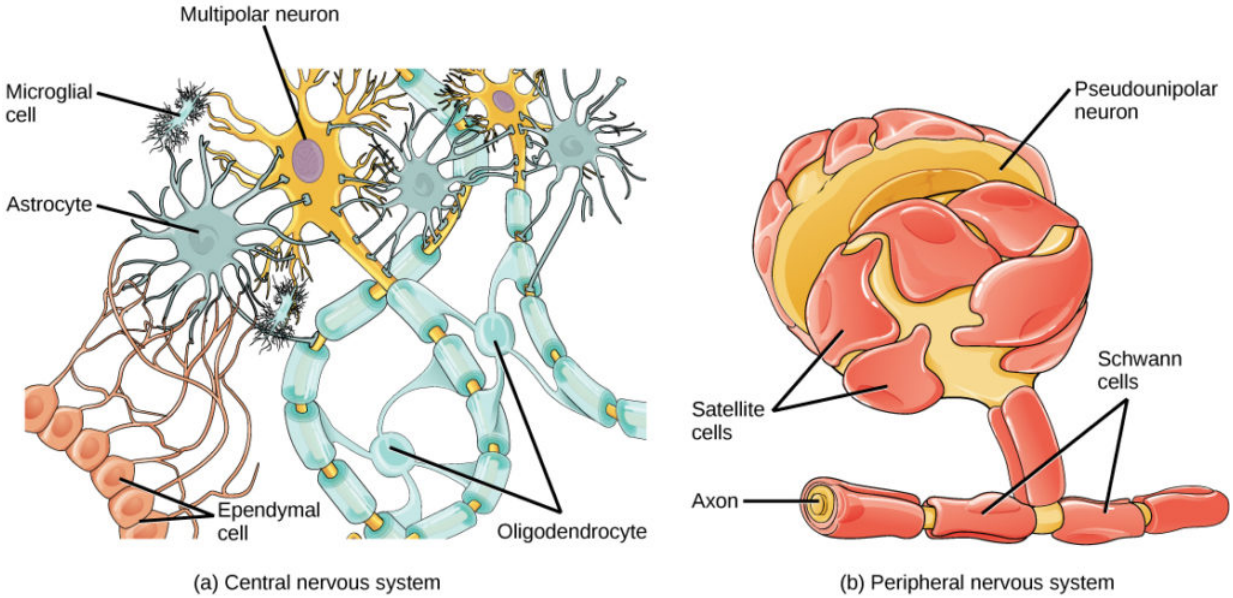
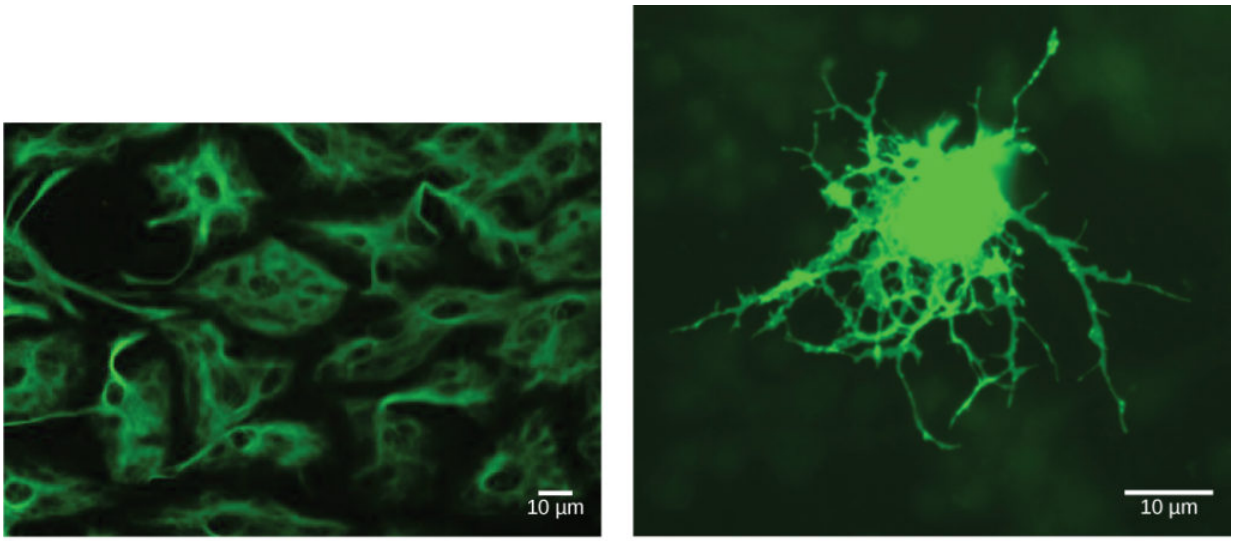


Figure 1. Glial cells support neurons and maintain their environment. Glial cells of the (a) central nervous system include oligodendrocytes, astrocytes, ependymal cells, and microglial cells. Oligodendrocytes form the myelin sheath around axons. Astrocytes provide nutrients to neurons, maintain their extracellular environment, and provide structural support. Microglia scavenge pathogens and dead cells. Ependymal cells produce cerebrospinal fluid that cushions the neurons. Glial cells of the (b) peripheral nervous system include Schwann cells, which form the myelin sheath, and satellite cells, which provide nutrients and structural support to neurons.

Astrocytes, shown in Figure 2a make contact with both capillaries and neurons in the CNS. They provide nutrients and other substances to neurons, regulate the concentrations of ions and chemicals in the extracellular fluid, and provide structural support for synapses. Astrocytes also form the blood-brain barrier—a structure that blocks entrance of toxic substances into the brain. Astrocytes, in particular, have been shown through calcium imaging experiments to become active in response to nerve activity, transmit calcium waves between astrocytes, and modulate the activity of surrounding synapses.

Satellite glia provide nutrients and structural support for neurons in the PNS. **Microglia** scavenge and degrade dead cells and protect the brain from invading microorganisms. **Oligodendrocytes**, shown in Figure 2b form myelin sheaths around axons in the CNS. One axon can be myelinated by several oligodendrocytes, and one oligodendrocyte can provide myelin for multiple neurons. This is distinctive from the PNS where a single **Schwann cell** provides myelin for only one axon as the entire Schwann cell surrounds the axon. **Radial glia** serve as scaffolds for developing neurons as they migrate to their end destinations. **Ependymal** cells line fluid-filled ventricles of the brain and the central canal of the spinal cord. They are involved in the production of cerebrospinal fluid, which serves as a cushion for the brain, moves the fluid between the spinal cord and the brain, and is a component of the choroid plexus.



(a) Astrocyte (b) Oligodendrocyte

Figure 2. (a) Astrocytes and (b) oligodendrocytes are glial cells of the central nervous system. (credit a: modification of work by Uniformed Services University; credit b: modification of work by Jurjen Broeke; scale-bar data from Matt Russell)

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17.8: Introduction to Neuron Communication

Explain the way neurons communicate

All functions performed by the nervous system—from a simple motor reflex to more advanced functions like making a memory or a decision—require neurons to communicate with one another. While humans use words and body language to communicate, neurons use electrical and chemical signals. Just like a person in a committee, one neuron usually receives and synthesizes messages from multiple other neurons before “making the decision” to send the message on to other neurons.

What You’ll Learn to Do

- Describe the basis of the resting membrane potential
- Explain the stages of an action potential and how action potentials are propagated
- Explain the similarities and differences between chemical and electrical synapses
- Describe the process of signal summation
- Discuss the processes involved in synaptic plasticity

Learning Activities

The learning activities for this section include the following:

- Resting Membrane Potential
- Action Potential
- Chemical and Electrical Synapses
- Signal Summation
- Synaptic Plasticity
- Self Check: Neuron Communication

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17.9: Resting Membrane Potential

For the nervous system to function, neurons must be able to send and receive signals. These signals are possible because each neuron has a charged cellular membrane (a voltage difference between the inside and the outside), and the charge of this membrane can change in response to neurotransmitter molecules released from other neurons and environmental stimuli. To understand how neurons communicate, one must first understand the basis of the baseline or "resting" membrane charge.

Neuronal Charged Membranes

The lipid bilayer membrane that surrounds a neuron is impermeable to charged molecules or ions. To enter or exit the neuron, ions must pass through special proteins called ion channels that span the membrane. Ion channels have different configurations: open, closed, and inactive, as illustrated in Figure 1. Some ion channels need to be activated in order to open and allow ions to pass into or out of the cell. These ion channels are sensitive to the environment and can change their shape accordingly. Ion channels that change their structure in response to voltage changes are called voltage-gated ion channels. Voltage-gated ion channels regulate the relative concentrations of different ions inside and outside the cell. The difference in total charge between the inside and outside of the cell is called the **membrane potential**.

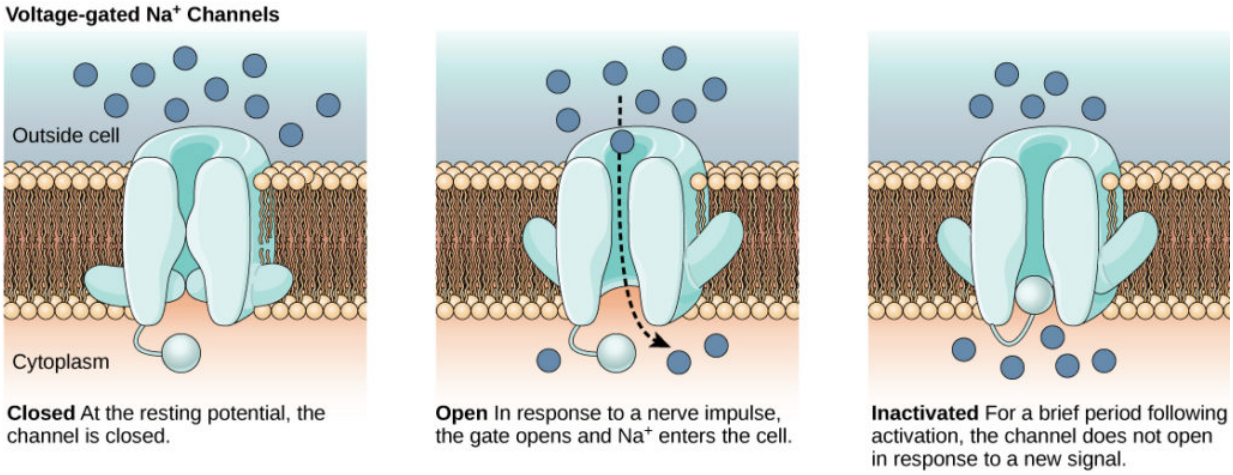


Figure 1. Voltage-gated ion channels open in response to changes in membrane voltage. After activation, they become inactivated for a brief period and will no longer open in response to a signal.

This video discusses the basis of the resting membrane potential.



A link to an interactive elements can be found at the bottom of this page.

Resting Membrane Potential

A neuron at rest is negatively charged: the inside of a cell is approximately 70 millivolts more negative than the outside (−70 mV, note that this number varies by neuron type and by species). This voltage is called the resting membrane potential; it is caused by differences in the concentrations of ions inside and outside the cell. If the membrane were equally permeable to all ions, each type of ion would flow across the membrane and the system would reach equilibrium. Because ions cannot simply cross the membrane at will, there are different concentrations of several ions inside and outside the cell, as shown in Table 1.

Table 1. Ion Concentration Inside and Outside Neurons

Ion	Extracellular concentration (mM)	Intracellular concentration (mM)	Ratio outside/inside
Na^+	145	12	12
K+	4	155	0.026
Cl^-	120	4	30
Organic anions (A−)	—	100	

The resting membrane potential is a result of different concentrations inside and outside the cell. The difference in the number of positively charged potassium ions (K^+) inside and outside the cell dominates the resting membrane potential (Figure 2).

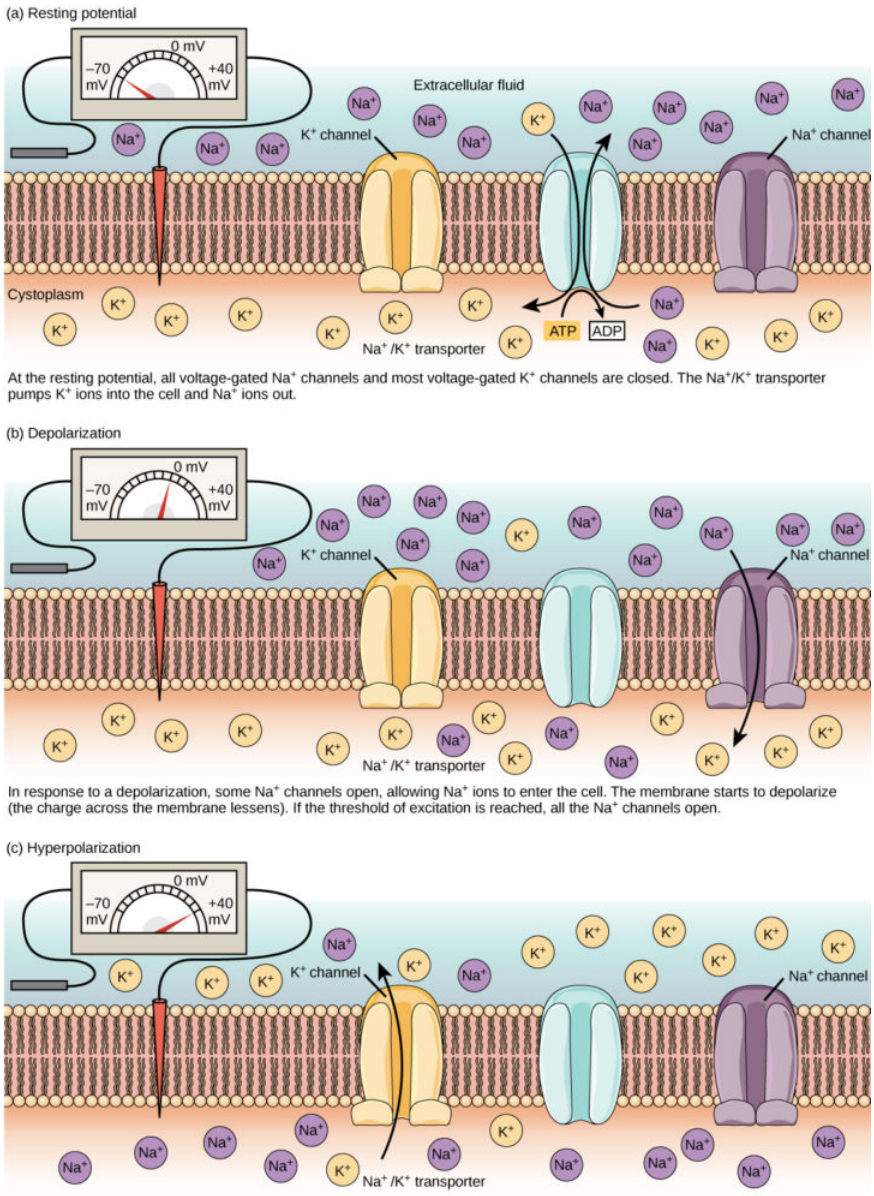


Figure 2. The (a) resting membrane potential is a result of different concentrations of Na^+ and K^+ ions inside and outside the cell. A nerve impulse causes Na^+ to enter the cell, resulting in (b) depolarization. At the peak action potential, K^+ channels open and the cell becomes (c) hyperpolarized.

When the membrane is at rest, K^+ ions accumulate inside the cell due to a net movement with the concentration gradient. The negative resting membrane potential is created and maintained by increasing the concentration of cations outside the cell (in the extracellular fluid) relative to inside the cell (in the cytoplasm). The negative charge within the cell is created by the cell membrane being more permeable to potassium ion movement than sodium ion movement. In neurons, potassium ions are maintained at high concentrations within the cell while sodium ions are maintained at high concentrations outside of the cell. The cell possesses potassium and sodium leakage channels that allow the two cations to diffuse down their concentration gradient.

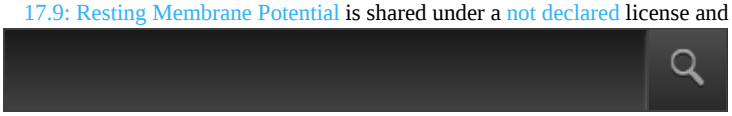
However, the neurons have far more potassium leakage channels than sodium leakage channels. Therefore, potassium diffuses out of the cell at a much faster rate than sodium leaks in. Because more cations are leaving the cell than are entering, this causes the interior of the cell to be negatively charged relative to the outside of the cell. The actions of the sodium potassium pump help to maintain the resting potential, once established. Recall that sodium potassium pumps brings two K^+ ions into the cell while removing three Na^+ ions per ATP consumed. As more cations are expelled from the cell than taken in, the inside of the cell remains negatively charged relative to the extracellular fluid. It should be noted that chloride ions (Cl^-) tend to accumulate outside of the cell because they are repelled by negatively-charged proteins within the cytoplasm.

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17.10: Action Potential

A neuron can receive input from other neurons and, if this input is strong enough, send the signal to downstream neurons. Transmission of a signal between neurons is generally carried by a chemical called a neurotransmitter. Transmission of a signal within a neuron (from dendrite to axon terminal) is carried by a brief reversal of the resting membrane potential called an **action potential**. When neurotransmitter molecules bind to receptors located on a neuron's dendrites, ion channels open. At excitatory synapses, this opening allows positive ions to enter the neuron and results in **depolarization** of the membrane—a decrease in the difference in voltage between the inside and outside of the neuron. A stimulus from a sensory cell or another neuron depolarizes the target neuron to its threshold potential (−55 mV). Na^+ channels in the axon hillock open, allowing positive ions to enter the cell (Figure 1).

Once the sodium channels open, the neuron completely depolarizes to a membrane potential of about +40 mV. Action potentials are considered an "all-or nothing" event, in that, once the threshold potential is reached, the neuron always completely depolarizes. Once depolarization is complete, the cell must now "reset" its membrane voltage back to the resting potential. To accomplish this, the Na^+channels close and cannot be opened. This begins the neuron's **refractory period**, in which it cannot produce another action potential because its sodium channels will not open. At the same time, voltage-gated K^+ channels open, allowing K^+ to leave the cell. As K^+ ions leave the cell, the membrane potential once again becomes negative. The diffusion of K^+ out of the cell actually **hyperpolarizes** the cell, in that the membrane potential becomes more negative than the cell's normal resting potential. At this point, the sodium channels will return to their resting state, meaning they are ready to open again if the membrane potential again exceeds the threshold potential. Eventually the extra K^+ ions diffuse out of the cell through the potassium leakage channels, bringing the cell from its hyperpolarized state, back to its resting membrane potential.

? Practice Question

The formation of an action potential can be divided into five steps, which can be seen in Figure 1.

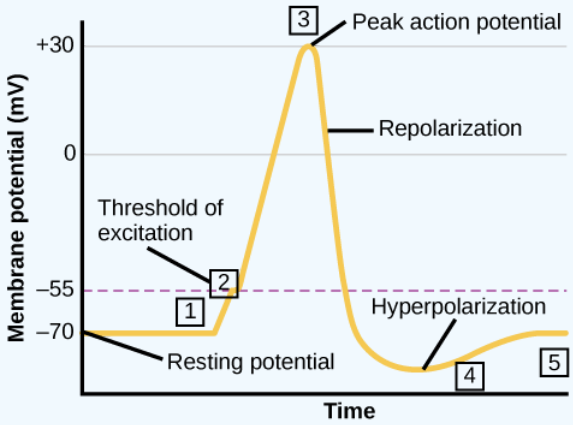


Figure 1. Action Potential

1. A stimulus from a sensory cell or another neuron causes the target cell to depolarize toward the threshold potential.
2. If the threshold of excitation is reached, all Na^+ channels open and the membrane depolarizes.
3. At the peak action potential, K^+ channels open and K^+ begins to leave the cell. At the same time, Na^+ channels close.
4. The membrane becomes hyperpolarized as K^+ ions continue to leave the cell. The hyperpolarized membrane is in a refractory period and cannot fire.
5. The K^+ channels close and the Na^+/K^+ transporter restores the resting potential.

Potassium channel blockers, such as amiodarone and procainamide, which are used to treat abnormal electrical activity in the heart, called cardiac dysrhythmia, impede the movement of K^+ through voltage-gated K^+ channels. Which part of the action potential would you expect potassium channels to affect?

[reveal-answer q="217786"]Show Answer[/reveal-answer]

[hidden-answer a="217786"]Potassium channel blockers slow the repolarization phase, but have no effect on depolarization.[/hidden-answer]

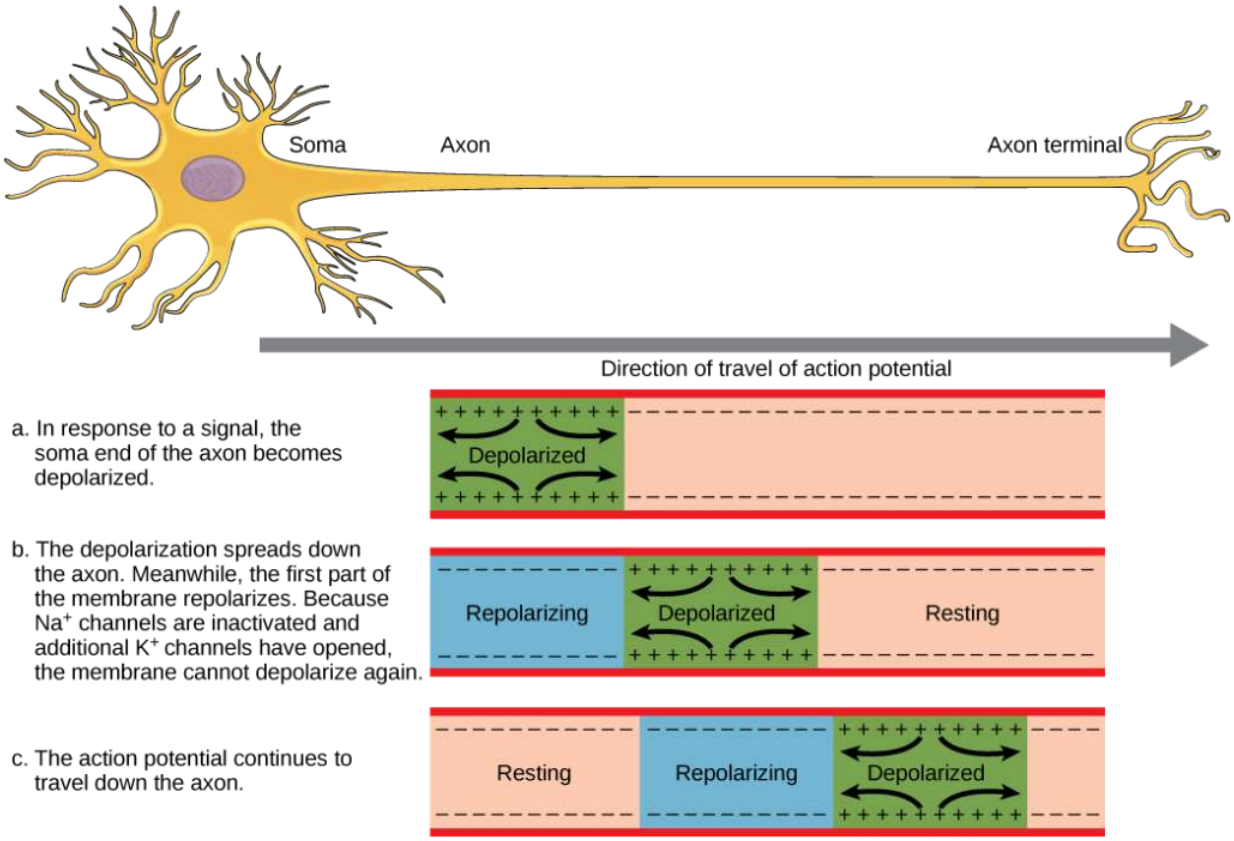


Figure 2. The action potential is conducted down the axon as the axon membrane depolarizes, then repolarizes.

This video presents an overview of action potential.

Myelin and the Propagation of the Action Potential

For an action potential to communicate information to another neuron, it must travel along the axon and reach the axon terminals where it can initiate neurotransmitter release. The speed of conduction of an action potential along an axon is influenced by both the diameter of the axon and the axon's resistance to current leak. Myelin acts as an insulator that prevents current from leaving the axon; this increases the speed of action potential conduction. In demyelinating diseases like multiple sclerosis, action potential conduction slows because current leaks from previously insulated axon areas.

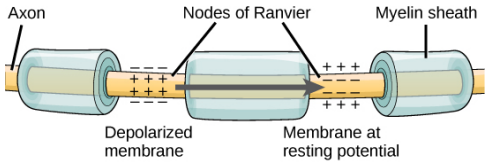


Figure 3. Nodes of Ranvier are gaps in myelin coverage along axons. Nodes contain voltage-gated K^+ and Na^+ channels. Action potentials travel down the axon by jumping from one node to the next.

The nodes of Ranvier, illustrated in Figure 3 are gaps in the myelin sheath along the axon. These unmyelinated spaces are about one micrometer long and contain voltage gated Na^+ and K^+ channels. Flow of ions through these channels, particularly the Na^+ channels, regenerates the action potential over and over again along the axon. This 'jumping' of the action potential from one node to the next is called **saltatory conduction**. If nodes of Ranvier were not present along an axon, the action potential would propagate very slowly since Na^+ and K^+ channels would have to continuously regenerate action potentials at every point along the axon instead of at specific points. Nodes of Ranvier also save energy for the neuron since the channels only need to be present at the nodes and not along the entire axon.

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17.11: Chemical and Electrical Synapses

The synapse or “gap” is the place where information is transmitted from one neuron to another. Synapses usually form between axon terminals and dendritic spines, but this is not universally true. There are also axon-to-axon, dendrite-to-dendrite, and axon-to-cell body synapses. The neuron transmitting the signal is called the presynaptic neuron, and the neuron receiving the signal is called the postsynaptic neuron. Note that these designations are relative to a particular synapse—most neurons are both presynaptic and postsynaptic. There are two types of synapses: chemical and electrical.

Chemical Synapse

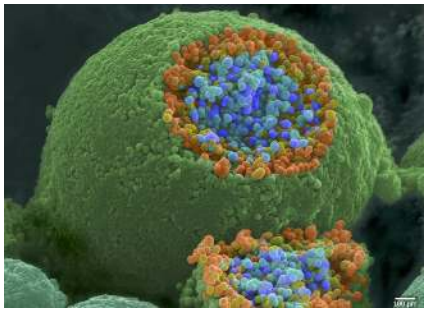


Figure 1. This pseudocolored image taken with a scanning electron microscope shows an axon terminal that was broken open to reveal synaptic vesicles (blue and orange) inside the neuron. (credit: modification of work by Tina Carvalho, NIH-NIGMS; scale-bar data from Matt Russell)

When an action potential reaches the axon terminal it depolarizes the membrane and opens voltage-gated Na^+ channels. Na^+ ions enter the cell, further depolarizing the presynaptic membrane. This depolarization causes voltage-gated Ca^{2+} channels to open. Calcium ions entering the cell initiate a signaling cascade that causes small membrane-bound vesicles, called **synaptic vesicles**, containing neurotransmitter molecules to fuse with the presynaptic membrane. Synaptic vesicles are shown in Figure 1, which is an image from a scanning electron microscope.

Fusion of a vesicle with the presynaptic membrane causes neurotransmitter to be released into the **synaptic cleft**, the extracellular space between the presynaptic and postsynaptic membranes, as illustrated in Figure 2. The neurotransmitter diffuses across the synaptic cleft and binds to receptor proteins on the postsynaptic membrane.

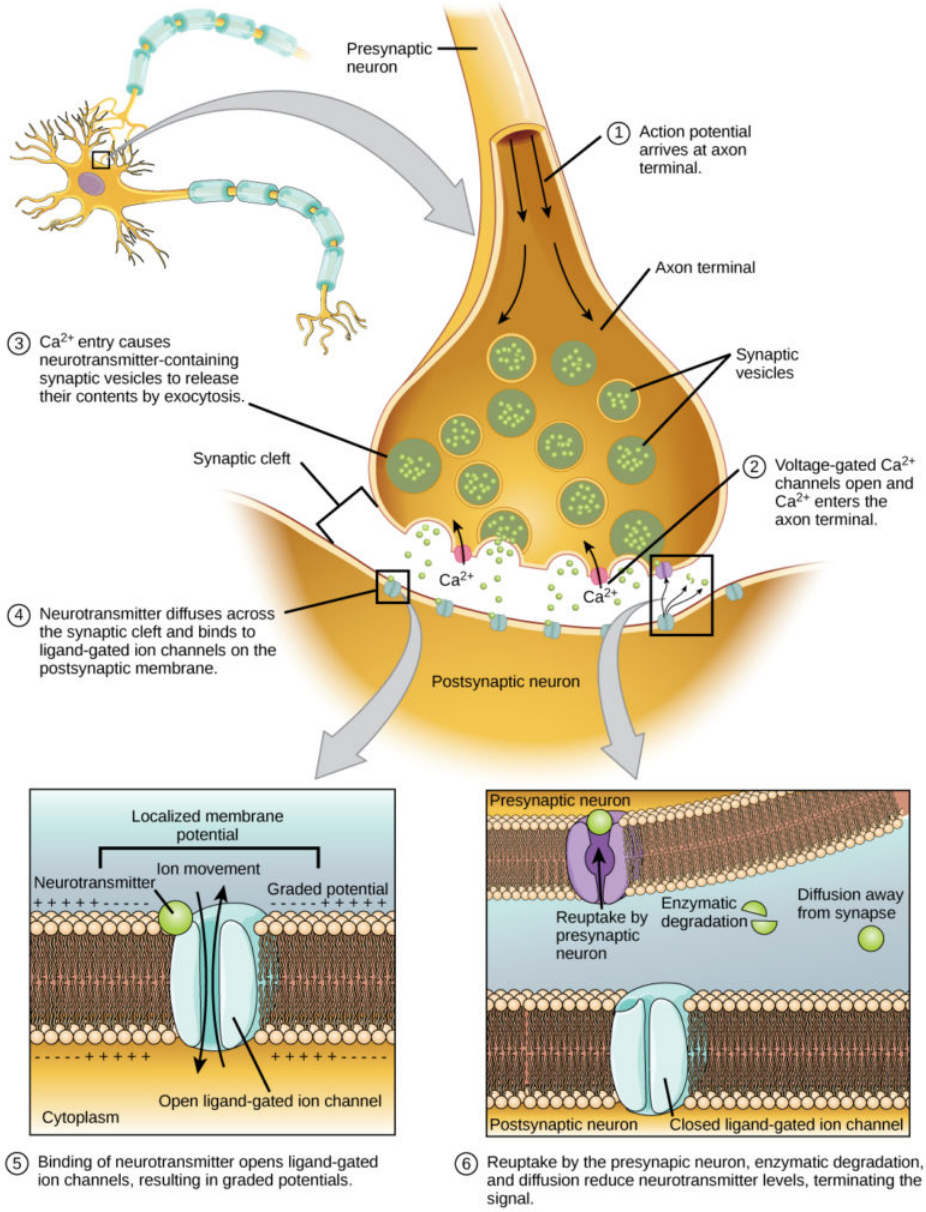


Figure 2. Communication at chemical synapses requires release of neurotransmitters. When the presynaptic membrane is depolarized, voltage-gated $Ca2^{+}$ channels open and allow $Ca2^{+}$ to enter the cell. The calcium entry causes synaptic vesicles to fuse with the membrane and release neurotransmitter molecules into the synaptic cleft. The neurotransmitter diffuses across the synaptic cleft and binds to ligand-gated ion channels in the postsynaptic membrane, resulting in a localized depolarization or hyperpolarization of the postsynaptic neuron.

The binding of a specific neurotransmitter causes particular ion channels, in this case ligand-gated channels, on the postsynaptic membrane to open. Neurotransmitters can either have excitatory or inhibitory effects on the postsynaptic membrane. There are several examples of well known neurotransmitters detailed in Table 1. For example, when acetylcholine is released at the synapse between a nerve and muscle (called the neuromuscular junction) by a presynaptic neuron, it causes postsynaptic Na^{+} channels to open. Na^{+} enters the postsynaptic cell and causes the postsynaptic membrane to depolarize. This depolarization is called an **excitatory postsynaptic potential (EPSP)** and makes the postsynaptic neuron more likely to fire an action potential. Release of neurotransmitter at inhibitory synapses causes **inhibitory postsynaptic potentials (IPSPs)**, a hyperpolarization of the presynaptic membrane. For example, when the neurotransmitter GABA (gamma-aminobutyric acid) is released from a presynaptic neuron, it binds to and opens Cl^{-} channels. Cl^{-} ions enter the cell and hyperpolarizes the membrane, making the neuron less likely to fire an action potential.

Once neurotransmission has occurred, the neurotransmitter must be removed from the synaptic cleft so the postsynaptic membrane can “reset” and be ready to receive another signal. This can be accomplished in three ways: the neurotransmitter can diffuse away from the synaptic cleft, it can be degraded by enzymes in the synaptic cleft, or it can be recycled (sometimes called reuptake) by the presynaptic neuron. Several drugs act at this step of neurotransmission. For example, some drugs that are given to Alzheimer’s patients work by inhibiting acetylcholinesterase, the enzyme that degrades acetylcholine. This inhibition of the enzyme essentially increases neurotransmission at synapses that release acetylcholine. Once released, the acetylcholine stays in the cleft and can continually bind and unbind to postsynaptic receptors.

Table 1. Neurotransmitters

Neurotransmitter	Function	Location
Acetylcholine	muscle control, memory	CNS and/or PNS
Serotonin	intestinal movement, mood regulation, sleep	gut, CNS
Dopamine	voluntary muscle movements, cognition, reward pathways	hypothalamus
Norepinephrine	fight or flight response	adrenal medulla
GABA	inhibits CNS	brain
Glutamate	generally an excitatory neurotransmitter, memory	CNS, PNS

Electrical Synapse

While electrical synapses are fewer in number than chemical synapses, they are found in all nervous systems and play important and unique roles. The mode of neurotransmission in electrical synapses is quite different from that in chemical synapses. In an electrical synapse, the presynaptic and postsynaptic membranes are very close together and are actually physically connected by channel proteins forming gap junctions. Gap junctions allow current to pass directly from one cell to the next. In addition to the ions that carry this current, other molecules, such as ATP, can diffuse through the large gap junction pores.

There are key differences between chemical and electrical synapses. Because chemical synapses depend on the release of neurotransmitter molecules from synaptic vesicles to pass on their signal, there is an approximately one millisecond delay between when the axon potential reaches the presynaptic terminal and when the neurotransmitter leads to opening of postsynaptic ion channels. Additionally, this signaling is unidirectional. Signaling in electrical synapses, in contrast, is virtually instantaneous (which is important for synapses involved in key reflexes), and some electrical synapses are bidirectional. Electrical synapses are also more reliable as they are less likely to be blocked, and they are important for synchronizing the electrical activity of a group of neurons. For example, electrical synapses in the thalamus are thought to regulate slow-wave sleep, and disruption of these synapses can cause seizures.

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17.12: Signal Summation

Sometimes a single EPSP is strong enough to induce an action potential in the postsynaptic neuron, but often multiple presynaptic inputs must create EPSPs around the same time for the postsynaptic neuron to be sufficiently depolarized to fire an action potential. This process is called **summation** and occurs at the axon hillock, as illustrated in Figure 1. Additionally, one neuron often has inputs from many presynaptic neurons—some excitatory and some inhibitory—so IPSPs can cancel out EPSPs and vice versa. It is the net change in postsynaptic membrane voltage that determines whether the postsynaptic cell has reached its threshold of excitation needed to fire an action potential. Together, synaptic summation and the threshold for excitation act as a filter so that random "noise" in the system is not transmitted as important information.

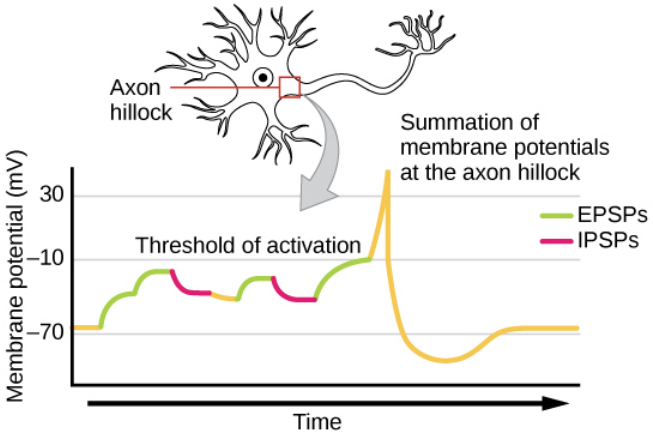


Figure 1. A single neuron can receive both excitatory and inhibitory inputs from multiple neurons, resulting in local membrane depolarization (EPSP input) and hyperpolarization (IPSP input). All these inputs are added together at the axon hillock. If the EPSPs are strong enough to overcome the IPSPs and reach the threshold of excitation, the neuron will fire.

Brain-computer interface

Amyotrophic lateral sclerosis (ALS, also called Lou Gehrig's Disease) is a neurological disease characterized by the degeneration of the motor neurons that control voluntary movements. The disease begins with muscle weakening and lack of coordination and eventually destroys the neurons that control speech, breathing, and swallowing; in the end, the disease can lead to paralysis. At that point, patients require assistance from machines to be able to breathe and to communicate. Several special technologies have been developed to allow "locked-in" patients to communicate with the rest of the world. One technology, for example, allows patients to type out sentences by twitching their cheek. These sentences can then be read aloud by a computer.

A relatively new line of research for helping paralyzed patients, including those with ALS, to communicate and retain a degree of self-sufficiency is called brain-computer interface (BCI) technology and is illustrated in Figure 2. This technology sounds like something out of science fiction: it allows paralyzed patients to control a computer using only their thoughts. There are several forms of BCI. Some forms use EEG recordings from electrodes taped onto the skull. These recordings contain information from large populations of neurons that can be decoded by a computer. Other forms of BCI require the implantation of an array of electrodes smaller than a postage stamp in the arm and hand area of the motor cortex. This form of BCI, while more invasive, is very powerful as each electrode can record actual action potentials from one or more neurons. These signals are then sent to a computer, which has been trained to decode the signal and feed it to a tool—such as a cursor on a computer screen. This means that a patient with ALS can use e-mail, read the Internet, and communicate with others by thinking of moving his or her hand or arm (even though the paralyzed patient cannot make that bodily movement). Recent advances have allowed a paralyzed locked-in patient who suffered a stroke 15 years ago to control a robotic arm and even to feed herself coffee using BCI technology.

Despite the amazing advancements in BCI technology, it also has limitations. The technology can require many hours of training and long periods of intense concentration for the patient; it can also require brain surgery to implant the devices.

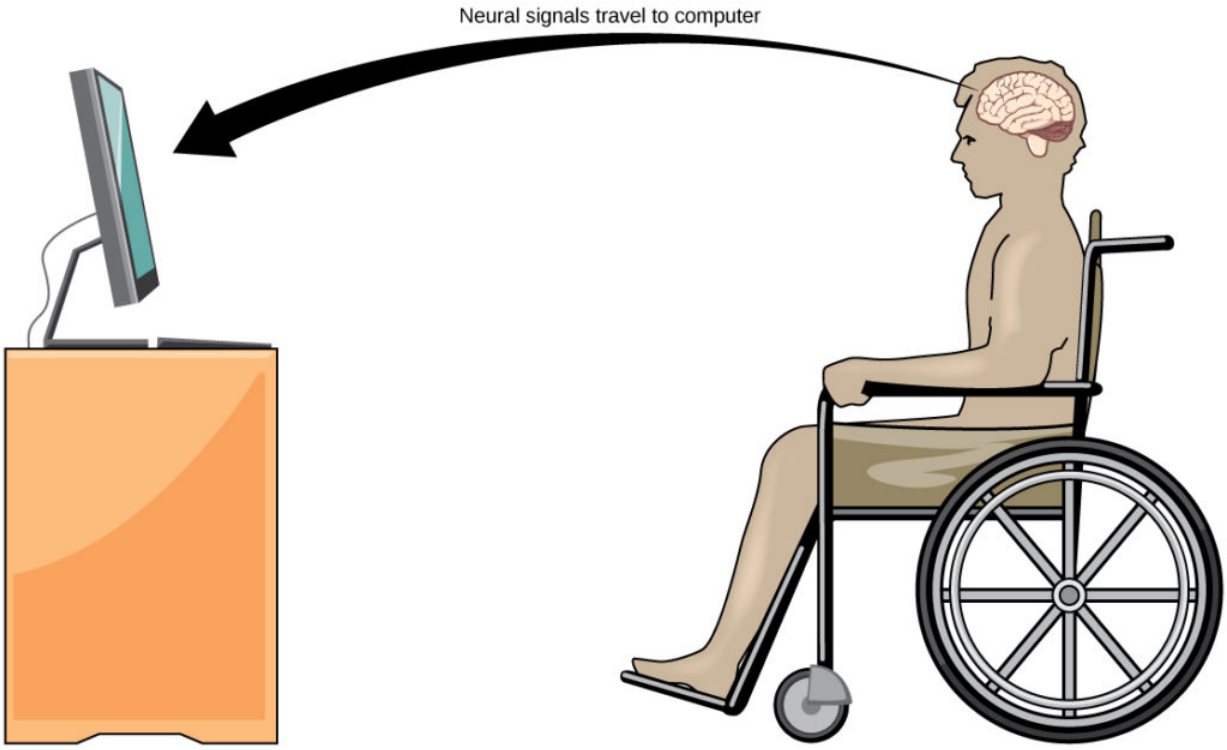


Figure 2. With brain-computer interface technology, neural signals from a paralyzed patient are collected, decoded, and then fed to a tool, such as a computer, a wheelchair, or a robotic arm.

A link to an interactive elements can be found at the bottom of this page.

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17.13: Synaptic Plasticity

Synapses are not static structures. They can be weakened or strengthened. They can be broken, and new synapses can be made. Synaptic plasticity allows for these changes, which are all needed for a functioning nervous system. In fact, synaptic plasticity is the basis of learning and memory. Two processes in particular, long-term potentiation (LTP) and long-term depression (LTD) are important forms of synaptic plasticity that occur in synapses in the hippocampus, a brain region that is involved in storing memories.

Long-term Potentiation (LTP)

Long-term potentiation (LTP) is a persistent strengthening of a synaptic connection. LTP is based on the Hebbian principle: cells that fire together wire together. There are various mechanisms, none fully understood, behind the synaptic strengthening seen with LTP. One known mechanism involves a type of postsynaptic glutamate receptor, called NMDA (N-Methyl-D-aspartate) receptors, shown in Figure 1.

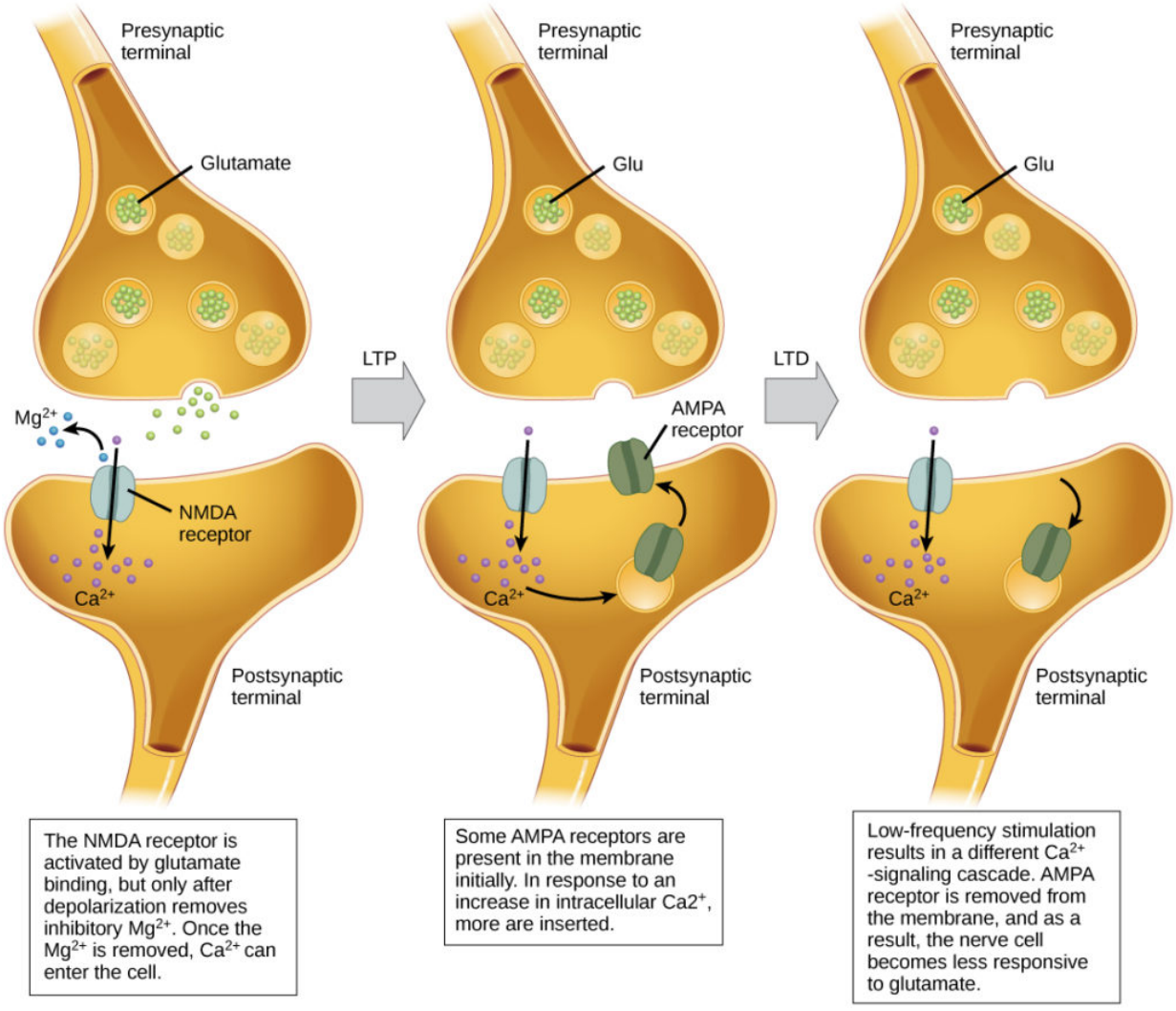


Figure 1. Calcium entry through postsynaptic NMDA receptors can initiate two different forms of synaptic plasticity: long-term potentiation (LTP) and long-term depression (LTD). LTP arises when a single synapse is repeatedly stimulated. This stimulation causes a calcium- and CaMKII-dependent cellular cascade, which results in the insertion of more AMPA receptors into the postsynaptic membrane. The next time glutamate is released from the presynaptic cell, it will bind to both NMDA and the newly inserted AMPA receptors, thus depolarizing the membrane more efficiently. LTD occurs when few glutamate molecules bind to NMDA receptors at a synapse (due to a low firing rate of the presynaptic neuron). The calcium that does flow through NMDA receptors initiates a different calcineurin and protein phosphatase 1-dependent cascade, which results in the endocytosis of AMPA receptors. This makes the postsynaptic neuron less responsive to glutamate released from the presynaptic neuron.

These receptors are normally blocked by magnesium ions; however, when the postsynaptic neuron is depolarized by multiple presynaptic inputs in quick succession (either from one neuron or multiple neurons), the magnesium ions are forced out allowing Ca ions to pass into the postsynaptic cell. Next, Ca^{2+} ions entering the cell initiate a signaling cascade that causes a different type of glutamate receptor, called AMPA (α-amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid) receptors, to be inserted into the postsynaptic membrane, since activated AMPA receptors allow positive ions to enter the cell. So, the next time glutamate is released from the presynaptic membrane, it will have a larger excitatory effect (EPSP) on the postsynaptic cell because the binding of glutamate to these AMPA receptors will allow more positive ions into the cell. The insertion of additional AMPA receptors strengthens the synapse and means that the postsynaptic neuron is more likely to fire in response to presynaptic neurotransmitter release. Some drugs of abuse co-opt the LTP pathway, and this synaptic strengthening can lead to addiction.

Long-term Depression (LTD)

Long-term depression (LTD) is essentially the reverse of LTP: it is a long-term weakening of a synaptic connection. One mechanism known to cause LTD also involves AMPA receptors. In this situation, calcium that enters through NMDA receptors initiates a different signaling cascade, which results in the removal of AMPA receptors from the postsynaptic membrane, as illustrated in Figure 1. The decrease in AMPA receptors in the membrane makes the postsynaptic neuron less responsive to glutamate released from the presynaptic neuron. While it may seem counterintuitive, LTD may be just as important for learning and memory as LTP. The weakening and pruning of unused synapses allows for unimportant connections to be lost and makes the synapses that have undergone LTP that much stronger by comparison.

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17.14: Introduction to the Central Nervous System

Identify the components of the central nervous system

The vertebrate central nervous system contains the brain and the spinal cord, which are covered and protected by three meninges. The brain contains structurally and functionally defined regions. While functions may be primarily localized to one structure in the brain, most complex functions, like language and sleep, involve neurons in multiple brain regions. The spinal cord is the information superhighway that connects the brain with the rest of the body through its connections with peripheral nerves. It transmits sensory and motor input and also controls motor reflexes.

What You'll Learn to Do

- Differentiate between the nervous systems of different animals
- Identify the components of the central nervous system
- Identify locations and basic function of the different parts of the brain
- Identify locations and basic function of the different parts of the spinal cord

Learning Activities

The learning activities for this section include the following:

- Components of the Central Nervous System
- Brain
- Spinal Cord
- Self Check: The Central Nervous System

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17.15: Components of the Central Nervous System

The central nervous system (CNS) is made up of the brain, a part of which is shown in Figure 1 and spinal cord and is covered with three layers of protective coverings called **meninges** (from the Greek word for membrane). The outermost layer is the **dura mater**(Latin for “hard mother”). As the Latin suggests, the primary function for this thick layer is to protect the brain and spinal cord. The dura mater also contains vein-like structures that carry blood from the brain back to the heart. The middle layer is the web-like **arachnoid mater**. The last layer is the **pia mater** (Latin for “soft mother”), which directly contacts and covers the brain and spinal cord like plastic wrap. The space between the arachnoid and pia maters is filled with **cerebrospinal fluid (CSF)**. CSF is produced by a tissue called **choroid plexus** in fluid-filled compartments in the CNS called **ventricles**. The brain floats in CSF, which acts as a cushion and shock absorber and makes the brain neutrally buoyant. CSF also functions to circulate chemical substances throughout the brain and into the spinal cord.

The entire brain contains only about 8.5 tablespoons of CSF, but CSF is constantly produced in the ventricles. This creates a problem when a ventricle is blocked—the CSF builds up and creates swelling and the brain is pushed against the skull. This swelling condition is called hydrocephalus (“water head”) and can cause seizures, cognitive problems, and even death if a shunt is not inserted to remove the fluid and pressure.

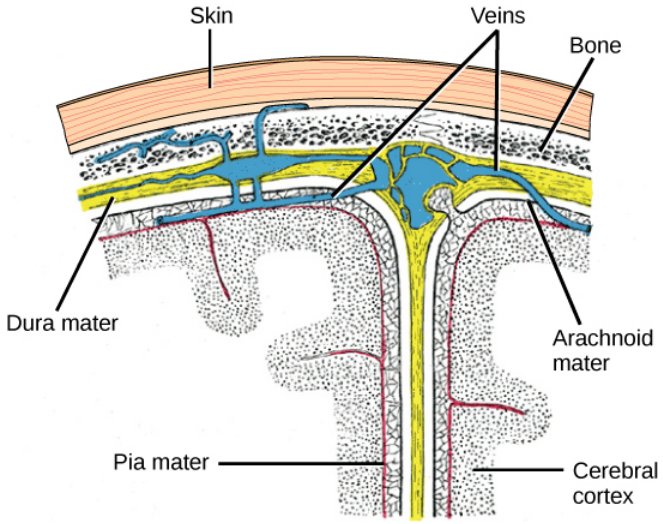


Figure 1. The cerebral cortex is covered by three layers of meninges: the dura, arachnoid, and pia maters. (credit: modification of work by Gray’s Anatomy)

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17.16: Brain

The brain is the part of the central nervous system that is contained in the cranial cavity of the skull. It includes the cerebral cortex, limbic system, basal ganglia, thalamus, hypothalamus, and cerebellum. There are three different ways that a brain can be sectioned in order to view internal structures: a sagittal section cuts the brain left to right, as shown in Figure 1b, a coronal section cuts the brain front to back, as shown in Figure 1a, and a horizontal section cuts the brain top to bottom.

Cerebral Cortex

The outermost part of the brain is a thick piece of nervous system tissue called the **cerebral cortex**, which is folded into hills called **gyri** (singular: gyrus) and valleys called **sulci** (singular: sulcus). The cortex is made up of two hemispheres—right and left—which are separated by a large sulcus. A thick fiber bundle called the **corpus callosum** (Latin: "tough body") connects the two hemispheres and allows information to be passed from one side to the other. Although there are some brain functions that are localized more to one hemisphere than the other, the functions of the two hemispheres are largely redundant. In fact, sometimes (very rarely) an entire hemisphere is removed to treat severe epilepsy. While patients do suffer some deficits following the surgery, they can have surprisingly few problems, especially when the surgery is performed on children who have very immature nervous systems.

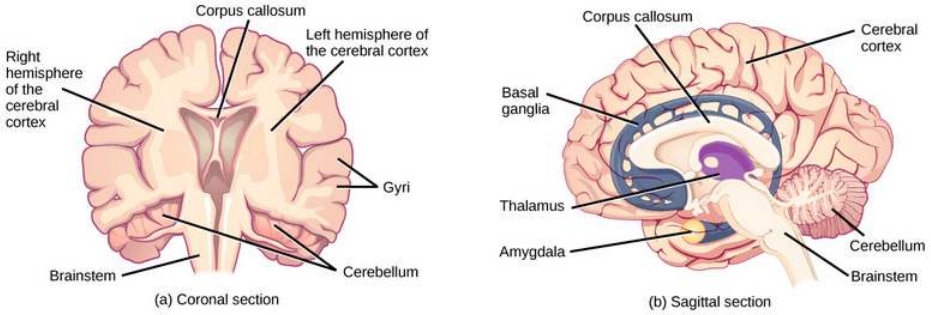


Figure 1. These illustrations show the (a) coronal and (b) sagittal sections of the human brain.

In other surgeries to treat severe epilepsy, the corpus callosum is cut instead of removing an entire hemisphere. This causes a condition called split-brain, which gives insights into unique functions of the two hemispheres. For example, when an object is presented to patients' left visual field, they may be unable to verbally name the object (and may claim to not have seen an object at all). This is because the visual input from the left visual field crosses and enters the right hemisphere and cannot then signal to the speech center, which generally is found in the left side of the brain. Remarkably, if a split-brain patient is asked to pick up a specific object out of a group of objects with the left hand, the patient will be able to do so but will still be unable to vocally identify it.

See this website to learn more about split-brain patients and to play a game where you can model the split-brain experiments yourself.

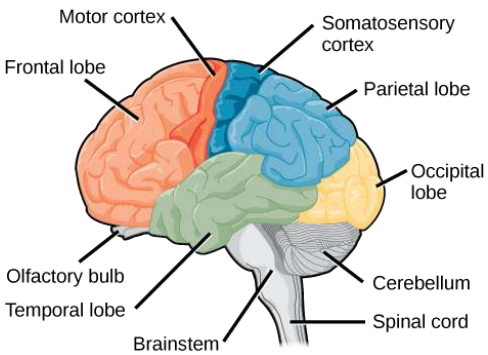


Figure 2. The human cerebral cortex includes the frontal, parietal, temporal, and occipital lobes.

Each cortical hemisphere contains regions called lobes that are involved in different functions. Scientists use various techniques to determine what brain areas are involved in different functions: they examine patients who have had injuries or diseases that affect

specific areas and see how those areas are related to functional deficits. They also conduct animal studies where they stimulate brain areas and see if there are any behavioral changes. They use a technique called transmagnetic stimulation (TMS) to temporarily deactivate specific parts of the cortex using strong magnets placed outside the head; and they use functional magnetic resonance imaging (fMRI) to look at changes in oxygenated blood flow in particular brain regions that correlate with specific behavioral tasks. These techniques, and others, have given great insight into the functions of different brain regions but have also showed that any given brain area can be involved in more than one behavior or process, and any given behavior or process generally involves neurons in multiple brain areas. That being said, each hemisphere of the mammalian cerebral cortex can be broken down into four functionally and spatially defined lobes: frontal, parietal, temporal, and occipital. Figure 2 illustrates these four lobes of the human cerebral cortex.

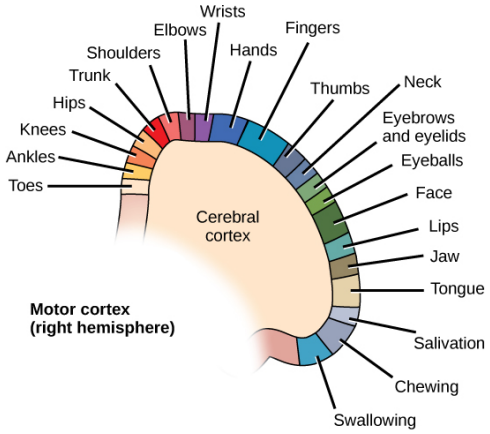


Figure 3. Different parts of the motor cortex control different muscle groups. Muscle groups that are neighbors in the body are generally controlled by neighboring regions of the motor cortex as well. For example, the neurons that control finger movement are near the neurons that control hand movement.

The **frontal lobe** is located at the front of the brain, over the eyes. This lobe contains the olfactory bulb, which processes smells. The frontal lobe also contains the motor cortex, which is important for planning and implementing movement. Areas within the motor cortex map to different muscle groups, and there is some organization to this map, as shown in Figure 3. For example, the neurons that control movement of the fingers are next to the neurons that control movement of the hand. Neurons in the frontal lobe also control cognitive functions like maintaining attention, speech, and decision-making. Studies of humans who have damaged their frontal lobes show that parts of this area are involved in personality, socialization, and assessing risk.

The **parietal lobe** is located at the top of the brain. Neurons in the parietal lobe are involved in speech and also reading. Two of the parietal lobe's main functions are processing **somatosensation**—touch sensations like pressure, pain, heat, cold—and processing **proprioception**—the sense of how parts of the body are oriented in space. The parietal lobe contains a somatosensory map of the body similar to the motor cortex.

The **occipital lobe** is located at the back of the brain. It is primarily involved in vision—seeing, recognizing, and identifying the visual world.

The **temporal lobe** is located at the base of the brain by your ears and is primarily involved in processing and interpreting sounds. It also contains the **hippocampus** (Greek for "seahorse")—a structure that processes memory formation. The hippocampus is illustrated in Figure 5. The role of the hippocampus in memory was partially determined by studying one famous epileptic patient, HM, who had both sides of his hippocampus removed in an attempt to cure his epilepsy. His seizures went away, but he could no longer form new memories (although he could remember some facts from before his surgery and could learn new motor tasks).

? Try It

Compared to other vertebrates, mammals have exceptionally large brains for their body size. An entire alligator's brain, for example, would fill about one and a half teaspoons. This increase in brain to body size ratio is especially pronounced in apes, whales, and dolphins. While this increase in overall brain size doubtlessly played a role in the evolution of complex behaviors unique to mammals, it does not tell the whole story. Scientists have found a relationship between the relatively high surface area of the cortex and the intelligence and complex social behaviors exhibited by some mammals. This increased surface area

is due, in part, to increased folding of the cortical sheet (more sulci and gyri). For example, a rat cortex is very smooth with very few sulci and gyri. Cat and sheep cortices have more sulci and gyri. Chimps, humans, and dolphins have even more.

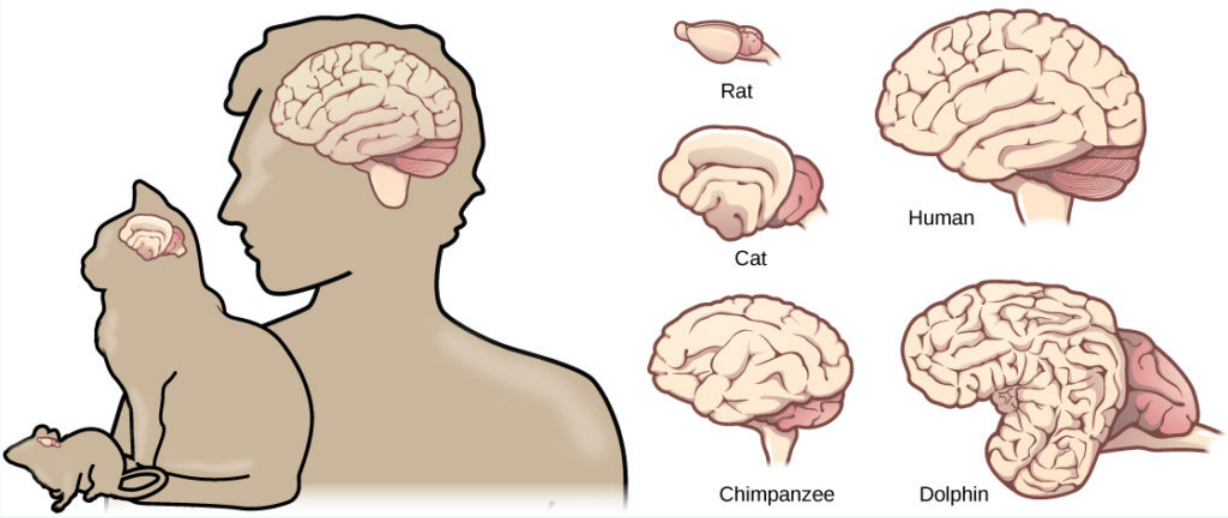


Figure 4. Mammals have larger brain-to-body ratios than other vertebrates. Within mammals, increased cortical folding and surface area is correlated with complex behavior.

Basal Ganglia

Interconnected brain areas called the **basal ganglia** (or **basal nuclei**), shown in Figure 1b, play important roles in movement control and posture. Damage to the basal ganglia, as in Parkinson's disease, leads to motor impairments like a shuffling gait when walking. The basal ganglia also regulate motivation. For example, when a wasp sting led to bilateral basal ganglia damage in a 25-year-old businessman, he began to spend all his days in bed and showed no interest in anything or anybody. But when he was externally stimulated—as when someone asked to play a card game with him—he was able to function normally. Interestingly, he and other similar patients do not report feeling bored or frustrated by their state.

Thalamus

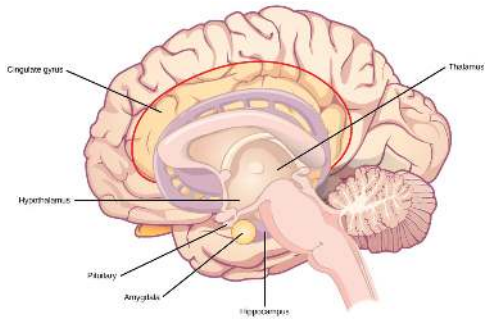


Figure 5. The limbic system regulates emotion and other behaviors. It includes parts of the cerebral cortex located near the center of the brain, including the cingulate gyrus and the hippocampus as well as the thalamus, hypothalamus and amygdala.

The **thalamus** (Greek for "inner chamber"), illustrated in Figure 5, acts as a gateway to and from the cortex. It receives sensory and motor inputs from the body and also receives feedback from the cortex. This feedback mechanism can modulate conscious awareness of sensory and motor inputs depending on the attention and arousal state of the animal. The thalamus helps regulate consciousness, arousal, and sleep states. A rare genetic disorder called fatal familial insomnia causes the degeneration of thalamic neurons and glia. This disorder prevents affected patients from being able to sleep, among other symptoms, and is eventually fatal.

Hypothalamus

Below the thalamus is the **hypothalamus**, shown in Figure 5. The hypothalamus controls the endocrine system by sending signals to the pituitary gland, a pea-sized endocrine gland that releases several different hormones that affect other glands as well as other cells. This relationship means that the hypothalamus regulates important behaviors that are controlled by these hormones. The

hypothalamus is the body's thermostat—it makes sure key functions like food and water intake, energy expenditure, and body temperature are kept at appropriate levels. Neurons within the hypothalamus also regulate circadian rhythms, sometimes called sleep cycles.

Limbic System

The **limbic system** is a connected set of structures that regulates emotion, as well as behaviors related to fear and motivation. It plays a role in memory formation and includes parts of the thalamus and hypothalamus as well as the hippocampus. One important structure within the limbic system is a temporal lobe structure called the **amygdala** (Greek for "almond"), illustrated in Figure 5. The two amygdala are important both for the sensation of fear and for recognizing fearful faces. The **cingulate gyrus** helps regulate emotions and pain.

Cerebellum

The **cerebellum** (Latin for "little brain"), shown in Figure 2, sits at the base of the brain on top of the brainstem. The cerebellum controls balance and aids in coordinating movement and learning new motor tasks.

Brainstem

The **brainstem**, illustrated in Figure 2, connects the rest of the brain with the spinal cord. It consists of the midbrain, medulla oblongata, and the pons. Motor and sensory neurons extend through the brainstem allowing for the relay of signals between the brain and spinal cord. Ascending neural pathways cross in this section of the brain allowing the left hemisphere of the cerebrum to control the right side of the body and vice versa. The brainstem coordinates motor control signals sent from the brain to the body. The brainstem controls several important functions of the body including alertness, arousal, breathing, blood pressure, digestion, heart rate, swallowing, walking, and sensory and motor information integration.

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17.17: Spinal Cord

Connecting to the brainstem and extending down the body through the spinal column is the **spinal cord**. The spinal cord is a thick bundle of nerve tissue that carries information about the body to the brain and from the brain to the body. The spinal cord is contained within the bones of the vertebrate column but is able to communicate signals to and from the body through its connections with spinal nerves (part of the peripheral nervous system). A cross-section of the spinal cord looks like a white oval containing a gray butterfly-shape, as illustrated in Figure 1. Myelinated axons make up the “white matter” and neuron and glial cell bodies make up the “gray matter.” Gray matter is also composed of interneurons, which connect two neurons each located in different parts of the body. Axons and cell bodies in the dorsal (facing the back of the animal) spinal cord convey mostly sensory information from the body to the brain. Axons and cell bodies in the ventral (facing the front of the animal) spinal cord primarily transmit signals controlling movement from the brain to the body.

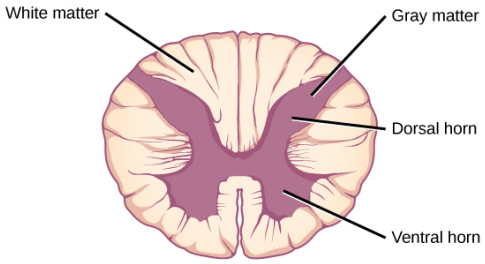


Figure 1. A cross-section of the spinal cord shows gray matter (containing cell bodies and interneurons) and white matter (containing axons).

The spinal cord also controls motor reflexes. These reflexes are quick, unconscious movements—like automatically removing a hand from a hot object. Reflexes are so fast because they involve local synaptic connections. For example, the knee reflex that a doctor tests during a routine physical is controlled by a single synapse between a sensory neuron and a motor neuron. While a reflex may only require the involvement of one or two synapses, synapses with interneurons in the spinal column transmit information to the brain to convey what happened (the knee jerked, or the hand was hot).

In the United States, there around 10,000 spinal cord injuries each year. Because the spinal cord is the information superhighway connecting the brain with the body, damage to the spinal cord can lead to paralysis. The extent of the paralysis depends on the location of the injury along the spinal cord and whether the spinal cord was completely severed. For example, if the spinal cord is damaged at the level of the neck, it can cause paralysis from the neck down, whereas damage to the spinal column further down may limit paralysis to the legs. Spinal cord injuries are notoriously difficult to treat because spinal nerves do not regenerate, although ongoing research suggests that stem cell transplants may be able to act as a bridge to reconnect severed nerves. Researchers are also looking at ways to prevent the inflammation that worsens nerve damage after injury. One such treatment is to pump the body with cold saline to induce hypothermia. This cooling can prevent swelling and other processes that are thought to worsen spinal cord injuries.

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17.18: Introduction to the Peripheral Nervous System

Identify the components of the peripheral nervous system

The peripheral nervous system (PNS) is the connection between the central nervous system and the rest of the body. The CNS is like the power plant of the nervous system. It creates the signals that control the functions of the body. The PNS is like the wires that go to individual houses. Without those “wires,” the signals produced by the CNS could not control the body (and the CNS would not be able to receive sensory information from the body either).

The PNS can be broken down into the **autonomic nervous system**, which controls bodily functions without conscious control, and the **sensory-somatic nervous system**, which transmits sensory information from the skin, muscles, and sensory organs to the CNS and sends motor commands from the CNS to the muscles.

What You’ll Learn to Do

- Describe the organization and functions of the sympathetic nervous systems
- Describe the organization and functions of the parasympathetic nervous systems
- Describe the organization and function of the sensory-somatic nervous system

Learning Activities

The learning activities for this section include the following:

- Autonomic Nervous System
- Sensory-Somatic Nervous System
- Self Check: The Peripheral Nervous System

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17.19: Autonomic Nervous System

In the autonomic nervous system, a preganglionic neuron of the CNS synapses with a postganglionic neuron of the PNS. The postganglionic neuron, in turn, acts on a target organ. Autonomic responses are mediated by the sympathetic and the parasympathetic systems, which are antagonistic to one another. The sympathetic system activates the “fight or flight” response, while the parasympathetic system activates the “rest and digest” response.

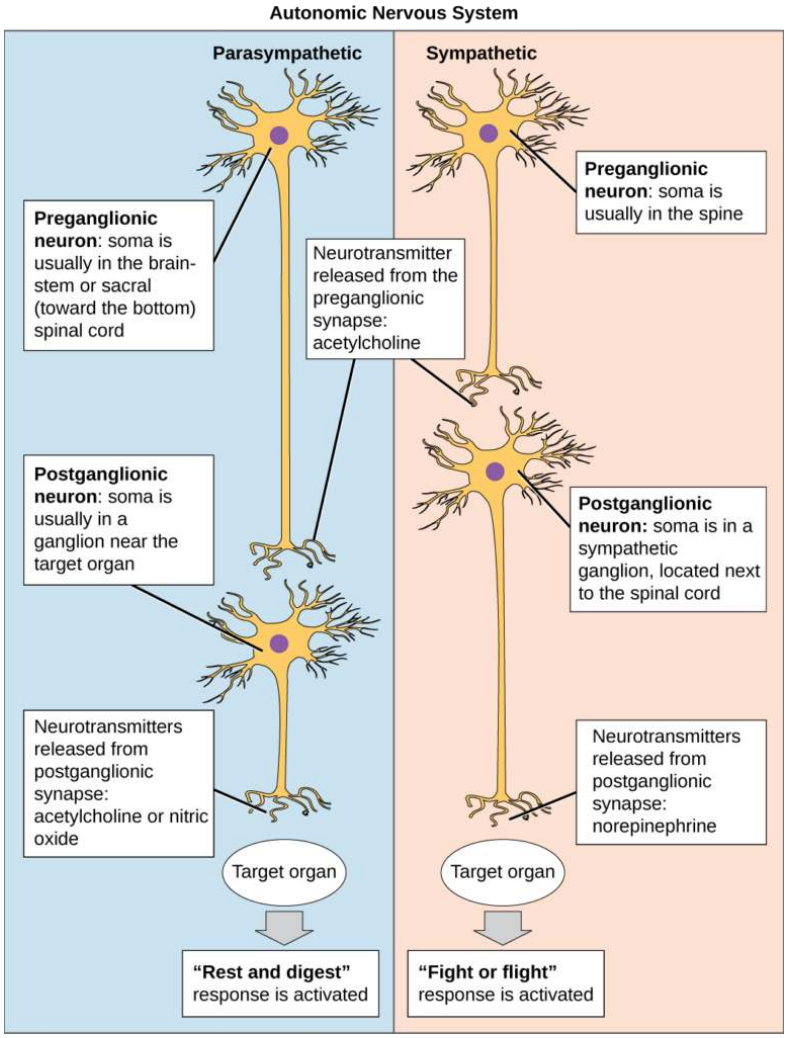


Figure 1. The sympathetic and parasympathetic systems

The autonomic nervous system serves as the relay between the CNS and the internal organs. It controls the lungs, the heart, smooth muscle, and exocrine and endocrine glands. The autonomic nervous system controls these organs largely without conscious control; it can continuously monitor the conditions of these different systems and implement changes as needed. Signaling to the target tissue usually involves two synapses: a preganglionic neuron (originating in the CNS) synapses to a neuron in a ganglion that, in turn, synapses on the target organ, as illustrated in Figure 1. There are two divisions of the autonomic nervous system that often have opposing effects: the sympathetic nervous system and the parasympathetic nervous system.

? Practice Question

Which of the following statements is false?

a. The parasympathetic pathway is responsible for resting the body, while the sympathetic pathway is responsible for preparing for an emergency.
b. Most preganglionic neurons in the sympathetic pathway originate in the spinal cord.

c. Slowing of the heartbeat is a parasympathetic response.
d. Parasympathetic neurons are responsible for releasing norepinephrine on the target organ, while sympathetic neurons are responsible for releasing acetylcholine.

[reveal-answer q="310489"]Show Answer[/reveal-answer]
[hidden-answer a="310489"]Statement d is false.[/hidden-answer]

Sympathetic Nervous System

The **sympathetic nervous system** is responsible for the "fight or flight" response that occurs when an animal encounters a dangerous situation. One way to remember this is to think of the surprise a person feels when encountering a snake ("snake" and "sympathetic" both begin with "s"). Examples of functions controlled by the sympathetic nervous system include an accelerated heart rate and inhibited digestion. These functions help prepare an organism's body for the physical strain required to escape a potentially dangerous situation or to fend off a predator.

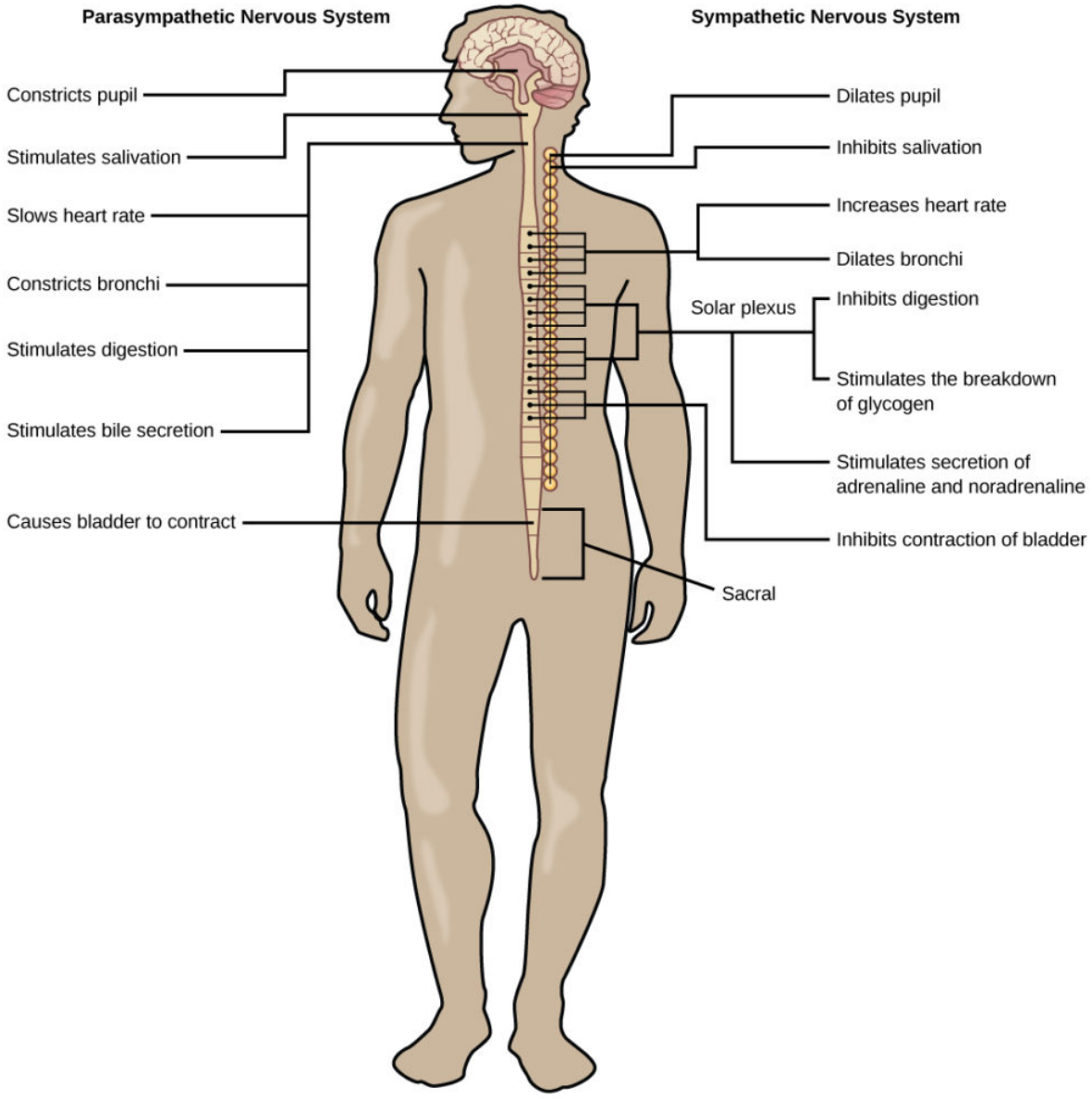


Figure 2. The sympathetic and parasympathetic nervous systems often have opposing effects on target organs.

Most preganglionic neurons in the sympathetic nervous system originate in the spinal cord, as illustrated in Figure 2. The axons of these neurons release **acetylcholine** on postganglionic neurons within sympathetic ganglia (the sympathetic ganglia form a chain

that extends alongside the spinal cord). The acetylcholine activates the postganglionic neurons. Postganglionic neurons then release **norepinephrine** onto target organs. As anyone who has ever felt a rush before a big test, speech, or athletic event can attest, the effects of the sympathetic nervous system are quite pervasive. This is both because one preganglionic neuron synapses on multiple postganglionic neurons, amplifying the effect of the original synapse, and because the adrenal gland also releases norepinephrine (and the closely related hormone epinephrine) into the blood stream. The physiological effects of this norepinephrine release include dilating the trachea and bronchi (making it easier for the animal to breathe), increasing heart rate, and moving blood from the skin to the heart, muscles, and brain (so the animal can think and run). The strength and speed of the sympathetic response helps an organism avoid danger, and scientists have found evidence that it may also increase LTP—allowing the animal to remember the dangerous situation and avoid it in the future.

Parasympathetic Nervous System

While the sympathetic nervous system is activated in stressful situations, the **parasympathetic nervous system** allows an animal to "rest and digest." The parasympathetic system's functions conserve energy: slowing down the heart rate, reducing contractile forces of both cardiac and gastrointestinal muscle, and reducing conduction velocity of the sinoatrial node and atrioventricular node.

One way to remember this is to think that during a restful situation like a picnic, the parasympathetic nervous system is in control ("picnic" and "parasympathetic" both start with "p"). Parasympathetic preganglionic neurons have cell bodies located in the brainstem and in the sacral (toward the bottom) spinal cord, as shown in Figure 2. The axons of the preganglionic neurons release acetylcholine on the postganglionic neurons, which are generally located very near the target organs. Most postganglionic neurons release acetylcholine onto target organs, although some release nitric oxide. Acetylcholine acts on two types of receptors, the muscarinic and nicotinic cholinergic receptors. Most transmissions occur in two stages: When stimulated, the preganglionic neuron releases acetylcholine at the ganglion, which acts on nicotinic receptors of postganglionic neurons. The postganglionic neuron then releases acetylcholine to stimulate the muscarinic receptors of the target organ.

The parasympathetic nervous system resets organ function after the sympathetic nervous system is activated (the common adrenaline dump you feel after a "fight-or-flight" event). Effects of acetylcholine release on target organs include slowing of heart rate, lowered blood pressure, and stimulation of digestion.

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17.20: Sensory-Somatic Nervous System

The sensory-somatic nervous system is made up of cranial and spinal nerves and contains both sensory and motor neurons. Sensory neurons transmit sensory information from the skin, skeletal muscle, and sensory organs to the CNS. Motor neurons transmit messages about desired movement from the CNS to the muscles to make them contract. Without its sensory-somatic nervous system, an animal would be unable to process any information about its environment (what it sees, feels, hears, and so on) and could not control motor movements. Unlike the autonomic nervous system, which has two synapses between the CNS and the target organ, sensory and motor neurons have only one synapse—one ending of the neuron is at the organ and the other directly contacts a CNS neuron. Acetylcholine is the main neurotransmitter released at these synapses.

Humans have 12 **cranial nerves**, nerves that emerge from or enter the skull (cranium), as opposed to the spinal nerves, which emerge from the vertebral column. Each cranial nerve is accorded a name, which are detailed in Figure 1.

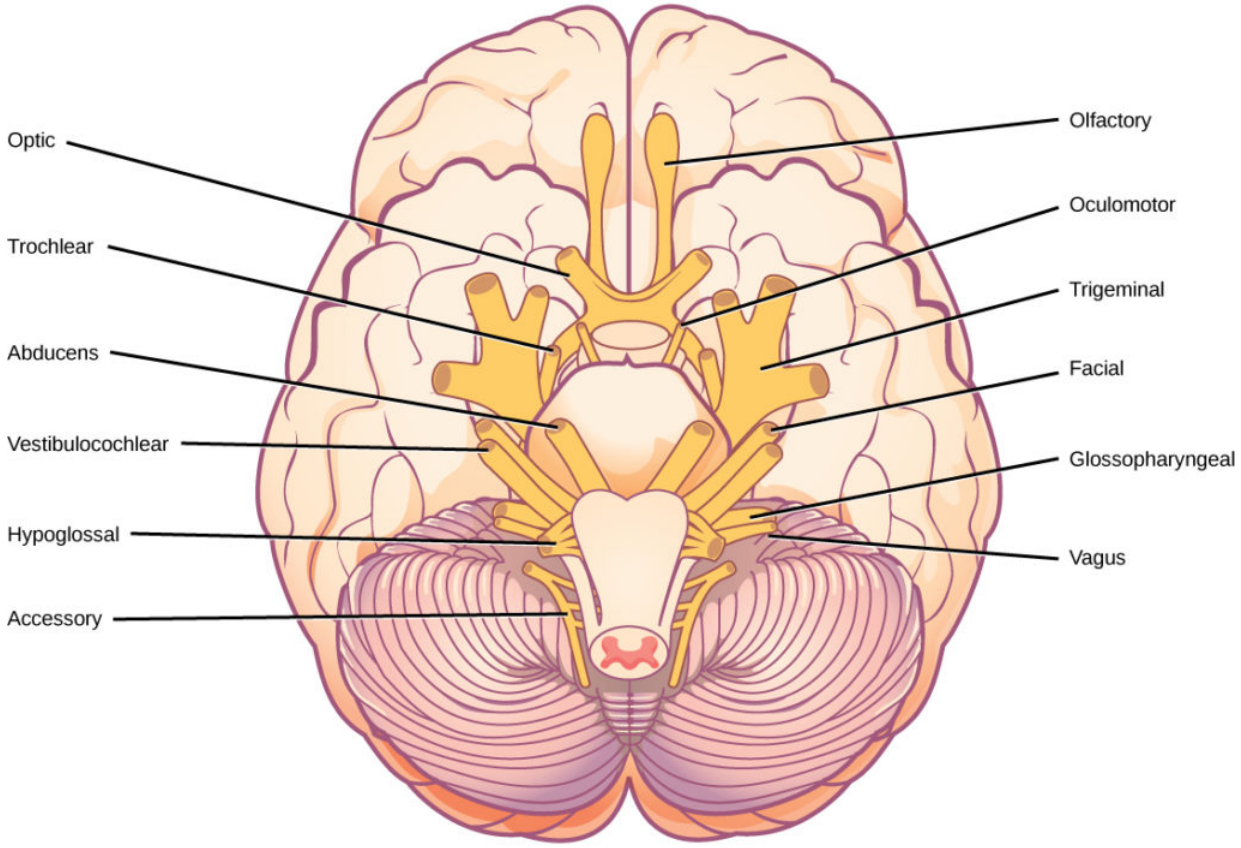


Figure 1. The human brain contains 12 cranial nerves that receive sensory input and control motor output for the head and neck.

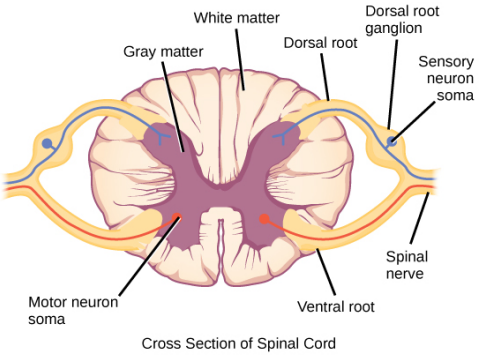


Figure 2. Spinal nerves contain both sensory and motor axons. The somas of sensory neurons are located in dorsal root ganglia. The somas of motor neurons are found in the ventral portion of the gray matter of the spinal cord.

Some cranial nerves transmit only sensory information. For example, the olfactory nerve transmits information about smells from the nose to the brainstem. Other cranial nerves transmit almost solely motor information. For example, the oculomotor nerve controls the opening and closing of the eyelid and some eye movements. Other cranial nerves contain a mix of sensory and motor fibers. For example, the glossopharyngeal nerve has a role in both taste (sensory) and swallowing (motor).

Spinal nerves transmit sensory and motor information between the spinal cord and the rest of the body. Each of the 31 spinal nerves (in humans) contains both sensory and motor axons. The sensory neuron cell bodies are grouped in structures called dorsal root ganglia and are shown in Figure 2.

Each sensory neuron has one projection—with a sensory receptor ending in skin, muscle, or sensory organs—and another that synapses with a neuron in the dorsal spinal cord. Motor neurons have cell bodies in the ventral gray matter of the spinal cord that project to muscle through the ventral root. These neurons are usually stimulated by interneurons within the spinal cord but are sometimes directly stimulated by sensory neurons.

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17.21: Introduction to Nervous System Disorders

Describe the symptoms, potential causes, and treatment of several examples of nervous system disorders

A nervous system that functions correctly is a fantastically complex, well-oiled machine—synapses fire appropriately, muscles move when needed, memories are formed and stored, and emotions are well regulated. Unfortunately, each year millions of people in the United States deal with some sort of nervous system disorder. While scientists have discovered potential causes of many of these diseases, and viable treatments for some, ongoing research seeks to find ways to better prevent and treat all of these disorders.

What You'll Learn to Do

- Identify key characteristics and symptoms of neurodegenerative disorders
- Identify key characteristics and symptoms of neurodevelopmental disorders
- Identify key characteristics and symptoms of mental illnesses
- Identify key characteristics and symptoms of other neurological disorders

Learning Activities

The learning activities for this section include the following:

- Neurodegenerative Disorders
- Neurodevelopmental Disorders
- Mental Illnesses
- Other Neurological Disorders
- Self Check: Nervous System Disorders

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17.22: Neurodegenerative Disorders

Neurodegenerative disorders are illnesses characterized by a loss of nervous system functioning that are usually caused by neuronal death. These diseases generally worsen over time as more and more neurons die. The symptoms of a particular neurodegenerative disease are related to where in the nervous system the death of neurons occurs. Spinocerebellar ataxia, for example, leads to neuronal death in the cerebellum. The death of these neurons causes problems in balance and walking. Neurodegenerative disorders include Huntington's disease, amyotrophic lateral sclerosis, Alzheimer's disease and other types of dementia disorders, and Parkinson's disease. Here, Alzheimer's and Parkinson's disease will be discussed in more depth.

Alzheimer's Disease

Alzheimer's disease is the most common cause of dementia in the elderly. In 2012, an estimated 5.4 million Americans suffered from Alzheimer's disease, and payments for their care are estimated at $200 billion. Roughly one in every eight people age 65 or older has the disease. Due to the aging of the baby-boomer generation, there are projected to be as many as 13 million Alzheimer's patients in the United States in the year 2050.

Symptoms of Alzheimer's disease include disruptive memory loss, confusion about time or place, difficulty planning or executing tasks, poor judgment, and personality changes. Problems smelling certain scents can also be indicative of Alzheimer's disease and may serve as an early warning sign. Many of these symptoms are also common in people who are aging normally, so it is the severity and longevity of the symptoms that determine whether a person is suffering from Alzheimer's.

Alzheimer's disease was named for Alois Alzheimer, a German psychiatrist who published a report in 1911 about a woman who showed severe dementia symptoms. Along with his colleagues, he examined the woman's brain following her death and reported the presence of abnormal clumps, which are now called amyloid plaques, along with tangled brain fibers called neurofibrillary tangles. Amyloid plaques, neurofibrillary tangles, and an overall shrinking of brain volume are commonly seen in the brains of Alzheimer's patients. Loss of neurons in the hippocampus is especially severe in advanced Alzheimer's patients. Figure 1 compares a normal brain to the brain of an Alzheimer's patient. Many research groups are examining the causes of these hallmarks of the disease.

One form of the disease is usually caused by mutations in one of three known genes. This rare form of early onset Alzheimer's disease affects fewer than five percent of patients with the disease and causes dementia beginning between the ages of 30 and 60. The more prevalent, late-onset form of the disease likely also has a genetic component. One particular gene, apolipoprotein E (APOE) has a variant (E4) that increases a carrier's likelihood of getting the disease. Many other genes have been identified that might be involved in the pathology.

Visit this website for video links discussing genetics and Alzheimer's disease.

Unfortunately, there is no cure for Alzheimer's disease. Current treatments focus on managing the symptoms of the disease. Because decrease in the activity of cholinergic neurons (neurons that use the neurotransmitter acetylcholine) is common in Alzheimer's disease, several drugs used to treat the disease work by increasing acetylcholine neurotransmission, often by inhibiting the enzyme that breaks down acetylcholine in the synaptic cleft. Other clinical interventions focus on behavioral therapies like psychotherapy, sensory therapy, and cognitive exercises. Since Alzheimer's disease appears to hijack the normal aging process, research into prevention is prevalent. Smoking, obesity, and cardiovascular problems may be risk factors for the disease, so treatments for those may also help to prevent Alzheimer's disease. Some studies have shown that people who remain intellectually active by playing games, reading, playing musical instruments, and being socially active in later life have a reduced risk of developing the disease.

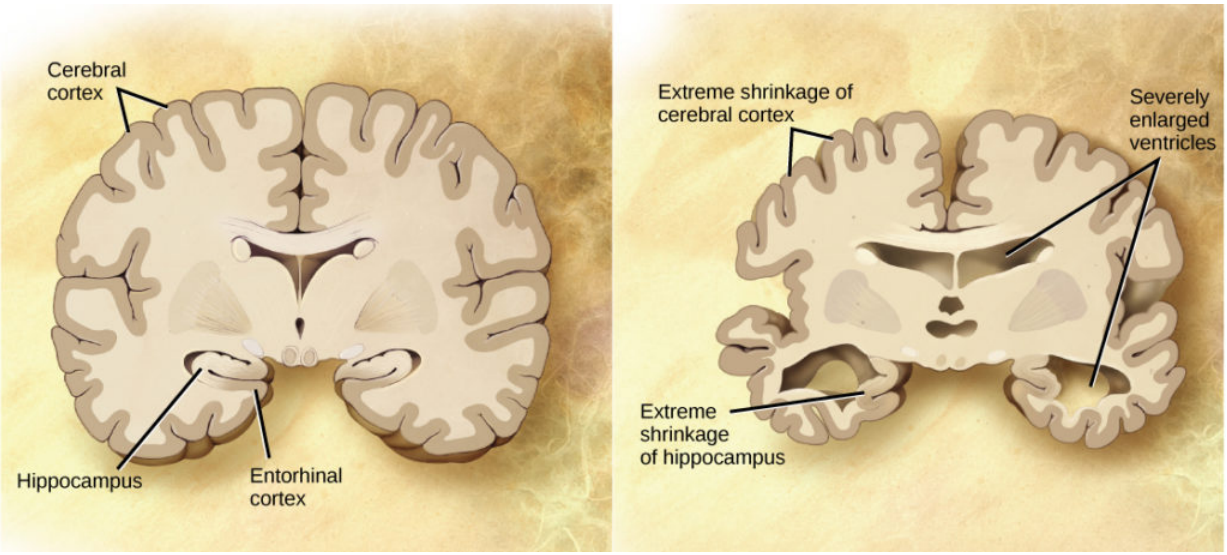


Figure 1. Compared to a normal brain (left), the brain from a patient with Alzheimer's disease (right) shows a dramatic neurodegeneration, particularly within the ventricles and hippocampus. (credit: modification of work by "Garrando"/Wikimedia Commons based on original images by ADEAR: "Alzheimer's Disease Education and Referral Center, a service of the National Institute on Aging")

Parkinson's Disease

Like Alzheimer's disease, **Parkinson's disease** is a neurodegenerative disease. It was first characterized by James Parkinson in 1817. Each year, 50,000-60,000 people in the United States are diagnosed with the disease. Parkinson's disease causes the loss of dopamine neurons in the substantia nigra, a midbrain structure that regulates movement. Loss of these neurons causes many symptoms including tremor (shaking of fingers or a limb), slowed movement, speech changes, balance and posture problems, and rigid muscles. The combination of these symptoms often causes a characteristic slow hunched shuffling walk, illustrated in Figure 2. Patients with Parkinson's disease can also exhibit psychological symptoms, such as dementia or emotional problems.



Figure 2. Parkinson's patients often have a characteristic hunched walk.

Although some patients have a form of the disease known to be caused by a single mutation, for most patients the exact causes of Parkinson's disease remain unknown: the disease likely results from a combination of genetic and environmental factors (similar to Alzheimer's disease). Post-mortem analysis of brains from Parkinson's patients shows the presence of Lewy bodies—abnormal protein clumps—in dopaminergic neurons. The prevalence of these Lewy bodies often correlates with the severity of the disease.

There is no cure for Parkinson's disease, and treatment is focused on easing symptoms. One of the most commonly prescribed drugs for Parkinson's is L-DOPA, which is a chemical that is converted into dopamine by neurons in the brain. This conversion increases the overall level of dopamine neurotransmission and can help compensate for the loss of dopaminergic neurons in the substantia nigra. Other drugs work by inhibiting the enzyme that breaks down dopamine.

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17.23: Neurodevelopmental Disorders

Neurodevelopmental disorders occur when the development of the nervous system is disturbed. There are several different classes of neurodevelopmental disorders. Some, like Down Syndrome, cause intellectual deficits. Others specifically affect communication, learning, or the motor system. Some disorders like autism spectrum disorder and attention deficit/hyperactivity disorder have complex symptoms.

Autism

Autism spectrum disorder (ASD) is a neurodevelopmental disorder. Its severity differs from person to person. Estimates for the prevalence of the disorder have changed rapidly in the past few decades. Current estimates suggest that one in 88 children will develop the disorder. ASD is four times more prevalent in males than females.

This video discusses possible reasons why there has been a recent increase in the number of people diagnosed with autism.



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=703

A characteristic symptom of ASD is impaired social skills. Children with autism may have difficulty making and maintaining eye contact and reading social cues. They also may have problems feeling empathy for others. Other symptoms of ASD include repetitive motor behaviors (such as rocking back and forth), preoccupation with specific subjects, strict adherence to certain rituals, and unusual language use. Up to 30 percent of patients with ASD develop epilepsy, and patients with some forms of the disorder (like Fragile X) also have intellectual disability. Because it is a spectrum disorder, other ASD patients are very functional and have good-to-excellent language skills. Many of these patients do not feel that they suffer from a disorder and instead think that their brains just process information differently.

Except for some well-characterized, clearly genetic forms of autism (like Fragile X and Rett's Syndrome), the causes of ASD are largely unknown. Variants of several genes correlate with the presence of ASD, but for any given patient, many different mutations in different genes may be required for the disease to develop. At a general level, ASD is thought to be a disease of "incorrect" wiring. Accordingly, brains of some ASD patients lack the same level of synaptic pruning that occurs in non-affected people. In the 1990s, a research paper linked autism to a common vaccine given to children. This paper was retracted when it was discovered that the author falsified data, and follow-up studies showed no connection between vaccines and autism.

Treatment for autism usually combines behavioral therapies and interventions, along with medications to treat other disorders common to people with autism (depression, anxiety, obsessive compulsive disorder). Although early interventions can help mitigate the effects of the disease, there is currently no cure for ASD.

Attention Deficit Hyperactivity Disorder (ADHD)

Approximately three to five percent of children and adults are affected by **attention deficit/hyperactivity disorder (ADHD)**. Like ASD, ADHD is more prevalent in males than females. Symptoms of the disorder include inattention (lack of focus), executive functioning difficulties, impulsivity, and hyperactivity beyond what is characteristic of the normal developmental stage. Some patients do not have the hyperactive component of symptoms and are diagnosed with a subtype of ADHD: attention deficit disorder

(ADD). Many people with ADHD also show comorbitity, in that they develop secondary disorders in addition to ADHD. Examples include depression or obsessive compulsive disorder (OCD). Figure 1 provides some statistics concerning comorbidity with ADHD.



Figure 1. Many people with ADHD have one or more other neurological disorders. (credit "chart design and illustration": modification of work by Leigh Coriale; credit "data": Drs. Biederman and Faraone, Massachusetts General Hospital)

The cause of ADHD is unknown, although research points to a delay and dysfunction in the development of the prefrontal cortex and disturbances in neurotransmission. According to studies of twins, the disorder has a strong genetic component. There are several candidate genes that may contribute to the disorder, but no definitive links have been discovered. Environmental factors, including exposure to certain pesticides, may also contribute to the development of ADHD in some patients. Treatment for ADHD often involves behavioral therapies and the prescription of stimulant medications, which paradoxically cause a calming effect in these patients.

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17.24: Mental Illnesses

Mental illnesses are nervous system disorders that result in problems with thinking, mood, or relating with other people. These disorders are severe enough to affect a person's quality of life and often make it difficult for people to perform the routine tasks of daily living. Debilitating mental disorders plague approximately 12.5 million Americans (about 1 in 17 people) at an annual cost of more than $300 billion. There are several types of mental disorders including schizophrenia, major depression, bipolar disorder, anxiety disorders and phobias, post-traumatic stress disorders, and obsessive-compulsive disorder (OCD), among others. The American Psychiatric Association publishes the Diagnostic and Statistical Manual of Mental Disorders (or DSM), which describes the symptoms required for a patient to be diagnosed with a particular mental disorder. Each newly released version of the DSM contains different symptoms and classifications as scientists learn more about these disorders, their causes, and how they relate to each other. A more detailed discussion of two mental illnesses—schizophrenia and major depression—is given below.

Schizophrenia

Schizophrenia is a serious and often debilitating mental illness affecting one percent of people in the United States. Symptoms of the disease include the inability to differentiate between reality and imagination, inappropriate and unregulated emotional responses, difficulty thinking, and problems with social situations. People with schizophrenia can suffer from hallucinations and hear voices; they may also suffer from delusions. Patients also have so-called "negative" symptoms like a flattened emotional state, loss of pleasure, and loss of basic drives. Many schizophrenic patients are diagnosed in their late adolescence or early 20s.

The development of schizophrenia is thought to involve malfunctioning dopaminergic neurons and may also involve problems with glutamate signaling. Treatment for the disease usually requires antipsychotic medications that work by blocking dopamine receptors and decreasing dopamine neurotransmission in the brain. This decrease in dopamine can cause Parkinson's disease-like symptoms in some patients. While some classes of antipsychotics can be quite effective at treating the disease, they are not a cure, and most patients must remain medicated for the rest of their lives.

Depression

Major depression affects approximately 6.7 percent of the adults in the United States each year and is one of the most common mental disorders. To be diagnosed with major depressive disorder, a person must have experienced a severely depressed mood lasting longer than two weeks along with other symptoms including a loss of enjoyment in activities that were previously enjoyed, changes in appetite and sleep schedules, difficulty concentrating, feelings of worthlessness, and suicidal thoughts.

The exact causes of major depression are unknown and likely include both genetic and environmental risk factors. Some research supports the "classic monoamine hypothesis," which suggests that depression is caused by a decrease in norepinephrine and serotonin neurotransmission. One argument against this hypothesis is the fact that some antidepressant medications cause an increase in norepinephrine and serotonin release within a few hours of beginning treatment—but clinical results of these medications are not seen until weeks later. This has led to alternative hypotheses: for example, dopamine may also be decreased in depressed patients, or it may actually be an increase in norepinephrine and serotonin that causes the disease, and antidepressants force a feedback loop that decreases this release.

Treatments for depression include psychotherapy, electroconvulsive therapy, deep-brain stimulation, and prescription medications. There are several classes of antidepressant medications that work through different mechanisms. For example, monoamine oxidase inhibitors (MAO inhibitors) block the enzyme that degrades many neurotransmitters (including dopamine, serotonin, norepinephrine), resulting in increased neurotransmitter in the synaptic cleft. Selective serotonin reuptake inhibitors (SSRIs) block the reuptake of serotonin into the presynaptic neuron. This blockage results in an increase in serotonin in the synaptic cleft. Other types of drugs such as norepinephrine-dopamine reuptake inhibitors and norepinephrine-serotonin reuptake inhibitors are also used to treat depression.

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17.25: Other Neurological Disorders

There are several other neurological disorders that cannot be easily placed in the above categories. These include chronic pain conditions, cancers of the nervous system, epilepsy disorders, and stroke. Epilepsy and stroke are discussed below.

Epilepsy

Estimates suggest that up to three percent of people in the United States will be diagnosed with **epilepsy** in their lifetime. While there are several different types of epilepsy, all are characterized by recurrent seizures. Epilepsy itself can be a symptom of a brain injury, disease, or other illness. For example, people who have intellectual disability or ASD can experience seizures, presumably because the developmental wiring malfunctions that caused their disorders also put them at risk for epilepsy. For many patients, however, the cause of their epilepsy is never identified and is likely to be a combination of genetic and environmental factors. Often, seizures can be controlled with anticonvulsant medications. However, for very severe cases, patients may undergo brain surgery to remove the brain area where seizures originate.

Stroke

A stroke results when blood fails to reach a portion of the brain for a long enough time to cause damage. Without the oxygen supplied by blood flow, neurons in this brain region die. This neuronal death can cause many different symptoms—depending on the brain area affected— including headache, muscle weakness or paralysis, speech disturbances, sensory problems, memory loss, and confusion. Stroke is often caused by blood clots and can also be caused by the bursting of a weak blood vessel. Strokes are extremely common and are the third most common cause of death in the United States. On average one person experiences a stroke every 40 seconds in the United States. Approximately 75 percent of strokes occur in people older than 65. Risk factors for stroke include high blood pressure, diabetes, high cholesterol, and a family history of stroke. Smoking doubles the risk of stroke. Because a stroke is a medical emergency, patients with symptoms of a stroke should immediately go to the emergency room, where they can receive drugs that will dissolve any clot that may have formed. These drugs will not work if the stroke was caused by a burst blood vessel or if the stroke occurred more than three hours before arriving at the hospital. Treatment following a stroke can include blood pressure medication (to prevent future strokes) and (sometimes intense) physical therapy.

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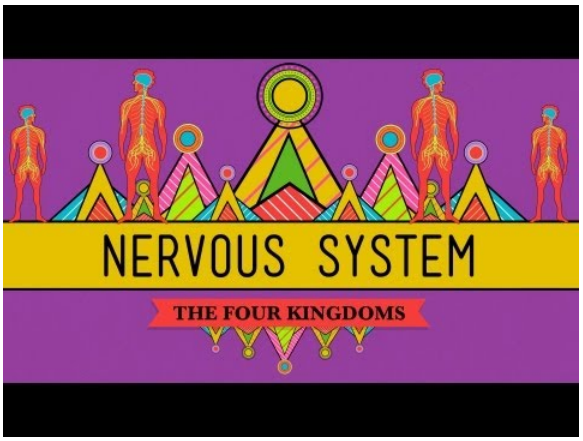
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17.26: Putting It Together- The Nervous System

Now that we've learned all about the different parts and functions of the nervous system, let's take a quick moment to review how the system works as a whole. This video takes a look at the nervous system and all of the things that it is responsible for in the body.



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=709

Career Connection

There are a lot of professions that require knowledge of the nervous system, but perhaps the most evident is neurology.

? Try It

Neurologists are physicians who specialize in disorders of the nervous system. They diagnose and treat disorders such as epilepsy, stroke, dementia, nervous system injuries, Parkinson's disease, sleep disorders, and multiple sclerosis. Neurologists are medical doctors who have attended college, medical school, and completed three to four years of neurology residency.

When examining a new patient, a neurologist takes a full medical history and performs a complete physical exam. The physical exam contains specific tasks that are used to determine what areas of the brain, spinal cord, or peripheral nervous system may be damaged. For example, to check whether the hypoglossal nerve is functioning correctly, the neurologist will ask the patient to move his or her tongue in different ways. If the patient does not have full control over tongue movements, then the hypoglossal nerve may be damaged or there may be a lesion in the brainstem where the cell bodies of these neurons reside (or there could be damage to the tongue muscle itself).

Neurologists have other tools besides a physical exam they can use to diagnose particular problems in the nervous system. If the patient has had a seizure, for example, the neurologist can use electroencephalography (EEG), which involves taping electrodes to the scalp to record brain activity, to try to determine which brain regions are involved in the seizure. In suspected stroke patients, a neurologist can use a computerized tomography (CT) scan, which is a type of X-ray, to look for bleeding in the brain or a possible brain tumor. To treat patients with neurological problems, neurologists can prescribe medications or refer the patient to a neurosurgeon for surgery.

This website allows you to see the different tests a neurologist might use to see what regions of the nervous system may be damaged in a patient.

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17.27: Cerego- The Nervous System

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for The Nervous System. You'll need to create a free log-in to practice these items, if you haven't already.

https://cerego.com/sets/796522/learn

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CHAPTER OVERVIEW

18: Module 15- The Endocrine System

18.1: Why It Matters- The Endocrine System
18.2: Introduction to Types of Hormones
18.3: Lipid-Derived Hormones
18.4: Amino Acid-Derived Hormones
18.5: Peptide Hormones
18.6: Hormone Regulation
18.7: Introduction to How Hormones Work
18.8: Hormones
18.9: Intracellular Hormone Receptors
18.10: Plasma Membrane Hormone Receptors
18.11: Introduction to Regulation of Body Processes
18.12: Hormonal Regulation of the Excretory System
18.13: Hormonal Regulation of the Reproductive System
18.14: Hormonal Regulation of Metabolism
18.15: Blood Calcium Levels and Growth
18.16: Hormonal Regulation of Stress
18.17: Introduction to Endocrine Glands
18.18: Hypothalamic-Pituitary Axis
18.19: Thyroids
18.20: Adrenal Glands
18.21: The Pancreas, Pineal Gland, and Gonads
18.22: Organs with Secondary Endocrine Functions
18.23: Putting It Together- The Endocrine System
18.24: Cerego- The Endocrine System

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18.1: Why It Matters- The Endocrine System

Why describe the components and role of the endocrine system?

The endocrine system includes the glands of the body and the hormones that they produce. The nervous system controls the glands directly by stimulation. The glands of the endocrine system can also be controlled as by chemical receptors in the blood. The endocrine system controls body processes through the production, secretion, and regulation of hormones, which serve as chemical "messengers" functioning in cellular and organ activity and, ultimately, maintaining the body's homeostasis. The endocrine system plays a role in growth, metabolism, and sexual development. In humans, common endocrine system diseases include thyroid disease and diabetes mellitus. In organisms that undergo metamorphosis, the process is controlled by the endocrine system. The transformation from tadpole to frog, for example, is complex and nuanced to adapt to specific environments and ecological circumstances.



Figure 1. The process of amphibian metamorphosis, as seen in the tadpole-to-frog stages shown here, is driven by hormones. (credit "tadpole": modification of work by Brian Gratwicke)

Learning Outcomes

- Identify different types of hormones and explain the regulation of hormone production
- Describe the two types of hormone receptors
- Describe how hormones regulate body processes
- Describe the role of different glands in the endocrine system

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18.2: Introduction to Types of Hormones

Identify different types of hormones and explain the regulation of hormone production

Although there are many different hormones in the human body, they can be divided into three classes based on their chemical structure: lipid-derived, amino acid-derived, and peptide (peptide and proteins) hormones. One of the key distinguishing features of lipid-derived hormones is that they can diffuse across plasma membranes whereas the amino acid-derived and peptide hormones cannot.

What You'll Learn to Do

- Explain the role of lipid-derived hormones in maintaining homeostasis
- Explain the role of amino acid-derived hormones in maintaining homeostasis
- Explain the role of peptide hormones in maintaining homeostasis
- Explain how hormone production is regulated

Learning Activities

The learning activities for this section include the following:

- Lipid-Derived Hormones
- Amino Acid-Derived Hormones
- Peptide Hormones
- Hormone Regulation
- Self Check: Types of Hormones

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18.3: Lipid-Derived Hormones

Maintaining homeostasis within the body requires the coordination of many different systems and organs. Communication between neighboring cells, and between cells and tissues in distant parts of the body, occurs through the release of chemicals called hormones. Hormones are released into body fluids (usually blood) that carry these chemicals to their target cells. At the target cells, which are cells that have a receptor for a signal or ligand from a signal cell, the hormones elicit a response. The cells, tissues, and organs that secrete hormones make up the endocrine system. Examples of glands of the endocrine system include the adrenal glands, which produce hormones such as epinephrine and norepinephrine that regulate responses to stress, and the thyroid gland, which produces thyroid hormones that regulate metabolic rates.

Most **lipid hormones** are derived from cholesterol and thus are structurally similar to it, as illustrated in Figure 1. The primary class of lipid hormones in humans is the steroid hormones. Chemically, these hormones are usually ketones or alcohols; their chemical names will end in "-ol" for alcohols or "-one" for ketones. Examples of steroid hormones include estradiol, which is an **estrogen**, or female sex hormone, and testosterone, which is an androgen, or male sex hormone. These two hormones are released by the female and male reproductive organs, respectively. Other steroid hormones include aldosterone and cortisol, which are released by the adrenal glands along with some other types of androgens. Steroid hormones are insoluble in water, and they are transported by transport proteins in blood. As a result, they remain in circulation longer than peptide hormones. For example, cortisol has a half-life of 60 to 90 minutes, while epinephrine, an amino acid derived-hormone, has a half-life of approximately one minute.

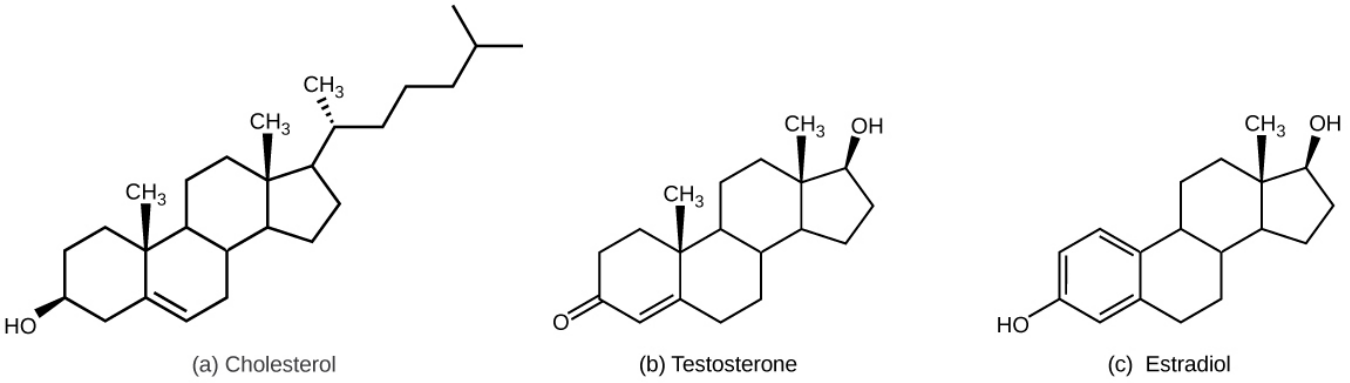


Figure 1. The structures shown here represent (a) cholesterol, plus the steroid hormones (b) testosterone and (c) estradiol.

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18.4: Amino Acid-Derived Hormones

The **amino acid-derived hormones** are relatively small molecules that are derived from the amino acids tyrosine and tryptophan, shown in Figure 1. If a hormone is amino acid-derived, its chemical name will end in *–ine*. Examples of amino acid-derived hormones include epinephrine and norepinephrine, which are synthesized in the medulla of the adrenal glands, and thyroxine, which is produced by the thyroid gland. The pineal gland in the brain makes and secretes melatonin which regulates sleep cycles.

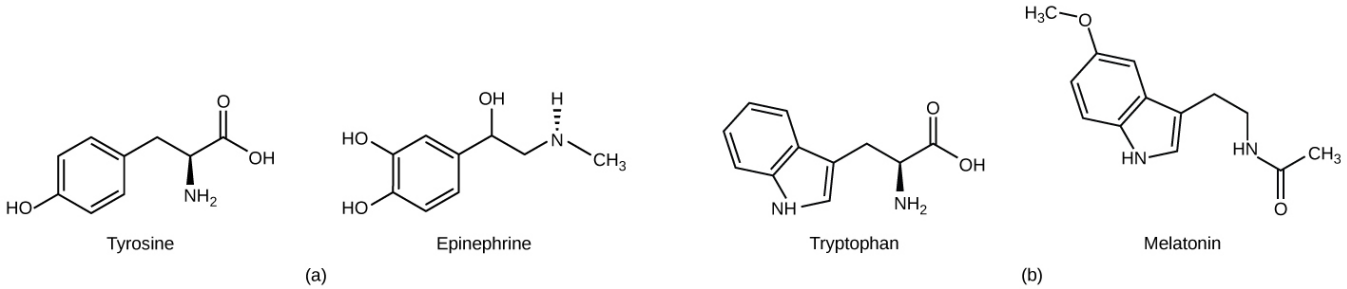


Figure 1. (a) The hormone epinephrine, which triggers the fight-or-flight response, is derived from the amino acid tyrosine. (b) The hormone melatonin, which regulates circadian rhythms, is derived from the amino acid tryptophan.

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18.5: Peptide Hormones

The structure of **peptide hormones** is that of a polypeptide chain (chain of amino acids). The peptide hormones include molecules that are short polypeptide chains, such as antidiuretic hormone and oxytocin produced in the brain and released into the blood in the posterior pituitary gland. This class also includes small proteins, like growth hormones produced by the pituitary, and large glycoproteins such as follicle-stimulating hormone produced by the pituitary. Figure 1 illustrates these peptide hormones.

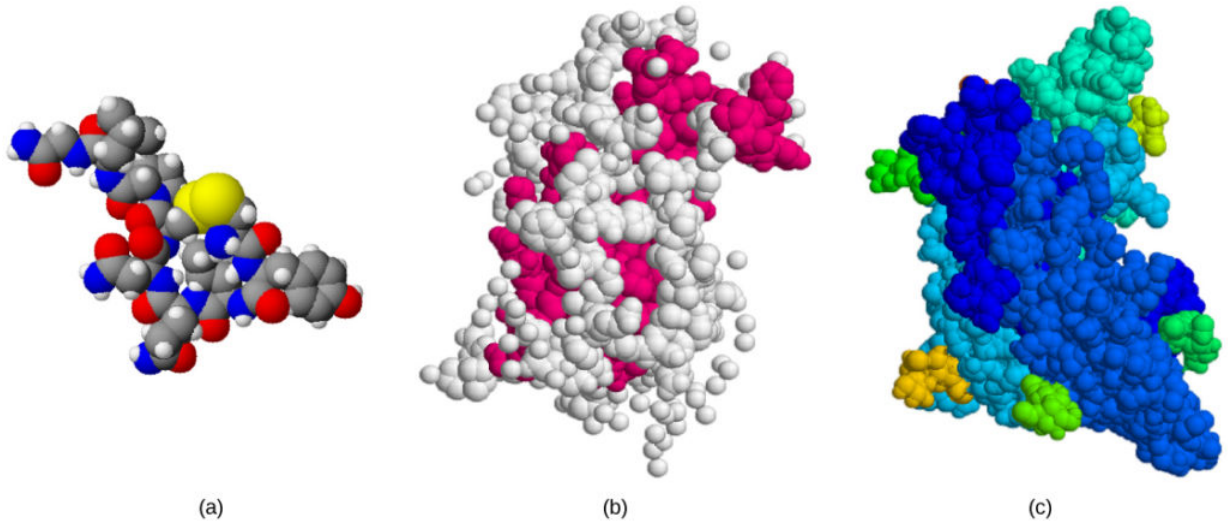


Figure 1. The structures of peptide hormones (a) oxytocin, (b) growth hormone, and (c) follicle-stimulating hormone are shown. These peptide hormones are much larger than those derived from cholesterol or amino acids.

Secreted peptides like insulin are stored within vesicles in the cells that synthesize them. They are then released in response to stimuli such as high blood glucose levels in the case of insulin. Amino acid-derived and polypeptide hormones are water-soluble and insoluble in lipids. These hormones cannot pass through plasma membranes of cells; therefore, their receptors are found on the surface of the target cells.

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18.6: Hormone Regulation

Hormone production and release are primarily controlled by negative feedback. In negative feedback systems, a stimulus elicits the release of a substance; once the substance reaches a certain level, it sends a signal that stops further release of the substance. In this way, the concentration of hormones in blood is maintained within a narrow range. For example, the amount of glucose in the blood controls the secretion of insulin and glucagons via negative feedback.

During hormone regulation, hormones are released, either directly by an endocrine gland or indirectly through the action of the hypothalamus of the brain, which stimulates other endocrine glands to release hormones in order to maintain homeostasis. The hormones activate target cells, which initiate physiological changes that adjust the body conditions. When normal conditions have been recovered, the corrective action – the production of hormones – is discontinued. Thus, in negative feedback, when the original (abnormal) condition has been repaired, or negated, corrective actions decrease or discontinue.

In another example of hormone regulation, the anterior pituitary signals the thyroid to release thyroid hormones. Increasing levels of these hormones in the blood then give feedback to the hypothalamus and anterior pituitary to inhibit further signaling to the thyroid gland, as illustrated in Figure 1.

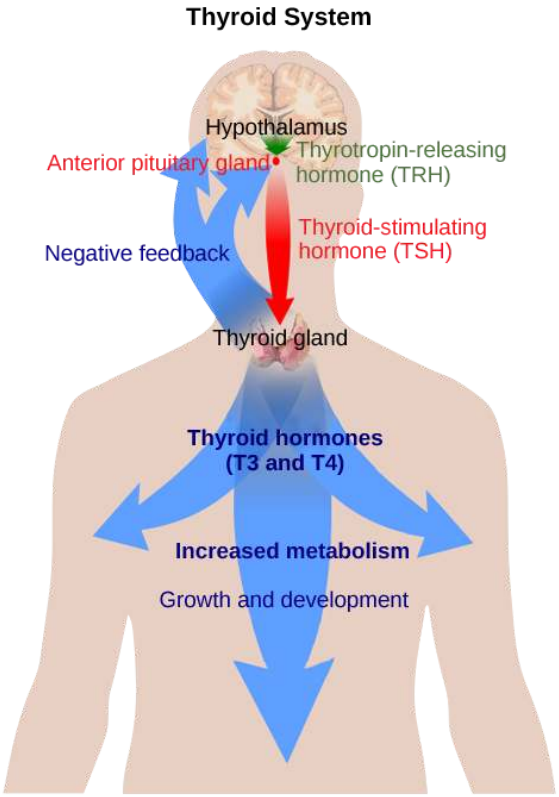


Figure 1. The anterior pituitary stimulates the thyroid gland to release thyroid hormones T_3 and T_4. Increasing levels of these hormones in the blood results in feedback to the hypothalamus and anterior pituitary to inhibit further signaling to the thyroid gland. (credit: modification of work by Mikael Häggström)

Stimuli

There are three mechanisms by which endocrine glands are stimulated to synthesize and release hormones: humoral stimuli, hormonal stimuli, and neural stimuli.

Humoral Stimuli

The term “humoral” is derived from the term “humor,” which refers to bodily fluids such as blood. A **humoral stimuli** refers to the control of hormone release in response to changes in extracellular fluids such as blood or the ion concentration in the blood. For example, a rise in blood glucose levels triggers the pancreatic release of insulin. Insulin causes blood glucose levels to drop, which signals the pancreas to stop producing insulin in a negative feedback loop.

Hormonal Stimuli

Hormonal stimuli refers to the release of a hormone in response to another hormone. A number of endocrine glands release hormones when stimulated by hormones released by other endocrine glands. For example, the hypothalamus produces hormones that stimulate the anterior portion of the pituitary gland. The anterior pituitary in turn releases hormones that regulate hormone production by other endocrine glands. The anterior pituitary releases the thyroid-stimulating hormone, which then stimulates the thyroid gland to produce the hormones T_3 and T_4. As blood concentrations of T_3 and T_4 rise, they inhibit both the pituitary and the hypothalamus in a negative feedback loop.

Neural Stimuli

In some cases, the nervous system directly stimulates endocrine glands to release hormones, which is referred to as **neural stimuli**. Recall that in a short-term stress response, the hormones epinephrine and norepinephrine are important for providing the bursts of energy required for the body to respond. Here, neuronal signaling from the sympathetic nervous system directly stimulates the adrenal medulla to release the hormones epinephrine and norepinephrine in response to stress.

? Practice Question

Hyperthyroidism is a condition in which the thyroid gland is overactive. Hypothyroidism is a condition in which the thyroid gland is underactive. Which of the conditions are the following two patients most likely to have?

- Patient A has symptoms including weight gain, cold sensitivity, low heart rate and fatigue.
- Patient B has symptoms including weight loss, profuse sweating, increased heart rate and difficulty sleeping.

[reveal-answer q="71349"]Show Answer[/reveal-answer]
[hidden-answer a="71349"]Patient A has symptoms associated with decreased metabolism, and may be suffering from hypothyroidism. Patient B has symptoms associated with increased metabolism, and may be suffering from hyperthyroidism.[/hidden-answer]

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18.7: Introduction to How Hormones Work

Describe the two types of hormone receptors

Hormones cause cellular changes by binding to receptors on target cells. The number of receptors on a target cell can increase or decrease in response to hormone activity. Hormones can affect cells directly through intracellular hormone receptors or indirectly through plasma membrane hormone receptors.

What You'll Learn to Do

- Explain how hormones work
- Describe the structure and function of intracellular hormone receptors
- Describe the structure and function of plasma membrane hormone receptors

Learning Activities

The learning activities for this section include the following:

- Hormones
- Intracellular Hormone Receptors
- Plasma Membrane Hormone Receptors
- Self Check: How Hormones Work

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18.8: Hormones

Hormones mediate changes in target cells by binding to specific **hormone receptors**. In this way, even though hormones circulate throughout the body and come into contact with many different cell types, they only affect cells that possess the necessary receptors. Receptors for a specific hormone may be found on many different cells or may be limited to a small number of specialized cells. For example, thyroid hormones act on many different tissue types, stimulating metabolic activity throughout the body. Cells can have many receptors for the same hormone but often also possess receptors for different types of hormones. The number of receptors that respond to a hormone determines the cell's sensitivity to that hormone, and the resulting cellular response. Additionally, the number of receptors that respond to a hormone can change over time, resulting in increased or decreased cell sensitivity. In **up-regulation**, the number of receptors increases in response to rising hormone levels, making the cell more sensitive to the hormone and allowing for more cellular activity. When the number of receptors decreases in response to rising hormone levels, called **down-regulation**, cellular activity is reduced.

Receptor binding alters cellular activity and results in an increase or decrease in normal body processes. Depending on the location of the protein receptor on the target cell and the chemical structure of the hormone, hormones can mediate changes directly by binding to **intracellular hormone receptors** and modulating gene transcription, or indirectly by binding to cell surface receptors and stimulating signaling pathways.

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18.9: Intracellular Hormone Receptors

Lipid-derived (soluble) hormones such as steroid hormones diffuse across the membranes of the endocrine cell. Once outside the cell, they bind to transport proteins that keep them soluble in the bloodstream. At the target cell, the hormones are released from the carrier protein and diffuse across the lipid bilayer of the plasma membrane of cells. The steroid hormones pass through the plasma membrane of a target cell and adhere to intracellular receptors residing in the cytoplasm or in the nucleus. The cell signaling pathways induced by the steroid hormones regulate specific genes on the cell's DNA. The hormones and receptor complex act as transcription regulators by increasing or decreasing the synthesis of mRNA molecules of specific genes. This, in turn, determines the amount of corresponding protein that is synthesized by altering gene expression. This protein can be used either to change the structure of the cell or to produce enzymes that catalyze chemical reactions. In this way, the steroid hormone regulates specific cell processes as illustrated in Figure 1.



Figure 1. An intracellular nuclear receptor (NR) is located in the cytoplasm bound to a heat shock protein (HSP). Upon hormone binding, the receptor dissociates from the heat shock protein and translocates to the nucleus. In the nucleus, the hormone-receptor complex binds to a DNA sequence called a hormone response element (HRE), which triggers gene transcription and translation. The corresponding protein product can then mediate changes in cell function.

Practice Question

Heat shock proteins (HSP) are so named because they help refold misfolded proteins. In response to increased temperature (a "heat shock"), heat shock proteins are activated by release from the NR/HSP complex. At the same time, transcription of HSP genes is activated. Why do you think the cell responds to a heat shock by increasing the activity of proteins that help refold misfolded proteins?

[reveal-answer q="23179″]Show Answer[/reveal-answer]

[hidden-answer a="23179″]Proteins unfold, or denature, at higher temperatures.[/hidden-answer]

Other lipid-soluble hormones that are not steroid hormones, such as vitamin D and thyroxine, have receptors located in the nucleus. The hormones diffuse across both the plasma membrane and the nuclear envelope, then bind to receptors in the nucleus. The hormone-receptor complex stimulates transcription of specific genes.

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18.10: Plasma Membrane Hormone Receptors

Amino acid derived hormones and polypeptide hormones are not lipid-derived (lipid-soluble) and therefore cannot diffuse through the plasma membrane of cells. Lipid insoluble hormones bind to receptors on the outer surface of the plasma membrane, via **plasma membrane hormone receptors**. Unlike steroid hormones, lipid insoluble hormones do not directly affect the target cell because they cannot enter the cell and act directly on DNA. Binding of these hormones to a cell surface receptor results in activation of a signaling pathway; this triggers intracellular activity and carries out the specific effects associated with the hormone. In this way, nothing passes through the cell membrane; the hormone that binds at the surface remains at the surface of the cell while the intracellular product remains inside the cell. The hormone that initiates the signaling pathway is called a **first messenger**, which activates a second messenger in the cytoplasm, as illustrated in Figure 1.

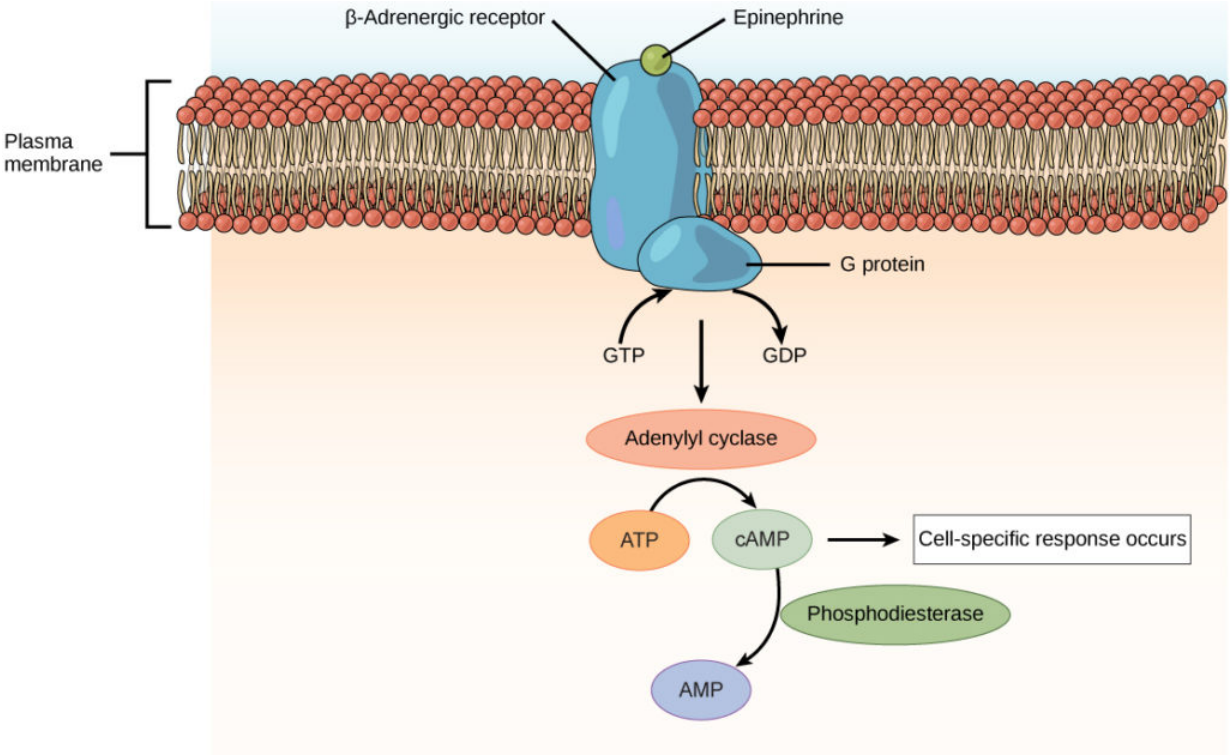


Figure 1. The amino acid-derived hormones epinephrine and norepinephrine bind to beta-adrenergic receptors on the plasma membrane of cells. Hormone binding to receptor activates a G-protein, which in turn activates adenylyl cyclase, converting ATP to cAMP. cAMP is a second messenger that mediates a cell-specific response. An enzyme called phosphodiesterase breaks down cAMP, terminating the signal.

One very important second messenger is cyclic AMP (cAMP). When a hormone binds to its membrane receptor, a **G-protein** that is associated with the receptor is activated; G-proteins are proteins separate from receptors that are found in the cell membrane. When a hormone is not bound to the receptor, the G-protein is inactive and is bound to guanosine diphosphate, or GDP. When a hormone binds to the receptor, the G-protein is activated by binding guanosine triphosphate, or GTP, in place of GDP. After binding, GTP is hydrolysed by the G-protein into GDP and becomes inactive.

The activated G-protein in turn activates a membrane-bound enzyme called **adenylyl cyclase**. Adenylyl cyclase catalyzes the conversion of ATP to cAMP. cAMP, in turn, activates a group of proteins called protein kinases, which transfer a phosphate group from ATP to a substrate molecule in a process called phosphorylation. The phosphorylation of a substrate molecule changes its structural orientation, thereby activating it. These activated molecules can then mediate changes in cellular processes.

The effect of a hormone is amplified as the signaling pathway progresses. The binding of a hormone at a single receptor causes the activation of many G-proteins, which activates adenylyl cyclase. Each molecule of adenylyl cyclase then triggers the formation of many molecules of cAMP. Further amplification occurs as protein kinases, once activated by cAMP, can catalyze many reactions. In this way, a small amount of hormone can trigger the formation of a large amount of cellular product. To stop hormone activity,

cAMP is deactivated by the cytoplasmic enzyme **phosphodiesterase**, or PDE. PDE is always present in the cell and breaks down cAMP to control hormone activity, preventing overproduction of cellular products.

The specific response of a cell to a lipid insoluble hormone depends on the type of receptors that are present on the cell membrane and the substrate molecules present in the cell cytoplasm. Cellular responses to hormone binding of a receptor include altering membrane permeability and metabolic pathways, stimulating synthesis of proteins and enzymes, and activating hormone release.

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18.11: Introduction to Regulation of Body Processes

Describe how hormones regulate body processes

Hormones have a wide range of effects and modulate many different body processes. The key regulatory processes that will be examined here are those affecting the excretory system, the reproductive system, metabolism, blood calcium concentrations, growth, and the stress response.

What You'll Learn to Do

- Explain how hormones regulate the excretory system
- Discuss the role of hormones in the reproductive system
- Describe how hormones regulate metabolism
- Explain the role of hormones in blood calcium levels
- Explain the role of hormones in growth
- Explain the role of hormones in stress

Learning Activities

The learning activities for this section include the following:

- Hormonal Regulation of the Excretory System
- Hormonal Regulation of the Reproductive System
- Hormonal Regulation of Metabolism
- Blood Calcium Levels and Growth
- Hormonal Regulation of Stress
- Self Check: Neurons and Glial Cells

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18.12: Hormonal Regulation of the Excretory System

Maintaining a proper water balance in the body is important to avoid dehydration or over-hydration (hyponatremia). The water concentration of the body is monitored by **osmoreceptors** in the hypothalamus, which detect the concentration of electrolytes in the extracellular fluid. The concentration of electrolytes in the blood rises when there is water loss caused by excessive perspiration, inadequate water intake, or low blood volume due to blood loss. An increase in blood electrolyte levels results in a neuronal signal being sent from the osmoreceptors in hypothalamic nuclei. The pituitary gland has two components: anterior and posterior. The anterior pituitary is composed of glandular cells that secrete protein hormones. The posterior pituitary is an extension of the hypothalamus. It is composed largely of neurons that are continuous with the hypothalamus.

The hypothalamus produces a polypeptide hormone known as **antidiuretic hormone (ADH)**, which is transported to and released from the posterior pituitary gland. The principal action of ADH is to regulate the amount of water excreted by the kidneys. As ADH (which is also known as vasopressin) causes direct water reabsorption from the kidney tubules, salts and wastes are concentrated in what will eventually be excreted as urine. The hypothalamus controls the mechanisms of ADH secretion, either by regulating blood volume or the concentration of water in the blood. Dehydration or physiological stress can cause an increase of osmolarity above 300 mOsm/L, which in turn, raises ADH secretion and water will be retained, causing an increase in blood pressure. ADH travels in the bloodstream to the kidneys. Once at the kidneys, ADH changes the kidneys to become more permeable to water by temporarily inserting water channels, aquaporins, into the kidney tubules. Water moves out of the kidney tubules through the aquaporins, reducing urine volume. The water is reabsorbed into the capillaries lowering blood osmolarity back toward normal. As blood osmolarity decreases, a negative feedback mechanism reduces osmoreceptor activity in the hypothalamus, and ADH secretion is reduced. ADH release can be reduced by certain substances, including alcohol, which can cause increased urine production and dehydration.

Chronic underproduction of ADH or a mutation in the ADH receptor results in **diabetes insipidus**. If the posterior pituitary does not release enough ADH, water cannot be retained by the kidneys and is lost as urine. This causes increased thirst, but water taken in is lost again and must be continually consumed. If the condition is not severe, dehydration may not occur, but severe cases can lead to electrolyte imbalances due to dehydration.

Another hormone responsible for maintaining electrolyte concentrations in extracellular fluids is **aldosterone**, a steroid hormone that is produced by the adrenal cortex. In contrast to ADH, which promotes the reabsorption of water to maintain proper water balance, aldosterone maintains proper water balance by enhancing Na^+ reabsorption and K^+ secretion from extracellular fluid of the cells in kidney tubules. Because it is produced in the cortex of the adrenal gland and affects the concentrations of minerals Na^+ and K^+, aldosterone is referred to as a **mineralocorticoid**, a corticosteroid that affects ion and water balance. Aldosterone release is stimulated by a decrease in blood sodium levels, blood volume, or blood pressure, or an increase in blood potassium levels. It also prevents the loss of Na^+ from sweat, saliva, and gastric juice. The reabsorption of Na^+ also results in the osmotic reabsorption of water, which alters blood volume and blood pressure.

Aldosterone production can be stimulated by low blood pressure, which triggers a sequence of chemical release, as illustrated in Figure 1. When blood pressure drops, the renin-angiotensin-aldosterone system (RAAS) is activated. Cells in the juxtaglomerular apparatus, which regulates the functions of the nephrons of the kidney, detect this and release **renin**. Renin, an enzyme, circulates in the blood and reacts with a plasma protein produced by the liver called angiotensinogen. When angiotensinogen is cleaved by renin, it produces angiotensin I, which is then converted into angiotensin II in the lungs. Angiotensin II functions as a hormone and then causes the release of the hormone aldosterone by the adrenal cortex, resulting in increased Na^+ reabsorption, water retention, and an increase in blood pressure. Angiotensin II in addition to being a potent vasoconstrictor also causes an increase in ADH and increased thirst, both of which help to raise blood pressure.

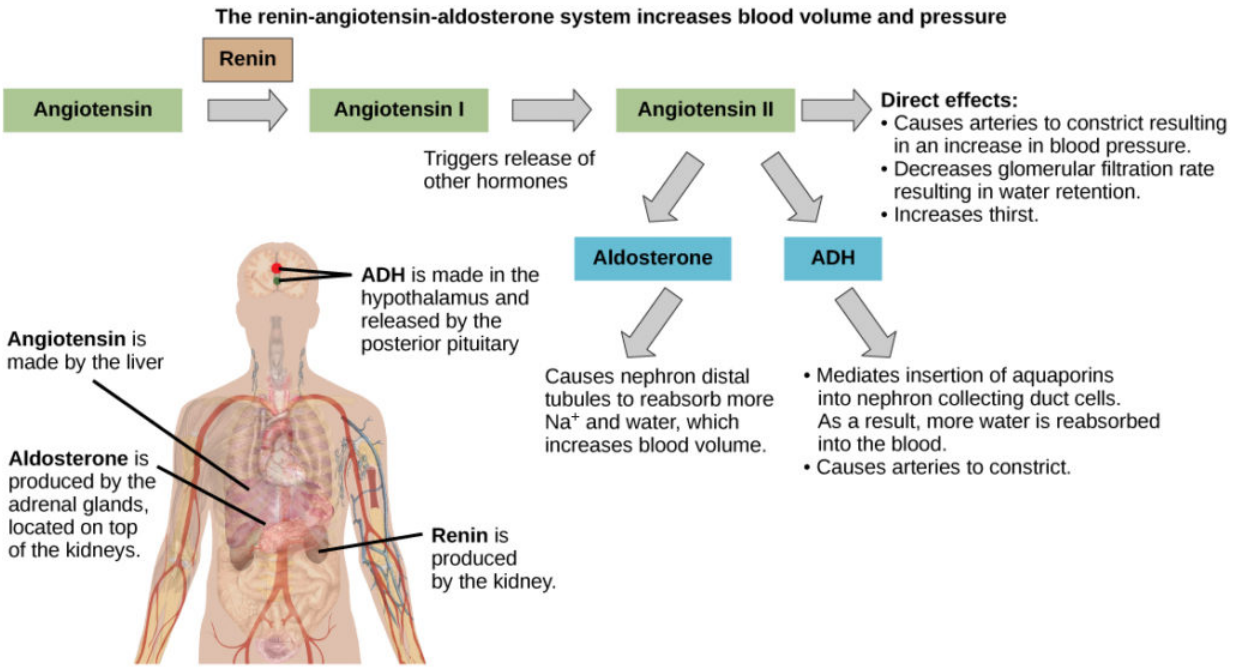


Figure 1. ADH and aldosterone increase blood pressure and volume. Angiotensin II stimulates release of these hormones. Angiotensin II, in turn, is formed when renin cleaves angiotensin. (credit: modification of work by Mikael Häggström)

In summary: Hormonal Regulation of the Excretory System

Water levels in the body are controlled by antidiuretic hormone (ADH), which is produced in the hypothalamus and triggers the reabsorption of water by the kidneys. Underproduction of ADH can cause diabetes insipidus. Aldosterone, a hormone produced by the adrenal cortex of the kidneys, enhances Na^+ reabsorption from the extracellular fluids and subsequent water reabsorption by diffusion. The renin-angiotensin-aldosterone system is one way that aldosterone release is controlled.

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18.13: Hormonal Regulation of the Reproductive System

Regulation of the reproductive system is a process that requires the action of hormones from the pituitary gland, the adrenal cortex, and the gonads. During puberty in both males and females, the hypothalamus produces gonadotropin-releasing hormone (GnRH), which stimulates the production and release of **follicle-stimulating hormone (FSH)** and luteinizing hormone (LH) from the anterior pituitary gland. These hormones regulate the gonads (testes in males and ovaries in females) and therefore are called **gonadotropins**. In both males and females, FSH stimulates gamete production and LH stimulates production of hormones by the gonads. An increase in gonad hormone levels inhibits GnRH production through a negative feedback loop.

Regulation of the Male Reproductive System

In males, FSH stimulates the maturation of sperm cells. FSH production is inhibited by the hormone inhibin, which is released by the testes. LH stimulates production of the sex hormones (**androgens**) by the interstitial cells of the testes and therefore is also called interstitial cell-stimulating hormone.

The most widely known androgen in males is testosterone. Testosterone promotes the production of sperm and masculine characteristics. The adrenal cortex also produces small amounts of testosterone precursor, although the role of this additional hormone production is not fully understood.

? Try It



Figure 1. Professional baseball player Jason Giambi publically admitted to, and apologized for, his use of anabolic steroids supplied by a trainer.(credit: Bryce Edwards)

Some athletes attempt to boost their performance by using artificial hormones that enhance muscle performance. Anabolic steroids, a form of the male sex hormone testosterone, are one of the most widely known performance-enhancing drugs. Steroids are used to help build muscle mass. Other hormones that are used to enhance athletic performance include erythropoietin, which triggers the production of red blood cells, and human growth hormone, which can help in building muscle mass. Most performance enhancing drugs are illegal for non-medical purposes. They are also banned by national and international governing bodies including the International Olympic Committee, the U.S. Olympic Committee, the National Collegiate Athletic Association, the Major League Baseball, and the National Football League.

The side effects of synthetic hormones are often significant and non-reversible, and in some cases, fatal. Androgens produce several complications such as liver dysfunctions and liver tumors, prostate gland enlargement, difficulty urinating, premature closure of epiphyseal cartilages, testicular atrophy, infertility, and immune system depression. The physiological strain caused by these substances is often greater than what the body can handle, leading to unpredictable and dangerous effects and linking their use to heart attacks, strokes, and impaired cardiac function.

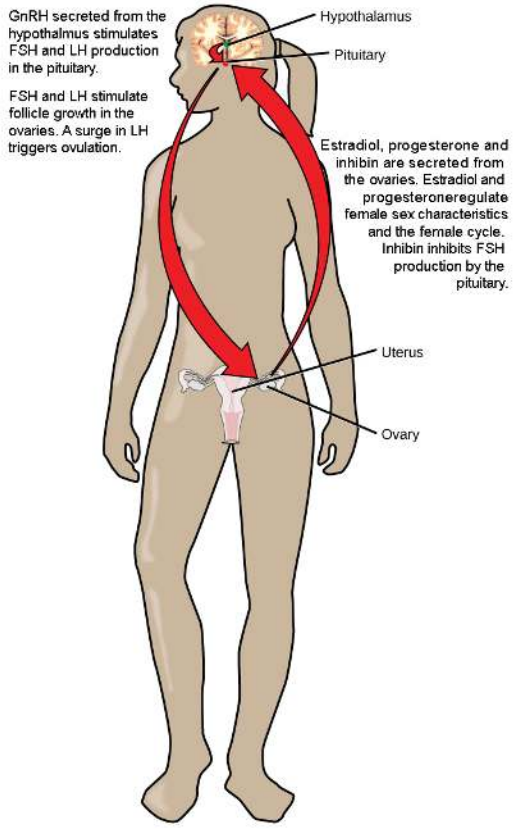


Figure 2. Hormonal regulation of the female reproductive system involves hormones from the hypothalamus, pituitary, and ovaries.

In females, FSH stimulates development of egg cells, called ova, which develop in structures called follicles. Follicle cells produce the hormone inhibin, which inhibits FSH production. LH also plays a role in the development of ova, induction of ovulation, and stimulation of estradiol and progesterone production by the ovaries, as illustrated in Figure 2.

Estradiol and progesterone are steroid hormones that prepare the body for pregnancy. Estradiol produces secondary sex characteristics in females, while both estradiol and progesterone regulate the menstrual cycle.

In addition to producing FSH and LH, the anterior portion of the pituitary gland also produces the hormone **prolactin (PRL)** in females. Prolactin stimulates the production of milk by the mammary glands following childbirth. Prolactin levels are regulated by the hypothalamic hormones **prolactin-releasing hormone (PRH)** and **prolactin-inhibiting hormone (PIH)**, which is now known to be dopamine. PRH stimulates the release of prolactin and PIH inhibits it.

The posterior pituitary releases the hormone **oxytocin**, which stimulates uterine contractions during childbirth. The uterine smooth muscles are not very sensitive to oxytocin until late in pregnancy when the number of oxytocin receptors in the uterus peaks. Stretching of tissues in the uterus and cervix stimulates oxytocin release during childbirth. Contractions increase in intensity as blood levels of oxytocin rise via a positive feedback mechanism until the birth is complete.

Oxytocin also stimulates the contraction of myoepithelial cells around the milk-producing mammary glands. As these cells contract, milk is forced from the secretory alveoli into milk ducts and is ejected from the breasts in milk ejection (“let-down”) reflex. Oxytocin release is stimulated by the suckling of an infant, which triggers the synthesis of oxytocin in the hypothalamus and its release into circulation at the posterior pituitary.

Learning Objectives

The reproductive system is controlled by the gonadotropins follicle-stimulating hormone (FSH) and luteinizing hormone (LH), which are produced by the pituitary gland. Gonadotropin release is controlled by the hypothalamic hormone gonadotropin-releasing hormone (GnRH). FSH stimulates the maturation of sperm cells in males and is inhibited by the hormone inhibin,

while LH stimulates the production of the androgen testosterone. FSH stimulates egg maturation in females, while LH stimulates the production of estrogens and progesterone. **Estrogens** are a group of steroid hormones produced by the ovaries that trigger the development of secondary sex characteristics in females as well as control the maturation of the ova. In females, the pituitary also produces prolactin, which stimulates milk production after childbirth, and oxytocin, which stimulates uterine contraction during childbirth and milk let-down during suckling.

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18.14: Hormonal Regulation of Metabolism

Blood glucose levels vary widely over the course of a day as periods of food consumption alternate with periods of fasting. Insulin and glucagon are the two hormones primarily responsible for maintaining homeostasis of blood glucose levels. Additional regulation is mediated by the thyroid hormones.

Regulation of Blood Glucose Levels by Insulin and Glucagon

Cells of the body require nutrients in order to function, and these nutrients are obtained through feeding. In order to manage nutrient intake, storing excess intake and utilizing reserves when necessary, the body uses hormones to moderate energy stores. **Insulin** is produced by the beta cells of the pancreas, which are stimulated to release insulin as blood glucose levels rise (for example, after a meal is consumed). Insulin lowers blood glucose levels by enhancing the rate of glucose uptake and utilization by target cells, which use glucose for ATP production. It also stimulates the liver to convert glucose to glycogen, which is then stored by cells for later use. Insulin also increases glucose transport into certain cells, such as muscle cells and the liver. This results from an insulin-mediated increase in the number of glucose transporter proteins in cell membranes, which remove glucose from circulation by facilitated diffusion. As insulin binds to its target cell via insulin receptors and signal transduction, it triggers the cell to incorporate glucose transport proteins into its membrane. This allows glucose to enter the cell, where it can be used as an energy source. However, this does not occur in all cells: some cells, including those in the kidneys and brain, can access glucose without the use of insulin. Insulin also stimulates the conversion of glucose to fat in adipocytes and the synthesis of proteins. These actions mediated by insulin cause blood glucose concentrations to fall, called a hypoglycemic “low sugar” effect, which inhibits further insulin release from beta cells through a negative feedback loop.

This animation describe the role of insulin and the pancreas in diabetes.

A link to an interactive elements can be found at the bottom of this page.

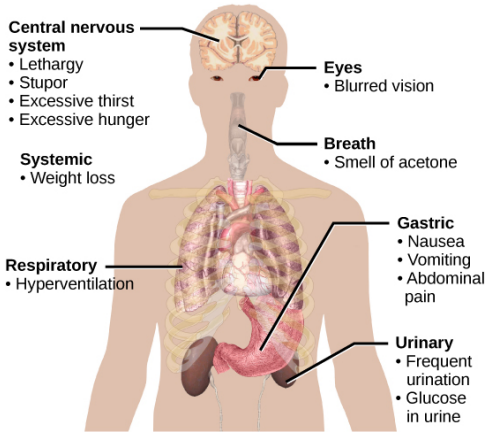


Figure 1. The main symptoms of diabetes are shown. (credit: modification of work by Mikael Häggström)

Impaired insulin function can lead to a condition called **diabetes mellitus**, the main symptoms of which are illustrated in Figure 1. This can be caused by low levels of insulin production by the beta cells of the pancreas, or by reduced sensitivity of tissue cells to insulin. This prevents glucose from being absorbed by cells, causing high levels of blood glucose, or **hyperglycemia** (high sugar). High blood glucose levels make it difficult for the kidneys to recover all the glucose from nascent urine, resulting in glucose being lost in urine. High glucose levels also result in less water being reabsorbed by the kidneys, causing high amounts of urine to be produced; this may result in dehydration. Over time, high blood glucose levels can cause nerve damage to the eyes and peripheral body tissues, as well as damage to the kidneys and cardiovascular system. Oversecretion of insulin can cause **hypoglycemia**, low blood glucose levels. This causes insufficient glucose availability to cells, often leading to muscle weakness, and can sometimes cause unconsciousness or death if left untreated.

When blood glucose levels decline below normal levels, for example between meals or when glucose is utilized rapidly during exercise, the hormone **glucagon** is released from the alpha cells of the pancreas. Glucagon raises blood glucose levels, eliciting what is called a hyperglycemic effect, by stimulating the breakdown of glycogen to glucose in skeletal muscle cells and liver cells

in a process called **glycogenolysis**. Glucose can then be utilized as energy by muscle cells and released into circulation by the liver cells. Glucagon also stimulates absorption of amino acids from the blood by the liver, which then converts them to glucose. This process of glucose synthesis is called **gluconeogenesis**. Glucagon also stimulates adipose cells to release fatty acids into the blood. These actions mediated by glucagon result in an increase in blood glucose levels to normal homeostatic levels. Rising blood glucose levels inhibit further glucagon release by the pancreas via a negative feedback mechanism. In this way, insulin and glucagon work together to maintain homeostatic glucose levels, as shown in Figure 2.

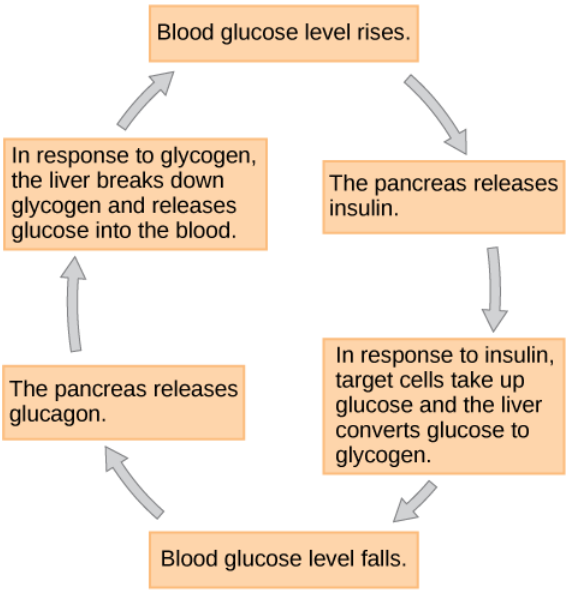


Figure 2. Insulin and glucagon regulate blood glucose levels.

? Practice Question

Pancreatic tumors may cause excess secretion of glucagon. Type I diabetes results from the failure of the pancreas to produce insulin. Which of the following statement about these two conditions is true?

a. A pancreatic tumor and type I diabetes will have the opposite effects on blood sugar levels.
b. A pancreatic tumor and type I diabetes will both cause hyperglycemia.
c. A pancreatic tumor and type I diabetes will both cause hypoglycemia.
d. Both pancreatic tumors and type I diabetes result in the inability of cells to take up glucose.

[reveal-answer q=”625162″]Show Answer[/reveal-answer]
[hidden-answer a=”625162″]Statement b is true.[/hidden-answer]

Regulation of Blood Glucose Levels by Thyroid Hormones

The basal metabolic rate, which is the amount of calories required by the body at rest, is determined by two hormones produced by the thyroid gland: **thyroxine**, also known as tetraiodothyronine or T_4, and **triiodothyronine**, also known as T_3. These hormones affect nearly every cell in the body except for the adult brain, uterus, testes, blood cells, and spleen. They are transported across the plasma membrane of target cells and bind to receptors on the mitochondria resulting in increased ATP production. In the nucleus, T_3 and T_4activate genes involved in energy production and glucose oxidation. This results in increased rates of metabolism and body heat production, which is known as the hormone’s calorigenic effect.

T_3 and T_4 release from the thyroid gland is stimulated by **thyroid-stimulating hormone (TSH)**, which is produced by the anterior pituitary. TSH binding at the receptors of the follicle of the thyroid triggers the production of T_3 and T_4 from a glycoprotein called **thyroglobulin**. Thyroglobulin is present in the follicles of the thyroid, and is converted into thyroid hormones with the addition of iodine. Iodine is formed from iodide ions that are actively transported into the thyroid follicle from the bloodstream. A peroxidase enzyme then attaches the iodine to the tyrosine amino acid found in thyroglobulin. T_3 has three iodine ions attached, while T_4 has four iodine ions attached. T_3 and T_4 are then released into the bloodstream, with T_4 being released in much greater amounts than

T_3. As $T_3$is more active than T_4 and is responsible for most of the effects of thyroid hormones, tissues of the body convert T_4 to T_3 by the removal of an iodine ion. Most of the released T_3 and T_4 becomes attached to transport proteins in the bloodstream and is unable to cross the plasma membrane of cells. These protein-bound molecules are only released when blood levels of the unattached hormone begin to decline. In this way, a week's worth of reserve hormone is maintained in the blood. Increased T_3 and T_4 levels in the blood inhibit the release of TSH, which results in lower T_3 and T_4 release from the thyroid.

The follicular cells of the thyroid require iodides (anions of iodine) in order to synthesize T_3 and T_4. Iodides obtained from the diet are actively transported into follicle cells resulting in a concentration that is approximately 30 times higher than in blood. The typical diet in North America provides more iodine than required due to the addition of iodide to table salt. Inadequate iodine intake, which occurs in many developing countries, results in an inability to synthesize T_3 and T_4 hormones. The thyroid gland enlarges in a condition called **goiter**, which is caused by overproduction of TSH without the formation of thyroid hormone. Thyroglobulin is contained in a fluid called colloid, and TSH stimulation results in higher levels of colloid accumulation in the thyroid. In the absence of iodine, this is not converted to thyroid hormone, and colloid begins to accumulate more and more in the thyroid gland, leading to goiter.

Disorders can arise from both the underproduction and overproduction of thyroid hormones. **Hypothyroidism**, underproduction of the thyroid hormones, can cause a low metabolic rate leading to weight gain, sensitivity to cold, and reduced mental activity, among other symptoms. In children, hypothyroidism can cause cretinism, which can lead to mental retardation and growth defects. **Hyperthyroidism**, the overproduction of thyroid hormones, can lead to an increased metabolic rate and its effects: weight loss, excess heat production, sweating, and an increased heart rate. Graves' disease is one example of a hyperthyroid condition.

Learning Objectives

Insulin is produced by the pancreas in response to rising blood glucose levels and allows cells to utilize blood glucose and store excess glucose for later use. Diabetes mellitus is caused by reduced insulin activity and causes high blood glucose levels, or hyperglycemia. Glucagon is released by the pancreas in response to low blood glucose levels and stimulates the breakdown of glycogen into glucose, which can be used by the body. The body's basal metabolic rate is controlled by the thyroid hormones thyroxine (T_4) and triiodothyronine (T_3). The anterior pituitary produces thyroid stimulating hormone (TSH), which controls the release of T_3 and T_4 from the thyroid gland. Iodine is necessary in the production of thyroid hormone, and the lack of iodine can lead to a condition called goiter.

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18.15: Blood Calcium Levels and Growth

Hormonal Control of Blood Calcium Levels

Regulation of blood calcium concentrations is important for generation of muscle contractions and nerve impulses, which are electrically stimulated. If calcium levels get too high, membrane permeability to sodium decreases and membranes become less responsive. If calcium levels get too low, membrane permeability to sodium increases and convulsions or muscle spasms can result.

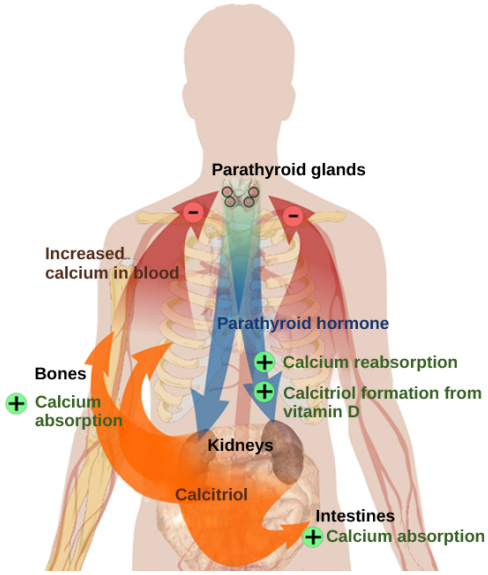


Figure 1. Parathyroid hormone (PTH) is released in response to low blood calcium levels. It increases blood calcium levels by targeting the skeleton, the kidneys, and the intestine. (credit: modification of work by Mikael Häggström)

Blood calcium levels are regulated by **parathyroid hormone (PTH)**, which is produced by the parathyroid glands, as illustrated in Figure 1. PTH is released in response to low blood Ca^{2+} levels. PTH increases Ca^{2+} levels by targeting the skeleton, the kidneys, and the intestine. In the skeleton, PTH stimulates osteoclasts, which causes bone to be reabsorbed, releasing Ca^{2+} from bone into the blood. PTH also inhibits osteoblasts, reducing Ca^{2+} deposition in bone. In the intestines, PTH increases dietary CA^{2+} absorption, and in the kidneys, PTH stimulates reabsorption of the CA^{2+}. While PTH acts directly on the kidneys to increase Ca^{2+} reabsorption, its effects on the intestine are indirect. PTH triggers the formation of calcitriol, an active form of vitamin D, which acts on the intestines to increase absorption of dietary calcium. PTH release is inhibited by rising blood calcium levels.

Hyperparathyroidism results from an overproduction of parathyroid hormone. This results in excessive calcium being removed from bones and introduced into blood circulation, producing structural weakness of the bones, which can lead to deformation and fractures, plus nervous system impairment due to high blood calcium levels. Hypoparathyroidism, the underproduction of PTH, results in extremely low levels of blood calcium, which causes impaired muscle function and may result in tetany (severe sustained muscle contraction).

The hormone **calcitonin**, which is produced by the parafollicular or C cells of the thyroid, has the opposite effect on blood calcium levels as does PTH. Calcitonin decreases blood calcium levels by inhibiting osteoclasts, stimulating osteoblasts, and stimulating calcium excretion by the kidneys. This results in calcium being added to the bones to promote structural integrity. Calcitonin is most important in children (when it stimulates bone growth), during pregnancy (when it reduces maternal bone loss), and during prolonged starvation (because it reduces bone mass loss). In healthy nonpregnant, unstarved adults, the role of calcitonin is unclear.

Hormonal Regulation of Growth

Hormonal regulation is required for the growth and replication of most cells in the body. **Growth hormone (GH)**, produced by the anterior portion of the pituitary gland, accelerates the rate of protein synthesis, particularly in skeletal muscle and bones. Growth hormone has direct and indirect mechanisms of action. The first direct action of GH is stimulation of triglyceride breakdown (lipolysis) and release into the blood by adipocytes. This results in a switch by most tissues from utilizing glucose as an energy source to utilizing fatty acids. This process is called a **glucose-sparing effect**. In another direct mechanism, GH stimulates

glycogen breakdown in the liver; the glycogen is then released into the blood as glucose. Blood glucose levels increase as most tissues are utilizing fatty acids instead of glucose for their energy needs. The GH mediated increase in blood glucose levels is called a **diabetogenic effect** because it is similar to the high blood glucose levels seen in diabetes mellitus.

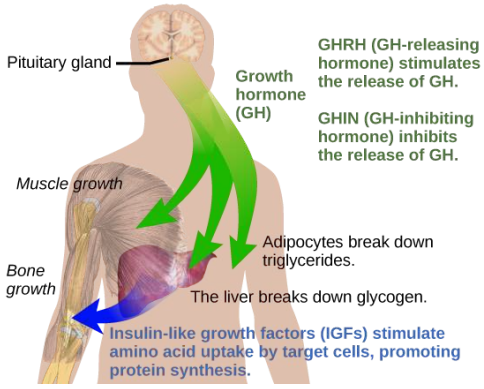


Figure 2. Growth hormone directly accelerates the rate of protein synthesis in skeletal muscle and bones. Insulin-like growth factor 1 (IGF-1) is activated by growth hormone and also allows formation of new proteins in muscle cells and bone. (credit: modification of work by Mikael Häggström)

The indirect mechanism of GH action is mediated by **insulin-like growth factors (IGFs)** or somatomedins, which are a family of growth-promoting proteins produced by the liver, which stimulates tissue growth. IGFs stimulate the uptake of amino acids from the blood, allowing the formation of new proteins, particularly in skeletal muscle cells, cartilage cells, and other target cells, as shown in Figure 2. This is especially important after a meal, when glucose and amino acid concentration levels are high in the blood. GH levels are regulated by two hormones produced by the hypothalamus. GH release is stimulated by **growth hormone-releasing hormone (GHRH)** and is inhibited by **growth hormone-inhibiting hormone (GHIH)**, also called somatostatin.

A balanced production of growth hormone is critical for proper development. Underproduction of GH in adults does not appear to cause any abnormalities, but in children it can result in **pituitary dwarfism**, in which growth is reduced. Pituitary dwarfism is characterized by symmetric body formation. In some cases, individuals are under 30 inches in height. Oversecretion of growth hormone can lead to **gigantism** in children, causing excessive growth. In some documented cases, individuals can reach heights of over eight feet. In adults, excessive GH can lead to **acromegaly**, a condition in which there is enlargement of bones in the face, hands, and feet that are still capable of growth.

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18.16: Hormonal Regulation of Stress

When a threat or danger is perceived, the body responds by releasing hormones that will ready it for the “fight-or-flight” response. The effects of this response are familiar to anyone who has been in a stressful situation: increased heart rate, dry mouth, and hair standing up.

? Try It

Interactions of the endocrine hormones have evolved to ensure the body’s internal environment remains stable. Stressors are stimuli that disrupt homeostasis. The sympathetic division of the vertebrate autonomic nervous system has evolved the fight-or-flight response to counter stress-induced disruptions of homeostasis. In the initial alarm phase, the sympathetic nervous system stimulates an increase in energy levels through increased blood glucose levels. This prepares the body for physical activity that may be required to respond to stress: to either fight for survival or to flee from danger.

However, some stresses, such as illness or injury, can last for a long time. Glycogen reserves, which provide energy in the short-term response to stress, are exhausted after several hours and cannot meet long-term energy needs. If glycogen reserves were the only energy source available, neural functioning could not be maintained once the reserves became depleted due to the nervous system’s high requirement for glucose. In this situation, the body has evolved a response to counter long-term stress through the actions of the glucocorticoids, which ensure that long-term energy requirements can be met. The glucocorticoids mobilize lipid and protein reserves, stimulate gluconeogenesis, conserve glucose for use by neural tissue, and stimulate the conservation of salts and water. The mechanisms to maintain homeostasis that are described here are those observed in the human body. However, the fight-or-flight response exists in some form in all vertebrates.

The sympathetic nervous system regulates the stress response via the hypothalamus. Stressful stimuli cause the hypothalamus to signal the adrenal medulla (which mediates short-term stress responses) via nerve impulses, and the adrenal cortex, which mediates long-term stress responses, via the hormone **adrenocorticotropic hormone (ACTH)**, which is produced by the anterior pituitary.

Short-Term Stress Response

When presented with a stressful situation, the body responds by calling for the release of hormones that provide a burst of energy. The hormones **epinephrine** (also known as adrenaline) and **norepinephrine** (also known as noradrenaline) are released by the adrenal medulla. How do these hormones provide a burst of energy? Epinephrine and norepinephrine increase blood glucose levels by stimulating the liver and skeletal muscles to break down glycogen and by stimulating glucose release by liver cells. Additionally, these hormones increase oxygen availability to cells by increasing the heart rate and dilating the bronchioles. The hormones also prioritize body function by increasing blood supply to essential organs such as the heart, brain, and skeletal muscles, while restricting blood flow to organs not in immediate need, such as the skin, digestive system, and kidneys. Epinephrine and norepinephrine are collectively called catecholamines.

Watch this Discovery Channel animation describing the flight-or-flight response.

A link to an interactive elements can be found at the bottom of this page.

Long-Term Stress Response

Long-term stress response differs from short-term stress response. The body cannot sustain the bursts of energy mediated by epinephrine and norepinephrine for long times. Instead, other hormones come into play. In a long-term stress response, the hypothalamus triggers the release of ACTH from the anterior pituitary gland. The adrenal cortex is stimulated by ACTH to release steroid hormones called **corticosteroids**. Corticosteroids turn on transcription of certain genes in the nuclei of target cells. They change enzyme concentrations in the cytoplasm and affect cellular metabolism. There are two main corticosteroids: glucocorticoids such as **cortisol**, and mineralocorticoids such as aldosterone. These hormones target the breakdown of fat into fatty acids in the adipose tissue. The fatty acids are released into the bloodstream for other tissues to use for ATP production. The **glucocorticoids**primarily affect glucose metabolism by stimulating glucose synthesis. Glucocorticoids also have anti-inflammatory

properties through inhibition of the immune system. For example, cortisone is used as an anti-inflammatory medication; however, it cannot be used long term as it increases susceptibility to disease due to its immune-suppressing effects.

Mineralocorticoids function to regulate ion and water balance of the body. The hormone aldosterone stimulates the reabsorption of water and sodium ions in the kidney, which results in increased blood pressure and volume.

Hypersecretion of glucocorticoids can cause a condition known as **Cushing's disease**, characterized by a shifting of fat storage areas of the body. This can cause the accumulation of adipose tissue in the face and neck, and excessive glucose in the blood. Hyposecretion of the corticosteroids can cause **Addison's disease**, which may result in bronzing of the skin, hypoglycemia, and low electrolyte levels in the blood.

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18.17: Introduction to Endocrine Glands

Describe the role of different glands in the endocrine system

Both the endocrine and nervous systems use chemical signals to communicate and regulate the body's physiology. The endocrine system releases hormones that act on target cells to regulate development, growth, energy metabolism, reproduction, and many behaviors. The nervous system releases neurotransmitters or neurohormones that regulate neurons, muscle cells, and endocrine cells. Because the neurons can regulate the release of hormones, the nervous and endocrine systems work in a coordinated manner to regulate the body's physiology.

What You'll Learn to Do

- Describe the role of the hypothalamic-pituitary axis in the endocrine system
- Describe the role of the thyroid and parathyroid glands in the endocrine system
- Describe the role of the adrenal gland in the endocrine system
- Describe the role of the pancreas, pineal gland and gonads in the endocrine system
- Identify different organs that have secondary endocrine functions

Learning Activities

The learning activities for this section include the following:

- Hypothalamic-Pituitary Axis
- Thyroids
- Adrenal Glands
- The Pancreas, Pineal Gland, and Gonads
- Organs with Secondary Endocrine Functions
- Self Check: Endocrine Glands

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18.18: Hypothalamic-Pituitary Axis

The **hypothalamus** in vertebrates integrates the endocrine and nervous systems. The hypothalamus is an endocrine organ located in the diencephalon of the brain. It receives input from the body and other brain areas and initiates endocrine responses to environmental changes. The hypothalamus acts as an endocrine organ, synthesizing hormones and transporting them along axons to the posterior pituitary gland. It synthesizes and secretes regulatory hormones that control the endocrine cells in the anterior pituitary gland. The hypothalamus contains autonomic centers that control endocrine cells in the adrenal medulla via neuronal control.

The **pituitary gland**, sometimes called the hypophysis or "master gland" is located at the base of the brain in the sella turcica, a groove of the sphenoid bone of the skull, illustrated in Figure 1. It is attached to the hypothalamus via a stalk called the **pituitary stalk** (or infundibulum). The anterior portion of the pituitary gland is regulated by releasing or release-inhibiting hormones produced by the hypothalamus, and the posterior pituitary receives signals via neurosecretory cells to release hormones produced by the hypothalamus. The pituitary has two distinct regions—the anterior pituitary and the posterior pituitary—which between them secrete nine different peptide or protein hormones. The posterior lobe of the pituitary gland contains axons of the hypothalamic neurons.

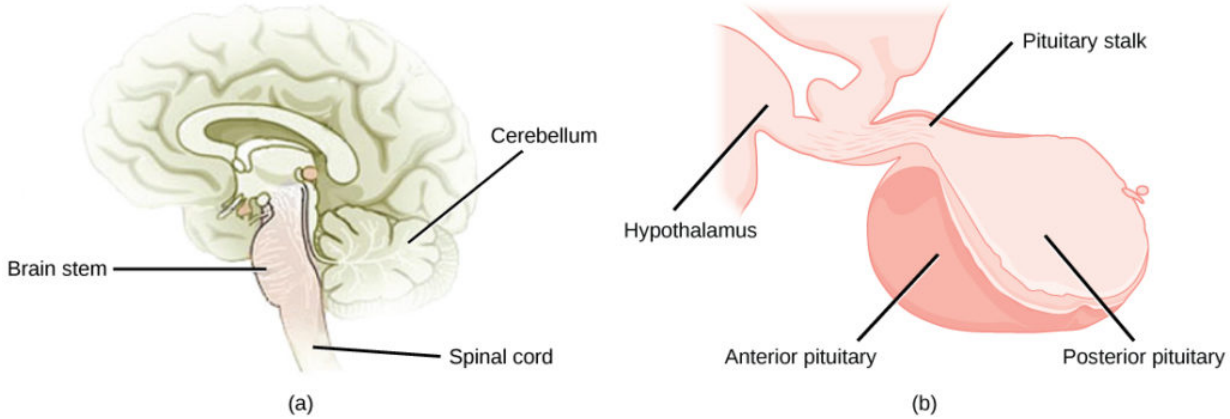


Figure 1. The pituitary gland is located at (a) the base of the brain and (b) connected to the hypothalamus by the pituitary stalk. (credit a: modification of work by NCI; credit b: modification of work by Gray's Anatomy)

Anterior Pituitary

The **anterior pituitary** gland, or adenohypophysis, is surrounded by a capillary network that extends from the hypothalamus, down along the infundibulum, and to the anterior pituitary. This capillary network is a part of the **hypophyseal portal system** that carries substances from the hypothalamus to the anterior pituitary and hormones from the anterior pituitary into the circulatory system. A portal system carries blood from one capillary network to another; therefore, the hypophyseal portal system allows hormones produced by the hypothalamus to be carried directly to the anterior pituitary without first entering the circulatory system.

The anterior pituitary produces seven hormones: growth hormone (GH), prolactin (PRL), thyroid-stimulating hormone (TSH), melanin-stimulating hormone (MSH), adrenocorticotropic hormone (ACTH), follicle-stimulating hormone (FSH), and luteinizing hormone (LH). Anterior pituitary hormones are sometimes referred to as tropic hormones, because they control the functioning of other organs. While these hormones are produced by the anterior pituitary, their production is controlled by regulatory hormones produced by the hypothalamus. These regulatory hormones can be releasing hormones or inhibiting hormones, causing more or less of the anterior pituitary hormones to be secreted. These travel from the hypothalamus through the hypophyseal portal system to the anterior pituitary where they exert their effect. Negative feedback then regulates how much of these regulatory hormones are released and how much anterior pituitary hormone is secreted.

Posterior Pituitary

The **posterior pituitary** is significantly different in structure from the anterior pituitary. It is a part of the brain, extending down from the hypothalamus, and contains mostly nerve fibers and neuroglial cells, which support axons that extend from the

hypothalamus to the posterior pituitary. The posterior pituitary and the infundibulum together are referred to as the neurohypophysis.

The hormones antidiuretic hormone (ADH), also known as vasopressin, and oxytocin are produced by neurons in the hypothalamus and transported within these axons along the infundibulum to the posterior pituitary. They are released into the circulatory system via neural signaling from the hypothalamus. These hormones are considered to be posterior pituitary hormones, even though they are produced by the hypothalamus, because that is where they are released into the circulatory system. The posterior pituitary itself does not produce hormones, but instead stores hormones produced by the hypothalamus and releases them into the blood stream.

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18.19: Thyroids

Thyroid Gland

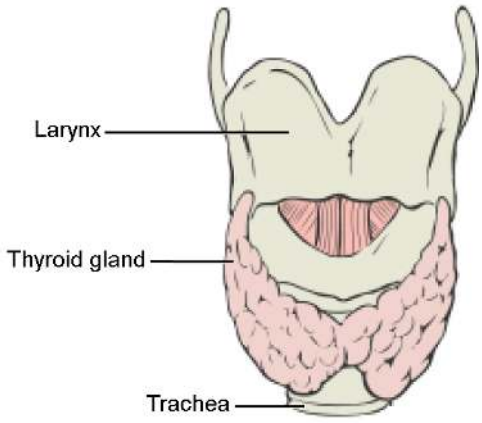


Figure 1. This illustration shows the location of the thyroid gland.

The **thyroid gland** is located in the neck, just below the larynx and in front of the trachea, as shown in Figure 1. It is a butterfly-shaped gland with two lobes that are connected by the **isthmus**. It has a dark red color due to its extensive vascular system. When the thyroid swells due to dysfunction, it can be felt under the skin of the neck.

The thyroid gland is made up of many spherical thyroid follicles, which are lined with a simple cuboidal epithelium. These follicles contain a viscous fluid, called **colloid**, which stores the glycoprotein thyroglobulin, the precursor to the thyroid hormones. The follicles produce hormones that can be stored in the colloid or released into the surrounding capillary network for transport to the rest of the body via the circulatory system.

Thyroid follicle cells synthesize the hormone thyroxine, which is also known as T_4 because it contains four atoms of iodine, and triiodothyronine, also known as T_3 because it contains three atoms of iodine. Follicle cells are stimulated to release stored T_3 and T_4 by thyroid stimulating hormone (TSH), which is produced by the anterior pituitary. These thyroid hormones increase the rates of mitochondrial ATP production.

A third hormone, calcitonin, is produced by **parafollicular cells** of the thyroid either releasing hormones or inhibiting hormones. Calcitonin release is not controlled by TSH, but instead is released when calcium ion concentrations in the blood rise. Calcitonin functions to help regulate calcium concentrations in body fluids.

Parathyroid Glands

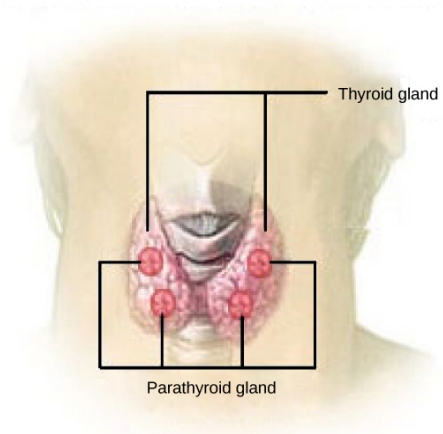


Figure 2. The parathyroid glands are located on the posterior of the thyroid gland. (credit: modification of work by NCI)

Most people have four **parathyroid glands**; however, the number can vary from two to six. These glands are located on the posterior surface of the thyroid gland, as shown in Figure 2. Normally, there is a superior gland and an inferior gland associated

with each of the thyroid's two lobes. Each parathyroid gland is covered by connective tissue and contains many secretory cells that are associated with a capillary network.

The parathyroid glands produce parathyroid hormone (PTH). PTH increases blood calcium concentrations when calcium ion levels fall below normal. PTH and calcitonin work in opposition to one another to maintain homeostatic Ca^{2+}levels in body fluids. These hormones encourage bone growth, muscle mass, and blood cell formation in children and women. PTH is produced by chief cells of the parathyroid. Another type of cells, oxyphil cells, exist in the parathyroid but their function is not known.

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18.20: Adrenal Glands

The **adrenal glands** are associated with the kidneys; one gland is located on top of each kidney as illustrated in Figure 1. The adrenal glands consist of an outer adrenal cortex and an inner adrenal medulla. These regions secrete different hormones.

Adrenal Cortex

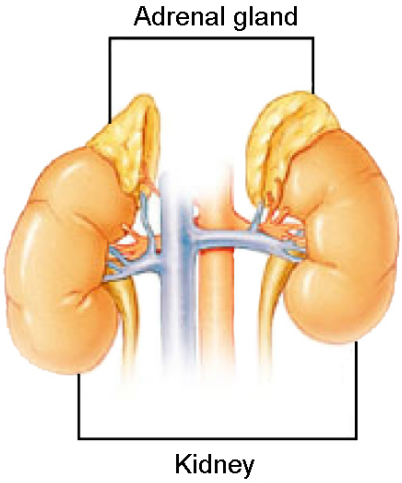


Figure 1. The location of the adrenal glands on top of the kidneys is shown. (credit: modification of work by NCI)

The **adrenal cortex** is made up of layers of epithelial cells and associated capillary networks. These layers form three distinct regions: an outer zona glomerulosa that produces mineralocorticoids, a middle zona fasciculata that produces glucocorticoids, and an inner zona reticularis that produces androgens.

The main mineralocorticoid is aldosterone, which regulates the concentration of Na^+ ions in urine, sweat, pancreas, and saliva. Aldosterone release from the adrenal cortex is stimulated by a decrease in blood concentrations of sodium ions, blood volume, or blood pressure, or by an increase in blood potassium levels.

The three main glucocorticoids are cortisol, corticosterone, and cortisone. The glucocorticoids stimulate the synthesis of glucose and gluconeogenesis (converting a non-carbohydrate to glucose) by liver cells and they promote the release of fatty acids from adipose tissue. These hormones increase blood glucose levels to maintain levels within a normal range between meals. These hormones are secreted in response to ACTH and levels are regulated by negative feedback.

Androgens are sex hormones that promote masculinity. They are produced in small amounts by the adrenal cortex in both males and females. They do not affect sexual characteristics and may supplement sex hormones released from the gonads.

Adrenal Medulla

The **adrenal medulla** contains large, irregularly shaped cells that are closely associated with blood vessels. These cells are innervated by preganglionic autonomic nerve fibers from the central nervous system.

The adrenal medulla contains two types of secretory cells: one that produces epinephrine (adrenaline) and another that produces norepinephrine (noradrenaline). Epinephrine is the primary adrenal medulla hormone accounting for 75 to 80 percent of its secretions. Epinephrine and norepinephrine increase heart rate, breathing rate, cardiac muscle contractions, blood pressure, and blood glucose levels. They also accelerate the breakdown of glucose in skeletal muscles and stored fats in adipose tissue.

The release of epinephrine and norepinephrine is stimulated by neural impulses from the sympathetic nervous system. Secretion of these hormones is stimulated by acetylcholine release from preganglionic sympathetic fibers innervating the adrenal medulla. These neural impulses originate from the hypothalamus in response to stress to prepare the body for the fight-or-flight response.

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18.21: The Pancreas, Pineal Gland, and Gonads

Pancreas

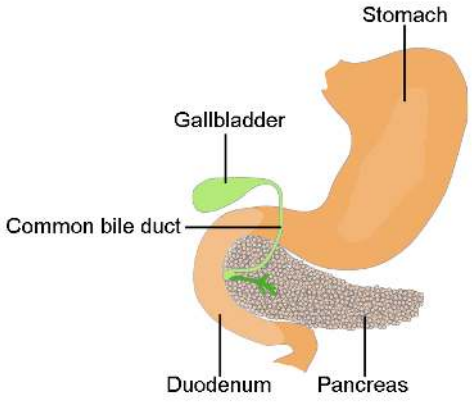


Figure 1. The pancreas is found underneath the stomach and points toward the spleen. (credit: modification of work by NCI)

The **pancreas**, illustrated in Figure 1, is an elongated organ that is located between the stomach and the proximal portion of the small intestine. It contains both exocrine cells that excrete digestive enzymes and endocrine cells that release hormones. It is sometimes referred to as a heterocrine gland because it has both endocrine and exocrine functions.

The endocrine cells of the pancreas form clusters called pancreatic islets or the **islets of Langerhans**, as visible in the micrograph shown in Figure 2. The pancreatic islets contain two primary cell types: **alpha cells**, which produce the hormone glucagon, and **beta cells**, which produce the hormone insulin. These hormones regulate blood glucose levels. As blood glucose levels decline, alpha cells release glucagon to raise the blood glucose levels by increasing rates of glycogen breakdown and glucose release by the liver. When blood glucose levels rise, such as after a meal, beta cells release insulin to lower blood glucose levels by increasing the rate of glucose uptake in most body cells, and by increasing glycogen synthesis in skeletal muscles and the liver. Together, glucagon and insulin regulate blood glucose levels.

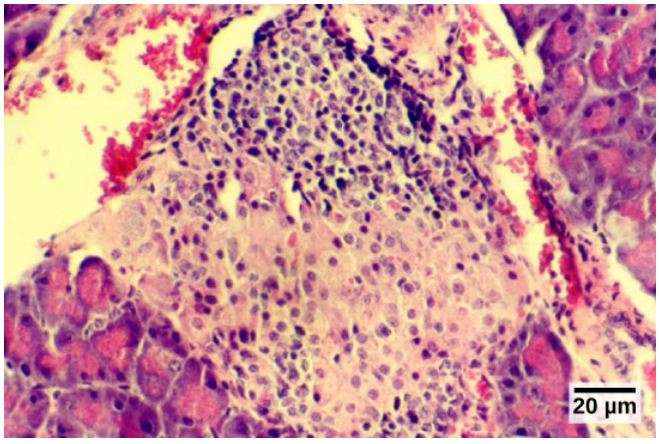


Figure 2. The islets of Langerhans are clusters of endocrine cells found in the pancreas; they stain lighter than surrounding cells. (credit: modification of work by Muhammad T. Tabiin, Christopher P. White, Grant Morahan, and Bernard E. Tuch; scale-bar data from Matt Russell)

Pineal Gland

The pineal gland produces melatonin. The rate of melatonin production is affected by the photoperiod. Collaterals from the visual pathways innervate the pineal gland. During the day photoperiod, little melatonin is produced; however, melatonin production increases during the dark photoperiod (night). In some mammals, melatonin has an inhibitory affect on reproductive functions by decreasing production and maturation of sperm, oocytes, and reproductive organs. Melatonin is an effective antioxidant, protecting

the CNS from free radicals such as nitric oxide and hydrogen peroxide. Lastly, melatonin is involved in biological rhythms, particularly circadian rhythms such as the sleep-wake cycle and eating habits.

Gonads

The gonads—the male testes and female ovaries—produce steroid hormones. The testes produce androgens, testosterone being the most prominent, which allow for the development of secondary sex characteristics and the production of sperm cells. The ovaries produce estradiol and progesterone, which cause secondary sex characteristics and prepare the body for childbirth.

Table 1. Endocrine Glands and their Associated Hormones

Endocrine Gland	Associated Hormones	Effect
Hypothalamus	releasing and inhibiting hormones	regulate hormone release from pituitary gland; produce oxytocin; produce uterine contractions and milk secretion in females
	antidiuretic hormone (ADH)	water reabsorption from kidneys; vasoconstriction to increase blood pressure
Pituitary (Anterior)	growth hormone (GH)	promotes growth of body tissues, protein synthesis; metabolic functions
	prolactin (PRL)	promotes milk production
	thyroid stimulating hormone (TSH)	stimulates thyroid hormone release
	adrenocorticotropic hormone (ACTH)	stimulates hormone release by adrenal cortex, glucocorticoids
	follicle-stimulating hormone (FSH)	stimulates gamete production (both ova and sperm); secretion of estradiol
	luteinizing hormone (LH)	stimulates androgen production by gonads; ovulation, secretion of progesterone
	melanocyte-stimulating hormone (MSH)	stimulates melanocytes of the skin increasing melanin pigment production.
Pituitary (Posterior)	antidiuretic hormone (ADH)	stimulates water reabsorption by kidneys
	oxytocin	stimulates uterine contractions during childbirth; milk ejection; stimulates ductus deferens and prostate gland contraction during emission
Thyroid	thyroxine, triiodothyronine	stimulate and maintain metabolism; growth and development
	calcitonin	reduces blood Ca^{2+} levels
Parathyroid	parathyroid hormone (PTH)	increases blood Ca^{2+} levels
Adrenal (Cortex)	aldosterone	increases blood Na^{+} levels; increase K^{+} secretion
	cortisol, corticosterone, cortisone	increase blood glucose levels; anti-inflammatory effects
Adrenal (Medulla)	epinephrine, norepinephrine	stimulate fight-or-flight response; increase blood gluclose levels; increase metabolic activities
Pancreas	insulin	reduces blood glucose levels
	glucagon	increases blood glucose levels
Pineal gland	melatonin	regulates some biological rhythms and protects CNS from free radicals
Testes	androgens	regulate, promote, increase or maintain sperm production; male secondary sexual

Table 1. Endocrine Glands and their Associated Hormones

Endocrine Gland	Associated Hormones	Effect
		characteristics
Ovaries	estrogen	promotes uterine lining growth; female secondary sexual characteristics
	progestins	promote and maintain uterine lining growth

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18.22: Organs with Secondary Endocrine Functions

There are several organs whose primary functions are non-endocrine but that also possess endocrine functions. These include the heart, kidneys, intestines, thymus, gonads, and adipose tissue.

The heart possesses endocrine cells in the walls of the atria that are specialized cardiac muscle cells. These cells release the hormone **atrial natriuretic peptide (ANP)** in response to increased blood volume. High blood volume causes the cells to be stretched, resulting in hormone release. ANP acts on the kidneys to reduce the reabsorption of Na^+, causing Na^+ and water to be excreted in the urine. ANP also reduces the amounts of renin released by the kidneys and aldosterone released by the adrenal cortex, further preventing the retention of water. In this way, ANP causes a reduction in blood volume and blood pressure, and reduces the concentration of Na^+ in the blood.

The gastrointestinal tract produces several hormones that aid in digestion. The endocrine cells are located in the mucosa of the GI tract throughout the stomach and small intestine. Some of the hormones produced include gastrin, secretin, and cholecystokinin, which are secreted in the presence of food, and some of which act on other organs such as the pancreas, gallbladder, and liver. They trigger the release of gastric juices, which help to break down and digest food in the GI tract.

While the adrenal glands associated with the kidneys are major **endocrine glands**, the kidneys themselves also possess endocrine function. Renin is released in response to decreased blood volume or pressure and is part of the renin-angiotensin-aldosterone system that leads to the release of aldosterone. Aldosterone then causes the retention of Na^+ and water, raising blood volume. The kidneys also release calcitriol, which aids in the absorption of Ca^{2+} and phosphate ions. **Erythropoietin (EPO)** is a protein hormone that triggers the formation of red blood cells in the bone marrow. EPO is released in response to low oxygen levels. Because red blood cells are oxygen carriers, increased production results in greater oxygen delivery throughout the body. EPO has been used by athletes to improve performance, as greater oxygen delivery to muscle cells allows for greater endurance. Because red blood cells increase the viscosity of blood, artificially high levels of EPO can cause severe health risks.

The **thymus** is found behind the sternum; it is most prominent in infants, becoming smaller in size through adulthood. The thymus produces hormones referred to as thymosins, which contribute to the development of the immune response.

Adipose tissue is a connective tissue found throughout the body. It produces the hormone **leptin** in response to food intake. Leptin increases the activity of anorexigenic neurons and decreases that of orexigenic neurons, producing a feeling of satiety after eating, thus affecting appetite and reducing the urge for further eating. Leptin is also associated with reproduction. It must be present for GnRH and gonadotropin synthesis to occur. Extremely thin females may enter puberty late; however, if adipose levels increase, more leptin will be produced, improving fertility.

In Summary: Organs with Secondary Endocrine Functions

Some organs possess endocrine activity as a secondary function but have another primary function. The heart produces the hormone atrial natriuretic peptide, which functions to reduce blood volume, pressure, and Na^+ concentration. The gastrointestinal tract produces various hormones that aid in digestion. The kidneys produce renin, calcitriol, and erythropoietin. Adipose tissue produces leptin, which promotes satiety signals in the brain.

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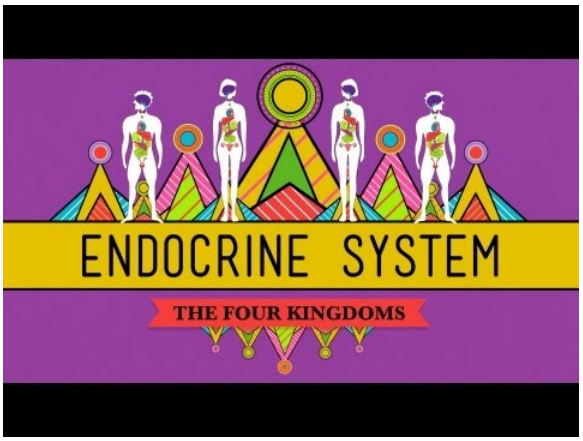
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18.23: Putting It Together- The Endocrine System

This video fills us in on the endocrine system—the system of glands which produce and secrete different types of hormones directly into the bloodstream to regulate the body's growth, metabolism, and sexual development & function.



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=759

Table 1 summarizes the major hormones, their target and their function.

Table 1. Major Horomes

Endocrine Gland	Hormone Released	Chemical Class	Target Tissue/Organ	Major Function of Hormone
Hypothalamus	Hypothalamic releasing and inhibiting hormones	Peptide	Anterior pituitary	Regulate anterior pituitary hormone
Posterior Pituitary	Antidiuretic (ADH)	Peptide	Kidneys	Stimulates water reabsorption by kidneys
	Oxytocin	Peptide	Uterus, mammary glands	Stimulates uterine muscle contractions and release of milk by mammary glands
Anterior Pituitary	Thyroid stimulating (TSH)	Glycoprotein	Thyroid	Stimulates thyroid
	Adrenocorticotropic (ACTH)	Peptide	Adrenal cortex	Stimulates adrenal cortex
	Gonadotropic (FSH, LH)	Glycoprotein	Gonads	Egg and sperm production, sex hormone production
	Prolactin (PRL)	Protein	Mammary glands	Milk production
	Growth (GH)	Protein	Soft tissue, bones	Cell division, protein synthesis and bone growth
Thyroid	Thyroxine (T4) and Triiodothyronie (T3)	Iodinated amino acid	All tissue	Increase metabolic rate, regulates growth and development
	Calcitonin	Peptide	Bones, kidneys and intestine	Lowers blood calcium level
Parathyroids	Parathyroid (PTH)	Peptide	Bones, kidneys and intestine	Raises blood calcium level
Adrenal Cortex	Glucocorticoids (cortisol)	Steroid	All tissue	Raise blood glucose level, stimulates breakdown of protein
	Mineralocorticoids (aldosterone)	Steroid	Kidneys	Reabsorb sodium and excrete potassium
	Sex Hormones	Steroid	Gonads, skin, muscles and bones	Stimulates reproductive organs and brings on sex characteristics
Adrenal Medulla	Epinephrine and norepinephrine	Modified amino acid	Cardiac and other muscles	Released in emergency situations, raises blood glucose level, “fight or flight” response
Pancreas	Insulin	Protein	Liver, muscles, adipose tissue	Lowers blood glucose levels, promotes formation of glycogen

Table 1. Major Horomes

Endocrine Gland	Hormone Released	Chemical Class	Target Tissue/Organ	Major Function of Hormone
	Glucagon	Protein	Liver, muscles, adipose tissue	Raises blood glucose levels
Testes	Androgens (testosterone)	Steroid	Gonads, skin, muscles and bone	Stimulates male sex characteristics
Ovaries	Estrogen and progesterone	Steroid	Gonads, skin, muscles and bones	Stimulates female sex characteristics
Thymus	Thymosins	Peptide	T lymphocytes	Stimulates production and maturation of T lymphocytes
Pineal Gland	Melatonin	Modified amino acid	Brain	Controls circadian and circannual rhythms, possibly involved in maturation of sexual organs

Career Connection

Fittingly, the profession that works closely with the endocrine system is known as endocrinology. If you found this body system interesting, you may want to look into this field.

? Try It

An endocrinologist is a medical doctor who specializes in treating disorders of the endocrine glands, hormone systems, and glucose and lipid metabolic pathways. An endocrine surgeon specializes in the surgical treatment of endocrine diseases and glands. Some of the diseases that are managed by endocrinologists: disorders of the pancreas (diabetes mellitus), disorders of the pituitary (gigantism, acromegaly, and pituitary dwarfism), disorders of the thyroid gland (goiter and Graves' disease), and disorders of the adrenal glands (Cushing's disease and Addison's disease).

Endocrinologists are required to assess patients and diagnose endocrine disorders through extensive use of laboratory tests. Many endocrine diseases are diagnosed using tests that stimulate or suppress endocrine organ functioning. Blood samples are then drawn to determine the effect of stimulating or suppressing an endocrine organ on the production of hormones. For example, to diagnose diabetes mellitus, patients are required to fast for 12 to 24 hours. They are then given a sugary drink, which stimulates the pancreas to produce insulin to decrease blood glucose levels. A blood sample is taken one to two hours after the sugar drink is consumed. If the pancreas is functioning properly, the blood glucose level will be within a normal range. Another example is the A1C test, which can be performed during blood screening. The A1C test measures average blood glucose levels over the past two to three months by examining how well the blood glucose is being managed over a long time.

Once a disease has been diagnosed, endocrinologists can prescribe lifestyle changes and/or medications to treat the disease. Some cases of diabetes mellitus can be managed by exercise, weight loss, and a healthy diet; in other cases, medications may be required to enhance insulin release. If the disease cannot be controlled by these means, the endocrinologist may prescribe insulin injections.

In addition to clinical practice, endocrinologists may also be involved in primary research and development activities. For example, ongoing islet transplant research is investigating how healthy pancreas islet cells may be transplanted into diabetic patients. Successful islet transplants may allow patients to stop taking insulin injections.

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18.24: Cerego- The Endocrine System

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for The Endocrine System. You'll need to create a free log-in to practice these items, if you haven't already.

https://cerego.com/sets/796524/learn

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CHAPTER OVERVIEW

19: Module 16- The Reproductive System

19.1: Why It Matters- The Reproductive System
19.2: Introduction to Reproduction Methods
19.3: Asexual Reproduction
19.4: Sexual Reproduction
19.5: Introduction to Human Reproductive Anatomy
19.6: Male Reproductive Anatomy
19.7: Female Reproductive Anatomy
19.8: Sexual Response
19.9: Gametogenesis
19.10: Introduction to Hormonal Control of Human Reproduction
19.11: Reproductive Hormones
19.12: The Ovarian Cycle, the Menstrual Cycle, and Menopause
19.13: Introduction to Fertilization
19.14: Fertilization
19.15: External and Internal Fertilization
19.16: The Evolution of Reproduction
19.17: Introduction to Early Embryonic Development
19.18: Cleavage and Blastula Stage
19.19: Gastrulation
19.20: Organogenesis
19.21: Vertebrate Axis Formation
19.22: Introduction to Human Pregnancy and Birth
19.23: Human Gestation
19.24: Labor and Birth
19.25: Contraception and Birth Control
19.26: Infertility
19.27: Putting It Together- The Reproductive System
19.28: Cerego- The Reproductive System

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19.1: Why It Matters- The Reproductive System

Why describe the components and role of the reproductive system?



Figure 1. Female seahorses produce eggs for reproduction that are then fertilized by the male. Unlike almost all other animals, the male seahorse then gestates the young until birth. (credit: modification of work by "cliff1066″/Flickr)

Animal reproduction is necessary for the survival of a species. In the animal kingdom, there are innumerable ways that species reproduce. Asexual reproduction produces genetically identical organisms (clones), whereas in sexual reproduction, the genetic material of two individuals combines to produce offspring that are genetically different from their parents. During sexual reproduction the male gamete (sperm) may be placed inside the female's body for internal fertilization, or the sperm and eggs may be released into the environment for external fertilization. Seahorses, like the one shown in Figure 1, provide an example of the latter. Following a mating dance, the female lays eggs in the male seahorse's abdominal brood pouch where they are fertilized. The eggs hatch and the offspring develop in the pouch for several weeks.

Learning Outcomes

- Describe advantages and disadvantages of asexual and sexual reproduction
- Describe human male and female reproductive anatomies
- Describe the roles of male and female reproductive hormones
- Discuss internal and external methods of fertilization
- Explain how the embryo forms from the zygote
- Describe the process of organogenesis and vertebrate formation
- Explain fetal development during the three trimesters of gestation

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19.2: Introduction to Reproduction Methods

Describe advantages and disadvantages of asexual and sexual reproduction

Animals produce offspring through asexual or sexual reproduction; both methods have advantages and disadvantages. Reproduction may be asexual when one individual produces genetically identical offspring, or sexual when the genetic material from two individuals is combined to produce genetically diverse offspring.

What You'll Learn to Do

- Discuss asexual reproduction methods
- Discuss sexual reproduction methods
- Describe how sex is determined in different organisms

Learning Activities

The learning activities for this section include the following:

- Asexual Reproduction
- Sexual Reproduction
- Self Check: Reproduction Methods

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19.3: Asexual Reproduction

Asexual reproduction occurs in prokaryotic microorganisms (bacteria) and in some eukaryotic single-celled and multi-celled organisms. **Asexual reproduction** produces offspring that are genetically identical to the parent because the offspring are all clones of the original parent. A single individual can produce offspring asexually and large numbers of offspring can be produced quickly.

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

Fission

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

Budding

Budding is a form of asexual reproduction that results from the outgrowth of a part of a cell or body region leading to a separation from the original organism into two individuals. Budding occurs commonly in some invertebrate animals such as corals and hydras. In hydras, a bud forms that develops into an adult and breaks away from the main body, as illustrated in Figure 1b, whereas in coral budding, the bud does not detach and multiplies as part of a new colony.

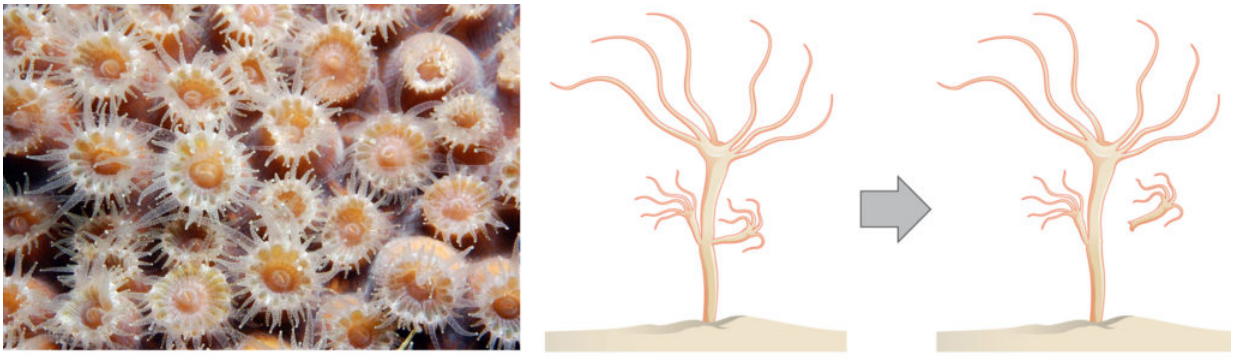


Figure 1. (a) Coral polyps reproduce asexually by fission. (b) Hydra reproduce asexually through budding. (credit a: G. P. Schmahl, NOAA FGBNMS Manager)

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



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=769

Fragmentation



Figure 2. Sea stars can reproduce through fragmentation. The large arm, a fragment from another sea star, is developing into a new individual.

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

For example, in many sea stars, asexual reproduction is accomplished by fragmentation. Figure 2 illustrates a sea star for which an arm of the individual is broken off and regenerates a new sea star. Fisheries workers have been known to try to kill the sea stars eating their clam or oyster beds by cutting them in half and throwing them back into the ocean. Unfortunately for the workers, the two parts can each regenerate a new half, resulting in twice as many sea stars to prey upon the oysters and clams. Fragmentation also occurs in annelid worms, turbellarians, and poriferans.

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

Parthenogenesis

Parthenogenesis is a form of asexual reproduction where an egg develops into a complete individual without being fertilized. The resulting offspring can be either haploid or diploid, depending on the process and the species. Parthenogenesis occurs in invertebrates such as water flees, rotifers, aphids, stick insects, some ants, wasps, and bees. Bees use parthenogenesis to produce haploid males (drones) and diploid females (workers). If an egg is fertilized, a queen is produced. The queen bee controls the reproduction of the hive bees to regulate the type of bee produced.

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

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19.4: Sexual Reproduction

Sexual reproduction is the combination of (usually haploid) reproductive cells from two individuals to form a third (usually diploid) unique offspring. Sexual reproduction produces offspring with novel combinations of genes. This can be an adaptive advantage in unstable or unpredictable environments. Species that reproduce sexually must maintain two different types of individuals, males and females, which can limit the ability to colonize new habitats as both sexes must be present. As humans, we are used to thinking of animals as having two separate sexes—male and female—determined at conception. However, in the animal kingdom, there are many variations on this theme.

Hermaphroditism



Figure 1. Many snails are hermaphrodites. When two individuals mate, they can produce up to one hundred eggs each. (credit: Assaf Shtilman)

Hermaphroditism occurs in animals where one individual has both male and female reproductive parts. Invertebrates such as earthworms, slugs, tapeworms and snails, shown in Figure 1, are often hermaphroditic. Hermaphrodites may self-fertilize or may mate with another of their species, fertilizing each other and both producing offspring. Self fertilization is common in animals that have limited mobility or are not motile, such as barnacles and clams.

Sex Determination

Mammalian sex determination is determined genetically by the presence of X and Y chromosomes. Individuals homozygous for X (XX) are female and heterozygous individuals (XY) are male. The presence of a Y chromosome causes the development of male characteristics and its absence results in female characteristics. The XY system is also found in some insects and plants.

Avian sex determination is dependent on the presence of Z and W chromosomes. Homozygous for Z (ZZ) results in a male and heterozygous (ZW) results in a female. The W appears to be essential in determining the sex of the individual, similar to the Y chromosome in mammals. Some fish, crustaceans, insects (such as butterflies and moths), and reptiles use this system.

The sex of some species is not determined by genetics but by some aspect of the environment. Sex determination in some crocodiles and turtles, for example, is often dependent on the temperature during critical periods of egg development. This is referred to as environmental sex determination, or more specifically as temperature-dependent sex determination. In many turtles, cooler temperatures during egg incubation produce males and warm temperatures produce females. In some crocodiles, moderate temperatures produce males and both warm and cool temperatures produce females. In some species, sex is both genetic- and temperature-dependent.

Individuals of some species change their sex during their lives, alternating between male and female. If the individual is female first, it is termed protogyny or “first female,” if it is male first, its termed protandry or “first male.” Oysters, for example, are born male, grow, and become female and lay eggs; some oyster species change sex multiple times.

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19.5: Introduction to Human Reproductive Anatomy

Describe human male and female reproductive anatomies

As animals became more complex, specific organs and organ systems developed to support specific functions for the organism. The reproductive structures that evolved in land animals allow males and females to mate, fertilize internally, and support the growth and development of offspring.

The reproductive tissues of male and female humans develop similarly *in utero* until a low level of the hormone testosterone is released from male gonads. Testosterone causes the undeveloped tissues to differentiate into male sexual organs. When testosterone is absent, the tissues develop into female sexual tissues. Primitive gonads become testes or ovaries. Tissues that produce a penis in males produce a clitoris in females. The tissue that will become the scrotum in a male becomes the labia in a female; that is, they are homologous structures.

What You'll Learn to Do

- Describe human male reproductive anatomies
- Describe human female reproductive anatomies
- Discuss the human sexual response
- Discuss the differences and similarities between spermatogenesis and oogenesis

Learning Activities

The learning activities for this section include the following:

- Male Reproductive Anatomy
- Female Reproductive Anatomy
- Sexual Response
- Gametogenesis
- Self Check: Human Reproductive Anatomy

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19.6: Male Reproductive Anatomy

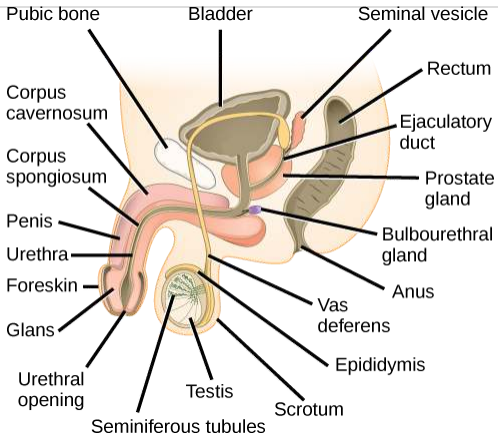


Figure 1. The reproductive structures of the human male are shown.

In the male reproductive system, the **scrotum** houses the testicles or testes (singular: testis), including providing passage for blood vessels, nerves, and muscles related to testicular function. The **testes** are a pair of male reproductive organs that produce sperm and some reproductive hormones. Each testis is approximately 2.5 by 3.8 cm (1.5 by 1 in) in size and divided into wedge-shaped lobules by connective tissue called septa. Coiled in each wedge are seminiferous tubules that produce sperm.

Sperm are immobile at body temperature; therefore, the scrotum and penis are external to the body, as illustrated in Figure 1 so that a proper temperature is maintained for motility. In land mammals, the pair of testes must be suspended outside the body at about 2° C lower than body temperature to produce viable sperm. Infertility can occur in land mammals when the testes do not descend through the abdominal cavity during fetal development.

Practice Question

Which of the following statements about the male reproductive system is false?

a. The vas deferens carries sperm from the testes to the penis.
b. Sperm mature in seminiferous tubules in the testes.
c. Both the prostate and the bulbourethral glands produce components of the semen.
d. The prostate gland is located in the testes.

[reveal-answer q=”795597″]Show Answer[/reveal-answer]
[hidden-answer a=”795597″]Statement d is false.[/hidden-answer]

Sperm mature in **seminiferous tubules** that are coiled inside the testes, as illustrated in Figure 1. The walls of the seminiferous tubules are made up of the developing sperm cells, with the least developed sperm at the periphery of the tubule and the fully developed sperm in the lumen. The sperm cells are mixed with “nursemaid” cells called Sertoli cells which protect the germ cells and promote their development. Other cells mixed in the wall of the tubules are the interstitial cells of Leydig. These cells produce high levels of testosterone once the male reaches adolescence.

When the sperm have developed flagella and are nearly mature, they leave the testicles and enter the epididymis, shown in Figure 1. This structure resembles a comma and lies along the top and posterior portion of the testes; it is the site of sperm maturation. The sperm leave the epididymis and enter the vas deferens (or ductus deferens), which carries the sperm, behind the bladder, and forms the ejaculatory duct with the duct from the seminal vesicles. During a vasectomy, a section of the vas deferens is removed, preventing sperm from being passed out of the body during ejaculation and preventing fertilization.

Semen is a mixture of sperm and spermatic duct secretions (about 10 percent of the total) and fluids from accessory glands that contribute most of the semen’s volume. Sperm are haploid cells, consisting of a flagellum as a tail, a neck that contains the cell’s energy-producing mitochondria, and a head that contains the genetic material. Figure 2 shows a micrograph of human sperm as well as a diagram of the parts of the sperm. An acrosome is found at the top of the head of the sperm. This structure contains

lysosomal enzymes that can digest the protective coverings that surround the egg to help the sperm penetrate and fertilize the egg. An ejaculate will contain from two to five milliliters of fluid with from 50–120 million sperm per milliliter.

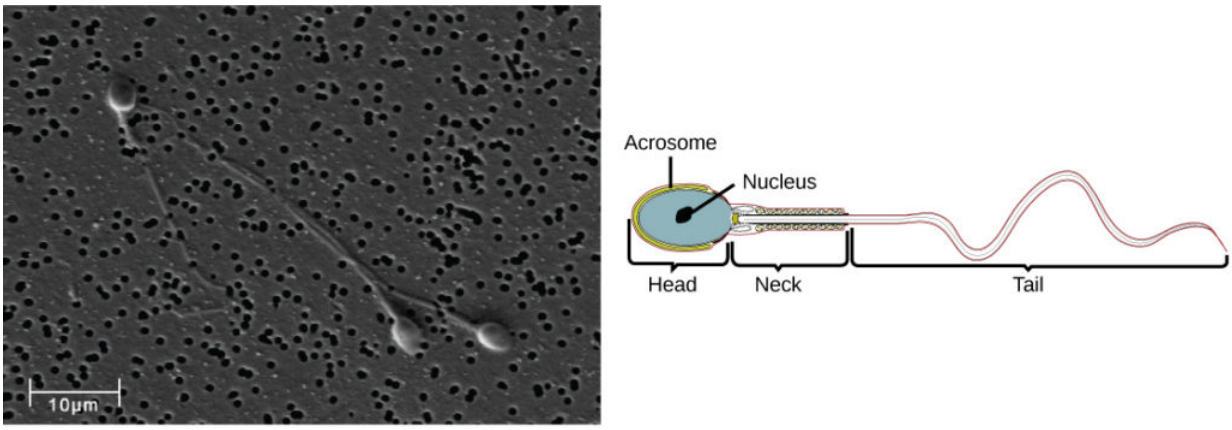


Figure 2. Human sperm, visualized using scanning electron microscopy, have a flagellum, neck, and head. (credit b: modification of work by Mariana Ruiz Villareal; scale-bar data from Matt Russell)

The bulk of the semen comes from the accessory glands associated with the male reproductive system. These are the seminal vesicles, the prostate gland, and the bulbourethral gland, all of which are illustrated in Figure 1. The **seminal vesicles** are a pair of glands that lie along the posterior border of the urinary bladder. The glands make a solution that is thick, yellowish, and alkaline. As sperm are only motile in an alkaline environment, a basic pH is important to reverse the acidity of the vaginal environment. The solution also contains mucus, fructose (a sperm mitochondrial nutrient), a coagulating enzyme, ascorbic acid, and local-acting hormones called prostaglandins. The seminal vesicle glands account for 60 percent of the bulk of semen.

The **penis**, illustrated in Figure 1, is an organ that drains urine from the renal bladder and functions as a copulatory organ during intercourse. The penis contains three tubes of erectile tissue running through the length of the organ. These consist of a pair of tubes on the dorsal side, called the corpus cavernosum, and a single tube of tissue on the ventral side, called the corpus spongiosum. This tissue will become engorged with blood, becoming erect and hard, in preparation for intercourse. The organ is inserted into the vagina culminating with an ejaculation. During intercourse, the smooth muscle sphincters at the opening to the renal bladder close and prevent urine from entering the penis. An orgasm is a two-stage process: first, glands and accessory organs connected to the testes contract, then semen (containing sperm) is expelled through the urethra during ejaculation. After intercourse, the blood drains from the erectile tissue and the penis becomes flaccid.

The walnut-shaped **prostate gland** surrounds the urethra, the connection to the urinary bladder. It has a series of short ducts that directly connect to the urethra. The gland is a mixture of smooth muscle and glandular tissue. The muscle provides much of the force needed for ejaculation to occur. The glandular tissue makes a thin, milky fluid that contains citrate (a nutrient), enzymes, and prostate specific antigen (PSA). PSA is a proteolytic enzyme that helps to liquefy the ejaculate several minutes after release from the male. Prostate gland secretions account for about 30 percent of the bulk of semen.

The **bulbourethral gland**, or Cowper’s gland, releases its secretion prior to the release of the bulk of the semen. It neutralizes any acid residue in the urethra left over from urine. This usually accounts for a couple of drops of fluid in the total ejaculate and may contain a few sperm. Withdrawal of the penis from the vagina before ejaculation to prevent pregnancy may not work if sperm are present in the bulbourethral gland secretions. The location and functions of the male reproductive organs are summarized in Table 1.

Table 1. Male Reproductive Anatomy		
Organ	Location	Function
Scrotum	External	Carry and support testes
Penis	External	Deliver urine, copulating organ
Testes	Internal	Produce sperm and male hormones
Seminal Vesicles	Internal	Contribute to semen production
Prostate Gland	Internal	Contribute to semen production
Bulbourethral Glands	Internal	Clean urethra at ejaculation

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19.7: Female Reproductive Anatomy

A number of reproductive structures are exterior to the female's body. These include the breasts and the vulva, which consists of the mons pubis, clitoris, labia majora, labia minora, and the vestibular glands, all illustrated in Figure 1. The location and functions of the female reproductive organs are summarized in Table 1. The vulva is an area associated with the vestibule which includes the structures found in the inguinal (groin) area of women. The mons pubis is a round, fatty area that overlies the pubic symphysis. The **clitoris** is a structure with erectile tissue that contains a large number of sensory nerves and serves as a source of stimulation during intercourse. The **labia majora** are a pair of elongated folds of tissue that run posterior from the mons pubis and enclose the other components of the vulva. The labia majora derive from the same tissue that produces the scrotum in a male. The **labia minora** are thin folds of tissue centrally located within the labia majora. These labia protect the openings to the vagina and urethra. The mons pubis and the anterior portion of the labia majora become covered with hair during adolescence; the labia minora is hairless. The greater vestibular glands are found at the sides of the vaginal opening and provide lubrication during intercourse.

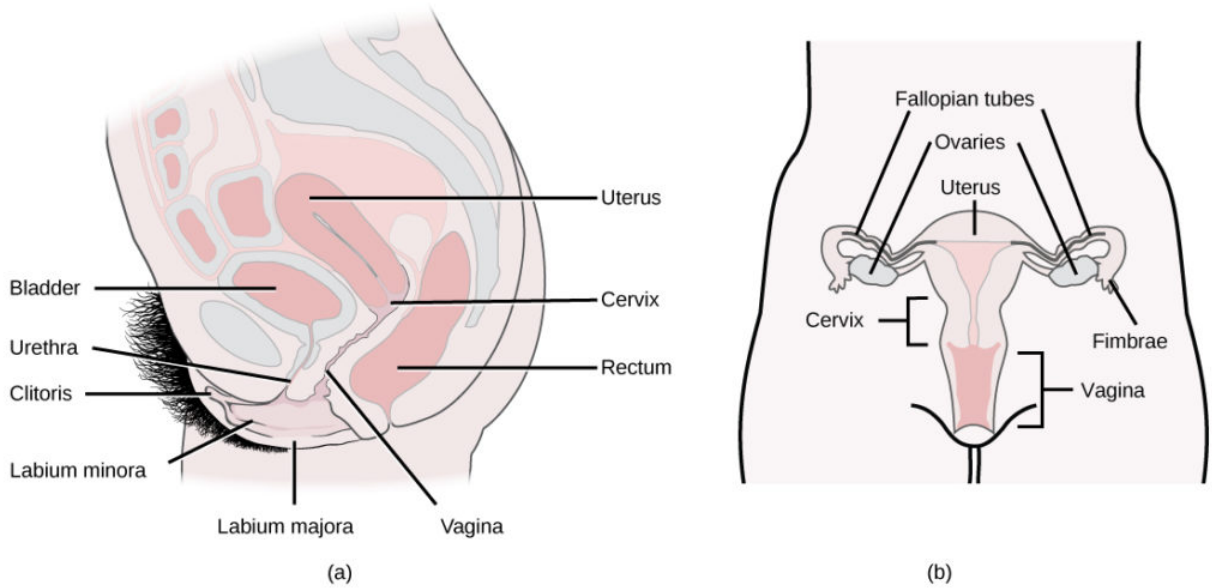


Figure 1. The reproductive structures of the human female are shown. (credit a: modification of work by Gray's Anatomy; credit b: modification of work by CDC)

Table 1. Female Reproductive Anatomy

Organ	Location	Function
Clitoris	External	Sensory organ
Mons pubis	External	Fatty area overlying pubic bone
Labia majora	External	Covers labia minora
Labia minora	External	Covers vestibule
Greater vestibular glands	External	Secrete mucus; lubricate vagina
Breast	External	Produce and deliver milk
Ovaries	Internal	Carry and develop eggs
Oviducts (Fallopian tubes)	Internal	Transport egg to uterus
Uterus	Internal	Support developing embryo
Vagina	Internal	Common tube for intercourse, birth canal, passing menstrual flow

The breasts consist of mammary glands and fat. The size of the breast is determined by the amount of fat deposited behind the gland. Each gland consists of 15 to 25 lobes that have ducts that empty at the nipple and that supply the nursing child with nutrient- and antibody-rich milk to aid development and protect the child.

Internal female reproductive structures include ovaries, oviducts, the **uterus**, and the vagina, shown in Figure 1. The pair of ovaries is held in place in the abdominal cavity by a system of ligaments. Ovaries consist of a medulla and cortex: the medulla contains nerves and blood vessels to supply the cortex with nutrients and remove waste. The outer layers of cells of the cortex are the functional parts of the ovaries. The cortex is made up of follicular cells that surround eggs that develop during fetal development *in utero*. During the menstrual period, a batch of follicular cells develops and prepares the eggs for release. At ovulation, one follicle ruptures and one egg is released, as illustrated in Figure 2a.

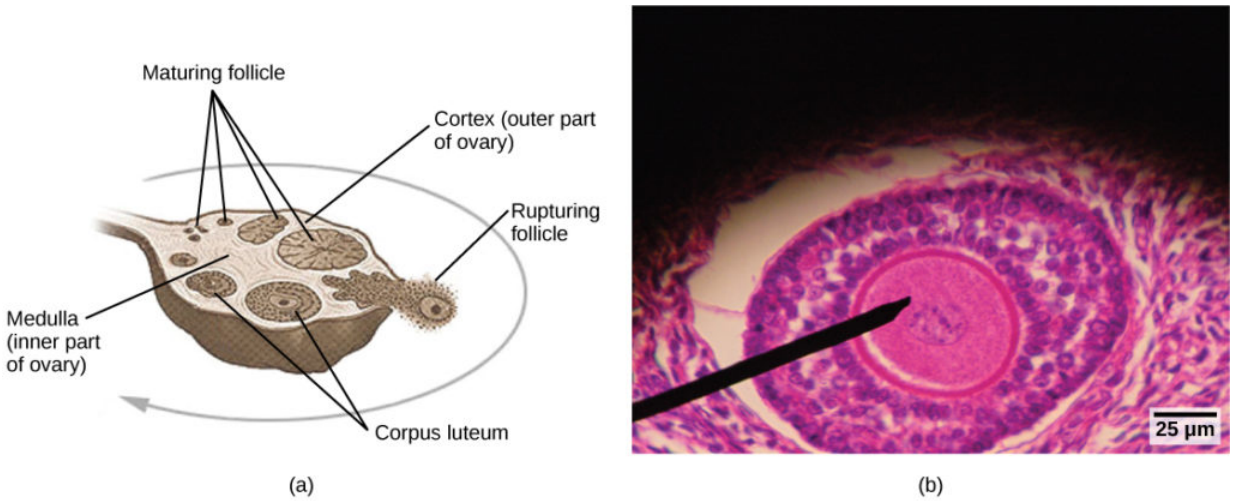


Figure 2. Oocytes develop in (a) follicles, located in the ovary. At the beginning of the menstrual cycle, the follicle matures. At ovulation, the follicle ruptures, releasing the egg. The follicle becomes a corpus luteum, which eventually degenerates. The (b) follicle in this light micrograph has an oocyte at its center. (credit a: modification of work by NIH; scale-bar data from Matt Russell)

The **oviducts**, or fallopian tubes, extend from the uterus in the lower abdominal cavity to the ovaries, but they are not in contact with the ovaries. The lateral ends of the oviducts flare out into a trumpet-like structure and have a fringe of finger-like projections called fimbriae, illustrated in Figure 2b. When an egg is released at ovulation, the fimbrae help the non-motile egg enter into the tube and passage to the uterus. The walls of the oviducts are ciliated and are made up mostly of smooth muscle. The cilia beat toward the middle, and the smooth muscle contracts in the same direction, moving the egg toward the uterus. Fertilization usually takes place within the oviducts and the developing embryo is moved toward the uterus for development. It usually takes the egg or embryo a week to travel through the oviduct. Sterilization in women is called a tubal ligation; it is analogous to a vasectomy in males in that the oviducts are severed and sealed.

The uterus is a structure about the size of a woman's fist. This is lined with an endometrium rich in blood vessels and mucus glands. The uterus supports the developing embryo and fetus during gestation. The thickest portion of the wall of the uterus is made of smooth muscle. Contractions of the smooth muscle in the uterus aid in passing the baby through the vagina during labor. A portion of the lining of the uterus sloughs off during each menstrual period, and then builds up again in preparation for an implantation. Part of the uterus, called the cervix, protrudes into the top of the vagina. The cervix functions as the birth canal.

The **vagina** is a muscular tube that serves several purposes. It allows menstrual flow to leave the body. It is the receptacle for the penis during intercourse and the vessel for the delivery of offspring. It is lined by stratified squamous epithelial cells to protect the underlying tissue.

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19.8: Sexual Response

The sexual response in humans is both psychological and physiological. Both sexes experience sexual arousal through psychological and physical stimulation. There are four phases of the sexual response. During phase one, called excitement, vasodilation leads to vasocongestion in erectile tissues in both men and women. The nipples, clitoris, labia, and penis engorge with blood and become enlarged. Vaginal secretions are released to lubricate the vagina to facilitate intercourse. During the second phase, called the plateau, stimulation continues, the outer third of the vaginal wall enlarges with blood, and breathing and heart rate increase.

During phase three, or orgasm, rhythmic, involuntary contractions of muscles occur in both sexes. In the male, the reproductive accessory glands and tubules constrict placing semen in the urethra, then the urethra contracts expelling the semen through the penis. In women, the uterus and vaginal muscles contract in waves that may last slightly less than a second each. During phase four, or resolution, the processes described in the first three phases reverse themselves and return to their normal state. Men experience a refractory period in which they cannot maintain an erection or ejaculate for a period of time ranging from minutes to hours.

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19.9: Gametogenesis

Gametogenesis, the production of sperm and eggs, takes place through the process of meiosis. During meiosis, two cell divisions separate the paired chromosomes in the nucleus and then separate the chromatids that were made during an earlier stage of the cell's life cycle. Meiosis produces haploid cells with half of each pair of chromosomes normally found in diploid cells. The production of sperm is called **spermatogenesis** and the production of eggs is called **oogenesis**.

Spermatogenesis

Spermatogenesis, illustrated in Figure 1, occurs in the wall of the seminiferous tubules, with stem cells at the periphery of the tube and the spermatozoa at the lumen of the tube. Immediately under the capsule of the tubule are diploid, undifferentiated cells. These stem cells, called spermatogonia (singular: spermatagonium), go through mitosis with one offspring going on to differentiate into a sperm cell and the other giving rise to the next generation of sperm.

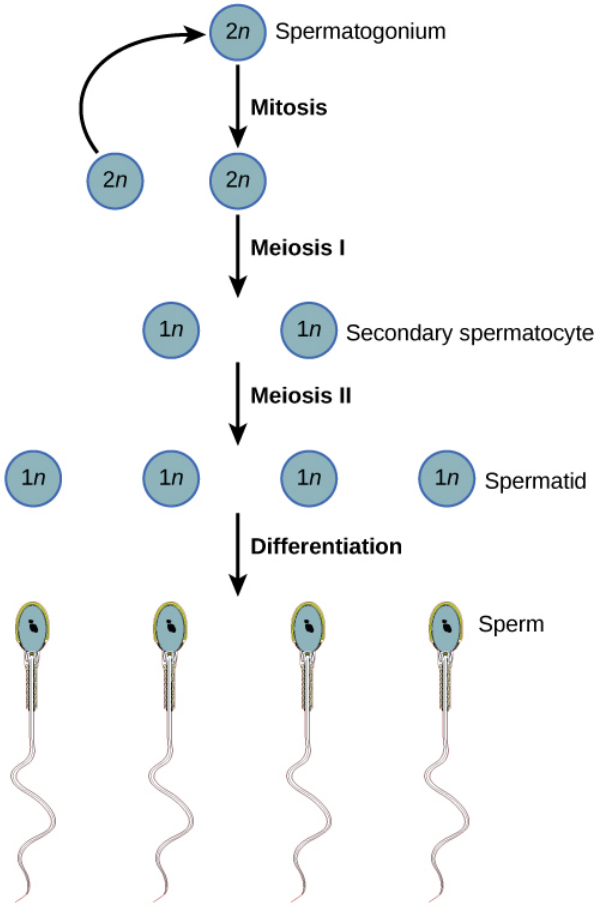


Figure 1. During spermatogenesis, four sperm result from each primary spermatocyte.

Meiosis starts with a cell called a primary spermatocyte. At the end of the first meiotic division, a haploid cell is produced called a secondary spermatocyte. This cell is haploid and must go through another meiotic cell division. The cell produced at the end of meiosis is called a spermatid and when it reaches the lumen of the tubule and grows a flagellum, it is called a sperm cell. Four sperm result from each primary spermatocyte that goes through meiosis.

Stem cells are deposited during gestation and are present at birth through the beginning of adolescence, but in an inactive state. During adolescence, gonadotropic hormones from the anterior pituitary cause the activation of these cells and the production of viable sperm. This continues into old age.

Visit this site to see the process of spermatogenesis.

Oogenesis

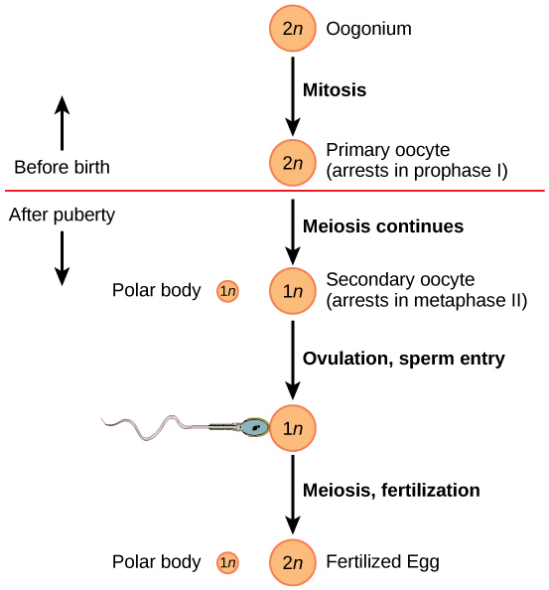


Figure 2. The process of oogenesis occurs in the ovary's outermost layer.

Oogenesis, illustrated in Figure 2, occurs in the outermost layers of the ovaries. As with sperm production, oogenesis starts with a germ cell, called an oogonium (plural: oogonia), but this cell undergoes mitosis to increase in number, eventually resulting in up to about one to two million cells in the embryo.

The cell starting meiosis is called a primary oocyte, as shown in Figure 2. This cell will start the first meiotic division and be arrested in its progress in the first prophase stage. At the time of birth, all future eggs are in the prophase stage. At adolescence, anterior pituitary hormones cause the development of a number of follicles in an ovary. This results in the primary oocyte finishing the first meiotic division. The cell divides unequally, with most of the cellular material and organelles going to one cell, called a secondary oocyte, and only one set of chromosomes and a small amount of cytoplasm going to the other cell. This second cell is called a polar body and usually dies. A secondary meiotic arrest occurs, this time at the metaphase II stage. At ovulation, this secondary oocyte will be released and travel toward the uterus through the oviduct. If the secondary oocyte is fertilized, the cell continues through the meiosis II, producing a second polar body and a fertilized egg containing all 46 chromosomes of a human being, half of them coming from the sperm.

Egg production begins before birth, is arrested during meiosis until puberty, and then individual cells continue through at each menstrual cycle. One egg is produced from each meiotic process, with the extra chromosomes and chromatids going into polar bodies that degenerate and are reabsorbed by the body.

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19.10: Introduction to Hormonal Control of Human Reproduction

Describe the roles of male and female reproductive hormones

The human male and female reproductive cycles are controlled by the interaction of hormones from the hypothalamus and anterior pituitary with hormones from reproductive tissues and organs. In both sexes, the hypothalamus monitors and causes the release of hormones from the pituitary gland. When the reproductive hormone is required, the hypothalamus sends a **gonadotropin-releasing hormone (GnRH)** to the anterior pituitary. This causes the release of **follicle stimulating hormone (FSH)** and **luteinizing hormone (LH)** from the anterior pituitary into the blood. Note that the body must reach puberty in order for the adrenals to release the hormones that must be present for GnRH to be produced. Although FSH and LH are named after their functions in female reproduction, they are produced in both sexes and play important roles in controlling reproduction. Other hormones have specific functions in the male and female reproductive systems.

What You'll Learn to Do

- Describe the roles of male reproductive hormones
- Describe the roles of female reproductive hormones
- Discuss the interplay of the ovarian and menstrual cycles, and how both end at menopause

Learning Activities

The learning activities for this section include the following:

- Reproductive Hormones
- The Ovarian Cycle, the Menstrual Cycle, and Menopause
- Self Check: Hormonal Control of Human Reproduction

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19.11: Reproductive Hormones

Male Hormones

At the onset of puberty, the hypothalamus causes the release of FSH and LH into the male system for the first time. FSH enters the testes and stimulates the **Sertoli cells** to begin facilitating spermatogenesis using negative feedback, as illustrated in Figure 1. LH also enters the testes and stimulates the **interstitial cells of Leydig** to make and release testosterone into the testes and the blood.

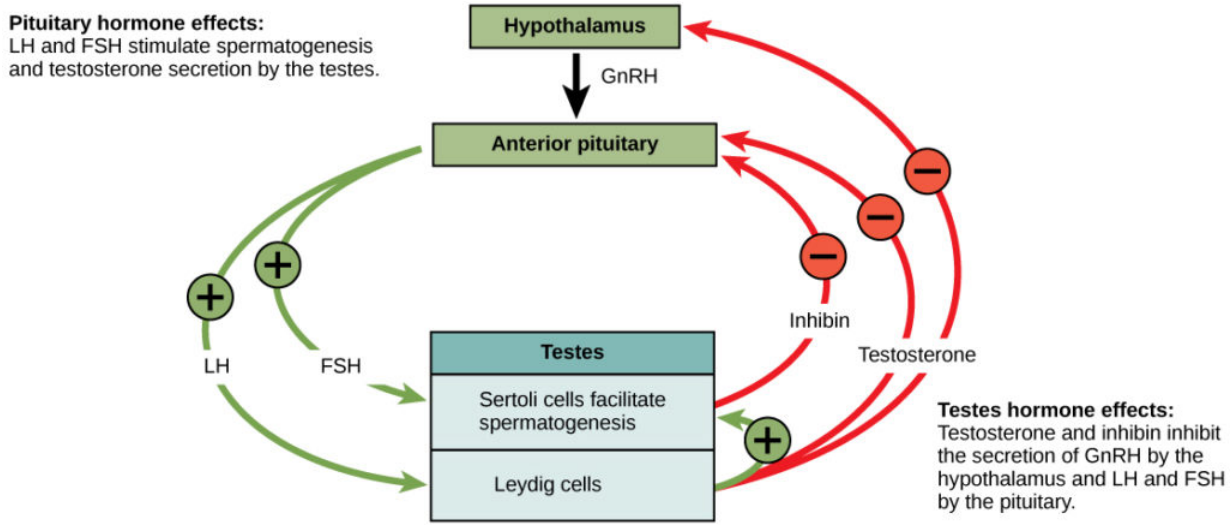


Figure 1. Hormones control sperm production in a negative feedback system.

Testosterone, the hormone responsible for the secondary sexual characteristics that develop in the male during adolescence, stimulates spermatogenesis. These secondary sex characteristics include a deepening of the voice, the growth of facial, axillary, and pubic hair, and the beginnings of the sex drive.

A negative feedback system occurs in the male with rising levels of testosterone acting on the hypothalamus and anterior pituitary to inhibit the release of GnRH, FSH, and LH. The Sertoli cells produce the hormone **inhibin**, which is released into the blood when the sperm count is too high. This inhibits the release of GnRH and FSH, which will cause spermatogenesis to slow down. If the sperm count reaches 20 million/ml, the Sertoli cells cease the release of inhibin, and the sperm count increases.

Female Hormones

The control of reproduction in females is more complex. As with the male, the anterior pituitary hormones cause the release of the hormones FSH and LH. In addition, estrogens and progesterone are released from the developing follicles. **Estrogen** is the reproductive hormone in females that assists in endometrial regrowth, ovulation, and calcium absorption; it is also responsible for the secondary sexual characteristics of females. These include breast development, flaring of the hips, and a shorter period necessary for bone maturation. **Progesterone** assists in endometrial re-growth and inhibition of FSH and LH release.

In females, FSH stimulates development of egg cells, called ova, which develop in structures called follicles. Follicle cells produce the hormone inhibin, which inhibits FSH production. LH also plays a role in the development of ova, induction of ovulation, and stimulation of estradiol and progesterone production by the ovaries. Estradiol and progesterone are steroid hormones that prepare the body for pregnancy. Estradiol produces secondary sex characteristics in females, while both estradiol and progesterone regulate the menstrual cycle.

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19.12: The Ovarian Cycle, the Menstrual Cycle, and Menopause

The Ovarian Cycle and the Menstrual Cycle

The **ovarian cycle** governs the preparation of endocrine tissues and release of eggs, while the **menstrual cycle** governs the preparation and maintenance of the uterine lining. These cycles occur concurrently and are coordinated over a 22–32 day cycle, with an average length of 28 days.

The first half of the ovarian cycle is the follicular phase shown in Figure 1. Slowly rising levels of FSH and LH cause the growth of follicles on the surface of the ovary. This process prepares the egg for ovulation. As the follicles grow, they begin releasing estrogens and a low level of progesterone. Progesterone maintains the endometrium to help ensure pregnancy. The trip through the fallopian tube takes about seven days. At this stage of development, called the morula, there are 30-60 cells. If pregnancy implantation does not occur, the lining is sloughed off. After about five days, estrogen levels rise and the menstrual cycle enters the proliferative phase. The endometrium begins to regrow, replacing the blood vessels and glands that deteriorated during the end of the last cycle.

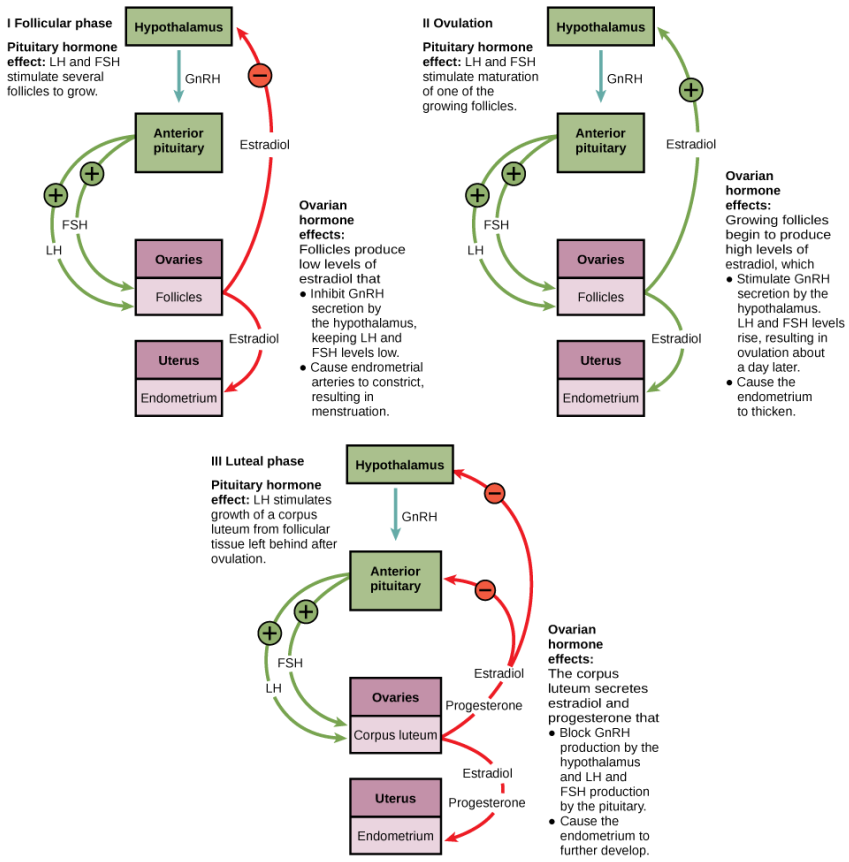


Figure 1. Click for a larger image. The ovarian and menstrual cycles of female reproduction are regulated by hormones produced by the hypothalamus, pituitary, and ovaries.

? Practice Question

Which of the following statements about hormone regulation of the female reproductive cycle is false?

a. LH and FSH are produced in the pituitary, and estradiol and progesterone are produced in the ovaries.
b. Estradiol and progesterone secreted from the corpus luteum cause the endometrium to thicken.
c. Both progesterone and estradiol are produced by the follicles.
d. Secretion of GnRH by the hypothalamus is inhibited by low levels of estradiol but stimulated by high levels of estradiol.

[reveal-answer q="87184"]Show Answer[/reveal-answer]
[hidden-answer a="87184"]Statement c is false.[/hidden-answer]



Figure 2. This mature egg follicle may rupture and release an egg. (credit: scale-bar data from Matt Russell)

Just prior to the middle of the cycle (approximately day 14), the high level of estrogen causes FSH and especially LH to rise rapidly, then fall. The spike in LH causes **ovulation**: the most mature follicle, like that shown in Figure 2, ruptures and releases its egg. The follicles that did not rupture degenerate and their eggs are lost. The level of estrogen decreases when the extra follicles degenerate.

Following ovulation, the ovarian cycle enters its luteal phase, illustrated in Figure 1 and the menstrual cycle enters its secretory phase, both of which run from about day 15 to 28. The luteal and secretory phases refer to changes in the ruptured follicle. The cells in the follicle undergo physical changes and produce a structure called a corpus luteum. The corpus luteum produces estrogen and progesterone. The progesterone facilitates the regrowth of the uterine lining and inhibits the release of further FSH and LH. The uterus is being prepared to accept a fertilized egg, should it occur during this cycle. The inhibition of FSH and LH prevents any further eggs and follicles from developing, while the progesterone is elevated. The level of estrogen produced by the corpus luteum increases to a steady level for the next few days.

If no fertilized egg is implanted into the uterus, the corpus luteum degenerates and the levels of estrogen and progesterone decrease. The endometrium begins to degenerate as the progesterone levels drop, initiating the next menstrual cycle. The decrease in progesterone also allows the hypothalamus to send GnRH to the anterior pituitary, releasing FSH and LH and starting the cycles again. Figure 3 visually compares the ovarian and uterine cycles as well as the commensurate hormone levels.

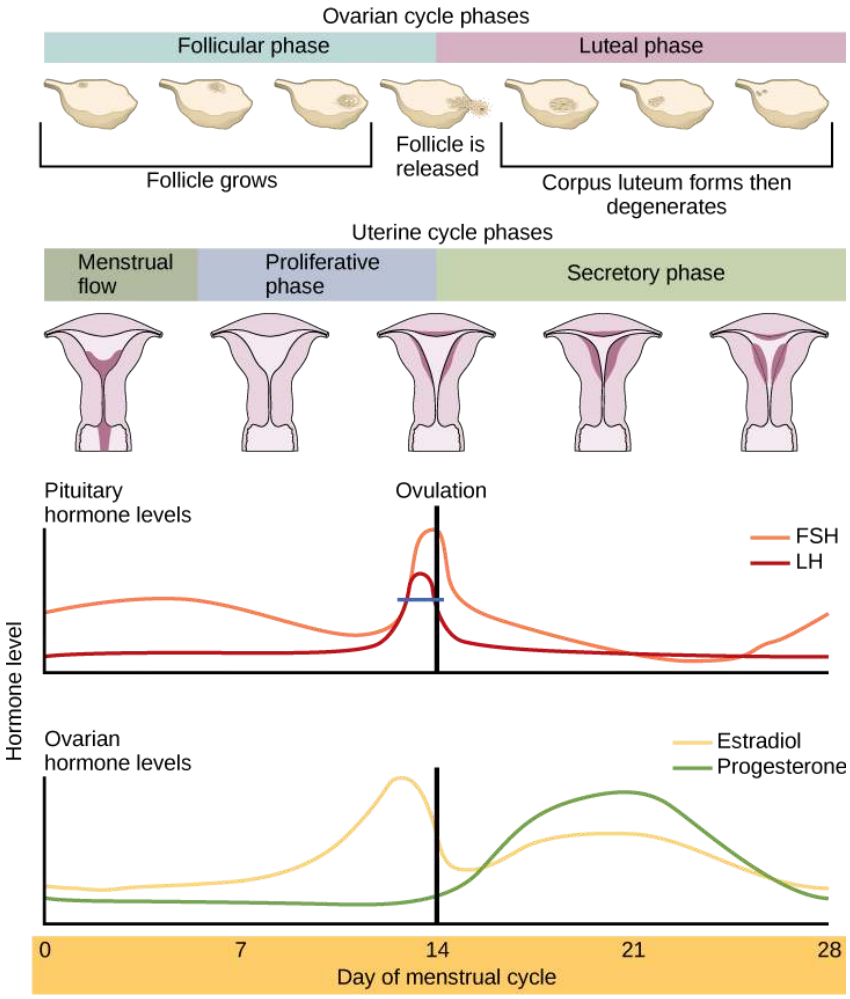


Figure 3. Rising and falling hormone levels result in progression of the ovarian and menstrual cycles. (credit: modification of work by Mikael Häggström)

? Practice Question

Which of the following statements about the menstrual cycle is false?

a. Progesterone levels rise during the luteal phase of the ovarian cycle and the secretory phase of the uterine cycle.
b. Menstruation occurs just after LH and FSH levels peak.
c. Menstruation occurs after progesterone levels drop.
d. Estrogen levels rise before ovulation, while progesterone levels rise after.

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[hidden-answer a="94688"]Statement b is false.[/hidden-answer]

Menopause

As women approach their mid-40s to mid-50s, their ovaries begin to lose their sensitivity to FSH and LH. Menstrual periods become less frequent and finally cease; this is **menopause**. There are still eggs and potential follicles on the ovaries, but without the stimulation of FSH and LH, they will not produce a viable egg to be released. The outcome of this is the inability to have children.

The side effects of menopause include hot flashes, heavy sweating (especially at night), headaches, some hair loss, muscle pain, vaginal dryness, insomnia, depression, weight gain, and mood swings. Estrogen is involved in calcium metabolism and, without it, blood levels of calcium decrease. To replenish the blood, calcium is lost from bone which may decrease the bone density and lead

to osteoporosis. Supplementation of estrogen in the form of hormone replacement therapy (HRT) can prevent bone loss, but the therapy can have negative side effects. While HRT is thought to give some protection from colon cancer, osteoporosis, heart disease, macular degeneration, and possibly depression, its negative side effects include increased risk of: stroke or heart attack, blood clots, breast cancer, ovarian cancer, endometrial cancer, gall bladder disease, and possibly dementia.

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19.13: Introduction to Fertilization

Discuss internal and external methods of fertilization

Sexual reproduction starts with the combination of a sperm and an egg in a process called fertilization. This can occur either outside the bodies or inside the female. Both methods have advantages and disadvantages. Once fertilized, the eggs can develop inside the female or outside. If the egg develops outside the body, it usually has a protective covering over it. Animal anatomy evolved various ways to fertilize, hold, or expel the egg. The method of fertilization varies among animals. Some species release the egg and sperm into the environment, some species retain the egg and receive the sperm into the female body and then expel the developing embryo covered with shell, while still other species retain the developing offspring through the gestation period.

What You'll Learn to Do

- Define the term fertilization
- Discuss external methods of fertilization
- Discuss internal methods of fertilization
- Describe the anatomical adaptations that occurred in animals to facilitate reproduction

Learning Activities

The learning activities for this section include the following:

- Fertilization
- External and Internal Fertilization
- The Evolution of Reproduction
- Self Check: Fertilization

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19.14: Fertilization

Sexual reproduction starts with the combination of a sperm and an egg in a process called fertilization. This can occur either inside (**internal fertilization**) or outside (**external fertilization**) the body of the female. Humans provide an example of the former whereas seahorse reproduction is an example of the latter.

Fertilization, pictured in Figure 1a is the process in which gametes (an egg and sperm) fuse to form a zygote. The egg and sperm each contain one set of chromosomes. To ensure that the offspring has only one complete diploid set of chromosomes, only one sperm must fuse with one egg. In mammals, the egg is protected by a layer of extracellular matrix consisting mainly of glycoproteins called the **zona pellucida**. When a sperm binds to the zona pellucida, a series of biochemical events, called the **acrosomal reactions**, take place. In placental mammals, the acrosome contains digestive enzymes that initiate the degradation of the glycoprotein matrix protecting the egg and allowing the sperm plasma membrane to fuse with the egg plasma membrane, as illustrated in Figure 1b. The fusion of these two membranes creates an opening through which the sperm nucleus is transferred into the ovum. The nuclear membranes of the egg and sperm break down and the two haploid genomes condense to form a diploid genome.

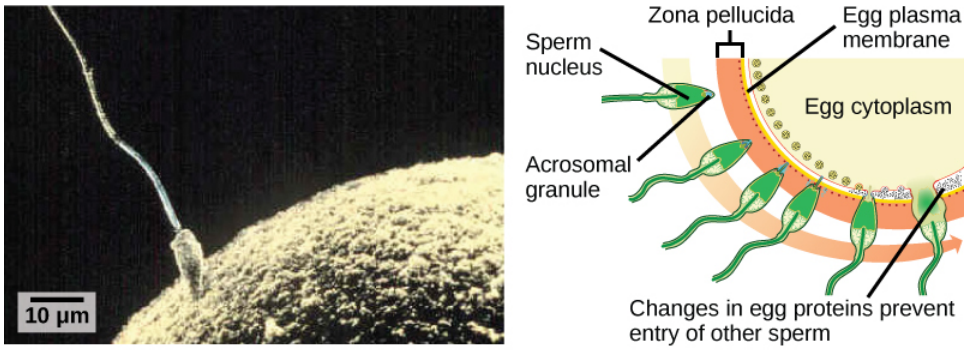


Figure 1. (a) Fertilization is the process in which sperm and egg fuse to form a zygote. (b) Acrosomal reactions help the sperm degrade the glycoprotein matrix protecting the egg and allow the sperm to transfer its nucleus. (credit: (b) modification of work by Mariana Ruiz Villareal; scale-bar data from Matt Russell)

To ensure that no more than one sperm fertilizes the egg, once the acrosomal reactions take place at one location of the egg membrane, the egg releases proteins in other locations to prevent other sperm from fusing with the egg. If this mechanism fails, multiple sperm can fuse with the egg, resulting in **polyspermy**. The resulting embryo is not genetically viable and dies within a few days.

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19.15: External and Internal Fertilization

External Fertilization

External fertilization usually occurs in aquatic environments where both eggs and sperm are released into the water. After the sperm reaches the egg, fertilization takes place. Most external fertilization happens during the process of spawning where one or several females release their eggs and the male(s) release sperm in the same area, at the same time. The release of the reproductive material may be triggered by water temperature or the length of daylight. Nearly all fish spawn, as do crustaceans (such as crabs and shrimp), mollusks (such as oysters), squid, and echinoderms (such as sea urchins and sea cucumbers). Figure 1a shows salmon spawning in a shallow stream. Frogs, like those shown in Figure 1b, corals, mayflies, and mosquitoes also spawn.



Figure 1. (a) Salmon reproduce through spawning. (b) During sexual reproduction in toads, the male grasps the female from behind and externally fertilizes the eggs as they are deposited. (credit a: Dan Bennett; credit b: “OakleyOriginals”/Flickr)

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

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

Internal Fertilization

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

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

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

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

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19.16: The Evolution of Reproduction

Once multicellular organisms evolved and developed specialized cells, some also developed tissues and organs with specialized functions. An early development in reproduction occurred in the Annelids. These organisms produce sperm and eggs from undifferentiated cells in their coelom and store them in that cavity. When the coelom becomes filled, the cells are released through an excretory opening or by the body splitting open. Reproductive organs evolved with the development of gonads that produce sperm and eggs. These cells went through meiosis, an adaption of mitosis, which reduced the number of chromosomes in each reproductive cell by half, while increasing the number of cells through cell division.

Complete reproductive systems were developed in insects, with separate sexes. Sperm are made in testes and then travel through coiled tubes to the epididymis for storage. Eggs mature in the ovary. When they are released from the ovary, they travel to the uterine tubes for fertilization. Some insects have a specialized sac, called a **spermatheca**, which stores sperm for later use, sometimes up to a year. Fertilization can be timed with environmental or food conditions that are optimal for offspring survival.

Vertebrates have similar structures, with a few differences. Non-mammals, such as birds and reptiles, have a common body opening, called a **cloaca**, for the digestive, excretory and reproductive systems. Coupling between birds usually involves positioning the cloaca openings opposite each other for transfer of sperm. Mammals have separate openings for the systems in the female and a uterus for support of developing offspring. The uterus has two chambers in species that produce large numbers of offspring at a time, while species that produce one offspring, such as primates, have a single uterus.

Sperm transfer from the male to the female during reproduction ranges from releasing the sperm into the watery environment for external fertilization, to the joining of cloaca in birds, to the development of a penis for direct delivery into the female's vagina in mammals.

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19.17: Introduction to Early Embryonic Development

Explain how the embryo forms from the zygote

After an egg is fertilized, and has fused with sperm to form a zygote, an embryo begins to develop. The process in which an organism develops from a single-celled zygote to a multi-cellular organism is complex and well-regulated. The early stages of embryonic development are also crucial for ensuring the fitness of the organism.

What You'll Learn to Do

- Discuss the role of cleavage in animal development
- Discuss the role of gastrulation in animal development
- Describe the process of organogenesis
- Identify the anatomical axes formed in vertebrates

Learning Activities

The learning activities for this section include the following:

- Cleavage and Blastula Stage
- Gastrulation
- Organogenesis
- Vertebrate Formation
- Self Check: Early Embryonic Development

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19.18: Cleavage and Blastula Stage

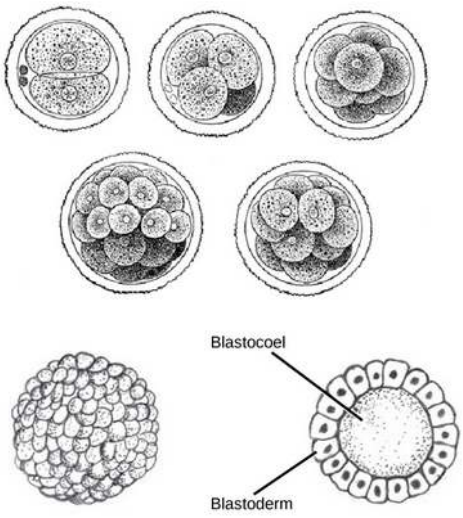


Figure 1. (a) During cleavage, the zygote rapidly divides into multiple cells without increasing in size. (b) The cells rearrange themselves to form a hollow ball with a fluid-filled or yolk-filled cavity called the blastula. (credit a: modification of work by Gray's Anatomy; credit b: modification of work by Pearson Scott Foresman, donated to the Wikimedia Foundation)

The development of multi-cellular organisms begins from a single-celled zygote, which undergoes rapid cell division to form the blastula. The rapid, multiple rounds of cell division are termed cleavage. Cleavage is illustrated in (Figure 1a). After the cleavage has produced over 100 cells, the embryo is called a blastula. The blastula is usually a spherical layer of cells (the blastoderm) surrounding a fluid-filled or yolk-filled cavity (the blastocoel). Mammals at this stage form a structure called the blastocyst, characterized by an inner cell mass that is distinct from the surrounding blastula, shown in Figure 1b. During cleavage, the cells divide without an increase in mass; that is, one large single-celled zygote divides into multiple smaller cells. Each cell within the blastula is called a blastomere.

Cleavage can take place in two ways: **holoblastic** (total) cleavage or **meroblastic** (partial) cleavage. The type of cleavage depends on the amount of yolk in the eggs. In placental mammals (including humans) where nourishment is provided by the mother's body, the eggs have a very small amount of yolk and undergo holoblastic cleavage. Other species, such as birds, with a lot of yolk in the egg to nourish the embryo during development, undergo meroblastic cleavage.

In mammals, the blastula forms the **blastocyst** in the next stage of development. Here the cells in the blastula arrange themselves in two layers: the **inner cell mass**, and an outer layer called the **trophoblast**. The inner cell mass is also known as the embryoblast and this mass of cells will go on to form the embryo.

At this stage of development, illustrated in Figure 2 the inner cell mass consists of embryonic stem cells that will differentiate into the different cell types needed by the organism. The trophoblast will contribute to the placenta and nourish the embryo.

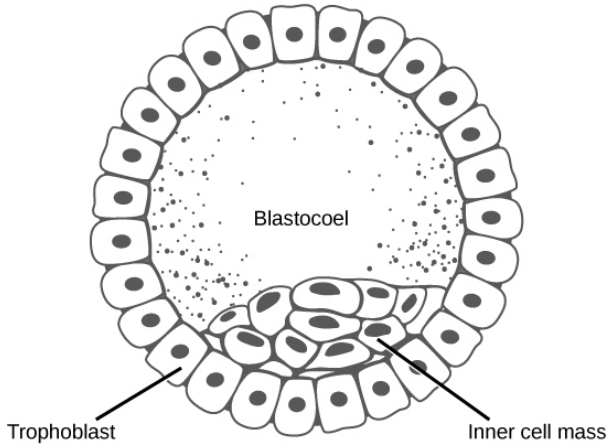


Figure 2. The rearrangement of the cells in the mammalian blastula to two layers—the inner cell mass and the trophoblast—results in the formation of the blastocyst.

Visit the Virtual Human Embryo project at the Endowment for Human Development site to step through an interactive that shows the stages of embryo development, including micrographs and rotating 3-D images.

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19.19: Gastrulation

The typical blastula is a ball of cells. The next stage in embryonic development is the formation of the body plan. The cells in the blastula rearrange themselves spatially to form three layers of cells. This process is called **gastrulation**. During gastrulation, the blastula folds upon itself to form the three layers of cells. Each of these layers is called a germ layer and each germ layer differentiates into different organ systems.

The three germs layers, shown in Figure 1, are the endoderm, the ectoderm, and the mesoderm. The ectoderm gives rise to the nervous system and the epidermis. The mesoderm gives rise to the muscle cells and connective tissue in the body. The endoderm gives rise to columnar cells found in the digestive system and many internal organs.

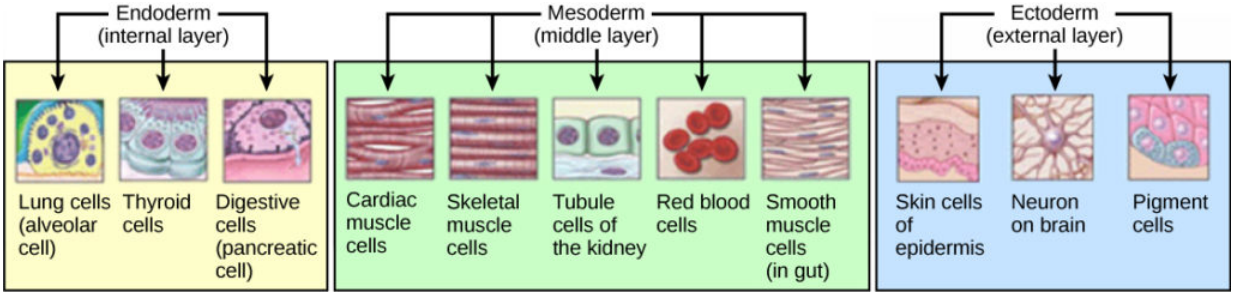


Figure 1. The three germ layers give rise to different cell types in the animal body. (credit: modification of work by NIH, NCBI)

Are Designer Babies in Our Future?

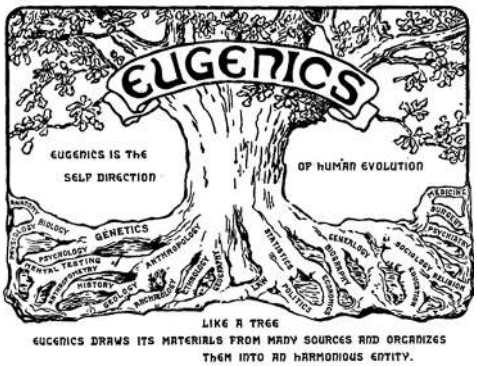


Figure 2. This logo from the Second International Eugenics Conference in New York City in September of 1921 shows how eugenics attempted to merge several fields of study with the goal of producing a genetically superior human race.

If you could prevent your child from getting a devastating genetic disease, would you do it? Would you select the sex of your child or select for their attractiveness, strength, or intelligence? How far would you go to maximize the possibility of resistance to disease? The genetic engineering of a human child, the production of “designer babies” with desirable phenotypic characteristics, was once a topic restricted to science fiction. This is the case no longer: science fiction is now overlapping into science fact. Many phenotypic choices for offspring are already available, with many more likely to be possible in the not too distant future. Which traits should be selected and how they should be selected are topics of much debate within the worldwide medical community. The ethical and moral line is not always clear or agreed upon, and some fear that modern reproductive technologies could lead to a new form of eugenics.

Eugenics is the use of information and technology from a variety of sources to improve the genetic makeup of the human race. The goal of creating genetically superior humans was quite prevalent (although controversial) in several countries during the early 20th century, but fell into disrepute when Nazi Germany developed an extensive eugenics program in the 1930’s and 40’s. As part of their program, the Nazis forcibly sterilized hundreds of thousands of the so-called “unfit” and killed tens of thousands of institutionally disabled people as part of a systematic program to develop a genetically superior race of Germans known as Aryans. Ever since, eugenic ideas have not been as publicly expressed, but there are still those who promote them.

Efforts have been made in the past to control traits in human children using donated sperm from men with desired traits. In fact, eugenicist Robert Klark Graham established a sperm bank in 1980 that included samples exclusively from donors with high IQs.

The “genius” sperm bank failed to capture the public’s imagination and the operation closed in 1999.

In more recent times, the procedure known as prenatal genetic diagnosis (PGD) has been developed. PGD involves the screening of human embryos as part of the process of *in vitro* fertilization, during which embryos are conceived and grown outside the mother’s body for some period of time before they are implanted. The term PGD usually refers to both the diagnosis, selection, and the implantation of the selected embryos.

In the least controversial use of PGD, embryos are tested for the presence of alleles which cause genetic diseases such as sickle cell disease, muscular dystrophy, and hemophilia, in which a single disease-causing allele or pair of alleles has been identified. By excluding embryos containing these alleles from implantation into the mother, the disease is prevented, and the unused embryos are either donated to science or discarded. There are relatively few in the worldwide medical community that question the ethics of this type of procedure, which allows individuals scared to have children because of the alleles they carry to do so successfully. The major limitation to this procedure is its expense. Not usually covered by medical insurance and thus out of reach financially for most couples, only a very small percentage of all live births use such complicated methodologies. Yet, even in cases like these where the ethical issues may seem to be clear-cut, not everyone agrees with the morality of these types of procedures. For example, to those who take the position that human life begins at conception, the discarding of unused embryos, a necessary result of PGD, is unacceptable under any circumstances.

A murkier ethical situation is found in the selection of a child’s sex, which is easily performed by PGD. Currently, countries such as Great Britain have banned the selection of a child’s sex for reasons other than preventing sex-linked diseases. Other countries allow the procedure for “family balancing”, based on the desire of some parents to have at least one child of each sex. Still others, including the United States, have taken a scattershot approach to regulating these practices, essentially leaving it to the individual practicing physician to decide which practices are acceptable and which are not.

Even murkier are rare instances of disabled parents, such as those with deafness or dwarfism, who select embryos via PGD to ensure that they share their disability. These parents usually cite many positive aspects of their disabilities and associated culture as reasons for their choice, which they see as their moral right. To others, to purposely cause a disability in a child violates the basic medical principle of *Primum non nocere*, “first, do no harm.” This procedure, although not illegal in most countries, demonstrates the complexity of ethical issues associated with choosing genetic traits in offspring.

Where could this process lead? Will this technology become more affordable and how should it be used? With the ability of technology to progress rapidly and unpredictably, a lack of definitive guidelines for the use of reproductive technologies before they arise might make it difficult for legislators to keep pace once they are in fact realized, assuming the process needs any government regulation at all. Other bioethicists argue that we should only deal with technologies that exist now, and not in some uncertain future. They argue that these types of procedures will always be expensive and rare, so the fears of eugenics and “master” races are unfounded and overstated. The debate continues.

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19.20: Organogenesis

Organs form from the germ layers through the process of differentiation. During differentiation, the embryonic stem cells express specific sets of genes which will determine their ultimate cell type. For example, some cells in the ectoderm will express the genes specific to skin cells. As a result, these cells will differentiate into epidermal cells. The process of differentiation is regulated by cellular signaling cascades.

Scientists study organogenesis extensively in the lab in fruit flies (*Drosophila*) and the nematode *Caenorhabditis elegans*. *Drosophila* have segments along their bodies, and the patterning associated with the segment formation has allowed scientists to study which genes play important roles in organogenesis along the length of the embryo at different time points. The nematode *C.elegans* has roughly 1000 somatic cells and scientists have studied the fate of each of these cells during their development in the nematode life cycle. There is little variation in patterns of cell lineage between individuals, unlike in mammals where cell development from the embryo is dependent on cellular cues.

In vertebrates, one of the primary steps during organogenesis is the formation of the neural system. The ectoderm forms epithelial cells and tissues, and neuronal tissues. During the formation of the neural system, special signaling molecules called growth factors signal some cells at the edge of the ectoderm to become epidermis cells. The remaining cells in the center form the neural plate. If the signaling by growth factors were disrupted, then the entire ectoderm would differentiate into neural tissue.

The neural plate undergoes a series of cell movements where it rolls up and forms a tube called the **neural tube**, as illustrated in Figure 1. In further development, the neural tube will give rise to the brain and the spinal cord.

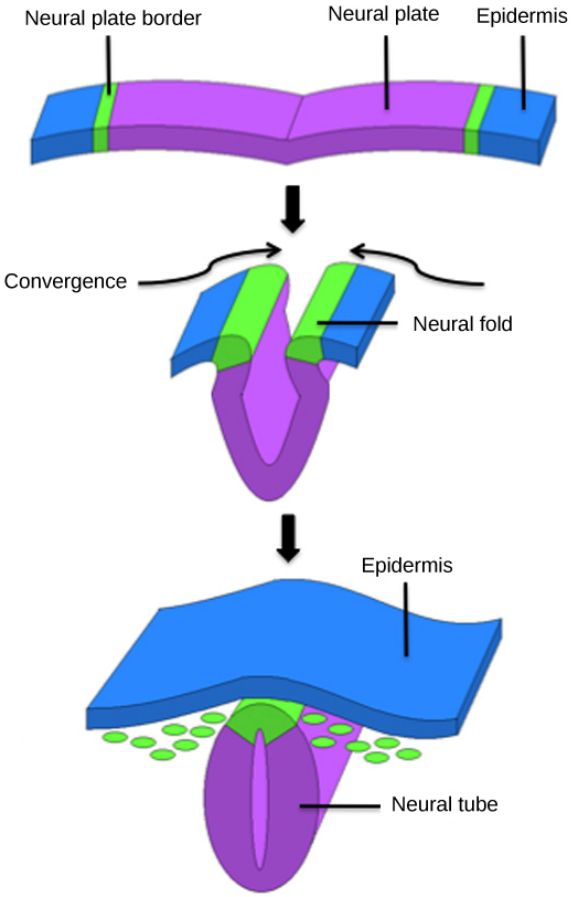


Figure 1. The central region of the ectoderm forms the neural tube, which gives rise to the brain and the spinal cord.

The mesoderm that lies on either side of the vertebrate neural tube will develop into the various connective tissues of the animal body. A spatial pattern of gene expression reorganizes the mesoderm into groups of cells called **somites** with spaces between them. The somites, illustrated in Figure 2 will further develop into the ribs, lungs, and segmental (spine) muscle. The mesoderm also forms a structure called the notochord, which is rod-shaped and forms the central axis of the animal body.



Figure 2. In this five-week old human embryo, somites are segments along the length of the body. (credit: modification of work by Ed Uthman)

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19.21: Vertebrate Axis Formation

Even as the germ layers form, the ball of cells still retains its spherical shape. However, animal bodies have lateral-medial (left-right), dorsal-ventral (back-belly), and anterior-posterior (head-feet) axes, illustrated in Figure 1.

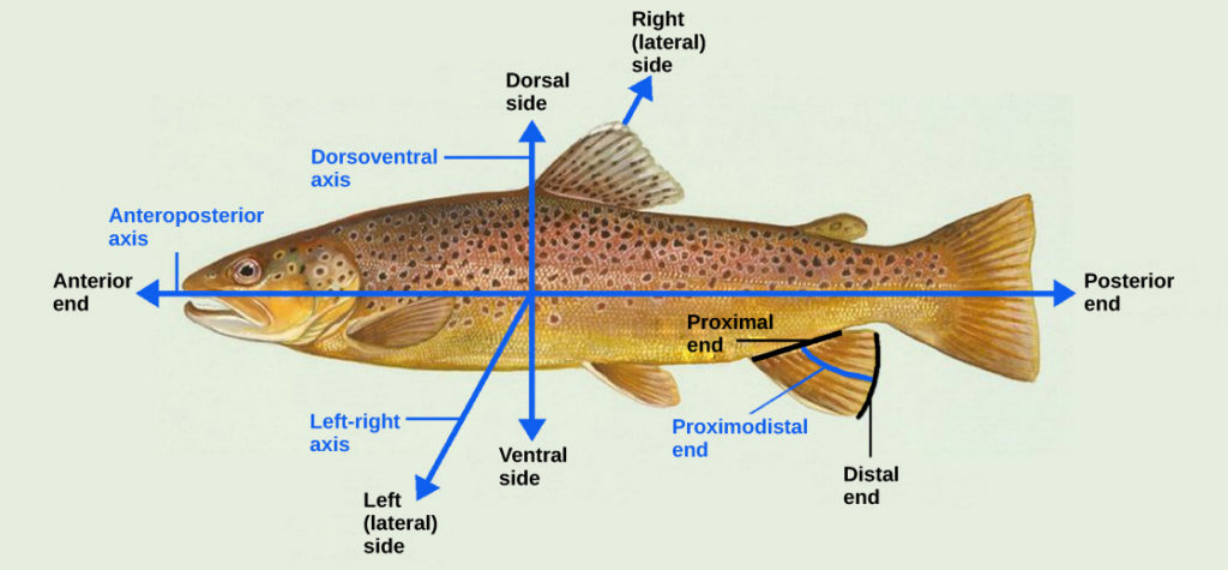


Figure 1. Animal bodies have three axes for symmetry. (credit: modification of work by NOAA)

How are these established? In one of the most seminal experiments ever to be carried out in developmental biology, Spemann and Mangold took dorsal cells from one embryo and transplanted them into the belly region of another embryo. They found that the transplanted embryo now had two notochords: one at the dorsal site from the original cells and another at the transplanted site. This suggested that the dorsal cells were genetically programmed to form the notochord and define the axis. Since then, researchers have identified many genes that are responsible for axis formation. Mutations in these genes leads to the loss of symmetry required for organism development.

Animal bodies have externally visible symmetry. However, the internal organs are not symmetric. For example, the heart is on the left side and the liver on the right. The formation of the central left-right axis is an important process during development. This internal asymmetry is established very early during development and involves many genes. Research is still ongoing to fully understand the developmental implications of these genes.

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19.22: Introduction to Human Pregnancy and Birth

Explain fetal development during the three trimesters of gestation

Pregnancy begins with the fertilization of an egg and continues through to the birth of the individual. The length of time of gestation varies among animals, but is very similar among the great apes: human gestation is 266 days, while chimpanzee gestation is 237 days, a gorilla's is 257 days, and orangutan gestation is 260 days long. The fox has a 57-day gestation. Dogs and cats have similar gestations averaging 60 days. The longest gestation for a land mammal is an African elephant at 640 days. The longest gestations among marine mammals are the beluga and sperm whales at 460 days.

What You'll Learn to Do

- Explain fetal development during the three trimesters of gestation
- Describe labor and delivery
- Compare the efficacy and duration of various types of contraception
- Discuss causes of infertility and the therapeutic options available

Learning Activities

The learning activities for this section include the following:

- Human Gestation
- Labor and Birth
- Contraception and Birth Control
- Infertility
- Self Check: Human Pregnancy and Birth

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19.23: Human Gestation

Twenty-four hours before fertilization, the egg has finished meiosis and becomes a mature oocyte. When fertilized (at conception) the egg becomes known as a zygote. The zygote travels through the oviduct to the uterus (Figure 1). The developing embryo must implant into the wall of the uterus within seven days, or it will deteriorate and die. The outer layers of the zygote (blastocyst) grow into the endometrium by digesting the endometrial cells, and wound healing of the endometrium closes up the blastocyst into the tissue. Another layer of the blastocyst, the chorion, begins releasing a hormone called **human beta chorionic gonadotropin (*β*-HCG)** which makes its way to the corpus luteum and keeps that structure active. This ensures adequate levels of progesterone that will maintain the endometrium of the uterus for the support of the developing embryo. Pregnancy tests determine the level of *β*-HCG in urine or serum. If the hormone is present, the test is positive.

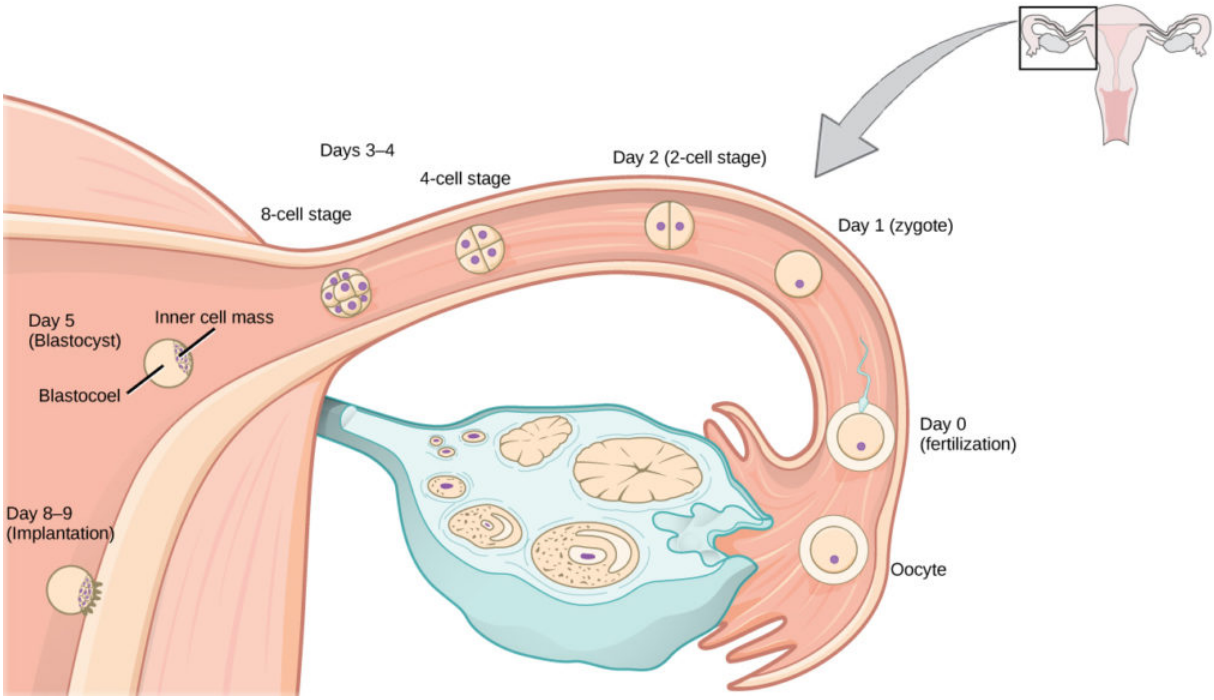


Figure 1. In humans, fertilization occurs soon after the oocyte leaves the ovary. Implantation occurs eight or nine days later.(credit: Ed Uthman)

The gestation period is divided into three equal periods or trimesters. During the first two to four weeks of the first trimester, nutrition and waste are handled by the endometrial lining through diffusion. As the trimester progresses, the outer layer of the embryo begins to merge with the endometrium, and the **placenta** forms. This organ takes over the nutrient and waste requirements of the embryo and fetus, with the mother's blood passing nutrients to the placenta and removing waste from it.



Figure 2. Fetal development is shown at nine weeks gestation. (credit: Ed Uthman)

Chemicals from the fetus, such as bilirubin, are processed by the mother's liver for elimination. Some of the mother's immunoglobulins will pass through the placenta, providing passive immunity against some potential infections.

Internal organs and body structures begin to develop during the first trimester. By five weeks, limb buds, eyes, the heart, and liver have been basically formed. By eight weeks, the term fetus applies, and the body is essentially formed, as shown in Figure 2.

The individual is about five centimeters (two inches) in length and many of the organs, such as the lungs and liver, are not yet functioning. Exposure to any toxins is especially dangerous during the first trimester, as all of the body's organs and structures are going through initial development. Anything that affects that development can have a severe effect on the fetus' survival.



Figure 3. This fetus is just entering the second trimester, when the placenta takes over more of the functions performed as the baby develops. (credit: National Museum of Health and Medicine)

During the second trimester, the fetus grows to about 30 cm (12 inches), as shown in Figure 3. It becomes active and the mother usually feels the first movements. All organs and structures continue to develop.

The placenta has taken over the functions of nutrition and waste and the production of estrogen and progesterone from the corpus luteum, which has degenerated. The placenta will continue functioning up through the delivery of the baby.

During the third trimester, the fetus grows to 3 to 4 kg (6 ½–8 ½ lbs.) and about 50 cm (19–20 inches) long, as illustrated in Figure 4. This is the period of the most rapid growth during the pregnancy. Organ development continues to birth (and some systems, such as the nervous system and liver, continue to develop after birth).

The mother will be at her most uncomfortable during this trimester. She may urinate frequently due to pressure on the bladder from the fetus. There may also be intestinal blockage and circulatory problems, especially in her legs. Clots may form in her legs due to pressure from the fetus on returning veins as they enter the abdominal cavity.

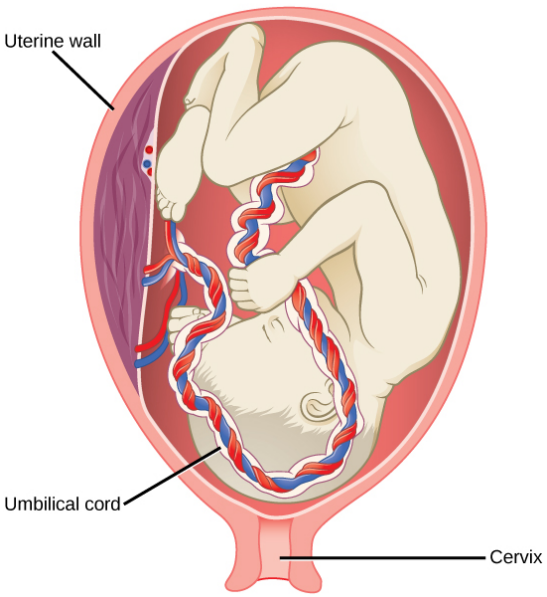


Figure 4. There is rapid fetal growth during the third trimester. (credit: modification of work by Gray's Anatomy)

Visit this site to see the stages of human fetal development.

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19.24: Labor and Birth

Labor is the physical efforts of expulsion of the fetus and the placenta from the uterus during birth (parturition). Toward the end of the third trimester, estrogen causes receptors on the uterine wall to develop and bind the hormone oxytocin. At this time, the baby reorients, facing forward and down with the back or crown of the head engaging the cervix (uterine opening). This causes the cervix to stretch and nerve impulses are sent to the hypothalamus, which signals for the release of oxytocin from the posterior pituitary. The oxytocin causes the smooth muscle in the uterine wall to contract. At the same time, the placenta releases prostaglandins into the uterus, increasing the contractions. A positive feedback relay occurs between the uterus, hypothalamus, and the posterior pituitary to assure an adequate supply of oxytocin. As more smooth muscle cells are recruited, the contractions increase in intensity and force.

There are three stages to labor. During stage one, the cervix thins and dilates. This is necessary for the baby and placenta to be expelled during birth. The cervix will eventually dilate to about 10 cm. During stage two, the baby is expelled from the uterus. The uterus contracts and the mother pushes as she compresses her abdominal muscles to aid the delivery. The last stage is the passage of the placenta after the baby has been born and the organ has completely disengaged from the uterine wall. If labor should stop before stage two is reached, synthetic oxytocin, known as Pitocin, can be administered to restart and maintain labor.

An alternative to labor and delivery is the surgical delivery of the baby through a procedure called a Caesarian section. This is major abdominal surgery and can lead to post-surgical complications for the mother, but in some cases it may be the only way to safely deliver the baby.

The mother’s mammary glands go through changes during the third trimester to prepare for lactation and breastfeeding. When the baby begins suckling at the breast, signals are sent to the hypothalamus causing the release of prolactin from the anterior pituitary. Prolactin causes the mammary glands to produce milk. Oxytocin is also released, promoting the release of the milk. The milk contains nutrients for the baby’s development and growth as well as immunoglobulins to protect the child from bacterial and viral infections.

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19.25: Contraception and Birth Control

The prevention of a pregnancy comes under the terms contraception or birth control. Strictly speaking, **contraception** refers to preventing the sperm and egg from joining. Both terms are, however, frequently used interchangeably.

Table 1. Contraceptive Methods

Method	Examples	Failure Rate in Typical Use Over 12 Months
Barrier	male condom, female condom, sponge, cervical cap, diaphragm, spermicides	15 to 24%
Hormonal	oral, patch, vaginal ring	8%
	injection	3%
	implant	less than 1%
Other	IUD (intrauterine device)	less than 1%
	natural family planning	12 to 25%
	withdrawal	27%
	sterilization	less than 1%

Table 1 lists common methods of contraception. The failure rates listed are not the ideal rates that could be realized, but the typical rates that occur. A failure rate is the number of pregnancies resulting from the method's use over a twelve-month period. Barrier methods, such as condoms, cervical caps, and diaphragms, block sperm from entering the uterus, preventing fertilization. Spermicides are chemicals that are placed in the vagina that kill sperm. Sponges, which are saturated with spermicides, are placed in the vagina at the cervical opening. Combinations of spermicidal chemicals and barrier methods achieve lower failure rates than do the methods when used separately.

Nearly a quarter of the couples using barrier methods, natural family planning, or withdrawal can expect a failure of the method. Natural family planning is based on the monitoring of the menstrual cycle and having intercourse only during times when the egg is not available. A woman's body temperature may rise a degree Celsius at ovulation and the cervical mucus may increase in volume and become more pliable. These changes give a general indication of when intercourse is more or less likely to result in fertilization. Withdrawal involves the removal of the penis from the vagina during intercourse, before ejaculation occurs. This is a risky method with a high failure rate due to the possible presence of sperm in the bulbourethral gland's secretion, which may enter the vagina prior to removing the penis.

Hormonal methods use synthetic progesterone (sometimes in combination with estrogen), to inhibit the hypothalamus from releasing FSH or LH, and thus prevent an egg from being available for fertilization. The method of administering the hormone affects failure rate. The most reliable method, with a failure rate of less than 1 percent, is the implantation of the hormone under the skin. The same rate can be achieved through the sterilization procedures of vasectomy in the man or of tubal ligation in the woman, or by using an intrauterine device (IUD). IUDs are inserted into the uterus and establish an inflammatory condition that prevents fertilized eggs from implanting into the uterine wall.

Compliance with the contraceptive method is a strong contributor to the success or failure rate of any particular method. The only method that is completely effective at preventing conception is abstinence. The choice of contraceptive method depends on the goals of the woman or couple. Tubal ligation and vasectomy are considered permanent prevention, while other methods are reversible and provide short-term contraception.

Termination of an existing pregnancy can be spontaneous or voluntary. Spontaneous termination is a miscarriage and usually occurs very early in the pregnancy, usually within the first few weeks. This occurs when the fetus cannot develop properly and the

gestation is naturally terminated. Voluntary termination of a pregnancy is an abortion. Laws regulating abortion vary between states and tend to view fetal viability as the criteria for allowing or preventing the procedure.

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19.26: Infertility

Infertility is the inability to conceive a child or carry a child to birth. About 75 percent of causes of infertility can be identified; these include diseases, such as sexually transmitted diseases that can cause scarring of the reproductive tubes in either men or women, or developmental problems frequently related to abnormal hormone levels in one of the individuals. Inadequate nutrition, especially starvation, can delay menstruation. Stress can also lead to infertility. Short-term stress can affect hormone levels, while long-term stress can delay puberty and cause less frequent menstrual cycles. Other factors that affect fertility include toxins (such as cadmium), tobacco smoking, marijuana use, gonadal injuries, and aging.

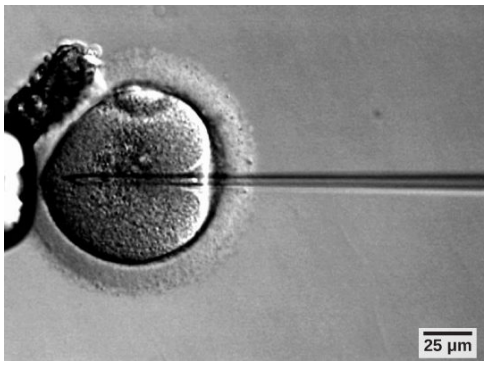


Figure 1. A sperm is inserted into an egg for fertilization during intracytoplasmic sperm injection (ICSI). (credit: scale-bar data from Matt Russell)

If infertility is identified, several assisted reproductive technologies (ART) are available to aid conception. A common type of ART is *in vitro* fertilization (IVF) where an egg and sperm are combined outside the body and then placed in the uterus. Eggs are obtained from the woman after extensive hormonal treatments that prepare mature eggs for fertilization and prepare the uterus for implantation of the fertilized egg. Sperm are obtained from the man and they are combined with the eggs and supported through several cell divisions to ensure viability of the zygotes. When the embryos have reached the eight-cell stage, one or more is implanted into the woman's uterus. If fertilization is not accomplished by simple IVF, a procedure that injects the sperm into an egg can be used. This is called intracytoplasmic sperm injection (ICSI) and is shown in Figure 1. IVF procedures produce a surplus of fertilized eggs and embryos that can be frozen and stored for future use. The procedures can also result in multiple births.

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19.27: Putting It Together- The Reproductive System

Hank lets us in on the meaning of life, at least from a biological perspective—it's reproduction, which answers the essential question of all organisms: how do I make more of myself? So, sex, how does it work?



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Reproductive Endocrinologist

A reproductive endocrinologist is a physician who treats a variety of hormonal disorders related to reproduction and infertility in both men and women. The disorders include menstrual problems, infertility, pregnancy loss, sexual dysfunction, and menopause. Doctors may use fertility drugs, surgery, or assisted reproductive techniques (ART) in their therapy. ART involves the use of procedures to manipulate the egg or sperm to facilitate reproduction, such as *in vitro* fertilization.

Reproductive endocrinologists undergo extensive medical training, first in a four-year residency in obstetrics and gynecology, then in a three-year fellowship in reproductive endocrinology. To be board certified in this area, the physician must pass written and oral exams in both areas.

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19.28: Cerego- The Reproductive System

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for The Reproductive System. You'll need to create a free log-in to practice these items, if you haven't already.

https://cerego.com/sets/796530/learn

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CHAPTER OVERVIEW

20: Module 17- Sensory Systems

20.1: Why It Matters- The Sensory Systems
20.2: Introduction to the Senses
20.3: Human Senses
20.4: Sensation
20.5: Just-Noticeable Difference
20.6: Introduction to Somatosensation
20.7: Somatosensory Receptors
20.8: Thermoreception and Pain
20.9: Introduction to Taste and Smell
20.10: Tastes and Odors
20.11: Tastes
20.12: Smell and Taste in the Brain
20.13: Introduction to Hearing and Vestibular Sensation
20.14: Sound and Reception
20.15: Transduction of Sound
20.16: Vestibular Information
20.17: Introduction to Vision
20.18: Light
20.19: Anatomy of the Eye
20.20: Transduction of Light
20.21: Vision in the Brain
20.22: Putting It Together- The Sensory System
20.23: Cerego- Sensory Systems

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20.1: Why It Matters- The Sensory Systems

Why describe the components and role of the sensory system?



Figure 1. This shark uses its senses of sight, vibration (lateral-line system), and smell to hunt, but it also relies on its ability to sense the electric fields of prey, a sense not present in most land animals. (credit: modification of work by Hermanus Backpackers Hostel, South Africa)

In more advanced animals, the senses are constantly at work, making the animal aware of stimuli—such as light, or sound, or the presence of a chemical substance in the external environment—and monitoring information about the organism's internal environment. All bilaterally symmetric animals have a sensory system, and the development of any species' sensory system has been driven by natural selection; thus, sensory systems differ among species according to the demands of their environments. The shark, unlike most fish predators, is electrosensitive—that is, sensitive to electrical fields produced by other animals in its environment. While it is helpful to this underwater predator, electrosensitivity is a sense not found in most land animals.

Learning Outcomes

- Identify the general and special senses in humans
- Describe how somatosensation, the sense of touch, works
- Explain how taste and smell work together
- Trace the path of sound through the auditory system to the site of transduction of sound
- Trace the path of light through the eye to the point of the optic nerve

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20.2: Introduction to the Senses

Identify the general and special senses in humans

Humans have special senses: olfaction, gustation, equilibrium, and hearing, plus the general senses of somatosensation. Each of these senses allow us to perceive something about the world around us.

What You'll Learn to Do

- Identify the general and special senses in humans
- Describe three important steps in sensation
- Explain the concept of just-noticeable difference in sensory perception

Learning Activities

The learning activities for this section include the following:

- Human Senses
- Sensation
- Just-Noticeable Difference
- Self Check: The Senses

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20.3: Human Senses

A sense is a physiological capacity of organisms that provides data for perception. The senses and their operation, classification, and theory are overlapping topics studied by a variety of fields, most notably neuroscience, cognitive psychology (or cognitive science), and philosophy of perception. The nervous system has a specific sensory nervous system, and a sense organ, dedicated to each sense.

Humans have a multitude of senses. Sight (vision), hearing (audition), taste (gustation), smell (olfaction), and touch (somatosensation) are the five traditionally recognized senses. The ability to detect other stimuli beyond those governed by these most broadly recognized senses also exists, and these sensory modalities include temperature (thermoception), kinesthetic sense (proprioception), pain (nociception), balance (equilibrioception), vibration (mechanoreception), and various internal stimuli (e.g. the different chemoreceptors for detecting salt and carbon dioxide concentrations in the blood). However, what constitutes a sense is a matter of some debate, leading to difficulties in defining what exactly a distinct sense is, and where the borders between responses to related stimuli lay. This process is called **sensory transduction**.

There are two broad types of cellular systems that perform sensory transduction. In one, a neuron works with a **sensory receptor**, a cell, or cell process that is specialized to engage with and detect a specific stimulus. Stimulation of the sensory receptor activates the associated afferent neuron, which carries information about the stimulus to the central nervous system. In the second type of sensory transduction, a sensory nerve ending responds to a stimulus in the internal or external environment: this neuron constitutes the sensory receptor itself. Free nerve endings can be stimulated by several different stimuli, thus showing little receptor specificity. For example, pain receptors in your gums and teeth may be stimulated by temperature changes, chemical stimulation, or pressure.

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20.4: Sensation

Reception

The first step in sensation is **reception**, which is the activation of sensory receptors by stimuli such as mechanical stimuli (being bent or squished, for example), chemicals, or temperature. The receptor can then respond to the stimuli. The region in space in which a given sensory receptor can respond to a stimulus, be it far away or in contact with the body, is that receptor's **receptive field**. Think for a moment about the differences in receptive fields for the different senses. For the sense of touch, a stimulus must come into contact with body. For the sense of hearing, a stimulus can be a moderate distance away (some baleen whale sounds can propagate for many kilometers). For vision, a stimulus can be very far away; for example, the visual system perceives light from stars at enormous distances.

Transduction

The most fundamental function of a sensory system is the translation of a sensory signal to an electrical signal in the nervous system. This takes place at the sensory receptor, and the change in electrical potential that is produced is called the **receptor potential**. How is sensory input, such as pressure on the skin, changed to a receptor potential? In this example, a type of receptor called a **mechanoreceptor** (as shown in Figure 1) possesses specialized membranes that respond to pressure. Disturbance of these dendrites by compressing them or bending them opens gated ion channels in the plasma membrane of the sensory neuron, changing its electrical potential. Recall that in the nervous system, a positive change of a neuron's electrical potential (also called the membrane potential), depolarizes the neuron. Receptor potentials are graded potentials: the magnitude of these graded (receptor) potentials varies with the strength of the stimulus. If the magnitude of depolarization is sufficient (that is, if membrane potential reaches a threshold), the neuron will fire an action potential. In most cases, the correct stimulus impinging on a sensory receptor will drive membrane potential in a positive direction, although for some receptors, such as those in the visual system, this is not always the case.

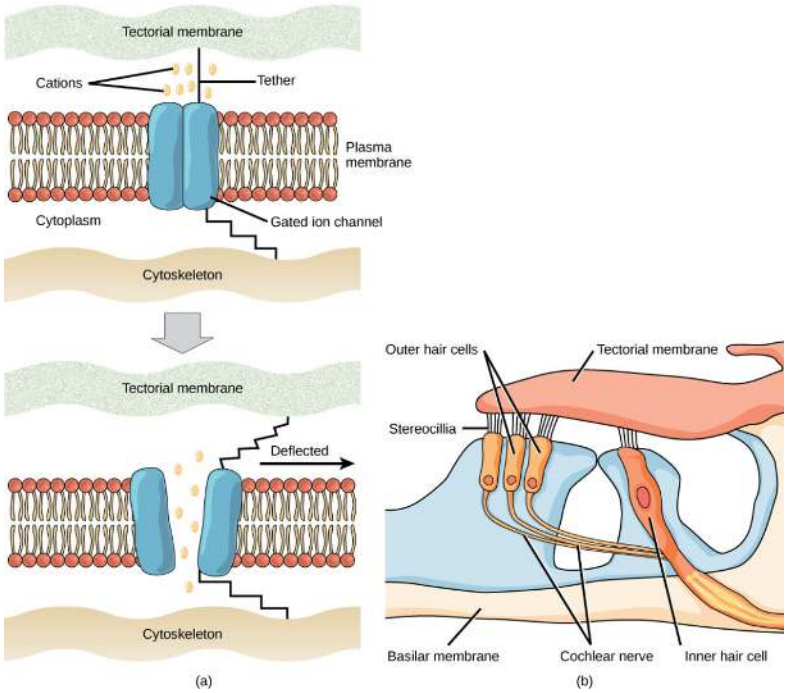


Figure 1. (a) Mechanosensitive ion channels are gated ion channels that respond to mechanical deformation of the plasma membrane. A mechanosensitive channel is connected to the plasma membrane and the cytoskeleton by hair-like tethers. When pressure causes the extracellular matrix to move, the channel opens, allowing ions to enter or exit the cell. (b) Stereocilia in the human ear are connected to mechanosensitive ion channels. When a sound causes the stereocilia to move, mechanosensitive ion channels transduce the signal to the cochlear nerve.

Sensory receptors for different senses are very different from each other, and they are specialized according to the type of stimulus they sense: they have receptor specificity. For example, touch receptors, light receptors, and sound receptors are each activated by

different stimuli. Touch receptors are not sensitive to light or sound; they are sensitive only to touch or pressure. However, stimuli may be combined at higher levels in the brain, as happens with olfaction, contributing to our sense of taste.

Encoding and Transmission of Sensory Information

Four aspects of sensory information are encoded by sensory systems: the type of stimulus, the location of the stimulus in the receptive field, the duration of the stimulus, and the relative intensity of the stimulus. Thus, action potentials transmitted over a sensory receptor's afferent axons encode one type of stimulus, and this segregation of the senses is preserved in other sensory circuits. For example, auditory receptors transmit signals over their own dedicated system, and electrical activity in the axons of the auditory receptors will be interpreted by the brain as an auditory stimulus—a sound.

The intensity of a stimulus is often encoded in the rate of action potentials produced by the sensory receptor. Thus, an intense stimulus will produce a more rapid train of action potentials, and reducing the stimulus will likewise slow the rate of production of action potentials. A second way in which intensity is encoded is by the number of receptors activated. An intense stimulus might initiate action potentials in a large number of adjacent receptors, while a less intense stimulus might stimulate fewer receptors. Integration of sensory information begins as soon as the information is received in the CNS, and the brain will further process incoming signals.

Perception

Perception is an individual's interpretation of a sensation. Although perception relies on the activation of sensory receptors, perception happens not at the level of the sensory receptor, but at higher levels in the nervous system, in the brain. The brain distinguishes sensory stimuli through a sensory pathway: action potentials from sensory receptors travel along neurons that are dedicated to a particular stimulus. These neurons are dedicated to that particular stimulus and synapse with particular neurons in the brain or spinal cord.

All sensory signals, except those from the olfactory system, are transmitted though the central nervous system and are routed to the thalamus and to the appropriate region of the cortex. Recall that the thalamus is a structure in the forebrain that serves as a clearinghouse and relay station for sensory (as well as motor) signals. When the sensory signal exits the thalamus, it is conducted to the specific area of the cortex (Figure 2) dedicated to processing that particular sense.

How are neural signals interpreted? Interpretation of sensory signals between individuals of the same species is largely similar, owing to the inherited similarity of their nervous systems; however, there are some individual differences. A good example of this is individual tolerances to a painful stimulus, such as dental pain, which certainly differ.

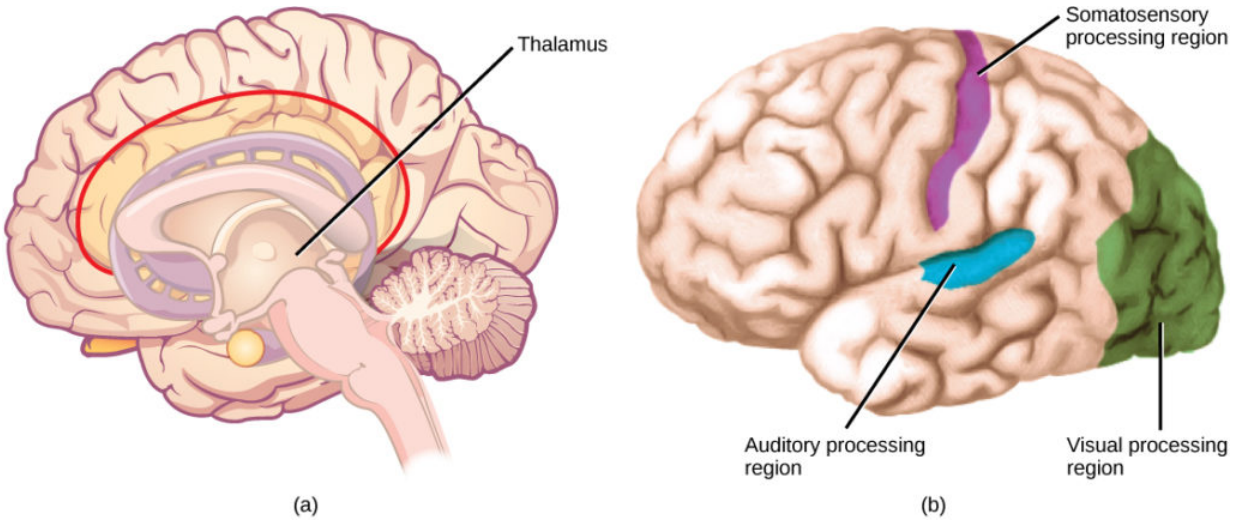


Figure 2. In humans, with the exception of olfaction, all sensory signals are routed from the (a) thalamus to (b) final processing regions in the cortex of the brain. (credit b: modification of work by Polina Tishina)

Learning Objectives

Sensory receptors are either specialized cells associated with sensory neurons or the specialized ends of sensory neurons that are a part of the peripheral nervous system, and they are used to receive information about the environment (internal or external). Each sensory receptor is modified for the type of stimulus it detects. For example, neither gustatory receptors nor auditory receptors are sensitive to light. Each sensory receptor is responsive to stimuli within a specific region in space, which is known as that receptor's receptive field. The most fundamental function of a sensory system is the translation of a sensory signal to an electrical signal in the nervous system.

All sensory signals, except those from the olfactory system, enter the central nervous system and are routed to the thalamus. When the sensory signal exits the thalamus, it is conducted to the specific area of the cortex dedicated to processing that particular sense.

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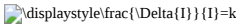
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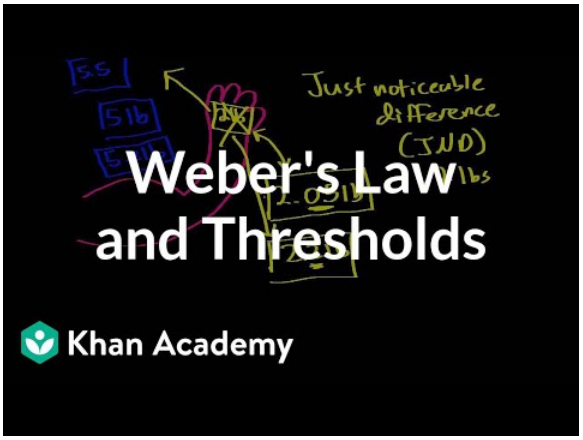
20.5: Just-Noticeable Difference

In the branch of experimental psychology focused on sense, sensation, and perception, which is called psychophysics, a **just-noticeable difference** (JND) is the amount something must be changed in order for a difference to be noticeable, or detectable at least half the time (absolute threshold). This limen (another word for threshold) is also known as the difference limen, differential threshold, or least perceptible difference.

For many sensory modalities, over a wide range of stimulus magnitudes sufficiently far from the upper and lower limits of perception, the JND is a fixed proportion of the reference sensory level, and so the ratio of the JND/reference is roughly constant (that is the JND is a constant proportion/percentage of the reference level). Measured in physical units, we have:



where I is the original intensity of the particular stimulation, ΔI is the addition to it required for the change to be perceived (the JND), and k is a constant. This rule was first discovered by Ernst Heinrich Weber (1795–1878), an anatomist and physiologist, in experiments on the thresholds of perception of lifted weights. A theoretical rationale (not universally accepted) was subsequently provided by Gustav Fechner, so the rule is therefore known either as the Weber Law or as the Weber–Fechner law; the constant k is called the **Weber constant**. It is true, at least to a good approximation, of many but not all sensory dimensions, for example the brightness of lights, and the intensity and the pitch of sounds. It is not true, however, of the wavelength of light. Stanley Smith Stevens argued that it would hold only for what he called *prothetic* sensory continua, where change of input takes the form of increase in intensity or something obviously analogous; it would not hold for *metathetic* continua, where change of input produces a qualitative rather than a quantitative change of the percept. Stevens developed his own law, called Stevens' Power Law, that raises the stimulus to a constant power while, like Weber, also multiplying it by a constant factor in order to achieve the perceived stimulus.



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The JND is a statistical, rather than an exact quantity: from trial to trial, the difference that a given person notices will vary somewhat, and it is therefore necessary to conduct many trials in order to determine the threshold. The JND usually reported is the difference that a person notices on 50% of trials. If a different proportion is used, this would be included in the description—for example a study might report the value of the 75 percent JND.

Modern approaches to psychophysics, for example signal detection theory, imply that the observed JND is not an absolute quantity, but will depend on situational and motivational as well as perceptual factors. For example, when a researcher flashes a very dim light, a participant may report seeing it on some trials but not on others.

Try It Yourself

It is easy to differentiate between a one-pound bag of rice and a two-pound bag of rice. There is a one-pound difference, and one bag is twice as heavy as the other. However, would it be as easy to differentiate between a 20- and a 21-pound bag?

Question: What is the smallest detectible weight difference between a one-pound bag of rice and a larger bag? What is the smallest detectible difference between a 20-pound bag and a larger bag? In both cases, at what weights are the differences detected? This smallest detectible difference in stimuli is known as the just-noticeable difference (JND).

Background: Research background literature on JND and on Weber's Law, a description of a proposed mathematical relationship between the overall magnitude of the stimulus and the JND. You will be testing JND of different weights of rice in bags. Choose a convenient increment that is to be stepped through while testing. For example, you could choose 10 percent increments between one and two pounds (1.1, 1.2, 1.3, 1.4, and so on) or 20 percent increments (1.2, 1.4, 1.6, and 1.8).

Hypothesis: Develop a hypothesis about JND in terms of percentage of the whole weight being tested (such as "the JND between the two small bags and between the two large bags is proportionally the same," or ". . . is not proportionally the same.") So, for the first hypothesis, if the JND between the one-pound bag and a larger bag is 0.2 pounds (that is, 20 percent; 1.0 pound feels the same as 1.1 pounds, but 1.0 pound feels less than 1.2 pounds), then the JND between the 20-pound bag and a larger bag will also be 20 percent. (So, 20 pounds feels the same as 22 pounds or 23 pounds, but 20 pounds feels less than 24 pounds.)

Test the hypothesis: Enlist 24 participants, and split them into two groups of 12. To set up the demonstration, assuming a 10 percent increment was selected, have the first group be the one-pound group. As a counter-balancing measure against a systematic error, however, six of the first group will compare one pound to two pounds, and step down in weight (1.0 to 2.0, 1.0 to 1.9, and so on.), while the other six will step up (1.0 to 1.1, 1.0 to 1.2, and so on). Apply the same principle to the 20-pound group (20 to 40, 20 to 38, and so on, and 20 to 22, 20 to 24, and so on). Given the large difference between 20 and 40 pounds, you may wish to use 30 pounds as your larger weight. In any case, use two weights that are easily detectable as different.

Record the observations: Record the data in a table similar to the table below. For the one-pound and 20-pound groups (base weights) record a plus sign (+) for each participant that detects a difference between the base weight and the step weight. Record a minus sign (−) for each participant that finds no difference. If one-tenth steps were not used, then replace the steps in the "Step Weight" columns with the step you are using.

Table 1. Results of JND Testing (+ = difference; − = no difference)

Step Weight	One pound	20 pounds	Step Weight
1.1	22		
1.2	24		
1.3	26		
1.4	28		
1.5	30		
1.6	32		
1.7	34		
1.8	36		
1.9	38		
2.0	40		

Analyze the data/report the results: What step weight did all participants find to be equal with one-pound base weight? What about the 20-pound group?

Draw a conclusion: Did the data support the hypothesis? Are the final weights proportionally the same? If not, why not? Do the findings adhere to Weber's Law? Weber's Law states that the concept that a just-noticeable difference in a stimulus is proportional to the magnitude of the original stimulus.

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20.6: Introduction to Somatosensation

Describe how somatosensation, the sense of touch, works

Somatosensation is a mixed sensory category and includes all sensation received from the skin and mucous membranes, as well from as the limbs and joints. Somatosensation is also known as tactile sense, or more familiarly, as the sense of touch. Somatosensation occurs all over the exterior of the body and at some interior locations as well. A variety of receptor types—embedded in the skin, mucous membranes, muscles, joints, internal organs, and cardiovascular system—play a role.

What You'll Learn to Do

- Describe four important mechanoreceptors in human skin
- Describe the topographical distribution of somatosensory receptors
- Describe how thermoreception, the detection of heat and cold, works
- Explain why the perception of pain is subjective

Learning Activities

The learning activities for this section include the following:

- Somatosensory Receptors
- Thermoreception and Pain
- Self Check: Somatosensation

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20.7: Somatosensory Receptors

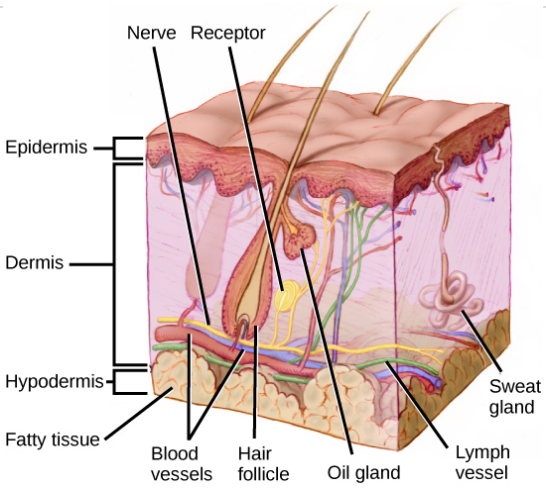


Figure 1. Mammalian skin has three layers: an epidermis, a dermis, and a hypodermis. (credit: modification of work by Don Bliss, National Cancer Institute)

Recall that the epidermis is the outermost layer of skin in mammals. It is relatively thin, is composed of keratin-filled cells, and has no blood supply. The epidermis serves as a barrier to water and to invasion by pathogens. Below this, the much thicker dermis contains blood vessels, sweat glands, hair follicles, lymph vessels, and lipid-secreting sebaceous glands (Figure 1). Below the epidermis and dermis is the subcutaneous tissue, or hypodermis, the fatty layer that contains blood vessels, connective tissue, and the axons of sensory neurons. The hypodermis, which holds about 50 percent of the body's fat, attaches the dermis to the bone and muscle, and supplies nerves and blood vessels to the dermis.

Sensory receptors are classified into five categories: mechanoreceptors, thermoreceptors, proprioceptors, pain receptors, and chemoreceptors. These categories are based on the nature of stimuli each receptor class transduces. What is commonly referred to as "touch" involves more than one kind of stimulus and more than one kind of receptor. Mechanoreceptors in the skin are described as encapsulated (that is, surrounded by a capsule) or unencapsulated (a group that includes free nerve endings). A **free nerve ending**, as its name implies, is an unencapsulated dendrite of a sensory neuron. Free nerve endings are the most common nerve endings in skin, and they extend into the middle of the epidermis. Free nerve endings are sensitive to painful stimuli, to hot and cold, and to light touch. They are slow to adjust to a stimulus and so are less sensitive to abrupt changes in stimulation.

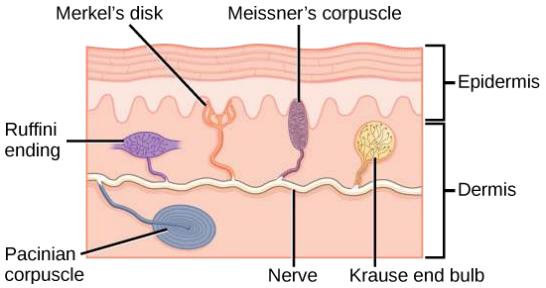


Figure 2. Four of the primary mechanoreceptors in human skin are shown. Merkel's disks, which are unencapsulated, respond to light touch. Meissner's corpuscles, Ruffini endings, Pacinian corpuscles, and Krause end bulbs are all encapsulated. Meissner's corpuscles respond to touch and low-frequency vibration. Ruffini endings detect stretch, deformation within joints, and warmth. Pacinian corpuscles detect transient pressure and high-frequency vibration. Krause end bulbs detect cold.

There are three classes of mechanoreceptors: tactile, proprioceptors, and baroreceptors. Mechanoreceptors sense stimuli due to physical deformation of their plasma membranes. They contain mechanically gated ion channels whose gates open or close in response to pressure, touch, stretching, and sound." There are four primary tactile mechanoreceptors in human skin: Merkel's disks, Meissner's corpuscles, Ruffini endings, and Pacinian corpuscle; two are located toward the surface of the skin and two are located deeper. A fifth type of mechanoreceptor, Krause end bulbs, are found only in specialized regions. **Merkel's disks** (shown in Figure 2) are found in the upper layers of skin near the base of the epidermis, both in skin that has hair and on **glabrous** skin, that is, the hairless skin found on the palms and fingers, the soles of the feet, and the lips of humans and other primates. Merkel's disks are

densely distributed in the fingertips and lips. They are slow-adapting, encapsulated nerve endings, and they respond to light touch. Light touch, also known as discriminative touch, is a light pressure that allows the location of a stimulus to be pinpointed. The receptive fields of Merkel's disks are small with well-defined borders. That makes them finely sensitive to edges and they come into use in tasks such as typing on a keyboard.

? Practice Question

Which of the following statements about mechanoreceptors is false?

a. Pacini corpuscles are found in both glabrous and hairy skin.
b. Merkel's disks are abundant on the fingertips and lips.
c. Ruffini endings are encapsulated mechanoreceptors.
d. Meissner's corpuscles extend into the lower dermis.

[reveal-answer q="20233"]Show Answer[/reveal-answer]
[hidden-answer a="20233"]Statement d is false.[/hidden-answer]

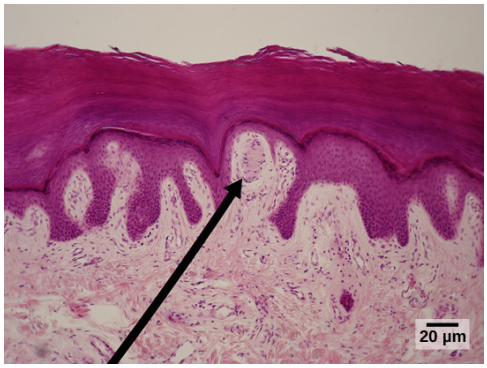


Figure 3. Meissner corpuscles in the fingertips, such as the one viewed here using bright field light microscopy, allow for touch discrimination of fine detail. (credit: modification of work by "Wbensmith"/Wikimedia Commons; scale-bar data from Matt Russell)

Meissner's corpuscles, (shown in Figure 3) also known as tactile corpuscles, are found in the upper dermis, but they project into the epidermis. They, too, are found primarily in the glabrous skin on the fingertips and eyelids. They respond to fine touch and pressure, but they also respond to low-frequency vibration or flutter. They are rapidly adapting, fluid-filled, encapsulated neurons with small, well-defined borders and are responsive to fine details. Like Merkel's disks, Meissner's corpuscles are not as plentiful in the palms as they are in the fingertips.

Deeper in the epidermis, near the base, are **Ruffini endings**, which are also known as bulbous corpuscles. They are found in both glabrous and hairy skin. These are slow-adapting, encapsulated mechanoreceptors that detect skin stretch and deformations within joints, so they provide valuable feedback for gripping objects and controlling finger position and movement. Thus, they also contribute to proprioception and kinesthesia. Ruffini endings also detect warmth. Note that these warmth detectors are situated deeper in the skin than are the cold detectors. It is not surprising, then, that humans detect cold stimuli before they detect warm stimuli.

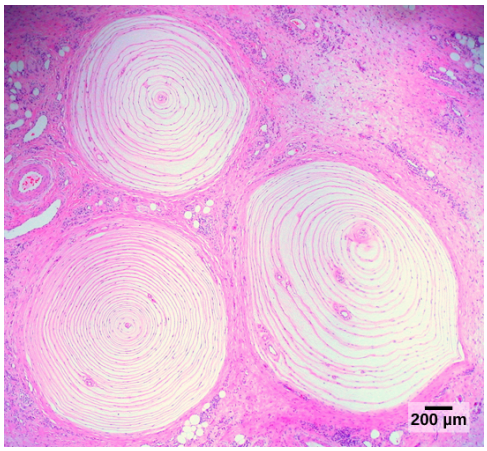


Figure 4. Pacinian corpuscles, such as these visualized using bright field light microscopy, detect pressure (touch) and high-frequency vibration. (credit: modification of work by Ed Uthman; scale-bar data from Matt Russell)

Pacinian corpuscles (seen in Figure 4) are located deep in the dermis of both glabrous and hairy skin and are structurally similar to Meissner's corpuscles; they are found in the bone periosteum, joint capsules, pancreas and other viscera, breast, and genitals. They are rapidly adapting mechanoreceptors that sense deep transient (but not prolonged) pressure and high-frequency vibration. Pacinian receptors detect pressure and vibration by being compressed, stimulating their internal dendrites. There are fewer Pacinian corpuscles and Ruffini endings in skin than there are Merkel's disks and Meissner's corpuscles.

In proprioception, proprioceptive and kinesthetic signals travel through myelinated afferent neurons running from the spinal cord to the medulla. Neurons are not physically connected, but communicate via neurotransmitters secreted into synapses or "gaps" between communicating neurons. Once in the medulla, the neurons continue carrying the signals to the thalamus.

Muscle spindles are stretch receptors that detect the amount of stretch, or lengthening of muscles. Related to these are **Golgi tendon organs**, which are tension receptors that detect the force of muscle contraction. Proprioceptive and kinesthetic signals come from limbs. Unconscious proprioceptive signals run from the spinal cord to the cerebellum, the brain region that coordinates muscle contraction, rather than to the thalamus, like most other sensory information.

Barorecptors detect pressure changes in an organ. They are found in the walls of the carotid artery and the aorta where they monitor blood pressure, and in the lungs where they detect the degree of lung expansion. Stretch receptors are found at various sites in the digestive and urinary systems.

In addition to these two types of deeper receptors, there are also rapidly adapting hair receptors, which are found on nerve endings that wrap around the base of hair follicles. There are a few types of hair receptors that detect slow and rapid hair movement, and they differ in their sensitivity to movement. Some hair receptors also detect skin deflection, and certain rapidly adapting hair receptors allow detection of stimuli that have not yet touched the skin.

Integration of Signals from Mechanoreceptors

The configuration of the different types of receptors working in concert in human skin results in a very refined sense of touch. The nociceptive receptors—those that detect pain—are located near the surface. Small, finely calibrated mechanoreceptors—Merkel's disks and Meissner's corpuscles—are located in the upper layers and can precisely localize even gentle touch. The large mechanoreceptors—Pacinian corpuscles and Ruffini endings—are located in the lower layers and respond to deeper touch. (Consider that the deep pressure that reaches those deeper receptors would not need to be finely localized.) Both the upper and lower layers of the skin hold rapidly and slowly adapting receptors. Both primary somatosensory cortex and secondary cortical areas are responsible for processing the complex picture of stimuli transmitted from the interplay of mechanoreceptors.

Density of Mechanoreceptors

The distribution of touch receptors in human skin is not consistent over the body. In humans, touch receptors are less dense in skin covered with any type of hair, such as the arms, legs, torso, and face. Touch receptors are denser in glabrous skin (the type found on human fingertips and lips, for example), which is typically more sensitive and is thicker than hairy skin (4 to 5 mm versus 2 to 3 mm).

How is receptor density estimated in a human subject? The relative density of pressure receptors in different locations on the body can be demonstrated experimentally using a two-point discrimination test. In this demonstration, two sharp points, such as two thumbtacks, are brought into contact with the subject's skin (though not hard enough to cause pain or break the skin). The subject reports if he or she feels one point or two points. If the two points are felt as one point, it can be inferred that the two points are both in the receptive field of a single sensory receptor. If two points are felt as two separate points, each is in the receptive field of two separate sensory receptors. The points could then be moved closer and re-tested until the subject reports feeling only one point, and the size of the receptive field of a single receptor could be estimated from that distance.

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20.8: Thermoreception and Pain

Thermoreception

Thermoception or **thermoreception** is the sense by which an organism perceives temperatures. The details of how temperature receptors work are still being investigated. Ciliopathy is associated with decreased ability to sense heat, thus cilia may aid in the process. Transient receptor potential channels (TRP channels) are believed to play a role in many species in sensation of hot, cold, and pain. Mammals have at least two types of sensor: those that detect heat (i.e., temperatures above body temperature) and those that detect cold (i.e. temperatures below body temperature).

In addition to Krause end bulbs that detect cold and Ruffini endings that detect warmth, there are different types of cold receptors on some free nerve endings: thermoreceptors, located in the dermis, skeletal muscles, liver, and hypothalamus, that are activated by different temperatures. Their pathways into the brain run from the spinal cord through the thalamus to the primary somatosensory cortex. Warmth and cold information from the face travels through one of the cranial nerves to the brain. You know from experience that a tolerably cold or hot stimulus can quickly progress to a much more intense stimulus that is no longer tolerable. Any stimulus that is too intense can be perceived as pain because temperature sensations are conducted along the same pathways that carry pain sensations

Pain

Pain is the name given to **nociception**, which is the neural processing of injurious stimuli in response to tissue damage. Pain is caused by true sources of injury, such as contact with a heat source that causes a thermal burn or contact with a corrosive chemical. But pain also can be caused by harmless stimuli that mimic the action of damaging stimuli, such as contact with capsaicins, the compounds that cause peppers to taste hot and which are used in self-defense pepper sprays and certain topical medications. Peppers taste “hot” because the protein receptors that bind capsaicin open the same calcium channels that are activated by warm receptors.

Nociception starts at the sensory receptors, but pain, inasmuch as it is the perception of nociception, does not start until it is communicated to the brain. There are several nociceptive pathways to and through the brain. Most axons carrying nociceptive information into the brain from the spinal cord project to the thalamus (as do other sensory neurons) and the neural signal undergoes final processing in the primary somatosensory cortex. Interestingly, one nociceptive pathway projects not to the thalamus but directly to the hypothalamus in the forebrain, which modulates the cardiovascular and neuroendocrine functions of the autonomic nervous system. Recall that threatening—or painful—stimuli stimulate the sympathetic branch of the visceral sensory system, readying a fight-or-flight response.

View this video that animates the five phases of nociceptive pain.

A link to an interactive elements can be found at the bottom of this page.

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20.9: Introduction to Taste and Smell

Explain how taste and smell work together

Taste, also called **gustation**, and smell, also called **olfaction**, are the most interconnected senses in that both involve molecules of the stimulus entering the body and bonding to receptors. Smell lets an animal sense the presence of food or other animals—whether potential mates, predators, or prey—or other chemicals in the environment that can impact their survival. Similarly, the sense of taste allows animals to discriminate between types of foods. While the value of a sense of smell is obvious, what is the value of a sense of taste? Different tasting foods have different attributes, both helpful and harmful. For example, sweet-tasting substances tend to be highly caloric, which could be necessary for survival in lean times. Bitterness is associated with toxicity, and sourness is associated with spoiled food. Salty foods are valuable in maintaining homeostasis by helping the body retain water and by providing ions necessary for cells to function.

What You'll Learn to Do

- Explain in what way smell and taste differ from other senses
- Identify the five primary tastes that can be distinguished by humans
- Identify the parts of the brain associated with taste and smell

Learning Activities

The learning activities for this section include the following:

- Tastes and Odors
- Tastes
- Smell and Taste in the Brain
- Self Check: Taste and Smell

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20.10: Tastes and Odors

Both taste and odor stimuli are molecules taken in from the environment. The primary tastes detected by humans are sweet, sour, bitter, salty and umami. The first four tastes need little explanation. The identification of **umami** as a fundamental taste occurred fairly recently—it was identified in 1908 by Japanese scientist Kikunae Ikeda while he worked with seaweed broth, but it was not widely accepted as a taste that could be physiologically distinguished until many years later. The taste of umami, also known as savoriness, is attributable to the taste of the amino acid L-glutamate. In fact, monosodium glutamate, or MSG, is often used in cooking to enhance the savory taste of certain foods. What is the adaptive value of being able to distinguish umami? Savory substances tend to be high in protein.

All odors that we perceive are molecules in the air we breathe. If a substance does not release molecules into the air from its surface, it has no smell. And if a human or other animal does not have a receptor that recognizes a specific molecule, then that molecule has no smell. Humans have about 350 olfactory receptor subtypes that work in various combinations to allow us to sense about 10,000 different odors. Compare that to mice, for example, which have about 1,300 olfactory receptor types, and therefore probably sense more odors. Both odors and tastes involve molecules that stimulate specific chemoreceptors. Although humans commonly distinguish taste as one sense and smell as another, they work together to create the perception of flavor. A person's perception of flavor is reduced if he or she has congested nasal passages.

Reception and Transduction

Odorants (odor molecules) enter the nose and dissolve in the olfactory epithelium, the mucosa at the back of the nasal cavity (as illustrated in Figure 1). The **olfactory epithelium** is a collection of specialized olfactory receptors in the back of the nasal cavity that spans an area about 5 cm^2 in humans. Recall that sensory cells are neurons. An **olfactory receptor**, which is a dendrite of a specialized neuron, responds when it binds certain molecules inhaled from the environment by sending impulses directly to the olfactory bulb of the brain. Humans have about 12 million olfactory receptors, distributed among hundreds of different receptor types that respond to different odors. Twelve million seems like a large number of receptors, but compare that to other animals: rabbits have about 100 million, most dogs have about 1 billion, and bloodhounds—dogs selectively bred for their sense of smell—have about 4 billion. The overall size of the olfactory epithelium also differs between species, with that of bloodhounds, for example, being many times larger than that of humans.

Olfactory neurons are **bipolar neurons** (neurons with two processes from the cell body). Each neuron has a single dendrite buried in the olfactory epithelium, and extending from this dendrite are 5 to 20 receptor-laden, hair-like cilia that trap odorant molecules. The sensory receptors on the cilia are proteins, and it is the variations in their amino acid chains that make the receptors sensitive to different odorants. Each olfactory sensory neuron has only one type of receptor on its cilia, and the receptors are specialized to detect specific odorants, so the bipolar neurons themselves are specialized. When an odorant binds with a receptor that recognizes it, the sensory neuron associated with the receptor is stimulated. Olfactory stimulation is the only sensory information that directly reaches the cerebral cortex, whereas other sensations are relayed through the thalamus.

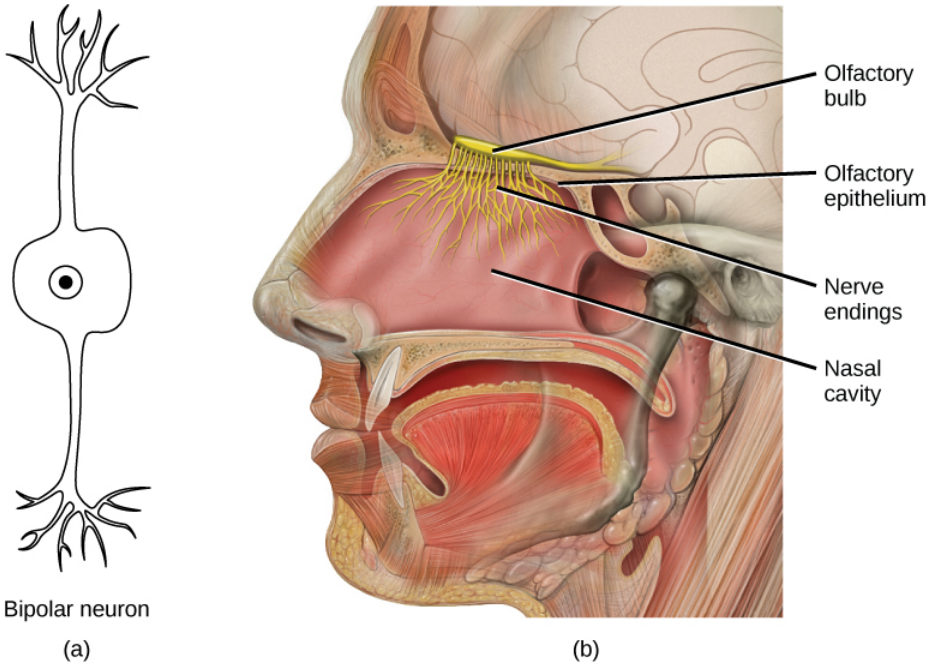


Figure 1. In the human olfactory system, (a) bipolar olfactory neurons extend from (b) the olfactory epithelium, where olfactory receptors are located, to the olfactory bulb. (credit: modification of work by Patrick J. Lynch, medical illustrator; C. Carl Jaffe, MD, cardiologist)

? Try It

A **pheromone** is a chemical released by an animal that affects the behavior or physiology of animals of the same species. Pheromonal signals can have profound effects on animals that inhale them, but pheromones apparently are not consciously perceived in the same way as other odors. There are several different types of pheromones, which are released in urine or as glandular secretions. Certain pheromones are attractants to potential mates, others are repellants to potential competitors of the same sex, and still others play roles in mother-infant attachment. Some pheromones can also influence the timing of puberty, modify reproductive cycles, and even prevent embryonic implantation. While the roles of pheromones in many nonhuman species are important, pheromones have become less important in human behavior over evolutionary time compared to their importance to organisms with more limited behavioral repertoires.



Figure 2. The flehmen response in this tiger results in the curling of the upper lip and helps airborne pheromone molecules enter the vomeronasal organ. (credit: modification of work by “chadh”/Flickr)

The vomeronasal organ (VNO, or Jacobson’s organ) is a tubular, fluid-filled, olfactory organ present in many vertebrate animals that sits adjacent to the nasal cavity. It is very sensitive to pheromones and is connected to the nasal cavity by a duct. When molecules dissolve in the mucosa of the nasal cavity, they then enter the VNO where the pheromone molecules among them bind with specialized pheromone receptors. Upon exposure to pheromones from their own species or others, many animals, including cats, may display the flehmen response (shown in Figure 2), a curling of the upper lip that helps pheromone molecules enter the VNO.

Pheromonal signals are sent, not to the main olfactory bulb, but to a different neural structure that projects directly to the amygdala (recall that the amygdala is a brain center important in emotional reactions, such as fear). The pheromonal signal then continues to areas of the hypothalamus that are key to reproductive physiology and behavior. While some scientists assert that the VNO is apparently functionally vestigial in humans, even though there is a similar structure located near human nasal cavities, others are researching it as a possible functional system that may, for example, contribute to synchronization of menstrual cycles in women living in close proximity.

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20.11: Tastes

Detecting a taste (gustation) is fairly similar to detecting an odor (olfaction), given that both taste and smell rely on chemical receptors being stimulated by certain molecules. The primary organ of taste is the taste bud. A **taste bud** is a cluster of gustatory receptors (taste cells) that are located within the bumps on the tongue called **papillae** (singular: papilla) (illustrated in Figure 1). There are several structurally distinct papillae. Filiform papillae, which are located across the tongue, are tactile, providing friction that helps the tongue move substances, and contain no taste cells. In contrast, fungiform papillae, which are located mainly on the anterior two-thirds of the tongue, each contain one to eight taste buds and also have receptors for pressure and temperature. The large circumvallate papillae contain up to 100 taste buds and form a V near the posterior margin of the tongue.

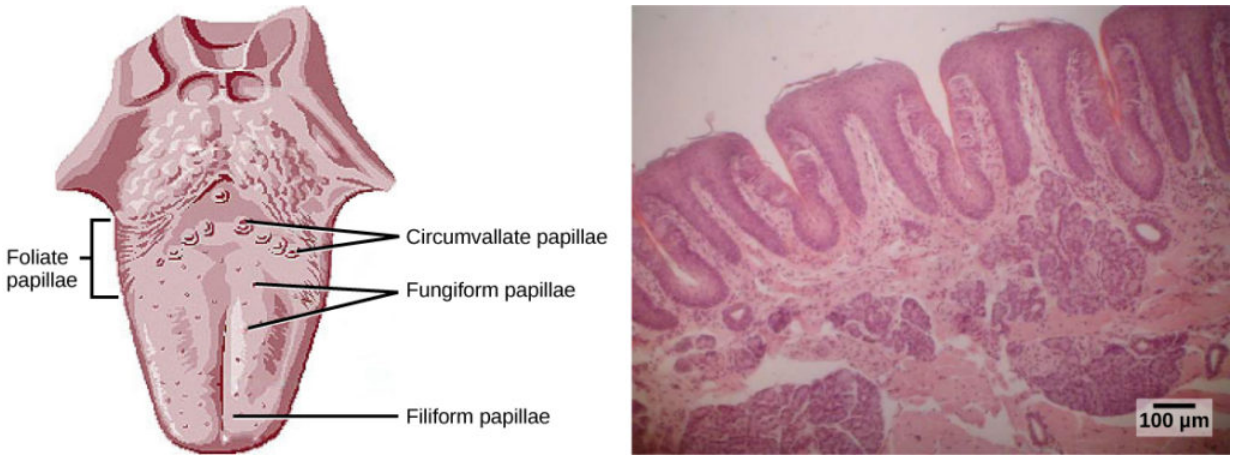


Figure 1. (a) Foliate, circumvallate, and fungiform papillae are located on different regions of the tongue. (b) Foliate papillae are prominent protrusions on this light micrograph. (credit a: modification of work by NCI; scale-bar data from Matt Russell)

In addition to those two types of chemically and mechanically sensitive papillae are foliate papillae—leaf-like papillae located in parallel folds along the edges and toward the back of the tongue, as seen in the Figure 1 micrograph. Foliate papillae contain about 1,300 taste buds within their folds. Finally, there are circumvallate papillae, which are wall-like papillae in the shape of an inverted "V" at the back of the tongue. Each of these papillae is surrounded by a groove and contains about 250 taste buds.

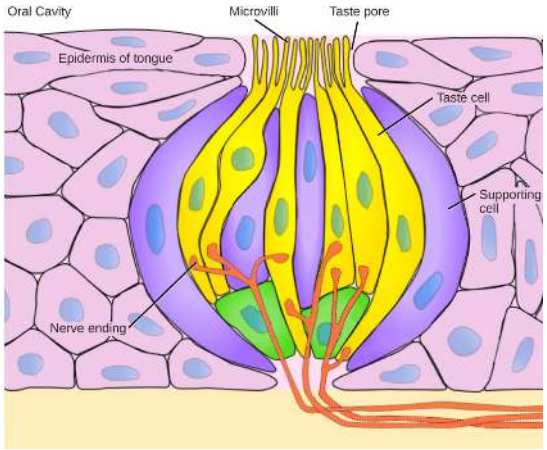


Figure 2. Pores in the tongue allow tastants to enter taste pores in the tongue. (credit: modification of work by Vincenzo Rizzo)

Each taste bud's taste cells are replaced every 10 to 14 days. These are elongated cells with hair-like processes called microvilli at the tips that extend into the taste bud pore (illustrate in Figure 2). Food molecules (**tastants**) are dissolved in saliva, and they bind with and stimulate the receptors on the microvilli. The receptors for tastants are located across the outer portion and front of the tongue, outside of the middle area where the filiform papillae are most prominent.

In humans, there are five primary tastes, and each taste has only one corresponding type of receptor. Thus, like olfaction, each receptor is specific to its stimulus (tastant). Transduction of the five tastes happens through different mechanisms that reflect the molecular composition of the tastant. A salty tastant (containing NaCl) provides the sodium ions (Na^+) that enter the taste neurons

and excite them directly. Sour tastants are acids and belong to the thermoreceptor protein family. Binding of an acid or other sour-tasting molecule triggers a change in the ion channel and these increase hydrogen ion (H^+) concentrations in the taste neurons, thus depolarizing them. Sweet, bitter, and umami tastants require a G-protein coupled receptor. These tastants bind to their respective receptors, thereby exciting the specialized neurons associated with them.

Both tasting abilities and sense of smell change with age. In humans, the senses decline dramatically by age 50 and continue to decline. A child may find a food to be too spicy, whereas an elderly person may find the same food to be bland and unappetizing.

View this animation that shows how the sense of taste works.

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20.12: Smell and Taste in the Brain

Olfactory neurons project from the olfactory epithelium to the olfactory bulb as thin, unmyelinated axons. The **olfactory bulb** is composed of neural clusters called **glomeruli**, and each glomerulus receives signals from one type of olfactory receptor, so each glomerulus is specific to one odorant. From glomeruli, olfactory signals travel directly to the olfactory cortex and then to the frontal cortex and the thalamus. Recall that this is a different path from most other sensory information, which is sent directly to the thalamus before ending up in the cortex. Olfactory signals also travel directly to the amygdala, thereafter reaching the hypothalamus, thalamus, and frontal cortex. The last structure that olfactory signals directly travel to is a cortical center in the temporal lobe structure important in spatial, autobiographical, declarative, and episodic memories. Olfaction is finally processed by areas of the brain that deal with memory, emotions, reproduction, and thought.

Taste neurons project from taste cells in the tongue, esophagus, and palate to the medulla, in the brainstem. From the medulla, taste signals travel to the thalamus and then to the primary gustatory cortex. Information from different regions of the tongue is segregated in the medulla, thalamus, and cortex.

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20.13: Introduction to Hearing and Vestibular Sensation

Trace the path of sound through the auditory system to the site of transduction of sound

Audition, or hearing, is important to humans and to other animals for many different interactions. It enables an organism to detect and receive information about danger, such as an approaching predator, and to participate in communal exchanges like those concerning territories or mating. On the other hand, although it is physically linked to the auditory system, the vestibular system is not involved in hearing. Instead, an animal's vestibular system detects its own movement, both linear and angular acceleration and deceleration, and balance.

What You'll Learn to Do

- Describe the relationship of amplitude and frequency of a sound wave to attributes of sound
- Trace the path of sound through the auditory system
- Describe the process of creating sound
- Identify the structures of the vestibular system that respond to gravity

Learning Activities

The learning activities for this section include the following:

- Sound and Reception
- Transduction of Sound
- Vestibular Information
- Self Check: Hearing and Vestibular Sensation

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20.14: Sound and Reception

Auditory stimuli are sound waves, which are mechanical, pressure waves that move through a medium, such as air or water. There are no sound waves in a vacuum since there are no air molecules to move in waves. The speed of sound waves differs, based on altitude, temperature, and medium, but at sea level and a temperature of 20º C (68º F), sound waves travel in the air at about 343 meters per second.

As is true for all waves, there are four main characteristics of a sound wave: frequency, wavelength, period, and amplitude. Frequency is the number of waves per unit of time, and in sound is heard as pitch. High-frequency (≥15.000Hz) sounds are higher-pitched (short wavelength) than low-frequency (long wavelengths; ≤100Hz) sounds. Frequency is measured in cycles per second, and for sound, the most commonly used unit is hertz (Hz), or cycles per second. Most humans can perceive sounds with frequencies between 30 and 20,000 Hz. Women are typically better at hearing high frequencies, but everyone's ability to hear high frequencies decreases with age. Dogs detect up to about 40,000 Hz; cats, 60,000 Hz; bats, 100,000 Hz; and dolphins 150,000 Hz, and American shad (*Alosa sapidissima*), a fish, can hear 180,000 Hz. Those frequencies above the human range are called **ultrasound**.

Amplitude, or the dimension of a wave from peak to trough, in sound is heard as volume and is illustrated in Figure 1. The sound waves of louder sounds have greater amplitude than those of softer sounds. For sound, volume is measured in decibels (dB). The softest sound that a human can hear is the zero point. Humans speak normally at 60 decibels.

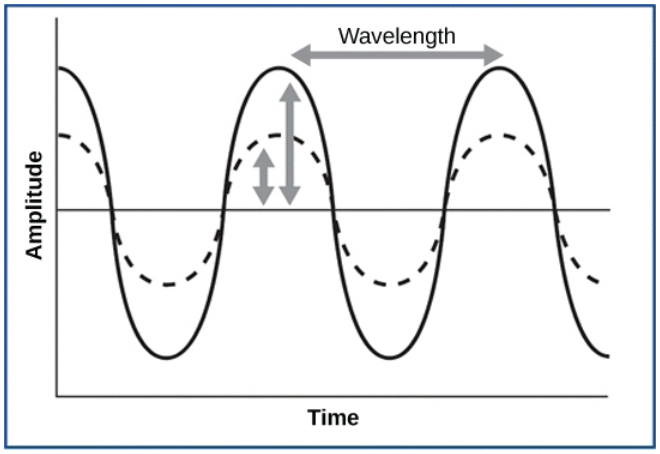


Figure 1. For sound waves, wavelength corresponds to pitch. Amplitude of the wave corresponds to volume. The sound wave shown with a dashed line is softer in volume than the sound wave shown with a solid line. (credit: NIH)

Reception of Sound

In mammals, sound waves are collected by the external, cartilaginous part of the ear called the **pinna**, then travel through the auditory canal and cause vibration of the thin diaphragm called the **tympanum** or ear drum, the innermost part of the **outer ear** (illustrated in Figure 2). Interior to the tympanum is the **middle ear**. The middle ear holds three small bones called the **ossicles**, which transfer energy from the moving tympanum to the inner ear. The three ossicles are the **malleus** (also known as the hammer), the **incus** (the anvil), and **stapes** (the stirrup). The aptly named stapes looks very much like a stirrup. The three ossicles are unique to mammals, and each plays a role in hearing. The malleus attaches at three points to the interior surface of the tympanic membrane. The incus attaches the malleus to the stapes. In humans, the stapes is not long enough to reach the tympanum. If we did not have the malleus and the incus, then the vibrations of the tympanum would never reach the inner ear. These bones also function to collect force and amplify sounds. The ear ossicles are homologous to bones in a fish mouth: the bones that support gills in fish are thought to be adapted for use in the vertebrate ear over evolutionary time. Many animals (frogs, reptiles, and birds, for example) use the stapes of the middle ear to transmit vibrations to the middle ear.

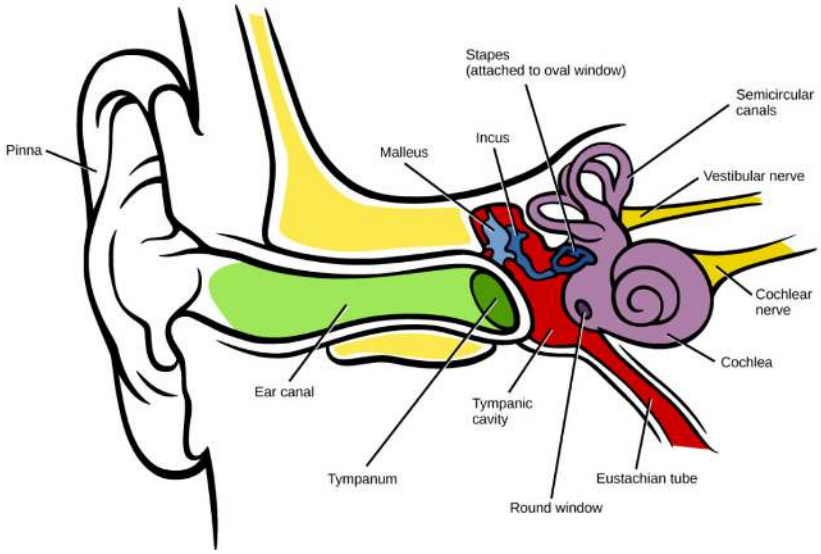


Figure 2. Sound travels through the outer ear to the middle ear, which is bounded on its exterior by the tympanic membrane. The middle ear contains three bones called ossicles that transfer the sound wave to the oval window, the exterior boundary of the inner ear. The organ of Corti, which is the organ of sound transduction, lies inside the cochlea. (credit: modification of work by Lars Chittka, Axel Brockmann)

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20.15: Transduction of Sound

Vibrating objects, such as vocal cords, create sound waves or pressure waves in the air. When these pressure waves reach the ear, the ear transduces this mechanical stimulus (pressure wave) into a nerve impulse (electrical signal) that the brain perceives as sound. The pressure waves strike the tympanum, causing it to vibrate. The mechanical energy from the moving tympanum transmits the vibrations to the three bones of the middle ear. The stapes transmits the vibrations to a thin diaphragm called the **oval window**, which is the outermost structure of the **inner ear**. The structures of the inner ear are found in the **labyrinth**, a bony, hollow structure that is the most interior portion of the ear. Here, the energy from the sound wave is transferred from the stapes through the flexible oval window and to the fluid of the cochlea. The vibrations of the oval window create pressure waves in the fluid (perilymph) inside the cochlea. The **cochlea** is a whorled structure, like the shell of a snail, and it contains receptors for transduction of the mechanical wave into an electrical signal (as illustrated in Figure 1). Inside the cochlea, the **basilar membrane** is a mechanical analyzer that runs the length of the cochlea, curling toward the cochlea's center.

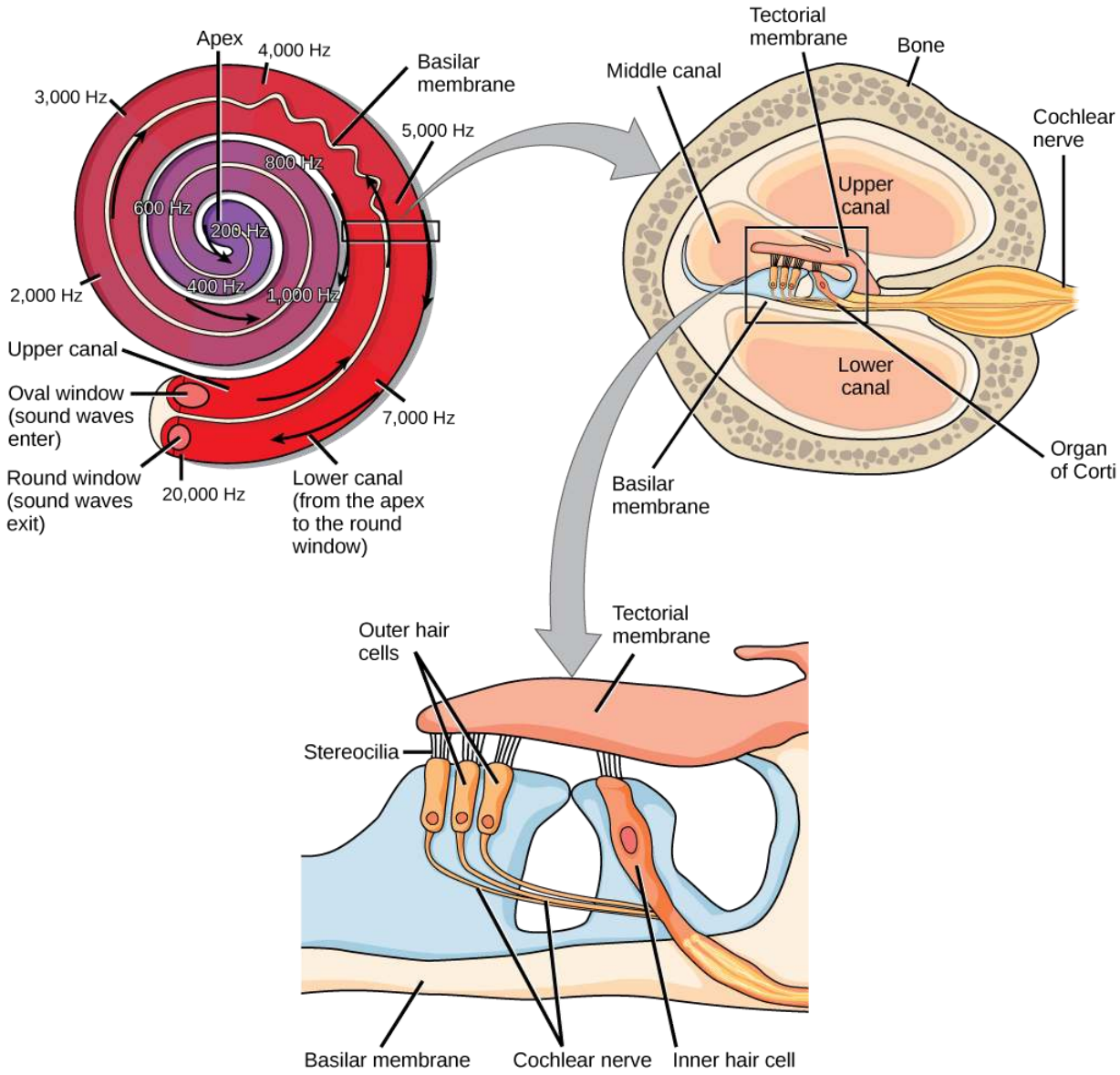


Figure 1. In the human ear, sound waves cause the stapes to press against the oval window. Vibrations travel up the fluid-filled interior of the cochlea. The basilar membrane that lines the cochlea gets continuously thinner toward the apex of the cochlea. Different thicknesses of membrane vibrate in response to different frequencies of sound. Sound waves then exit through the round window. In the cross section of the cochlea (top right figure), note that in addition to the upper canal and lower canal, the cochlea also has a middle canal. The organ of Corti (bottom image) is the site of sound transduction. Movement of stereocilia on hair cells results in an action potential that travels along the auditory nerve.

The mechanical properties of the basilar membrane change along its length, such that it is thicker, tauter, and narrower at the outside of the whorl (where the cochlea is largest), and thinner, floppier, and broader toward the apex, or center, of the whorl (where the cochlea is smallest). Different regions of the basilar membrane vibrate according to the frequency of the sound wave conducted through the fluid in the cochlea. For these reasons, the fluid-filled cochlea detects different wave frequencies (pitches) at different regions of the membrane. When the sound waves in the cochlear fluid contact the basilar membrane, it flexes back and forth in a wave-like fashion. Above the basilar membrane is the **tectorial membrane**.

? Practice Question

Cochlear implants can restore hearing in people who have a nonfunctional cochlear. The implant consists of a microphone that picks up sound. A speech processor selects sounds in the range of human speech, and a transmitter converts these sounds to electrical impulses, which are then sent to the auditory nerve. Which of the following types of hearing loss would not be restored by a cochlear implant?

a. Hearing loss resulting from absence or loss of hair cells in the organ of Corti.
b. Hearing loss resulting from an abnormal auditory nerve.
c. Hearing loss resulting from fracture of the cochlea.
d. Hearing loss resulting from damage to bones of the middle ear.

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[hidden-answer a="603186"]Option b would not be restored by a cochlear implant.[/hidden-answer]

The site of transduction is in the **organ of Corti** (spiral organ). It is composed of hair cells held in place above the basilar membrane like flowers projecting up from soil, with their exposed short, hair-like **stereocilia** contacting or embedded in the tectorial membrane above them. The inner hair cells are the primary auditory receptors and exist in a single row, numbering approximately 3,500. The stereocilia from inner hair cells extend into small dimples on the tectorial membrane's lower surface. The outer hair cells are arranged in three or four rows. They number approximately 12,000, and they function to fine tune incoming sound waves. The longer stereocilia that project from the outer hair cells actually attach to the tectorial membrane. All of the stereocilia are mechanoreceptors, and when bent by vibrations they respond by opening a gated ion channel. As a result, the hair cell membrane is depolarized, and a signal is transmitted to the cochlear nerve. Intensity (volume) of sound is determined by how many hair cells at a particular location are stimulated.

The hair cells are arranged on the basilar membrane in an orderly way. The basilar membrane vibrates in different regions, according to the frequency of the sound waves impinging on it. Likewise, the hair cells that lay above it are most sensitive to a specific frequency of sound waves. Hair cells can respond to a small range of similar frequencies, but they require stimulation of greater intensity to fire at frequencies outside of their optimal range. The difference in response frequency between adjacent inner hair cells is about 0.2 percent. Compare that to adjacent piano strings, which are about six percent different. Place theory, which is the model for how biologists think pitch detection works in the human ear, states that high frequency sounds selectively vibrate the basilar membrane of the inner ear near the entrance port (the oval window). Lower frequencies travel farther along the membrane before causing appreciable excitation of the membrane. The basic pitch-determining mechanism is based on the location along the membrane where the hair cells are stimulated. The place theory is the first step toward an understanding of pitch perception. Considering the extreme pitch sensitivity of the human ear, it is thought that there must be some auditory "sharpening" mechanism to enhance the pitch resolution.

When sound waves produce fluid waves inside the cochlea, the basilar membrane flexes, bending the stereocilia that attach to the tectorial membrane. Their bending results in action potentials in the hair cells, and auditory information travels along the neural endings of the bipolar neurons of the hair cells (collectively, the auditory nerve) to the brain. When the hairs bend, they release an excitatory neurotransmitter at a synapse with a sensory neuron, which then conducts action potentials to the central nervous system. The cochlear branch of the vestibulocochlear cranial nerve sends information on hearing. The auditory system is very refined, and there is some modulation or "sharpening" built in. The brain can send signals back to the cochlea, resulting in a change of length in the outer hair cells, sharpening or dampening the hair cells' response to certain frequencies.

Watch an animation of sound entering the outer ear, moving through the ear structure, stimulating cochlear nerve impulses, and eventually sending signals to the temporal lobe.

Higher Processing

The inner hair cells are most important for conveying auditory information to the brain. About 90 percent of the afferent neurons carry information from inner hair cells, with each hair cell synapsing with 10 or so neurons. Outer hair cells connect to only 10 percent of the afferent neurons, and each afferent neuron innervates many hair cells. The afferent, bipolar neurons that convey auditory information travel from the cochlea to the medulla, through the pons and midbrain in the brainstem, finally reaching the primary auditory cortex in the temporal lobe.

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20.16: Vestibular Information

The stimuli associated with the vestibular system are linear acceleration (gravity) and angular acceleration and deceleration. Gravity, acceleration, and deceleration are detected by evaluating the inertia on receptive cells in the vestibular system. Gravity is detected through head position. Angular acceleration and deceleration are expressed through turning or tilting of the head.

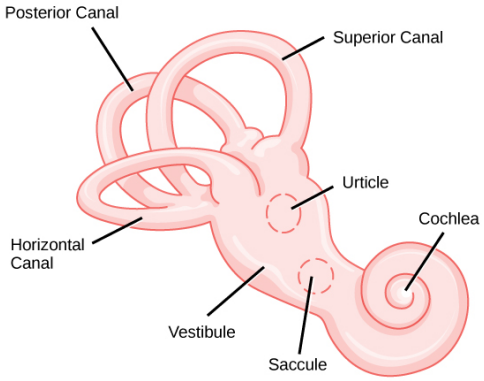


Figure 1. The structure of the vestibular labyrinth is shown. (credit: modification of work by NIH)

The vestibular system has some similarities with the auditory system. It utilizes hair cells just like the auditory system, but it excites them in different ways. There are five vestibular receptor organs in the inner ear: the utricle, the saccule, and three semicircular canals. Together, they make up what's known as the vestibular labyrinth that is shown in Figure 1. The utricle and saccule respond to acceleration in a straight line, such as gravity. The roughly 30,000 hair cells in the utricle and 16,000 hair cells in the saccule lie below a gelatinous layer, with their stereocilia projecting into the gelatin. Embedded in this gelatin are calcium carbonate crystals—like tiny rocks. When the head is tilted, the crystals continue to be pulled straight down by gravity, but the new angle of the head causes the gelatin to shift, thereby bending the stereocilia. The bending of the stereocilia stimulates the neurons, and they signal to the brain that the head is tilted, allowing the maintenance of balance. It is the vestibular branch of the vestibulocochlear cranial nerve that deals with balance.

The fluid-filled **semicircular canals** are tubular loops set at oblique angles. They are arranged in three spatial planes. The base of each canal has a swelling that contains a cluster of hair cells. The hairs project into a gelatinous cap called the cupula and monitor angular acceleration and deceleration from rotation. They would be stimulated by driving your car around a corner, turning your head, or falling forward. One canal lies horizontally, while the other two lie at about 45 degree angles to the horizontal axis, as illustrated in Figure 1. When the brain processes input from all three canals together, it can detect angular acceleration or deceleration in three dimensions. When the head turns, the fluid in the canals shifts, thereby bending stereocilia and sending signals to the brain. Upon cessation accelerating or decelerating—or just moving—the movement of the fluid within the canals slows or stops. For example, imagine holding a glass of water. When moving forward, water may splash backwards onto the hand, and when motion has stopped, water may splash forward onto the fingers. While in motion, the water settles in the glass and does not splash. Note that the canals are not sensitive to velocity itself, but to changes in velocity, so moving forward at 60mph with your eyes closed would not give the sensation of movement, but suddenly accelerating or braking would stimulate the receptors.

Higher Processing

Hair cells from the utricle, saccule, and semicircular canals also communicate through bipolar neurons to the cochlear nucleus in the medulla. Cochlear neurons send descending projections to the spinal cord and ascending projections to the pons, thalamus, and cerebellum. Connections to the cerebellum are important for coordinated movements. There are also projections to the temporal cortex, which account for feelings of dizziness; projections to autonomic nervous system areas in the brainstem, which account for motion sickness; and projections to the primary somatosensory cortex, which monitors subjective measurements of the external world and self-movement. People with lesions in the vestibular area of the somatosensory cortex see vertical objects in the world as being tilted. Finally, the vestibular signals project to certain optic muscles to coordinate eye and head movements.

Click through this interactive tutorial to review the parts of the ear and how they function to process sound.

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20.17: Introduction to Vision

Trace the path of light through the eye to the point of the optic nerve

Vision is the ability to detect light patterns from the outside environment and interpret them into images. Animals are bombarded with sensory information, and the sheer volume of visual information can be problematic. Fortunately, the visual systems of species have evolved to attend to the most-important stimuli. The importance of vision to humans is further substantiated by the fact that about one-third of the human cerebral cortex is dedicated to analyzing and perceiving visual information.

What You'll Learn to Do

- Explain how electromagnetic waves differs from sound waves
- Identify the structures found in an eye
- Trace the path of light through the eye to the point of the optic nerve
- Identify the parts of the brain associated with vision

Learning Activities

The learning activities for this section include the following:

- Light
- Anatomy of the Eye
- Transduction of Light
- Vision in the Brain
- Self Check: Vision

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20.18: Light

As with auditory stimuli, light travels in waves. The compression waves that compose sound must travel in a medium—a gas, a liquid, or a solid. In contrast, light is composed of electromagnetic waves and needs no medium; light can travel in a vacuum (Figure 1). The behavior of light can be discussed in terms of the behavior of waves and also in terms of the behavior of the fundamental unit of light—a packet of electromagnetic radiation called a photon. A glance at the electromagnetic spectrum shows that visible light for humans is just a small slice of the entire spectrum, which includes radiation that we cannot see as light because it is below the frequency of visible red light and above the frequency of visible violet light.

Certain variables are important when discussing perception of light. Wavelength (which varies inversely with frequency) manifests itself as hue. Light at the red end of the visible spectrum has longer wavelengths (and is lower frequency), while light at the violet end has shorter wavelengths (and is higher frequency). The wavelength of light is expressed in nanometers (abbreviated nm); one nanometer is one billionth of a meter. Humans perceive light that ranges between approximately 380 nm and 740 nm. Some other animals, though, can detect wavelengths outside of the human range. For example, bees see near-ultraviolet light in order to locate nectar guides on flowers, and some non-avian reptiles sense infrared light (heat that prey gives off).

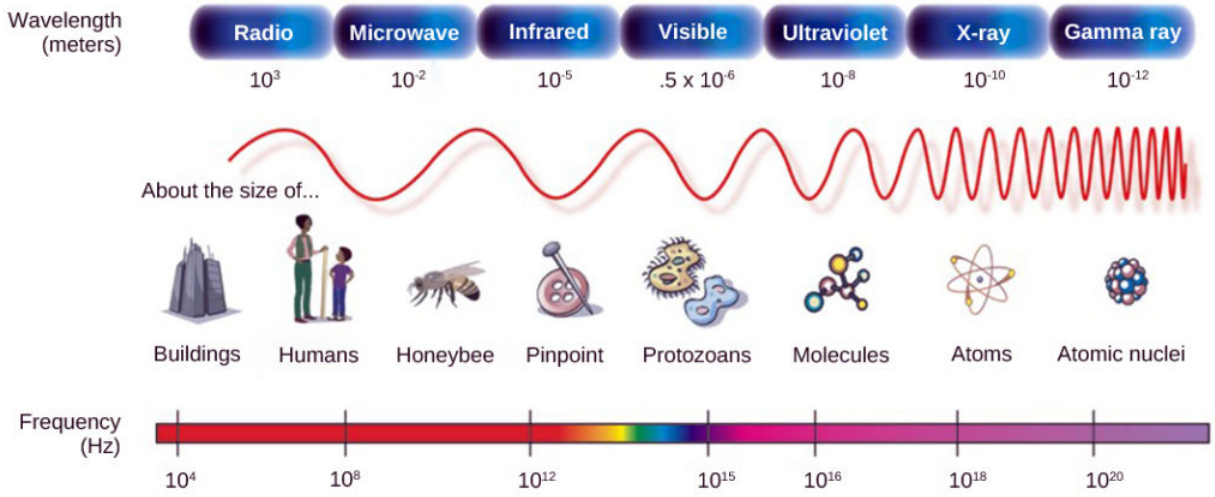


Figure 1. In the electromagnetic spectrum, visible light lies between 380 nm and 740 nm. (credit: modification of work by NASA)

Wave amplitude is perceived as luminous intensity, or brightness. The standard unit of intensity of light is the **candela**, which is approximately the luminous intensity of a one common candle.

Light waves travel 299,792 km per second in a vacuum, (and somewhat slower in various media such as air and water), and those waves arrive at the eye as long (red), medium (green), and short (blue) waves. What is termed “white light” is light that is perceived as white by the human eye. This effect is produced by light that stimulates equally the color receptors in the human eye. The apparent color of an object is the color (or colors) that the object reflects. Thus a red object reflects the red wavelengths in mixed (white) light and absorbs all other wavelengths of light.

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20.19: Anatomy of the Eye

The photoreceptive cells of the eye, where transduction of light to nervous impulses occurs, are located in the **retina** (shown in Figure 1) on the inner surface of the back of the eye. But light does not impinge on the retina unaltered. It passes through other layers that process it so that it can be interpreted by the retina (Figure 1b). The **cornea**, the front transparent layer of the eye, and the crystalline **lens**, a transparent convex structure behind the cornea, both refract (bend) light to focus the image on the retina. The **iris**, which is conspicuous as the colored part of the eye, is a circular muscular ring lying between the lens and cornea that regulates the amount of light entering the eye. In conditions of high ambient light, the iris contracts, reducing the size of the pupil at its center. In conditions of low light, the iris relaxes and the pupil enlarges.

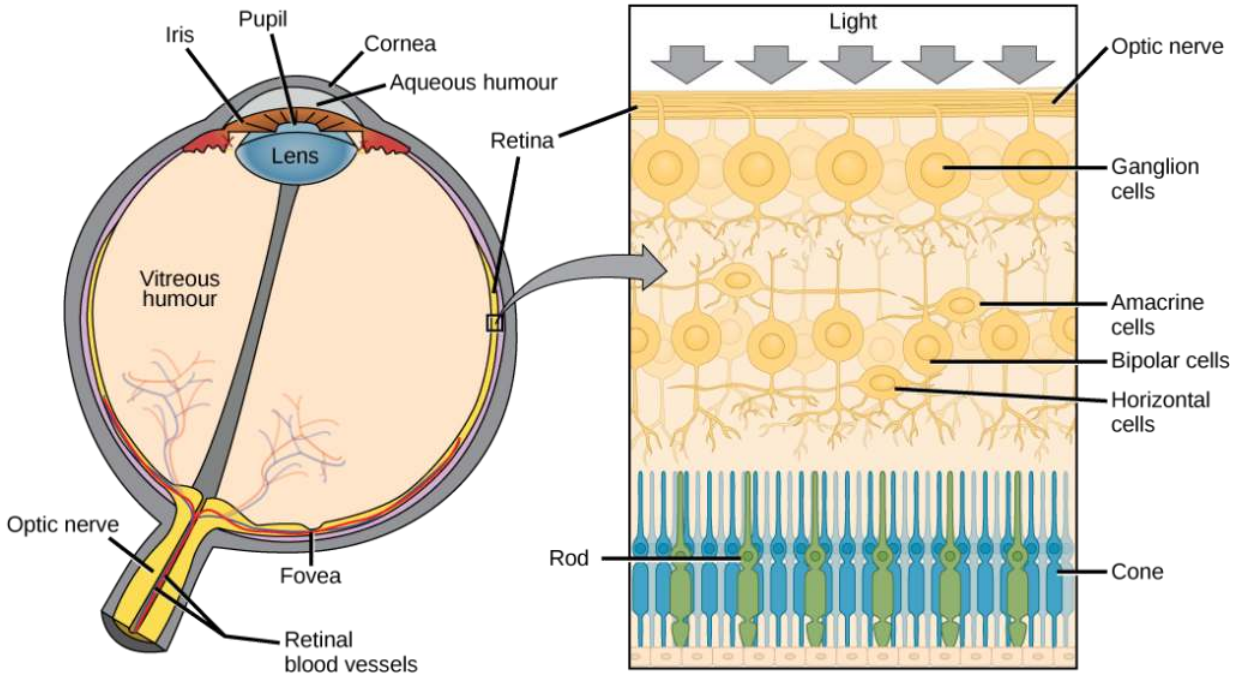


Figure 1. (a) The human eye is shown in cross section. (b) A blowup shows the layers of the retina.

Practice Question

Which of the following statements about the human eye is false?

a. Rods detect color, while cones detect only shades of gray.
b. When light enters the retina, it passes the ganglion cells and bipolar cells before reaching photoreceptors at the rear of the eye.
c. The iris adjusts the amount of light coming into the eye.
d. The cornea is a protective layer on the front of the eye.

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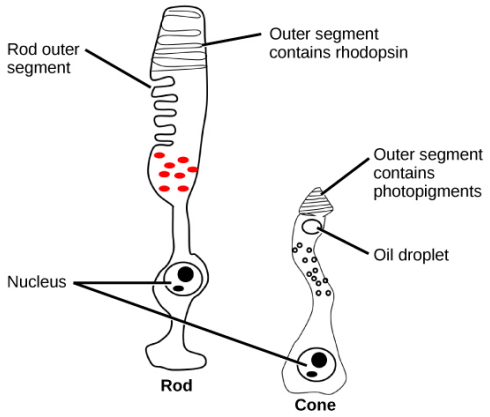


Figure 2. Rods and cones are photoreceptors in the retina. Rods respond in low light and can detect only shades of gray. Cones respond in intense light and are responsible for color vision. (credit: modification of work by Piotr Sliwa)

The main function of the lens is to focus light on the retina and fovea centralis. The lens is dynamic, focusing and re-focusing light as the eye rests on near and far objects in the visual field. The lens is operated by muscles that stretch it flat or allow it to thicken, changing the focal length of light coming through it to focus it sharply on the retina. With age comes the loss of the flexibility of the lens, and a form of farsightedness called **presbyopia** results. Presbyopia occurs because the image focuses behind the retina. Presbyopia is a deficit similar to a different type of farsightedness called **hyperopia** caused by an eyeball that is too short. For both defects, images in the distance are clear but images nearby are blurry. **Myopia** (nearsightedness) occurs when an eyeball is elongated and the image focus falls in front of the retina. In this case, images in the distance are blurry but images nearby are clear.

There are two types of photoreceptors in the retina: **rods** and **cones**, named for their general appearance as illustrated in Figure 2. Rods are strongly photosensitive and are located in the outer edges of the retina. They detect dim light and are used primarily for peripheral and nighttime vision. Cones are weakly photosensitive and are located near the center of the retina. They respond to bright light, and their primary role is in daytime, color vision.

The **fovea** is the region in the center back of the eye that is responsible for acute vision. The fovea has a high density of cones. When you bring your gaze to an object to examine it intently in bright light, the eyes orient so that the object's image falls on the fovea. However, when looking at a star in the night sky or other object in dim light, the object can be better viewed by the peripheral vision because it is the rods at the edges of the retina, rather than the cones at the center, that operate better in low light. In humans, cones far outnumber rods in the fovea.

Review the anatomical structure of the eye, clicking on each part to practice identification.

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20.20: Transduction of Light

The rods and cones are the site of transduction of light to a neural signal. Both rods and cones contain photopigments. In vertebrates, the main photopigment, **rhodopsin**, has two main parts Figure 1): an opsin, which is a membrane protein (in the form of a cluster of α-helices that span the membrane), and retinal—a molecule that absorbs light.

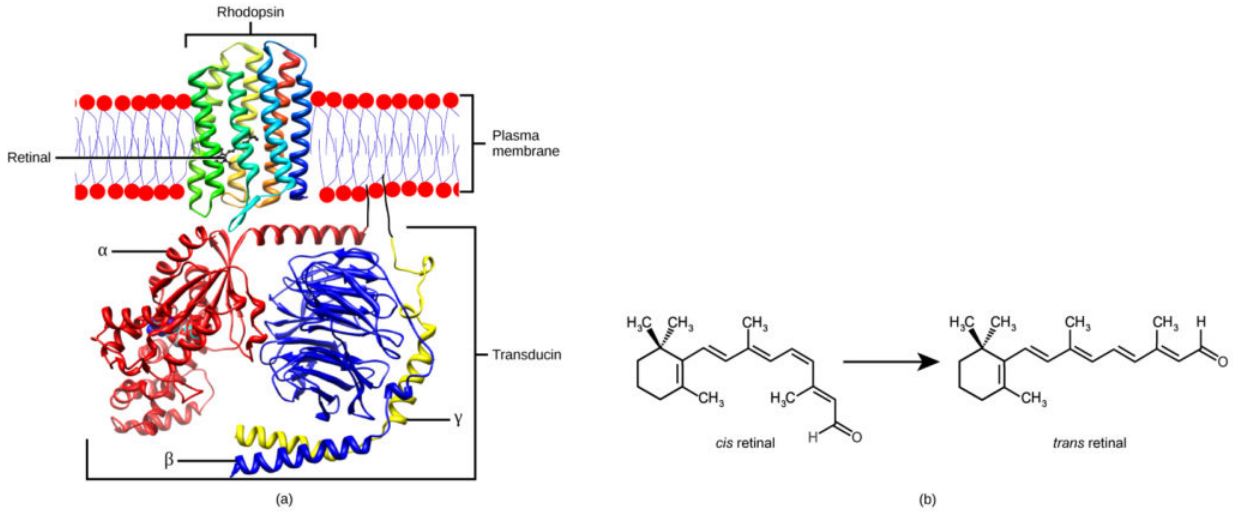


Figure 1. (a) Rhodopsin, the photoreceptor in vertebrates, has two parts: the trans-membrane protein opsin, and retinal. When light strikes retinal, it changes shape from (b) a cis to a trans form. The signal is passed to a G-protein called transducin, triggering a series of downstream events.

When light hits a photoreceptor, it causes a shape change in the retinal, altering its structure from a bent (*cis*) form of the molecule to its linear (*trans*) isomer. This isomerization of retinal activates the rhodopsin, starting a cascade of events that ends with the closing of Na^+ channels in the membrane of the photoreceptor. Thus, unlike most other sensory neurons (which become depolarized by exposure to a stimulus) visual receptors become hyperpolarized and thus driven away from threshold (Figure 2).

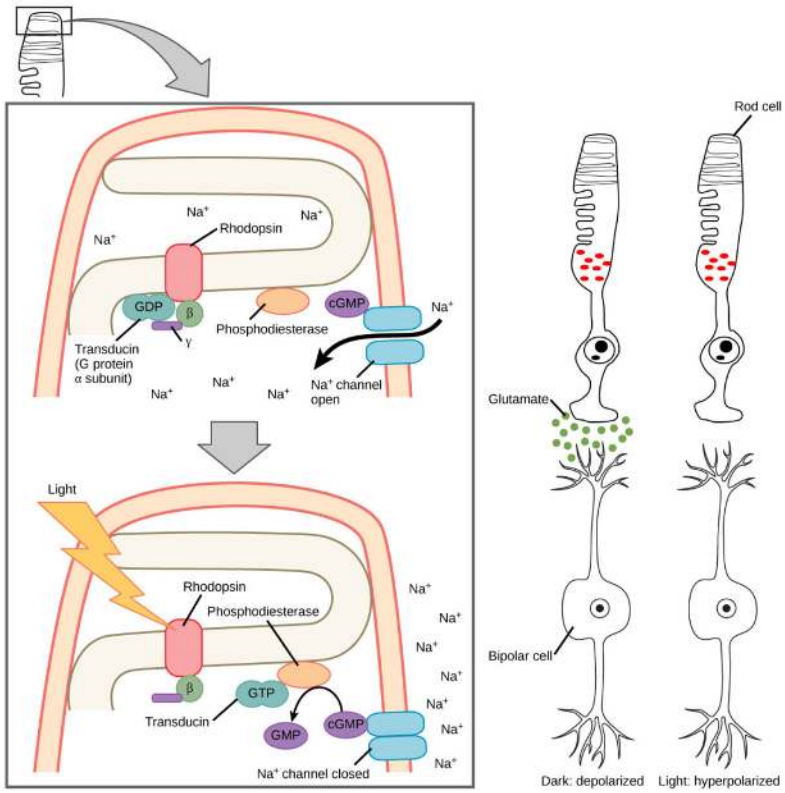


Figure 2. When light strikes rhodopsin, the G-protein transducin is activated, which in turn activates phosphodiesterase. Phosphodiesterase converts cGMP to GMP, thereby closing sodium channels. As a result, the membrane becomes hyperpolarized. The hyperpolarized membrane does not release glutamate to the bipolar cell.

Trichromatic Coding

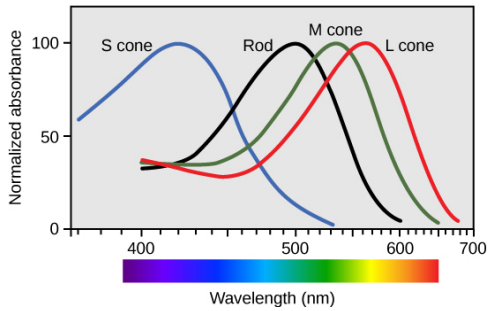


Figure 3. Human rod cells and the different types of cone cells each have an optimal wavelength. However, there is considerable overlap in the wavelengths of light detected.

There are three types of cones (with different photopsins), and they differ in the wavelength to which they are most responsive, as shown in Figure 3. Some cones are maximally responsive to short light waves of 420 nm, so they are called S cones (“S” for “short”); others respond maximally to waves of 530 nm (M cones, for “medium”); a third group responds maximally to light of longer wavelengths, at 560 nm (L, or “long” cones). With only one type of cone, color vision would not be possible, and a two-cone (dichromatic) system has limitations. Primates use a three-cone (trichromatic) system, resulting in full color vision.

The color we perceive is a result of the ratio of activity of our three types of cones. The colors of the visual spectrum, running from long-wavelength light to short, are red (700 nm), orange (600 nm), yellow (565 nm), green (497 nm), blue (470 nm), indigo (450 nm), and violet (425 nm). Humans have very sensitive perception of color and can distinguish about 500 levels of brightness, 200 different hues, and 20 steps of saturation, or about 2 million distinct colors.

Retinal Processing

Visual signals leave the cones and rods, travel to the bipolar cells, and then to ganglion cells. A large degree of processing of visual information occurs in the retina itself, before visual information is sent to the brain.

Photoreceptors in the retina continuously undergo **tonic activity**. That is, they are always slightly active even when not stimulated by light. In neurons that exhibit tonic activity, the absence of stimuli maintains a firing rate at a baseline; while some stimuli increase firing rate from the baseline, and other stimuli decrease firing rate. In the absence of light, the bipolar neurons that connect rods and cones to ganglion cells are continuously and actively inhibited by the rods and cones. Exposure of the retina to light hyperpolarizes the rods and cones and removes their inhibition of bipolar cells. The now active bipolar cells in turn stimulate the ganglion cells, which send action potentials along their axons (which leave the eye as the optic nerve). Thus, the visual system relies on change in retinal activity, rather than the absence or presence of activity, to encode visual signals for the brain. Sometimes horizontal cells carry signals from one rod or cone to other photoreceptors and to several bipolar cells. When a rod or cone stimulates a horizontal cell, the horizontal cell inhibits more distant photoreceptors and bipolar cells, creating lateral inhibition. This inhibition sharpens edges and enhances contrast in the images by making regions receiving light appear lighter and dark surroundings appear darker. Amacrine cells can distribute information from one bipolar cell to many ganglion cells.

You can demonstrate this using an easy demonstration to “trick” your retina and brain about the colors you are observing in your visual field. Look fixedly at Figure 4 for about 45 seconds. Then quickly shift your gaze to a sheet of blank white paper or a white wall. You should see an afterimage of the Norwegian flag in its correct colors. At this point, close your eyes for a moment, then reopen them, looking again at the white paper or wall; the afterimage of the flag should continue to appear as red, white, and blue.

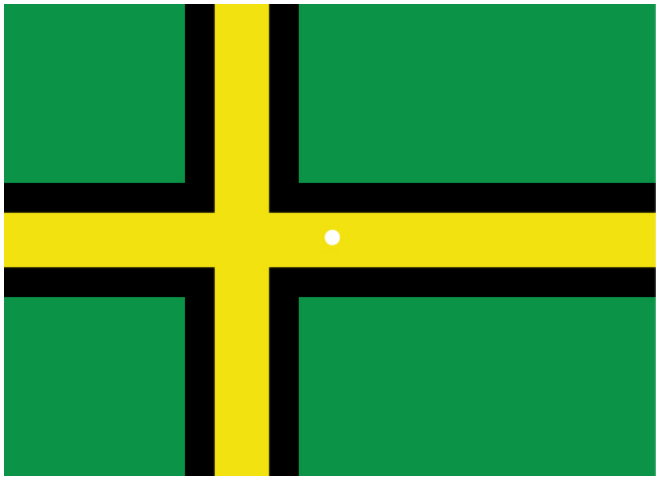


Figure 4. View this flag to understand how retinal processing works. Stare at the center of the flag (indicated by the white dot) for 45 seconds, and then quickly look at a white background, noticing how colors appear.

What causes this? According to an explanation called opponent process theory, as you gazed fixedly at the green, black, and yellow flag, your retinal ganglion cells that respond positively to green, black, and yellow increased their firing dramatically. When you shifted your gaze to the neutral white ground, these ganglion cells abruptly decreased their activity and the brain interpreted this abrupt downshift as if the ganglion cells were responding now to their “opponent” colors: red, white, and blue, respectively, in the visual field. Once the ganglion cells return to their baseline activity state, the false perception of color will disappear.

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20.21: Vision in the Brain

The myelinated axons of ganglion cells make up the optic nerves. Within the nerves, different axons carry different qualities of the visual signal. Some axons constitute the magnocellular (big cell) pathway, which carries information about form, movement, depth, and differences in brightness. Other axons constitute the parvocellular (small cell) pathway, which carries information on color and fine detail. Some visual information projects directly back into the brain, while other information crosses to the opposite side of the brain. This crossing of optical pathways produces the distinctive optic chiasma (Greek, for “crossing”) found at the base of the brain and allows us to coordinate information from both eyes.

Once in the brain, visual information is processed in several places, and its routes reflect the complexity and importance of visual information to humans and other animals. One route takes the signals to the thalamus, which serves as the routing station for all incoming sensory impulses except olfaction. In the thalamus, the magnocellular and parvocellular distinctions remain intact, and there are different layers of the thalamus dedicated to each. When visual signals leave the thalamus, they travel to the primary visual cortex at the rear of the brain. From the visual cortex, the visual signals travel in two directions. One stream that projects to the parietal lobe, in the side of the brain, carries magnocellular (“where”) information. A second stream projects to the temporal lobe and carries both magnocellular (“where”) and parvocellular (“what”) information.

Another important visual route is a pathway from the retina to the **superior colliculus** in the midbrain, where eye movements are coordinated and integrated with auditory information. Finally, there is the pathway from the retina to the **suprachiasmatic nucleus** (SCN) of the hypothalamus. The SCN is a cluster of cells that is considered to be the body’s internal clock, which controls our **circadian** (day-long) cycle. The SCN sends information to the pineal gland, which is important in sleep/wake patterns and annual cycles.

View this interactive presentation to review what you have learned about how vision functions.

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20.22: Putting It Together- The Sensory System

These videos walk you through the way we experience our major special senses. It all boils down to one thing: sensory cells translating chemical, electromagnetic, and mechanical stimuli into action potentials that our nervous system can make sense of.



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Career Connection

There are different professions that focus on human senses. Most likely, the profession you're most familiar with in this category is optometrists (eye doctors).

? Try It

Optometrists examine the eyes and other parts of the visual system. They also diagnose and treat visual problems and manage diseases, injuries, and other disorders of the eyes. They prescribe eyeglasses or contact lenses as needed.

Some optometrists spend much of their time providing specialized care, particularly if they are working in a group practice with other optometrists or physicians. For example, some optometrists mostly treat patients with only partial sight, a condition known as low vision. Others may focus on treating infants and children.

Optometrists promote eye health and counsel patients on how general health can affect eyesight. For example, they may counsel patients on how smoking cessation or weight loss can reduce vision problems.

Many optometrists own their practice and those who do may spend more time on general business activities, such as hiring employees, ordering supplies, and marketing their business.

Optometrists should not be confused with ophthalmologists or dispensing opticians. Ophthalmologists are physicians who perform eye surgery and treat eye diseases in addition to performing eye exams and prescribing eyeglasses and contact lenses. For more information on ophthalmologists, see the physicians and surgeons profile. Dispensing opticians fit and adjust eyeglasses and, in some states, fill contact lens prescriptions that an optometrist or ophthalmologist has written.

There are also audiologists, who diagnose, manage, and treat a patient's hearing, balance, or ear problems.

? Try It

Audiologists use audiometers, computers, and other devices to test patients' hearing ability and balance. They work to determine the extent of hearing damage and identify the underlying cause. Audiologists measure the loudness at which a person begins to hear sounds and the person's ability to distinguish between sounds and understand speech.

Before determining treatment options, audiologists evaluate psychological information to measure the impact of hearing loss on a patient. Treatment may include cleaning wax out of ear canals, fitting and checking hearing aids, or fitting the patient with cochlear implants to improve hearing. Cochlear implants are tiny devices that are placed under the skin near the ear and deliver electrical impulses directly to the auditory nerve in the brain. This allows a person with certain types of deafness to be able to hear.

Audiologists also counsel patients on other ways to cope with profound hearing loss, such as by learning to lip read or by using technology.

Audiologists can help a patient suffering from vertigo or other balance problems. They work with patients and provide them with exercises involving head movement or positioning that might relieve some of their symptoms.

Some audiologists specialize in working with the elderly or with children. Others educate the public on hearing loss prevention. Audiologists may design products to help protect the hearing of workers on the job. Audiologists who are self-employed hire employees, keep records, order equipment and supplies, and complete other tasks related to running a business.

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20.23: Cerego- Sensory Systems

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for Sensory Systems. You'll need to create a free log-in to practice these items, if you haven't already.

https://cerego.com/sets/796523/learn

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CHAPTER OVERVIEW

21: Module 18- The Circulatory System

21.1: Why It Matters- The Circulatory System
21.2: Introduction to the Circulatory System
21.3: Circulatory System Architecture
21.4: Circulatory System Variation in Animals
21.5: Introduction to Structure and Function of Blood
21.6: The Role of Blood in the Body
21.7: Blood Cells
21.8: Components of Blood
21.9: Introduction to the Mammalian Heart
21.10: Structure of the Heart
21.11: The Cardiac Cycle
21.12: Introduction to Blood Flow and Blood Pressure Regulation
21.13: Blood Vessels
21.14: Blood Circulation
21.15: Blood Pressure
21.16: Putting It Together- The Circulatory System
21.17: Cerego- The Circulatory System

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21.1: Why It Matters- The Circulatory System

Why describe the components and role of the circulatory system?



Figure 1. Just as highway systems transport people and goods through a complex network, the circulatory system transports nutrients, gases, and wastes throughout the animal body. (credit: modification of work by Andrey Belenko)

Most animals are complex multicellular organisms that require a mechanism for transporting nutrients throughout their bodies and removing waste products. The circulatory system has evolved over time from simple diffusion through cells in the early evolution of animals to a complex network of blood vessels that reach all parts of the human body. This extensive network supplies the cells, tissues, and organs with oxygen and nutrients, and removes carbon dioxide and waste, which are byproducts of respiration.

At the core of the human circulatory system is the heart. The size of a clenched fist, the human heart is protected beneath the rib cage. Made of specialized and unique cardiac muscle, it pumps blood throughout the body and to the heart itself. Heart contractions are driven by intrinsic electrical impulses that the brain and endocrine hormones help to regulate. Understanding the heart's basic anatomy and function is important to understanding the body's circulatory and respiratory systems.

Gas exchange is one essential function of the circulatory system. A circulatory system is not needed in organisms with no specialized respiratory organs because oxygen and carbon dioxide diffuse directly between their body tissues and the external environment. However, in organisms that possess lungs and gills, oxygen must be transported from these specialized respiratory organs to the body tissues via a circulatory system. Therefore, circulatory systems have had to evolve to accommodate the great diversity of body sizes and body types present among animals.

Learning Outcomes

- Describe the organization of the vertebrate circulatory system
- Describe the structure and function of blood in the body
- Describe the structure of the heart and explain how cardiac muscle is different from other muscles
- Explain the structure of arteries, veins, and capillaries, and how blood flows through the body

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21.2: Introduction to the Circulatory System

Describe the organization of the vertebrate circulatory system

In all animals, except a few simple types, the circulatory system is used to transport nutrients and gases through the body. Simple diffusion allows some water, nutrient, waste, and gas exchange into primitive animals that are only a few cell layers thick; however, bulk flow is the only method by which the entire body of larger more complex organisms is accessed.

What You'll Learn to Do

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

Learning Activities

The learning activities for this section include the following:

- Circulatory System Architecture
- Circulatory System Variation in Animals
- Self Check: The Circulatory System

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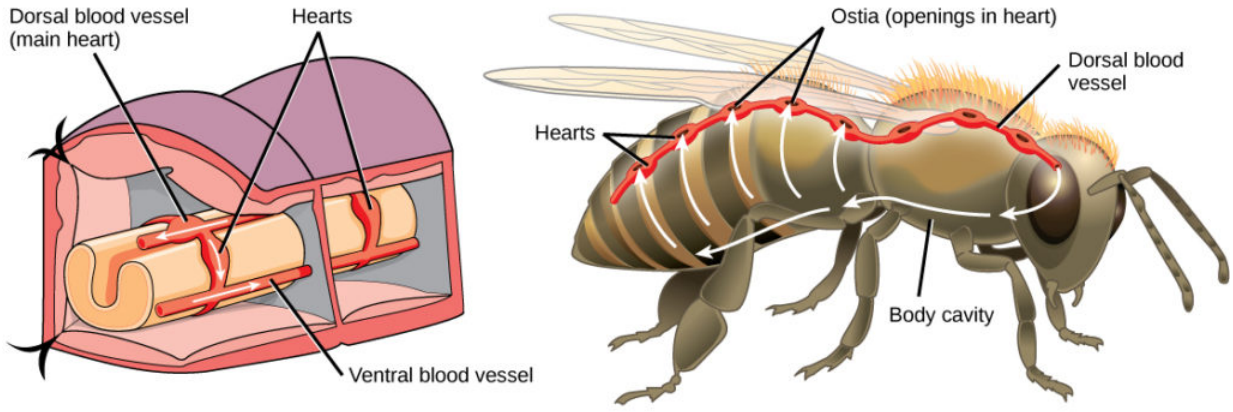
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21.3: Circulatory System Architecture

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

Closed Circulatory Systems

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



(a) Closed circulatory system (b) Open circulatory system

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

Open Circulatory Systems

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

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21.4: Circulatory System Variation in Animals

The circulatory system varies from simple systems in invertebrates to more complex systems in vertebrates. The simplest animals, such as the sponges (Porifera) and rotifers (Rotifera), do not need a circulatory system because diffusion allows adequate exchange of water, nutrients, and waste, as well as dissolved gases, as shown in Figure 1a. Organisms that are more complex but still only have two layers of cells in their body plan, such as jellies (Cnidaria) and comb jellies (Ctenophora) also use diffusion through their epidermis and internally through the gastrovascular compartment. Both their internal and external tissues are bathed in an aqueous environment and exchange fluids by diffusion on both sides, as illustrated in Figure 1b. Exchange of fluids is assisted by the pulsing of the jellyfish body.

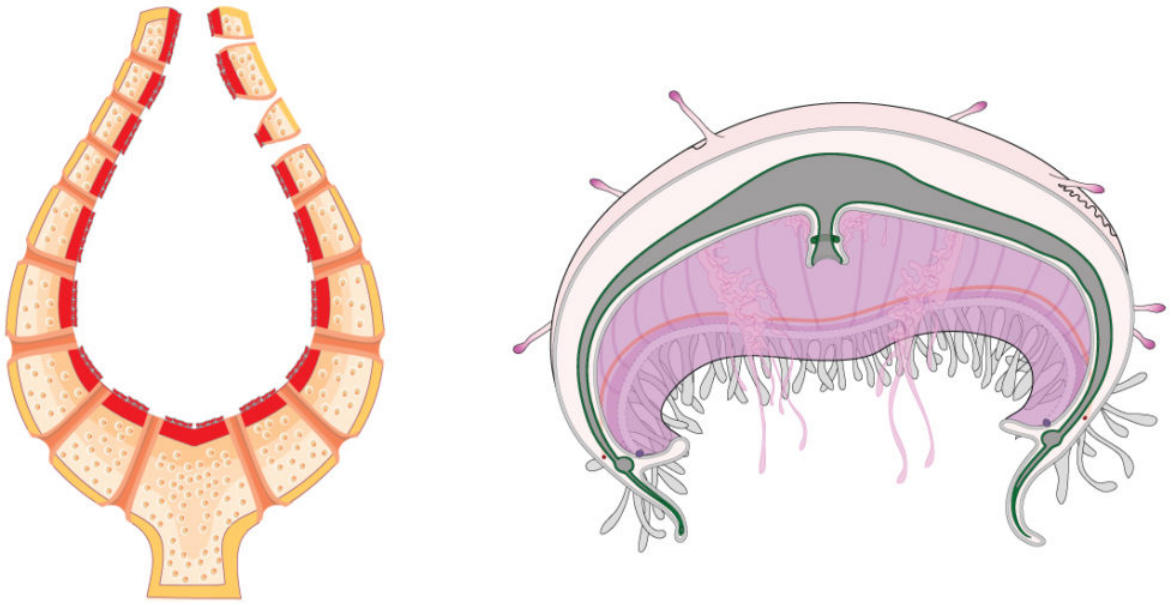


Figure 1. Simple animals consisting of a single cell layer such as the (a) sponge or only a few cell layers such as the (b) jellyfish do not have a circulatory system. Instead, gases, nutrients, and wastes are exchanged by diffusion.

For more complex organisms, diffusion is not efficient for cycling gases, nutrients, and waste effectively through the body; therefore, more complex circulatory systems evolved. Most arthropods and many mollusks have open circulatory systems. In an open system, an elongated beating heart pushes the hemolymph through the body and muscle contractions help to move fluids. The larger more complex crustaceans, including lobsters, have developed arterial-like vessels to push blood through their bodies, and the most active mollusks, such as squids, have evolved a closed circulatory system and are able to move rapidly to catch prey. Closed circulatory systems are a characteristic of vertebrates; however, there are significant differences in the structure of the heart and the circulation of blood between the different vertebrate groups due to adaptation during evolution and associated differences in anatomy. Figures 2 and 3 illustrates the basic circulatory systems of some vertebrates: fish, amphibians, reptiles, and mammals.

As illustrated in Figure 2a, fish have a single circuit for blood flow and a two-chambered heart that has only a single atrium and a single ventricle. The atrium collects blood that has returned from the body and the ventricle pumps the blood to the gills where gas exchange occurs and the blood is re-oxygenated; this is called **gill circulation**. The blood then continues through the rest of the body before arriving back at the atrium; this is called **systemic circulation**. This unidirectional flow of blood produces a gradient of oxygenated to deoxygenated blood around the fish's systemic circuit. The result is a limit in the amount of oxygen that can reach some of the organs and tissues of the body, reducing the overall metabolic capacity of fish.

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

As shown in Figure 2b, amphibians have a three-chambered heart that has two atria and one ventricle rather than the two-chambered heart of fish. The two **atria** (superior heart chambers) receive blood from the two different circuits (the lungs and the systems), and then there is some mixing of the blood in the heart's **ventricle** (inferior heart chamber), which reduces the efficiency of oxygenation. The advantage to this arrangement is that high pressure in the vessels pushes blood to the lungs and body. The mixing is mitigated by a ridge within the ventricle that diverts oxygen-rich blood through the systemic circulatory system and deoxygenated blood to the pulmocutaneous circuit. For this reason, amphibians are often described as having **double circulation**.

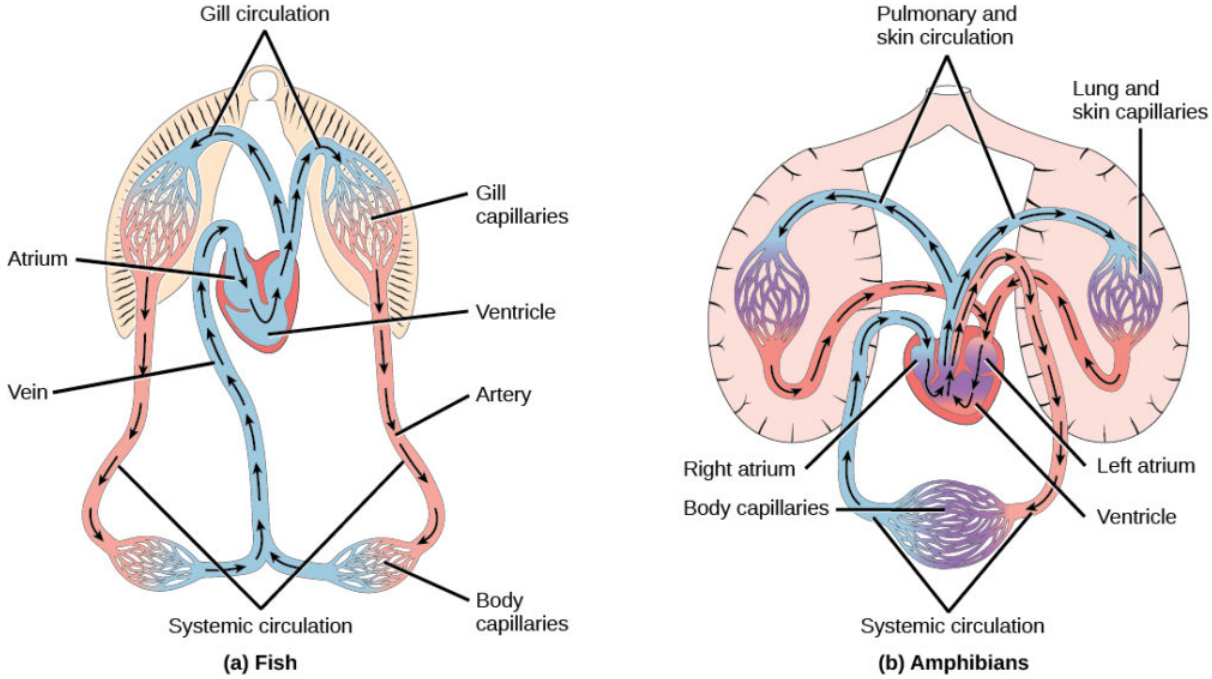


Figure 2. (a) Fish have the simplest circulatory systems of the vertebrates: blood flows unidirectionally from the two-chambered heart through the gills and then the rest of the body. (b) Amphibians have two circulatory routes: one for oxygenation of the blood through the lungs and skin, and the other to take oxygen to the rest of the body. The blood is pumped from a three-chambered heart with two atria and a single ventricle.

Most reptiles also have a three-chambered heart similar to the amphibian heart that directs blood to the pulmonary and systemic circuits, as shown in Figure 3a. The ventricle is divided more effectively by a partial septum, which results in less mixing of oxygenated and deoxygenated blood. Some reptiles (alligators and crocodiles) are the most primitive animals to exhibit a four-chambered heart. Crocodilians have a unique circulatory mechanism where the heart shunts blood from the lungs toward the stomach and other organs during long periods of submergence, for instance, while the animal waits for prey or stays underwater waiting for prey to rot. One adaptation includes two main arteries that leave the same part of the heart: one takes blood to the lungs and the other provides an alternate route to the stomach and other parts of the body. Two other adaptations include a hole in the heart between the two ventricles, called the foramen of Panizza, which allows blood to move from one side of the heart to the other, and specialized connective tissue that slows the blood flow to the lungs. Together these adaptations have made crocodiles and alligators one of the most evolutionarily successful animal groups on earth.

In mammals and birds, the heart is also divided into four chambers: two atria and two ventricles, as illustrated in Figure 3b. The oxygenated blood is separated from the deoxygenated blood, which improves the efficiency of double circulation and is probably required for the warm-blooded lifestyle of mammals and birds. The four-chambered heart of birds and mammals evolved independently from a three-chambered heart. The independent evolution of the same or a similar biological trait is referred to as convergent evolution.

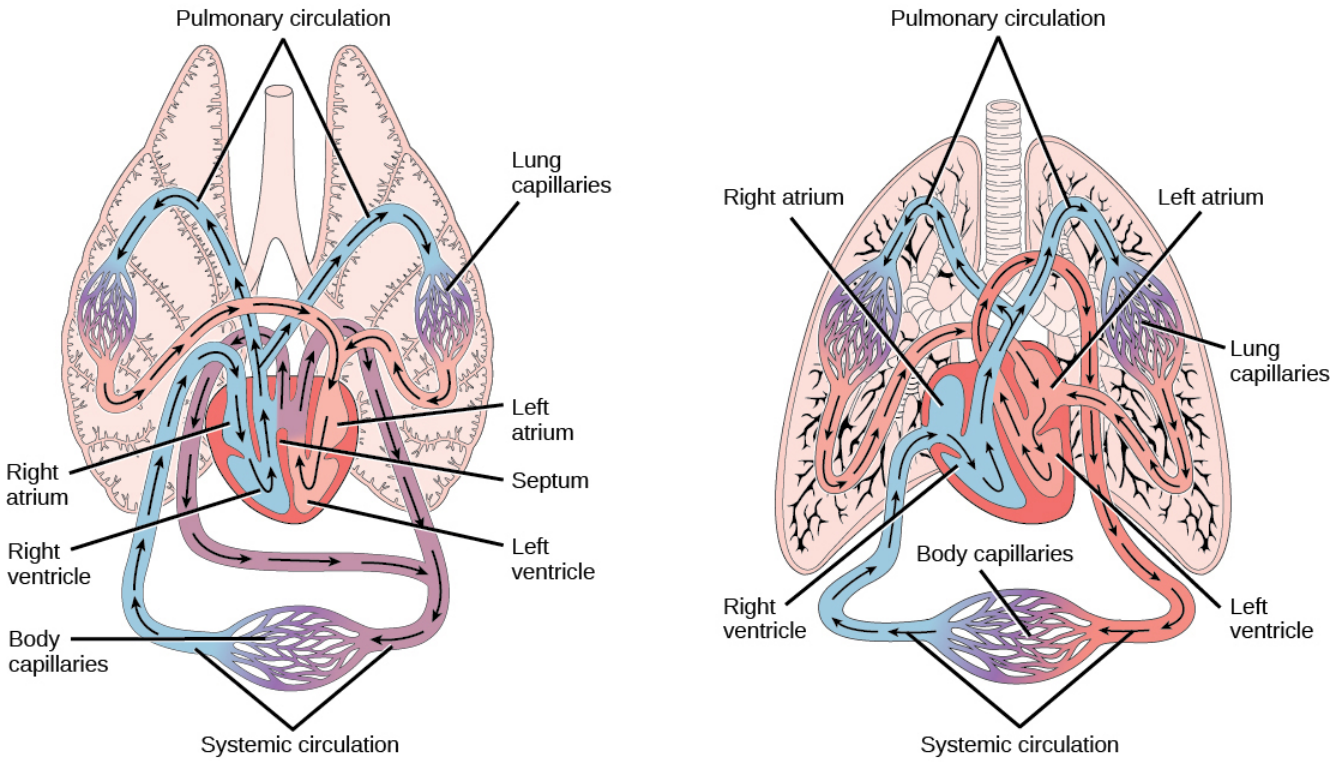


Figure 3. (a) Reptiles also have two circulatory routes; however, blood is only oxygenated through the lungs. The heart is three chambered, but the ventricles are partially separated so some mixing of oxygenated and deoxygenated blood occurs except in crocodilians and birds. (b) Mammals and birds have the most efficient heart with four chambers that completely separate the oxygenated and deoxygenated blood; it pumps only oxygenated blood through the body and deoxygenated blood to the lungs.

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21.5: Introduction to Structure and Function of Blood

Describe the structure and function of blood in the body

Blood is important for regulation of the body's pH, temperature, osmotic pressure, the circulation of nutrients and removal of waste, the distribution of hormones from endocrine glands, and the elimination of excess heat; it also contains components for blood clotting. Blood is made of of several components, including red blood cells, white blood cells, platelets, and the plasma, which contains coagulation factors and serum.

What You'll Learn to Do

- Identify the role of blood in the body
- Compare red and white blood cells
- Describe the basic components of the blood

Learning Activities

The learning activities for this section include the following:

- The Role of Blood in the Body
- Blood Cells
- Components of Blood
- Self Check: Structure and Function of Blood

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21.6: The Role of Blood in the Body

Blood, like the human blood illustrated in Figure 1 is important for regulation of the body's systems and homeostasis. Blood helps maintain homeostasis by stabilizing pH, temperature, osmotic pressure, and by eliminating excess heat. Blood supports growth by distributing nutrients and hormones, and by removing waste. **Red blood cells** contain hemoglobin, which binds oxygen. These cells deliver oxygen to the cells and remove carbon dioxide.

Blood plays a protective role by transporting clotting factors and **platelets** to prevent blood loss after injury. Blood also transports the disease-fighting agents **white blood cells** to sites of infection. These cells—including neutrophils, monocytes, lymphocytes, eosinophils, and basophils—are involved in the immune response.

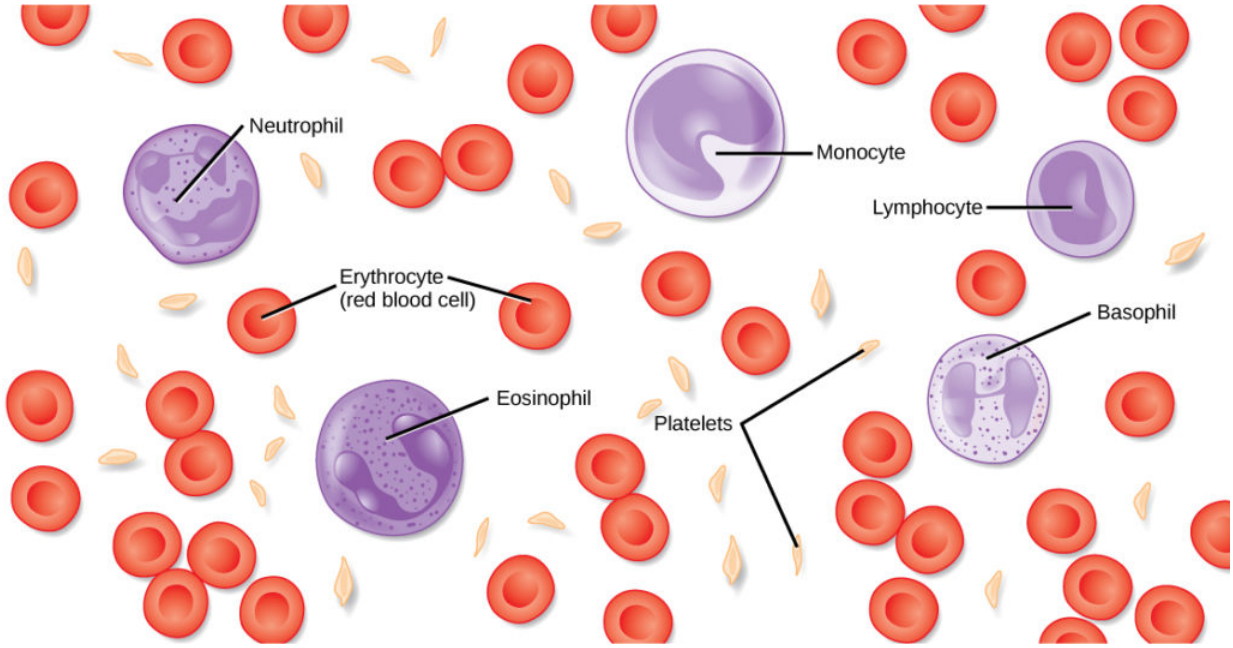


Figure 1. The cells and cellular components of human blood are shown.

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21.7: Blood Cells

Red Blood Cells

Red blood cells, or erythrocytes (*erythro–* = "red"; *–cyte* = "cell"), are specialized cells that circulate through the body delivering oxygen to cells; they are formed from stem cells in the bone marrow. In mammals, red blood cells are small biconcave cells that at maturity do not contain a nucleus or mitochondria and are only 7–8 µm in size. In birds and non-avian reptiles, a nucleus is still maintained in red blood cells.

The red coloring of blood comes from the iron-containing protein hemoglobin, illustrated in Figure 1a. The principal job of this protein is to carry oxygen, but it also transports carbon dioxide as well. Hemoglobin is packed into red blood cells at a rate of about 250 million molecules of hemoglobin per cell. Each hemoglobin molecule binds four oxygen molecules so that each red blood cell carries one billion molecules of oxygen. There are approximately 25 trillion red blood cells in the five liters of blood in the human body, which could carry up to 25 sextillion (25×10^{21}) molecules of oxygen in the body at any time. In mammals, the lack of organelles in erythrocytes leaves more room for the hemoglobin molecules, and the lack of mitochondria also prevents use of the oxygen for metabolic respiration. Only mammals have anucleated red blood cells, and some mammals (camels, for instance) even have nucleated red blood cells. The advantage of nucleated red blood cells is that these cells can undergo mitosis. Anucleated red blood cells metabolize anaerobically (without oxygen), making use of a primitive metabolic pathway to produce ATP and increase the efficiency of oxygen transport.

Not all organisms use hemoglobin as the method of oxygen transport. Invertebrates that utilize hemolymph rather than blood use different pigments to bind to the oxygen. These pigments use copper or iron to the oxygen. Invertebrates have a variety of other respiratory pigments. Hemocyanin, a blue-green, copper-containing protein, illustrated in Figure 1b is found in mollusks, crustaceans, and some of the arthropods. Chlorocruorin, a green-colored, iron-containing pigment is found in four families of polychaete tubeworms. Hemerythrin, a red, iron-containing protein is found in some polychaete worms and annelids and is illustrated in Figure 1c. Despite the name, hemerythrin does not contain a heme group and its oxygen-carrying capacity is poor compared to hemoglobin.

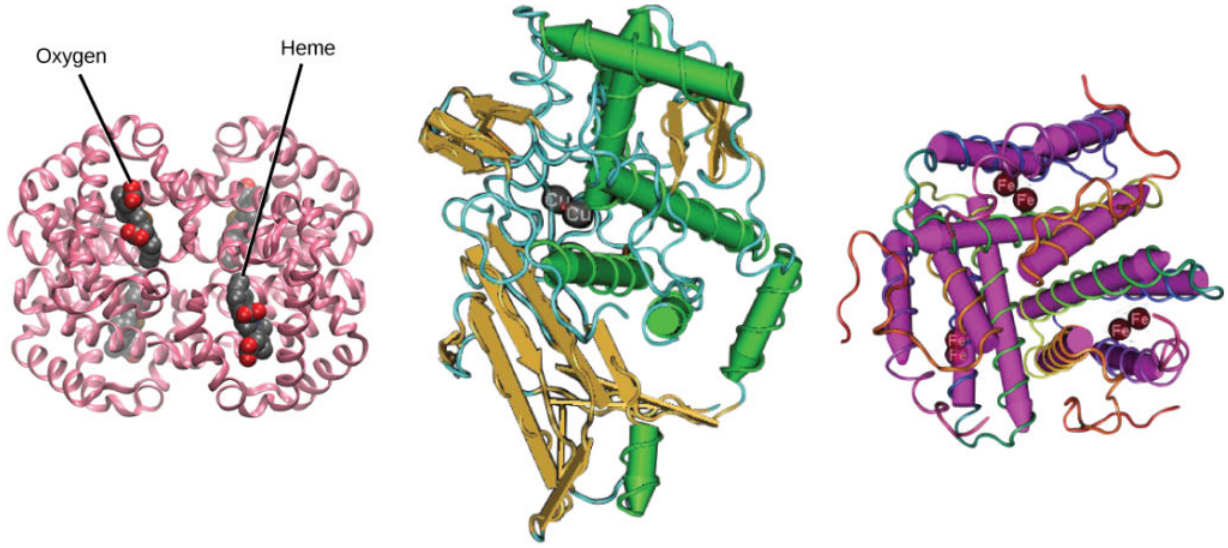


Figure 1. In most vertebrates, (a) hemoglobin delivers oxygen to the body and removes some carbon dioxide. Hemoglobin is composed of four protein subunits, two alpha chains and two beta chains, and a heme group that has iron associated with it. The iron reversibly associates with oxygen, and in so doing is oxidized from Fe^{2+} to Fe^{3+}. In most mollusks and some arthropods, (b) hemocyanin delivers oxygen. Unlike hemoglobin, hemolymph is not carried in blood cells, but floats free in the hemolymph. Copper instead of iron binds the oxygen, giving the hemolymph a blue-green color. In annelids, such as the earthworm, and some other invertebrates, (c) hemerythrin carries oxygen. Like hemoglobin, hemerythrin is carried in blood cells and has iron associated with it, but despite its name, hemerythrin does not contain heme.

The small size and large surface area of red blood cells allows for rapid diffusion of oxygen and carbon dioxide across the plasma membrane. In the lungs, carbon dioxide is released and oxygen is taken in by the blood. In the tissues, oxygen is released from the blood and carbon dioxide is bound for transport back to the lungs. Studies have found that hemoglobin also binds nitrous oxide (NO). NO is a vasodilator that relaxes the blood vessels and capillaries and may help with gas exchange and the passage of red blood cells through narrow vessels. Nitroglycerin, a heart medication for angina and heart attacks, is converted to NO to help relax the blood vessels and increase oxygen flow through the body.

A characteristic of red blood cells is their glycolipid and glycoprotein coating; these are lipids and proteins that have carbohydrate molecules attached. In humans, the surface glycoproteins and glycolipids on red blood cells vary between individuals, producing the different blood types, such as A, B, and O. Red blood cells have an average life span of 120 days, at which time they are broken down and recycled in the liver and spleen by phagocytic macrophages, a type of white blood cell.

White Blood Cells

White blood cells, also called leukocytes (leuko = white), make up approximately one percent by volume of the cells in blood. The role of white blood cells is very different than that of red blood cells: they are primarily involved in the immune response to identify and target pathogens, such as invading bacteria, viruses, and other foreign organisms. White blood cells are formed continually; some only live for hours or days, but some live for years.

The morphology of white blood cells differs significantly from red blood cells. They have nuclei and do not contain hemoglobin. The different types of white blood cells are identified by their microscopic appearance after histologic staining, and each has a different specialized function. The two main groups, both illustrated in Figure 2 are the granulocytes, which include the neutrophils, eosinophils, and basophils, and the agranulocytes, which include the monocytes and lymphocytes.



Figure 2. (a) Granulocytes—including neutrophils, eosinophils and basophils—are characterized by a lobed nucleus and granular inclusions in the cytoplasm. Granulocytes are typically first-responders during injury or infection. (b) Agranulocytes include lymphocytes and monocytes. Lymphocytes, including B and T cells, are responsible for adaptive immune response. Monocytes differentiate into macrophages and dendritic cells, which in turn respond to infection or injury.

Granulocytes contain granules in their cytoplasm; the agranulocytes are so named because of the lack of granules in their cytoplasm. Some leukocytes become macrophages that either stay at the same site or move through the blood stream and gather at sites of infection or inflammation where they are attracted by chemical signals from foreign particles and damaged cells. Lymphocytes are the primary cells of the immune system and include B cells, T cells, and natural killer cells. B cells destroy bacteria and inactivate their toxins. They also produce antibodies. T cells attack viruses, fungi, some bacteria, transplanted cells, and cancer cells. T cells attack viruses by releasing toxins that kill the viruses. Natural killer cells attack a variety of infectious microbes and certain tumor cells.

One reason that HIV poses significant management challenges is because the virus directly targets T cells by gaining entry through a receptor. Once inside the cell, HIV then multiplies using the T cell’s own genetic machinery. After the HIV virus replicates, it is transmitted directly from the infected T cell to macrophages. The presence of HIV can remain unrecognized for an extensive period of time before full disease symptoms develop

Learning Objectives

Red blood cells are specialized cells that contain hemoglobin and circulate through the body delivering oxygen to cells. White blood cells are involved in the immune response to identify and target invading bacteria, viruses, and other foreign organisms; they also recycle waste components, such as old red blood cells.

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21.8: Components of Blood

Hemoglobin is responsible for distributing oxygen, and to a lesser extent, carbon dioxide, throughout the circulatory systems of humans, vertebrates, and many invertebrates. The blood is more than the proteins, though. Blood is actually a term used to describe the liquid that moves through the vessels and includes **plasma** (the liquid portion, which contains water, proteins, salts, lipids, and glucose) and the cells (red and white cells) and cell fragments called **platelets**. Blood plasma is actually the dominant component of blood and contains the water, proteins, electrolytes, lipids, and glucose. The cells are responsible for carrying the gases (red cells) and immune the response (white). The platelets are responsible for blood clotting. Interstitial fluid that surrounds cells is separate from the blood, but in hemolymph, they are combined. In humans, cellular components make up approximately 45 percent of the blood and the liquid plasma 55 percent. Blood is 20 percent of a person's extracellular fluid and eight percent of weight.

Platelets and Coagulation Factors

Blood must clot to heal wounds and prevent excess blood loss. Small cell fragments called platelets (thrombocytes) are attracted to the wound site where they adhere by extending many projections and releasing their contents. These contents activate other platelets and also interact with other coagulation factors, which convert fibrinogen, a water-soluble protein present in blood serum into fibrin (a non-water soluble protein), causing the blood to clot. Many of the clotting factors require vitamin K to work, and vitamin K deficiency can lead to problems with blood clotting. Many platelets converge and stick together at the wound site forming a platelet plug (also called a fibrin clot), as illustrated in Figure 1b. The plug or clot lasts for a number of days and stops the loss of blood. Platelets are formed from the disintegration of larger cells called megakaryocytes, like that shown in Figure 1a. For each megakaryocyte, 2000–3000 platelets are formed with 150,000 to 400,000 platelets present in each cubic millimeter of blood. Each platelet is disc shaped and 2–4 μm in diameter. They contain many small vesicles but do not contain a nucleus.

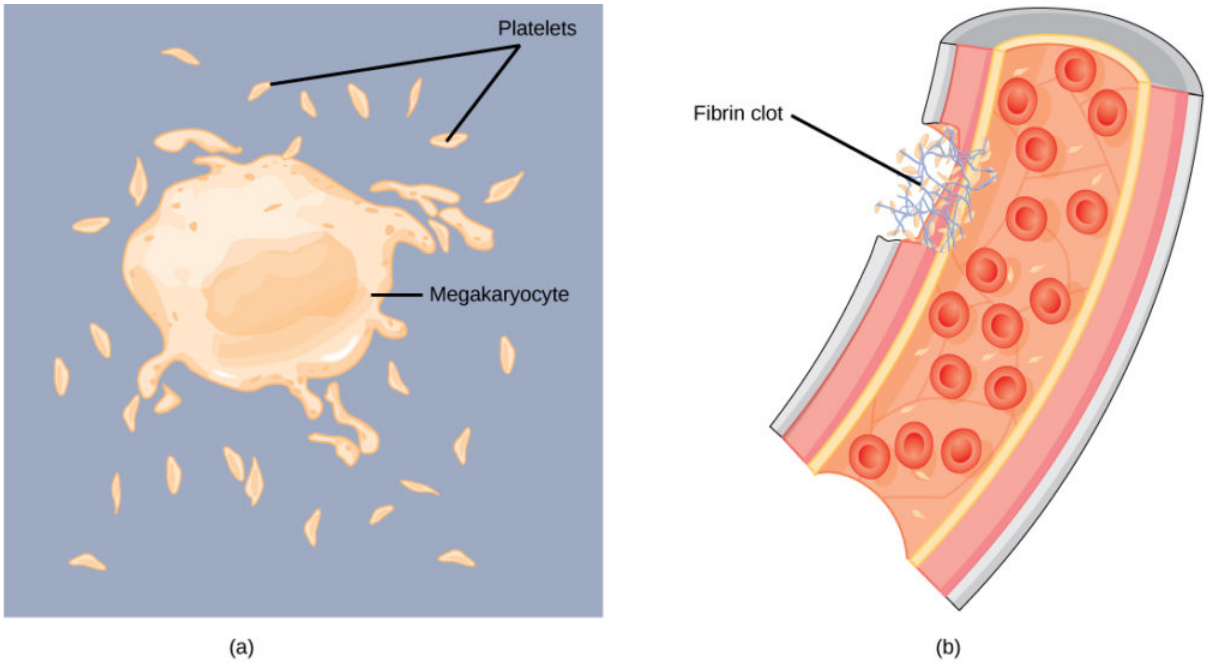


Figure 1. (a) Platelets are formed from large cells called megakaryocytes. The megakaryocyte breaks up into thousands of fragments that become platelets. (b) Platelets are required for clotting of the blood. The platelets collect at a wound site in conjunction with other clotting factors, such as fibrinogen, to form a fibrin clot that prevents blood loss and allows the wound to heal.

Plasma and Serum

The liquid component of blood is called plasma, and it is separated by spinning or centrifuging the blood at high rotations (3000 rpm or higher). The blood cells and platelets are separated by centrifugal forces to the bottom of a specimen tube. The upper liquid layer, the plasma, consists of 90 percent water along with various substances required for maintaining the body's pH, osmotic load, and for protecting the body. The plasma also contains the coagulation factors and antibodies.

The plasma component of blood without the coagulation factors is called the **serum**. Serum is similar to interstitial fluid in which the correct composition of key ions acting as electrolytes is essential for normal functioning of muscles and nerves. Other components in the serum include proteins that assist with maintaining pH and osmotic balance while giving viscosity to the blood. The serum also contains antibodies, specialized proteins that are important for defense against viruses and bacteria. Lipids, including cholesterol, are also transported in the serum, along with various other substances including nutrients, hormones, metabolic waste, plus external substances, such as, drugs, viruses, and bacteria.

Human serum albumin is the most abundant protein in human blood plasma and is synthesized in the liver. Albumin, which constitutes about half of the blood serum protein, transports hormones and fatty acids, buffers pH, and maintains osmotic pressures. Immunoglobin is a protein antibody produced in the mucosal lining and plays an important role in antibody mediated immunity.

Try It

Red blood cells are coated in antigens made of glycolipids and glycoproteins. The composition of these molecules is determined by genetics, which have evolved over time. In humans, the different surface antigens are grouped into 24 different blood groups with more than 100 different antigens on each red blood cell. The two most well known blood groups are the ABO, shown in Figure 2, and Rh systems. The surface antigens in the ABO blood group are glycolipids, called antigen A and antigen B. People with blood type A have antigen A, those with blood type B have antigen B, those with blood type AB have both antigens, and people with blood type O have neither antigen. Antibodies called agglutinougens are found in the blood plasma and react with the A or B antigens, if the two are mixed. When type A and type B blood are combined, agglutination (clumping) of the blood occurs because of antibodies in the plasma that bind with the opposing antigen; this causes clots that coagulate in the kidney causing kidney failure. Type O blood has neither A or B antigens, and therefore, type O blood can be given to all blood types. Type O negative blood is the universal donor. Type AB positive blood is the universal acceptor because it has both A and B antigen. The ABO blood groups were discovered in 1900 and 1901 by Karl Landsteiner at the University of Vienna.

The Rh blood group was first discovered in Rhesus monkeys. Most people have the Rh antigen (Rh+) and do not have anti-Rh antibodies in their blood. The few people who do not have the Rh antigen and are Rh– can develop anti-Rh antibodies if exposed to Rh+ blood. This can happen after a blood transfusion or after an Rh– woman has an Rh+ baby. The first exposure does not usually cause a reaction; however, at the second exposure, enough antibodies have built up in the blood to produce a reaction that causes agglutination and breakdown of red blood cells. An injection can prevent this reaction.

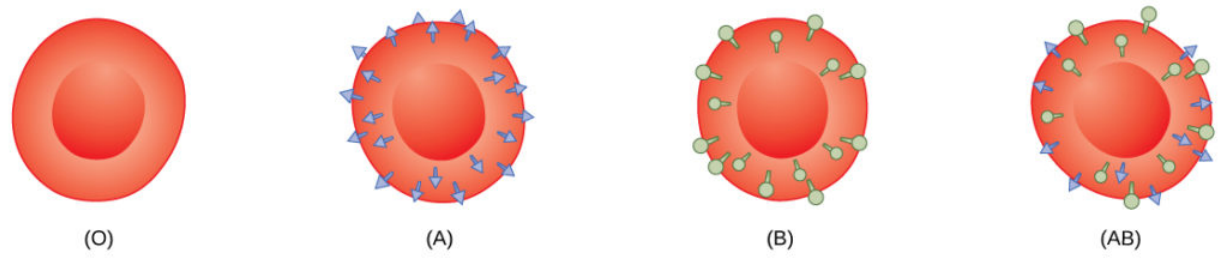


Figure 2. Human red blood cells may have either type A or B glycoproteins on their surface, both glycoproteins combined (AB), or neither (O). The glycoproteins serve as antigens and can elicit an immune response in a person who receives a transfusion containing unfamiliar antigens. Type O blood, which has no A or B antigens, does not elicit an immune response when injected into a person of any blood type. Thus, O is considered the universal donor. Persons with type AB blood can accept blood from any blood type, and type AB is considered the universal acceptor.

Play a blood typing game on the Nobel Prize website to solidify your understanding of blood types.

Learning Objectives

Platelets and blood clotting factors cause the change of the soluble protein fibrinogen to the insoluble protein fibrin at a wound site forming a plug. Plasma consists of 90 percent water along with various substances, such as coagulation factors and antibodies. The serum is the plasma component of the blood without the coagulation factors.

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21.9: Introduction to the Mammalian Heart

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

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

What You'll Learn to Do

- Describe the structure of the heart
- Describe the cardiac cycle

Learning Activities

The learning activities for this section include the following:

- Structure of the Heart
- The Cardiac Cycle
- Self Check: The Mammalian Heart

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21.10: Structure of the Heart

The heart muscle is asymmetrical due to the distance blood must travel in the pulmonary and systemic circuits. Since the right side of the heart sends blood to the pulmonary circuit, it is smaller than the left side which must send blood out to the whole body in the systemic circuit, as shown in Figure 1.

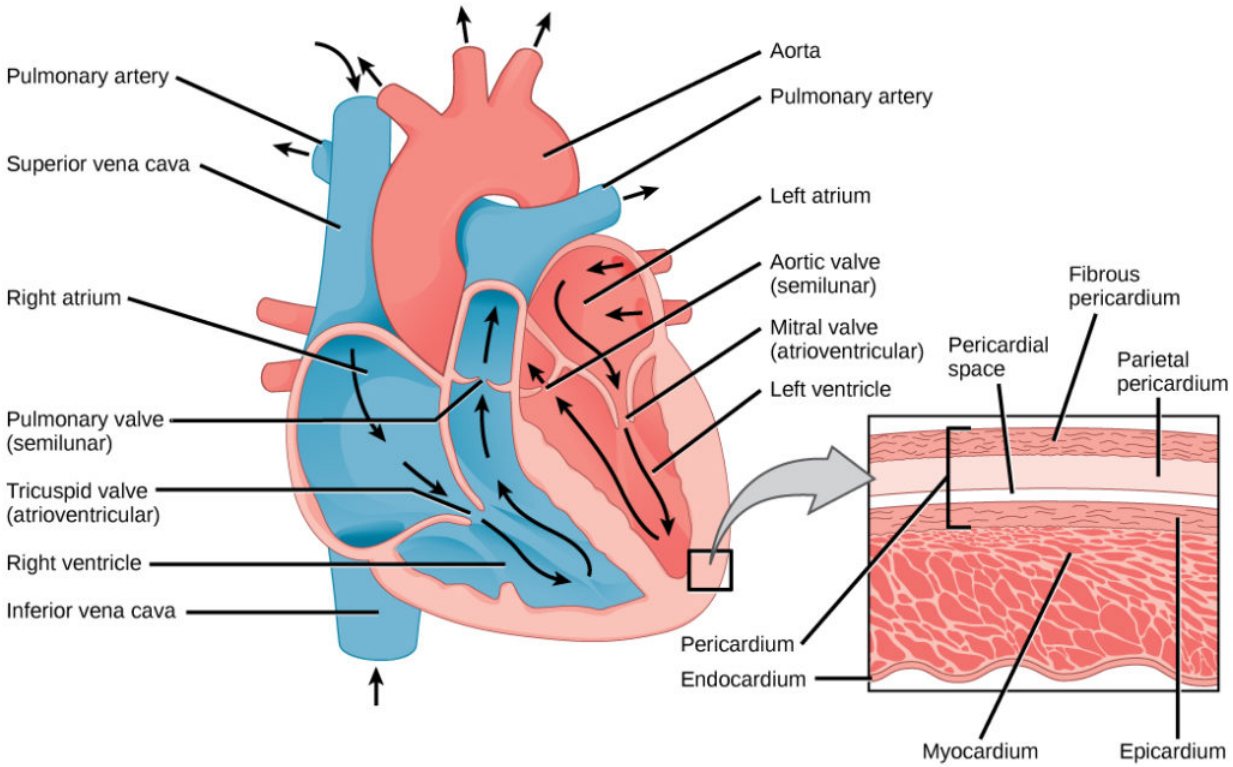


Figure 1. The heart is primarily made of a thick muscle layer, called the myocardium, surrounded by membranes. One-way valves separate the four chambers.

In humans, the heart is about the size of a clenched fist, and it is divided into four chambers: two atria and two ventricles. There is one atrium and one ventricle on the right side and one atrium and one ventricle on the left side. The atria are the chambers that receive blood, and the ventricles are the chambers that pump blood. The right atrium receives deoxygenated blood from the **superior vena cava**, which drains blood from the jugular vein that comes from the brain and from the veins that come from the arms, as well as from the **inferior vena cava** which drains blood from the veins that come from the lower organs and the legs.

In addition, the right atrium receives blood from the coronary sinus which drains deoxygenated blood from the heart itself. This deoxygenated blood then passes to the right ventricle through the **atrioventricular valve** or the **tricuspid valve**, a flap of connective tissue that opens in only one direction to prevent the backflow of blood. The valve separating the chambers on the left side of the heart valve is called the bicuspid or mitral valve. After it is filled, the right ventricle pumps the blood through the pulmonary arteries, by-passing the **semilunar valve** (or pulmonic valve) to the lungs for re-oxygenation.

After blood passes through the pulmonary arteries, the right semilunar valves close preventing the blood from flowing backwards into the right ventricle. The left atrium then receives the oxygen-rich blood from the lungs via the pulmonary veins. This blood passes through the **bicuspid valve** or mitral valve (the atrioventricular valve on the left side of the heart) to the left ventricle where the blood is pumped out through **aorta**, the major artery of the body, taking oxygenated blood to the organs and muscles of the body. Once blood is pumped out of the left ventricle and into the aorta, the aortic semilunar valve (or aortic valve) closes preventing blood from flowing backward into the left ventricle. This pattern of pumping is referred to as double circulation and is found in all mammals.

Practice Question

Which of the following statements about the heart is false?

a. The mitral valve separates the left ventricle from the left atrium.
b. Blood travels through the bicuspid valve to the left atrium.
c. Both the aortic and the pulmonary valves are semilunar valves.
d. The mitral valve is an atrioventricular valve.

[reveal-answer q="486904"]Show Answer[/reveal-answer]
[hidden-answer a="486904"]Statement b is false.[/hidden-answer]

The heart is composed of three layers; the epicardium, the myocardium, and the endocardium, illustrated in Figure 1. The inner wall of the heart has a lining called the **endocardium**. The **myocardium** consists of the heart muscle cells that make up the middle layer and the bulk of the heart wall. The outer layer of cells is called the **epicardium**, of which the second layer is a membranous layered structure called the **pericardium** that surrounds and protects the heart; it allows enough room for vigorous pumping but also keeps the heart in place to reduce friction between the heart and other structures.

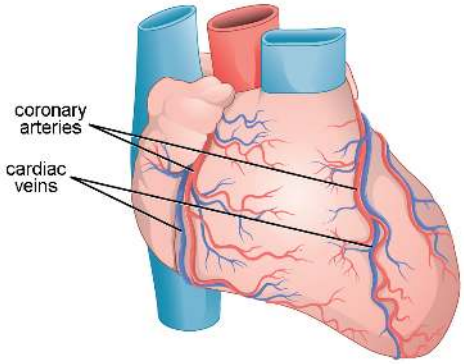


Figure 2. Blood vessels of the coronary system, including the coronary arteries and veins, keep the heart musculature oxygenated.

The heart has its own blood vessels that supply the heart muscle with blood (Figure 2). The **coronary arteries** branch from the aorta and surround the outer surface of the heart like a crown. They diverge into capillaries where the heart muscle is supplied with oxygen before converging again into the **coronary veins** to take the deoxygenated blood back to the right atrium where the blood will be re-oxygenated through the pulmonary circuit. The heart muscle will die without a steady supply of blood. **Atherosclerosis** is the blockage of an artery by the buildup of fatty plaques. Because of the size (narrow) of the coronary arteries and their function in serving the heart itself, atherosclerosis can be deadly in these arteries. The slowdown of blood flow and subsequent oxygen deprivation that results from atherosclerosis causes severe pain, known as **angina**, and complete blockage of the arteries will cause **myocardial infarction**: the death of cardiac muscle tissue, commonly known as a heart attack.

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21.11: The Cardiac Cycle

The main purpose of the heart is to pump blood through the body; it does so in a repeating sequence called the cardiac cycle. The **cardiac cycle** is the coordination of the filling and emptying of the heart of blood by electrical signals that cause the heart muscles to contract and relax. The human heart beats over 100,000 times per day. In each cardiac cycle, the heart contracts (**systole**), pushing out the blood and pumping it through the body; this is followed by a relaxation phase (**diastole**), where the heart fills with blood, as illustrated in Figure 1. The atria contract at the same time, forcing blood through the atrioventricular valves into the ventricles. Closing of the atrioventricular valves produces a monosyllabic “lup” sound. Following a brief delay, the ventricles contract at the same time forcing blood through the semilunar valves into the aorta and the artery transporting blood to the lungs (via the pulmonary artery). Closing of the semilunar valves produces a monosyllabic “dup” sound.

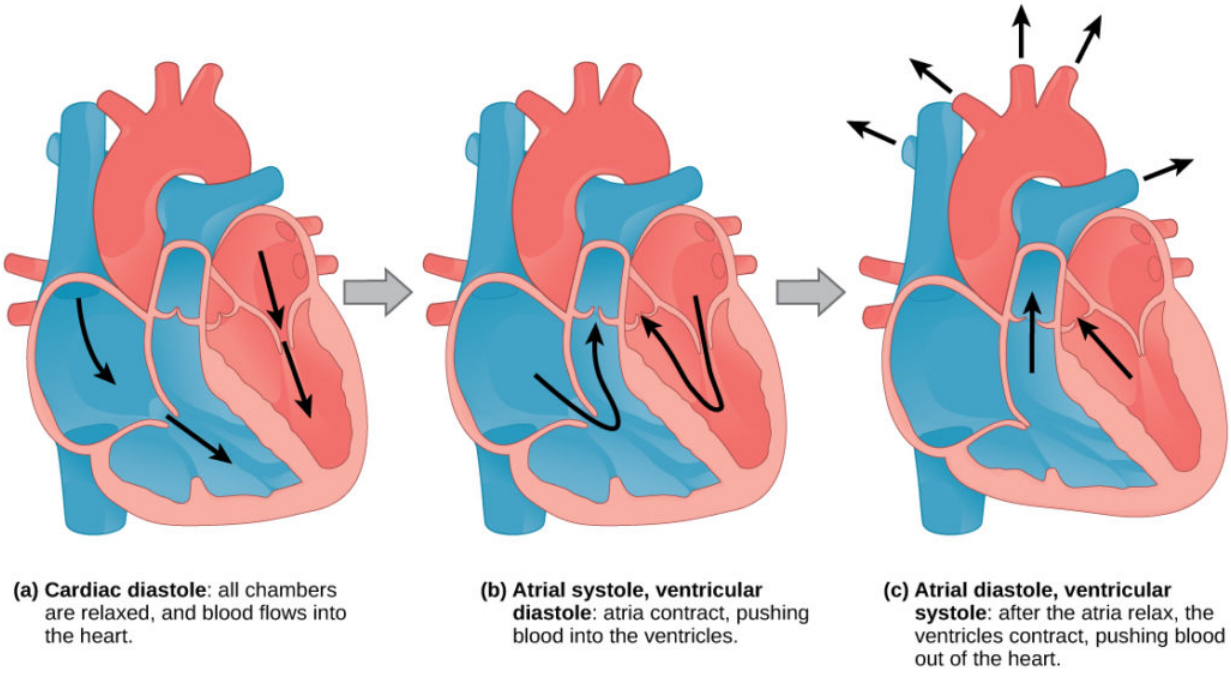


Figure 1. During (a) cardiac diastole, the heart muscle is relaxed and blood flows into the heart. During (b) atrial systole, the atria contract, pushing blood into the ventricles. During (c) atrial diastole, the ventricles contract, forcing blood out of the heart.

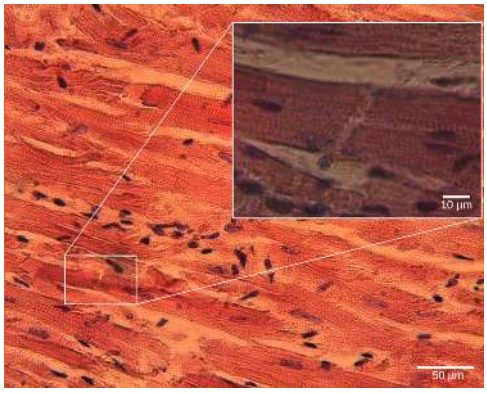


Figure 2. Cardiomyocytes are striated muscle cells found in cardiac tissue. (credit: modification of work by Dr. S. Girod, Anton Becker; scale-bar data from Matt Russell)

The pumping of the heart is a function of the cardiac muscle cells, or cardiomyocytes, that make up the heart muscle. **Cardiomyocytes**, shown in Figure 2, are distinctive muscle cells that are striated like skeletal muscle but pump rhythmically and involuntarily like smooth muscle; they are connected by intercalated disks exclusive to cardiac muscle. They are self-stimulated for a period of time and isolated cardiomyocytes will beat if given the correct balance of nutrients and electrolytes.

The autonomous beating of cardiac muscle cells is regulated by the heart's internal pacemaker that uses electrical signals to time the beating of the heart. The electrical signals and mechanical actions, illustrated in Figure 3, are intimately intertwined. The internal pacemaker starts at the **sinoatrial (SA) node**, which is located near the wall of the right atrium. Electrical charges spontaneously pulse from the SA node causing the two atria to contract in unison. The pulse reaches a second node, called the atrioventricular (AV) node, between the right atrium and right ventricle where it pauses for approximately 0.1 second before spreading to the walls of the ventricles. From the AV node, the electrical impulse enters the bundle of His, then to the left and right bundle branches extending through the interventricular septum. Finally, the Purkinje fibers conduct the impulse from the apex of the heart up the ventricular myocardium, and then the ventricles contract. This pause allows the atria to empty completely into the ventricles before the ventricles pump out the blood. The electrical impulses in the heart produce electrical currents that flow through the body and can be measured on the skin using electrodes. This information can be observed as an **electrocardiogram (ECG)**—a recording of the electrical impulses of the cardiac muscle.

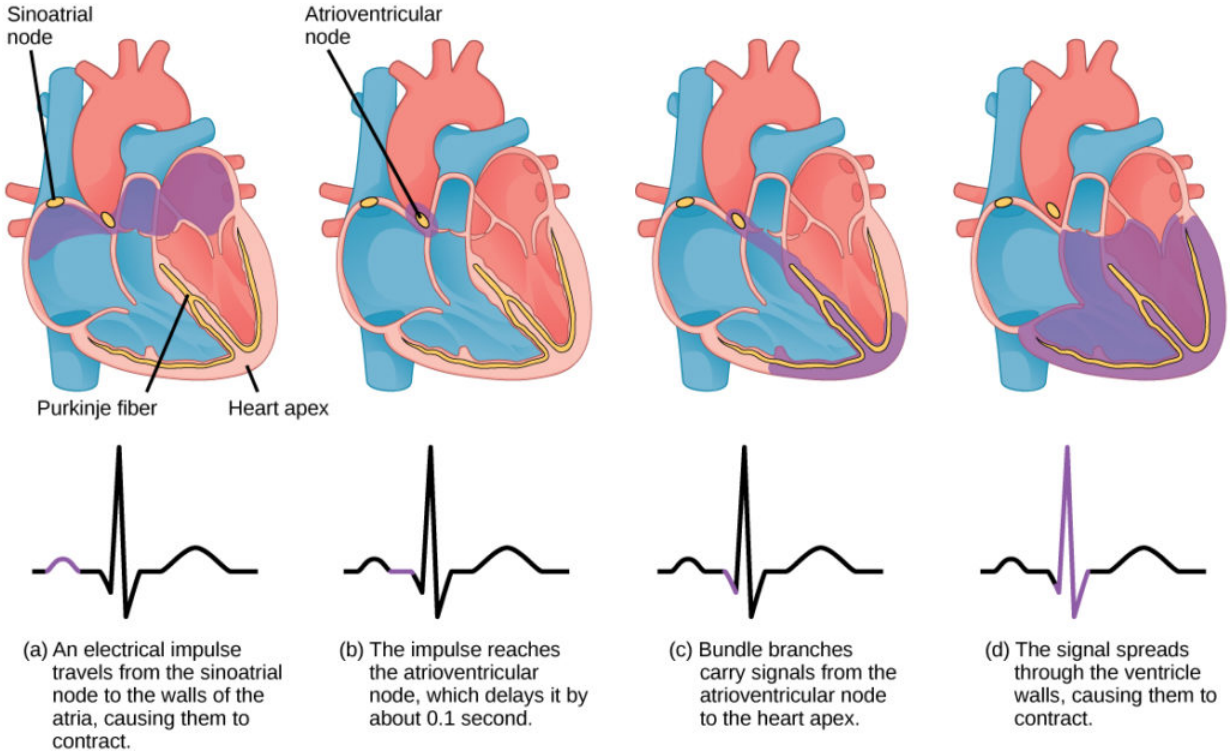


Figure 3. The beating of the heart is regulated by an electrical impulse that causes the characteristic reading of an ECG. The signal is initiated at the sinoatrial valve. The signal then (a) spreads to the atria, causing them to contract. The signal is (b) delayed at the atrioventricular node before it is passed on to the (c) heart apex. The delay allows the atria to relax before the (d) ventricles contract. The final part of the ECG cycle prepares the heart for the next beat.

Visit this site to see the heart's "pacemaker" in action

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21.12: Introduction to Blood Flow and Blood Pressure Regulation

Explain the structure of arteries, veins, and capillaries, and how blood flows through the body

Blood primarily moves through the body by the rhythmic movement of smooth muscle in the vessel wall and by the action of the skeletal muscle as the body moves. Blood is prevented from flowing backward in the veins by one-way valves. Blood flow through the capillary beds is controlled by precapillary sphincters to increase and decrease flow depending on the body's needs and is directed by nerve and hormone signals. Lymph vessels take fluid that has leaked out of the blood to the lymph nodes where it is cleaned before returning to the heart. During systole, blood enters the arteries, and the artery walls stretch to accommodate the extra blood. During diastole, the artery walls return to normal. The blood pressure of the systole phase and the diastole phase gives the two pressure readings for blood pressure.

What You'll Learn to Do

- Explain the structure of arteries, veins, and capillaries
- Describe the system of blood flow through the body
- Identify the importance of blood pressure
- Describe how blood pressure is regulated

Learning Activities

The learning activities for this section include the following:

- Blood Vessels
- Blood Circulation
- Blood Pressure
- Self Check: Blood Flow and Blood Pressure Regulation

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21.13: Blood Vessels

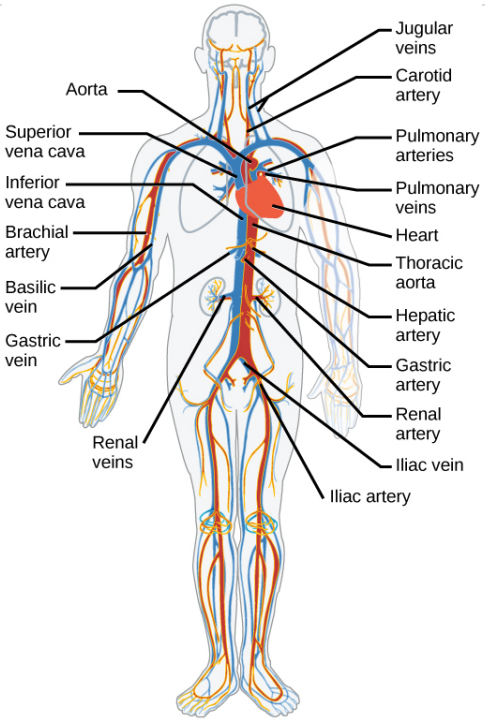


Figure 1. The major human arteries and veins are shown. (credit: modification of work by Mariana Ruiz Villareal)

The blood from the heart is carried through the body by a complex network of blood vessels (Figure 1). **Arteries** take blood away from the heart. The main artery is the aorta that branches into major arteries that take blood to different limbs and organs. These major arteries include the carotid artery that takes blood to the brain, the brachial arteries that take blood to the arms, and the thoracic artery that takes blood to the thorax and then into the hepatic, renal, and gastric arteries for the liver, kidney, and stomach, respectively. The iliac artery takes blood to the lower limbs. The major arteries diverge into minor arteries, and then smaller vessels called **arterioles**, to reach more deeply into the muscles and organs of the body.

Arterioles diverge into capillary beds. **Capillary beds** contain a large number (10 to 100) of **capillaries** that branch among the cells and tissues of the body. Capillaries are narrow-diameter tubes that can fit red blood cells through in single file and are the sites for the exchange of nutrients, waste, and oxygen with tissues at the cellular level. Fluid also crosses into the interstitial space from the capillaries. The capillaries converge again into **venules** that connect to minor veins that finally connect to major veins that take blood high in carbon dioxide back to the heart. **Veins** are blood vessels that bring blood back to the heart. The major veins drain blood from the same organs and limbs that the major arteries supply. Fluid is also brought back to the heart via the lymphatic system.

The structure of the different types of blood vessels reflects their function or layers. There are three distinct layers, or tunics, that form the walls of blood vessels (Figure 2). The first tunic is a smooth, inner lining of endothelial cells that are in contact with the red blood cells. The endothelial tunic is continuous with the endocardium of the heart. In capillaries, this single layer of cells is the location of diffusion of oxygen and carbon dioxide between the endothelial cells and red blood cells, as well as the exchange site via endocytosis and exocytosis. The movement of materials at the site of capillaries is regulated by **vasoconstriction**, narrowing of the blood vessels, and **vasodilation**, widening of the blood vessels; this is important in the overall regulation of blood pressure.

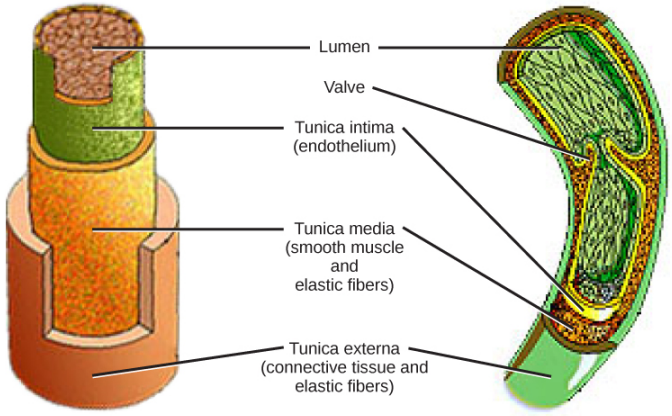


Figure 2. Arteries and veins consist of three layers: an outer tunica externa, a middle tunica media, and an inner tunica intima. Capillaries consist of a single layer of epithelial cells, the tunica intima. (credit: modification of work by NCI, NIH)

Veins and arteries both have two further tunics that surround the endothelium: the middle tunic is composed of smooth muscle and the outermost layer is connective tissue (collagen and elastic fibers). The elastic connective tissue stretches and supports the blood vessels, and the smooth muscle layer helps regulate blood flow by altering vascular resistance through vasoconstriction and vasodilation. The arteries have thicker smooth muscle and connective tissue than the veins to accommodate the higher pressure and speed of freshly pumped blood. The veins are thinner walled as the pressure and rate of flow are much lower. In addition, veins are structurally different than arteries in that veins have valves to prevent the backflow of blood. Because veins have to work against gravity to get blood back to the heart, contraction of skeletal muscle assists with the flow of blood back to the heart.

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21.14: Blood Circulation

Blood is pushed through the body by the action of the pumping heart. With each rhythmic pump, blood is pushed under high pressure and velocity away from the heart, initially along the main artery, the aorta. In the aorta, the blood travels at 30 cm/sec. As blood moves into the arteries, arterioles, and ultimately to the capillary beds, the rate of movement slows dramatically to about 0.026 cm/sec, one-thousand times slower than the rate of movement in the aorta. While the diameter of each individual arteriole and capillary is far narrower than the diameter of the aorta, and according to the law of continuity, fluid should travel faster through a narrower diameter tube, the rate is actually slower due to the overall diameter of all the combined capillaries being far greater than the diameter of the individual aorta.

The slow rate of travel through the capillary beds, which reach almost every cell in the body, assists with gas and nutrient exchange and also promotes the diffusion of fluid into the interstitial space. After the blood has passed through the capillary beds to the venules, veins, and finally to the main venae cavae, the rate of flow increases again but is still much slower than the initial rate in the aorta. Blood primarily moves in the veins by the rhythmic movement of smooth muscle in the vessel wall and by the action of the skeletal muscle as the body moves. Because most veins must move blood against the pull of gravity, blood is prevented from flowing backward in the veins by one-way valves. Because skeletal muscle contraction aids in venous blood flow, it is important to get up and move frequently after long periods of sitting so that blood will not pool in the extremities.

Blood flow through the capillary beds is regulated depending on the body's needs and is directed by nerve and hormone signals. For example, after a large meal, most of the blood is diverted to the stomach by vasodilation of vessels of the digestive system and vasoconstriction of other vessels. During exercise, blood is diverted to the skeletal muscles through vasodilation while blood to the digestive system would be lessened through vasoconstriction. The blood entering some capillary beds is controlled by small muscles, called precapillary sphincters, illustrated in Figure 1. If the sphincters are open, the blood will flow into the associated branches of the capillary blood. If all of the sphincters are closed, then the blood will flow directly from the arteriole to the venule through the thoroughfare channel (see Figure 1). These muscles allow the body to precisely control when capillary beds receive blood flow. At any given moment only about 5–10 percent of our capillary beds actually have blood flowing through them.

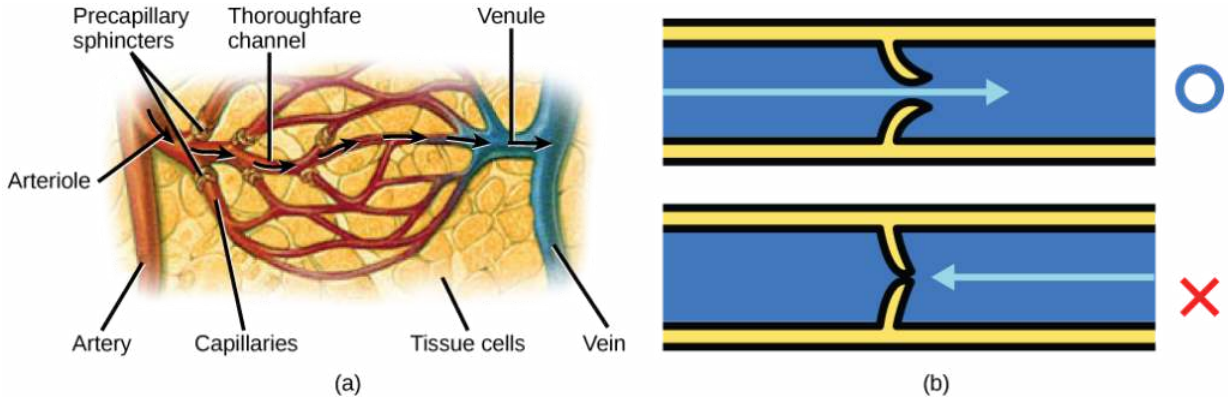


Figure 1. (a) Precapillary sphincters are rings of smooth muscle that regulate the flow of blood through capillaries; they help control the location of blood flow to where it is needed. (b) Valves in the veins prevent blood from moving backward. (credit a: modification of work by NCI)

Practice Question

Varicose veins are veins that become enlarged because the valves no longer close properly, allowing blood to flow backward. Varicose veins are often most prominent on the legs. Why do you think this is the case?

[reveal-answer q="480975"]Show Answer[/reveal-answer]

[hidden-answer a="480975"]Blood in the legs is farthest away from the heart and has to flow up to reach it.[/hidden-answer]

Watch this video to see the circulatory system's blood flow.

A link to an interactive elements can be found at the bottom of this page.

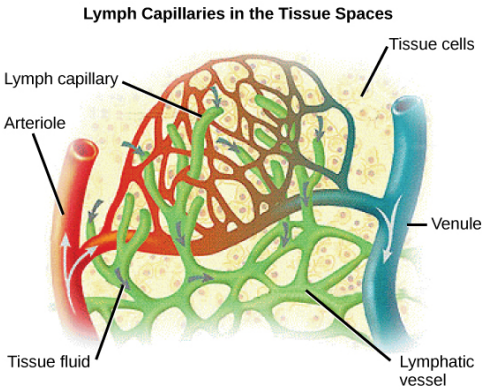


Figure 2. Fluid from the capillaries moves into the interstitial space and lymph capillaries by diffusion down a pressure gradient and also by osmosis. Out of 7,200 liters of fluid pumped by the average heart in a day, over 1,500 liters is filtered. (credit: modification of work by NCI, NIH)

Proteins and other large solutes cannot leave the capillaries. The loss of the watery plasma creates a hyperosmotic solution within the capillaries, especially near the venules. This causes about 85 percent of the plasma that leaves the capillaries to eventually diffuses back into the capillaries near the venules. The remaining 15 percent of blood plasma drains out from the interstitial fluid into nearby lymphatic vessels (Figure 2).

The fluid in the lymph is similar in composition to the interstitial fluid. The lymph fluid passes through lymph nodes before it returns to the heart via the vena cava. **Lymph nodes** are specialized organs that filter the lymph by percolation through a maze of connective tissue filled with white blood cells. The white blood cells remove infectious agents, such as bacteria and viruses, to clean the lymph before it returns to the bloodstream. After it is cleaned, the lymph returns to the heart by the action of smooth muscle pumping, skeletal muscle action, and one-way valves joining the returning blood near the junction of the venae cavae entering the right atrium of the heart.

Vertebrate Diversity in Blood Circulation

Blood circulation has evolved differently in vertebrates and may show variation in different animals for the required amount of pressure, organ and vessel location, and organ size. Animals with longs necks and those that live in cold environments have distinct blood pressure adaptations.

Long necked animals, such as giraffes, need to pump blood upward from the heart against gravity. The blood pressure required from the pumping of the left ventricle would be equivalent to 250 mm Hg (mm Hg = millimeters of mercury, a unit of pressure) to reach the height of a giraffe's head, which is 2.5 meters higher than the heart. However, if checks and balances were not in place, this blood pressure would damage the giraffe's brain, particularly if it was bending down to drink. These checks and balances include valves and feedback mechanisms that reduce the rate of cardiac output. Long-necked dinosaurs such as the sauropods had to pump blood even higher, up to ten meters above the heart. This would have required a blood pressure of more than 600 mm Hg, which could only have been achieved by an enormous heart. Evidence for such an enormous heart does not exist and mechanisms to reduce the blood pressure required include the slowing of metabolism as these animals grew larger. It is likely that they did not routinely feed on tree tops but grazed on the ground.

Living in cold water, whales need to maintain the temperature in their blood. This is achieved by the veins and arteries being close together so that heat exchange can occur. This mechanism is called a countercurrent heat exchanger. The blood vessels and the whole body are also protected by thick layers of blubber to prevent heat loss. In land animals that live in cold environments, thick fur and hibernation are used to retain heat and slow metabolism.

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21.15: Blood Pressure

Blood pressure (BP) is the pressure exerted by blood on the walls of a blood vessel that helps to push blood through the body. Systolic blood pressure measures the amount of pressure that blood exerts on vessels while the heart is beating. The optimal systolic blood pressure is 120 mmHg. Diastolic blood pressure measures the pressure in the vessels between heartbeats. The optimal diastolic blood pressure is 80 mmHg. Many factors can affect blood pressure, such as hormones, stress, exercise, eating, sitting, and standing. Blood flow through the body is regulated by the size of blood vessels, by the action of smooth muscle, by one-way valves, and by the fluid pressure of the blood itself.

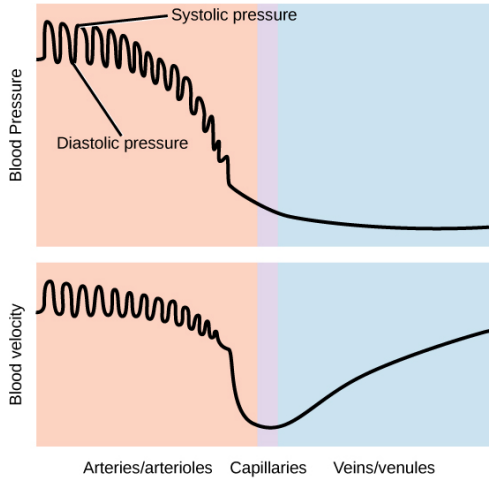


Figure 1. Blood pressure is related to the blood velocity in the arteries and arterioles. In the capillaries and veins, the blood pressure continues to decease but velocity increases.

The pressure of the blood flow in the body is produced by the hydrostatic pressure of the fluid (blood) against the walls of the blood vessels. Fluid will move from areas of high to low hydrostatic pressures. In the arteries, the hydrostatic pressure near the heart is very high and blood flows to the arterioles where the rate of flow is slowed by the narrow openings of the arterioles. During systole, when new blood is entering the arteries, the artery walls stretch to accommodate the increase of pressure of the extra blood; during diastole, the walls return to normal because of their elastic properties. The blood pressure of the systole phase and the diastole phase, graphed in Figure 1, gives the two pressure readings for blood pressure. For example, 120/80 indicates a reading of 120 mm Hg during the systole and 80 mm Hg during diastole. Throughout the cardiac cycle, the blood continues to empty into the arterioles at a relatively even rate. This resistance to blood flow is called **peripheral resistance**.

Blood Pressure Regulation

Cardiac output is the volume of blood pumped by the heart in one minute. It is calculated by multiplying the number of heart contractions that occur per minute (heart rate) times the **stroke volume** (the volume of blood pumped into the aorta per contraction of the left ventricle). Therefore, cardiac output can be increased by increasing heart rate, as when exercising. However, cardiac output can also be increased by increasing stroke volume, such as if the heart contracts with greater strength. Stroke volume can also be increased by speeding blood circulation through the body so that more blood enters the heart between contractions. During heavy exertion, the blood vessels relax and increase in diameter, offsetting the increased heart rate and ensuring adequate oxygenated blood gets to the muscles. Stress triggers a decrease in the diameter of the blood vessels, consequently increasing blood pressure. These changes can also be caused by nerve signals or hormones, and even standing up or lying down can have a great effect on blood pressure.

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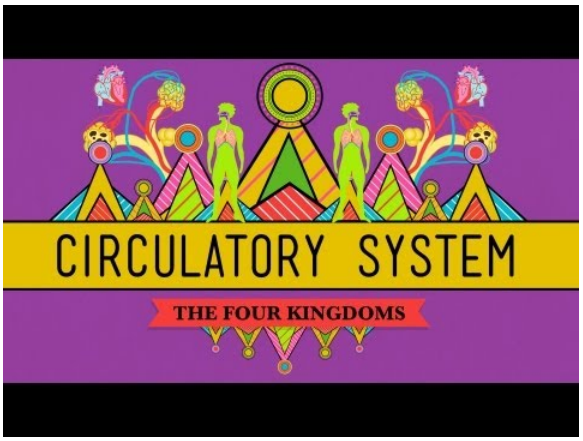
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21.16: Putting It Together- The Circulatory System

Now that we've learned about the parts and functions of the circulatory system, let's take a look at the system as a whole. This video takes us on a trip around the body—we follow the circulatory and respiratory systems as they deliver oxygen and remove carbon dioxide from cells, and help make it possible for our bodies to function.



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=901

Heart Disease

Heart disease is among the top ten causes of death in the United States. The term "heart disease" refers to several types of heart conditions. The most common type is coronary artery disease, which can cause heart attack. Other kinds of heart disease may involve the valves in the heart, or the heart may not pump well and cause heart failure. Some people are born with heart disease.

Anyone, including children, can develop heart disease. It occurs when a substance called plaque builds up in your arteries. When this happens, your arteries can narrow over time, reducing blood flow to the heart. Smoking, eating an unhealthy diet, and not getting enough exercise all increase your risk for having heart disease.

Having high cholesterol, high blood pressure, or diabetes also can increase your risk for heart disease. Ask your doctor about preventing or treating these medical conditions.

What are the signs and symptoms?

The symptoms vary depending on the type of heart disease. For many people, chest discomfort or a heart attack is the first sign. Someone having a heart attack may experience several symptoms, including:

- Chest pain or discomfort that doesn't go away after a few minutes
- Pain or discomfort in the jaw, neck, or back
- Weakness, light-headedness, nausea, or a cold sweat
- Pain or discomfort in the arms or shoulder
- Shortness of breath

Can it be prevented?

You can take several steps to reduce your risk for heart disease:

- Don't smoke.
- Maintain a healthy weight.
- Eat a healthy diet.
- Exercise regularly.

If you have heart disease, lifestyle changes, like those just listed, can help lower your risk for complications. Your doctor also may prescribe medication to treat the disease. Talk with your doctor about the best ways to reduce your heart disease risk.

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21.17: Cerego- The Circulatory System

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for The Circulatory System. You'll need to create a free log-in to practice these items, if you haven't already.

https://cerego.com/sets/796527/learn

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CHAPTER OVERVIEW

22: Module 19- The Respiratory System

22.1: Why It Matters- The Respiratory System
22.2: Introduction to Systems of Gas Exchange
22.3: Different Types of Respiratory Systems
22.4: Mammalian Systems
22.5: Protective Mechanisms
22.6: Introduction to Gas Exchange across Respiratory Surfaces
22.7: Breathing Capacity
22.8: Gas Pressure and Respiration
22.9: Gas Exchange across the Alveoli
22.10: Introduction to Breathing
22.11: Types of Breathing
22.12: The Mechanics of Human Breathing
22.13: The Work of Breathing
22.14: Dead Space
22.15: Introduction to Transport of Gases in Human Bodily Fluids
22.16: Transport of Oxygen in the Blood
22.17: Transport of Carbon Dioxide in the Blood
22.18: Putting It Together- The Respiratory System
22.19: Cerego- The Respiratory System

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22.1: Why It Matters- The Respiratory System

Why describe the components and role of the respiratory system?

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



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

Learning Objectives

- Describe the passage of air from the outside environment to the lungs
- Understand how gas pressure influences how gases move into and out of the body
- Describe how the structures of the respiratory system control the mechanics of breathing
- Explain how gases are transported in the body

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22.2: Introduction to Systems of Gas Exchange

Describe the passage of air from the outside environment to the lungs

The primary function of the respiratory system is to deliver oxygen to the cells of the body's tissues and remove carbon dioxide, a cell waste product. The main structures of the human respiratory system are the nasal cavity, the trachea, and lungs.

What You'll Learn to Do

- Discuss the respiratory processes used by animals without lungs
- Identify common structures in mammalian respiratory systems
- Explain how the lungs are protected from particulate matter

Learning Activities

The learning activities for this section include the following:

- Different Types of Respiratory Systems
- Mammalian Systems
- Protective Mechanisms
- Self Check: Systems of Gas Exchange

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22.3: Different Types of Respiratory Systems

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

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

Direct Diffusion



Figure 1. This flatworm's process of respiration works by diffusion across the outer membrane. (credit: Stephen Childs)

For small multicellular organisms, diffusion across the outer membrane is sufficient to meet their oxygen needs. Gas exchange by direct diffusion across surface membranes is efficient for organisms less than 1 mm in diameter. In simple organisms, such as cnidarians and flatworms, every cell in the body is close to the external environment. Their cells are kept moist and gases diffuse quickly via direct diffusion. Flatworms are small, literally flat worms, which "breathe" through diffusion across the outer membrane (Figure 1). The flat shape of these organisms increases the surface area for diffusion, ensuring that each cell within the body is close to the outer membrane surface and has access to oxygen. If the flatworm had a cylindrical body, then the cells in the center would not be able to get oxygen.

Skin and Gills

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



Figure 2. This common carp, like many other aquatic organisms, has gills that allow it to obtain oxygen from water. (credit: "Guitardude012"/Wikimedia Commons)

Organisms that live in water need to obtain oxygen from the water. Oxygen dissolves in water but at a lower concentration than in the atmosphere. The atmosphere has roughly 21 percent oxygen. In water, the oxygen concentration is much smaller than that. Fish and many other aquatic organisms have evolved gills to take up the dissolved oxygen from water (Figure 2). Gills are thin tissue

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

The folded surfaces of the gills provide a large surface area to ensure that the fish gets sufficient oxygen. Diffusion is a process in which material travels from regions of high concentration to low concentration until equilibrium is reached. In this case, blood with a low concentration of oxygen molecules circulates through the gills. The concentration of oxygen molecules in water is higher than the concentration of oxygen molecules in gills. As a result, oxygen molecules diffuse from water (high concentration) to blood (low concentration), as shown in Figure 3. Similarly, carbon dioxide molecules in the blood diffuse from the blood (high concentration) to water (low concentration).

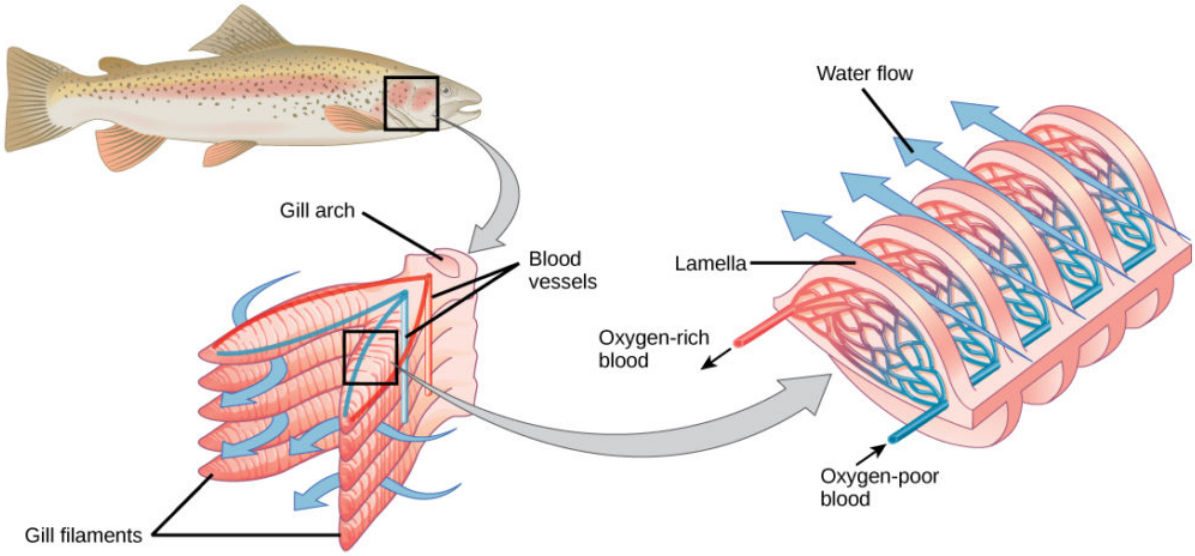


Figure 3. As water flows over the gills, oxygen is transferred to blood via the veins. (credit “fish”: modification of work by Duane Raver, NOAA)

Tracheal Systems

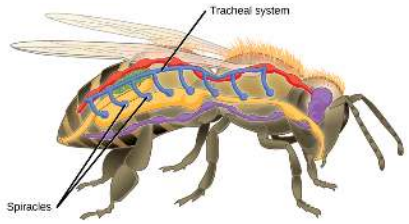


Figure 4. Insects perform respiration via a tracheal system.

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

Insect bodies have openings, called spiracles, along the thorax and abdomen. These openings connect to the tubular network, allowing oxygen to pass into the body (Figure 4) and regulating the diffusion of CO_2 and water vapor. Air enters and leaves the tracheal system through the spiracles. Some insects can ventilate the tracheal system with body movements.

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22.4: Mammalian Systems

In mammals, pulmonary ventilation occurs via inhalation (breathing). During inhalation, air enters the body through the **nasal cavity** located just inside the nose (Figure 1). As air passes through the nasal cavity, the air is warmed to body temperature and humidified. The respiratory tract is coated with mucus to seal the tissues from direct contact with air. Mucus is high in water. As air crosses these surfaces of the mucous membranes, it picks up water. These processes help equilibrate the air to the body conditions, reducing any damage that cold, dry air can cause. Particulate matter that is floating in the air is removed in the nasal passages via mucus and cilia. The processes of warming, humidifying, and removing particles are important protective mechanisms that prevent damage to the trachea and lungs. Thus, inhalation serves several purposes in addition to bringing oxygen into the respiratory system.

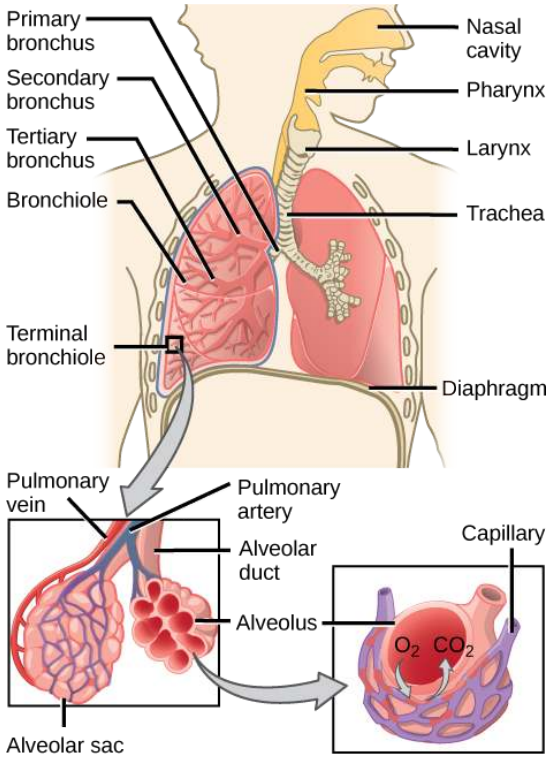


Figure 1. Air enters the respiratory system through the nasal cavity and pharynx, and then passes through the trachea and into the bronchi, which bring air into the lungs. (credit: modification of work by NCI)

? Practice Question

Which of the following statements about the mammalian respiratory system is false?

a. When we breathe in, air travels from the pharynx to the trachea.
b. The bronchioles branch into bronchi.
c. Alveolar ducts connect to alveolar sacs.
d. Gas exchange between the lung and blood takes place in the alveolus.

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[hidden-answer a="997523"]Statement b is false.[/hidden-answer]

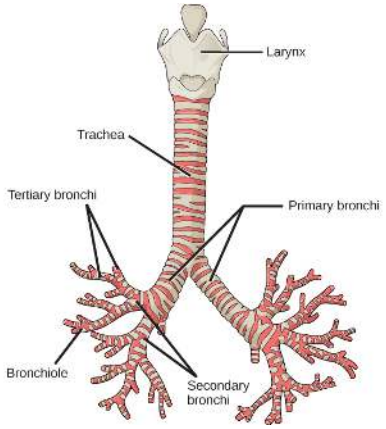


Figure 2. The trachea and bronchi are made of incomplete rings of cartilage. (credit: modification of work by Gray's Anatomy)

From the nasal cavity, air passes through the **pharynx** (throat) and the **larynx** (voice box), as it makes its way to the **trachea** (Figure 1). The main function of the trachea is to funnel the inhaled air to the lungs and the exhaled air back out of the body. The human trachea is a cylinder about 10 to 12 cm long and 2 cm in diameter that sits in front of the esophagus and extends from the larynx into the chest cavity where it divides into the two primary bronchi at the midthorax. It is made of incomplete rings of hyaline cartilage and smooth muscle (Figure 2).

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

Lungs: Bronchi and Alveoli

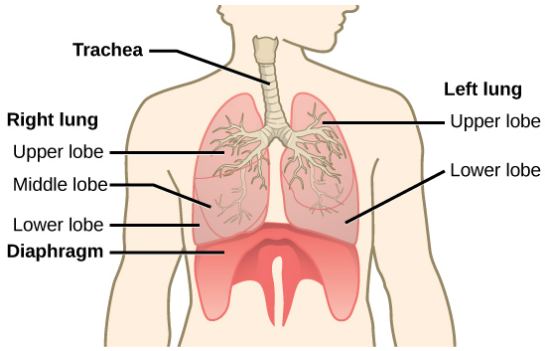


Figure 3. The trachea bifurcates into the right and left bronchi in the lungs. The right lung is made of three lobes and is larger. To accommodate the heart, the left lung is smaller and has only two lobes.

The end of the trachea bifurcates (divides) to the right and left lungs. The lungs are not identical. The right lung is larger and contains three lobes, whereas the smaller left lung contains two lobes (Figure 3). The muscular **diaphragm**, which facilitates breathing, is inferior (below) to the lungs and marks the end of the thoracic cavity.

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

The **terminal bronchioles** subdivide into microscopic branches called respiratory bronchioles. The respiratory bronchioles subdivide into several alveolar ducts. Numerous alveoli and alveolar sacs surround the alveolar ducts. The alveolar sacs resemble bunches of grapes tethered to the end of the bronchioles (Figure 4).

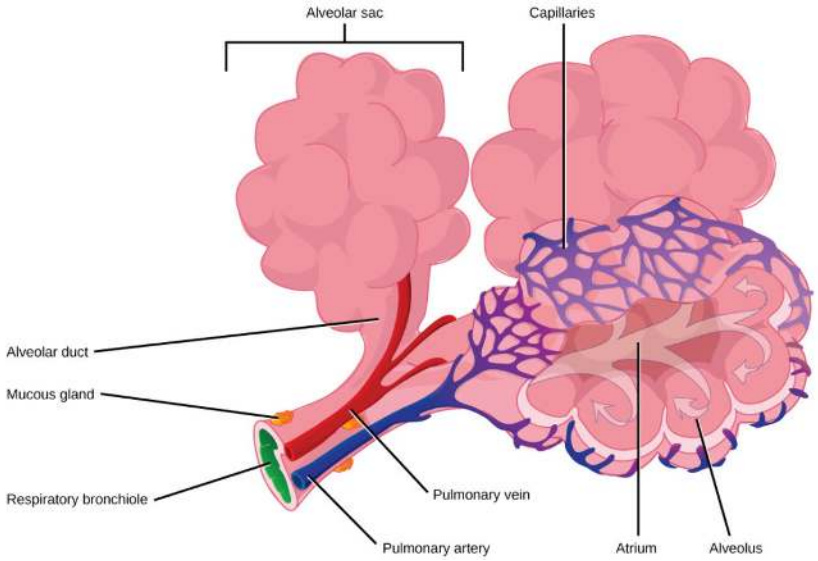


Figure 4. Terminal bronchioles are connected by respiratory bronchioles to alveolar ducts and alveolar sacs. Each alveolar sac contains 20 to 30 spherical alveoli and has the appearance of a bunch of grapes. Air flows into the atrium of the alveolar sac, then circulates into alveoli where gas exchange occurs with the capillaries. Mucous glands secrete mucous into the airways, keeping them moist and flexible. (credit: modification of work by Mariana Ruiz Villareal)

In the acinar region, the **alveolar ducts** are attached to the end of each bronchiole. At the end of each duct are approximately 100 **alveolar sacs**, each containing 20 to 30 **alveoli** that are 200 to 300 microns in diameter. Gas exchange occurs only in alveoli. Alveoli are made of thin-walled parenchymal cells, typically one-cell thick, that look like tiny bubbles within the sacs. Alveoli are in direct contact with capillaries (one-cell thick) of the circulatory system. Such intimate contact ensures that oxygen will diffuse from alveoli into the blood and be distributed to the cells of the body. In addition, the carbon dioxide that was produced by cells as a waste product will diffuse from the blood into alveoli to be exhaled. The anatomical arrangement of capillaries and alveoli emphasizes the structural and functional relationship of the respiratory and circulatory systems. Because there are so many alveoli (~300 million per lung) within each alveolar sac and so many sacs at the end of each alveolar duct, the lungs have a sponge-like consistency. This organization produces a very large surface area that is available for gas exchange. The surface area of alveoli in the lungs is approximately 75 m^2. This large surface area, combined with the thin-walled nature of the alveolar parenchymal cells, allows gases to easily diffuse across the cells.

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22.5: Protective Mechanisms

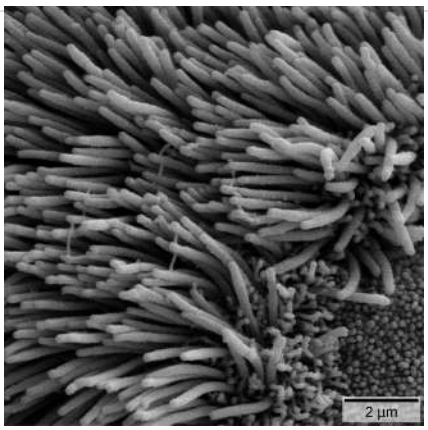


Figure 1. The bronchi and bronchioles contain cilia that help move mucus and other particles out of the lungs. (credit: Louisa Howard, modification of work by Dartmouth Electron Microscope Facility)

The air that organisms breathe contains **particulate matter** such as dust, dirt, viral particles, and bacteria that can damage the lungs or trigger allergic immune responses. The respiratory system contains several protective mechanisms to avoid problems or tissue damage. In the nasal cavity, hairs and mucus trap small particles, viruses, bacteria, dust, and dirt to prevent their entry.

If particulates do make it beyond the nose, or enter through the mouth, the bronchi and bronchioles of the lungs also contain several protective devices. The lungs produce **mucus**—a sticky substance made of **mucin**, a complex glycoprotein, as well as salts and water—that traps particulates. The bronchi and bronchioles contain cilia, small hair-like projections that line the walls of the bronchi and bronchioles (Figure 1). These cilia beat in unison and move mucus and particles out of the bronchi and bronchioles back up to the throat where it is swallowed and eliminated via the esophagus.

In humans, for example, tar and other substances in cigarette smoke destroy or paralyze the cilia, making the removal of particles more difficult. In addition, smoking causes the lungs to produce more mucus, which the damaged cilia are not able to move. This causes a persistent cough, as the lungs try to rid themselves of particulate matter, and makes smokers more susceptible to respiratory ailments.

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22.6: Introduction to Gas Exchange across Respiratory Surfaces

Understand how gas pressure influences how gases move into and out of the body

The structure of the lung maximizes its surface area to increase gas diffusion. Because of the enormous number of alveoli (approximately 300 million in each human lung), the surface area of the lung is very large (75 m^2). Having such a large surface area increases the amount of gas that can diffuse into and out of the lungs.

What You'll Learn to Do

- Identify the basic principles of gas exchange
- Name and describe lung volumes and capacities
- Describe how gas pressure influences how gases move into and out of the body
- Discuss how gases move across the alveoli

Learning Activities

The learning activities for this section include the following:

- Breathing Capacity
- Gas Pressure and Respiration
- Gas Exchange across the Alveoli
- Self Check: Gas Exchange across Respiratory Surfaces

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22.7: Breathing Capacity

Basic Principles of Gas Exchange

Gas exchange during respiration occurs primarily through diffusion. Diffusion is a process in which transport is driven by a concentration gradient. Gas molecules move from a region of high concentration to a region of low concentration. Blood that is low in oxygen concentration and high in carbon dioxide concentration undergoes gas exchange with air in the lungs. The air in the lungs has a higher concentration of oxygen than that of oxygen-depleted blood and a lower concentration of carbon dioxide. This concentration gradient allows for gas exchange during respiration.

Partial pressure is a measure of the concentration of the individual components in a mixture of gases. The total pressure exerted by the mixture is the sum of the partial pressures of the components in the mixture. The rate of diffusion of a gas is proportional to its partial pressure within the total gas mixture. This concept is discussed further in detail below.

Lung Volumes and Capacities

Different animals have different lung capacities based on their activities. Cheetahs have evolved a much higher lung capacity than humans; it helps provide oxygen to all the muscles in the body and allows them to run very fast. Elephants also have a high lung capacity. In this case, it is not because they run fast but because they have a large body and must be able to take up oxygen in accordance with their body size.

Human lung size is determined by genetics, gender, and height. At maximal capacity, an average lung can hold almost six liters of air, but lungs do not usually operate at maximal capacity. Air in the lungs is measured in terms of **lung volumes** and **lung capacities** (see Figure 1 and Table 1). Volume measures the amount of air for one function (such as inhalation or exhalation). Capacity is any two or more volumes (for example, how much can be inhaled from the end of a maximal exhalation).

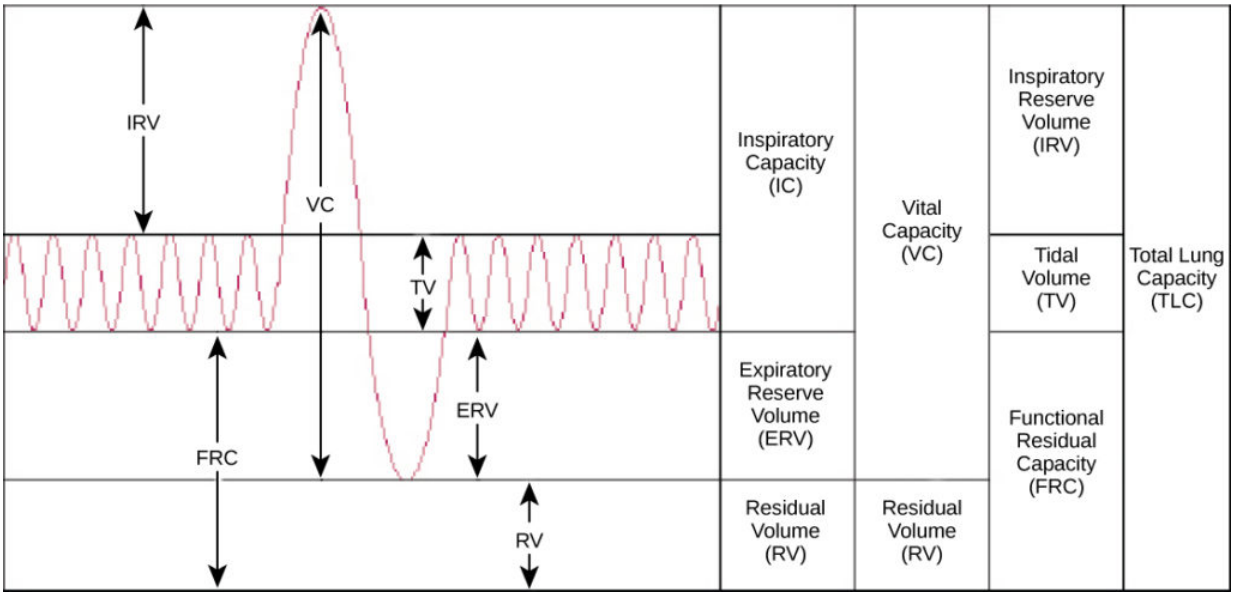


Figure 1. Human lung volumes and capacities are shown. The total lung capacity of the adult male is six liters. Tidal volume is the volume of air inhaled in a single, normal breath. Inspiratory capacity is the amount of air taken in during a deep breath, and residual volume is the amount of air left in the lungs after forceful respiration.

Table 1. Lung Volumes and Capacities (Avg Adult Male)

Volume/Capacity	Definition	Volume (liters)	Equations
Tidal volume (TV)	Amount of air inhaled during a normal breath	0.5	–
Expiratory reserve volume (ERV)	Amount of air that can be exhaled after a normal exhalation	1.2	–
Inspiratory reserve volume (IRV)	Amount of air that can be further inhaled after a normal inhalation	3.1	–
Residual volume (RV)	Air left in the lungs after a forced exhalation	1.2	–
Vital capacity (VC)	Maximum amount of air that can be moved in or out of the lungs in a single respiratory cycle	4.8	ERV+TV+IRV
Inspiratory capacity (IC)	Volume of air that can be inhaled in addition to a normal exhalation	3.6	TV+IRV
Functional residual capacity (FRC)	Volume of air remaining after a normal exhalation	2.4	ERV+RV
Total lung capacity (TLC)	Total volume of air in the lungs after a maximal inspiration	6.0	RV+ERV+TV+IRV
Forced expiratory volume (FEV1)	How much air can be forced out of the lungs over a specific time period, usually one second	~4.1 to 5.5	–

The volume in the lung can be divided into four units: tidal volume, expiratory reserve volume, inspiratory reserve volume, and residual volume. **Tidal volume (TV)** measures the amount of air that is inspired and expired during a normal breath. On average, this volume is around one-half liter, which is a little less than the capacity of a 20-ounce drink bottle. The **expiratory reserve volume (ERV)** is the additional amount of air that can be exhaled after a normal exhalation. It is the reserve amount that can be exhaled beyond what is normal. Conversely, the **inspiratory reserve volume (IRV)** is the additional amount of air that can be inhaled after a normal inhalation. The **residual volume (RV)** is the amount of air that is left after expiratory reserve volume is exhaled. The lungs are never completely empty: There is always some air left in the lungs after a maximal exhalation. If this residual volume did not exist and the lungs emptied completely, the lung tissues would stick together and the energy necessary to re-inflate the lung could be too great to overcome. Therefore, there is always some air remaining in the lungs. Residual volume is also important for preventing large fluctuations in respiratory gases (O_2 and CO_2). The residual volume is the only lung volume that cannot be measured directly because it is impossible to completely empty the lung of air. This volume can only be calculated rather than measured.

Capacities are measurements of two or more volumes. The **vital capacity (VC)** measures the maximum amount of air that can be inhaled or exhaled during a respiratory cycle. It is the sum of the expiratory reserve volume, tidal volume, and inspiratory reserve volume. The **inspiratory capacity (IC)** is the amount of air that can be inhaled after the end of a normal expiration. It is, therefore, the sum of the tidal volume and inspiratory reserve volume. The **functional residual capacity (FRC)** includes the expiratory reserve volume and the residual volume. The FRC measures the amount of additional air that can be exhaled after a normal

exhalation. Lastly, the **total lung capacity (TLC)** is a measurement of the total amount of air that the lung can hold. It is the sum of the residual volume, expiratory reserve volume, tidal volume, and inspiratory reserve volume.

Lung volumes are measured by a technique called **spirometry**. An important measurement taken during spirometry is the **forced expiratory volume (FEV)**, which measures how much air can be forced out of the lung over a specific period, usually one second (FEV1). In addition, the forced vital capacity (FVC), which is the total amount of air that can be forcibly exhaled, is measured. The ratio of these values (**FEV1/FVC ratio**) is used to diagnose lung diseases including asthma, emphysema, and fibrosis. If the FEV1/FVC ratio is high, the lungs are not compliant (meaning they are stiff and unable to bend properly), and the patient most likely has lung fibrosis. Patients exhale most of the lung volume very quickly. Conversely, when the FEV1/FVC ratio is low, there is resistance in the lung that is characteristic of asthma. In this instance, it is hard for the patient to get the air out of his or her lungs, and it takes a long time to reach the maximal exhalation volume. In either case, breathing is difficult and complications arise.

Practice Questions

The inspiratory reserve volume measures the _____.

a. amount of air remaining in the lung after a maximal exhalation
b. amount of air that the lung holds
c. amount of air the can be further exhaled after a normal breath
d. amount of air that can be further inhaled after a normal breath

[reveal-answer q="759869"]Show Answer[/reveal-answer]
[hidden-answer a="759869"]Answer d: The inspiratory reserve volume measures the amount of air that can be further inhaled after a normal breath.

[/hidden-answer]

Of the following, which does not explain why the partial pressure of oxygen is lower in the lung than in the external air?

a. Air in the lung is humidified; therefore, water vapor pressure alters the pressure.
b. Carbon dioxide mixes with oxygen.
c. Lungs exert a pressure on the air to reduce the oxygen pressure.
d. Oxygen is moved into the blood and is headed to the tissues.

[reveal-answer q="644127"]Show Answer[/reveal-answer]
[hidden-answer a="644127"]Answer c: Lungs exert a pressure on the air to reduce the oxygen pressure.

[/hidden-answer]

The total lung capacity is calculated using which of the following formulas?

a. residual volume + expiratory reserve volume + tidal volume + inspiratory reserve volume
b. residual volume + tidal volume + inspiratory reserve volume
c. residual volume + expiratory reserve volume + inspiratory reserve volume
d. expiratory reserve volume + tidal volume + inspiratory reserve volume

[reveal-answer q="889265"]Show Answer[/reveal-answer]
[hidden-answer a="889265"]Answer a: The total lung capacity is calculated using the following formula:

residual volume + expiratory reserve volume + tidal volume + inspiratory reserve volume[/hidden-answer]

Learning Objectives

The lungs can hold a large volume of air, but they are not usually filled to maximal capacity. Lung volume measurements include tidal volume, expiratory reserve volume, inspiratory reserve volume, and residual volume. The sum of these equals the total lung capacity.

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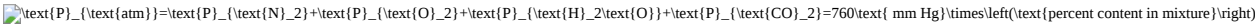
22.8: Gas Pressure and Respiration

The respiratory process can be better understood by examining the properties of gases. Gases move freely, but gas particles are constantly hitting the walls of their vessel, thereby producing gas pressure.

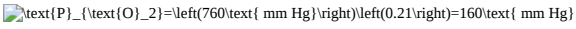
Air is a mixture of gases, primarily nitrogen (N_2; 78.6 percent), oxygen (O_2; 20.9 percent), water vapor (H_2O; 0.5 percent), and carbon dioxide (CO_2; 0.04 percent). Each gas component of that mixture exerts a pressure. The pressure for an individual gas in the mixture is the partial pressure of that gas. Approximately 21 percent of atmospheric gas is oxygen. Carbon dioxide, however, is found in relatively small amounts, 0.04 percent. The partial pressure for oxygen is much greater than that of carbon dioxide. The partial pressure of any gas can be calculated by:



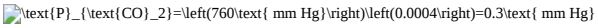
$$\mathrm{P_{atm}} \tag{22.8.1}$$



The pressure of the atmosphere at sea level is 760 mm Hg. Therefore, the partial pressure of oxygen is:

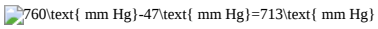


and for carbon dioxide:

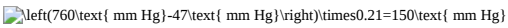


At high altitudes,  decreases, but concentration does not change; the partial pressure decrease is due to the reduction in  .

When the air mixture reaches the lung, it has been humidified. The pressure of the water vapor in the lung does not change the pressure of the air, but it must be included in the partial pressure equation. For this calculation, the water pressure (47 mm Hg) is subtracted from the atmospheric pressure:



and the partial pressure of oxygen is:



These partial pressures determine the rate of gas exchange, or the flow of gas, in the system. Oxygen and carbon dioxide will flow according to their pressure gradient from high to low. Therefore, understanding the partial pressure of each gas will aid in understanding how gases move in the respiratory system.

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22.9: Gas Exchange across the Alveoli

In the body, oxygen is used by cells of the body's tissues and carbon dioxide is produced as a waste product. The ratio of carbon dioxide production to oxygen consumption is the **respiratory quotient (RQ)**. RQ varies between 0.7 and 1.0. If just glucose were used to fuel the body, the RQ would equal one. One mole of carbon dioxide would be produced for every mole of oxygen consumed. Glucose, however, is not the only fuel for the body. Protein and fat are also used as fuels for the body. Because of this, less carbon dioxide is produced than oxygen is consumed and the RQ is, on average, about 0.7 for fat and about 0.8 for protein.

The RQ is used to calculate the partial pressure of oxygen in the alveolar spaces within the lung, the **alveolar** P_{O_2} . Above, the partial pressure of oxygen in the lungs was calculated to be 150 mm Hg. However, lungs never fully deflate with an exhalation; therefore, the inspired air mixes with this residual air and lowers the partial pressure of oxygen within the alveoli. This means that there is a lower concentration of oxygen in the lungs than is found in the air outside the body. Knowing the RQ, the partial pressure of oxygen in the alveoli can be calculated:

$$\text{alveolar P}_{\text{O}_2}=\text{inspired P}_{\text{O}_2}-\left(\frac{\text{alveolar P}_{\text{O}_2}}{\text{RQ}}\right)$$

With an RQ of 0.8 and a P_{CO_2} in the alveoli of 40 mm Hg, the alveolar P_{O_2} is equal to:

$$\text{alveolar P}_{\text{O}_2}=150\text{ mm Hg}-\left(\frac{40\text{ mm Hg}}{0.8}\right)=\text{mm Hg}$$

Notice that this pressure is less than the external air. Therefore, the oxygen will flow from the inspired air in the lung $\left(\text{P}_{\text{O}_2}=150\text{ mm Hg}\right)$ into the bloodstream $\left(\text{P}_{\text{O}_2}=100\text{ mm Hg}\right)$.

In the lungs, oxygen diffuses out of the alveoli and into the capillaries surrounding the alveoli. Oxygen (about 98 percent) binds reversibly to the respiratory pigment hemoglobin found in red blood cells (RBCs). RBCs carry oxygen to the tissues where oxygen dissociates from the hemoglobin and diffuses into the cells of the tissues. More specifically, alveolar P_{O_2} is higher in the alveoli $\left(\text{P}_{\text{ALVO}_2}=100\text{ mm Hg}\right)$ than blood $\text{P}_{\text{O}_2}\left(40\text{ mm Hg}\right)$ in the capillaries. Because this pressure gradient exists, oxygen diffuses down its pressure gradient, moving out of the alveoli and entering the blood of the capillaries where O_2 binds to hemoglobin. At the same time, alveolar P_{CO_2} is lower $\left(\text{P}_{\text{ALVO}_2}=40\text{ mm Hg}\right)$ than blood $\text{P}_{\text{CO}_2}=\left(45\text{ mm Hg}\right)$. CO_2 diffuses down its pressure gradient, moving out of the capillaries and entering the alveoli.

Oxygen and carbon dioxide move independently of each other; they diffuse down their own pressure gradients.

As blood leaves the lungs through the pulmonary veins, the **venous** $\mathbf{\text{P}_{\text{O}_2}}$= 100 mm Hg, whereas the **venous** $\mathbf{\text{P}_{\text{CO}_2}}$ = 40 mm Hg. As blood enters the systemic capillaries, the blood will lose oxygen and gain carbon dioxide because of the pressure difference of the tissues and blood. In systemic capillaries, $\text{P}_{\text{O}_2}=100\text{ mm Hg}$, but in the tissue cells, $\text{P}_{\text{O}_2}=40\text{ mm Hg}$. This pressure gradient drives the diffusion of oxygen out of the capillaries and into the tissue cells. At the same time, blood $\text{P}_{\text{CO}_2}=40\text{ mm Hg}$ and systemic tissue $\text{P}_{\text{CO}_2}=45\text{ mm Hg}$. The pressure gradient drives CO_2 out of tissue cells and into the capillaries. The blood returning to the lungs through the pulmonary arteries has a venous $\text{P}_{\text{O}_2}=40\text{ mm Hg}$ and a $\text{P}_{\text{CO}_2}=45\text{ mm Hg}$. The blood enters the lung capillaries where the process of exchanging gases between the capillaries and alveoli begins again (Figure 1).

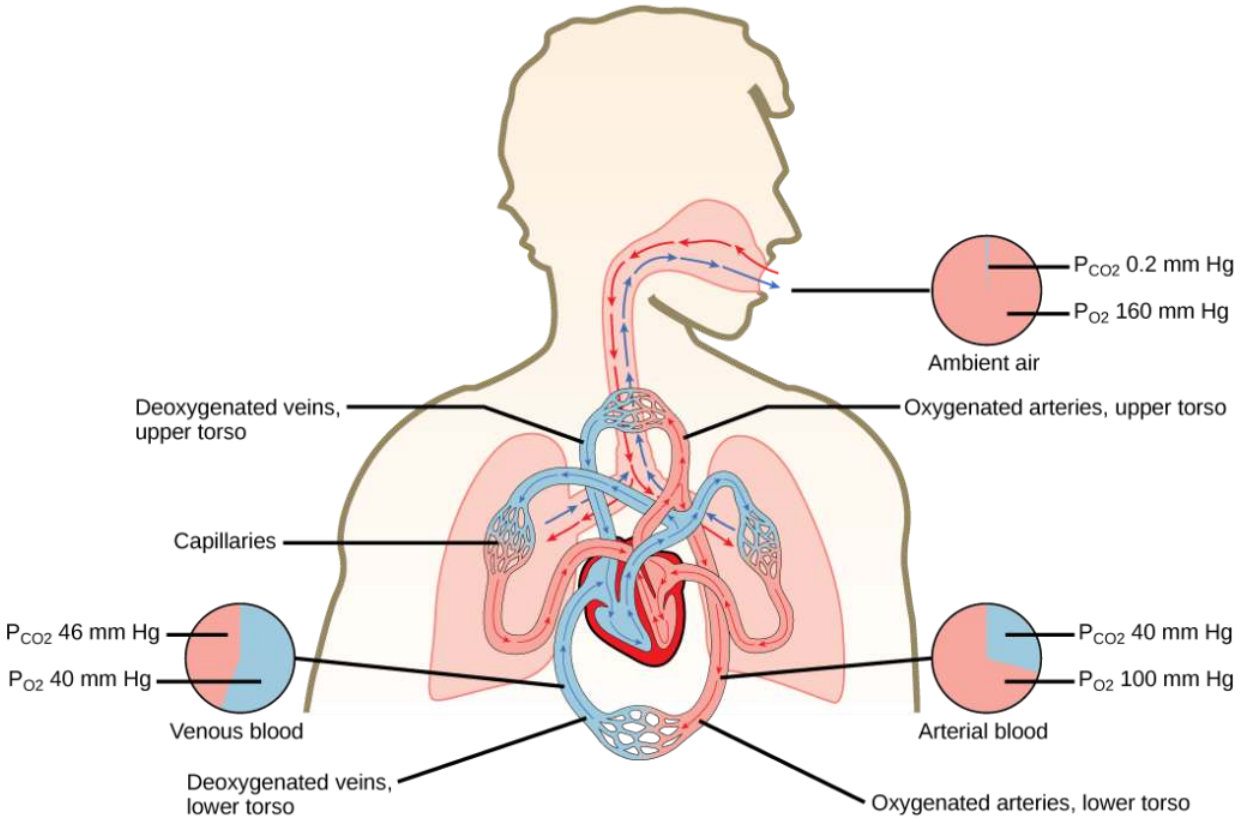


Figure 1. The partial pressures of oxygen and carbon dioxide change as blood moves through the body.

Practice Question

Which of the following statements is false?

a. In the tissues, P_{O_2} drops as blood passes from the arteries to the veins, while P_{CO_2} increases.
b. Blood travels from the lungs to the heart to body tissues, then back to the heart, then the lungs.
c. Blood travels from the lungs to the heart to body tissues, then back to the lungs, then the heart.
d. P_{O_2} is higher in air than in the lungs.

[reveal-answer q="660519"]Show Answer[/reveal-answer]
[hidden-answer a="660519"]Statement c is false.[/hidden-answer]

In short, the change in partial pressure from the alveoli to the capillaries drives the oxygen into the tissues and the carbon dioxide into the blood from the tissues. The blood is then transported to the lungs where differences in pressure in the alveoli result in the movement of carbon dioxide out of the blood into the lungs, and oxygen into the blood.

Watch this video to learn how to carry out spirometry.

A link to an interactive elements can be found at the bottom of this page.

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22.10: Introduction to Breathing

Describe how the structures of the respiratory system control the mechanics of breathing

Mammalian lungs are located in the thoracic cavity where they are surrounded and protected by the rib cage, intercostal muscles, and bound by the chest wall. The bottom of the lungs is contained by the diaphragm, a skeletal muscle that facilitates breathing. Breathing requires the coordination of the lungs, the chest wall, and most importantly, the diaphragm.

What You'll Learn to Do

- Identify common types of breathing, including that of mammals and amphibians
- Describe how the structures of the lungs and thoracic cavity control the mechanics of breathing
- Explain the importance of compliance and resistance in the lungs
- Discuss problems that may arise due to a V/Q mismatch

Learning Activities

The learning activities for this section include the following:

- Types of Breathing
- The Mechanics of Human Breathing
- The Work of Breathing
- Dead Space
- Self Check: Breathing

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22.11: Types of Breathing

Amphibian Respiration

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

Avian Respiration

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

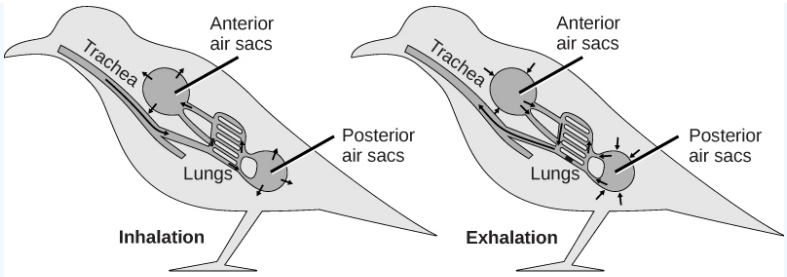
In addition to lungs, birds have air sacs inside their body. Air flows in one direction from the posterior air sacs to the lungs and out of the anterior air sacs. The flow of air is in the opposite direction from blood flow, and gas exchange takes place much more efficiently. This type of breathing enables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

? Try It

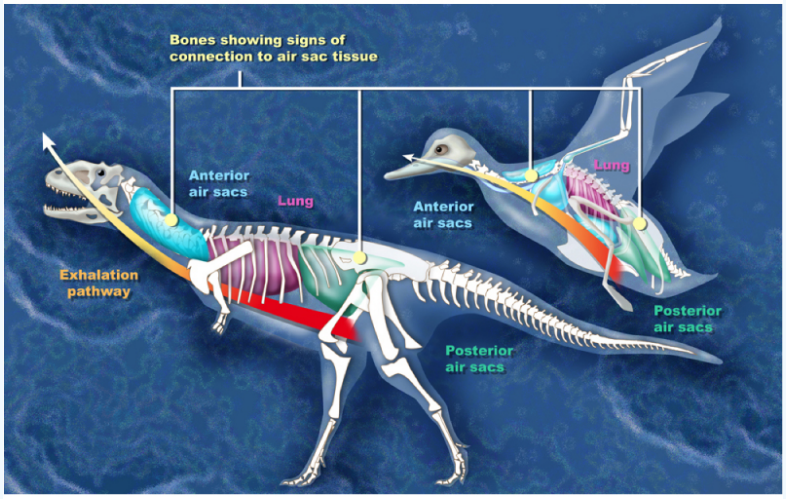
Birds have evolved a respiratory system that enables them to fly. Flying is a high-energy process and requires a lot of oxygen. Furthermore, many birds fly in high altitudes where the concentration of oxygen in low. How did birds evolve a respiratory system that is so unique?

Decades of research by paleontologists have shown that birds evolved from therapods, meat-eating dinosaurs (Figure 1). In fact, fossil evidence shows that meat-eating dinosaurs that lived more than 100 million years ago had a similar flow-through respiratory system with lungs and air sacs. *Archaeopteryx*and *Xiaotingia*, for example, were flying dinosaurs and are believed to be early precursors of birds.

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



(a)



(b)

Figure 1. (a) Birds have a flow-through respiratory system in which air flows unidirectionally from the posterior sacs into the lungs, then into the anterior air sacs. The air sacs connect to openings in hollow bones. (b) Dinosaurs, from which birds descended, have similar hollow bones and are believed to have had a similar respiratory system. (credit b: modification of work by Zina Deretsky, National Science Foundation)

Mammalian Respiration

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

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22.12: The Mechanics of Human Breathing

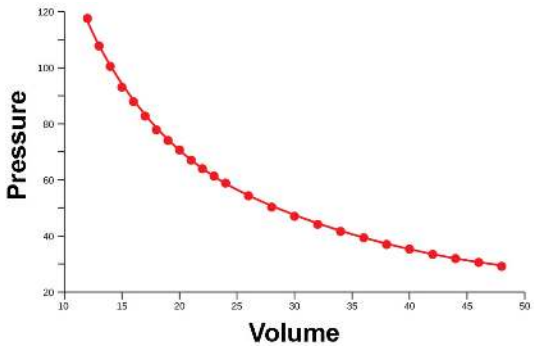


Figure 1. This graph shows data from Boyle's original 1662 experiment, which shows that pressure and volume are inversely related. No units are given as Boyle used arbitrary units in his experiments.

Boyle's Law is the gas law that states that in a closed space, pressure and volume are inversely related. As volume decreases, pressure increases and vice versa (Figure 1). The relationship between gas pressure and volume helps to explain the mechanics of breathing.

There is always a slightly negative pressure within the thoracic cavity, which aids in keeping the airways of the lungs open. During inhalation, volume increases as a result of contraction of the diaphragm, and pressure decreases (according to Boyle's Law). This decrease of pressure in the thoracic cavity relative to the environment makes the cavity less than the atmosphere (Figure 2a). Because of this drop in pressure, air rushes into the respiratory passages. To increase the volume of the lungs, the chest wall expands. This results from the contraction of the **intercostal muscles**, the muscles that are connected to the rib cage. Lung volume expands because the diaphragm contracts and the intercostals muscles contract, thus expanding the thoracic cavity. This increase in the volume of the thoracic cavity lowers pressure compared to the atmosphere, so air rushes into the lungs, thus increasing its volume. The resulting increase in volume is largely attributed to an increase in alveolar space, because the bronchioles and bronchi are stiff structures that do not change in size.

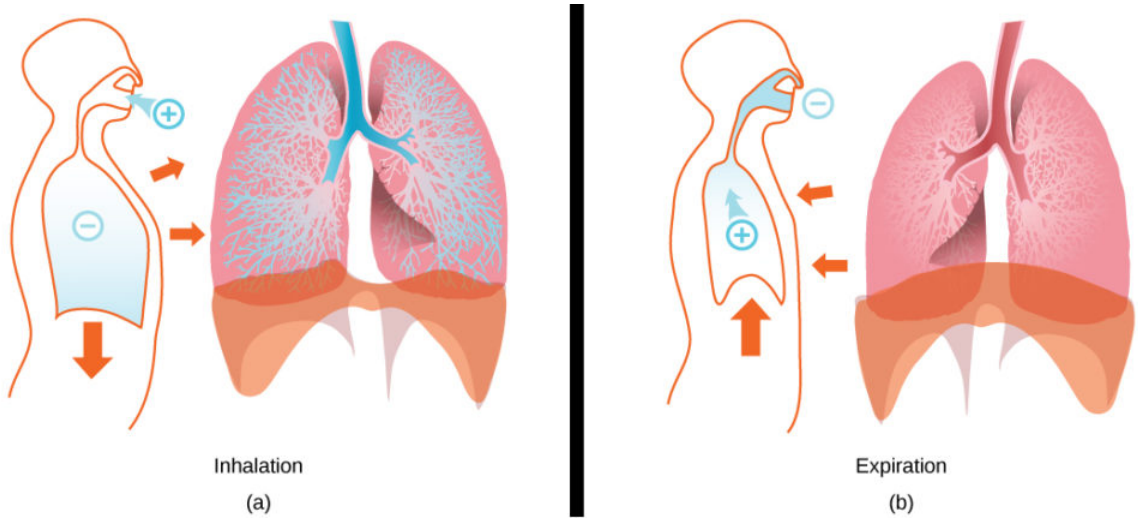


Figure 2. The lungs, chest wall, and diaphragm are all involved in respiration, both (a) inhalation and (b) expiration. (credit: modification of work by Mariana Ruiz Villareal)

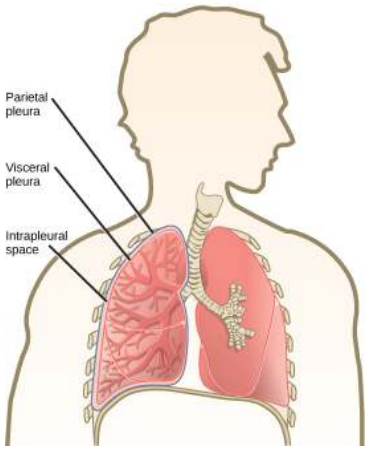


Figure 3. A tissue layer called pleura surrounds the lung and interior of the thoracic cavity. (credit: modification of work by NCI)

The chest wall expands out and away from the lungs. The lungs are elastic; therefore, when air fills the lungs, the **elastic recoil** within the tissues of the lung exerts pressure back toward the interior of the lungs and pushes air back out of the lungs. These outward and inward forces compete to inflate and deflate the lung with every breath. Upon exhalation, the lungs recoil to force the air out of the lungs, and the intercostal muscles relax, returning the chest wall back to its original position (Figure 2b).

The diaphragm also relaxes and moves higher into the thoracic cavity. This increases the pressure within the thoracic cavity relative to the environment, and air rushes out of the lungs. The movement of air out of the lungs is a passive event; no muscles are contracting to expel the air.

Each lung is surrounded by an invaginated sac. The layer of tissue that covers the lung and dips into spaces is called the visceral **pleura**. A second layer of parietal pleura lines the interior of the thorax (Figure 3). The space between these layers, the **intrapleural space**, contains a small amount of fluid that protects the tissue and reduces the friction generated from rubbing the tissue layers together as the lungs contract and relax. **Pleurisy** results when these layers of tissue become inflamed; it is painful because the inflammation increases the pressure within the thoracic cavity and reduces the volume of the lung.

View how Boyle's Law is related to breathing and watch this video:

A link to an interactive elements can be found at the bottom of this page.

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22.13: The Work of Breathing

The number of breaths per minute is the **respiratory rate**. On average, under non-exertion conditions, the human respiratory rate is 12–15 breaths/minute. The respiratory rate contributes to the **alveolar ventilation**, or how much air moves into and out of the alveoli. Alveolar ventilation prevents carbon dioxide buildup in the alveoli. There are two ways to keep the alveolar ventilation constant: increase the respiratory rate while decreasing the tidal volume of air per breath (shallow breathing), or decrease the respiratory rate while increasing the tidal volume per breath. In either case, the ventilation remains the same, but the work done and type of work needed are quite different. Both tidal volume and respiratory rate are closely regulated when oxygen demand increases.

There are two types of work conducted during respiration, flow-resistive and elastic work. **Flow-resistive** refers to the work of the alveoli and tissues in the lung, whereas **elastic work** refers to the work of the intercostal muscles, chest wall, and diaphragm. Increasing the respiration rate increases the flow-resistive work of the airways and decreases the elastic work of the muscles. Decreasing the respiratory rate reverses the type of work required.

Surfactant

The air-tissue/water interface of the alveoli has a high surface tension. This surface tension is similar to the surface tension of water at the liquid-air interface of a water droplet that results in the bonding of the water molecules together. **Surfactant** is a complex mixture of phospholipids and lipoproteins that works to reduce the surface tension that exists between the alveoli tissue and the air found within the alveoli. By lowering the surface tension of the alveolar fluid, it reduces the tendency of alveoli to collapse.

Surfactant works like a detergent to reduce the surface tension and allows for easier inflation of the airways. When a balloon is first inflated, it takes a large amount of effort to stretch the plastic and start to inflate the balloon. If a little bit of detergent was applied to the interior of the balloon, then the amount of effort or work needed to begin to inflate the balloon would decrease, and it would become much easier to start blowing up the balloon. This same principle applies to the airways. A small amount of surfactant to the airway tissues reduces the effort or work needed to inflate those airways. Babies born prematurely sometimes do not produce enough surfactant. As a result, they suffer from **respiratory distress syndrome**, because it requires more effort to inflate their lungs. Surfactant is also important for preventing collapse of small alveoli relative to large alveoli.

Lung Resistance and Compliance

Pulmonary diseases reduce the rate of gas exchange into and out of the lungs. Two main causes of decreased gas exchange are **compliance** (how elastic the lung is) and **resistance** (how much obstruction exists in the airways). A change in either can dramatically alter breathing and the ability to take in oxygen and release carbon dioxide.

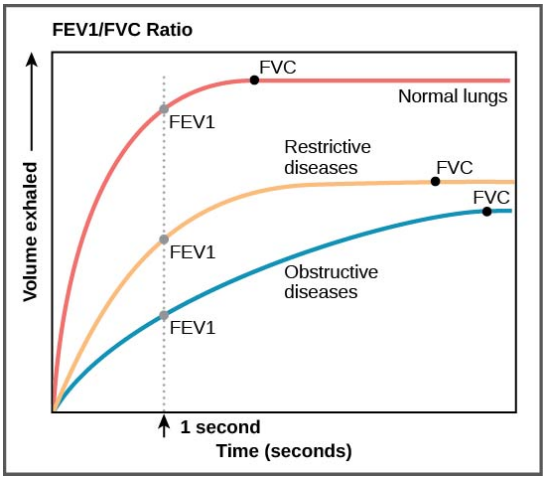


Figure 1. The ratio of FEV1 to FVC.

The ratio of FEV1 (the amount of air that can be forcibly exhaled in one second after taking a deep breath) to FVC (the total amount of air that can be forcibly exhaled) can be used to diagnose whether a person has restrictive or obstructive lung disease. In restrictive lung disease, FVC is reduced but airways are not obstructed, so the person is able to expel air reasonably fast. In

obstructive lung disease, airway obstruction results in slow exhalation as well as reduced FVC. Thus, the FEV1/FVC ratio is lower in persons with obstructive lung disease (less than 69 percent) than in persons with restrictive disease (88 to 90 percent).

Restrictive Diseases

Examples of **restrictive diseases** are respiratory distress syndrome and pulmonary fibrosis. In both diseases, the airways are less compliant and they are stiff or fibrotic. There is a decrease in compliance because the lung tissue cannot bend and move. In these types of restrictive diseases, the intrapleural pressure is more positive and the airways collapse upon exhalation, which traps air in the lungs. Forced or **functional vital capacity (FVC)**, which is the amount of air that can be forcibly exhaled after taking the deepest breath possible, is much lower than in normal patients, and the time it takes to exhale most of the air is greatly prolonged (Figure 1). A patient suffering from these diseases cannot exhale the normal amount of air.

Obstructive Diseases

Obstructive diseases and conditions include emphysema, asthma, and pulmonary edema. In emphysema, which mostly arises from smoking tobacco, the walls of the alveoli are destroyed, decreasing the surface area for gas exchange. The overall compliance of the lungs is increased, because as the alveolar walls are damaged, lung elastic recoil decreases due to a loss of elastic fibers, and more air is trapped in the lungs at the end of exhalation. Asthma is a disease in which inflammation is triggered by environmental factors. Inflammation obstructs the airways. The obstruction may be due to edema (fluid accumulation), smooth muscle spasms in the walls of the bronchioles, increased mucus secretion, damage to the epithelia of the airways, or a combination of these events. Those with asthma or edema experience increased occlusion from increased inflammation of the airways. This tends to block the airways, preventing the proper movement of gases (Figure 1). Those with obstructive diseases have large volumes of air trapped after exhalation and breathe at a very high lung volume to compensate for the lack of airway recruitment.

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22.14: Dead Space

Pulmonary circulation pressure is very low compared to that of the systemic circulation. It is also independent of cardiac output. This is because of a phenomenon called **recruitment**, which is the process of opening airways that normally remain closed when cardiac output increases. As cardiac output increases, the number of capillaries and arteries that are perfused (filled with blood) increases. These capillaries and arteries are not always in use but are ready if needed. At times, however, there is a mismatch between the amount of air (ventilation, V) and the amount of blood (perfusion, Q) in the lungs.

This difference between the amounts of air and blood reaching the lungs is referred to as **ventilation/perfusion (V/Q) mismatch**.

There are two types of V/Q mismatch. Both produce **dead space or shunts**, regions of ineffective lung tissue. Dead spaces can severely impact breathing, because they reduce the surface area available for gas diffusion. As a result, the amount of oxygen in the blood decreases, whereas the carbon dioxide level increases. Dead space is created when no ventilation and/or perfusion takes place.

1. **Anatomical dead space** and **anatomical shunts** arise from an anatomical deficiencies. Anatomical dead space occurs naturally in areas of the lungs that don't come in contact with alveoli (like the trachea). In these spaces, the lungs are ventilated and receiving enough air, but blood is not being oxygenated in that space because the air is not reaching perfused areas. An example of an anatomical shunt is the effect of gravity on the lungs. The lung is particularly susceptible to changes in the magnitude and direction of gravitational forces. When someone is standing or sitting upright, the pleural pressure gradient leads to increased ventilation further down in the lung. Likewise, it takes less energy to pump blood to the bottom of the lung than to the top when in a prone position. Perfusion of the lung is not uniform while standing or sitting, and some of the circulating blood doesn't make it past the lungs to be oxygenated. An anatomical shunt develops because the ventilation of the airways does not match the perfusion of the arteries surrounding those airways. As a result, the rate of gas exchange is reduced. Note that this does not occur when lying down, because in this position, gravity does not preferentially pull the bottom of the lung down.
2. **Physiological dead space** or **physiological shunts**, arise from a functional impairment of the lung or arteries. This happens when there is a lack of blood flow where the alveoli have enough air to oxygenate blood or there is a lack of air in an area where the blood flow is normal. A physiological shunt can develop if there is infection or edema in the lung that obstructs an area. This will decrease ventilation but not affect perfusion; therefore, the V/Q ratio changes and gas exchange is affected. A physiological dead space could be something like a blood clot that cuts down perfusion around well-ventilated alveoli. Emphysema, which causes a deterioration of capillaries around alveoli will also create physiological dead space.

The lung can compensate for these mismatches in ventilation and perfusion. If ventilation is greater than perfusion, the arterioles dilate and the bronchioles constrict. This increases perfusion and reduces ventilation. Likewise, if ventilation is less than perfusion, the arterioles constrict and the bronchioles dilate to correct the imbalance.

Watch this video to view the mechanics of breathing.

A link to an interactive elements can be found at the bottom of this page.

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22.15: Introduction to Transport of Gases in Human Bodily Fluids

Explain how gases are transported in the body

Once the oxygen diffuses across the alveoli, it enters the bloodstream and is transported to the tissues where it is unloaded, and carbon dioxide diffuses out of the blood and into the alveoli to be expelled from the body. Although gas exchange is a continuous process, the oxygen and carbon dioxide are transported by different mechanisms.

What You'll Learn to Do

- Describe how oxygen is bound to hemoglobin and transported to body tissues
- Explain how carbon dioxide is transported from body tissues to the lungs

Learning Activities

The learning activities for this section include the following:

- Transport of Oxygen in the Blood
- Transport of Carbon Dioxide in the Blood
- Self Check: Transport of Gases in Human Bodily Fluids

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22.16: Transport of Oxygen in the Blood

Although oxygen dissolves in blood, only a small amount of oxygen is transported this way. Only 1.5 percent of oxygen in the blood is dissolved directly into the blood itself. Most oxygen—98.5 percent—is bound to a protein called hemoglobin and carried to the tissues.

Hemoglobin

Hemoglobin, or Hb, is a protein molecule found in red blood cells (erythrocytes) made of four subunits: two alpha subunits and two beta subunits (Figure 1). Each subunit surrounds a central **heme group** that contains iron and binds one oxygen molecule, allowing each hemoglobin molecule to bind four oxygen molecules. Molecules with more oxygen bound to the heme groups are brighter red. As a result, oxygenated arterial blood where the Hb is carrying four oxygen molecules is bright red, while venous blood that is deoxygenated is darker red.

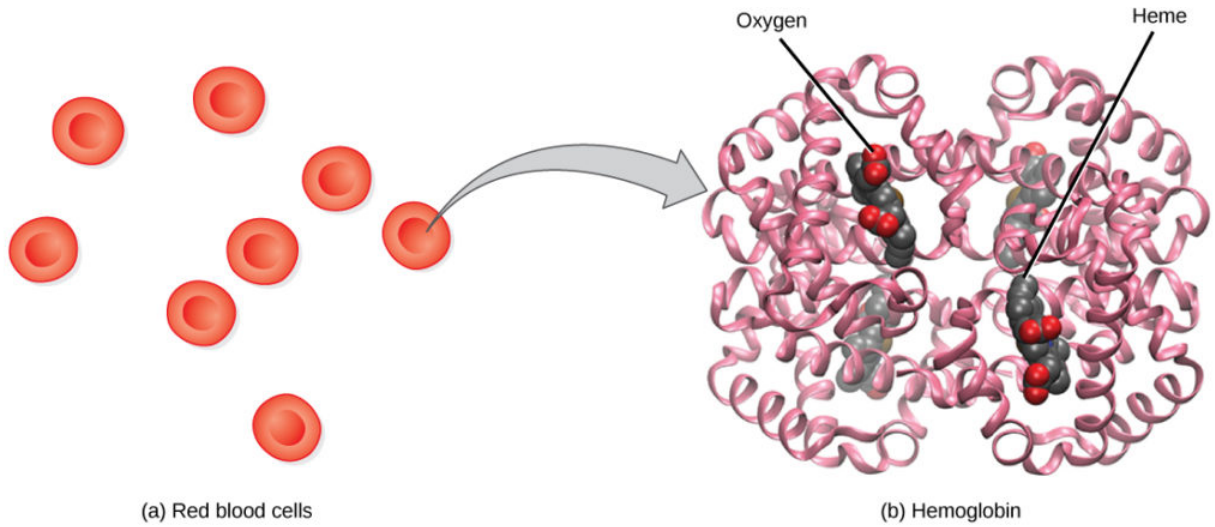


Figure 1. The protein inside (a) red blood cells that carries oxygen to cells and carbon dioxide to the lungs is (b) hemoglobin. Hemoglobin is made up of four symmetrical subunits and four heme groups. Iron associated with the heme binds oxygen. It is the iron in hemoglobin that gives blood its red color.

It is easier to bind a second and third oxygen molecule to Hb than the first molecule. This is because the hemoglobin molecule changes its shape, or conformation, as oxygen binds. The fourth oxygen is then more difficult to bind. The binding of oxygen to hemoglobin can be plotted as a function of the partial pressure of oxygen in the blood (x-axis) versus the relative Hb-oxygen saturation (y-axis). The resulting graph—an **oxygen dissociation curve**—is sigmoidal, or S-shaped (Figure 2). As the partial pressure of oxygen increases, the hemoglobin becomes increasingly saturated with oxygen.

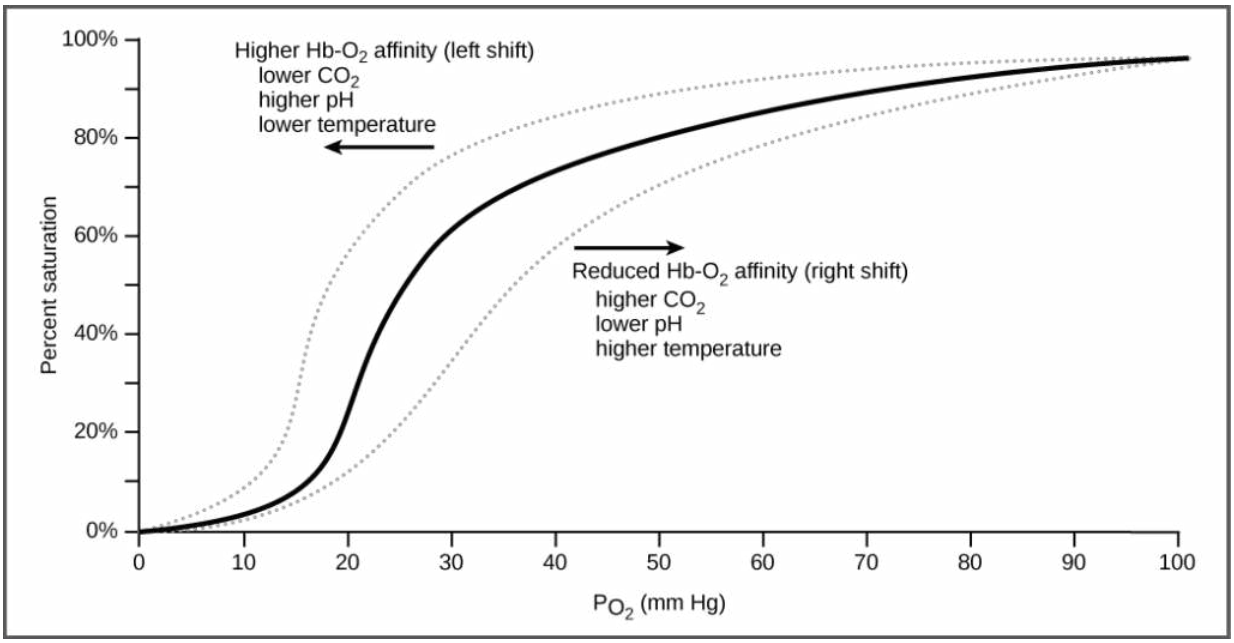


Figure 2. The oxygen dissociation curve demonstrates that, as the partial pressure of oxygen increases, more oxygen binds hemoglobin. However, the affinity of hemoglobin for oxygen may shift to the left or the right depending on environmental conditions.

? Practice Question

The kidneys are responsible for removing excess H+ ions from the blood. If the kidneys fail, what would happen to blood pH and to hemoglobin affinity for oxygen?

[reveal-answer q="521300"]Show Answer[/reveal-answer]

[hidden-answer a="521300"]The blood pH will drop and hemoglobin affinity for oxygen will decrease.[/hidden-answer]

Factors That Affect Oxygen Binding

The **oxygen-carrying capacity** of hemoglobin determines how much oxygen is carried in the blood. In addition to P_{O_2}, other environmental factors and diseases can affect oxygen carrying capacity and delivery.

Carbon dioxide levels, blood pH, and body temperature affect oxygen-carrying capacity (Figure 2). When carbon dioxide is in the blood, it reacts with water to form bicarbonate $\left(\text{HCO}^-_3\right)$ and hydrogen ions (H^+). As the level of carbon dioxide in the blood increases, more H^+ is produced and the pH decreases. This increase in carbon dioxide and subsequent decrease in pH reduce the affinity of hemoglobin for oxygen. The oxygen dissociates from the Hb molecule, shifting the oxygen dissociation curve to the right. Therefore, more oxygen is needed to reach the same hemoglobin saturation level as when the pH was higher. A similar shift in the curve also results from an increase in body temperature. Increased temperature, such as from increased activity of skeletal muscle, causes the affinity of hemoglobin for oxygen to be reduced.

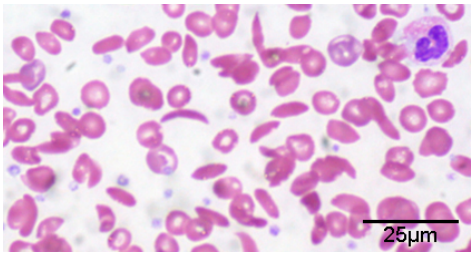


Figure 3. Individuals with sickle cell anemia have crescent-shaped red blood cells. (credit: modification of work by Ed Uthman; scale-bar data from Matt Russell)

Diseases like sickle cell anemia and thalassemia decrease the blood's ability to deliver oxygen to tissues and its oxygen-carrying capacity. In **sickle cell anemia**, the shape of the red blood cell is crescent-shaped, elongated, and stiffened, reducing its ability to

deliver oxygen (Figure 3).

In this form, red blood cells cannot pass through the capillaries. This is painful when it occurs. **Thalassemia** is a rare genetic disease caused by a defect in either the alpha or the beta subunit of Hb. Patients with thalassemia produce a high number of red blood cells, but these cells have lower-than-normal levels of hemoglobin. Therefore, the oxygen-carrying capacity is diminished.

Learning Objectives

Hemoglobin is a protein found in red blood cells that is comprised of two alpha and two beta subunits that surround an iron-containing heme group. Oxygen readily binds this heme group. The ability of oxygen to bind increases as more oxygen molecules are bound to heme. Disease states and altered conditions in the body can affect the binding ability of oxygen, and increase or decrease its ability to dissociate from hemoglobin.

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22.17: Transport of Carbon Dioxide in the Blood

Carbon dioxide molecules are transported in the blood from body tissues to the lungs by one of three methods: dissolution directly into the blood, binding to hemoglobin, or carried as a bicarbonate ion. Several properties of carbon dioxide in the blood affect its transport. First, carbon dioxide is more soluble in blood than oxygen. About 5 to 7 percent of all carbon dioxide is dissolved in the plasma. Second, carbon dioxide can bind to plasma proteins or can enter red blood cells and bind to hemoglobin. This form transports about 10 percent of the carbon dioxide. When carbon dioxide binds to hemoglobin, a molecule called **carbaminohemoglobin** is formed. Binding of carbon dioxide to hemoglobin is reversible. Therefore, when it reaches the lungs, the carbon dioxide can freely dissociate from the hemoglobin and be expelled from the body.

Third, the majority of carbon dioxide molecules (85 percent) are carried as part of the **bicarbonate buffer system**. In this system, carbon dioxide diffuses into the red blood cells. **Carbonic anhydrase (CA)** within the red blood cells quickly converts the carbon dioxide into carbonic acid (H_2CO_3). Carbonic acid is an unstable intermediate molecule that immediately dissociates into **bicarbonate ions** $\left(\text{HCO}^{-}_{3}\right)$ and hydrogen (H^+) ions. Since carbon dioxide is quickly converted into bicarbonate ions, this reaction allows for the continued uptake of carbon dioxide into the blood down its concentration gradient. It also results in the production of H^+ions. If too much H^+ is produced, it can alter blood pH. However, hemoglobin binds to the free H^+ ions and thus limits shifts in pH. The newly synthesized bicarbonate ion is transported out of the red blood cell into the liquid component of the blood in exchange for a chloride ion (Cl^-); this is called the **chloride shift**. When the blood reaches the lungs, the bicarbonate ion is transported back into the red blood cell in exchange for the chloride ion. The H^+ ion dissociates from the hemoglobin and binds to the bicarbonate ion. This produces the carbonic acid intermediate, which is converted back into carbon dioxide through the enzymatic action of CA. The carbon dioxide produced is expelled through the lungs during exhalation.

$$\text{CO}_2+\text{H}_2\text{O}\longleftrightarrow\underset{\left(\text{carbonic acid}\right)}{\text{H}_2\text{CO}_3}\longleftrightarrow\underset{\left(\text{bicarbonate}\right)}{\text{HCO}_3+\text{H}^+}$$

The benefit of the bicarbonate buffer system is that carbon dioxide is “soaked up” into the blood with little change to the pH of the system. This is important because it takes only a small change in the overall pH of the body for severe injury or death to result. The presence of this bicarbonate buffer system also allows for people to travel and live at high altitudes: When the partial pressure of oxygen and carbon dioxide change at high altitudes, the bicarbonate buffer system adjusts to regulate carbon dioxide while maintaining the correct pH in the body.

Carbon Monoxide Poisoning

While carbon dioxide can readily associate and dissociate from hemoglobin, other molecules such as carbon monoxide (CO) cannot. Carbon monoxide has a greater affinity for hemoglobin than oxygen. Therefore, when carbon monoxide is present, it binds to hemoglobin preferentially over oxygen. As a result, oxygen cannot bind to hemoglobin, so very little oxygen is transported through the body (Figure 1).

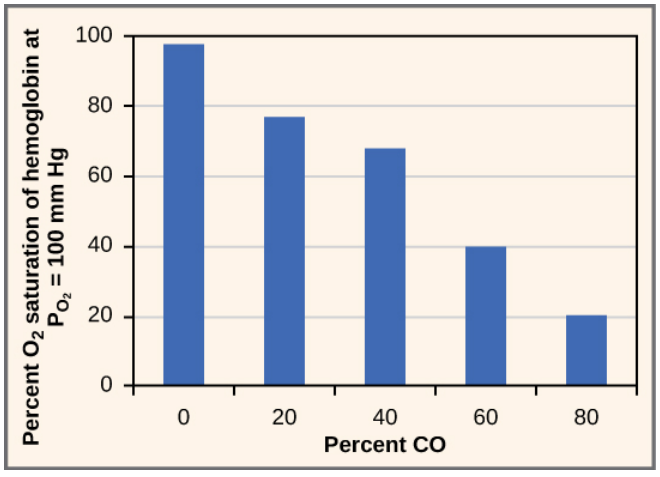


Figure 1. As percent CO increases, the oxygen saturation of hemoglobin decreases.

Carbon monoxide is a colorless, odorless gas and is therefore difficult to detect. It is produced by gas-powered vehicles and tools. Carbon monoxide can cause headaches, confusion, and nausea; long-term exposure can cause brain damage or death.

Administering 100 percent (pure) oxygen is the usual treatment for carbon monoxide poisoning. Administration of pure oxygen speeds up the separation of carbon monoxide from hemoglobin.

Learning Objectives

Carbon dioxide can be transported through the blood via three methods. It is dissolved directly in the blood, bound to plasma proteins or hemoglobin, or converted into bicarbonate.

The majority of carbon dioxide is transported as part of the bicarbonate system. Carbon dioxide diffuses into red blood cells. Inside, carbonic anhydrase converts carbon dioxide into carbonic acid (H_2CO_3), which is subsequently hydrolyzed into bicarbonate $\left(\text{HCO}^{-}_{3}\right)$ and H^+. The H^+ ion binds to hemoglobin in red blood cells, and bicarbonate is transported out of the red blood cells in exchange for a chloride ion. This is called the chloride shift.

Bicarbonate leaves the red blood cells and enters the blood plasma. In the lungs, bicarbonate is transported back into the red blood cells in exchange for chloride. The H^+ dissociates from hemoglobin and combines with bicarbonate to form carbonic acid with the help of carbonic anhydrase, which further catalyzes the reaction to convert carbonic acid back into carbon dioxide and water. The carbon dioxide is then expelled from the lungs.

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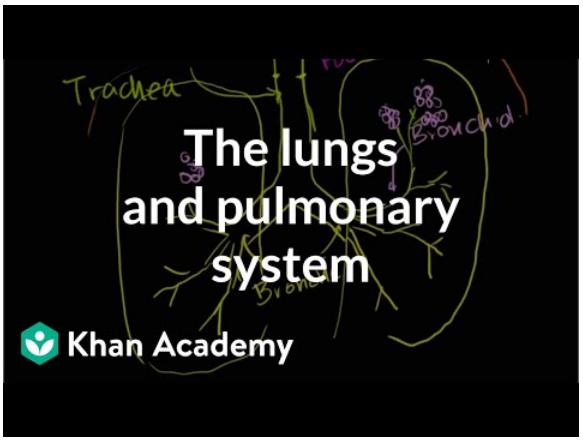
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22.18: Putting It Together- The Respiratory System

Now that we've learned all about the different parts and functions of the respiratory system, let's take a quick moment to review the system as a whole:



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=941

Career Connection

There are several different professions that work with the respiratory system. One of these is the respiratory therapist.

? Try It

Respiratory therapists or respiratory practitioners evaluate and treat patients with lung and cardiovascular diseases. They work as part of a medical team to develop treatment plans for patients. Respiratory therapists may treat premature babies with underdeveloped lungs, patients with chronic conditions such as asthma, or older patients suffering from lung disease such as emphysema and chronic obstructive pulmonary disease (COPD). They may operate advanced equipment such as compressed gas delivery systems, ventilators, blood gas analyzers, and resuscitators. Specialized programs to become a respiratory therapist generally lead to a bachelor's degree with a respiratory therapist specialty. Because of a growing aging population, career opportunities as a respiratory therapist are expected to remain strong.

Respiratory therapists use various tests to evaluate patients. For example, they test lung capacity by having patients breathe into an instrument that measures the volume and flow of oxygen when they inhale and exhale. Respiratory therapists also may take blood samples and use a blood gas analyzer to test oxygen and carbon dioxide levels.

Respiratory therapists also perform chest physiotherapy on patients to remove mucus from their lungs and make it easier for them to breathe. Removing mucus is necessary for patients suffering from lung diseases, such as cystic fibrosis, and it involves the therapist vibrating the patient's rib cage, often by tapping the patient's chest and encouraging him or her to cough. Respiratory therapists may connect patients who cannot breathe on their own to ventilators that deliver oxygen to the lungs. Therapists insert a tube in the patient's windpipe (trachea) and connect the tube to ventilator equipment. They set up and monitor the equipment to ensure that the patient is receiving the correct amount of oxygen at the correct rate.

Respiratory therapists who work in home care teach patients and their families to use ventilators and other life-support systems in their homes. During these visits, they may inspect and clean equipment, check the home for environmental hazards, and ensure that patients know how to use their medications. Therapists also make emergency home visits when necessary.

In some hospitals, respiratory therapists are involved in related areas, such as diagnosing breathing problems for people with sleep apnea and counseling people on how to stop smoking.

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22.19: Cerego- The Respiratory System

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for The Respiratory System. You'll need to create a free log-in to practice these items, if you haven't already.

https://cerego.com/sets/796526/learn

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CHAPTER OVERVIEW

23: Module 20- The Immune System

23.1: Why It Matters- The Immune System
23.2: Introduction to the Innate Immune Response
23.3: Physical and Chemical Barriers
23.4: Pathogen Recognition
23.5: Natural Killer Cells
23.6: Complement System
23.7: Introduction to the Adaptive Immune Response
23.8: Antigen-Presenting Cells
23.9: T and B Lymphocytes
23.10: Mucosal Surfaces and Immune Tolerance
23.11: Immunological Memory
23.12: Primary Centers of the Immune System
23.13: Introduction to Antibodies
23.14: Antibody Structure
23.15: Antibody Classes
23.16: Antibody Functions
23.17: Disruptions in the Immune System
23.18: Putting It Together- The Immune System
23.19: Cerego- The Immune System

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23.1: Why It Matters- The Immune System

Why describe the components and role of the immune system?

The environment consists of numerous **pathogens**, which are agents, usually microorganisms, that cause diseases in their hosts. A **host** is the organism that is invaded and often harmed by a pathogen. Pathogens include bacteria, protists, fungi and other infectious organisms. We are constantly exposed to pathogens in food and water, on surfaces, and in the air. Mammalian immune systems evolved for protection from such pathogens; they are composed of an extremely diverse array of specialized cells and soluble molecules that coordinate a rapid and flexible defense system capable of providing protection from a majority of these disease agents.

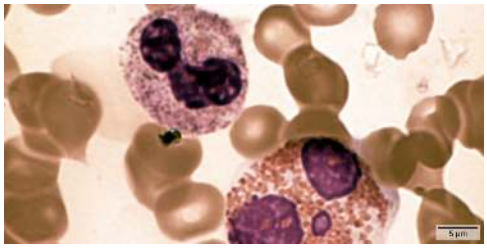


Figure 1. In this compound light micrograph purple-stained neutrophil (upper left) and eosinophil (lower right) are white blood cells that float among red blood cells in this blood smear. Neutrophils provide an early, rapid, and nonspecific defense against invading pathogens. Eosinophils play a variety of roles in the immune response. Red blood cells are about 7–8 µm in diameter, and a neutrophil is about 10–12µm. (credit: modification of work by Dr. David Csaba)

Components of the immune system constantly search the body for signs of pathogens. When pathogens are found, immune factors are mobilized to the site of an infection. The immune factors identify the nature of the pathogen, strengthen the corresponding cells and molecules to combat it efficiently, and then halt the immune response after the infection is cleared to avoid unnecessary host cell damage. The immune system can remember pathogens to which it has been exposed to create a more efficient response upon re-exposure. This memory can last several decades. Features of the immune system, such as pathogen identification, specific response, amplification, retreat, and remembrance are essential for survival against pathogens. The immune response can be classified as either innate or active. The innate immune response is always present and attempts to defend against all pathogens rather than focusing on specific ones. Conversely, the adaptive immune response stores information about past infections and mounts pathogen-specific defenses.

Learning Outcomes

- Explain immediate and induced innate immune responses
- Explain adaptive immunity
- Describe the structure and function of antibodies
- Describe immunodeficiency and hypersensitivity

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23.2: Introduction to the Innate Immune Response

Explain immediate and induced innate immune responses

The immune system comprises both innate and adaptive immune responses. **Innate immunity** occurs naturally because of genetic factors or physiology; it is not induced by infection or vaccination but works to reduce the workload for the adaptive immune response. Both the innate and adaptive levels of the immune response involve secreted proteins, receptor-mediated signaling, and intricate cell-to-cell communication. The innate immune system developed early in animal evolution, roughly a billion years ago, as an essential response to infection. Innate immunity has a limited number of specific targets: any pathogenic threat triggers a consistent sequence of events that can identify the type of pathogen and either clear the infection independently or mobilize a highly specialized adaptive immune response. For example, tears and mucus secretions contain microbicidal factors.

What You'll Learn to Do

- Describe physical and chemical immune barriers
- Describe different ways that host organisms recognize and combat pathogens
- Discuss natural killer cells
- Summarize how the proteins in a complement system function to destroy extracellular pathogens

Learning Activities

The learning activities for this section include the following:

- Physical and Chemical Barriers
- Pathogen Recognition
- Natural Killer Cells
- Complement System
- Self Check: The Innate Immune Response

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23.3: Physical and Chemical Barriers

Before any immune factors are triggered, the skin functions as a continuous, impassable barrier to potentially infectious pathogens. Pathogens are killed or inactivated on the skin by desiccation (drying out) and by the skin's acidity. In addition, beneficial microorganisms that coexist on the skin compete with invading pathogens, preventing infection. Regions of the body that are not protected by skin (such as the eyes and mucus membranes) have alternative methods of defense, such as tears and mucus secretions that trap and rinse away pathogens, and cilia in the nasal passages and respiratory tract that push the mucus with the pathogens out of the body. Throughout the body are other defenses, such as the low pH of the stomach (which inhibits the growth of pathogens), blood proteins that bind and disrupt bacterial cell membranes, and the process of urination (which flushes pathogens from the urinary tract).

Despite these barriers, pathogens may enter the body through skin abrasions or punctures, or by collecting on mucosal surfaces in large numbers that overcome the mucus or cilia. Some pathogens have evolved specific mechanisms that allow them to overcome physical and chemical barriers. When pathogens do enter the body, the innate immune system responds with inflammation, pathogen engulfment, and secretion of immune factors and proteins.

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23.4: Pathogen Recognition

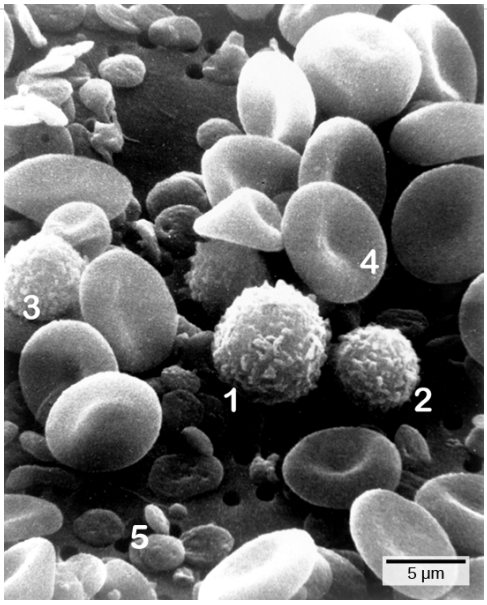


Figure 1. Cells of the blood include (1) monocytes, (2) lymphocytes, (3) neutrophils, (4) red blood cells, and (5) platelets. Note the very similar morphologies of the leukocytes (1, 2, 3). (credit: modification of work by Bruce Wetzel, Harry Schaefer, NCI; scale-bar data from Matt Russell)

An infection may be intracellular or extracellular, depending on the pathogen. All viruses infect cells and replicate within those cells (intracellularly), whereas bacteria and other parasites may replicate intracellularly or extracellularly, depending on the species. The innate immune system must respond accordingly: by identifying the extracellular pathogen and/or by identifying host cells that have already been infected. When a pathogen enters the body, cells in the blood and lymph detect the specific **pathogen-associated molecular patterns (PAMPs)** on the pathogen's surface. PAMPs are carbohydrate, polypeptide, and nucleic acid "signatures" that are expressed by viruses, bacteria, and parasites but which differ from molecules on host cells. The immune system has specific cells, described in Figure 1 and shown in Table 1, with receptors that recognize these PAMPs.

A **macrophage** is a large phagocytic cell that engulfs foreign particles and pathogens. Macrophages recognize PAMPs via complementary **pattern recognition receptors (PRRs)**. PRRs are molecules on macrophages and dendritic cells which are in contact with the external environment. A **monocyte** is a type of white blood cell that circulates in the blood and lymph and differentiates into macrophages after it moves into infected tissue. Dendritic cells bind molecular signatures of pathogens and promote pathogen engulfment and destruction. Toll-like receptors (TLRs) are a type of PRR that recognizes molecules that are shared by pathogens but distinguishable from host molecules). TLRs are present in invertebrates as well as vertebrates, and appear to be one of the most ancient components of the immune system. TLRs have also been identified in the mammalian nervous system.

Table 1. The characteristics and location of cells involved in the innate immune system are described (credit: modification of work by NIH).

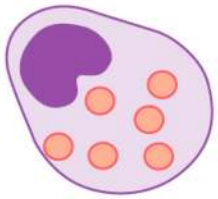
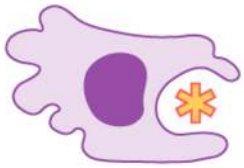
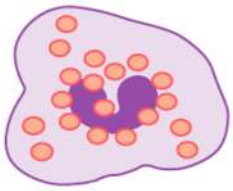
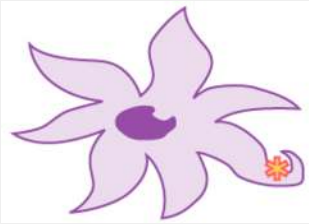
Cell Type	Characteristics	Location	Diagram
Mast cells	Dilate blood vessels and induce inflammation through release of histamines and heparin. Recruit macrophages and neutrophils. Involved in wound healing and defense against pathogens, but can also be responsible for allergic reactions.	Connective tissues, mucous membranes	
Macrophages	Phagocytic cells that consume foreign pathogens and cancer cells. Stimulate response of other immune cells.	Migrate from blood vessels into tissues	
Natural killer cells	Kill tumor cells and virus-infected cells	Circulate in blood and migrate into tissues	
Dendritic cells	Present antigens on their surface, thereby triggering adaptive immunity	Present in tissues in epithelial tissue, including skin, lung and tissues of the digestive tract. Migrate to lymph nodes upon activation.	
Monocytes	Differentiate into macrophages and dendritic cells in response to inflammation.	Stored in the spleen, move through blood vessels to infected tissues.	
Neutrophils	First responders at the site of infection or trauma, these abundant phagocytic cells represent 50–60% of all leukocytes. Release toxins that kill or inhibit bacteria and fungi and recruit other immune cells to the site of infection.	Migrate from blood vessels into tissues	

Table 1. The characteristics and location of cells involved in the innate immune system are described (credit: modification of work by NIH).

Cell Type	Characteristics	Location	Diagram
Basophils	Responsible for defense against parasites. Release histamines that cause inflammation and may be responsible for allergic reactions.	Circulate in blood and migrate to tissues	
Eosinophils	Release toxins that kill bacteria and parasites but also cause tissue damage.	Circulate in blood and migrate to tissues	

Cytokine Release Effect

The binding of PRRs with PAMPs triggers the release of cytokines, which signal that a pathogen is present and needs to be destroyed along with any infected cells. A **cytokine** is a chemical messenger that regulates cell differentiation (form and function), proliferation (production), and gene expression to affect immune responses. At least 40 types of cytokines exist in humans that differ in terms of the cell type that produces them, the cell type that responds to them, and the changes they produce. One type cytokine, interferon, is illustrated in Figure 2.

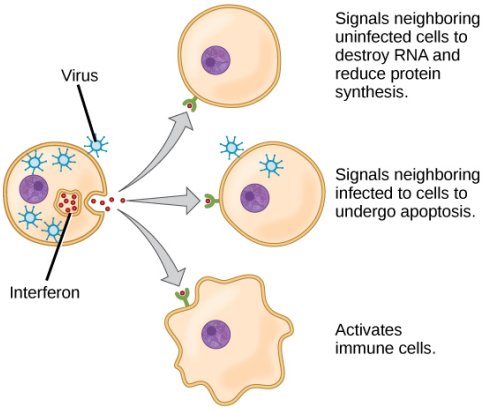


Figure 2. Interferons are cytokines that are released by a cell infected with a virus. Response of neighboring cells to interferon helps stem the infection.

One subclass of cytokines is the interleukin (IL), so named because they mediate interactions between leukocytes (white blood cells). Interleukins are involved in bridging the innate and adaptive immune responses. In addition to being released from cells after PAMP recognition, cytokines are released by the infected cells which bind to nearby uninfected cells and induce those cells to release cytokines, which results in a cytokine burst.

A second class of early-acting cytokines is interferons, which are released by infected cells as a warning to nearby uninfected cells. One of the functions of an **interferon** is to inhibit viral replication. They also have other important functions, such as tumor surveillance. Interferons work by signaling neighboring uninfected cells to destroy RNA and reduce protein synthesis, signaling neighboring infected cells to undergo apoptosis (programmed cell death), and activating immune cells.

In response to interferons, uninfected cells alter their gene expression, which increases the cells' resistance to infection. One effect of interferon-induced gene expression is a sharply reduced cellular protein synthesis. Virally infected cells produce more viruses by synthesizing large quantities of viral proteins. Thus, by reducing protein synthesis, a cell becomes resistant to viral infection.

Phagocytosis and Inflammation

The first cytokines to be produced are pro-inflammatory; that is, they encourage **inflammation**, the localized redness, swelling, heat, and pain that result from the movement of leukocytes and fluid through increasingly permeable capillaries to a site of infection. The population of leukocytes that arrives at an infection site depends on the nature of the infecting pathogen. Both macrophages and dendritic cells engulf pathogens and cellular debris through phagocytosis. A **neutrophil** is also a phagocytic leukocyte that engulfs and digests pathogens. Neutrophils, shown in Figure 1, are the most abundant leukocytes of the immune system. Neutrophils have a nucleus with two to five lobes, and they contain organelles, called lysosomes, that digest engulfed pathogens. An **eosinophil** is a leukocyte that works with other eosinophils to surround a parasite; it is involved in the allergic response and in protection against helminthes (parasitic worms).

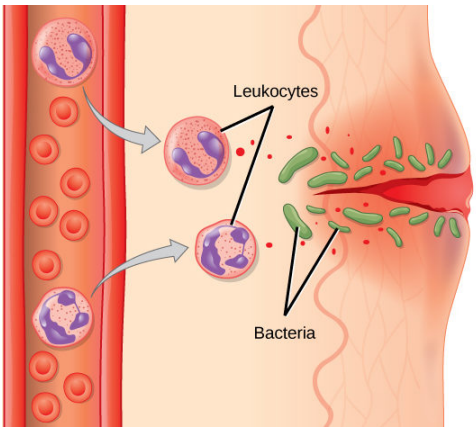


Figure 3. In response to a cut, mast cells secrete histamines that cause nearby capillaries to dilate. Neutrophils and monocytes leave the capillaries. Monocytes mature into macrophages. Neutrophils, dendritic cells and macrophages release chemicals to stimulate the inflammatory response. Neutrophils and macrophages also consume invading bacteria by phagocytosis.

Neutrophils and eosinophils are particularly important leukocytes that engulf large pathogens, such as bacteria and fungi. A **mast cell** is a leukocyte that produces inflammatory molecules, such as histamine, in response to large pathogens. A **basophil** is a leukocyte that, like a neutrophil, releases chemicals to stimulate the inflammatory response as illustrated in Figure 3. Basophils are also involved in allergy and hypersensitivity responses and induce specific types of inflammatory responses. Eosinophils and basophils produce additional inflammatory mediators to recruit more leukocytes. A hypersensitive immune response to harmless antigens, such as in pollen, often involves the release of histamine by basophils and mast cells.

Cytokines also send feedback to cells of the nervous system to bring about the overall symptoms of feeling sick, which include lethargy, muscle pain, and nausea. These effects may have evolved because the symptoms encourage the individual to rest and prevent them from spreading the infection to others. Cytokines also increase the core body temperature, causing a fever, which causes the liver to withhold iron from the blood. Without iron, certain pathogens, such as some bacteria, are unable to replicate; this is called nutritional immunity.

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23.5: Natural Killer Cells

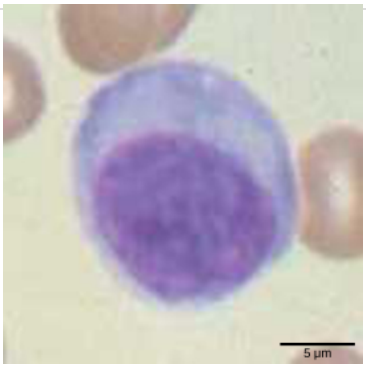


Figure 1. Lymphocytes, such as NK cells, are characterized by their large nuclei that actively absorb Wright stain and therefore appear dark colored under a microscope.

Lymphocytes are leukocytes that are histologically identifiable by their large, darkly staining nuclei; they are small cells with very little cytoplasm, as shown in Figure 1. Infected cells are identified and destroyed by **natural killer (NK) cells**, lymphocytes that can kill cells infected with viruses or tumor cells (abnormal cells that uncontrollably divide and invade other tissue). T cells and B cells of the adaptive immune system also are classified as lymphocytes. **T cells** are lymphocytes that mature in the thymus gland, and **B cells** are lymphocytes that mature in the bone marrow. NK cells identify intracellular infections, especially from viruses, by the altered expression of **major histocompatibility class (MHC) I molecules** on the surface of infected cells. MHC I molecules are proteins on the surfaces of all nucleated cells, thus they are scarce on red blood cells and platelets which are non-nucleated. The function of MHC I molecules is to display fragments of proteins from the infectious agents within the cell to T-cells; healthy cells will be ignored, while “non-self” or foreign proteins will be attacked by the immune system. MHC II molecules are found mainly on cells containing antigens (“non-self proteins”) and on lymphocytes. **MHC II molecules** interact with helper T-cells to trigger the appropriate immune response, which may include the inflammatory response.

An infected cell (or a tumor cell) is usually incapable of synthesizing and displaying MHC I molecules appropriately. The metabolic resources of cells infected by some viruses produce proteins that interfere with MHC I processing and/or trafficking to the cell surface. The reduced MHC I on host cells varies from virus to virus and results from active inhibitors being produced by the viruses. This process can deplete host MHC I molecules on the cell surface, which NK cells detect as “unhealthy” or “abnormal” while searching for cellular MHC I molecules. Similarly, the dramatically altered gene expression of tumor cells leads to expression of extremely deformed or absent MHC I molecules that also signal “unhealthy” or “abnormal.”

NK cells are always active; an interaction with normal, intact MHC I molecules on a healthy cell disables the killing sequence, and the NK cell moves on. After the NK cell detects an infected or tumor cell, its cytoplasm secretes granules comprised of **perforin**, a destructive protein that creates a pore in the target cell. Granzymes are released along with the perforin in the immunological synapse. A **granzyme** is a protease that digests cellular proteins and induces the target cell to undergo programmed cell death, or apoptosis. Phagocytic cells then digest the cell debris left behind. NK cells are constantly patrolling the body and are an effective mechanism for controlling potential infections and preventing cancer progression.

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23.6: Complement System

An array of approximately 20 types of soluble proteins, called a **complement system**, functions to destroy extracellular pathogens. Cells of the liver and macrophages synthesize complement proteins continuously; these proteins are abundant in the blood serum and are capable of responding immediately to infecting microorganisms. The complement system is so named because it is complementary to the antibody response of the adaptive immune system. Complement proteins bind to the surfaces of microorganisms and are particularly attracted to pathogens that are already bound by antibodies. Binding of complement proteins occurs in a specific and highly regulated sequence, with each successive protein being activated by cleavage and/or structural changes induced upon binding of the preceding protein(s). After the first few complement proteins bind, a cascade of sequential binding events follows in which the pathogen rapidly becomes coated in complement proteins.

Complement proteins perform several functions. The proteins serve as a marker to indicate the presence of a pathogen to phagocytic cells, such as macrophages and B cells, and enhance engulfment; this process is called **opsonization**. Opsonization refers to an immune process where particles such as bacteria are targeted for destruction by an immune cell known as a phagocyte. Certain complement proteins can combine to form attack complexes that open pores in microbial cell membranes. These structures destroy pathogens by causing their contents to leak, as illustrated in Figure 1.

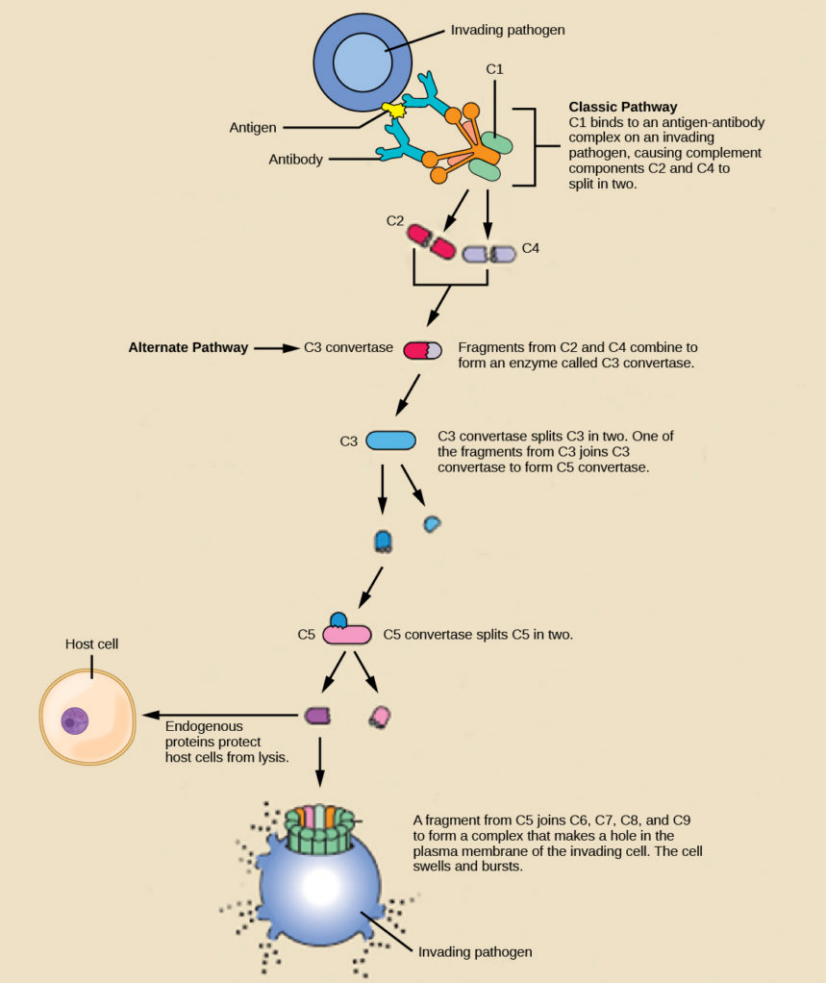


Figure 1. Click for a larger image. The classic pathway for the complement cascade involves the attachment of several initial complement proteins to an antibody-bound pathogen followed by rapid activation and binding of many more complement proteins and the creation of destructive pores in the microbial cell envelope and cell wall. The alternate pathway does not involve antibody activation. Rather, C3 convertase spontaneously breaks down C3. Endogenous regulatory proteins prevent the complement complex from binding to host cells. Pathogens lacking these regulatory proteins are lysed. (credit: modification of work by NIH)

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23.7: Introduction to the Adaptive Immune Response

Explain adaptive immunity

The adaptive, or acquired, immune response takes days or even weeks to become established—much longer than the innate response; however, adaptive immunity is more specific to pathogens and has memory. **Adaptive immunity** is an immunity that occurs after exposure to an antigen either from a pathogen or a vaccination. This part of the immune system is activated when the innate immune response is insufficient to control an infection. In fact, without information from the innate immune system, the adaptive response could not be mobilized.

There are two types of adaptive responses: the **cell-mediated immune response**, which is carried out by T cells, and the **humoral immune response**, which is controlled by activated B cells and antibodies. Activated T cells and B cells that are specific to molecular structures on the pathogen proliferate and attack the invading pathogen. Their attack can kill pathogens directly or secrete antibodies that enhance the phagocytosis of pathogens and disrupt the infection. Adaptive immunity also involves a memory to provide the host with long-term protection from reinfection with the same type of pathogen; on re-exposure, this memory will facilitate an efficient and quick response.

What You'll Learn to Do

- Describe the structure and function of antigen-presenting cells
- Describe the structure and function of T lymphocytes
- Describe the structure and function of B lymphocytes
- Describe immune tolerance
- Describe the role and importance of immunological memory
- Identify the primary centers of the immune system

Learning Activities

The learning activities for this section include the following:

- Antigen-Presenting Cells
- T and B Lymphocytes
- Mucosal Surfaces and Immune Tolerance
- Immunological Memory
- Primary Centers of the Immune System
- Self Check: The Adaptive Immune Response

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23.8: Antigen-Presenting Cells

Unlike NK cells of the innate immune system, B cells (B lymphocytes) are a type of white blood cell that gives rise to antibodies, whereas T cells (T lymphocytes) are a type of white blood cell that plays an important role in the immune response. T cells are a key component in the cell-mediated response—the specific immune response that utilizes T cells to neutralize cells that have been infected with viruses and certain bacteria. There are three types of T cells: cytotoxic, helper, and suppressor T cells. Cytotoxic T cells destroy virus-infected cells in the cell-mediated immune response, and helper T cells play a part in activating both the antibody and the cell-mediated immune responses. Suppressor T cells deactivate T cells and B cells when needed, and thus prevent the immune response from becoming too intense.

An **antigen** is a foreign or "non-self" macromolecule that reacts with cells of the immune system. Not all antigens will provoke a response. For instance, individuals produce innumerable "self" antigens and are constantly exposed to harmless foreign antigens, such as food proteins, pollen, or dust components. The suppression of immune responses to harmless macromolecules is highly regulated and typically prevents processes that could be damaging to the host, known as tolerance.

The innate immune system contains cells that detect potentially harmful antigens, and then inform the adaptive immune response about the presence of these antigens. An **antigen-presenting cell (APC)** is an immune cell that detects, engulfs, and informs the adaptive immune response about an infection. When a pathogen is detected, these APCs will phagocytose the pathogen and digest it to form many different fragments of the antigen. Antigen fragments will then be transported to the surface of the APC, where they will serve as an indicator to other immune cells. **Dendritic cells** are immune cells that process antigen material; they are present in the skin (Langerhans cells) and the lining of the nose, lungs, stomach, and intestines. Sometimes a dendritic cell presents on the surface of other cells to induce an immune response, thus functioning as an antigen-presenting cell. Macrophages also function as APCs. Before activation and differentiation, B cells can also function as APCs.

After phagocytosis by APCs, the phagocytic vesicle fuses with an intracellular lysosome forming phagolysosome. Within the phagolysosome, the components are broken down into fragments; the fragments are then loaded onto MHC class I or MHC class II molecules and are transported to the cell surface for antigen presentation, as illustrated in Figure 1. Note that T lymphocytes cannot properly respond to the antigen unless it is processed and embedded in an MHC II molecule. APCs express MHC on their surfaces, and when combined with a foreign antigen, these complexes signal a "non-self" invader. Once the fragment of antigen is embedded in the MHC II molecule, the immune cell can respond. Helper T- cells are one of the main lymphocytes that respond to antigen-presenting cells. Recall that all other nucleated cells of the body expressed MHC I molecules, which signal "healthy" or "normal."

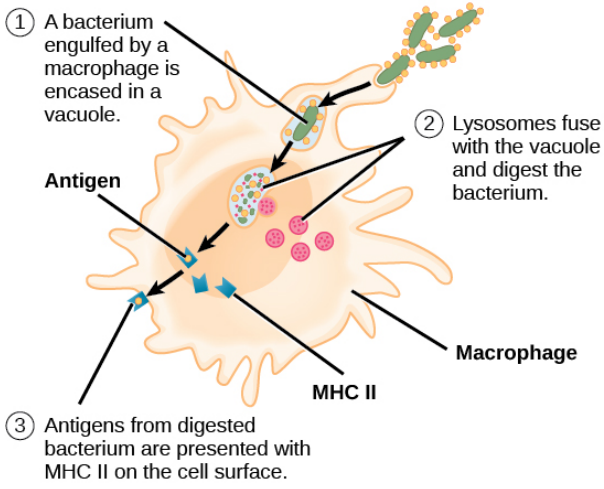


Figure 1. An APC, such as a macrophage, engulfs and digests a foreign bacterium. An antigen from the bacterium is presented on the cell surface in conjunction with an MHC II molecule Lymphocytes of the adaptive immune response interact with antigen-embedded MHC II molecules to mature into functional immune cells.

This animation from Rockefeller University shows how dendritic cells act as sentinels in the body's immune system.

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23.9: T and B Lymphocytes

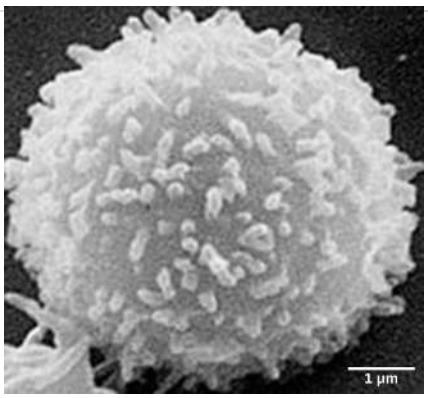


Figure 1. This scanning electron micrograph shows a T lymphocyte, which is responsible for the cell-mediated immune response. T cells are able to recognize antigens. (credit: modification of work by NCI; scale-bar data from Matt Russell)

Lymphocytes in human circulating blood are approximately 80 to 90 percent T cells, shown in Figure 1, and 10 to 20 percent B cells. Recall that the T cells are involved in the cell-mediated immune response, whereas B cells are part of the humoral immune response.

T cells encompass a heterogeneous population of cells with extremely diverse functions. Some T cells respond to APCs of the innate immune system, and indirectly induce immune responses by releasing cytokines. Other T cells stimulate B cells to prepare their own response. Another population of T cells detects APC signals and directly kills the infected cells. Other T cells are involved in suppressing inappropriate immune reactions to harmless or "self" antigens.

T and B cells exhibit a common theme of recognition/binding of specific antigens via a complementary receptor, followed by activation and self-amplification/maturation to specifically bind to the particular antigen of the infecting pathogen. T and B lymphocytes are also similar in that each cell only expresses one type of antigen receptor. Any individual may possess a population of T and B cells that together express a near limitless variety of antigen receptors that are capable of recognizing virtually any infecting pathogen. T and B cells are activated when they recognize small components of antigens, called **epitopes**, presented by APCs, illustrated in Figure 2.

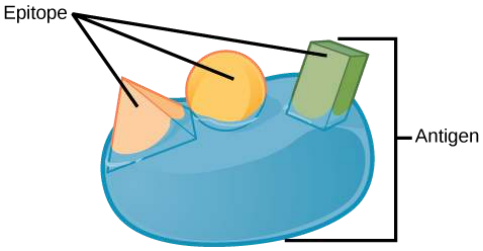


Figure 2. An antigen is a macromolecule that reacts with components of the immune system. A given antigen may contain several motifs that are recognized by immune cells. Each motif is an epitope. In this figure, the entire structure is an antigen, and the orange, salmon and green components projecting from it represent potential epitopes.

Note that recognition occurs at a specific epitope rather than on the entire antigen; for this reason, epitopes are known as "antigenic determinants." In the absence of information from APCs, T and B cells remain inactive, or naïve, and are unable to prepare an immune response. The requirement for information from the APCs of innate immunity to trigger B cell or T cell activation illustrates the essential nature of the innate immune response to the functioning of the entire immune system.

Naïve T cells can express one of two different molecules, CD4 or CD8, on their surface, as shown in Figure 3, and are accordingly classified as $CD4^+$ or $CD8^+$ cells. These molecules are important because they regulate how a T cell will interact with and respond to an APC. Naïve $CD4^+$ cells bind APCs via their antigen-embedded MHC II molecules and are stimulated to become **helper T (T_H) lymphocytes**, cells that go on to stimulate B cells (or cytotoxic T cells) directly or secrete cytokines to inform more and various target cells about the pathogenic threat. In contrast, $CD8^+$ cells engage antigen-embedded MHC I molecules on APCs and are stimulated to become **cytotoxic T lymphocytes (CTLs)**, which directly kill infected cells by apoptosis and emit cytokines to amplify the immune response. The two populations of T cells have different mechanisms of immune protection, but both bind

MHC molecules via their antigen receptors called T cell receptors (TCRs). The CD4 or CD8 surface molecules differentiate whether the TCR will engage an MHC II or an MHC I molecule. Because they assist in binding specificity, the CD4 and CD8 molecules are described as coreceptors.

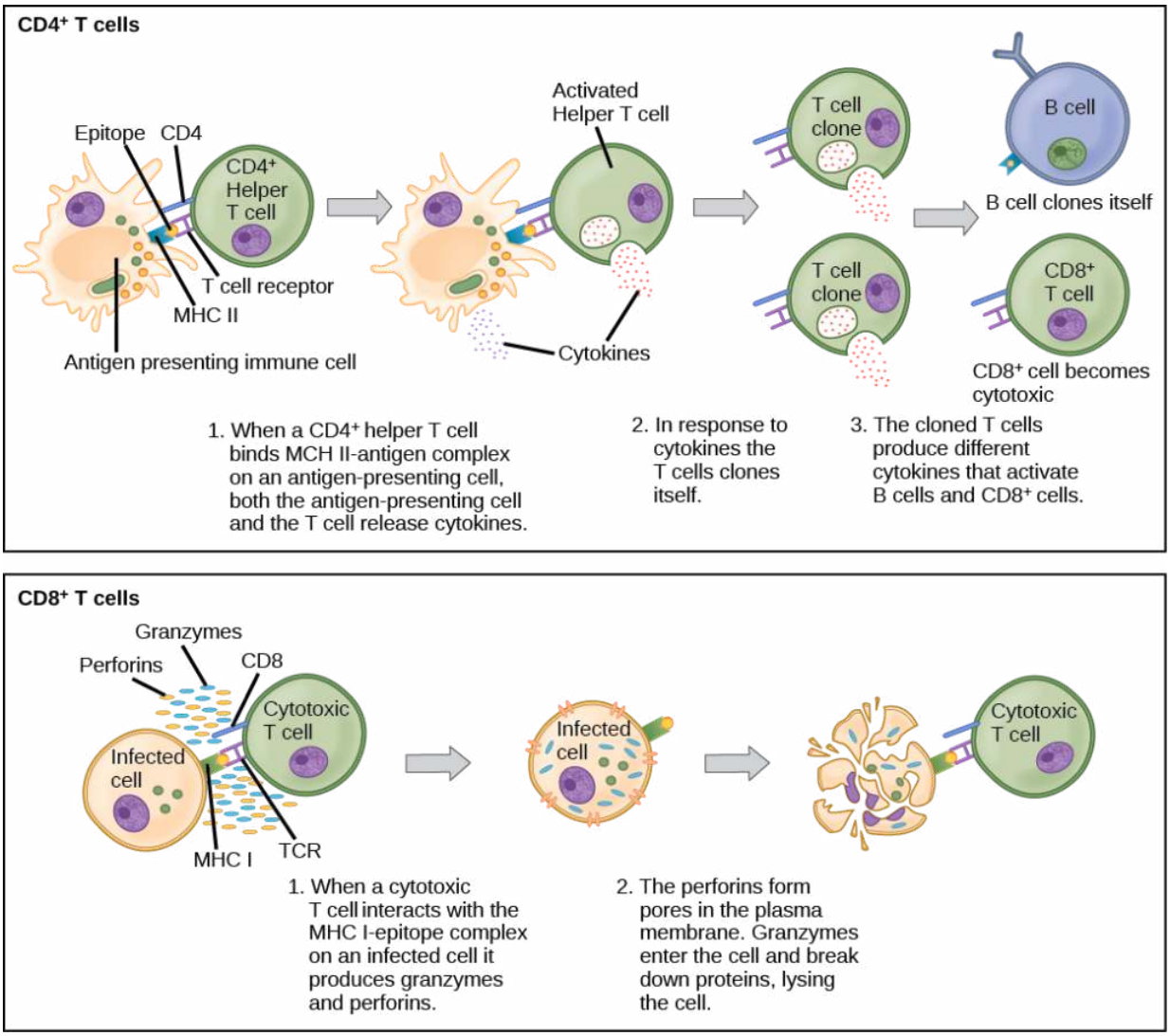


Figure 3. Naïve $CD4^+$ T cells engage MHC II molecules on antigen-presenting cells (APCs) and become activated. Clones of the activated helper T cell, in turn, activate B cells and $CD8^+$ T cells, which become cytotoxic T cells. Cytotoxic T cells kill infected cells.

? Practice Question

Which of the following statements about T cells is false?

a. Helper T cells release cytokines while cytotoxic T cells kill the infected cell.
b. Helper T cells are $CD4^+$, while cytotoxic T cells are $CD8^+$.
c. MHC II is a receptor found on most body cells, while MHC I is a receptor found on immune cells only.
d. The T cell receptor is found on both $CD4^+$ and $CD8^+$ T cells.

[reveal-answer q="849110"]Show Answer[/reveal-answer]
[hidden-answer a="849110"]Statement c is false.[/hidden-answer]

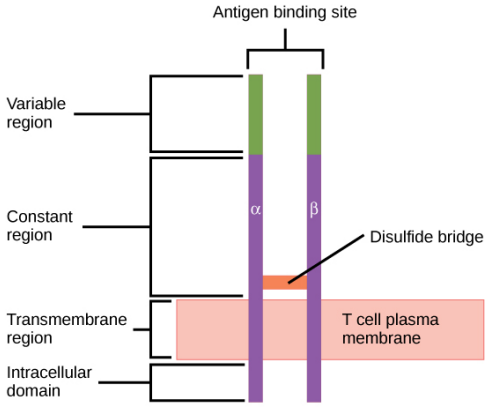


Figure 4. A T cell receptor spans the membrane and projects variable binding regions into the extracellular space to bind processed antigens via MHC molecules on APCs.

Consider the innumerable possible antigens that an individual will be exposed to during a lifetime. The mammalian adaptive immune system is adept in responding appropriately to each antigen. Mammals have an enormous diversity of T cell populations, resulting from the diversity of TCRs. Each TCR consists of two polypeptide chains that span the T cell membrane, as illustrated in Figure 4; the chains are linked by a disulfide bridge. Each polypeptide chain is comprised of a constant domain and a variable domain: a domain, in this sense, is a specific region of a protein that may be regulatory or structural. The intracellular domain is involved in intracellular signaling. A single T cell will express thousands of identical copies of one specific TCR variant on its cell surface. The specificity of the adaptive immune system occurs because it synthesizes millions of different T cell populations, each expressing a TCR that differs in its variable domain. This TCR diversity is achieved by the mutation and recombination of genes that encode these receptors in stem cell precursors of T cells. The binding between an antigen-displaying MHC molecule and a complementary TCR “match” indicates that the adaptive immune system needs to activate and produce that specific T cell because its structure is appropriate to recognize and destroy the invading pathogen.

Helper T Lymphocytes

The T_H lymphocytes function indirectly to identify potential pathogens for other cells of the immune system. These cells are important for extracellular infections, such as those caused by certain bacteria, helminths, and protozoa. T_H lymphocytes recognize specific antigens displayed in the MHC II complexes of APCs. There are two major populations of T_H cells: T_H1 and T_H2. T_H1 cells secrete cytokines to enhance the activities of macrophages and other T cells. T_H1 cells activate the action of cyotoxic T cells, as well as macrophages. T_H2 cells stimulate naïve B cells to destroy foreign invaders via antibody secretion. Whether a T_H1 or a T_H2 immune response develops depends on the specific types of cytokines secreted by cells of the innate immune system, which in turn depends on the nature of the invading pathogen.

The T_H1-mediated response involves macrophages and is associated with inflammation. Recall the frontline defenses of macrophages involved in the innate immune response. Some intracellular bacteria, such as *Mycobacterium tuberculosis*, have evolved to multiply in macrophages after they have been engulfed. These pathogens evade attempts by macrophages to destroy and digest the pathogen. When *M. tuberculosis* infection occurs, macrophages can stimulate naïve T cells to become T_H1 cells. These stimulated T cells secrete specific cytokines that send feedback to the macrophage to stimulate its digestive capabilities and allow it to destroy the colonizing *M. tuberculosis*. In the same manner, T_H1-activated macrophages also become better suited to ingest and kill tumor cells. In summary; T_H1 responses are directed toward intracellular invaders while T_H2 responses are aimed at those that are extracellular.

B Lymphocytes

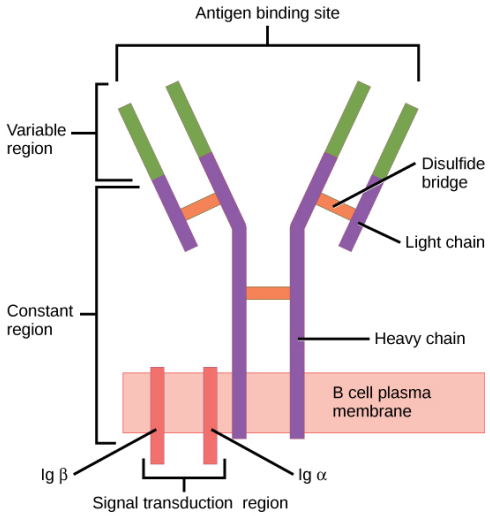


Figure 5. B cell receptors are embedded in the membranes of B cells and bind a variety of antigens through their variable regions. The signal transduction region transfers the signal into the cell.

When stimulated by the T_H2 pathway, naïve B cells differentiate into antibody-secreting plasma cells. A **plasma cell** is an immune cell that secrets antibodies; these cells arise from B cells that were stimulated by antigens. Similar to T cells, naïve B cells initially are coated in thousands of B cell receptors (BCRs), which are membrane-bound forms of Ig (immunoglobulin, or an antibody). The B cell receptor has two heavy chains and two light chains connected by disulfide linkages. Each chain has a constant and a variable region; the latter is involved in antigen binding. Two other membrane proteins, Ig alpha and Ig beta, are involved in signaling. The receptors of any particular B cell, as shown in Figure 5 are all the same, but the hundreds of millions of different B cells in an individual have distinct recognition domains that contribute to extensive diversity in the types of molecular structures to which they can bind. In this state, B cells function as APCs. They bind and engulf foreign antigens via their BCRs and then display processed antigens in the context of MHC II molecules to T_H2 cells. When a T_H2 cell detects that a B cell is bound to a relevant antigen, it secretes specific cytokines that induce the B cell to proliferate rapidly, which makes thousands of identical (clonal) copies of it, and then it synthesizes and secretes antibodies with the same antigen recognition pattern as the BCRs. The activation of B cells corresponding to one specific BCR variant and the dramatic proliferation of that variant is known as **clonal selection**. This phenomenon drastically, but briefly, changes the proportions of BCR variants expressed by the immune system, and shifts the balance toward BCRs specific to the infecting pathogen.

T and B cells differ in one fundamental way: whereas T cells bind antigens that have been digested and embedded in MHC molecules by APCs, B cells function as APCs that bind intact antigens that have not been processed. Although T and B cells both react with molecules that are termed “antigens,” these lymphocytes actually respond to very different types of molecules. B cells must be able to bind intact antigens because they secrete antibodies that must recognize the pathogen directly, rather than digested remnants of the pathogen. Bacterial carbohydrate and lipid molecules can activate B cells independently from the T cells.

Cytotoxic T Lymphocytes

CTLs, a subclass of T cells, function to clear infections directly. The cell-mediated part of the adaptive immune system consists of CTLs that attack and destroy infected cells. CTLs are particularly important in protecting against viral infections; this is because viruses replicate within cells where they are shielded from extracellular contact with circulating antibodies. When APCs phagocytize pathogens and present MHC I-embedded antigens to naïve $CD8^+$ T cells that express complementary TCRs, the $CD8^+$ T cells become activated to proliferate according to clonal selection. These resulting CTLs then identify non-APCs displaying the same MHC I-embedded antigens (for example, viral proteins)—for example, the CTLs identify infected host cells.

Intracellularly, infected cells typically die after the infecting pathogen replicates to a sufficient concentration and lyses the cell, as many viruses do. CTLs attempt to identify and destroy infected cells before the pathogen can replicate and escape, thereby halting the progression of intracellular infections. CTLs also support NK lymphocytes to destroy early cancers. Cytokines secreted by the

T_H1 response that stimulates macrophages also stimulate CTLs and enhance their ability to identify and destroy infected cells and tumors.

CTLs sense MHC I-embedded antigens by directly interacting with infected cells via their TCRs. Binding of TCRs with antigens activates CTLs to release perforin and granzyme, degradative enzymes that will induce apoptosis of the infected cell. Recall that this is a similar destruction mechanism to that used by NK cells. In this process, the CTL does not become infected and is not harmed by the secretion of perforin and granzymes. In fact, the functions of NK cells and CTLs are complementary and maximize the removal of infected cells, as illustrated in Figure 6. If the NK cell cannot identify the "missing self" pattern of down-regulated MHC I molecules, then the CTL can identify it by the complex of MHC I with foreign antigens, which signals "altered self." Similarly, if the CTL cannot detect antigen-embedded MHC I because the receptors are depleted from the cell surface, NK cells will destroy the cell instead. CTLs also emit cytokines, such as interferons, that alter surface protein expression in other infected cells, such that the infected cells can be easily identified and destroyed. Moreover, these interferons can also prevent virally infected cells from releasing virus particles.

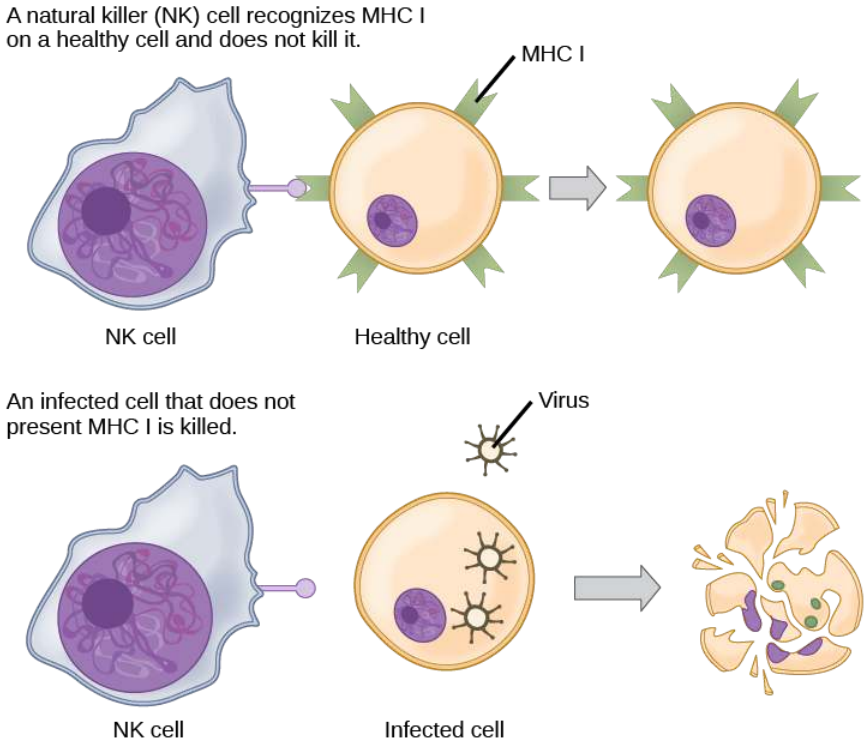


Figure 6. Natural killer (NK) cells recognize the MHC I receptor on healthy cells. If MHC I is absent, the cell is lysed.

? Practice Question

Based on what you know about MHC receptors, why do you think an organ transplanted from an incompatible donor to a recipient will be rejected?

[practice-area rows="2"][/practice-area]
[reveal-answer q="177880"]Show Answer[/reveal-answer]
[hidden-answer a="177880"]MHC receptors differ from person to person. Thus, MHC receptors on an incompatible donor are considered "non-self" and are rejected by the immune system.[/hidden-answer]

Plasma cells and CTLs are collectively called **effector cells**: they represent differentiated versions of their naïve counterparts, and they are involved in bringing about the immune defense of killing pathogens and infected host cells.

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23.10: Mucosal Surfaces and Immune Tolerance

The innate and adaptive immune responses discussed thus far comprise the systemic immune system (affecting the whole body), which is distinct from the mucosal immune system. Mucosal immunity is formed by mucosa-associated lymphoid tissue, which functions independently of the systemic immune system, and which has its own innate and adaptive components. **Mucosa-associated lymphoid tissue (MALT)**, illustrated in Figure 1, is a collection of lymphatic tissue that combines with epithelial tissue lining the mucosa throughout the body. This tissue functions as the immune barrier and response in areas of the body with direct contact to the external environment. The systemic and mucosal immune systems use many of the same cell types. Foreign particles that make their way to MALT are taken up by absorptive epithelial cells called M cells and delivered to APCs located directly below the mucosal tissue. M cells function in the transport described, and are located in the Peyer's patch, a lymphoid nodule. APCs of the mucosal immune system are primarily dendritic cells, with B cells and macrophages having minor roles. Processed antigens displayed on APCs are detected by T cells in the MALT and at various mucosal induction sites, such as the tonsils, adenoids, appendix, or the mesenteric lymph nodes of the intestine. Activated T cells then migrate through the lymphatic system and into the circulatory system to mucosal sites of infection.

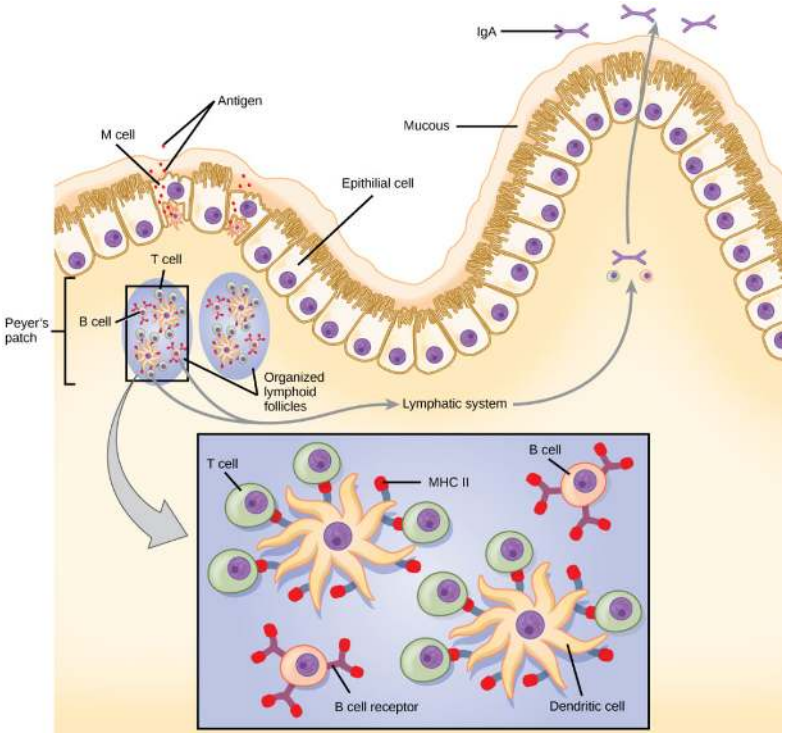


Figure 1. Click for a larger image. The topology and function of intestinal MALT is shown. Pathogens are taken up by M cells in the intestinal epithelium and excreted into a pocket formed by the inner surface of the cell. The pocket contains antigen-presenting cells such as dendritic cells, which engulf the antigens, then present them with MHC II molecules on the cell surface. The dendritic cells migrate to an underlying tissue called a Peyer's patch. Antigen-presenting cells, T cells, and B cells aggregate within the Peyer's patch, forming organized lymphoid follicles. There, some T cells and B cells are activated. Other antigen-loaded dendritic cells migrate through the lymphatic system where they activate B cells, T cells, and plasma cells in the lymph nodes. The activated cells then return to MALT tissue effector sites. IgA and other antibodies are secreted into the intestinal lumen.

MALT is a crucial component of a functional immune system because mucosal surfaces, such as the nasal passages, are the first tissues onto which inhaled or ingested pathogens are deposited. The mucosal tissue includes the mouth, pharynx, and esophagus, and the gastrointestinal, respiratory, and urogenital tracts.

The immune system has to be regulated to prevent wasteful, unnecessary responses to harmless substances, and more importantly so that it does not attack "self." The acquired ability to prevent an unnecessary or harmful immune response to a detected foreign substance known not to cause disease is described as **immune tolerance**. Immune tolerance is crucial for maintaining mucosal homeostasis given the tremendous number of foreign substances (such as food proteins) that APCs of the oral cavity, pharynx, and

gastrointestinal mucosa encounter. Immune tolerance is brought about by specialized APCs in the liver, lymph nodes, small intestine, and lung that present harmless antigens to an exceptionally diverse population of **regulatory T (T_{reg}) cells**, specialized lymphocytes that suppress local inflammation and inhibit the secretion of stimulatory immune factors. The combined result of T_{reg} cells is to prevent immunologic activation and inflammation in undesired tissue compartments and to allow the immune system to focus on pathogens instead. In addition to promoting immune tolerance of harmless antigens, other subsets of T_{reg} cells are involved in the prevention of the **autoimmune response**, which is an inappropriate immune response to host cells or self-antigens. Another T_{reg} class suppresses immune responses to harmful pathogens after the infection has cleared to minimize host cell damage induced by inflammation and cell lysis.

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23.11: Immunological Memory

The adaptive immune system possesses a memory component that allows for an efficient and dramatic response upon reinvasion of the same pathogen. Memory is handled by the adaptive immune system with little reliance on cues from the innate response. During the adaptive immune response to a pathogen that has not been encountered before, called a primary response, plasma cells secreting antibodies and differentiated T cells increase, then plateau over time. As B and T cells mature into effector cells, a subset of the naïve populations differentiates into B and T memory cells with the same antigen specificities, as illustrated in Figure 1.

A **memory cell** is an antigen-specific B or T lymphocyte that does not differentiate into effector cells during the primary immune response, but that can immediately become effector cells upon re-exposure to the same pathogen. During the primary immune response, memory cells do not respond to antigens and do not contribute to host defenses. As the infection is cleared and pathogenic stimuli subside, the effectors are no longer needed, and they undergo apoptosis. In contrast, the memory cells persist in the circulation.

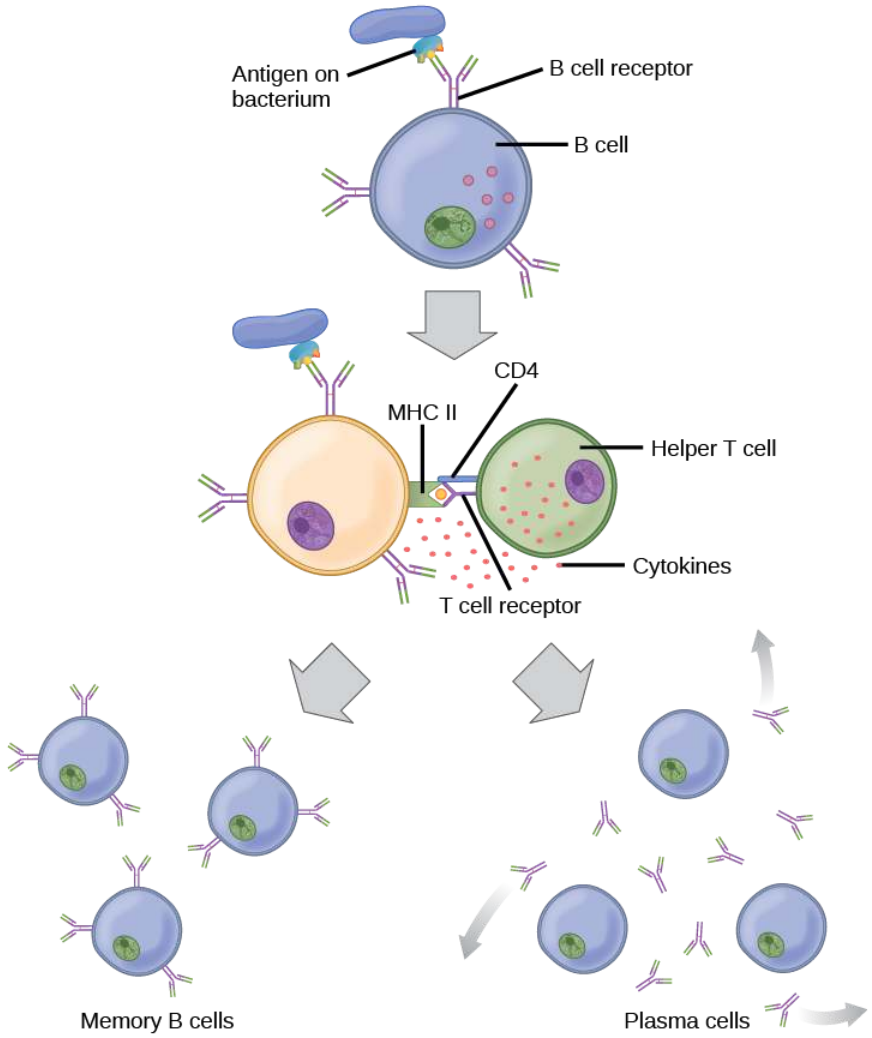


Figure 1. After initially binding an antigen to the B cell receptor (BCR), a B cell internalizes the antigen and presents it on MHC II. A helper T cell recognizes the MHC II–antigen complex and activates the B cell. As a result, memory B cells and plasma cells are made.

? Practice Question

The Rh antigen is found on Rh-positive red blood cells. An Rh-negative female can usually carry an Rh-positive fetus to term without difficulty. However, if she has a second Rh-positive fetus, her body may launch an immune attack that causes

hemolytic disease of the newborn. Why do you think hemolytic disease is only a problem during the second or subsequent pregnancies?

[practice-area rows="2"][/practice-area]
[reveal-answer q="251889"]Show Answer[/reveal-answer]
[hidden-answer a="251889"]If the blood of the mother and fetus mixes, memory cells that recognize the Rh antigen can form late in the first pregnancy. During subsequent pregnancies, these memory cells launch an immune attack on the fetal blood cells. Injection of anti-Rh antibody during the first pregnancy prevents the immune response from occurring.[/hidden-answer]

If the pathogen is never encountered again during the individual's lifetime, B and T memory cells will circulate for a few years or even several decades and will gradually die off, having never functioned as effector cells. However, if the host is re-exposed to the same pathogen type, circulating memory cells will immediately differentiate into plasma cells and CTLs without input from APCs or T_H cells. One reason the adaptive immune response is delayed is because it takes time for naïve B and T cells with the appropriate antigen specificities to be identified and activated. Upon reinfection, this step is skipped, and the result is a more rapid production of immune defenses. Memory B cells that differentiate into plasma cells output tens to hundreds-fold greater antibody amounts than were secreted during the primary response, as the graph in Figure 2 illustrates. This rapid and dramatic antibody response may stop the infection before it can even become established, and the individual may not realize they had been exposed.

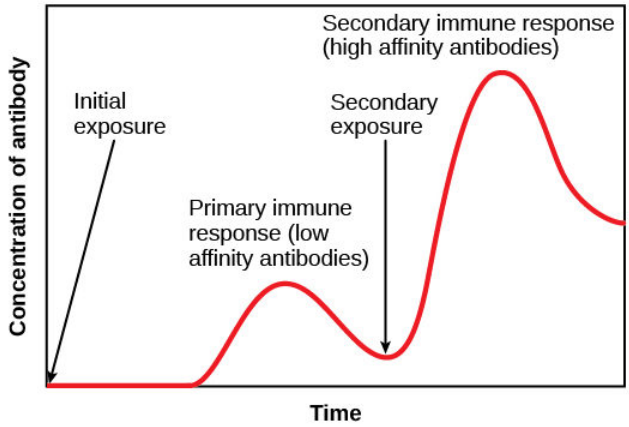


Figure 2. In the primary response to infection, antibodies are secreted first from plasma cells. Upon re-exposure to the same pathogen, memory cells differentiate into antibody-secreting plasma cells that output a greater amount of antibody for a longer period of time.

Vaccination is based on the knowledge that exposure to noninfectious antigens, derived from known pathogens, generates a mild primary immune response. The immune response to vaccination may not be perceived by the host as illness but still confers immune memory. When exposed to the corresponding pathogen to which an individual was vaccinated, the reaction is similar to a secondary exposure. Because each reinfection generates more memory cells and increased resistance to the pathogen, and because some memory cells die, certain vaccine courses involve one or more booster vaccinations to mimic repeat exposures: for instance, tetanus boosters are necessary every ten years because the memory cells only live that long.

Mucosal Immune Memory

A subset of T and B cells of the mucosal immune system differentiates into memory cells just as in the systemic immune system. Upon reinvasion of the same pathogen type, a pronounced immune response occurs at the mucosal site where the original pathogen deposited, but a collective defense is also organized within interconnected or adjacent mucosal tissue. For instance, the immune memory of an infection in the oral cavity would also elicit a response in the pharynx if the oral cavity was exposed to the same pathogen.

? Try It

Vaccination (or immunization) involves the delivery, usually by injection as shown in Figure 3a, of noninfectious antigen(s) derived from known pathogens. Other components, called adjuvants, are delivered in parallel to help stimulate the immune

response. Immunological memory is the reason vaccines work. Ideally, the effect of vaccination is to elicit immunological memory, and thus resistance to specific pathogens without the individual having to experience an infection.

Vaccinologists are involved in the process of vaccine development from the initial idea to the availability of the completed vaccine. This process can take decades, can cost millions of dollars, and can involve many obstacles along the way. For instance, injected vaccines stimulate the systemic immune system, eliciting humoral and cell-mediated immunity, but have little effect on the mucosal response, which presents a challenge because many pathogens are deposited and replicate in mucosal compartments, and the injection does not provide the most efficient immune memory for these disease agents. For this reason, vaccinologists are actively involved in developing new vaccines that are applied via intranasal, aerosol, oral, or transcutaneous (absorbed through the skin) delivery methods. Importantly, mucosal-administered vaccines elicit both mucosal and systemic immunity and produce the same level of disease resistance as injected vaccines. Currently, a version of intranasal influenza vaccine is available, and the polio and typhoid vaccines can be administered orally, as shown in Figure 3b.



Figure 3. (a) Vaccines are often delivered by injection into the arm. (b) The polio vaccine can be administered orally. (credit a: U.S. Navy Photographer's Mate Airman Apprentice Christopher D. Blachly; credit b: modification of work by UNICEF Sverige)

Similarly, the measles and rubella vaccines are being adapted to aerosol delivery using inhalation devices. Eventually, transgenic plants may be engineered to produce vaccine antigens that can be eaten to confer disease resistance. Other vaccines may be adapted to rectal or vaginal application to elicit immune responses in rectal, genitourinary, or reproductive mucosa.

Finally, vaccine antigens may be adapted to transdermal application in which the skin is lightly scraped and microneedles are used to pierce the outermost layer. In addition to mobilizing the mucosal immune response, this new generation of vaccines may end the anxiety associated with injections and, in turn, improve patient participation.

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23.12: Primary Centers of the Immune System

Although the immune system is characterized by circulating cells throughout the body, the regulation, maturation, and intercommunication of immune factors occur at specific sites. The blood circulates immune cells, proteins, and other factors through the body. Approximately 0.1 percent of all cells in the blood are leukocytes, which encompass monocytes (the precursor of macrophages) and lymphocytes. The majority of cells in the blood are erythrocytes (red blood cells). **Lymph** is a watery fluid that bathes tissues and organs with protective white blood cells and does not contain erythrocytes. Cells of the immune system can travel between the distinct lymphatic and blood circulatory systems, which are separated by interstitial space, by a process called extravasation (passing through to surrounding tissue).

The cells of the immune system originate from hematopoietic stem cells in the bone marrow. Cytokines stimulate these stem cells to differentiate into immune cells. B cell maturation occurs in the bone marrow, whereas naïve T cells transit from the bone marrow to the thymus for maturation. In the thymus, immature T cells that express TCRs complementary to self-antigens are destroyed. This process helps prevent autoimmune responses.

On maturation, T and B lymphocytes circulate to various destinations. Lymph nodes scattered throughout the body, as illustrated in Figure 1, house large populations of T and B cells, dendritic cells, and macrophages. Lymph gathers antigens as it drains from tissues. These antigens then are filtered through lymph nodes before the lymph is returned to circulation. APCs in the lymph nodes capture and process antigens and inform nearby lymphocytes about potential pathogens.

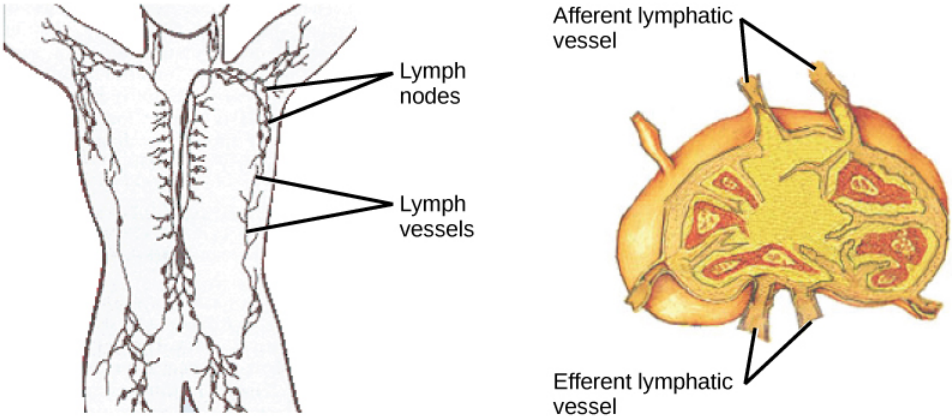


Figure 1. (a) Lymphatic vessels carry a clear fluid called lymph throughout the body. The liquid enters (b) lymph nodes through afferent vessels. Lymph nodes are filled with lymphocytes that purge infecting cells. The lymph then exits through efferent vessels. (credit: modification of work by NIH, NCI)

The spleen houses B and T cells, macrophages, dendritic cells, and NK cells. The spleen, shown in Figure 2, is the site where APCs that have trapped foreign particles in the blood can communicate with lymphocytes. Antibodies are synthesized and secreted by activated plasma cells in the spleen, and the spleen filters foreign substances and antibody-complexed pathogens from the blood. Functionally, the spleen is to the blood as lymph nodes are to the lymph.

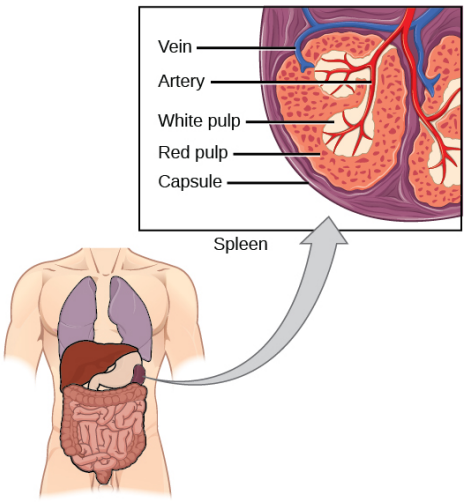


Figure 2. The spleen is similar to a lymph node but is much larger and filters blood instead of lymph. Blood enters the spleen through arteries and exits through veins. The spleen contains two types of tissue: red pulp and white pulp. Red pulp consists of cavities that store blood. Within the red pulp, damaged red blood cells are removed and replaced by new ones. White pulp is rich in lymphocytes that remove antigen-coated bacteria from the blood. (credit: modification of work by NCI)

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23.13: Introduction to Antibodies

Describe the structure and function of antibodies

An **antibody**, also known as an immunoglobulin (Ig), is a protein that is produced by plasma cells after stimulation by an antigen. Antibodies are the functional basis of humoral immunity. Antibodies occur in the blood, in gastric and mucus secretions, and in breast milk. Antibodies in these bodily fluids can bind pathogens and mark them for destruction by phagocytes before they can infect cells.

What You'll Learn to Do

- Describe the structure of antibodies
- Identify the different classes of antibodies
- Describe the function of antibodies
- Describe immunodeficiency and hypersensitivity

Learning Activities

The learning activities for this section include the following:

- Antibody Structure
- Antibody Classes
- Antibody Functions
- Disruptions in the Immune System
- Self Check: Antibodies

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23.14: Antibody Structure

An antibody molecule is comprised of four polypeptides: two identical heavy chains (large peptide units) that are partially bound to each other in a “Y” formation, which are flanked by two identical light chains (small peptide units), as illustrated in Figure 1. Bonds between the cysteine amino acids in the antibody molecule attach the polypeptides to each other. The areas where the antigen is recognized on the antibody are variable domains and the antibody base is composed of constant domains.

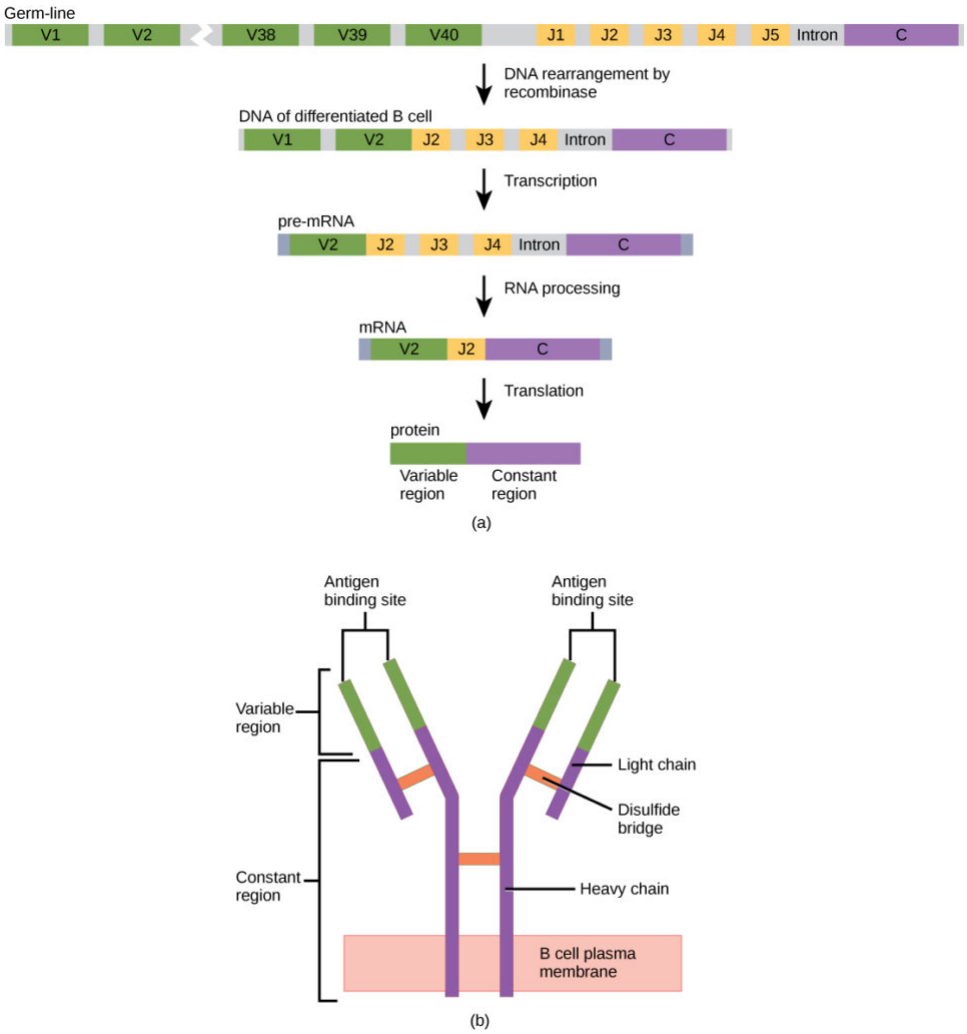


Figure 1. (a) As a germ-line B cell matures, an enzyme called DNA recombinase randomly excises V and J segments from the light chain gene. Splicing at the mRNA level results in further gene rearrangement. As a result, (b) each antibody has a unique variable region capable of binding a different antigen.

In germ-line B cells, the variable region of the light chain gene has 40 variable (V) and five joining (J) segments. An enzyme called DNA recombinase randomly excises most of these segments out of the gene, and splices one V segment to one J segment. During RNA processing, all but one V and J segment are spliced out. Recombination and splicing may result in over 10^6 possible VJ combinations. As a result, each differentiated B cell in the human body typically has a unique variable chain. The constant domain, which does not bind antibody, is the same for all antibodies.

Similar to TCRs and BCRs, antibody diversity is produced by the mutation and recombination of approximately 300 different gene segments encoding the light and heavy chain variable domains in precursor cells that are destined to become B cells. The variable domains from the heavy and light chains interact to form the binding site through which an antibody can bind a specific epitope on an antigen. The numbers of repeated constant domains in Ig classes are the same for all antibodies corresponding to a specific class. Antibodies are structurally similar to the extracellular component of the BCRs, and B cell maturation to plasma cells can be visualized in simple terms as the cell acquires the ability to secrete the extracellular portion of its BCR in large quantities.

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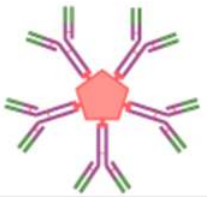
23.15: Antibody Classes

Antibodies can be divided into five classes—IgM, IgG, IgA, IgD, IgE—based on their physiochemical, structural, and immunological properties. IgGs, which make up about 80 percent of all antibodies, have heavy chains that consist of one variable domain and three identical constant domains. IgA and IgD also have three constant domains per heavy chain, whereas IgM and IgE each have four constant domains per heavy chain. The variable domain determines binding specificity and the constant domain of the heavy chain determines the immunological mechanism of action of the corresponding antibody class. It is possible for two antibodies to have the same binding specificities but be in different classes and, therefore, to be involved in different functions.

After an adaptive defense is produced against a pathogen, typically plasma cells first secrete IgM into the blood. BCRs on naïve B cells are of the IgM class and occasionally IgD class. IgM molecules make up approximately ten percent of all antibodies. Prior to antibody secretion, plasma cells assemble IgM molecules into pentamers (five individual antibodies) linked by a joining (J) chain, as shown in Figure 2. The pentamer arrangement means that these macromolecules can bind ten identical antigens. However, IgM molecules released early in the adaptive immune response do not bind to antigens as stably as IgGs, which are one of the possible types of antibodies secreted in large quantities upon re-exposure to the same pathogen.

Immunoglobulins have different functions, but all are composed of light and heavy chains that form a Y-shaped structure. Table 1 summarizes the properties of immunoglobulins and illustrates their basic structures.

Table 1. The Five Immunoglobulin (Ig) Classes

Name	Properties	Structure
IgA	Found in mucous, saliva, tears, and breast milk. Protects against pathogens.	
IgD	Part of the B cell receptor. Activates basophils and mast cells.	
IgE	Protects against parasitic worms. Responsible for allergic reactions.	
IgG	Secreted by plasma cells in the blood. Able to cross the placenta into the fetus.	
IgM	May be attached to the surface of a B cell or secreted into the blood. Responsible for early stages of immunity.	

IgAs populate the saliva, tears, breast milk, and mucus secretions of the gastrointestinal, respiratory, and genitourinary tracts. Collectively, these bodily fluids coat and protect the extensive mucosa (4000 square feet in humans). The total number of IgA molecules in these bodily secretions is greater than the number of IgG molecules in the blood serum. A small amount of IgA is also

secreted into the serum in monomeric form. Conversely, some IgM is secreted into bodily fluids of the mucosa. Similar to IgM, IgA molecules are secreted as polymeric structures linked with a J chain. However, IgAs are secreted mostly as dimeric molecules, not pentamers.

IgE is present in the serum in small quantities and is best characterized in its role as an allergy mediator. IgD is also present in small quantities. Similar to IgM, BCRs of the IgD class are found on the surface of naïve B cells. This class supports antigen recognition and maturation of B cells to plasma cells.

Antibodies of the Mucosal Immune System

Antibodies synthesized by the mucosal immune system include IgA and IgM. Activated B cells differentiate into mucosal plasma cells that synthesize and secrete dimeric IgA, and to a lesser extent, pentameric IgM. Secreted IgA is abundant in tears, saliva, breast milk, and in secretions of the gastrointestinal and respiratory tracts. Antibody secretion results in a local humoral response at epithelial surfaces and prevents infection of the mucosa by binding and neutralizing pathogens.

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23.16: Antibody Functions

Differentiated plasma cells are crucial players in the humoral response, and the antibodies they secrete are particularly significant against extracellular pathogens and toxins. Antibodies circulate freely and act independently of plasma cells. Antibodies can be transferred from one individual to another to temporarily protect against infectious disease. For instance, a person who has recently produced a successful immune response against a particular disease agent can donate blood to a nonimmune recipient and confer temporary immunity through antibodies in the donor's blood serum. This phenomenon is called **passive immunity**; it also occurs naturally during breastfeeding, which makes breastfed infants highly resistant to infections during the first few months of life.

Antibodies coat extracellular pathogens and neutralize them, as illustrated in Figure 1, by blocking key sites on the pathogen that enhance their infectivity (such as receptors that "dock" pathogens on host cells). Antibody neutralization can prevent pathogens from entering and infecting host cells, as opposed to the CTL-mediated approach of killing cells that are already infected to prevent progression of an established infection. The neutralized antibody-coated pathogens can then be filtered by the spleen and eliminated in urine or feces.

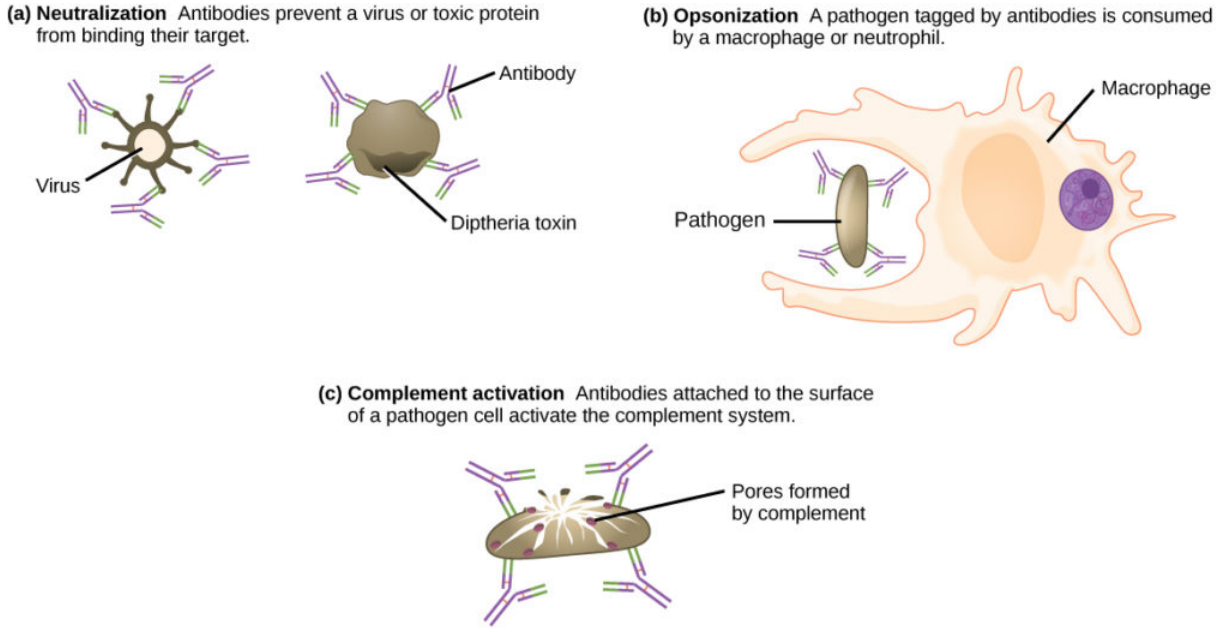


Figure 1. Antibodies may inhibit infection by (a) preventing the antigen from binding its target, (b) tagging a pathogen for destruction by macrophages or neutrophils, or (c) activating the complement cascade.

Antibodies also mark pathogens for destruction by phagocytic cells, such as macrophages or neutrophils, because phagocytic cells are highly attracted to macromolecules complexed with antibodies. Phagocytic enhancement by antibodies is called opsonization. In a process called complement fixation, IgM and IgG in serum bind to antigens and provide docking sites onto which sequential complement proteins can bind. The combination of antibodies and complement enhances opsonization even further and promotes rapid clearing of pathogens.

Affinity, Avidity, and Cross Reactivity

Not all antibodies bind with the same strength, specificity, and stability. In fact, antibodies exhibit different **affinities** (attraction) depending on the molecular complementarity between antigen and antibody molecules, as illustrated in Figure 2. An antibody with a higher affinity for a particular antigen would bind more strongly and stably, and thus would be expected to present a more challenging defense against the pathogen corresponding to the specific antigen.

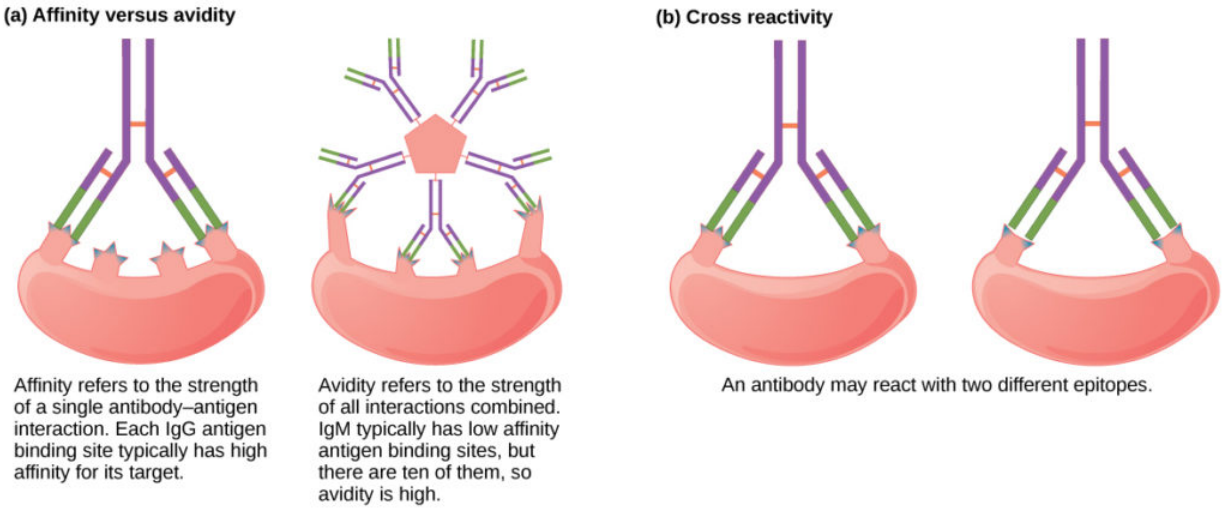


Figure 2. (a) Affinity refers to the strength of single interaction between antigen and antibody, while avidity refers to the strength of all interactions combined. (b) An antibody may cross react with different epitopes.

The term **avidity** describes binding by antibody classes that are secreted as joined, multivalent structures (such as IgM and IgA). Although avidity measures the strength of binding, just as affinity does, the avidity is not simply the sum of the affinities of the antibodies in a multimeric structure. The avidity depends on the number of identical binding sites on the antigen being detected, as well as other physical and chemical factors. Typically, multimeric antibodies, such as pentameric IgM, are classified as having lower affinity than monomeric antibodies, but high avidity. Essentially, the fact that multimeric antibodies can bind many antigens simultaneously balances their slightly lower binding strength for each antibody/antigen interaction.

Antibodies secreted after binding to one epitope on an antigen may exhibit cross reactivity for the same or similar epitopes on different antigens. Because an epitope corresponds to such a small region (the surface area of about four to six amino acids), it is possible for different macromolecules to exhibit the same molecular identities and orientations over short regions. **Cross reactivity** describes when an antibody binds not to the antigen that elicited its synthesis and secretion, but to a different antigen.

Cross reactivity can be beneficial if an individual develops immunity to several related pathogens despite having only been exposed to or vaccinated against one of them. For instance, antibody cross reactivity may occur against the similar surface structures of various Gram-negative bacteria. Conversely, antibodies raised against pathogenic molecular components that resemble self molecules may incorrectly mark host cells for destruction and cause autoimmune damage. Patients who develop systemic lupus erythematosus (SLE) commonly exhibit antibodies that react with their own DNA. These antibodies may have been initially raised against the nucleic acid of microorganisms but later cross-reacted with self-antigens. This phenomenon is also called molecular mimicry.

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23.17: Disruptions in the Immune System

Immune disruptions may involve insufficient immune responses or inappropriate immune targets. Immunodeficiency increases an individual's susceptibility to infections and cancers. Hypersensitivities are misdirected responses either to harmless foreign particles, as in the case of allergies, or to host factors, as in the case of autoimmunity. Reactions to self components may be the result of molecular mimicry.

Immunodeficiency

A functioning immune system is essential for survival, but even the sophisticated cellular and molecular defenses of the mammalian immune response can be defeated by pathogens at virtually every step. In the competition between immune protection and pathogen evasion, pathogens have the advantage of more rapid evolution because of their shorter generation time and other characteristics. For instance, *Streptococcus pneumoniae* (bacterium that cause pneumonia and meningitis) surrounds itself with a capsule that inhibits phagocytes from engulfing it and displaying antigens to the adaptive immune system. *Staphylococcus aureus* (bacterium that can cause skin infections, abscesses, and meningitis) synthesizes a toxin called leukocidin that kills phagocytes after they engulf the bacterium. Other pathogens can also hinder the adaptive immune system. HIV infects T_H cells via their CD4 surface molecules, gradually depleting the number of T_H cells in the body; this inhibits the adaptive immune system's capacity to generate sufficient responses to infection or tumors. As a result, HIV-infected individuals often suffer from infections that would not cause illness in people with healthy immune systems but which can cause devastating illness to immune-compromised individuals. Maladaptive responses of immune cells and molecules themselves can also disrupt the proper functioning of the entire system, leading to host cell damage that could become fatal.

Failures, insufficiencies, or delays at any level of the immune response can allow pathogens or tumor cells to gain a foothold and replicate or proliferate to high enough levels that the immune system becomes overwhelmed. **Immunodeficiency** is the failure, insufficiency, or delay in the response of the immune system, which may be acquired or inherited. Immunodeficiency can be acquired as a result of infection with certain pathogens (such as HIV), chemical exposure (including certain medical treatments), malnutrition, or possibly by extreme stress. For instance, radiation exposure can destroy populations of lymphocytes and elevate an individual's susceptibility to infections and cancer. Dozens of genetic disorders result in immunodeficiencies, including Severe Combined Immunodeficiency (SCID), Bare lymphocyte syndrome, and MHC II deficiencies. Rarely, primary immunodeficiencies that are present from birth may occur. Neutropenia is one form in which the immune system produces a below-average number of neutrophils, the body's most abundant phagocytes. As a result, bacterial infections may go unrestricted in the blood, causing serious complications.

Hypersensitivities

Maladaptive immune responses toward harmless foreign substances or self antigens that occur after tissue sensitization are termed **hypersensitivities**. The types of hypersensitivities include immediate, delayed, and autoimmunity. A large proportion of the population is affected by one or more types of hypersensitivity.

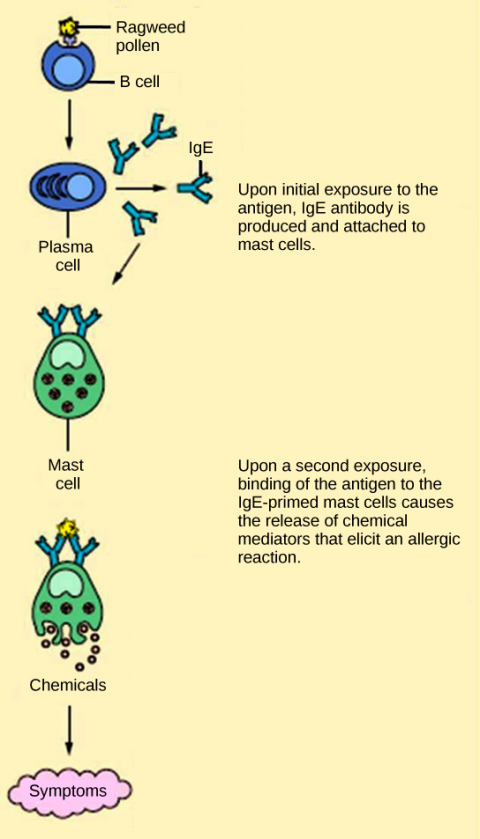


Figure 1. On first exposure to an allergen, an IgE antibody is synthesized by plasma cells in response to a harmless antigen. The IgE molecules bind to mast cells, and on secondary exposure, the mast cells release histamines and other modulators that affect the symptoms of allergy. (credit: modification of work by NIH)

The immune reaction that results from immediate hypersensitivities in which an antibody-mediated immune response occurs within minutes of exposure to a harmless antigen is called an **allergy**. In the United States, 20 percent of the population exhibits symptoms of allergy or asthma, whereas 55 percent test positive against one or more allergens. Upon initial exposure to a potential allergen, an allergic individual synthesizes antibodies of the IgE class via the typical process of APCs presenting processed antigen to T_H cells that stimulate B cells to produce IgE. This class of antibodies also mediates the immune response to parasitic worms. The constant domain of the IgE molecules interact with mast cells embedded in connective tissues. This process primes, or sensitizes, the tissue. Upon subsequent exposure to the same allergen, IgE molecules on mast cells bind the antigen via their variable domains and stimulate the mast cell to release the modified amino acids histamine and serotonin; these chemical mediators then recruit eosinophils which mediate allergic responses.

Figure 1 shows an example of an allergic response to ragweed pollen. The effects of an allergic reaction range from mild symptoms like sneezing and itchy, watery eyes to more severe or even life-threatening reactions involving intensely itchy welts or hives, airway contraction with severe respiratory distress, and plummeting blood pressure. This extreme reaction is known as anaphylactic shock. If not treated with epinephrine to counter the blood pressure and breathing effects, this condition can be fatal.

Delayed hypersensitivity is a cell-mediated immune response that takes approximately one to two days after secondary exposure for a maximal reaction to be observed. This type of hypersensitivity involves the T_H1 cytokine-mediated inflammatory response and may manifest as local tissue lesions or contact dermatitis (rash or skin irritation). Delayed hypersensitivity occurs in some individuals in response to contact with certain types of jewelry or cosmetics. Delayed hypersensitivity facilitates the immune response to poison ivy and is also the reason why the skin test for tuberculosis results in a small region of inflammation on individuals who were previously exposed to *Mycobacterium tuberculosis*. That is also why cortisone is used to treat such responses: it will inhibit cytokine production.

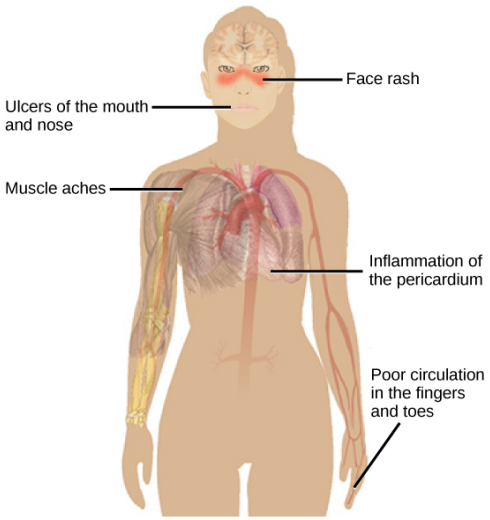


Figure 2. Systemic lupus erythematosus is characterized by autoimmunity to the individual's own DNA and/or proteins, which leads to varied dysfunction of the organs. (credit: modification of work by Mikael Häggström)

Autoimmunity is a type of hypersensitivity to self antigens that affects approximately five percent of the population. Most types of autoimmunity involve the humoral immune response. Antibodies that inappropriately mark self components as foreign are termed **autoantibodies**. In patients with the autoimmune disease myasthenia gravis, muscle cell receptors that induce contraction in response to acetylcholine are targeted by antibodies. The result is muscle weakness that may include marked difficultly with fine and/or gross motor functions. In systemic lupus erythematosus, a diffuse autoantibody response to the individual's own DNA and proteins results in various systemic diseases. As illustrated in Figure 2, systemic lupus erythematosus may affect the heart, joints, lungs, skin, kidneys, central nervous system, or other tissues, causing tissue damage via antibody binding, complement recruitment, lysis, and inflammation.

Autoimmunity can develop with time, and its causes may be rooted in molecular mimicry. Antibodies and TCRs may bind self antigens that are structurally similar to pathogen antigens, which the immune receptors first raised. As an example, infection with *Streptococcus pyogenes* (bacterium that causes strep throat) may generate antibodies or T cells that react with heart muscle, which has a similar structure to the surface of *S. pyogenes*. These antibodies can damage heart muscle with autoimmune attacks, leading to rheumatic fever. Insulin-dependent (Type 1) diabetes mellitus arises from a destructive inflammatory T_H1 response against insulin-producing cells of the pancreas. Patients with this autoimmunity must be injected with insulin that originates from other sources.

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23.18: Putting It Together- The Immune System

This video tells us about the team of deadly ninja assassins that is tasked with protecting our bodies from all the bad guys that want to kill us—also known as our immune system.



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=981

Autoimmune Diseases

Although the immune system protects the body by attacking invading “enemies” (pathogens), in some cases, the immune system can mistakenly identify the body’s own cells as the enemy, resulting in autoimmune disease.

Autoimmune diseases are those in which the body is attacked by its own specific adaptive immune response. In normal, healthy states, the immune system induces tolerance, which is a lack of an anti-self immune response. However, with autoimmunity, there is a loss of immune tolerance. Autoimmune diseases can have a variety of mixed symptoms that flare up and disappear, making diagnosis difficult.

The following are all examples of autoimmune diseases:

- celiac disease
- hyperthyroidism
- Type 1 Diabetes
- multiple sclerosis
- rheumatoid arthritis
- lupus

The causes of autoimmune disease are a combination of the individual’s genetic makeup and the effect of environmental influences, such as sunlight, infections, medications, and environmental chemicals. However, the vagueness of this list reflects our poor understanding of the etiology of these diseases. Except in a very few specific diseases, the initiation event(s) of most autoimmune states has not been fully characterized.

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23.19: Cerego- The Immune System

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for The Immune System. You'll need to create a free log-in to practice these items, if you haven't already.

https://cerego.com/sets/796529/learn

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CHAPTER OVERVIEW

24: Module 21- The Digestive System

24.1: Why It Matters- The Digestive System
24.2: Introduction to Digestive Systems
24.3: Herbivores, Carnivores, and Omnivores
24.4: Invertebrates and Vertebrate Digestive Systems
24.5: Parts of the Digestive System
24.6: Introduction to Nutrition and Energy Production
24.7: Food Requirements
24.8: Essential Nutrients
24.9: Food Energy and ATP
24.10: Introduction to Digestive System Processes and Regulation
24.11: Digestive System Processes
24.12: Neural Responses to Food
24.13: Hormonal Responses to Food
24.14: Putting It Together- The Digestive System
24.15: Cerego- The Digestive System

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24.1: Why It Matters- The Digestive System

Why describe the components and role of the digestive system?



Figure 1. For humans, fruits and vegetables are important in maintaining a balanced diet. (credit: modification of work by Julie Rybarczyk)

All living organisms need nutrients to survive. While plants can obtain the molecules required for cellular function through the process of photosynthesis, most animals obtain their nutrients by the consumption of other organisms. At the cellular level, the biological molecules necessary for animal function are amino acids, lipid molecules, nucleotides, and simple sugars. However, the food consumed consists of protein, fat, and complex carbohydrates. Animals must convert these macromolecules into the simple molecules required for maintaining cellular functions, such as assembling new molecules, cells, and tissues. The conversion of the food consumed to the nutrients required is a multi-step process involving digestion and absorption. During digestion, food particles are broken down to smaller components, and later, they are absorbed by the body.

One of the challenges in human nutrition is maintaining a balance between food intake, storage, and energy expenditure. Imbalances can have serious health consequences. For example, eating too much food while not expending much energy leads to obesity, which in turn will increase the risk of developing illnesses such as type-2 diabetes and cardiovascular disease. The recent rise in obesity and related diseases makes understanding the role of diet and nutrition in maintaining good health all the more important.

Learning Outcomes

- Compare and contrast different types of digestive systems
- Explain how energy is produced through diet and digestion
- Detail the steps involved in the digestive system processes
- Discuss the role of neural regulation in digestive processes

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24.2: Introduction to Digestive Systems

Compare and contrast different types of digestive systems

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

What You'll Learn to Do

- Identify the different structures required for herbivory and predatory diets
- Compare and contrast different types of digestive systems
- Explain the specialized functions of the organs involved in processing food in the body

Learning Activities

The learning activities for this section include the following:

- Herbivores, Carnivores, and Omnivores
- Invertebrates and Vertebrate Digestive Systems
- Parts of the Digestive System
- Self Check: Digestive Systems

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24.3: Herbivores, Carnivores, and Omnivores

Herbivores are animals whose primary food source is plant-based. Examples of herbivores, as shown in Figure 1 include vertebrates like deer, koalas, and some bird species, as well as invertebrates such as crickets and caterpillars. These animals have evolved digestive systems capable of handling large amounts of plant material. Herbivores can be further classified into frugivores (fruit-eaters), granivores (seed eaters), nectivores (nectar feeders), and folivores (leaf eaters).



Figure 1. Herbivores, like this (a) mule deer and (b) monarch caterpillar, eat primarily plant material. (credit a: modification of work by Bill Ebbesen; credit b: modification of work by Doug Bowman)

Carnivores are animals that eat other animals. The word carnivore is derived from Latin and literally means “meat eater.” Wild cats such as lions, shown in Figure 2a and tigers are examples of vertebrate carnivores, as are snakes and sharks, while invertebrate carnivores include sea stars, spiders, and ladybugs, shown in Figure 2b. Obligate carnivores are those that rely entirely on animal flesh to obtain their nutrients; examples of obligate carnivores are members of the cat family, such as lions and cheetahs. Facultative carnivores are those that also eat non-animal food in addition to animal food. Note that there is no clear line that differentiates facultative carnivores from omnivores; dogs would be considered facultative carnivores.



(a) (b)

Figure 2. Carnivores like the (a) lion eat primarily meat. The (b) ladybug is also a carnivore that consumes small insects called aphids. (credit a: modification of work by Kevin Pluck; credit b: modification of work by Jon Sullivan)

Omnivores are animals that eat both plant- and animal-derived food. In Latin, omnivore means to eat everything. Humans, bears (shown in Figure 3a), and chickens are example of vertebrate omnivores; invertebrate omnivores include cockroaches and crayfish (shown in Figure 3b).



(a) (b)

Figure 3. Omnivores like the (a) bear and (b) crayfish eat both plant and animal based food. (credit a: modification of work by Dave Menke; credit b: modification of work by Jon Sullivan)

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24.4: Invertebrates and Vertebrate Digestive Systems

Invertebrate Digestive Systems

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

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

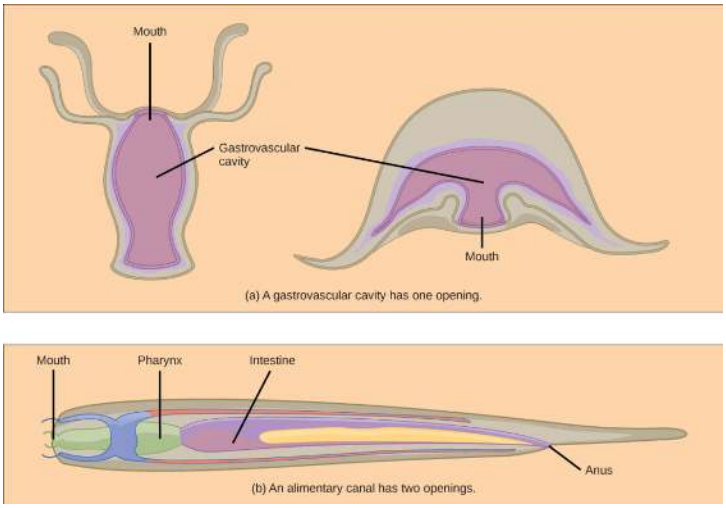


Figure 1. (a) A gastrovascular cavity has a single opening through which food is ingested and waste is excreted, as shown in this hydra and in this jellyfish medusa. (b) An alimentary canal has two openings: a mouth for ingesting food, and an anus for eliminating waste, as shown in this nematode.

Vertebrate Digestive Systems

Vertebrates have evolved more complex digestive systems to adapt to their dietary needs. Some animals have a single stomach, while others have multi-chambered stomachs. Birds have developed a digestive system adapted to eating unmasticated food.

Monogastric: Single-chambered Stomach

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

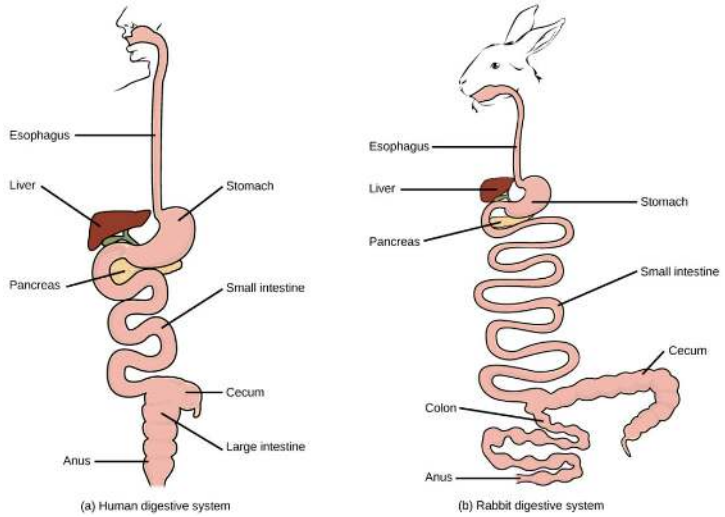


Figure 2. (a) Humans and herbivores, such as the (b) rabbit, have a monogastric digestive system. However, in the rabbit the small intestine and cecum are enlarged to allow more time to digest plant material. The enlarged organ provides more surface area for absorption of nutrients. Rabbits digest their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

Avian

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

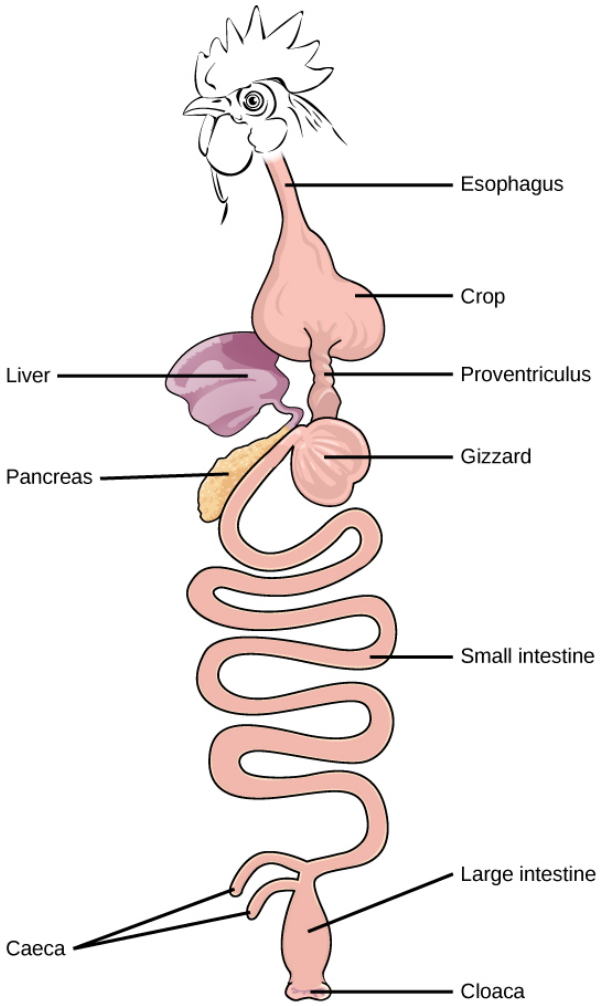


Figure 3. The avian esophagus has a pouch, called a crop, which stores food.

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

? Try It

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

Ruminants

Ruminants are mainly herbivores like cows, sheep, and goats, whose entire diet consists of eating large amounts of **roughage** or fiber. They have evolved digestive systems that help them digest vast amounts of cellulose. An interesting feature of the ruminants'

mouth is that they do not have upper incisor teeth. They use their lower teeth, tongue and lips to tear and chew their food. From the mouth, the food travels to the esophagus and on to the stomach.

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

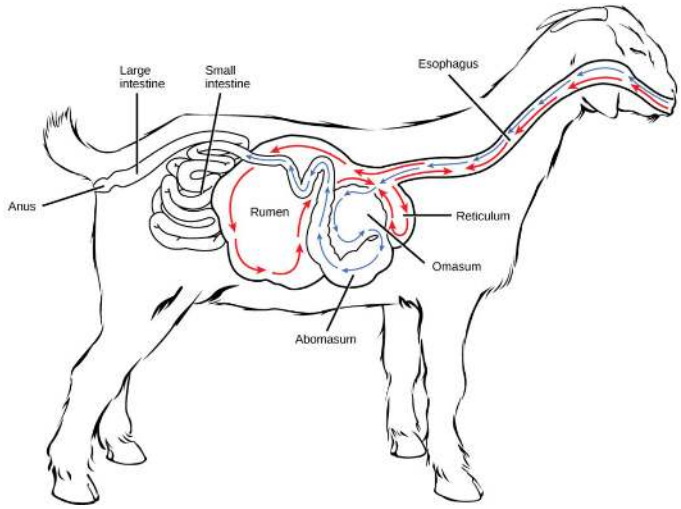


Figure 4. Ruminant animals, such as goats and cows, have four stomachs. The first two stomachs, the rumen and the reticulum, contain prokaryotes and protists that are able to digest cellulose fiber. The ruminant regurgitates cud from the reticulum, chews it, and swallows it into a third stomach, the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

Pseudo-ruminants

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

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24.5: Parts of the Digestive System

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

Oral Cavity

The oral cavity, or mouth, is the point of entry of food into the digestive system, illustrated in Figure 1. The food consumed is broken into smaller particles by mastication, the chewing action of the teeth. All mammals have teeth and can chew their food.

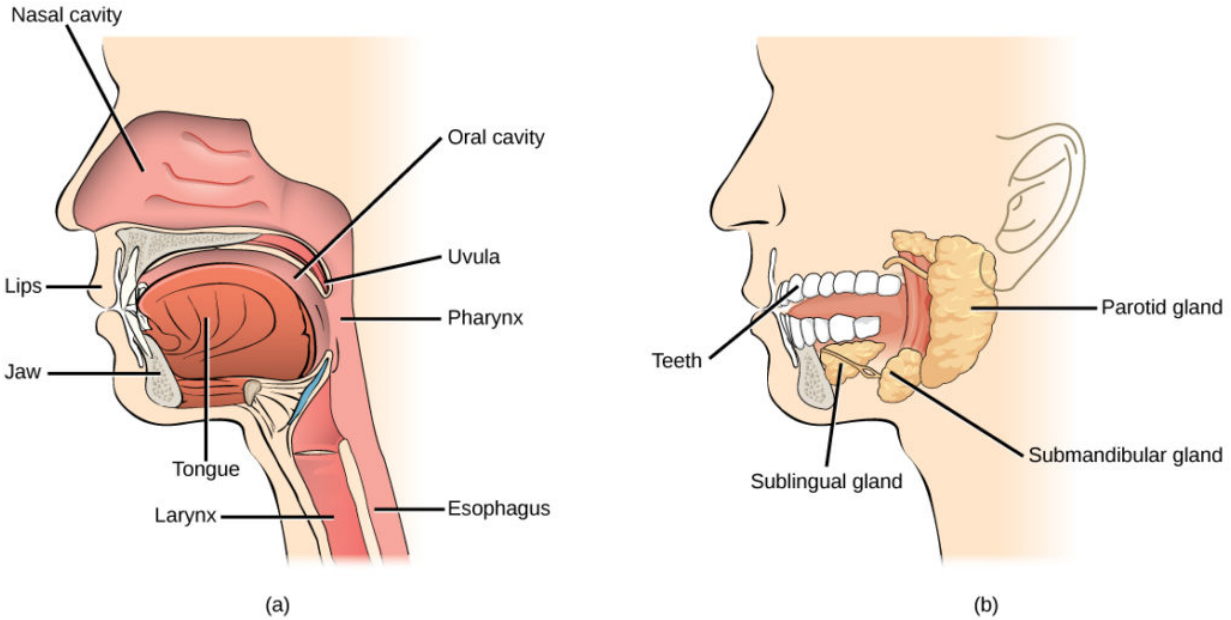


Figure 1. Digestion of food begins in the (a) oral cavity. Food is masticated by teeth and moistened by saliva secreted from the (b) salivary glands. Enzymes in the saliva begin to digest starches and fats. With the help of the tongue, the resulting bolus is moved into the esophagus by swallowing. (credit: modification of work by the National Cancer Institute)

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

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

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

Esophagus

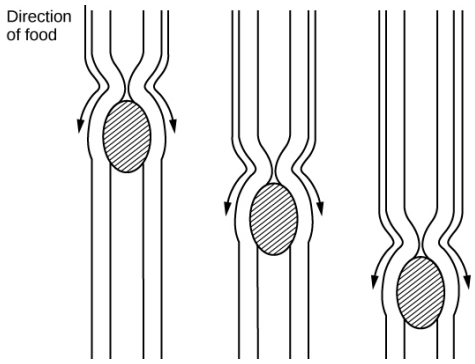


Figure 2. The esophagus transfers food from the mouth to the stomach through peristaltic movements.

The **esophagus** is a tubular organ that connects the mouth to the stomach. The chewed and softened food passes through the esophagus after being swallowed. The smooth muscles of the esophagus undergo a series of wave like movements called **peristalsis** that push the food toward the stomach, as illustrated in Figure 2. The peristalsis wave is unidirectional—it moves food from the mouth to the stomach, and reverse movement is not possible. The peristaltic movement of the esophagus is an involuntary reflex; it takes place in response to the act of swallowing.

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

Stomach

A large part of digestion occurs in the stomach, shown in Figure 3. The **stomach** is a saclike organ that secretes gastric digestive juices. The pH in the stomach is between 1.5 and 2.5. This highly acidic environment is required for the chemical breakdown of food and the extraction of nutrients. When empty, the stomach is a rather small organ; however, it can expand to up to 20 times its resting size when filled with food. This characteristic is particularly useful for animals that need to eat when food is available.

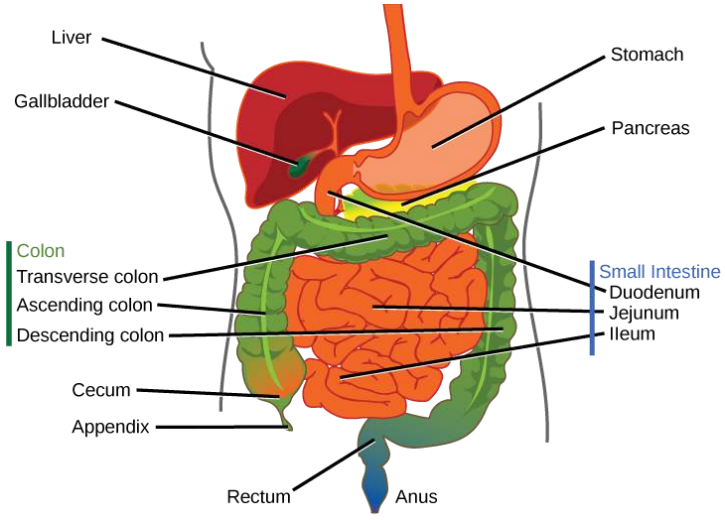


Figure 3. The human stomach has an extremely acidic environment where most of the protein gets digested. (credit: modification of work by Mariana Ruiz Villareal)

? Practice Question

Which of the following statements about the digestive system is false?

a. Chyme is a mixture of food and digestive juices that is produced in the stomach.
b. Food enters the large intestine before the small intestine.
c. In the small intestine, chyme mixes with bile, which emulsifies fats.
d. The stomach is separated from the small intestine by the pyloric sphincter.

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[hidden-answer a="475104"]Statement b is true.[/hidden-answer]

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

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

Small Intestine

Chyme moves from the stomach to the small intestine. The **small intestine** is the organ where the digestion of protein, fats, and carbohydrates is completed. The small intestine is a long tube-like organ with a highly folded surface containing finger-like projections called the **villi**. The apical surface of each villus has many microscopic projections called microvilli. These structures, illustrated in Figure 4, are lined with epithelial cells on the luminal side and allow for the nutrients to be absorbed from the digested food and absorbed into the blood stream on the other side. The villi and microvilli, with their many folds, increase the surface area of the intestine and increase absorption efficiency of the nutrients. Absorbed nutrients in the blood are carried into the hepatic portal vein, which leads to the liver. There, the liver regulates the distribution of nutrients to the rest of the body and removes toxic substances, including drugs, alcohol, and some pathogens.

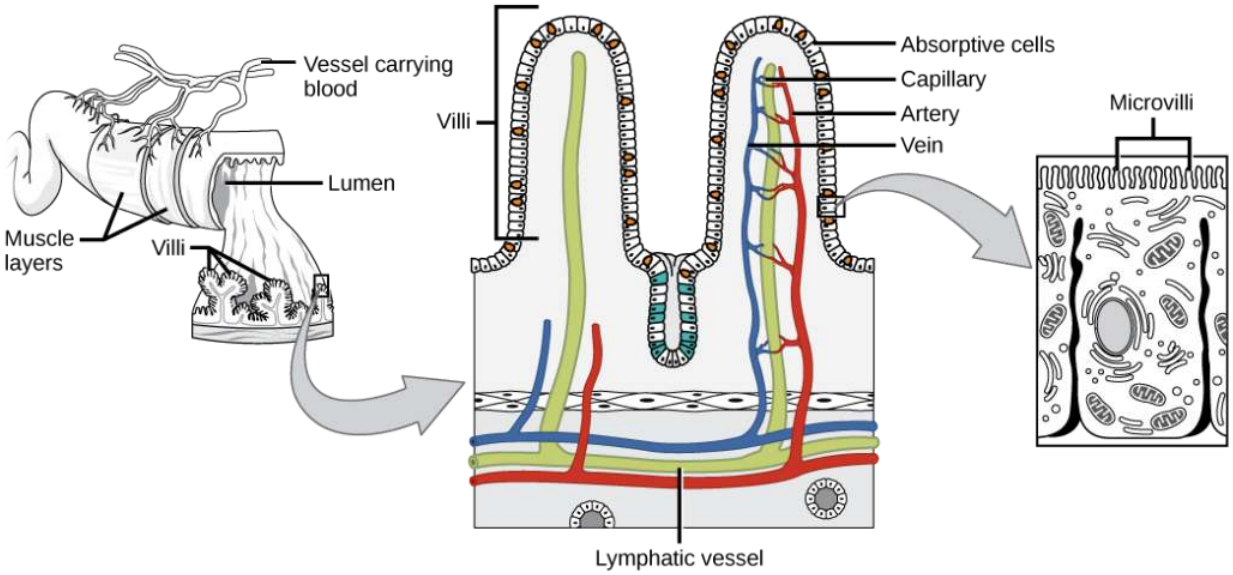


Figure 4. Villi are folds on the small intestine lining that increase the surface area to facilitate the absorption of nutrients.

? Practice Question

Which of the following statements about the small intestine is false?

a. Absorptive cells that line the small intestine have microvilli, small projections that increase surface area and aid in the absorption of food.
b. The inside of the small intestine has many folds, called villi.
c. Microvilli are lined with blood vessels as well as lymphatic vessels.
d. The inside of the small intestine is called the lumen.

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[hidden-answer a="650771"]Statement c is false.[/hidden-answer]

The human small intestine is over 6m long and is divided into three parts: the duodenum, the jejunum, and the ileum. The "C-shaped," fixed part of the small intestine is called the **duodenum** and is shown in Figure 3. The duodenum is separated from the stomach by the pyloric sphincter which opens to allow chyme to move from the stomach to the duodenum. In the duodenum, chyme is mixed with pancreatic juices in an alkaline solution rich in bicarbonate that neutralizes the acidity of chyme and acts as a buffer. Pancreatic juices also contain several digestive enzymes. Digestive juices from the pancreas, liver, and gallbladder, as well as from gland cells of the intestinal wall itself, enter the duodenum. **Bile** is produced in the liver and stored and concentrated in the gallbladder. Bile contains bile salts which emulsify lipids while the pancreas produces enzymes that catabolize starches, disaccharides, proteins, and fats. These digestive juices break down the food particles in the chyme into glucose, triglycerides, and amino acids. Some chemical digestion of food takes place in the duodenum. Absorption of fatty acids also takes place in the duodenum.

The second part of the small intestine is called the **jejunum**, shown in Figure 3. Here, hydrolysis of nutrients is continued while most of the carbohydrates and amino acids are absorbed through the intestinal lining. The bulk of chemical digestion and nutrient absorption occurs in the jejunum.

The **ileum**, also illustrated in Figure 3 is the last part of the small intestine and here the bile salts and vitamins are absorbed into blood stream. The undigested food is sent to the colon from the ileum via peristaltic movements of the muscle. The ileum ends and the large intestine begins at the ileocecal valve. The vermiform, "worm-like," appendix is located at the ileocecal valve. The appendix of humans secretes no enzymes and has an insignificant role in immunity.

Large Intestine

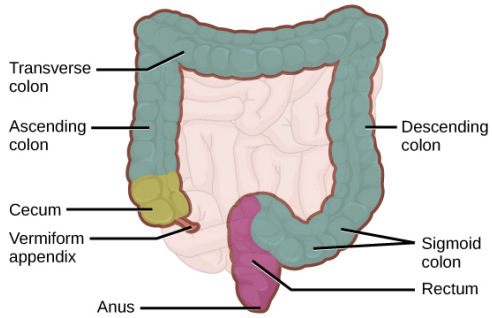


Figure 5. The large intestine reabsorbs water from undigested food and stores waste material until it is eliminated.

The **large intestine**, illustrated in Figure 5, reabsorbs the water from the undigested food material and processes the waste material. The human large intestine is much smaller in length compared to the small intestine but larger in diameter. It has three parts: the cecum, the colon, and the rectum. The cecum joins the ileum to the colon and is the receiving pouch for the waste matter. The colon is home to many bacteria or "intestinal flora" that aid in the digestive processes. The colon can be divided into four regions, the ascending colon, the transverse colon, the descending colon and the sigmoid colon. The main functions of the colon are to extract the water and mineral salts from undigested food, and to store waste material. Carnivorous mammals have a shorter large intestine compared to herbivorous mammals due to their diet.

Rectum and Anus

The **rectum** is the terminal end of the large intestine, as shown in Figure 5. The primary role of the rectum is to store the feces until defecation. The feces are propelled using peristaltic movements during elimination. The **anus** is an opening at the far-end of the digestive tract and is the exit point for the waste material. Two sphincters between the rectum and anus control elimination: the inner sphincter is involuntary and the outer sphincter is voluntary.

Accessory Organs

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

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

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

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

Learning Objectives

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

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24.6: Introduction to Nutrition and Energy Production

Explain how energy is produced through diet and digestion

Given the diversity of animal life on our planet, it is not surprising that the animal diet would also vary substantially. The animal diet is the source of materials needed for building DNA and other complex molecules needed for growth, maintenance, and reproduction; collectively these processes are called biosynthesis. The diet is also the source of materials for ATP production in the cells. The diet must be balanced to provide the minerals and vitamins that are required for cellular function.

What You'll Learn to Do

- Describe the essential nutrients required for cellular function that cannot be synthesized by the animal body
- Identify common nutrients essential to life
- Explain how energy is produced through diet and digestion

Learning Activities

The learning activities for this section include the following:

- Food Requirements
- Essential Nutrients
- Food Energy and ATP
- Self Check: Nutrition and Energy Production

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24.7: Food Requirements

What are the fundamental requirements of the animal diet? The animal diet should be well balanced and provide nutrients required for bodily function and the minerals and vitamins required for maintaining structure and regulation necessary for good health and reproductive capability. These requirements for a human are illustrated graphically in Figure 1.

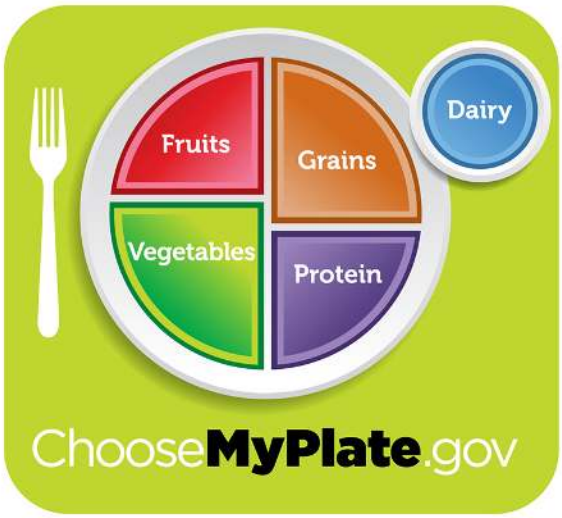


Figure 1. For humans, a balanced diet includes fruits, vegetables, grains, and protein. (credit: USDA)

The first step in ensuring that you are meeting the food requirements of your body is an awareness of the food groups and the nutrients they provide. To learn more about each food group and the recommended daily amounts, explore this interactive site by the United States Department of Agriculture.

? Try It

Obesity is a growing epidemic and the rate of obesity among children is rapidly rising in the United States. To combat childhood obesity and ensure that children get a healthy start in life, first lady Michelle Obama has launched the Let's Move! campaign. The goal of this campaign is to educate parents and caregivers on providing healthy nutrition and encouraging active lifestyles to future generations. This program aims to involve the entire community, including parents, teachers, and healthcare providers to ensure that children have access to healthy foods—more fruits, vegetables, and whole grains—and consume fewer calories from processed foods. Another goal is to ensure that children get physical activity. With the increase in television viewing and stationary pursuits such as video games, sedentary lifestyles have become the norm. Learn more at www.letsmove.gov.

Organic Precursors

The organic molecules required for building cellular material and tissues must come from food. Carbohydrates or sugars are the primary source of organic carbons in the animal body. During digestion, digestible carbohydrates are ultimately broken down into glucose and used to provide energy through metabolic pathways. Complex carbohydrates, including polysaccharides, can be broken down into glucose through biochemical modification; however, humans do not produce the enzyme cellulase and lack the ability to derive glucose from the polysaccharide cellulose. In humans, these molecules provide the fiber required for moving waste through the large intestine and a healthy colon. The intestinal flora in the human gut are able to extract some nutrition from these plant fibers. The excess sugars in the body are converted into glycogen and stored in the liver and muscles for later use. Glycogen stores are used to fuel prolonged exertions, such as long-distance running, and to provide energy during food shortage. Excess glycogen can be converted to fats, which are stored in the lower layer of the skin of mammals for insulation and energy storage. Excess digestible carbohydrates are stored by mammals in order to survive famine and aid in mobility.

Another important requirement is that of nitrogen. Protein catabolism provides a source of organic nitrogen. Amino acids are the building blocks of proteins and protein breakdown provides amino acids that are used for cellular function. The carbon and

nitrogen derived from these become the building block for nucleotides, nucleic acids, proteins, cells, and tissues. Excess nitrogen must be excreted as it is toxic. Fats add flavor to food and promote a sense of satiety or fullness. Fatty foods are also significant sources of energy because one gram of fat contains nine calories. Fats are required in the diet to aid the absorption of fat-soluble vitamins and the production of fat-soluble hormones.

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24.8: Essential Nutrients



Figure 1. A healthy diet should include a variety of foods to ensure that needs for essential nutrients are met. (credit: Keith Weller, USDA ARS)

While the animal body can synthesize many of the molecules required for function from the organic precursors, there are some nutrients that need to be consumed from food. These nutrients are termed **essential nutrients**, meaning they must be eaten, and the body cannot produce them.

The omega-3 alpha-linolenic acid and the omega-6 linoleic acid are essential fatty acids needed to make some membrane phospholipids. **Vitamins** are another class of essential organic molecules that are required in small quantities for many enzymes to function and, for this reason, are considered to be co-enzymes. Absence or low levels of vitamins can have a dramatic effect on health, as outlined in Table 1 and Table 2. Both fat-soluble and water-soluble vitamins must be obtained from food.

Table 1. Water-soluble Essential Vitamins

Vitamin	Function	Deficiencies Can Lead To	Sources
Vitamin B_1 (Thiamine)	Needed by the body to process lipids, proteins, and carbohydrates Coenzyme removes CO_2 from organic compounds	Muscle weakness, Beriberi: reduced heart function, CNS problems	Milk, meat, dried beans, whole grains
Vitamin B_2 (Riboflavin)	Takes an active role in metabolism, aiding in the conversion of food to energy (FAD and FMN)	Cracks or sores on the outer surface of the lips (cheliosis); inflammation and redness of the tongue; moist, scaly skin inflammation (seborrheic dermatitis)	Meat, eggs, enriched grains, vegetables
Vitamin B_3 (Niacin)	Used by the body to release energy from carbohydrates and to process alcohol; required for the synthesis of sex hormones; component of coenzyme NAD^+ and $NADP^+$	Pellagra, which can result in dermatitis, diarrhea, dementia, and death	Meat, eggs, grains, nuts, potatoes
Vitamin B_5 (Pantothenic acid)	Assists in producing energy from foods (lipids, in particular); component of coenzyme A	Fatigue, poor coordination, retarded growth, numbness, tingling of hands and feet	Meat, whole grains, milk, fruits, vegetables
Vitamin B_6 (Pyridoxine)	The principal vitamin for processing amino acids and lipids; also helps convert nutrients into energy	Irritability, depression, confusion, mouth sores or ulcers, anemia, muscular twitching	Meat, dairy products, whole grains, orange juice
Vitamin B_7 (Biotin)	Used in energy and amino acid metabolism, fat synthesis, and fat breakdown; helps the body use blood sugar	Hair loss, dermatitis, depression, numbness and tingling in the extremities; neuromuscular disorders	Meat, eggs, legumes and other vegetables
Vitamin B_9 (Folic acid)	Assists the normal development of cells, especially during fetal development; helps metabolize nucleic and amino acids	Deficiency during pregnancy is associated with birth defects, such as neural tube defects and anemia	Leafy green vegetables, whole wheat, fruits, nuts, legumes
Vitamin B_{12} (Cobalamin)	Maintains healthy nervous system and assists with blood cell formation; coenzyme in nucleic acid metabolism	Anemia, neurological disorders, numbness, loss of balance	Meat, eggs, animal products
Vitamin C (Ascorbic acid)	Helps maintain connective tissue: bone, cartilage, and dentin; boosts the immune system	Scurvy, which results in bleeding, hair and tooth loss; joint pain and swelling; delayed wound healing	Citrus fruits, broccoli, tomatoes, red sweet bell peppers

Table 2. Fat-soluble Essential Vitamins

Vitamin	Function	Deficiencies Can Lead To	Sources
Vitamin A (Retinol)	Critical to the development of bones, teeth, and skin; helps maintain eyesight, enhances the immune system, fetal development, gene expression	Night-blindness, skin disorders, impaired immunity	Dark green leafy vegetables, yellow-orange vegetables fruits, milk, butter
Vitamin D	Critical for calcium absorption for bone development and strength; maintains a stable nervous system; maintains a normal and strong heartbeat; helps in blood clotting	Rickets, osteomalacia, immunity	Cod liver oil, milk, egg yolk
Vitamin E (Tocopherol)	Lessens oxidative damage of cells,and prevents lung damage from pollutants; vital to the immune system	Deficiency is rare; anemia, nervous system degeneration	Wheat germ oil, unrefined vegetable oils, nuts, seeds, grains
Vitamin K (Phylloquinone)	Essential to blood clotting	Bleeding and easy bruising	Leafy green vegetables, tea

Minerals, listed in Table 3, are inorganic essential nutrients that must be obtained from food. Among their many functions, minerals help in structure and regulation and are considered co-factors.

Table 3. Minerals and Their Function in the Human Body

Vitamin	Function	Deficiencies Can Lead To	Sources
Calcium*	Needed for muscle and neuron function; heart health; builds bone and supports synthesis and function of blood cells; nerve function	Osteoporosis, rickets, muscle spasms, impaired growth	Milk, yogurt, fish, green leafy vegetables, legumes
Chlorine*	Needed for production of hydrochloric acid (HCl) in the stomach and nerve function; osmotic balance	Muscle cramps, mood disturbances, reduced appetite	Table salt
Copper (trace amounts)	Required component of many redox enzymes, including cytochrome c oxidase; cofactor for hemoglobin synthesis	Copper deficiency is rare	Liver, oysters, cocoa, chocolate, sesame, nuts
Iodine	Required for the synthesis of thyroid hormones	Goiter	Seafood, iodized salt, dairy products
Iron	Required for many proteins and enzymes, notably hemoglobin, to prevent anemia	Anemia, which causes poor concentration, fatigue, and poor immune function	Red meat, leafy green vegetables, fish (tuna, salmon), eggs, dried fruits, beans, whole grains
Magnesium*	Required co-factor for ATP formation; bone formation; normal membrane functions; muscle function	Mood disturbances, muscle spasms	Whole grains, leafy green vegetables
Manganese (trace amounts)	A cofactor in enzyme functions; trace amounts are required	Manganese deficiency is rare	Common in most foods
Molybdenum (trace amounts)	Acts as a cofactor for three essential enzymes in humans: sulfite oxidase, xanthine oxidase, and aldehyde oxidase	Molybdenum deficiency is rare	
Phosphorus*	A component of bones and teeth; helps regulate acid-base balance; nucleotide synthesis	Weakness, bone abnormalities, calcium loss	Milk, hard cheese, whole grains, meats
Potassium*	Vital for muscles, heart, and nerve function	Cardiac rhythm disturbance, muscle weakness	Legumes, potato skin, tomatoes, bananas
Selenium (trace amounts)	A cofactor essential to activity of antioxidant enzymes like glutathione peroxidase; trace amounts are required	Selenium deficiency is rare	Common in most foods
Sodium*	Systemic electrolyte required for many functions; acid-base	Muscle cramps, fatigue, reduced appetite	Table salt

*Greater than 200mg/day required

Table 3. Minerals and Their Function in the Human Body			
Vitamin	Function	Deficiencies Can Lead To	Sources
	balance; water balance; nerve function		
Zinc (trace amounts)	Required for several enzymes such as carboxypeptidase, liver alcohol dehydrogenase, and carbonic anhydrase	Anemia, poor wound healing, can lead to short stature	Common in most foods
*Greater than 200mg/day required			

Certain amino acids also must be procured from food and cannot be synthesized by the body. These amino acids are the “essential” amino acids. The human body can synthesize only 11 of the 20 required amino acids; the rest must be obtained from food. The essential amino acids are listed in Table 4.

Table 4. Essential Amino Acids	
Amino acids that must be consumed	Amino acids anabolized by the body
isoleucine	alanine
leucine	selenocysteine
lysine	aspartate
methionine	cysteine
phenylalanine	glutamate
tryptophan	glycine
valine	proline
histidine*	serine
threonine	tyrosine
arginine*	asparagine
*The human body can synthesize histidine and arginine, but not in the quantities required, especially for growing children.	

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24.9: Food Energy and ATP

Animals need food to obtain energy and maintain homeostasis. Homeostasis is the ability of a system to maintain a stable internal environment even in the face of external changes to the environment. For example, the normal body temperature of humans is 37°C (98.6°F). Humans maintain this temperature even when the external temperature is hot or cold. It takes energy to maintain this body temperature, and animals obtain this energy from food.

The primary source of energy for animals is carbohydrates, mainly glucose. Glucose is called the body's fuel. The digestible carbohydrates in an animal's diet are converted to glucose molecules through a series of catabolic chemical reactions.

Adenosine triphosphate, or ATP, is the primary energy currency in cells; ATP stores energy in phosphate ester bonds. ATP releases energy when the phosphodiester bonds are broken and ATP is converted to ADP and a phosphate group. ATP is produced by the oxidative reactions in the cytoplasm and mitochondrion of the cell, where carbohydrates, proteins, and fats undergo a series of metabolic reactions collectively called cellular respiration. For example, glycolysis is a series of reactions in which glucose is converted to pyruvic acid and some of its chemical potential energy is transferred to NADH and ATP.

ATP is required for all cellular functions. It is used to build the organic molecules that are required for cells and tissues; it provides energy for muscle contraction and for the transmission of electrical signals in the nervous system. When the amount of ATP is available in excess of the body's requirements, the liver uses the excess ATP and excess glucose to produce molecules called glycogen. Glycogen is a polymeric form of glucose and is stored in the liver and skeletal muscle cells. When blood sugar drops, the liver releases glucose from stores of glycogen. Skeletal muscle converts glycogen to glucose during intense exercise. The process of converting glucose and excess ATP to glycogen and the storage of excess energy is an evolutionarily important step in helping animals deal with mobility, food shortages, and famine.

Obesity

Obesity is a major health concern in the United States, and there is a growing focus on reducing obesity and the diseases it may lead to, such as type-2 diabetes, cancers of the colon and breast, and cardiovascular disease. How does the food consumed contribute to obesity?

Fatty foods are calorie-dense, meaning that they have more calories per unit mass than carbohydrates or proteins. One gram of carbohydrates has four calories, one gram of protein has four calories, and one gram of fat has nine calories. Animals tend to seek lipid-rich food for their higher energy content.

The signals of hunger ("time to eat") and satiety ("time to stop eating") are controlled in the hypothalamus region of the brain. Foods that are rich in fatty acids tend to promote satiety more than foods that are rich only in carbohydrates.

Excess carbohydrate and ATP are used by the liver to synthesize glycogen. The pyruvate produced during glycolysis is used to synthesize fatty acids. When there is more glucose in the body than required, the resulting excess pyruvate is converted into molecules that eventually result in the synthesis of fatty acids within the body. These fatty acids are stored in adipose cells—the fat cells in the mammalian body whose primary role is to store fat for later use.

It is important to note that some animals benefit from obesity. Polar bears and seals need body fat for insulation and to keep them from losing body heat during Arctic winters. When food is scarce, stored body fat provides energy for maintaining homeostasis. Fats prevent famine in mammals, allowing them to access energy when food is not available on a daily basis; fats are stored when a large kill is made or lots of food is available.

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24.10: Introduction to Digestive System Processes and Regulation

Discuss the processes and regulations involved in digestion

Obtaining nutrition and energy from food is a multi-step process. For true animals, the first step is ingestion, the act of taking in food. This is followed by digestion, absorption, and elimination. The brain is the control center for the sensation of hunger and satiety. The functions of the digestive system are regulated through neural and hormonal responses.

What You'll Learn to Do

- Detail the steps involved in the digestive system processes
- Discuss the role of neural regulation in digestive processes
- Explain how hormones regulate digestion

Learning Activities

The learning activities for this section include the following:

- Digestive System Processes
- Neural Responses to Food
- Hormonal Responses to Food
- Self Check: Digestive System Regulation

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24.11: Digestive System Processes

Ingestion

The large molecules found in intact food cannot pass through the cell membranes. Food needs to be broken into smaller particles so that animals can harness the nutrients and organic molecules. The first step in this process is **ingestion**. Ingestion is the process of taking in food through the mouth. In vertebrates, the teeth, saliva, and tongue play important roles in mastication (preparing the food into bolus). While the food is being mechanically broken down, the enzymes in saliva begin to chemically process the food as well. The combined action of these processes modifies the food from large particles to a soft mass that can be swallowed and can travel the length of the esophagus.

Digestion and Absorption

Digestion is the mechanical and chemical break down of food into small organic fragments. It is important to break down macromolecules into smaller fragments that are of suitable size for absorption across the digestive epithelium. Large, complex molecules of proteins, polysaccharides, and lipids must be reduced to simpler particles such as simple sugar before they can be absorbed by the digestive epithelial cells. Different organs play specific roles in the digestive process. The animal diet needs carbohydrates, protein, and fat, as well as vitamins and inorganic components for nutritional balance. How each of these components is digested is discussed in the following sections.

Carbohydrates

The digestion of carbohydrates begins in the mouth. The salivary enzyme amylase begins the breakdown of food starches into maltose, a disaccharide. As the bolus of food travels through the esophagus to the stomach, no significant digestion of carbohydrates takes place. The esophagus produces no digestive enzymes but does produce mucous for lubrication. The acidic environment in the stomach stops the action of the amylase enzyme.

The next step of carbohydrate digestion takes place in the duodenum. Recall that the chyme from the stomach enters the duodenum and mixes with the digestive secretion from the pancreas, liver, and gallbladder. Pancreatic juices also contain amylase, which continues the breakdown of starch and glycogen into maltose, a disaccharide. The disaccharides are broken down into monosaccharides by enzymes called **maltases**, **sucrases**, and **lactases**, which are also present in the brush border of the small intestinal wall. Maltase breaks down maltose into glucose. Other disaccharides, such as sucrose and lactose are broken down by sucrase and lactase, respectively. Sucrase breaks down sucrose (or “table sugar”) into glucose and fructose, and lactase breaks down lactose (or “milk sugar”) into glucose and galactose. The monosaccharides (glucose) thus produced are absorbed and then can be used in metabolic pathways to harness energy. The monosaccharides are transported across the intestinal epithelium into the bloodstream to be transported to the different cells in the body. The steps in carbohydrate digestion are summarized in Figure 1 and Table 1.

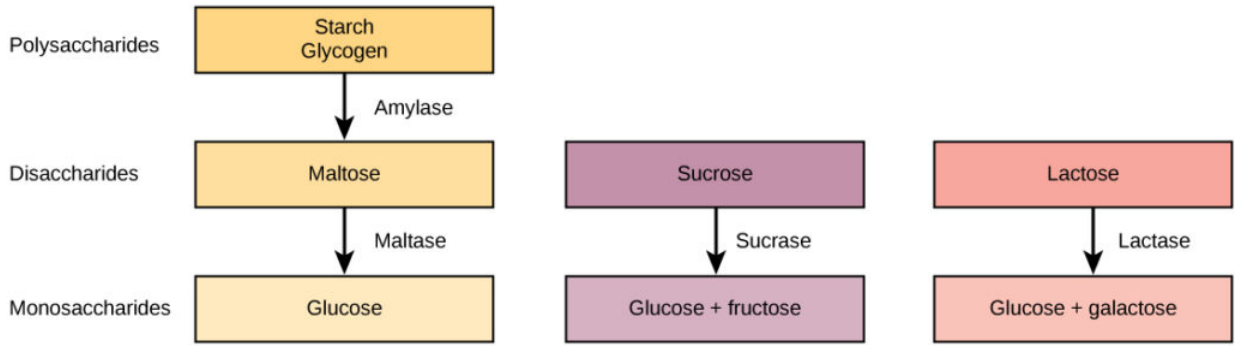


Figure 1. Digestion of carbohydrates is performed by several enzymes. Starch and glycogen are broken down into glucose by amylase and maltase. Sucrose (table sugar) and lactose (milk sugar) are broken down by sucrase and lactase, respectively.

Table 1. Digestion of Carbohydrates				
Enzyme	Produced By	Site of Action	Substrate Acting On	End Products
Salivary amylase	Salivary glands	Mouth	Polysaccharides (Starch)	Disaccharides (maltose), oligosaccharides
Pancreatic amylase	Pancreas	Small intestine	Polysaccharides (starch)	Disaccharides (maltose), monosaccharides
Oligosaccharidases	Lining of the intestine; brush border membrane	Small intestine	Disaccharides	Monosaccharides (e.g., glucose, fructose, galactose)

Protein

A large part of protein digestion takes place in the stomach. The enzyme pepsin plays an important role in the digestion of proteins by breaking down the intact protein to peptides, which are short chains of four to nine amino acids. In the duodenum, other enzymes—**trypsin**, **elastase**, and **chymotrypsin**—act on the peptides reducing them to smaller peptides. Trypsin elastase, carboxypeptidase, and chymotrypsin are produced by the pancreas and released into the duodenum where they act on the chyme. Further breakdown of peptides to single amino acids is aided by enzymes called peptidases (those that break down peptides). Specifically, **carboxypeptidase**, **dipeptidase**, and **aminopeptidase** play important roles in reducing the peptides to free amino acids. The amino acids are absorbed into the bloodstream through the small intestines. The steps in protein digestion are summarized in Figure 2 and Table 2.

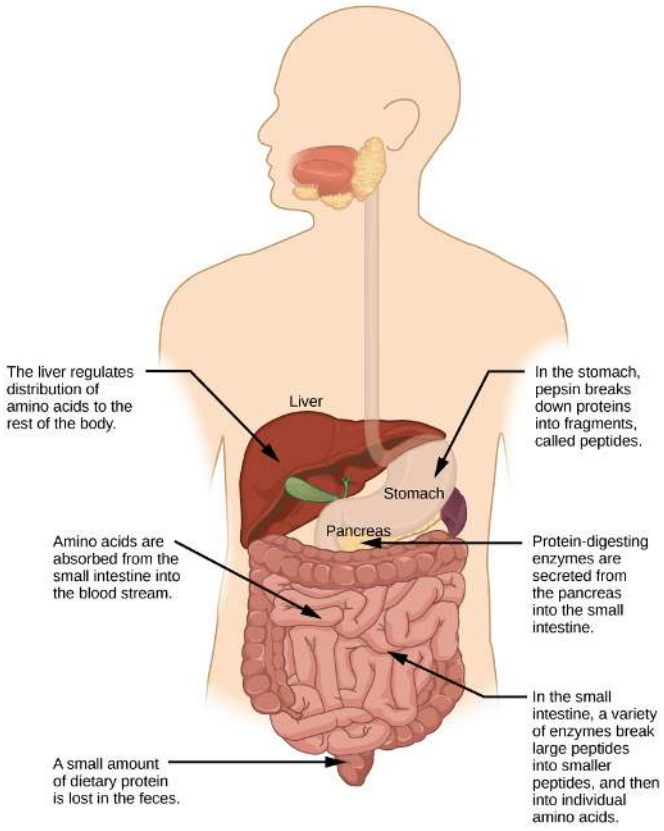


Figure 2. Protein digestion is a multistep process that begins in the stomach and continues through the intestines.

Table 2. Digestion of Protein

Enzyme	Produced By	Site of Action	Substrate Acting On	End Products
Pepsin	Stomach chief cells	Stomach	Proteins	Peptides
• Trypsin • Elastase Chymotrypsin	Pancreas	Small intestine	Proteins	Peptides
Carboxypeptidase	Pancreas	Small intestine	Peptides	Amino acids and peptides
• Aminopeptidase • Dipeptidase	Lining of intestine	Small intestine	Peptides	Amino acids

Lipids

Lipid digestion begins in the stomach with the aid of lingual lipase and gastric lipase. However, the bulk of lipid digestion occurs in the small intestine due to pancreatic lipase. When chyme enters the duodenum, the hormonal responses trigger the release of bile, which is produced in the liver and stored in the gallbladder. Bile aids in the digestion of lipids, primarily triglycerides by emulsification. Emulsification is a process in which large lipid globules are broken down into several small lipid globules. These small globules are more widely distributed in the chyme rather than forming large aggregates. Lipids are hydrophobic substances: in the presence of water, they will aggregate to form globules to minimize exposure to water. Bile contains bile salts, which are amphipathic, meaning they contain hydrophobic and hydrophilic parts. Thus, the bile salts hydrophilic side can interface with water on one side and the hydrophobic side interfaces with lipids on the other. By doing so, bile salts emulsify large lipid globules into small lipid globules.

Why is emulsification important for digestion of lipids? Pancreatic juices contain enzymes called lipases (enzymes that break down lipids). If the lipid in the chyme aggregates into large globules, very little surface area of the lipids is available for the lipases to act on, leaving lipid digestion incomplete. By forming an emulsion, bile salts increase the available surface area of the lipids many fold. The pancreatic lipases can then act on the lipids more efficiently and digest them, as detailed in Figure 3. Lipases break down the lipids into fatty acids and glycerides. These molecules can pass through the plasma membrane of the cell and enter the epithelial cells of the intestinal lining. The bile salts surround long-chain fatty acids and monoglycerides forming tiny spheres called micelles. The micelles move into the brush border of the small intestine absorptive cells where the long-chain fatty acids and monoglycerides diffuse out of the micelles into the absorptive cells leaving the micelles behind in the chyme. The long-chain fatty acids and monoglycerides recombine in the absorptive cells to form triglycerides, which aggregate into globules and become coated with proteins. These large spheres are called **chylomicrons**. Chylomicrons contain triglycerides, cholesterol, and other lipids and have proteins on their surface. The surface is also composed of the hydrophilic phosphate “heads” of phospholipids. Together, they enable the chylomicron to move in an aqueous environment without exposing the lipids to water. Chylomicrons leave the absorptive cells via exocytosis. Chylomicrons enter the lymphatic vessels, and then enter the blood in the subclavian vein.

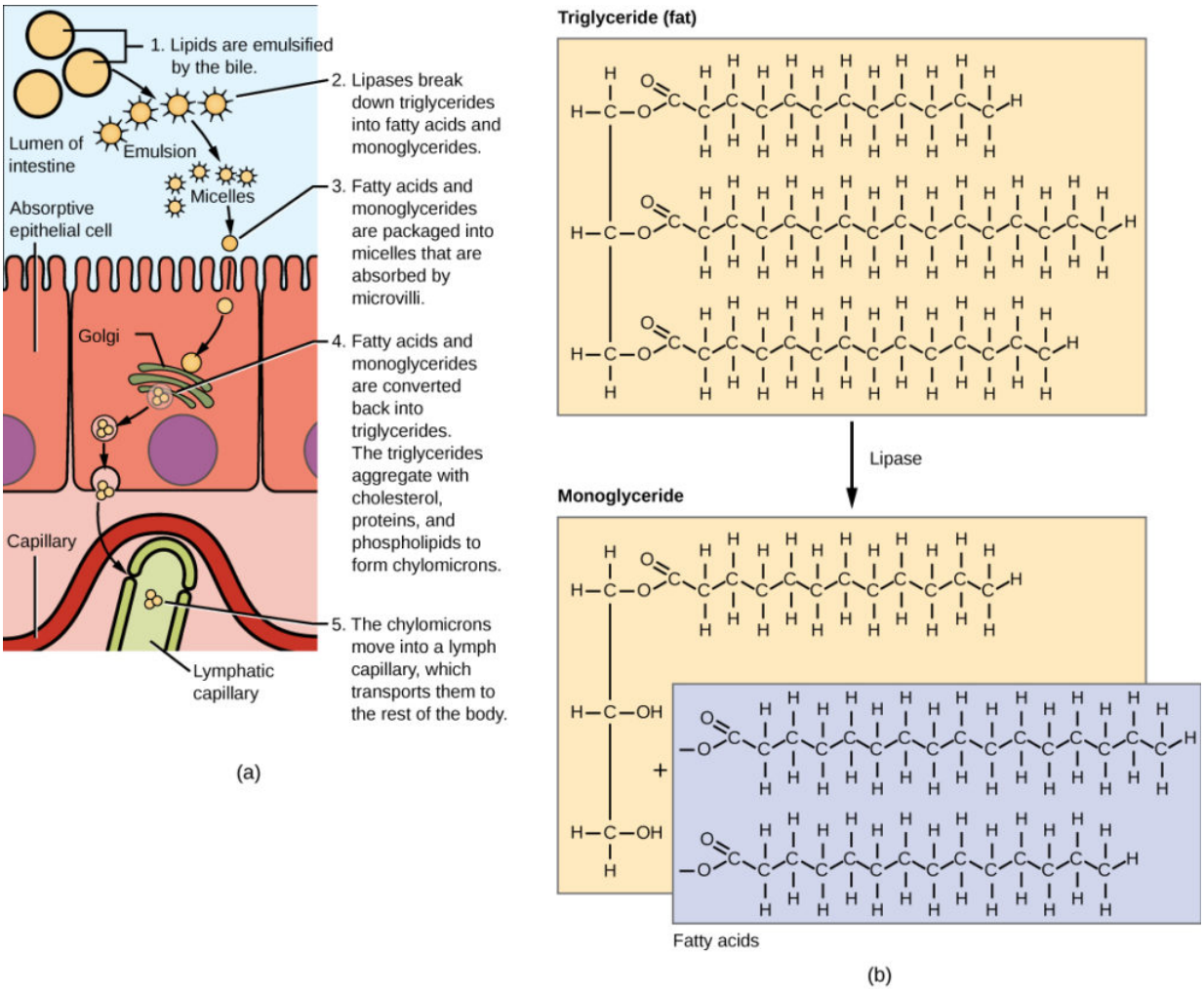


Figure 3. Lipids are digested and absorbed in the small intestine.

Vitamins

Vitamins can be either water-soluble or lipid-soluble. Fat soluble vitamins are absorbed in the same manner as lipids. It is important to consume some amount of dietary lipid to aid the absorption of lipid-soluble vitamins. Water-soluble vitamins can be directly absorbed into the bloodstream from the intestine.

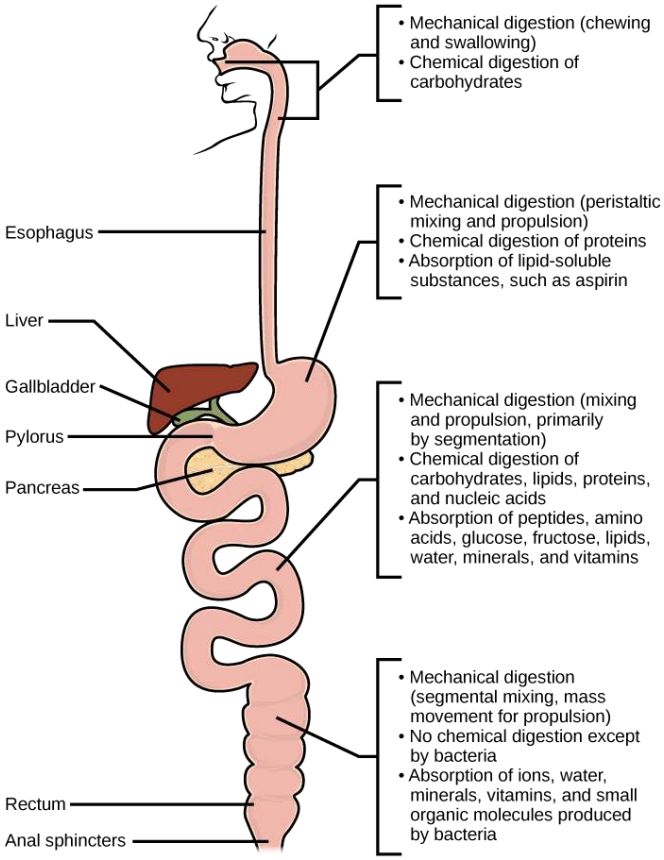


Figure 4. Mechanical and chemical digestion of food takes place in many steps, beginning in the mouth and ending in the rectum.

This website has an overview of the digestion of protein, fat, and carbohydrates.

? Practice Question

Which of the following statements about digestive processes is true?

a. Amylase, maltase, and lactase in the mouth digest carbohydrates.
b. Trypsin and lipase in the stomach digest protein.
c. Bile emulsifies lipids in the small intestine.
d. No food is absorbed until the small intestine.

[reveal-answer q="931879"]Show Answer[/reveal-answer]
[hidden-answer a="931879"]Statement c is true.[/hidden-answer]

Elimination

The final step in digestion is the elimination of undigested food content and waste products. The undigested food material enters the colon, where most of the water is reabsorbed. Recall that the colon is also home to the microflora called "intestinal flora" that aid in the digestion process. The semi-solid waste is moved through the colon by peristaltic movements of the muscle and is stored in the rectum. As the rectum expands in response to storage of fecal matter, it triggers the neural signals required to set up the urge to eliminate. The solid waste is eliminated through the anus using peristaltic movements of the rectum.

Common Problems with Elimination

Diarrhea and constipation are some of the most common health concerns that affect digestion. Constipation is a condition where the feces are hardened because of excess water removal in the colon. In contrast, if enough water is not removed from the feces, it results in diarrhea. Many bacteria, including the ones that cause cholera, affect the proteins involved in water reabsorption in the colon and result in excessive diarrhea.

Emesis

Emesis, or vomiting, is elimination of food by forceful expulsion through the mouth. It is often in response to an irritant that affects the digestive tract, including but not limited to viruses, bacteria, emotions, sights, and food poisoning. This forceful expulsion of the food is due to the strong contractions produced by the stomach muscles. The process of emesis is regulated by the medulla.

Learning Objectives

Digestion begins with ingestion, where the food is taken in the mouth. Digestion and absorption take place in a series of steps with special enzymes playing important roles in digesting carbohydrates, proteins, and lipids. Elimination describes removal of undigested food contents and waste products from the body. While most absorption occurs in the small intestines, the large intestine is responsible for the final removal of water that remains after the absorptive process of the small intestines. The cells that line the large intestine absorb some vitamins as well as any leftover salts and water. The large intestine (colon) is also where feces is formed.

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24.12: Neural Responses to Food



Figure 1. Seeing a plate of food triggers the secretion of saliva in the mouth and the production of HCL in the stomach. (credit: Kelly Bailey)

In reaction to the smell, sight, or thought of food, like that shown in Figure 1, the first hormonal response is that of salivation. The salivary glands secrete more saliva in response to the stimulus presented by food in preparation for digestion. Simultaneously, the stomach begins to produce hydrochloric acid to digest the food. Recall that the peristaltic movements of the esophagus and other organs of the digestive tract are under the control of the brain. The brain prepares these muscles for movement as well. When the stomach is full, the part of the brain that detects satiety signals fullness. There are three overlapping phases of gastric control—the cephalic phase, the gastric phase, and the intestinal phase—each requires many enzymes and is under neural control as well.

Digestive Phases

The response to food begins even before food enters the mouth. The first phase of ingestion, called the **cephalic phase**, is controlled by the neural response to the stimulus provided by food. All aspects—such as sight, sense, and smell—trigger the neural responses resulting in salivation and secretion of gastric juices. The gastric and salivary secretion in the cephalic phase can also take place due to the thought of food. Right now, if you think about a piece of chocolate or a crispy potato chip, the increase in salivation is a cephalic phase response to the thought. The central nervous system prepares the stomach to receive food.

The **gastric phase** begins once the food arrives in the stomach. It builds on the stimulation provided during the cephalic phase. Gastric acids and enzymes process the ingested materials. The gastric phase is stimulated by (1) distension of the stomach, (2) a decrease in the pH of the gastric contents, and (3) the presence of undigested material. This phase consists of local, hormonal, and neural responses. These responses stimulate secretions and powerful contractions.

The **intestinal phase** begins when chyme enters the small intestine triggering digestive secretions. This phase controls the rate of gastric emptying. In addition to gastrin emptying, when chyme enters the small intestine, it triggers other hormonal and neural events that coordinate the activities of the intestinal tract, pancreas, liver, and gallbladder.

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24.13: Hormonal Responses to Food

The **endocrine system** controls the response of the various glands in the body and the release of hormones at the appropriate times.

One of the important factors under hormonal control is the stomach acid environment. During the gastric phase, the hormone **gastrin** is secreted by G cells in the stomach in response to the presence of proteins. Gastrin stimulates the release of stomach acid, or hydrochloric acid (HCl) which aids in the digestion of the proteins. However, when the stomach is emptied, the acidic environment need not be maintained and a hormone called **somatostatin** stops the release of hydrochloric acid. This is controlled by a negative feedback mechanism.

In the duodenum, digestive secretions from the liver, pancreas, and gallbladder play an important role in digesting chyme during the intestinal phase. In order to neutralize the acidic chyme, a hormone called **secretin** stimulates the pancreas to produce alkaline bicarbonate solution and deliver it to the duodenum. Secretin acts in tandem with another hormone called **cholecystokinin** (CCK). Not only does CCK stimulate the pancreas to produce the requisite pancreatic juices, it also stimulates the gallbladder to release bile into the duodenum.

Visit this website to learn more about the endocrine system. Review the text and watch the animation of how control is implemented in the endocrine system.

Another level of hormonal control occurs in response to the composition of food. Foods high in lipids take a long time to digest. A hormone called **gastric inhibitory peptide** is secreted by the small intestine to slow down the peristaltic movements of the intestine to allow fatty foods more time to be digested and absorbed.

Understanding the hormonal control of the digestive system is an important area of ongoing research. Scientists are exploring the role of each hormone in the digestive process and developing ways to target these hormones. Advances could lead to knowledge that may help to battle the obesity epidemic.

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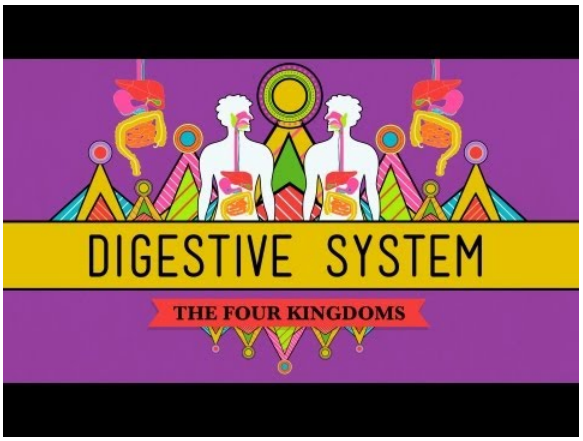
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24.14: Putting It Together- The Digestive System

Let's take a moment to quickly review the human digestive system. This video takes us through the bowels of the human digestive system and explains why it's all about surface area.



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/biom2/?p=1013

Disorders and Disease

Our digestive system is incredibly important: without it, we wouldn't be able to get the nutrients we need to survive. Unfortunately, there are a lot of ways things can go wrong, and doctors today are still learning more about why things go wrong when they do. Two of the most common stomach troubles are lactose intolerance and ulcers.

Lactose Intolerance

Lactose intolerance is a condition characterized by indigestion caused by dairy products. It occurs when the absorptive cells of the small intestine do not produce enough lactase, the enzyme that digests the milk sugar lactose. In most mammals, lactose intolerance increases with age. In contrast, some human populations, most notably Caucasians, are able to maintain the ability to produce lactase as adults.

In people with lactose intolerance, the lactose in chyme is not digested. Bacteria in the large intestine ferment the undigested lactose, a process that produces gas. In addition to gas, symptoms include abdominal cramps, bloating, and diarrhea. Symptom severity ranges from mild discomfort to severe pain; however, symptoms resolve once the lactose is eliminated in feces.

The hydrogen breath test is used to help diagnose lactose intolerance. Lactose-tolerant people have very little hydrogen in their breath. Those with lactose intolerance exhale hydrogen, which is one of the gases produced by the bacterial fermentation of lactose in the colon. After the hydrogen is absorbed from the intestine, it is transported through blood vessels into the lungs. There are a number of lactose-free dairy products available in grocery stores. In addition, dietary supplements are available. Taken with food, they provide lactase to help digest lactose.

Ulcers: When the Mucosal Barrier Breaks Down

As effective as the mucosal barrier is, it is not a "fail-safe" mechanism. Sometimes, gastric juice eats away at the superficial lining of the stomach mucosa, creating erosions, which mostly heal on their own. Deeper and larger erosions are called ulcers.

Why does the mucosal barrier break down? A number of factors can interfere with its ability to protect the stomach lining. The majority of all ulcers are caused by either excessive intake of non-steroidal anti-inflammatory drugs (NSAIDs), including aspirin, or *Helicobacter pylori* infection.

Antacids help relieve symptoms of ulcers such as "burning" pain and indigestion. When ulcers are caused by NSAID use, switching to other classes of pain relievers allows healing. When caused by *H. pylori* infection, antibiotics are effective.

A potential complication of ulcers is perforation: Perforated ulcers create a hole in the stomach wall, resulting in peritonitis (inflammation of the peritoneum). These ulcers must be repaired surgically.

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24.15: Cerego- The Digestive System

It is tempting to view different topics as completely separate, but in fact the ideas we cover in this course are often connected to one another. As you continue on, remember to come back and review the items you've learned in order to increase your depth of knowledge. The Cerego questions below are designed to help you remember the topics covered in this module. Using this practice set can help you do well both in this module and as you move through the course.

Click here to view the practice set for The Digestive System. You'll need to create a free log-in to practice these items, if you haven't already.

https://cerego.com/sets/796521/learn

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CHAPTER OVERVIEW

25: Module 22- The Excretory System

25.1: Why It Matters- The Excretory System
25.2: Introduction to Osmoregulation and Osmotic Balance

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25.1: Why It Matters- The Excretory System

Why describe the components and role of the excretory system?

The daily intake recommendation for human water consumption is eight to ten glasses of water. In order to achieve a healthy balance, the human body should excrete the eight to ten glasses of water every day. This occurs via the processes of urination, defecation, sweating and, to a small extent, respiration. The organs and tissues of the human body are soaked in fluids that are maintained at constant temperature, pH, and solute concentration, all crucial elements of homeostasis. The solutes in body fluids are mainly mineral salts and sugars, and osmotic regulation is the process by which the mineral salts and water are kept in balance. Osmotic homeostasis is maintained despite the influence of external factors like temperature, diet, and weather conditions.



Figure 1. Just as humans recycle what we can and dump the remains into landfills, our bodies use and recycle what they can and excrete the remaining waste products. Our bodies' complex systems have developed ways to treat waste and maintain a balanced internal environment. (credit: modification of work by Redwin Law)

Learning Outcomes

- Explain why osmoregulation and osmotic balance are important body functions
- Describe the structure of the kidneys and the functions of the parts of the kidney
- Explain how different excretion systems function
- Explain how hormonal cues help the kidneys synchronize the osmotic needs of the body

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25.2: Introduction to Osmoregulation and Osmotic Balance

Explain why osmoregulation and osmotic balance are important body functions

Osmoregulation and osmotic balance are important bodily functions, resulting in water and salt balance. This regulation equalizes the number of solute molecules across a semi-permeable membrane by the movement of water to the side of higher solute concentration.

What You'll Learn to Do

- Explain why osmoregulation and osmotic balance are important body functions
- Explain osmolarity and the way in which it is measured
- Describe osmoregulators or osmoconformers and how these tools allow animals to adapt to different environments
- Explain how hormonal cues help the kidneys synchronize the osmotic needs of the body

Learning Activities

The learning activities for this section include the following:

- Need for Osmoregulation
- Osmolality and Milliequivalent
- Osmoregulators and Osmoconformers
- Hormonal Cues
- Self Check: Osmoregulation and Osmotic Balance

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Index

Glossary

Sample Word 1 | Sample Definition 1

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- Biology for Majors II (Lumen) - *Undeclared*
  - Front Matter - *Undeclared*
    - TitlePage - *Undeclared*
    - InfoPage - *Undeclared*
    - Table of Contents - *Undeclared*
    - Licensing - *Undeclared*
  - 1: Course Contents - *Undeclared*
    - 1.1: About This Course - *Undeclared*
    - 1.2: Course Contents at a Glance - *Undeclared*
    - 1.3: Learning Outcomes - *Undeclared*
    - 1.4: Teaching this Course - *Undeclared*
  - 2: Faculty Resources - *Undeclared*
    - 2.1: Faculty Resource Overview - *Undeclared*
    - 2.2: Pacing - *Undeclared*
    - 2.3: PDF - *Undeclared*
    - 2.4: PowerPoints - *Undeclared*
    - 2.5: Assignments - *Undeclared*
    - 2.6: Question Banks - *Undeclared*
    - 2.7: I Need Help - *Undeclared*
  - 3: Resources- Course Assignments - *Undeclared*
    - 3.1: Assignment- Build a Cell - *Undeclared*
    - 3.2: Assignment- Nature's Recyclers - *Undeclared*
    - 3.3: Assignment- Hobby Horticulturalist - *Undeclared*
    - 3.4: Assignment- Morphological Phylogenetics - *Undeclared*
    - 3.5: Assignment- Public Relations- Invertebrates are Awesome! - *Undeclared*
    - 3.6: Assignment- Medical Experience - *Undeclared*
    - 3.7: Assignment- Synesthesia is an HR Issue? - *Undeclared*
    - 3.8: Assignment- Infertility- What's to Blame - *Undeclared*
    - 3.9: Assignment- High Altitude Athletic Training Advertisement - *Undeclared*
    - 3.10: Assignment- New AIDS Treatment Protocol - *Undeclared*
    - 3.11: Assignment- Celiac Disease vs IBS - *Undeclared*
    - 3.12: Assignment- Ecotourism - *Undeclared*
  - 4: Module 1- Introduction to Biology - *Undeclared*
    - 4.1: Why It Matters- Introduction to Biology - *Undeclared*
    - 4.2: Introduction to Characteristics of Life - *Undeclared*
    - 4.3: Properties of Life - *Undeclared*
    - 4.4: Levels of Organization of Living Things - *Undeclared*
    - 4.5: Introduction to Prokaryotes and Eukaryotes - *Undeclared*
    - 4.6: Comparing Prokaryotic and Eukaryotic Cells - *Undeclared*
    - 4.7: Introduction to Taxonomy - *Undeclared*
    - 4.8: The Diversity of Life - *Undeclared*
    - 4.9: Phylogenetic Trees - *Undeclared*
    - 4.10: Taxonomy - *Undeclared*
    - 4.11: Introduction to the Study of Biology - *Undeclared*
    - 4.12: The Branches of Biology - *Undeclared*
    - 4.13: Scientific Inquiry - *Undeclared*
    - 4.14: Experiments and Hypotheses - *Undeclared*
    - 4.15: Interpreting Results - *Undeclared*
    - 4.16: Putting It Together- Introduction to Biology - *Undeclared*
  - 5: Module 2- Viruses - *Undeclared*
    - 5.1: Why It Matters- Viruses - *Undeclared*
    - 5.2: Introduction to Viral Evolution, Morphology, and Classification - *Undeclared*
    - 5.3: History of Viruses - *Undeclared*
    - 5.4: Viral Morphology - *Undeclared*
    - 5.5: Virus Classification - *Undeclared*

- 5.6: Introduction to Virus Infections and Hosts - *Undeclared*
- 5.7: Steps of Virus Infections - *Undeclared*
- 5.8: Different Hosts and Their Viruses - *Undeclared*
- 5.9: Introduction to Prevention and Treatment of Viral Infections - *Undeclared*
- 5.10: Vaccines for Prevention - *Undeclared*
- 5.11: Vaccines and Anti-Viral Drugs for Treatment - *Undeclared*
- 5.12: Introduction to Prions and Viroids - *Undeclared*
- 5.13: Prions and Viroids - *Undeclared*
- 5.14: Putting It Together- Viruses - *Undeclared*
- 5.15: Cerego- Viruses - *Undeclared*

6: Module 3- History of Life - *Undeclared*

- 6.1: Why It Matters- History of Life - *Undeclared*
- 6.2: Introduction to Evolution - *Undeclared*
- 6.3: Natural Selection - *Undeclared*
- 6.4: Theory of Evolution - *Undeclared*
- 6.5: Evidence of Evolution - *Undeclared*
- 6.6: Misconceptions of Evolution - *Undeclared*
- 6.7: Introduction to Speciation - *Undeclared*
- 6.8: What is a Species? - *Undeclared*
- 6.9: Types of Speciation - *Undeclared*
- 6.10: Reconnection - *Undeclared*
- 6.11: Rates of Speciation - *Undeclared*
- 6.12: Introduction to the Evolution of Populations - *Undeclared*
- 6.13: Population Genetics - *Undeclared*
- 6.14: Hardy-Weinberg Principle of Equilibrium - *Undeclared*
- 6.15: Genetic Variation and Drift - *Undeclared*
- 6.16: Adaptive Evolution - *Undeclared*
- 6.17: Introduction to Phylogenies and the History of Life - *Undeclared*
- 6.18: Phylogenetic Trees - *Undeclared*
- 6.19: Taxonomy - *Undeclared*
- 6.20: Homologous and Analogous Traits - *Undeclared*
- 6.21: Cladistics - *Undeclared*
- 6.22: Perspectives on the Phylogenetic Tree - *Undeclared*
- 6.23: Putting It Together- History of Life - *Undeclared*
- 6.24: Cerego- History of Life - *Undeclared*

7: Module 4- Prokaryotes - *Undeclared*

- 7.1: Why It Matters- Prokaryotes - *Undeclared*
- 7.2: Introduction to Prokaryotic Diversity - *Undeclared*
- 7.3: Evolutionary History of Prokaryotes - *Undeclared*
- 7.4: Life in Moderate and Extreme Environments - *Undeclared*
- 7.5: Culturing Prokaryotes - *Undeclared*
- 7.6: Prokaryotic Biofilms - *Undeclared*
- 7.7: Introduction to the Structure of Prokaryotes - *Undeclared*
- 7.8: The Prokaryotic Cell - *Undeclared*
- 7.9: Archaea vs. Bacteria - *Undeclared*
- 7.10: Introduction to Prokaryotic Metabolism - *Undeclared*
- 7.11: Needs of Prokaryotes - *Undeclared*
- 7.12: How Prokaryotes Get Energy - *Undeclared*
- 7.13: Role of Prokaryotes in Ecosystems - *Undeclared*
- 7.14: Introduction to Bacterial Diseases in Humans - *Undeclared*
- 7.15: Long History of Bacterial Disease - *Undeclared*
- 7.16: Biofilms and Foodborne Diseases - *Undeclared*
- 7.17: Antibiotic Resistance - *Undeclared*
- 7.18: Introduction to Beneficial Prokaryotes - *Undeclared*
- 7.19: Nitrogen Fixation - *Undeclared*
- 7.20: Food from Bacteria - *Undeclared*
- 7.21: Bioremediation - *Undeclared*
- 7.22: Microbes and the Human Body - *Undeclared*
- 7.23: Putting It Together- Prokaryotes - *Undeclared*
- 7.24: Cerego- Prokaryotes - *Undeclared*

8: Module 5- Protists - *Undeclared*

- 8.1: Why It Matters- Protists - *Undeclared*
- 8.2: Introduction to the Characteristics of Protists - *Undeclared*
- 8.3: Cell Structure and Motility - *Undeclared*
- 8.4: Metabolism - *Undeclared*
- 8.5: Life Cycles and Habitats - *Undeclared*
- 8.6: Introduction to Groups of Protists - *Undeclared*
- 8.7: Excavata - *Undeclared*
- 8.8: Chromalveolata - *Undeclared*
- 8.9: Rhizaria - *Undeclared*
- 8.10: Archaeplastida - *Undeclared*
- 8.11: Amoebozoa - *Undeclared*
- 8.12: Opisthokonta - *Undeclared*
- 8.13: Introduction to the Ecology of Protists - *Undeclared*
- 8.14: Primary Producers - *Undeclared*
- 8.15: Protists as Decomposers - *Undeclared*
- 8.16: Pathogenic Protists - *Undeclared*
- 8.17: Putting It Together- Protists - *Undeclared*

- 8.18: Cerego- Protists - *Undeclared*

- 9: Module 6- Fungi - *Undeclared*
  - 9.1: Why It Matters- Fungi - *Undeclared*
  - 9.2: Introduction to the Characteristics of Fungi - *Undeclared*
  - 9.3: Fungal Structure and Habitats - *Undeclared*
  - 9.4: Nutrition and Growth - *Undeclared*
  - 9.5: Reproduction - *Undeclared*
  - 9.6: Introduction to the Classifications of Fungi - *Undeclared*
  - 9.7: Chytridiomycota- The Chytrids - *Undeclared*
  - 9.8: Zygomycota- The Conjugated Fungi - *Undeclared*
  - 9.9: Ascomycota- The Sac Fungi - *Undeclared*
  - 9.10: Basidiomycota- The Club Fungi - *Undeclared*
  - 9.11: Glomeromycota - *Undeclared*
  - 9.12: Deuteromycota- The Imperfect Fungi - *Undeclared*
  - 9.13: Introduction to the Ecology of Fungi - *Undeclared*
  - 9.14: Decomposers and Recyclers - *Undeclared*
  - 9.15: Mutualistic Relationships - *Undeclared*
  - 9.16: Introduction to Fungal Parasites and Pathogens - *Undeclared*
  - 9.17: Infections in Plants - *Undeclared*
  - 9.18: Infections in Humans - *Undeclared*
  - 9.19: Antifungal Therapy - *Undeclared*
  - 9.20: Putting It Together- Fungi - *Undeclared*
  - 9.21: Cerego- Fungi - *Undeclared*
- 10: Module 7- Plant Diversity - *Undeclared*
  - 10.1: Why It Matters- Plant Diversity - *Undeclared*
  - 10.2: Introduction to Seedless Plants - *Undeclared*
  - 10.3: Early Plant Life - *Undeclared*
  - 10.4: Green Algae- Precursors of Land Plants - *Undeclared*
  - 10.5: Bryophytes - *Undeclared*
  - 10.6: Seedless Vascular Plants - *Undeclared*
  - 10.7: Introduction to Seed Plants - *Undeclared*
  - 10.8: Evolution of Seed Plants - *Undeclared*
  - 10.9: Gymnosperms - *Undeclared*
  - 10.10: Angiosperms - *Undeclared*
  - 10.11: The Role of Seed Plants - *Undeclared*
  - 10.12: Putting It Together- Plant Diversity - *Undeclared*
  - 10.13: Cerego- Plant Diversity - *Undeclared*
- 11: Module 8- Plant Structure and Function - *Undeclared*
  - 11.1: Why It Matters- Plant Structure and Function - *Undeclared*
  - 11.2: Introduction to Plant Structures - *Undeclared*
  - 11.3: Plant Cells - *Undeclared*
  - 11.4: Plant Tissues and Organs - *Undeclared*
  - 11.5: Stems - *Undeclared*
  - 11.6: Leaves - *Undeclared*
  - 11.7: Roots - *Undeclared*
  - 11.8: Introduction to Transport of Water and Solutes in Plants - *Undeclared*
  - 11.9: Water Potential - *Undeclared*
  - 11.10: Transpiration - *Undeclared*
  - 11.11: Photosynthates - *Undeclared*
  - 11.12: Introduction to Plant Sensory Systems and Responses - *Undeclared*
  - 11.13: Plant Responses to Light - *Undeclared*
  - 11.14: Plant Responses to Gravity - *Undeclared*
  - 11.15: Plant Responses to Wind and Touch - *Undeclared*
  - 11.16: Defense Responses against Herbivores and Pathogens - *Undeclared*
  - 11.17: Introduction to Plant Growth - *Undeclared*
  - 11.18: How Plants Grow - *Undeclared*
  - 11.19: Stem Growth - *Undeclared*
  - 11.20: Growth Responses - *Undeclared*
  - 11.21: Introduction to Plant Nutrition - *Undeclared*
  - 11.22: Nutritional Requirements - *Undeclared*
  - 11.23: Autotrophic Plants - *Undeclared*
  - 11.24: Heterotrophic Plants - *Undeclared*
  - 11.25: Putting It Together- Plant Structure and Function - *Undeclared*
  - 11.26: Cerego- Plant Structure and Function - *Undeclared*
- 12: Module 9- Plant Reproduction - *Undeclared*
  - 12.1: Why It Matters- Plant Reproduction - *Undeclared*
  - 12.2: Introduction to Reproductive Development and Structure - *Undeclared*
  - 12.3: Stages of a Plant's Life Cycle - *Undeclared*
  - 12.4: Flower Structure - *Undeclared*
  - 12.5: Sexual Reproduction in Angiosperms - *Undeclared*
  - 12.6: Sexual Reproduction in Gymnosperms - *Undeclared*
  - 12.7: Angiosperms versus Gymnosperms - *Undeclared*
  - 12.8: Introduction to Asexual Reproduction in Plants - *Undeclared*
  - 12.9: Asexual Plants - *Undeclared*
  - 12.10: Natural and Artificial Asexual Reproduction - *Undeclared*
  - 12.11: Plant Life Spans - *Undeclared*

- 12.12: Introduction to Sexual Reproduction in Plants - *Undeclared*
- 12.13: Self-Pollination and Cross-Pollination - *Undeclared*
- 12.14: Methods of Pollination - *Undeclared*
- 12.15: Double Fertilization - *Undeclared*
- 12.16: Development Seeds and Fruit - *Undeclared*
- 12.17: Fruit and Seed Dispersal - *Undeclared*
- 12.18: Putting It Together- Plant Reproduction - *Undeclared*
- 12.19: Cerego- Plant Reproduction - *Undeclared*

13: Module 10- Animal Diversity - *Undeclared*

- 13.1: Why It Matters- Animal Diversity - *Undeclared*
- 13.2: Introduction to the Evolutionary History of the Animal Kingdom - *Undeclared*
- 13.3: Pre-Cambrian Animal Life - *Undeclared*
- 13.4: The Cambrian Explosion - *Undeclared*
- 13.5: Post-Cambrian Evolution - *Undeclared*
- 13.6: Introduction to Animal Phylogeny - *Undeclared*
- 13.7: Classifying Animals - *Undeclared*
- 13.8: Constructing an Animal Phylogenetic Tree - *Undeclared*
- 13.9: Modern Revisions of Phylogeny - *Undeclared*
- 13.10: Introduction to Animal Form and Function - *Undeclared*
- 13.11: Body Plans - *Undeclared*
- 13.12: Limits on Animal Size and Shape - *Undeclared*
- 13.13: Animal Bioenergetics - *Undeclared*
- 13.14: Introduction to Animal Primary Tissues - *Undeclared*
- 13.15: Complex Tissue Structure - *Undeclared*
- 13.16: Epithelial Tissues - *Undeclared*
- 13.17: Connective Tissues - *Undeclared*
- 13.18: Muscle and Nervous Tissues - *Undeclared*
- 13.19: Introduction to Animal Reproduction - *Undeclared*
- 13.20: Processes of Animal Reproduction and Development - *Undeclared*
- 13.21: Embryological Development - *Undeclared*
- 13.22: Hox Genes - *Undeclared*
- 13.23: Introduction to Homeostasis - *Undeclared*
- 13.24: What is Homeostasis? - *Undeclared*
- 13.25: Control of Homeostasis - *Undeclared*
- 13.26: Thermoregulation - *Undeclared*
- 13.27: Putting It Together- Animal Diversity - *Undeclared*
- 13.28: Cerego- Animal Diversity - *Undeclared*

14: Module 11- Invertebrates - *Undeclared*

- 14.1: Why It Matters- Invertebrates - *Undeclared*
- 14.2: Introduction to Phylum Porifera - *Undeclared*
- 14.3: Morphology of Sponges - *Undeclared*
- 14.4: Physiological Processes in Sponges - *Undeclared*
- 14.5: Introduction to Phylum Cnidaria - *Undeclared*
- 14.6: Characteristics of Phylum Cnidaria - *Undeclared*
- 14.7: Classes in the Phylum Cnidaria - *Undeclared*
- 14.8: Introduction to Superphylum Lophotrochozoa - *Undeclared*
- 14.9: Characteristics of Superphylum Lophotrochozoa - *Undeclared*
- 14.10: Phylum Platyhelminthes - *Undeclared*
- 14.11: Phylum Rotifera - *Undeclared*
- 14.12: Phylum Nemertea - *Undeclared*
- 14.13: Phylum Mollusca - *Undeclared*
- 14.14: Phylum Annelida - *Undeclared*
- 14.15: Introduction to Superphylum Ecdysozoa - *Undeclared*
- 14.16: Phylum Nematoda - *Undeclared*
- 14.17: Nematodes in Research - *Undeclared*
- 14.18: Phylum Arthropoda - *Undeclared*
- 14.19: Subphylums of Arthropoda - *Undeclared*
- 14.20: Introduction to Superphylum Deuterostomia - *Undeclared*
- 14.21: Characteristics of Superphylum Deuterostomia - *Undeclared*
- 14.22: Phylum Echinodermata - *Undeclared*
- 14.23: Putting It Together- Invertebrates - *Undeclared*
- 14.24: Cerego- Invertebrates - *Undeclared*

15: Module 12- Vertebrates - *Undeclared*

- 15.1: Why It Matters- Vertebrates - *Undeclared*
- 15.2: Introduction to Chordates - *Undeclared*
- 15.3: Characteristics of Chordates - *Undeclared*
- 15.4: Invertebrate Chordates - *Undeclared*
- 15.5: Craniates - *Undeclared*
- 15.6: Introduction to Fishes - *Undeclared*
- 15.7: Jawless Fishes - *Undeclared*
- 15.8: Jawed Fishes - *Undeclared*
- 15.9: Introduction to Amphibians - *Undeclared*
- 15.10: Amphibians - *Undeclared*
- 15.11: The Life Cycle of Amphibians - *Undeclared*
- 15.12: Clades of Amphibians - *Undeclared*
- 15.13: Introduction to Amniotes - *Undeclared*
- 15.14: Amniotic Animals - *Undeclared*
- 15.15: Evolution of Amniotes - *Undeclared*
- 15.16: Introduction to Reptiles - *Undeclared*
- 15.17: Characteristics of Reptiles - *Undeclared*

- 15.18: Classes of Reptiles - *Undeclared*
- 15.19: Evolutionary History of Reptiles - *Undeclared*
- 15.20: Introduction to Birds - *Undeclared*
- 15.21: Characteristics of Birds - *Undeclared*
- 15.22: Evolutionary History of Birds - *Undeclared*
- 15.23: Introduction to Mammals - *Undeclared*
- 15.24: Mammals - *Undeclared*
- 15.25: Primates - *Undeclared*
- 15.26: Evolution of Humans - *Undeclared*
- 15.27: Putting It Together- Vertebrates - *Undeclared*
- 15.28: Cerego- Vertebrates - *Undeclared*

16: Module 13- Overview of Body Systems - *Undeclared*

- 16.1: Why It Matters- Overview of Body Systems - *Undeclared*
- 16.2: Introduction to Integration of Systems - *Undeclared*
- 16.3: How Bodies Work - *Undeclared*
- 16.4: Maintaining Homeostasis - *Undeclared*
- 16.5: Blood Calcium and Glucose Levels - *Undeclared*
- 16.6: Introduction to Control Systems - *Undeclared*
- 16.7: Nervous System - *Undeclared*
- 16.8: Endocrine System - *Undeclared*
- 16.9: Reproductive System - *Undeclared*
- 16.10: Sensory Systems - *Undeclared*
- 16.11: Introduction to Cell Maintenance Systems - *Undeclared*
- 16.12: Circulatory System - *Undeclared*
- 16.13: Respiratory System - *Undeclared*
- 16.14: Immune System - *Undeclared*
- 16.15: Digestive System - *Undeclared*
- 16.16: Introduction to Support Systems - *Undeclared*
- 16.17: The Muscular System - *Undeclared*
- 16.18: The Skeletal System - *Undeclared*
- 16.19: Integumentary System - *Undeclared*
- 16.20: Putting It Together- Overview of Body Systems - *Undeclared*
- 16.21: Cerego- Overview of Body Systems - *Undeclared*

17: Module 14- The Nervous System - *Undeclared*

- 17.1: Why It Matters- The Nervous System - *Undeclared*
- 17.2: Introduction to Components of the Nervous System - *Undeclared*
- 17.3: Diversity of Nervous Systems - *Undeclared*
- 17.4: The Central and Peripheral Nervous Systems - *Undeclared*
- 17.5: Neurons - *Undeclared*
- 17.6: Neurogenesis - *Undeclared*
- 17.7: Glial Cells - *Undeclared*
- 17.8: Introduction to Neuron Communication - *Undeclared*
- 17.9: Resting Membrane Potential - *Undeclared*
- 17.10: Action Potential - *Undeclared*
- 17.11: Chemical and Electrical Synapses - *Undeclared*
- 17.12: Signal Summation - *Undeclared*
- 17.13: Synaptic Plasticity - *Undeclared*
- 17.14: Introduction to the Central Nervous System - *Undeclared*
- 17.15: Components of the Central Nervous System - *Undeclared*
- 17.16: Brain - *Undeclared*
- 17.17: Spinal Cord - *Undeclared*
- 17.18: Introduction to the Peripheral Nervous System - *Undeclared*
- 17.19: Autonomic Nervous System - *Undeclared*
- 17.20: Sensory-Somatic Nervous System - *Undeclared*
- 17.21: Introduction to Nervous System Disorders - *Undeclared*
- 17.22: Neurodegenerative Disorders - *Undeclared*
- 17.23: Neurodevelopmental Disorders - *Undeclared*
- 17.24: Mental Illnesses - *Undeclared*
- 17.25: Other Neurological Disorders - *Undeclared*
- 17.26: Putting It Together- The Nervous System - *Undeclared*
- 17.27: Cerego- The Nervous System - *Undeclared*

18: Module 15- The Endocrine System - *Undeclared*

- 18.1: Why It Matters- The Endocrine System - *Undeclared*
- 18.2: Introduction to Types of Hormones - *Undeclared*
- 18.3: Lipid-Derived Hormones - *Undeclared*
- 18.4: Amino Acid-Derived Hormones - *Undeclared*
- 18.5: Peptide Hormones - *Undeclared*
- 18.6: Hormone Regulation - *Undeclared*
- 18.7: Introduction to How Hormones Work - *Undeclared*
- 18.8: Hormones - *Undeclared*
- 18.9: Intracellular Hormone Receptors - *Undeclared*
- 18.10: Plasma Membrane Hormone Receptors - *Undeclared*
- 18.11: Introduction to Regulation of Body Processes - *Undeclared*
- 18.12: Hormonal Regulation of the Excretory System - *Undeclared*

- 18.13: Hormonal Regulation of the Reproductive System - *Undeclared*
- 18.14: Hormonal Regulation of Metabolism - *Undeclared*
- 18.15: Blood Calcium Levels and Growth - *Undeclared*
- 18.16: Hormonal Regulation of Stress - *Undeclared*
- 18.17: Introduction to Endocrine Glands - *Undeclared*
- 18.18: Hypothalamic-Pituitary Axis - *Undeclared*
- 18.19: Thyroids - *Undeclared*
- 18.20: Adrenal Glands - *Undeclared*
- 18.21: The Pancreas, Pineal Gland, and Gonads - *Undeclared*
- 18.22: Organs with Secondary Endocrine Functions - *Undeclared*
- 18.23: Putting It Together- The Endocrine System - *Undeclared*
- 18.24: Cerego- The Endocrine System - *Undeclared*

o 19: Module 16- The Reproductive System - *Undeclared*

- 19.1: Why It Matters- The Reproductive System - *Undeclared*
- 19.2: Introduction to Reproduction Methods - *Undeclared*
- 19.3: Asexual Reproduction - *Undeclared*
- 19.4: Sexual Reproduction - *Undeclared*
- 19.5: Introduction to Human Reproductive Anatomy - *Undeclared*
- 19.6: Male Reproductive Anatomy - *Undeclared*
- 19.7: Female Reproductive Anatomy - *Undeclared*
- 19.8: Sexual Response - *Undeclared*
- 19.9: Gametogenesis - *Undeclared*
- 19.10: Introduction to Hormonal Control of Human Reproduction - *Undeclared*
- 19.11: Reproductive Hormones - *Undeclared*
- 19.12: The Ovarian Cycle, the Menstrual Cycle, and Menopause - *Undeclared*
- 19.13: Introduction to Fertilization - *Undeclared*
- 19.14: Fertilization - *Undeclared*
- 19.15: External and Internal Fertilization - *Undeclared*
- 19.16: The Evolution of Reproduction - *Undeclared*
- 19.17: Introduction to Early Embryonic Development - *Undeclared*
- 19.18: Cleavage and Blastula Stage - *Undeclared*
- 19.19: Gastrulation - *Undeclared*
- 19.20: Organogenesis - *Undeclared*
- 19.21: Vertebrate Axis Formation - *Undeclared*
- 19.22: Introduction to Human Pregnancy and Birth - *Undeclared*
- 19.23: Human Gestation - *Undeclared*
- 19.24: Labor and Birth - *Undeclared*
- 19.25: Contraception and Birth Control - *Undeclared*
- 19.26: Infertility - *Undeclared*
- 19.27: Putting It Together- The Reproductive System - *Undeclared*
- 19.28: Cerego- The Reproductive System - *Undeclared*

o 20: Module 17- Sensory Systems - *Undeclared*

- 20.1: Why It Matters- The Sensory Systems - *Undeclared*
- 20.2: Introduction to the Senses - *Undeclared*
- 20.3: Human Senses - *Undeclared*
- 20.4: Sensation - *Undeclared*
- 20.5: Just-Noticeable Difference - *Undeclared*
- 20.6: Introduction to Somatosensation - *Undeclared*
- 20.7: Somatosensory Receptors - *Undeclared*
- 20.8: Thermoreception and Pain - *Undeclared*
- 20.9: Introduction to Taste and Smell - *Undeclared*
- 20.10: Tastes and Odors - *Undeclared*
- 20.11: Tastes - *Undeclared*
- 20.12: Smell and Taste in the Brain - *Undeclared*
- 20.13: Introduction to Hearing and Vestibular Sensation - *Undeclared*
- 20.14: Sound and Reception - *Undeclared*
- 20.15: Transduction of Sound - *Undeclared*
- 20.16: Vestibular Information - *Undeclared*
- 20.17: Introduction to Vision - *Undeclared*
- 20.18: Light - *Undeclared*
- 20.19: Anatomy of the Eye - *Undeclared*
- 20.20: Transduction of Light - *Undeclared*
- 20.21: Vision in the Brain - *Undeclared*
- 20.22: Putting It Together- The Sensory System - *Undeclared*
- 20.23: Cerego- Sensory Systems - *Undeclared*

o 21: Module 18- The Circulatory System - *Undeclared*

- 21.1: Why It Matters- The Circulatory System - *Undeclared*
- 21.2: Introduction to the Circulatory System - *Undeclared*
- 21.3: Circulatory System Architecture - *Undeclared*
- 21.4: Circulatory System Variation in Animals - *Undeclared*
- 21.5: Introduction to Structure and Function of Blood - *Undeclared*
- 21.6: The Role of Blood in the Body - *Undeclared*
- 21.7: Blood Cells - *Undeclared*

- 21.8: Components of Blood - *Undeclared*
- 21.9: Introduction to the Mammalian Heart - *Undeclared*
- 21.10: Structure of the Heart - *Undeclared*
- 21.11: The Cardiac Cycle - *Undeclared*
- 21.12: Introduction to Blood Flow and Blood Pressure Regulation - *Undeclared*
- 21.13: Blood Vessels - *Undeclared*
- 21.14: Blood Circulation - *Undeclared*
- 21.15: Blood Pressure - *Undeclared*
- 21.16: Putting It Together- The Circulatory System - *Undeclared*
- 21.17: Cerego- The Circulatory System - *Undeclared*

22: Module 19- The Respiratory System - *Undeclared*

- 22.1: Why It Matters- The Respiratory System - *Undeclared*
- 22.2: Introduction to Systems of Gas Exchange - *Undeclared*
- 22.3: Different Types of Respiratory Systems - *Undeclared*
- 22.4: Mammalian Systems - *Undeclared*
- 22.5: Protective Mechanisms - *Undeclared*
- 22.6: Introduction to Gas Exchange across Respiratory Surfaces - *Undeclared*
- 22.7: Breathing Capacity - *Undeclared*
- 22.8: Gas Pressure and Respiration - *Undeclared*
- 22.9: Gas Exchange across the Alveoli - *Undeclared*
- 22.10: Introduction to Breathing - *Undeclared*
- 22.11: Types of Breathing - *Undeclared*
- 22.12: The Mechanics of Human Breathing - *Undeclared*
- 22.13: The Work of Breathing - *Undeclared*
- 22.14: Dead Space - *Undeclared*
- 22.15: Introduction to Transport of Gases in Human Bodily Fluids - *Undeclared*
- 22.16: Transport of Oxygen in the Blood - *Undeclared*
- 22.17: Transport of Carbon Dioxide in the Blood - *Undeclared*
- 22.18: Putting It Together- The Respiratory System - *Undeclared*
- 22.19: Cerego- The Respiratory System - *Undeclared*

23: Module 20- The Immune System - *Undeclared*

- 23.1: Why It Matters- The Immune System - *Undeclared*
- 23.2: Introduction to the Innate Immune Response - *Undeclared*
- 23.3: Physical and Chemical Barriers - *Undeclared*
- 23.4: Pathogen Recognition - *Undeclared*
- 23.5: Natural Killer Cells - *Undeclared*
- 23.6: Complement System - *Undeclared*
- 23.7: Introduction to the Adaptive Immune Response - *Undeclared*
- 23.8: Antigen-Presenting Cells - *Undeclared*
- 23.9: T and B Lymphocytes - *Undeclared*
- 23.10: Mucosal Surfaces and Immune Tolerance - *Undeclared*
- 23.11: Immunological Memory - *Undeclared*
- 23.12: Primary Centers of the Immune System - *Undeclared*
- 23.13: Introduction to Antibodies - *Undeclared*
- 23.14: Antibody Structure - *Undeclared*
- 23.15: Antibody Classes - *Undeclared*
- 23.16: Antibody Functions - *Undeclared*
- 23.17: Disruptions in the Immune System - *CC BY 4.0*
- 23.18: Putting It Together- The Immune System - *Undeclared*
- 23.19: Cerego- The Immune System - *Undeclared*

24: Module 21- The Digestive System - *Undeclared*

- 24.1: Why It Matters- The Digestive System - *Undeclared*
- 24.2: Introduction to Digestive Systems - *Undeclared*
- 24.3: Herbivores, Carnivores, and Omnivores - *Undeclared*
- 24.4: Invertebrates and Vertebrate Digestive Systems - *Undeclared*
- 24.5: Parts of the Digestive System - *Undeclared*
- 24.6: Introduction to Nutrition and Energy Production - *Undeclared*
- 24.7: Food Requirements - *Undeclared*
- 24.8: Essential Nutrients - *Undeclared*
- 24.9: Food Energy and ATP - *Undeclared*
- 24.10: Introduction to Digestive System Processes and Regulation - *Undeclared*
- 24.11: Digestive System Processes - *Undeclared*
- 24.12: Neural Responses to Food - *Undeclared*
- 24.13: Hormonal Responses to Food - *Undeclared*
- 24.14: Putting It Together- The Digestive System - *Undeclared*
- 24.15: Cerego- The Digestive System - *Undeclared*

25: Module 22- The Excretory System - *Undeclared*

- 25.1: Why It Matters- The Excretory System - *Undeclared*
- 25.2: Introduction to Osmoregulation and Osmotic Balance - *Undeclared*

Back Matter - *Undeclared*

- Index - *Undeclared*

- Glossary - *Undeclared*
- Detailed Licensing - *Undeclared*