BIOLOGY FOR NON MAJORS II (LUMEN)



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Book- Biology for Non Majors II (Lumen)

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Licensing

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1.1: About This Course

Biology for Non-Majors II introduces students to the basics of the scientific process and covers some of biology's most compelling topics surrounding the history and diversity of life, including discussion on the different kingdoms of life, with focus on plants and animals, as well as an introduction to ecology. Designed for non-life science majors, this course is the second in a two-part series that completes a survey of biological principles.

This course was developed by Lumen Learning, with contributing work from Shelli Carter and Steven Mezik. Primary sources for course materials include 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.

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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: Biology

- Characteristics of Life
- The Study of Biology
- The Branches of Biology
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Module 2: History of Life

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

Module 3: Prokaryotes

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- Biotic and Abiotic Factors
- Biomes
- Population Ecology
- Community Ecology

Module 15: 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 Non-Majors II are aligned to the following learning outcomes. A full list of course learning outcomes can be viewed here: Biology for Non-Majors II Learning Outcomes.

Module 1: Define biology and apply its principles

Introduction to Biology

- List the defining characteristics of biological life
- Discuss the history of the study of life and the diversity of life on Earth
- Identify the main branches of biology
- Describe biology as a science and identify the key components of scientific inquiry

Module 2: Discuss the history of life on Earth

History of Life

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

Prokaryotes

- 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 4: Discuss the organisms in Kingdom Protista

Protists

- Identify the common characteristics of protists
- Describe the role that protists play in the ecosystem

Module 5: Discuss the organisms in Kingdom Fungi

Fungi

- Identify the common characteristics of fungi
- Describe the role that fungi play in the ecosystem
- Identify common fungal parasites and pathogens
- Discuss common human usage of fungi

Module 6: Differentiate between different types of plants

Plant Diversity

- Classify seedless plants
- Classify seed plants

Module 7: Discuss the structure and function of plants

Plant Structure and Function

- Identify basic common structures of plants
- Discuss common functions of plants

Module 8: Discuss the methods and structures of plant reproduction

Plant Reproduction

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

Module 9: Discuss the importance of animal diversity

Animal Diversity

- Discuss the evolutionary history of the animal kingdom
- Chart animal phylogeny

Module 10: Discuss the common features of organism in the animal kingdom

Features of the Animal Kingdom

- 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: Classify different types of invertebrates

Invertebrates

- Identify the common characteristics of phylum Porifera Phylum
- 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: Classify different types of vertebrates

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: Describe different body systems

Overview of 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: Define the scope and components of ecology

Ecology of Living Things

- 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 15: Discuss ecology as it relates to the environment

Ecology and 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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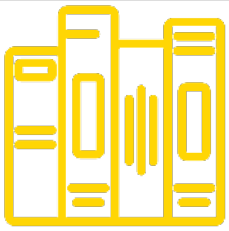
CHAPTER OVERVIEW

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2.1: Faculty Resources 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.

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2.2: Pacing



The Biology for Non-Majors II textbook contains fifteen modules—roughly one module per week for a 16-week semester. If you need to modify the pace and cover the material more quickly, the following modules work well together:

- **Module 6: Plant Diversity** and **Module 7: Plant Structure and Function**
- **Module 7: Plant Structure and Function** and **Module 8: Plant Reproduction**
- **Module 9: Animal Diversity** and **Module 10: Features of the Animal Kingdom**

We recommend NOT doubling up **Module 11: Invertebrates** or **Module 12: Vertebrates**, as they are long and especially challenging. Students will need more time for mastery and completion of assignments. In a longer semester, **Module 12: Vertebrates** can be taught over two weeks instead of one.

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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:

Download the course PDF (116.2 MB)

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2.4: PowerPoints

A full set of PowerPoint decks is provided for download below. All decks are tightly aligned to the modules in this course. Since they are openly licensed, you are welcome to retain, reuse, revise, remix, and redistribute as desired.

These PowerPoint files are 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 (110.8 MB), or download each individual deck below:

- Module 1: Introduction to Biology
- Module 2: History of Life
- Module 3: Prokaryotes
- Module 4: Protists
- Module 5: Fungi
- Module 6: Plant Diversity
- Module 7: Plant Structure and Function
- Module 8: Plant Reproduction
- Module 9: Animal Diversity
- Module 10: Features of the Animal Kingdom
- Module 11: Invertebrates
- Module 12: Vertebrates
- Module 13: Overview of Body Systems
- Module 14: Ecology of Living Things
- Module 15: 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. Grading guides are available to faculty who adopt Waymaker, OHM, or Candela courses with paid support from Lumen Learning. This approach helps us protect the academic integrity of these materials by ensuring they are shared only with authorized and institution-affiliated faculty and staff.

If you import this course into your learning management (Blackboard, Canvas, etc.), the assignments will automatically be loaded into the assignment tool. You can download print files of each assignment.

The assignments in this course cover content taught multiple modules. The alignment of each assignment can be seen below.

Assignment Files and Alignment		
Assignment	Student File	Covered Modules
Build a Cell	.docx, .rtf	Module 1: Introduction to Biology and Module 3: Prokaryotes
Nature's Recyclers	.docx, .rtf	Module 4: Protists, Module 5: Fungi, and Module 15: Ecology and the Environment
Hobby Horticulturalist	.docx, .rtf	Module 6: Plant Diversity, Module 7: Plant Structure and Function, and Module 8: Plant Reproduction
Morphological Phylogenetics	.docx, .rtf	Module 2: History of Life, Module 9: Animal Diversity, Module 10: Features of the Animal Kingdom, and Module 12: Vertebrates
Public Relations: Invertebrates are Awesome!	.docx, .rtf	Module 11: Invertebrates
Medical Experience	.docx, .rtf	Module 13: Overview of Body Systems
Ecotourism	.docx, .rtf	Module 14: Ecology of Living Things and Module 15: 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 "Using Waymaker" Knowledge Base 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 15 question banks with a total of 678 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- 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
Total points: 12				

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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
Total points: 12				

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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
Total points: 18				

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3.7: 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 The Study of Biology
4.6: The History of Biology
4.7: The Diversity of Life
4.8: Introduction to the Branches of Biology
4.9: The Branches of Biology
4.10: Introduction to the Process of Science
4.11: Scientific Inquiry
4.12: Basic and Applied Science
4.13: Summary- The Process of Science
4.14: Putting It Together- Introduction to Biology

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4.1: Why It Matters- Introduction to Biology

Why learn about biology and 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 about genetically modified foods and the dangers they inherently contain. Cristina was only halfway through reading the first paragraph of the article when Samuel sent her another article: this one lauding the paleo diet and its benefits. Cristina started to read the article, but before she got too far, she remembered that she had a paper due the next day. She made a mental note to come back to the articles from her cousin, and she bookmarked the animals article.

Though Cristina might not realize it, she's just been presented with three different biological questions. How did these animals develop such unique characteristics? Are GMOs dangerous? Are extreme diets (like the paleo diet) beneficial?

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.

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4.2: Introduction to Characteristics of Life

What you'll learn to do: 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?

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4.3: Properties of Life

Learning Objectives

- List the properties of life



Figure 1. This female monarch butterfly represents a highly organized structure consisting of cells, tissues, organs, and organ systems

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

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.

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.

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

Learning outcomes

- Order the 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. Two or more atoms are joined together by one or more chemical bonds to form **molecule.** 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.

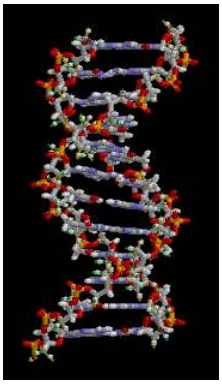


Figure 1. All molecules, including this DNA molecule, are composed of atoms. (credit: “brian0918″/Wikimedia Commons)

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 most multicellular 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.

Practice Question

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

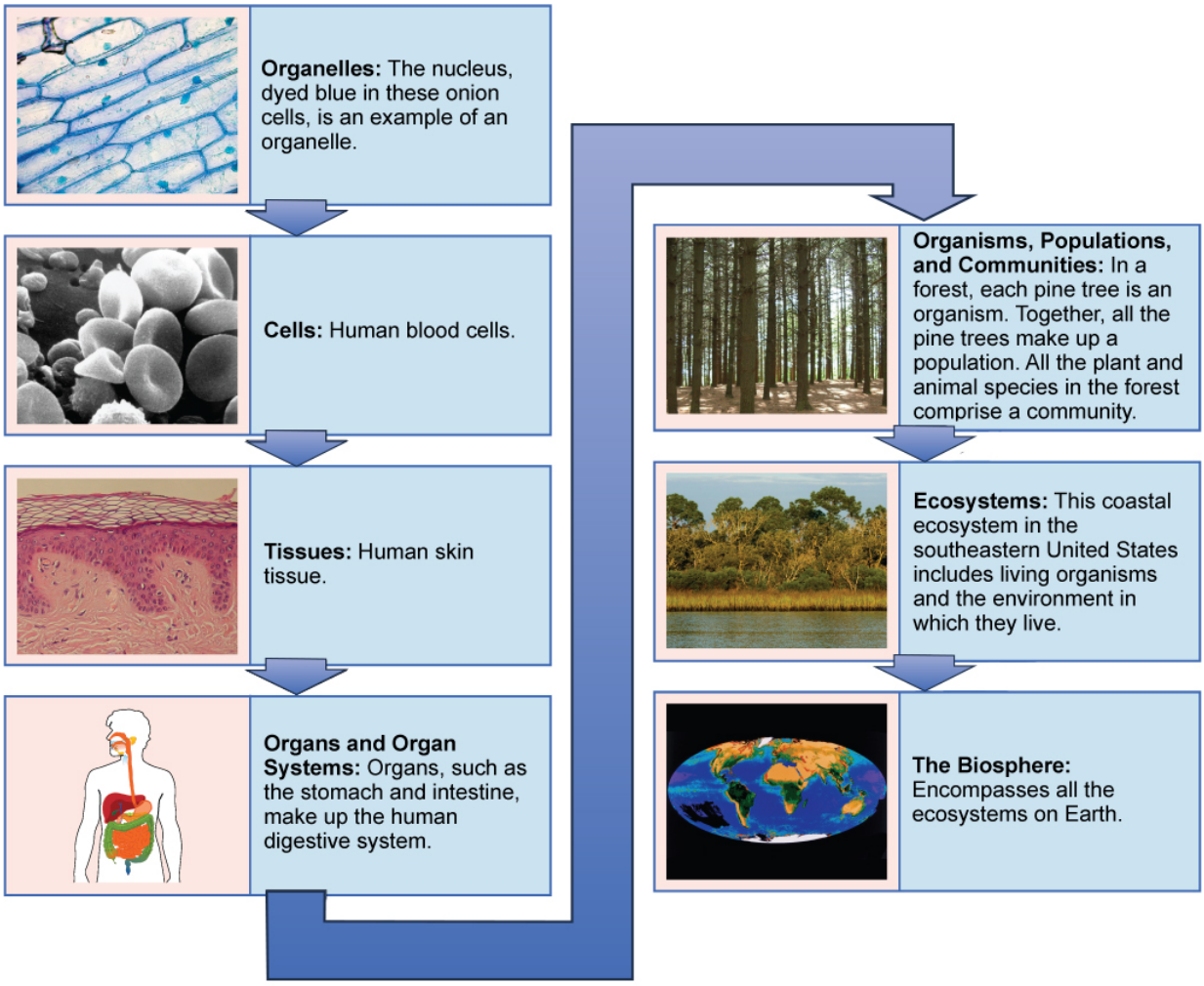


Figure 2. The biological levels of organization of living things are shown. From a single organelle to the entire biosphere, living organisms are parts of a highly structured hierarchy. (credit “organelles”: modification of work by Umberto Salvagnin; credit “cells”: modification of work by Bruce Wetzel, 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)

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 The Study of Biology

What you'll learn to do: Discuss the history of the study of life and the diversity of life on Earth



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.

All that said, the study of "life" has been practiced for hundreds of years and branches like the limbs of a great tree into a host of different areas and specialties. Before we can focus on the subdisciplines of biology, it is important that we first touch upon both the history of biology as well as the vast biological diversity on which it focuses.

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4.6: The History of Biology

Learning Outcome

Discuss the history of the study of life

The history of biology traces the study of the living world from ancient to modern times. Although the concept of biology as a single coherent field arose in the nineteenth century, the biological sciences emerged from traditions of medicine and natural history reaching back to ayurveda, ancient Egyptian medicine and the works of Aristotle and Galen in the ancient Greco-Roman world. This ancient work was further developed in the Middle Ages by Muslim physicians and scholars such as Avicenna. During the European Renaissance and early modern period, biological thought was revolutionized in Europe by a renewed interest in empiricism and the discovery of many novel organisms. Prominent in this movement were Vesalius and Harvey, who used experimentation and careful observation in physiology, and naturalists such as Linnaeus and Buffon who began to classify the diversity of life and the fossil record, as well as the development and behavior of organisms. Antonie van Leeuwenhoek revealed by means of microscopy the previously unknown world of microorganisms, laying the groundwork for cell theory. The growing importance of natural theology, partly a response to the rise of mechanical philosophy, encouraged the growth of natural history.

Over the eighteenth and nineteenth centuries, biological sciences such as botany and zoology became increasingly professional scientific disciplines. Lavoisier and other physical scientists began to connect the animate and inanimate worlds through physics and chemistry. Explorer-naturalists such as Alexander von Humboldt investigated the interaction between organisms and their environment, and the ways this relationship depends on geography—laying the foundations for biogeography, ecology, and ethology. Naturalists began to reject essentialism and consider the importance of extinction and the mutability of species. Cell theory provided a new perspective on the fundamental basis of life. These developments, as well as the results from embryology and paleontology, were synthesized in Charles Darwin's theory of evolution by natural selection. The end of the 19th century saw the fall of spontaneous generation and the rise of the germ theory of disease, though the mechanism of inheritance remained a mystery.

In the early twentieth century, the rediscovery of Gregor Mendel's work led to the rapid development of genetics by Thomas Hunt Morgan and his students, and by the 1930s the combination of population genetics and natural selection in the "neo-Darwinian synthesis". New disciplines developed rapidly, especially after James Watson and Francis Crick proposed the structure of DNA. Following the establishment of the Central Dogma and the cracking of the genetic code, biology was largely split between organismal biology—the fields that deal with whole organisms and groups of organisms—and the fields related to cellular and molecular biology. By the late twentieth century, new fields like genomics and proteomics were reversing this trend, with organismal biologists using molecular techniques, and molecular and cell biologists investigating the interplay between genes and the environment, as well as the genetics of natural populations of organisms.

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4.7: The Diversity of Life

Learning Objectives

- Explain the diversity of life



Figure 1. Life on earth is incredibly diverse.

If you were asked to categorize the living things on earth, how would you do so? Most likely, you would sort things into three groups: animals, plants, and microorganisms: these are the most visible divisions of life.

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.

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.

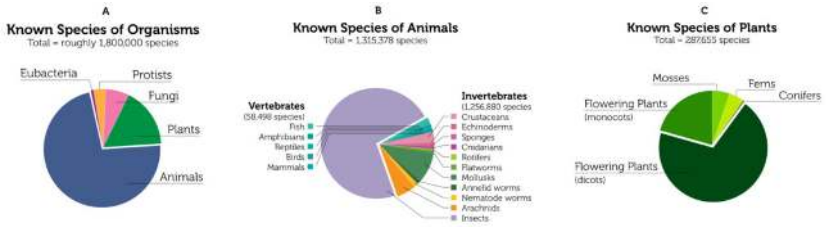


Figure 2. Known life on earth. Click for a larger image.

Learning Objectives

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

Scale of Biodiversity

Diversity may be measured at different scales. These are three indices used by ecologists:

- **Alpha diversity** refers to diversity within a particular area, community or ecosystem, and is measured by counting the number of taxa within the ecosystem (usually species).
- **Beta diversity** is species diversity between ecosystems; this involves comparing the number of taxa that are unique to each of the ecosystems.
- **Gamma diversity** is a measurement of the overall diversity for different ecosystems within a region.

Benefits of Biodiversity

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 3. 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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4.8: Introduction to the Branches of Biology

What you'll learn to do: Identify the main branches of biology

While this course provides a broad introduction to the science of biology, higher level study of the subject quickly breaks down into a vast number of sub-disciplines (e.g., microbiology, immunology, neurobiology, anatomy and physiology). Specialists in these different fields of biology include doctors, nutritionists, pharmacologists, botanists, astrobiologists, and many many more.

In this section, we'll learn about the different paths you can take as you study the science of life.

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4.9: The Branches of Biology

Learning Outcomes

- Identify the main 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. Biotechnologists apply the knowledge of biology to create useful products. Ecologists study the interactions of organisms in their environments. Physiologists study the workings of cells, tissues and organs. This is just a small sample of the many fields that biologists can pursue. From our own bodies to the world we live in, discoveries in biology can affect us in very direct and important ways. We depend on these discoveries for our health, our food sources, and the benefits provided by our ecosystem. Because of this, knowledge of biology can benefit us in making decisions in our day-to-day lives.

The development of technology in the twentieth century that continues today, particularly the technology to describe and manipulate the genetic material, DNA, has transformed biology. This transformation will allow biologists to continue to understand the history of life in greater detail, how the human body works, our human origins, and how humans can survive as a species on this planet despite the stresses caused by our increasing numbers. Biologists continue to decipher huge mysteries about life suggesting that we have only begun to understand life on the planet, its history, and our relationship to it. For this and other reasons, the knowledge of biology gained through this textbook and other printed and electronic media should be a benefit in whichever field you enter.

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4.10: Introduction to the Process of Science

What you'll learn to do: Describe biology as a science and identify the key components of scientific inquiry

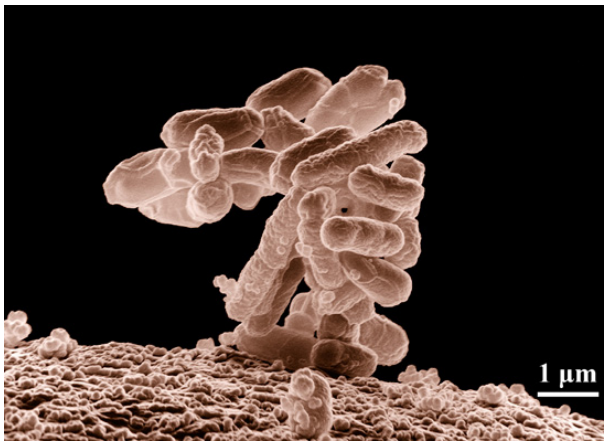


Figure 1. Biologists may choose to study *Escherichia coli* (*E. coli*), a bacterium that is a normal resident of our digestive tracts but which is also sometimes responsible for disease outbreaks. In this micrograph, the bacterium is visualized using a scanning electron microscope and digital colorization. (credit: Eric Erbe; digital colorization by Christopher Pooley, USDA-ARS)

Like geology, physics, and chemistry, biology is a science that gathers knowledge about the natural world. Specifically, biology is the study of life. The discoveries of biology are made by a community of researchers who work individually and together using agreed-on methods. In this sense, biology, like all sciences, is a social enterprise like politics or the arts. The methods of science include careful observation, record keeping, logical and mathematical reasoning, experimentation, and submitting conclusions to the scrutiny of others. Science also requires considerable imagination and creativity; a well-designed experiment is commonly described as elegant, or beautiful. Like politics, science has considerable practical implications and some science is dedicated to practical applications, such as the prevention of disease (see Figure 1). Other science proceeds largely motivated by curiosity. Whatever its goal, there is no doubt that science, including biology, has transformed human existence and will continue to do so.

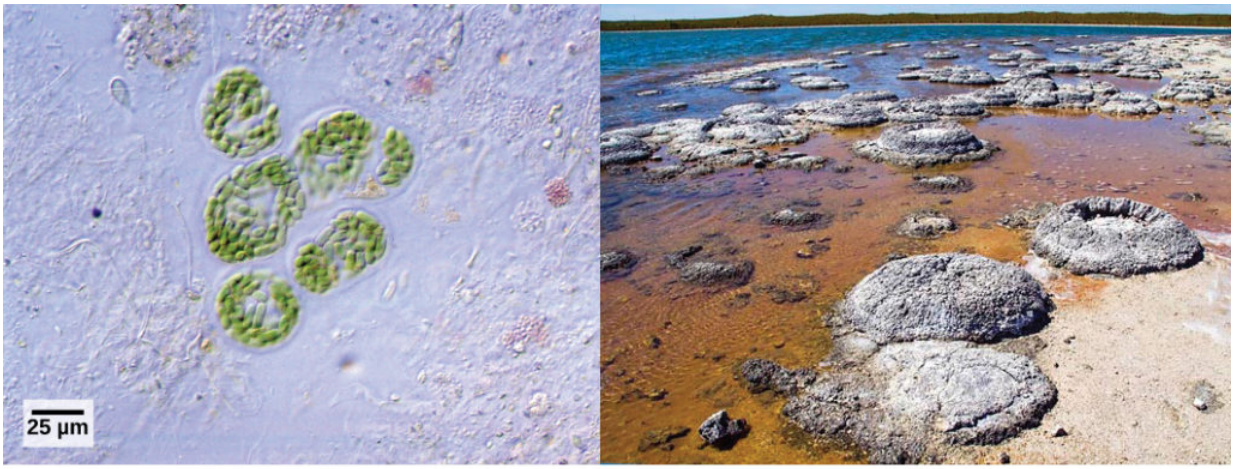


Figure 2. Formerly called blue-green algae, the (a) cyanobacteria seen through a light microscope are some of Earth's oldest life forms. These (b) stromatolites along the shores of Lake Thetis in Western Australia are ancient structures formed by the layering of cyanobacteria in shallow waters. (credit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

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4.11: Scientific Inquiry

Learning Objectives

- Compare inductive reasoning with deductive reasoning
- Describe the process of scientific inquiry

One thing is common to all forms of science: an ultimate goal “to know.” Curiosity and inquiry are the driving forces for the development of science. Scientists seek to understand the world and the way it operates. Two methods of logical thinking are used: inductive reasoning and deductive reasoning.

Inductive reasoning is a form of logical thinking that uses related observations to arrive at a general conclusion. This type of reasoning is common in descriptive science. A life scientist such as a biologist makes observations and records them. These data can be qualitative (descriptive) or quantitative (consisting of numbers), and the raw data can be supplemented with drawings, pictures, photos, or videos. From many observations, the scientist can infer conclusions (inductions) based on evidence. Inductive reasoning involves formulating generalizations inferred from careful observation and the analysis of a large amount of data. Brain studies often work this way. Many brains are observed while people are doing a task. The part of the brain that lights up, indicating activity, is then demonstrated to be the part controlling the response to that task.

Deductive reasoning or deduction is the type of logic used in hypothesis-based science. In deductive reasoning, the pattern of thinking moves in the opposite direction as compared to inductive reasoning. **Deductive reasoning** is a form of logical thinking that uses a general principle or law to forecast specific results. From those general principles, a scientist can extrapolate and predict the specific results that would be valid as long as the general principles are valid. For example, a prediction would be that if the climate is becoming warmer in a region, the distribution of plants and animals should change. Comparisons have been made between distributions in the past and the present, and the many changes that have been found are consistent with a warming climate. Finding the change in distribution is evidence that the climate change conclusion is a valid one.

Both types of logical thinking are related to the two main pathways of scientific study: descriptive science and hypothesis-based science. **Descriptive** (or discovery) **science** aims to observe, explore, and discover, while **hypothesis-based science** begins with a specific question or problem and a potential answer or solution that can be tested. The boundary between these two forms of study is often blurred, because most scientific endeavors combine both approaches. Observations lead to questions, questions lead to forming a hypothesis as a possible answer to those questions, and then the hypothesis is tested. Thus, descriptive science and hypothesis-based science are in continuous dialogue.

Hypothesis Testing



Figure 1. Sir Francis Bacon is credited with being the first to document the scientific method.

Biologists study the living world by posing questions about it and seeking science-based responses. This approach is common to other sciences as well and is often referred to as the scientific method. The scientific method was used even in ancient times, but it

was first documented by England's Sir Francis Bacon (1561–1626) (Figure 1), who set up inductive methods for scientific inquiry. The scientific method is not exclusively used by biologists but can be applied to almost anything as a logical problem-solving method.

The scientific process typically starts with an observation (often a problem to be solved) that leads to a question. Let's think about a simple problem that starts with an observation and apply the scientific method to solve the problem. One Monday morning, a student arrives at class and quickly discovers that the classroom is too warm. That is an observation that also describes a problem: the classroom is too warm. The student then asks a question: "Why is the classroom so warm?"

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

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

A hypothesis must be testable to ensure that it is valid. For example, a hypothesis that depends on what a bear thinks is not testable, because it can never be known what a bear thinks. It should also be **falsifiable**, meaning that it can be disproven by experimental results. An example of an unfalsifiable hypothesis is "Botticelli's *Birth of Venus* is beautiful." There is no experiment that might show this statement to be false. To test a hypothesis, a researcher will conduct one or more experiments designed to eliminate one or more of the hypotheses. This is important. A hypothesis can be disproven, or eliminated, but it can never be proven. Science does not deal in proofs like mathematics. If an experiment fails to disprove a hypothesis, then we find support for that explanation, but this is not to say that down the road a better explanation will not be found, or a more carefully designed experiment will be found to falsify the hypothesis.

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?



[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]

Each experiment will have one or more variables and one or more controls. A **variable** is any part of the experiment that can vary or change during the experiment. A **control** is a part of the experiment that does not change. Look for the variables and controls in the example that follows. As a simple example, an experiment might be conducted to test the hypothesis that phosphate limits the growth of algae in freshwater ponds. A series of artificial ponds are filled with water and half of them are treated by adding phosphate each week, while the other half are treated by adding a salt that is known not to be used by algae. The variable here is the phosphate (or lack of phosphate), the experimental or treatment cases are the ponds with added phosphate and the control ponds are those with something inert added, such as the salt. Just adding something is also a control against the possibility that adding extra matter to the pond has an effect. If the treated ponds show lesser growth of algae, then we have found support for our hypothesis. If they do not, then we reject our hypothesis. Be aware that rejecting one hypothesis does not determine whether or not the other hypotheses can be accepted; it simply eliminates one hypothesis that is not valid (Figure 2). Using the scientific method, the hypotheses that are inconsistent with experimental data are rejected.

? Practice Question

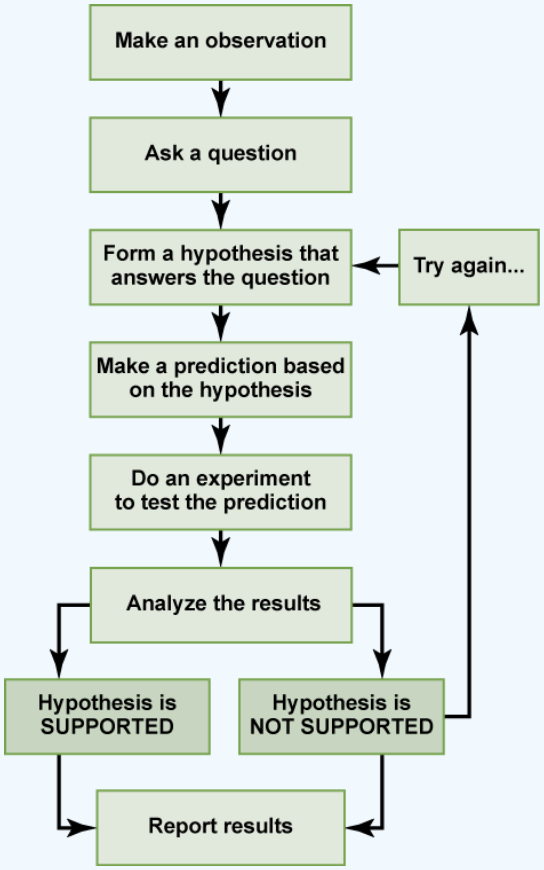


Figure 2. The scientific method is a series of defined steps that include experiments and careful observation. If a hypothesis is not supported by data, a new hypothesis can be proposed.

In the example below, the scientific method is used to solve an everyday problem. Which part in the example below is the hypothesis? Which is the prediction? Based on the results of the experiment, is the hypothesis supported? If it is not supported, propose some alternative hypotheses.

1. My toaster doesn't toast my bread.
2. Why doesn't my toaster work?
3. There is something wrong with the electrical outlet.
4. If something is wrong with the outlet, my coffeemaker also won't work when plugged into it.
5. I plug my coffeemaker into the outlet.
6. My coffeemaker works.

[practice-area rows=”4″][/practice-area]
[reveal-answer q=”41039″]Show Answer[/reveal-answer]
[hidden-answer a=”41039″]The hypothesis is #3 (there is something wrong with the electrical outlet), and the prediction is #4 (if something is wrong with the outlet, then the coffeemaker also won’t work when plugged into the outlet). The original hypothesis is not supported, as the coffee maker works when plugged into the outlet. Alternative hypotheses may include (1) the toaster might be broken or (2) the toaster wasn’t turned on.[/hidden-answer]

In practice, the scientific method is not as rigid and structured as it might at first appear. Sometimes an experiment leads to conclusions that favor a change in approach; often, an experiment brings entirely new scientific questions to the puzzle. Many times, science does not operate in a linear fashion; instead, scientists continually draw inferences and make generalizations, finding patterns as their research proceeds. Scientific reasoning is more complex than the scientific method alone suggests.

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4.12: Basic and Applied Science

Learning Objectives

- Describe the goals of basic science and applied science

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

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

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

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

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

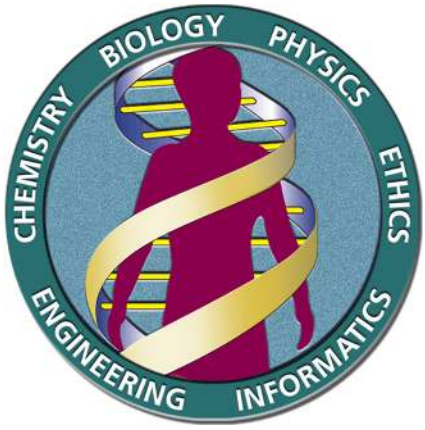


Figure 1. The Human Genome Project was a 13-year collaborative effort among researchers working in several different fields of science. The project was completed in 2003. (credit: the U.S. Department of Energy Genome Programs)

Another example of the link between basic and applied research is the Human Genome Project, a study in which each human chromosome was analyzed and mapped to determine the precise sequence of DNA subunits and the exact location of each gene. (The gene is the basic unit of heredity; an individual's complete collection of genes is his or her genome.) Other organisms have also been studied as part of this project to gain a better understanding of human chromosomes. The Human Genome Project (Figure

1) relied on basic research carried out with non-human organisms and, later, with the human genome. An important end goal eventually became using the data for applied research seeking cures for genetically related diseases.

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

Reporting Scientific Work

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

There are many journals and the popular press that do not use a peer-review system. A large number of online open-access journals, journals with articles available without cost, are now available many of which use rigorous peer-review systems, but some of which do not. Results of any studies published in these forums without peer review are not reliable and should not form the basis for other scientific work. In one exception, journals may allow a researcher to cite a personal communication from another researcher about unpublished results with the cited author's permission.

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4.13: Summary- The Process of Science

Learning Outcomes

- Compare inductive reasoning with deductive reasoning
- Describe the process of scientific inquiry
- Describe the goals of basic science and applied science

Biology is the science that studies living organisms and their interactions with one another and their environments. Science attempts to describe and understand the nature of the universe in whole or in part. Science has many fields; those fields related to the physical world and its phenomena are considered natural sciences.

A hypothesis is a tentative explanation for an observation. A scientific theory is a well-tested and consistently verified explanation for a set of observations or phenomena. A scientific law is a description, often in the form of a mathematical formula, of the behavior of an aspect of nature under certain circumstances. Two types of logical reasoning are used in science. Inductive reasoning uses results to produce general scientific principles. Deductive reasoning is a form of logical thinking that predicts results by applying general principles. The common thread throughout scientific research is the use of the scientific method. Scientists present their results in peer-reviewed scientific papers published in scientific journals.

Science can be basic or applied. The main goal of basic science is to expand knowledge without any expectation of short-term practical application of that knowledge. The primary goal of applied research, however, is to solve practical problems.

Practice Questions

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

a. hypothesis
b. variable
c. theory
d. control

[reveal-answer q="354047"]Show Answer[/reveal-answer]
[hidden-answer a="354047"]A suggested and testable explanation for an event is called a **hypothesis**.

[/hidden-answer]

Give an example of how applied science has had a direct effect on your daily life.
[reveal-answer q="886421"]Show Answer[/reveal-answer]
[hidden-answer a="886421"]Answers will vary. One example of how applied science has had a direct effect on daily life is the presence of vaccines. Vaccines to prevent diseases such polio, measles, tetanus, and even the influenza affect daily life by contributing to individual and societal health.[/hidden-answer]

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4.14: 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 Back

Cristina read an article about some of the world's weirdest animals. 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. We'll learn more about how these types of traits are selected for in Module 2: History of Life.

The next article Cristina read talked about GMOs (genetically modified organisms) and the risks they have. In order to truly understand potential risks of genetically modified foods, Cristina will need to first understand the science behind these foods. How are GMOs created? We won't address this topic here, but it draws upon our modern understanding of how organisms reproduce and pass along certain traits.

Cristina then looked at an article about the paleo diet. In order to survive, humans require specific nutrients. While we won't get into too much depth about nutrition in this course, we will learn about different body systems, including the digestive system, in Module 13: Overview of Body Systems. The digestive system is responsible for breaking down the macromolecules we eat and enabling those building blocks to be used throughout the body.

As you can see in Cristina's example, biology is all around us—after all, you're a living human being! In this course, we'll learn about key biological principles that can help you live your life the best you can.

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CHAPTER OVERVIEW

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5.5: Evidence of Evolution
5.6: Misconceptions of Evolution
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5.1: 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.

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5.2: Introduction to Evolution

What you'll learn to do: 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.

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

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5.3: Natural Selection

Learning Objectives

- Define natural selection

Darwin and Descent with Modification

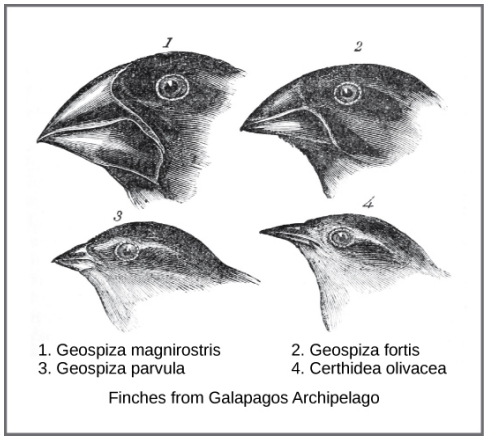


Figure 1. Darwin observed that beak shape varies among finch species. He postulated that the beak of an ancestral species had adapted over time to equip the finches to acquire different food sources.

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.

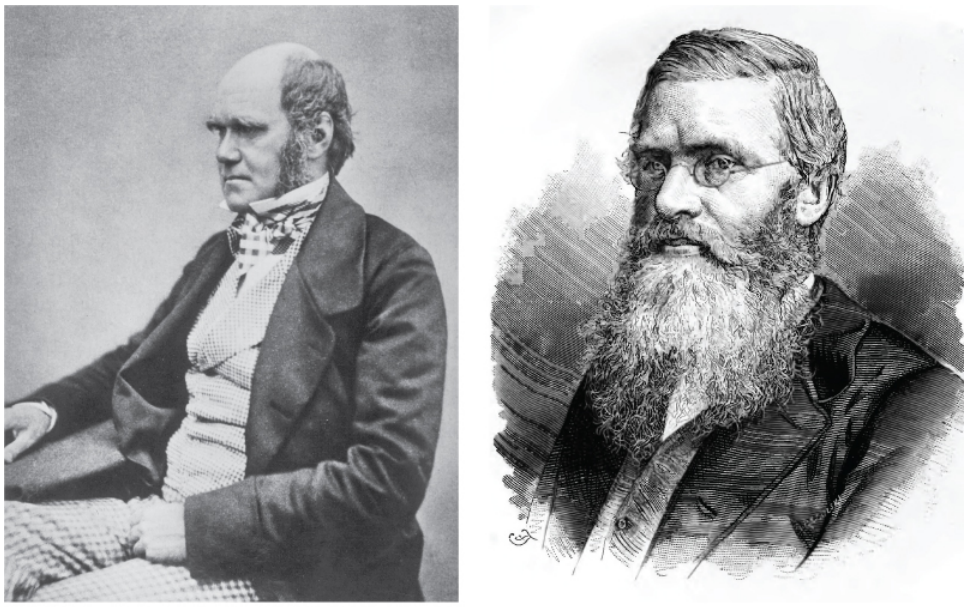
Wallace and Darwin both observed similar patterns in other organisms and they independently developed the same explanation for how and why such changes could take place. Darwin called this mechanism natural selection. **Natural selection**, also known as "survival of the fittest," is the more prolific 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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5.4: Theory of Evolution

Learning Objectives

- Describe the basis of the present-day 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).



(a) (b)

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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5.5: Evidence of Evolution

Learning Objectives

- Describe how the theory of evolution by natural selection is supported by evidence

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

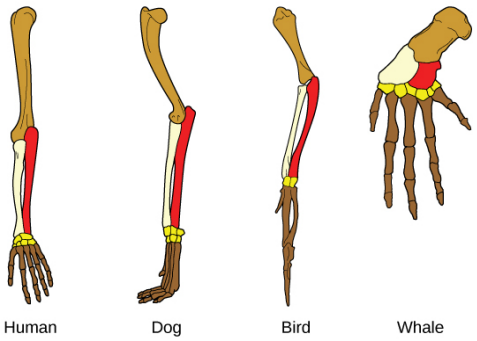


Figure 2. The similar construction of these appendages indicates that these organisms share a common ancestor.

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.

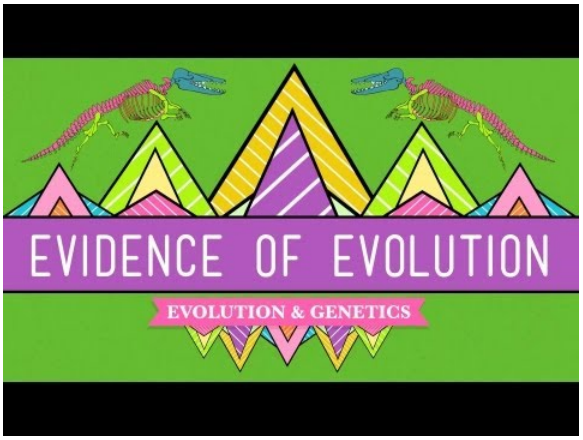
Molecular Biology

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/bionm2/?p=100

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5.6: Misconceptions of Evolution

Learning Objectives

- Refute common misconceptions about evolution

Although the theory of evolution generated some controversy when it was first proposed, it was almost universally accepted by biologists, particularly younger biologists, within 20 years after 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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5.7: Artificial Selection

Learning Outcome

- Define artificial selection

It is important to note that natural selection is not the only way that species evolve. In particular, humans can have quite drastic impacts on species' characteristics, especially in organisms with agricultural or economic benefit.

Artificial selection (also known as selective breeding) is the process by which humans use animal breeding and plant breeding to selectively develop particular phenotypic traits (characteristics) by choosing which typically animal or plant males and females will sexually reproduce and have offspring together. Domesticated animals are known as breeds, normally bred by a professional breeder, while domesticated plants are known as varieties, cultigens, or cultivars. Two purebred animals of different breeds produce a crossbreed, and crossbred plants are called hybrids. Flowers, vegetables and fruit-trees may be bred by amateurs and commercial or non-commercial professionals: major crops are usually the provenance of the professionals.

There are two approaches or types of artificial selection. First is the traditional "breeder's approach" in which the breeder or experimenter applies "a known amount of selection to a single phenotypic trait" by examining the chosen trait and choosing to breed only those that exhibit higher or "extreme values" of that trait. The second is called "controlled natural selection," which is essentially natural selection in a controlled environment. In this, the breeder does not choose which individuals being tested "survive or reproduce," as he or she could in the traditional approach. There are also "selection experiments," which is a third approach and these are conducted in order to determine the "strength of natural selection in the wild." However, this is more often an observational approach as opposed to an experimental approach.



Figure 1. A Belgian Blue cow. The defect in the breed's myostatin gene is maintained through linebreeding and is responsible for its accelerated lean muscle growth.

In animal breeding, techniques such as inbreeding, linebreeding, and outcrossing are utilized. In plant breeding, similar methods are used. Charles Darwin discussed how artificial selection had been successful in producing change over time in his 1859 book, *On the Origin of Species*. Its first chapter discusses artificial selection and domestication of such animals as pigeons, cats, cattle, and dogs. Darwin used artificial selection as a springboard to introduce and support the theory of natural selection.

The deliberate exploitation of artificial selection to produce desired results has become very common in agriculture and experimental biology.

Artificial selection can be unintentional, e.g., resulting from the process of human cultivation; and it may also produce unintended —desirable or undesirable—results. For example, in some grains, an increase in seed size may have resulted from certain ploughing practices rather than from the intentional selection of larger seeds. Most likely, there has been an interdependence between natural and artificial factors that have resulted in plant domestication.

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5.8: Introduction to Speciation

What you'll learn to do: 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.

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5.9: What is a Species?

Learning Objectives

- Define species and describe how species are identified as different

A basic and generally accepted definition of the term **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. It is important to note that this definition fits eukaryotic organisms fairly well, but that species are often defined quite differently in prokaryotic lineages. For the purposes of this lesson, we will focus on this definition of species applied to eukaryotes. Later in the course, we will touch upon prokaryotic species.

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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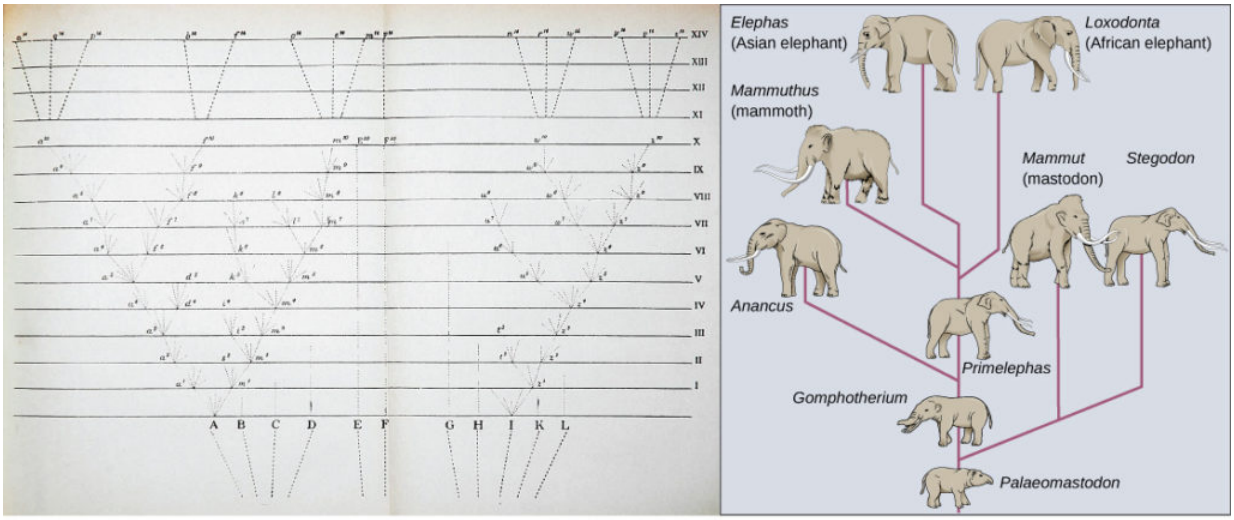
5.10: Types of Speciation

Learning Objectives

- Differentiate between 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.



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)

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.

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).

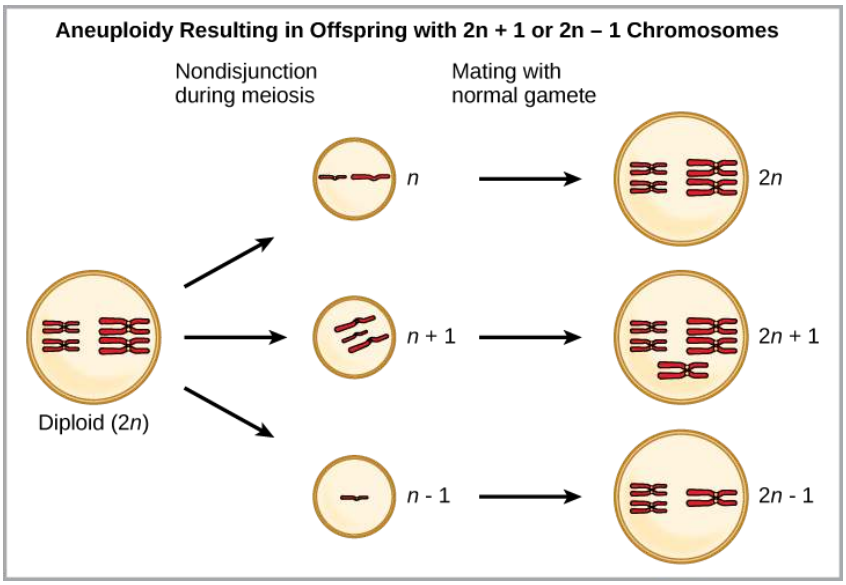


Figure 4. Aneuploidy results when the gametes have too many or too few chromosomes due to nondisjunction during meiosis. In the example shown here, the resulting offspring will have $2n+1$ or $2n-1$ chromosomes

? 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.

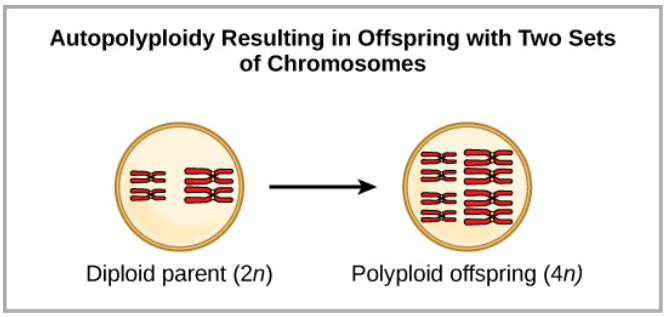


Figure 5. Autopolyploidy results when mitosis is not followed by cytokinesis.

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.

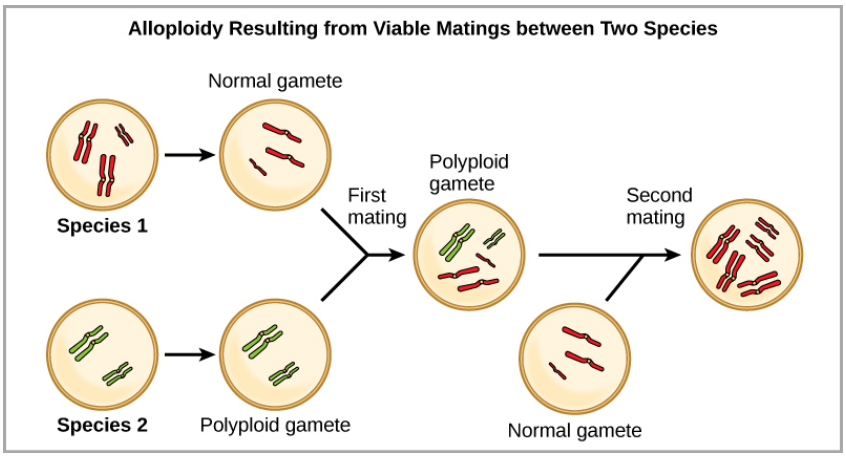


Figure 6. Alloploidy results when two species mate to produce viable offspring. In the example shown, a normal gamete from one species fuses with a polyploidy gamete from another. Two matings are necessary to produce viable offspring.

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).

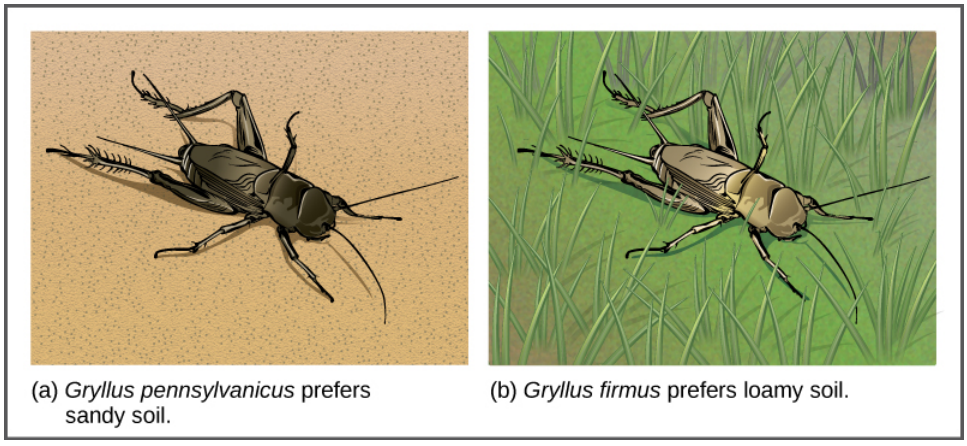


Figure 8. Speciation can occur when two populations occupy different habitats. The habitats need not be far apart. The cricket (a) *Gryllus pennsylvanicus* prefers sandy soil, and the cricket (b) *Gryllus firmus* prefers loamy soil. The two species can live in close proximity, but because of their different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

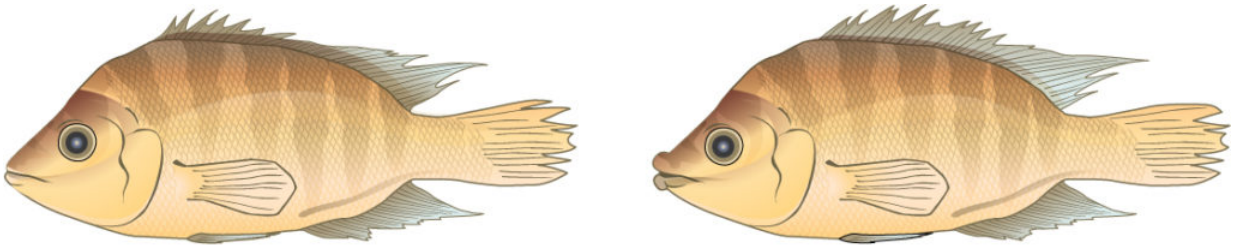
Figure 10. Some flowers have evolved to attract certain pollinators. The (a) wide foxglove flower is adapted for pollination by bees, while the (b) long, tube-shaped trumpet creeper flower is adapted for pollination by humming birds.

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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5.11: Reconnection

Learning Outcomes

- Describe the process of 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.

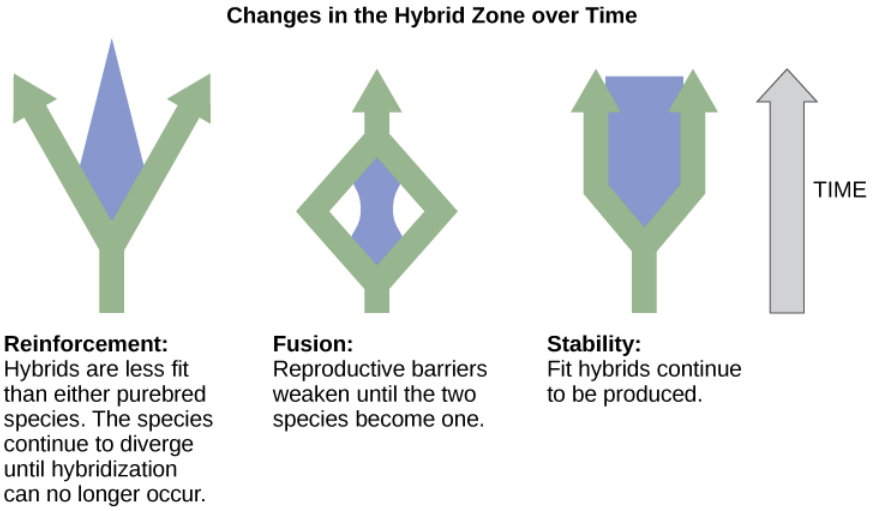


Figure 1. After speciation has occurred, the two separate but closely related species may continue to produce offspring in an area called the hybrid zone. Reinforcement, fusion, or stability may result, depending on reproductive barriers and the relative fitness of the hybrids.

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?

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[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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5.12: Rates of Speciation

Learning Outcomes

- Explain the two major theories on 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.

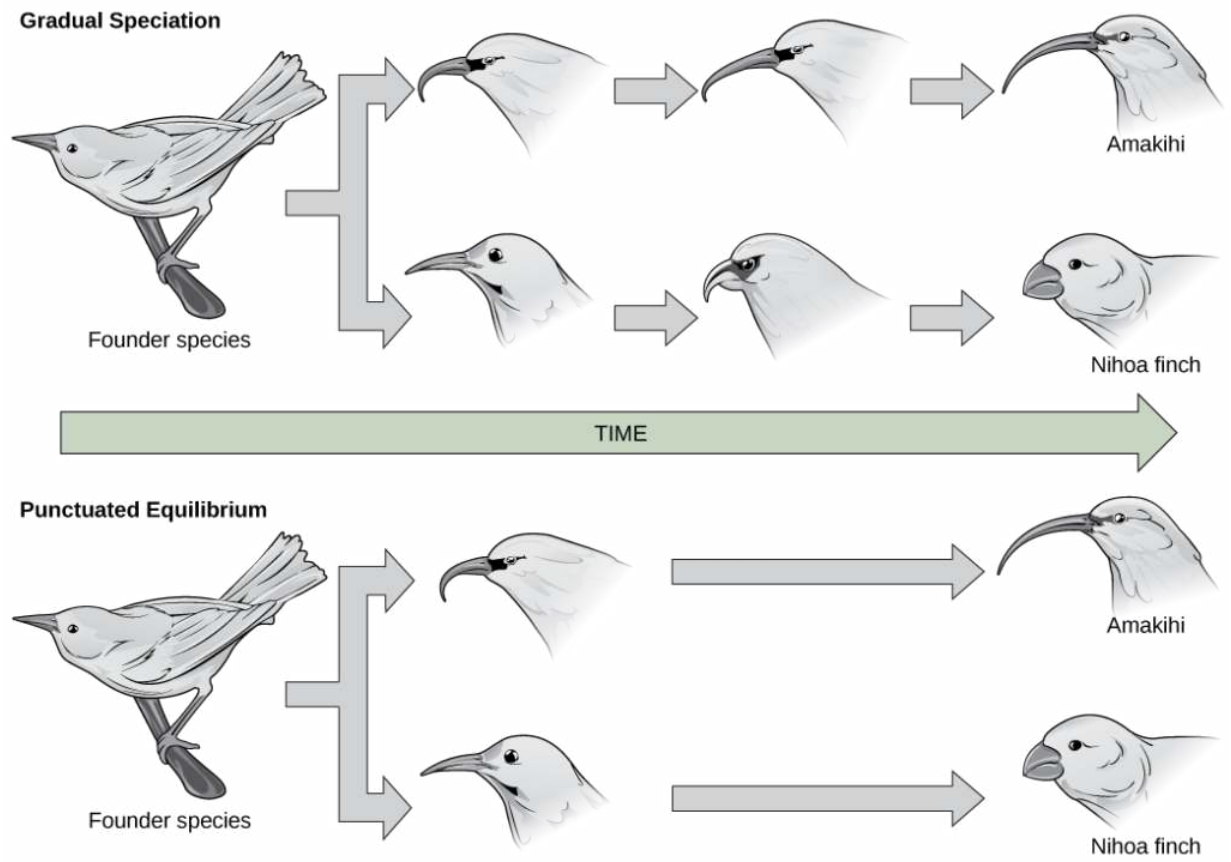


Figure 1. In (a) gradual speciation, species diverge at a slow, steady pace as traits change incrementally. In (b) punctuated equilibrium, species diverge quickly and then remain unchanged for long periods of time.

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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5.13: Introduction to the Evolution of Populations

What you'll learn to do: 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

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5.14: Population Genetics

Learning Outcomes

- Describe how population genetics is used in the study of the evolution of populations

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.

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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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5.15: Genetic Variation and Drift

Learning Objectives

- Describe the different types of variation in a population



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).

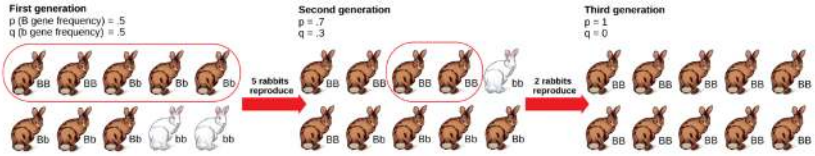


Figure 2. Click for a larger image. Genetic drift in a population can lead to the elimination of an allele from a population by chance. In this example, rabbits with the brown coat color allele (*B*) are dominant over rabbits with the white coat color allele (*b*). In the first generation, the two alleles 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?

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[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

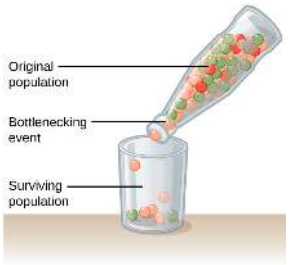


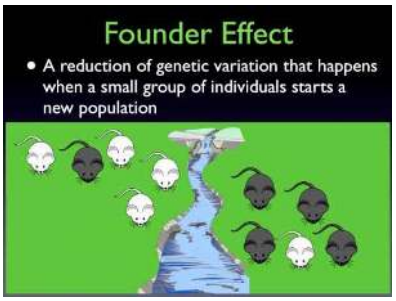
Figure 3. A chance event or catastrophe can reduce the genetic variability within a population.

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/bionm2/?p=120

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

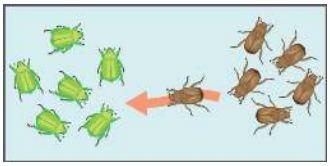


Figure 4. Gene flow can occur when an individual travels from one geographic location to another.

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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5.16: Adaptive Evolution

Learning Objectives

- Explain the different ways natural selection can shape populations

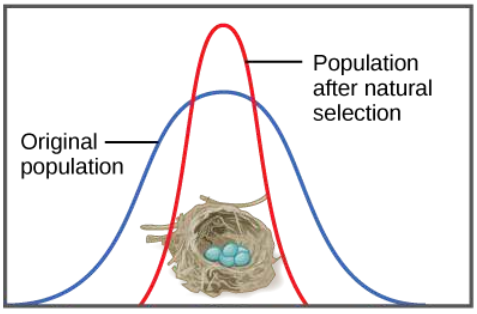
Natural selection only acts on the population's heritable traits: selecting for beneficial alleles and thus increasing their frequency in the population, while selecting against deleterious alleles and thereby decreasing their frequency—a process known as **adaptive evolution**. Natural selection does 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.



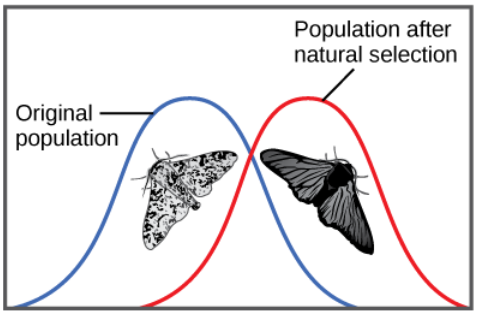
Robins typically lay four eggs, an example of stabilizing selection. Larger clutches may result in malnourished chicks, while smaller clutches may result in no viable offspring.

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.



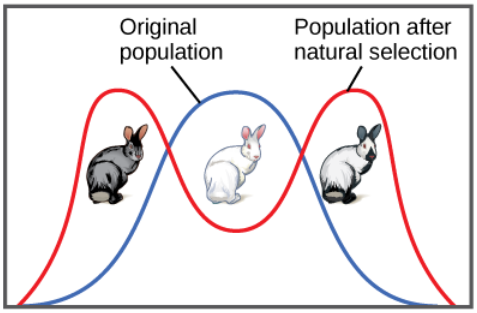
Light-colored peppered moths are better camouflaged against a pristine environment; likewise, dark-colored peppered moths are better camouflaged against a sooty environment. Thus, as the Industrial Revolution progressed in nineteenth-century England, the color of the moth population shifted from light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

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[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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5.17: Hardy-Weinberg Principle of Equilibrium

Learning Outcomes

- Define the Hardy-Weinberg principle and discuss its importance

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 mathematical models. 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.

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 the Hardy-Weinberg equation and mathematical calculations 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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5.18: Introduction to Phylogenies and the History of Life

What you'll learn to do: 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

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5.19: Phylogenetic Trees

Learning Objectives

- Discuss the components and purpose of a phylogenetic tree

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.

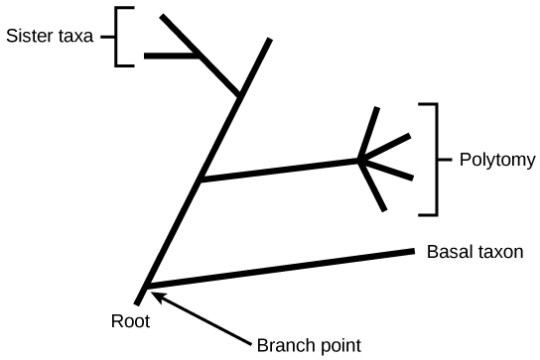


Figure 2. The root of a phylogenetic tree indicates that an ancestral lineage gave rise to all organisms on the tree. A branch point indicates where two lineages diverged. A lineage that evolved early and remains unbranched is a basal taxon. When two lineages stem from the same branch point, they are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

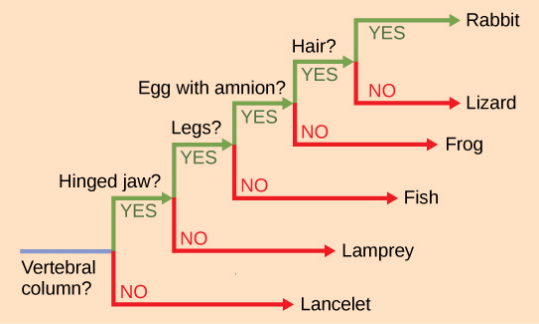


Figure 3. This ladder-like phylogenetic tree of vertebrates is rooted by an organism that lacked a vertebral column. At each branch point, organisms with different characters are placed in different groups based on the characteristics they share.

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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5.20: Taxonomy

Learning Outcomes

- List the different levels of the taxonomic classification system

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).

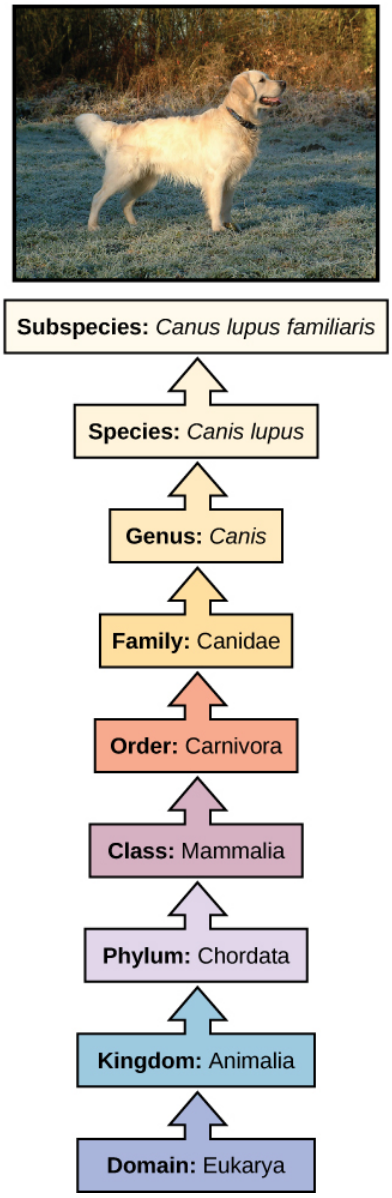


Figure 1. The taxonomic classification system uses a hierarchical model to organize living organisms into increasingly specific categories. The common dog, *Canis lupus familiaris*, is a subspecies of *Canis lupus*, which also includes the wolf and dingo. (credit "dog": modification of work by Janneke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

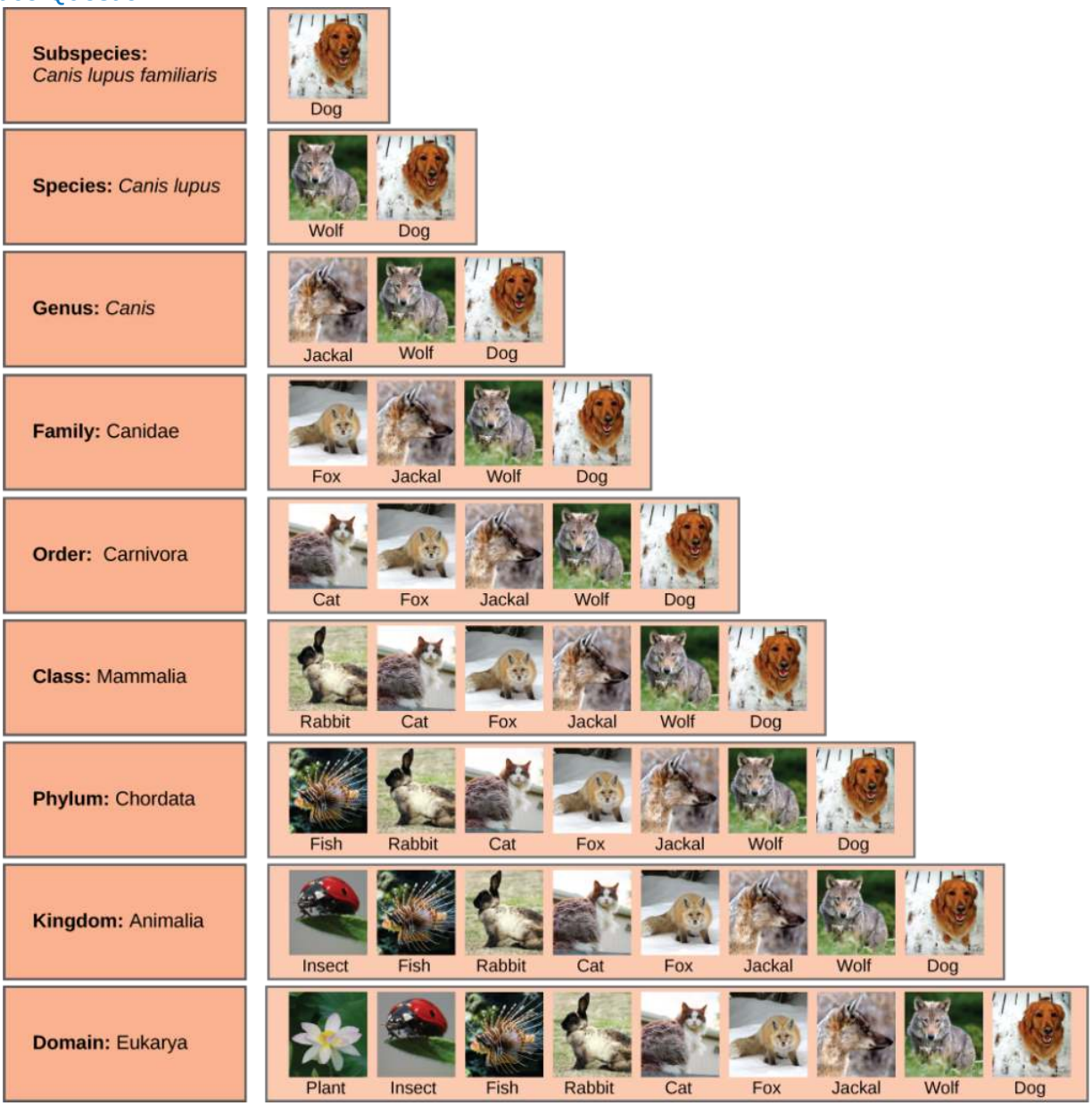


Figure 2. At each sublevel in the taxonomic classification system, organisms become more similar. Dogs and wolves are the same species because they can breed and produce viable offspring, but they are different enough to be classified as different subspecies. (credit “plant”: modification of work by “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/bionm2/?p=130

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5.21: Homologous and Analogous Traits

Learning Objectives

- Compare 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).

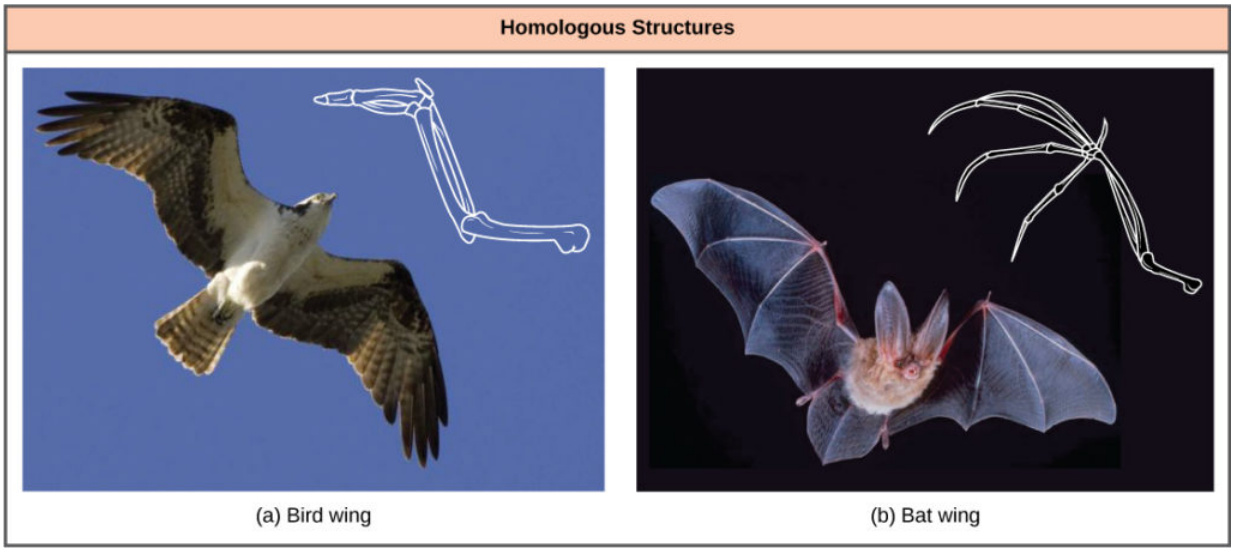


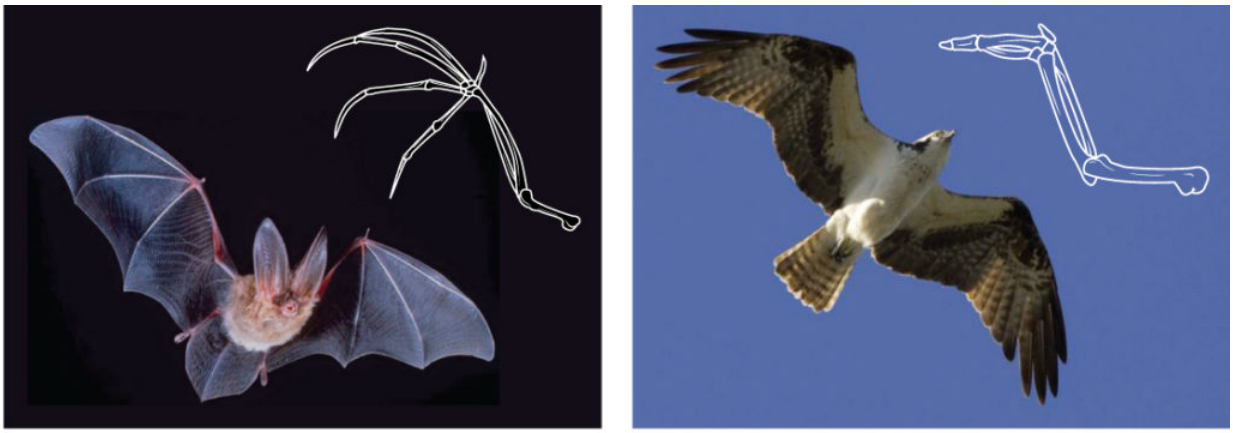
Figure 1. Bat and bird wings are homologous structures, indicating that bats and birds share a common evolutionary past. (credit a: modification of work by Steve Hillebrand, USFWS; credit b: modification of work by U.S. DOI BLM)

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.



(a) Bat wing

(b) Bird wing

(c) Insect wing

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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5.22: Cladistics

Learning Objectives

- Discuss the purpose of 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

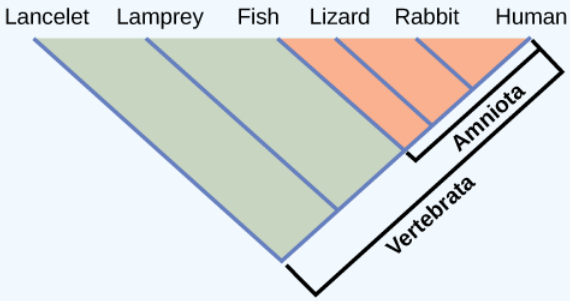


Figure 1. Lizards, rabbits, and humans all descend from a common ancestor that had an amniotic egg. Thus, lizards, rabbits, and humans all belong to the clade Amniota. Vertebrata is a larger clade that also includes fish and lamprey.

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

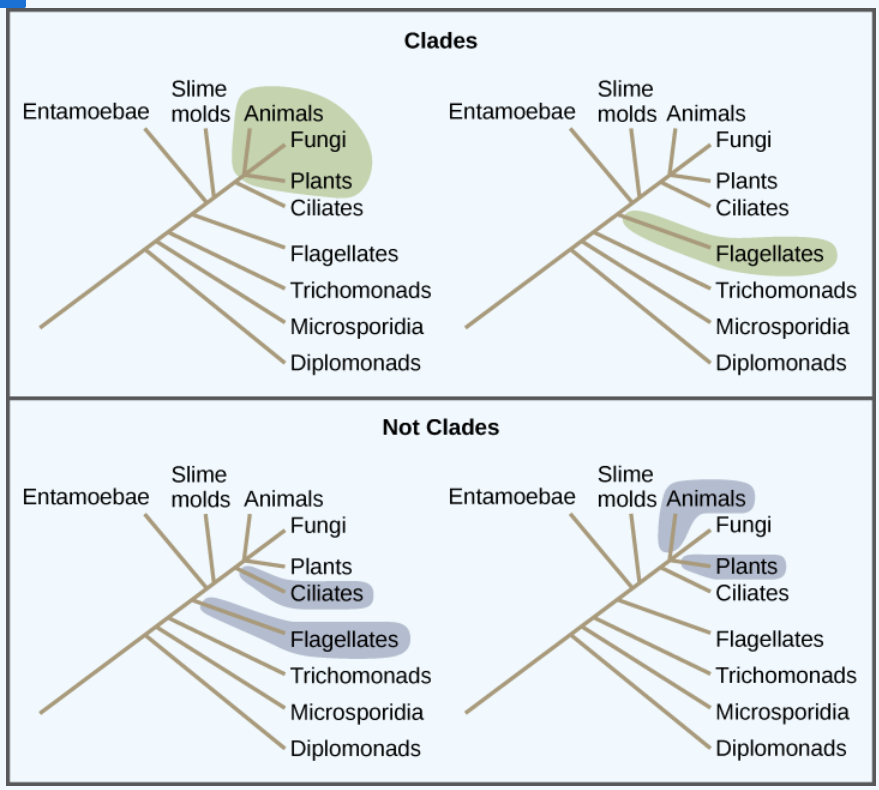


Figure 2. All the organisms within a clade stem from a single point on the tree. A clade may contain multiple groups, as in the case of animals, fungi and plants, or a single group, as in the case of flagellates. Groups that diverge at a different branch point, or that do not include all groups in a 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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5.23: Perspectives on the Phylogenetic Tree

Learning Objectives

- Identify different perspectives and criticisms of 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		

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.

The **nucleus-first** hypothesis proposes that the nucleus evolved in prokaryotes first (Figure 2**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 2**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 2**c**). All of these hypotheses are testable. Only time and more experimentation will determine which hypothesis is best supported by data.

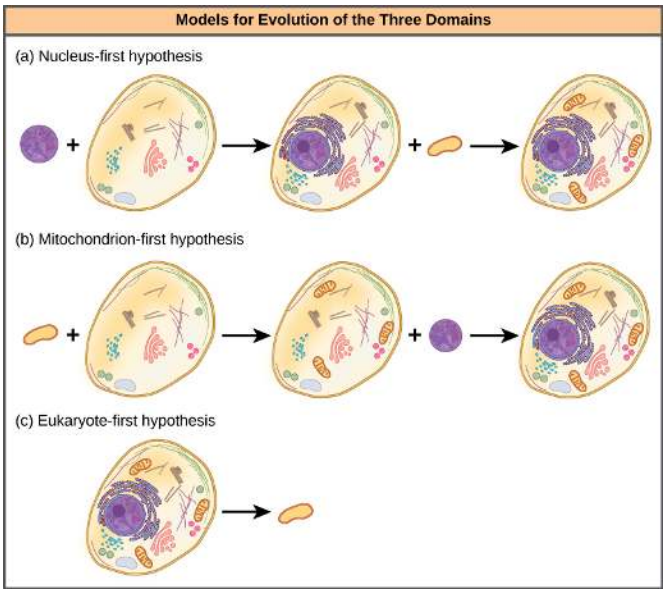


Figure 2. Three alternate hypotheses of eukaryotic and prokaryotic evolution are (a) the nucleus-first hypothesis, (b) the mitochondrion-first hypothesis, and (c) the eukaryote-first hypothesis.

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 3**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 3**b**) with its multiple trunks as a phylogenetic to represent a diminished evolutionary role for HGT.

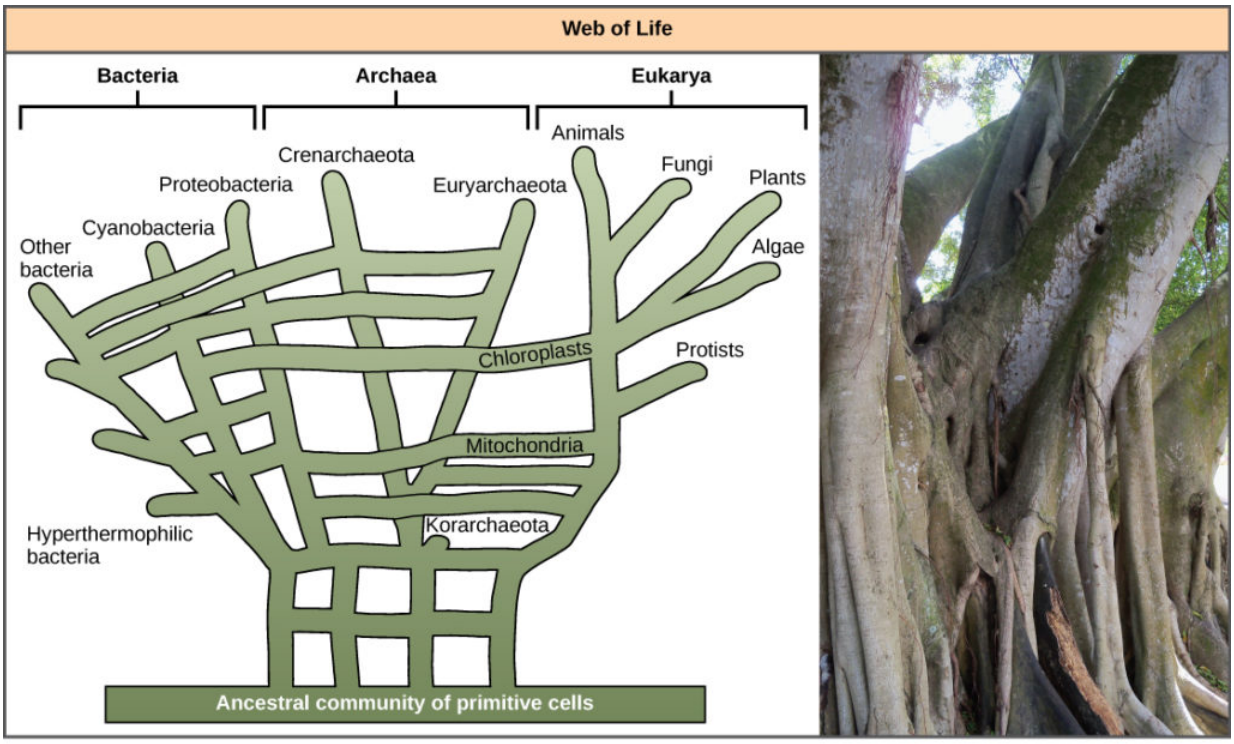


Figure 3. In the (a) phylogenetic model proposed by W. Ford Doolittle, the "tree of life" arose from a community of ancestral cells, has multiple trunks, and has connections between branches where horizontal gene transfer has occurred. Visually, this concept is better represented by (b) the multi-trunked 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

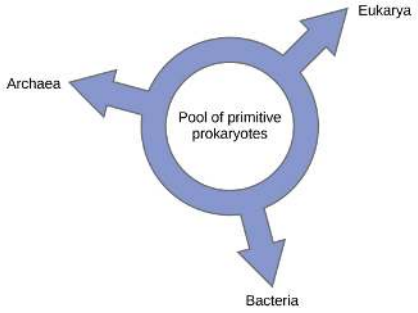


Figure 4. According to the "ring of life" phylogenetic model, the three domains of life evolved from a pool of primitive prokaryotes.

Others have proposed abandoning any tree-like model of phylogeny in favor of a ring structure, the so-called "**ring of life**" (Figure 4); 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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5.24: 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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CHAPTER OVERVIEW

6: Module 3- Prokaryotes

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6.1: Why It Matters- Prokaryotes

Why learn about different kinds of prokaryotes and bacteria?

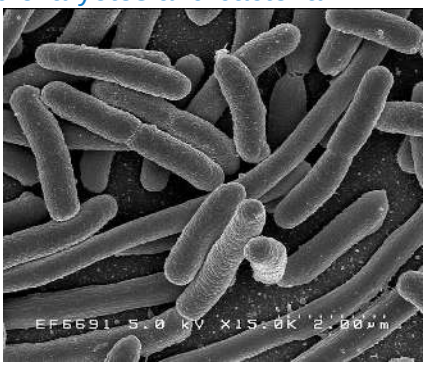


Figure 1. *Escherichia coli*, one of the many species of bacteria present in the human gut

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.

In this module we will focus on a limited number of both the beneficial and the harmful prokaryotes around us.

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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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6.2: Introduction to Prokaryotic Diversity

What you'll learn to do: 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.

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6.3: Evolutionary History of Prokaryotes

Learning Objectives

- Describe the evolutionary history of prokaryotes

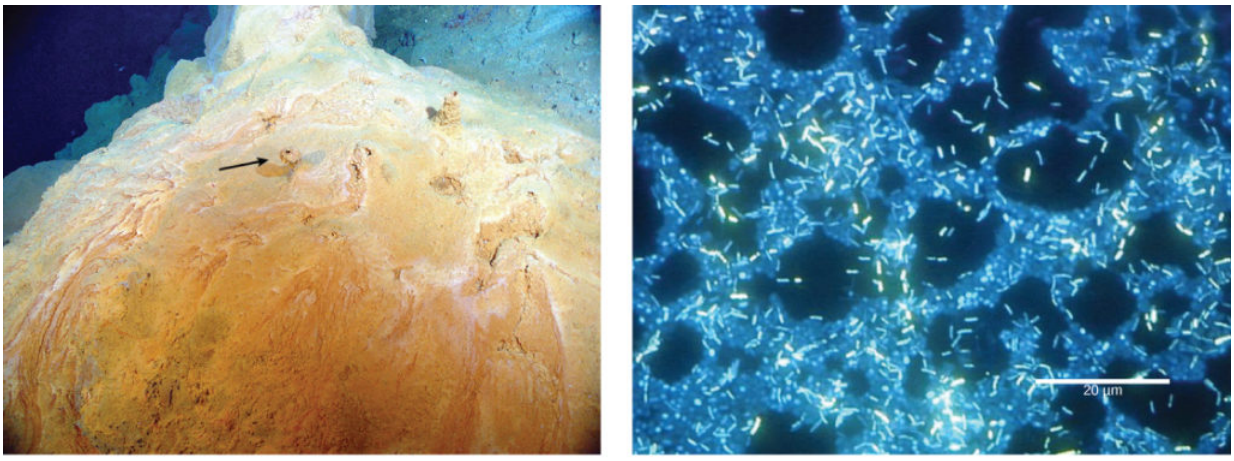
Prokaryotes are ubiquitous. They cover every imaginable surface where there is sufficient moisture, and they live on and inside of other living things. In the typical human body, prokaryotic cells outnumber human body cells by about ten to one. They comprise the majority of living things in all ecosystems. 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

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

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6.4: Life in Moderate and Extreme Environments

Learning Outcomes

- Discuss the distinguishing features of extremophiles

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.

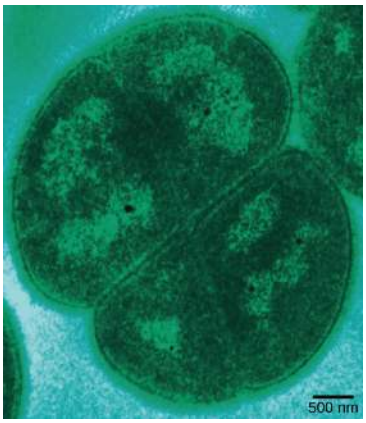


Figure 1. *Deinococcus radiodurans*, visualized in a false color transmission electron micrograph (credit: modification of work by Michael Daly; scale-bar data from Matt Russell)

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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6.5: Introduction to the Structure of Prokaryotes

What you'll learn to do: 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).

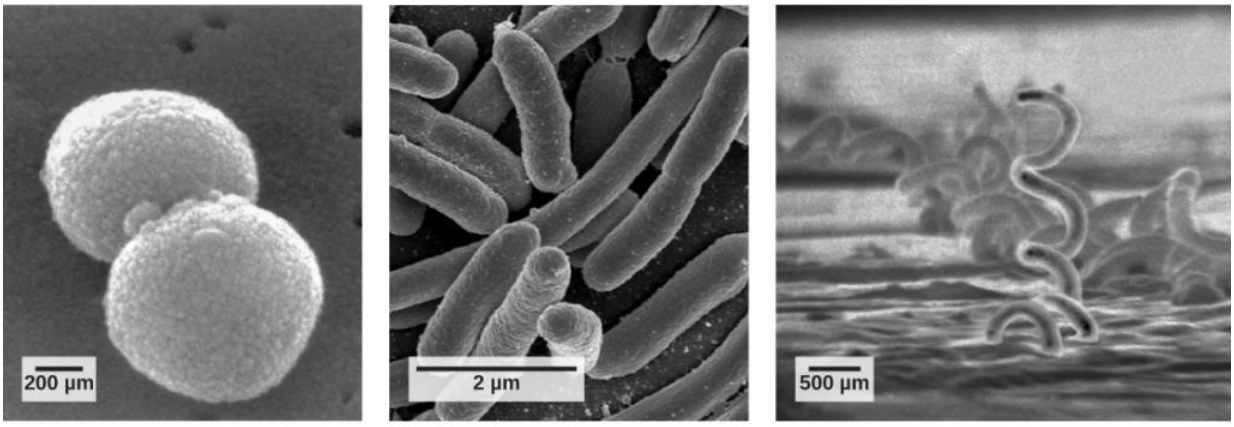


Figure 1. Prokaryotes fall into three basic categories based on their shape, visualized here using scanning electron microscopy: (a) cocci, or spherical (a pair is shown); (b) bacilli, or rod-shaped; and (c) spirilli, or spiral-shaped. (credit a: modification of work by Janice Haney Carr, Dr. Richard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

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6.6: The Prokaryotic Cell

Learning Objectives

- Describe the basic structure of a typical prokaryote

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.

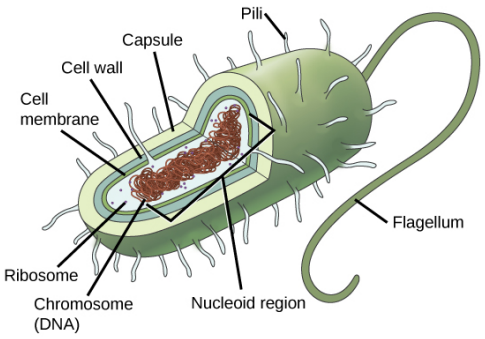


Figure 1. The features of a typical prokaryotic cell are shown.

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.

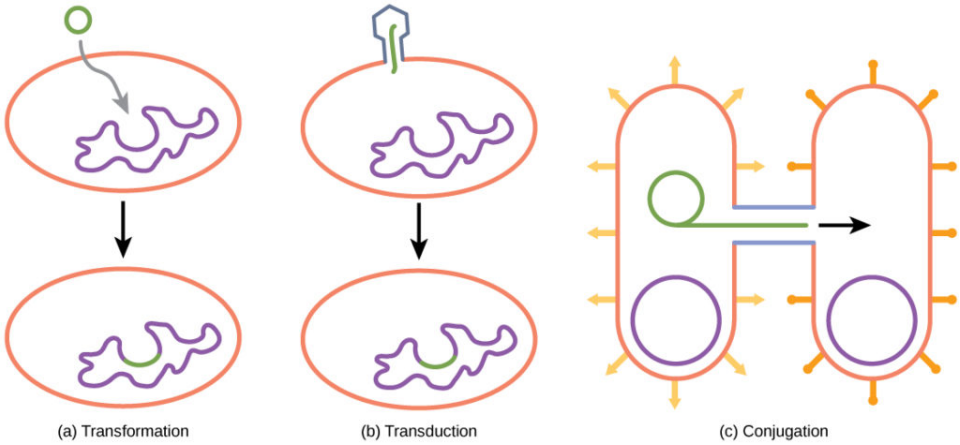


Figure 2. Besides binary fission, there are three other mechanisms by which prokaryotes can exchange DNA. In (a) transformation, the cell takes up prokaryotic DNA directly from the environment. The DNA may remain separate as plasmid DNA or be incorporated into the host genome. In (b) transduction, a 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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6.7: Archaea vs. Bacteria

Learning Objectives

- Describe important differences in structure between Archaea and Bacteria

Prokaryotes are divided into two different domains, Bacteria and Archaea, which together with Eukarya, comprise the three domains of life (Figure 1).

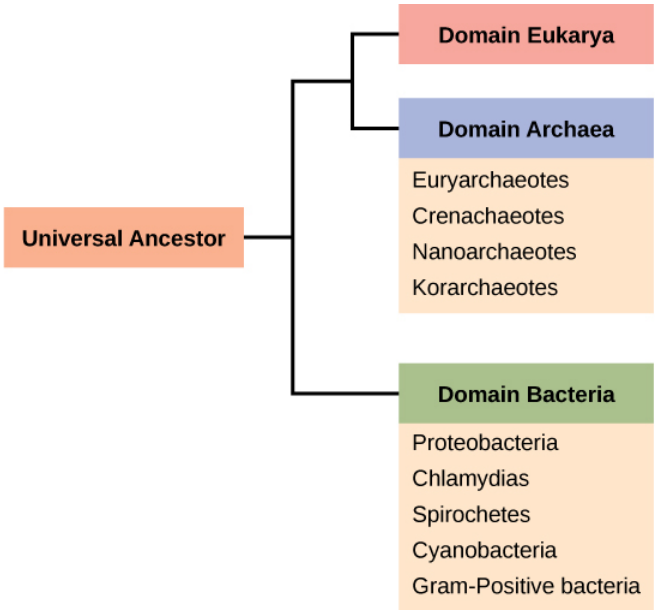


Figure 1. Bacteria and Archaea are both prokaryotes but differ enough to be placed in separate domains. An ancestor of modern Archaea is believed to have given rise to Eukarya, the third domain of life. Archaeal and bacterial phyla are shown; the evolutionary relationship between these phyla is still 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

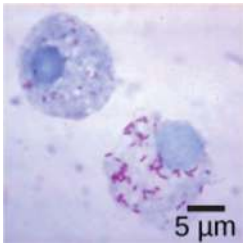
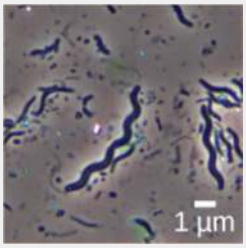
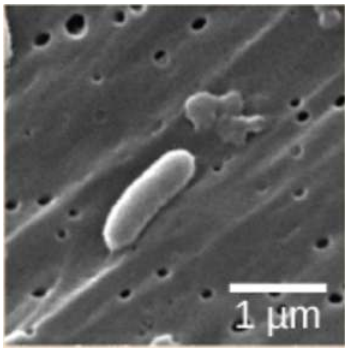
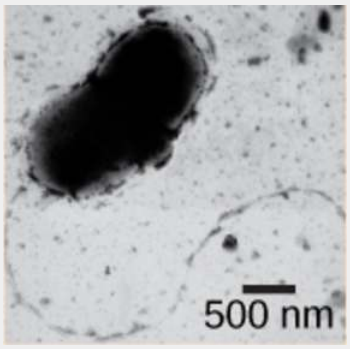
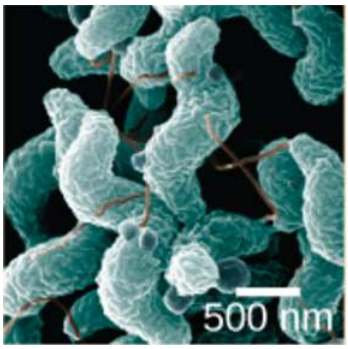
Class	Representative organisms	Representative micrograph
Alpha proteobacteria: Some species are photoautotrophic, but some are symbionts of plants and animals, and others are pathogens. Eukaryotic mitochondria are thought to be derived from bacteria in this group.	*Rhizobium*: Nitrogen-fixing endosymbiont 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

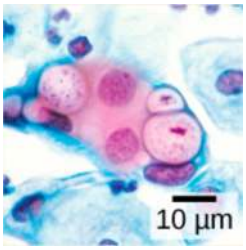
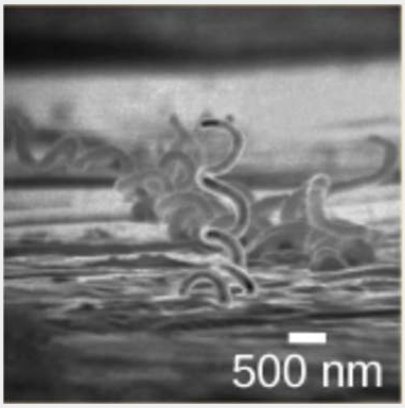
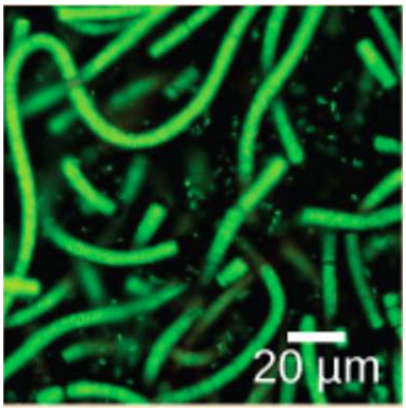
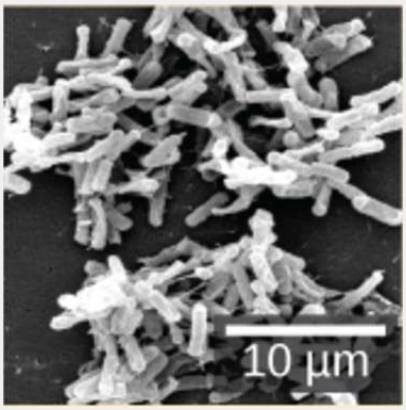
Phylum	Representative organisms	Representative micrograph
Chlamydias All members of this group are obligate intracellular parasites of animal cells. Cell walls lack peptidoglycan	*Chlamydia trachomatis*: Common sexually transmitted disease that can lead to blindness	 In this pap smear, *Chlamydia trachomatis* 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*

Table 2. Bacteria: Chlamydia, Spirochetes, Cyanobacteria, and Gram-positive

Phylum	Representative organisms	Representative micrograph
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*

(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

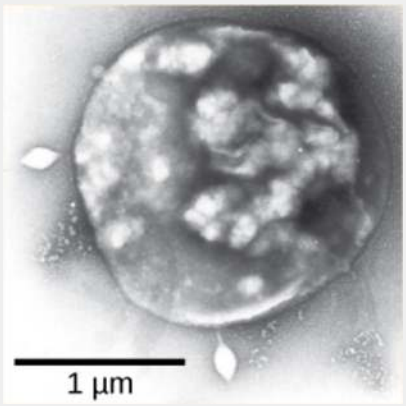
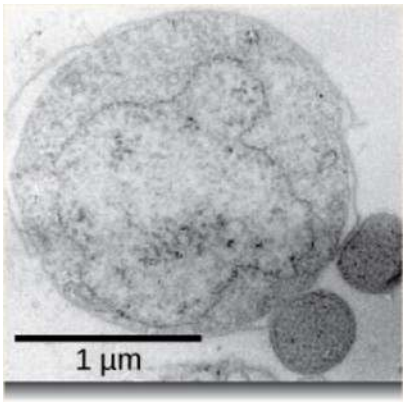
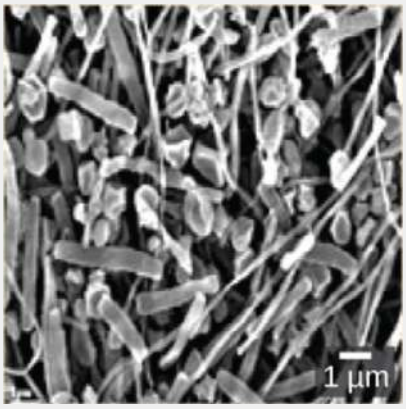
Phylum	Representative organisms	Representative micrograph
Euryarchaeota This phylum includes methanogens, which produce methane as a metabolic waste product, and halobacteria, which live in an extreme saline environment.	*Methanogens*: Methane production causes flatulence in humans and other animals. *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*

Table 3. Archaea

Phylum	Representative organisms	Representative micrograph
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.	 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).

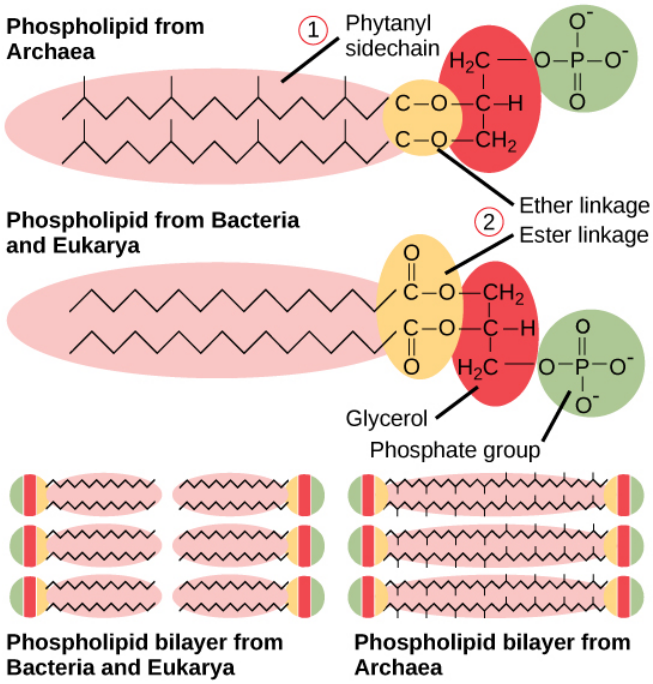


Figure 2. Archaeal phospholipids differ from those found in Bacteria and Eukarya in two ways. First, they have branched phytanyl sidechains instead of linear ones. Second, an ether bond instead of an ester bond connects the lipid to the glycerol.

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.

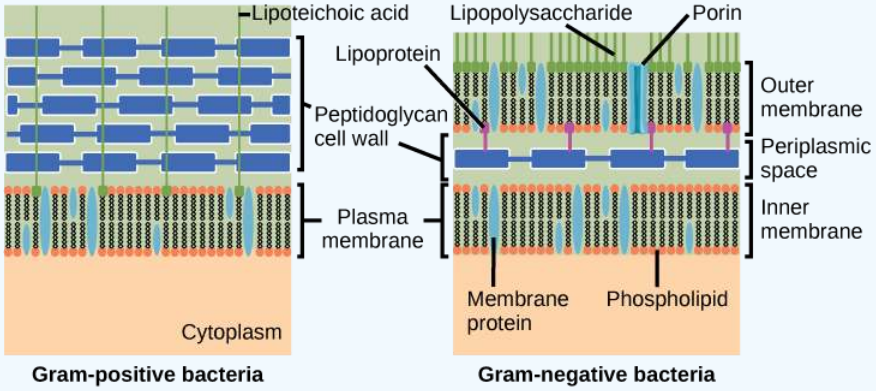


Figure 3. Gram-positive and -negative bacteria (credit: modification of work by "Franciscosp2"/Wikimedia Commons)

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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6.8: Prokaryotic Species Identification

Learning Objectives

- Explain how prokaryotic species are identified

To this point we have talked about the two broad domains of prokaryotes: Archaea and Bacteria. Before continuing our study of these organisms, it is important to address a basic question: *how does one define a prokaryotic species*? This may seem like a basic question, but it's a complex and even controversial one if you're a microbiologist.

For eukaryotes, most scientists define a species as a group of organisms that can interbreed and have fertile offspring. This definition makes sense for species that reproduce sexually, but it doesn't work so well for organisms like bacteria. Bacteria reproduce asexually to make clones of themselves—they don't interbreed.

Scientists instead classify bacteria and archaea into taxonomic groups based on similarities in appearance, physiology, and genes.[1] Many are given names using traditional Linnean taxonomy, wiith a genus and species. Still, the question of how and whether prokaryotes should be grouped into species remains a topic of debate among scientists. The right "species concept" for these organisms is still a work in progress.[2]

Metagenomics: A new window on microbes

Scientists estimate there may be millions of prokaryotic species (or species-like groups), but we know very little about most of them. This is starting to change thanks to large-scale DNA sequencing.

DNA sequencing makes it possible for scientists to study entire prokaryotic communities in their natural habitat—including the many prokaryotes that are unculturable, and would previously have been "invisible" to researchers.

The collective genome of such a community is called its metagenome, and the analysis of metagenome sequences is known as metagenomics. For example, a DNA sample can be taken from a hot spring microbial mat, such as the beautiful, multicolored mats found in Yellowstone National Park. Even a tiny sample from this rich community includes many, many individuals of different species.[3]



By sequencing and analyzing metagenome DNA samples, scientists can sometimes piece together entire genomes of previously unknown species. In other cases, they use sequence information from specific genes to figure out what types of prokaryotes are present (and how they are related to each other or to known species). The genes found in the DNA samples can also provide clues about the metabolic strategies of the organisms in the community.[4]

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6.9: Introduction to Prokaryotic Metabolism

What you'll learn to do: 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.

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6.10: Needs of Prokaryotes

Learning Objectives

- Identify the macronutrients needed by prokaryotes, and explain their importance

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

[reveal-answer q=”957849″]Show Answer[/reveal-answer]
[hidden-answer a=”957849″]Answer c. Nutrients are the substances needed to sustain life.[/hidden-answer]

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6.11: How Prokaryotes Get Energy

Learning Objectives

- Describe the ways in which prokaryotes get energy and carbon for life processes

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).

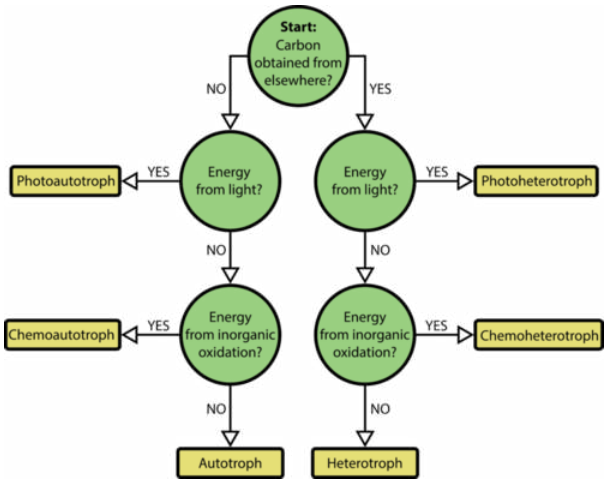


Figure 1. This flowchart helps to determine if a species is an autotroph or a heterotroph, a phototroph or a chemotroph. For example, "Obtain carbon elsewhere?" asks if the source of carbon is another organism. If the answer is "yes", the organism is heterotrophic. If the answer is "no," the organisms 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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6.12: Role of Prokaryotes in Ecosystems

Learning Objectives

- Describe the roles of prokaryotes in the carbon cycle
- Describe the roles of prokaryotes in the nitrogen cycle

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.

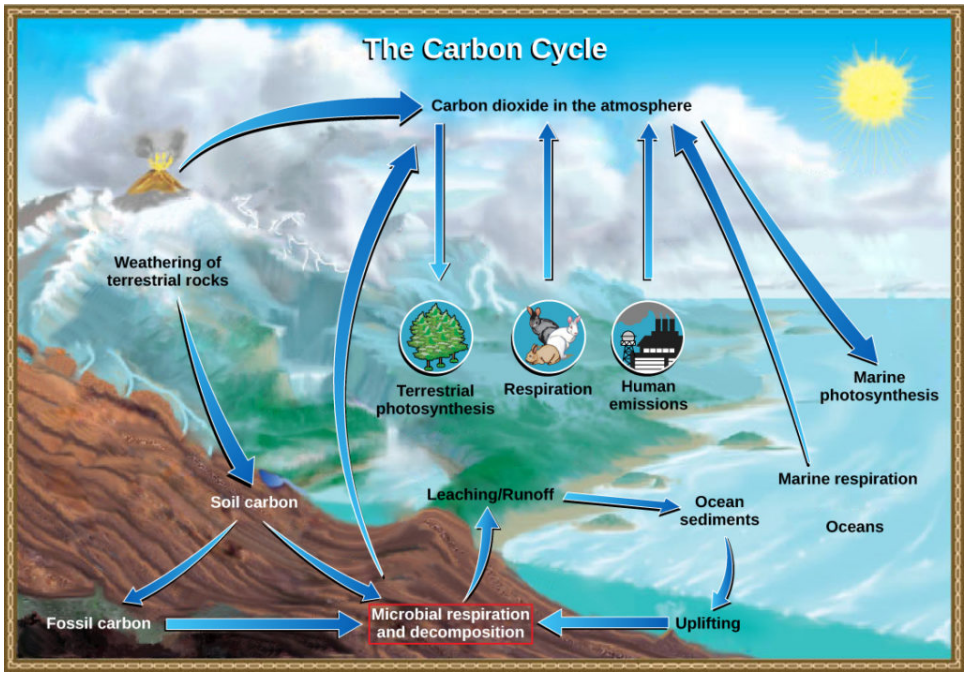


Figure 1. Prokaryotes play a significant role in continuously moving carbon through the biosphere. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

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**.

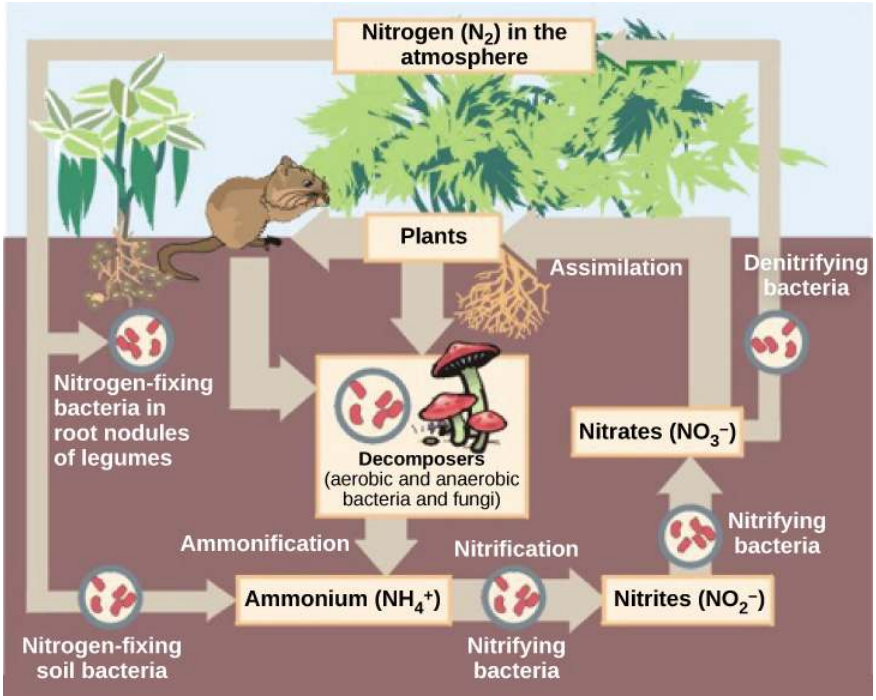


Figure 2. Prokaryotes play a key role in the nitrogen cycle. (credit: Environmental Protection Agency)

? 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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6.13: Introduction to Bacterial Diseases in Humans

What you'll learn to do: 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.

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6.14: Long History of Bacterial Disease

Learning Objectives

- Identify bacterial diseases that caused historically important plagues and epidemics

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.

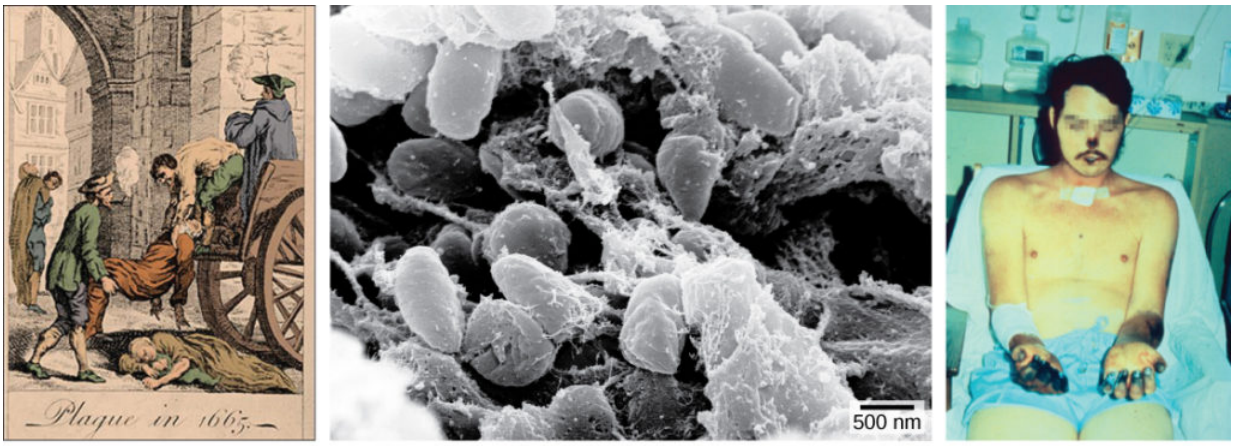


Figure 2. The (a) Great Plague of London killed an estimated 200,000 people, or about twenty percent of the city's population. The causative agent, the (b) bacterium *Yersinia pestis*, is a Gram-negative, rod-shaped bacterium from the class Gamma Proteobacteria. The disease is transmitted through the 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**), or 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.

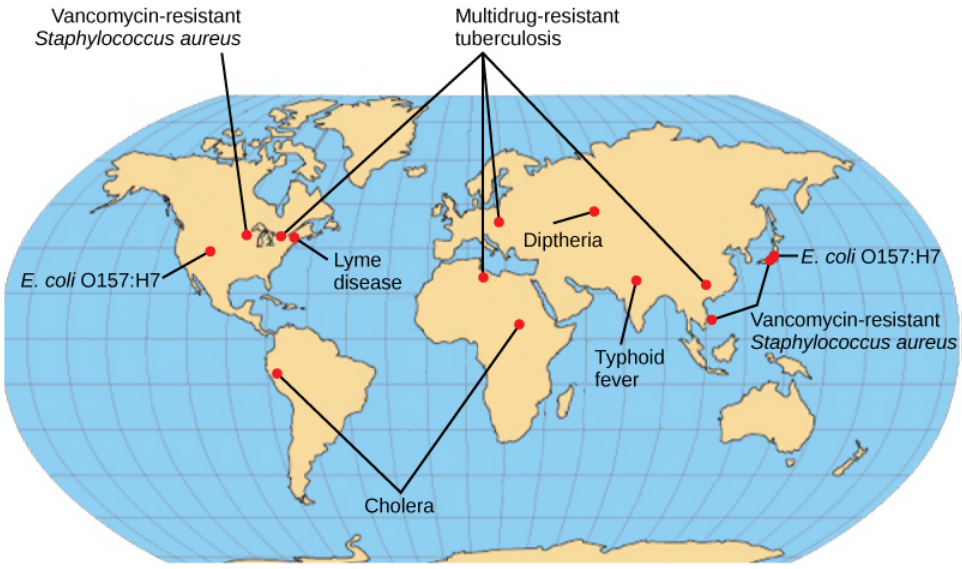


Figure 3. The map shows regions where bacterial diseases are emerging or reemerging. (credit: modification of work by NIH)

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.

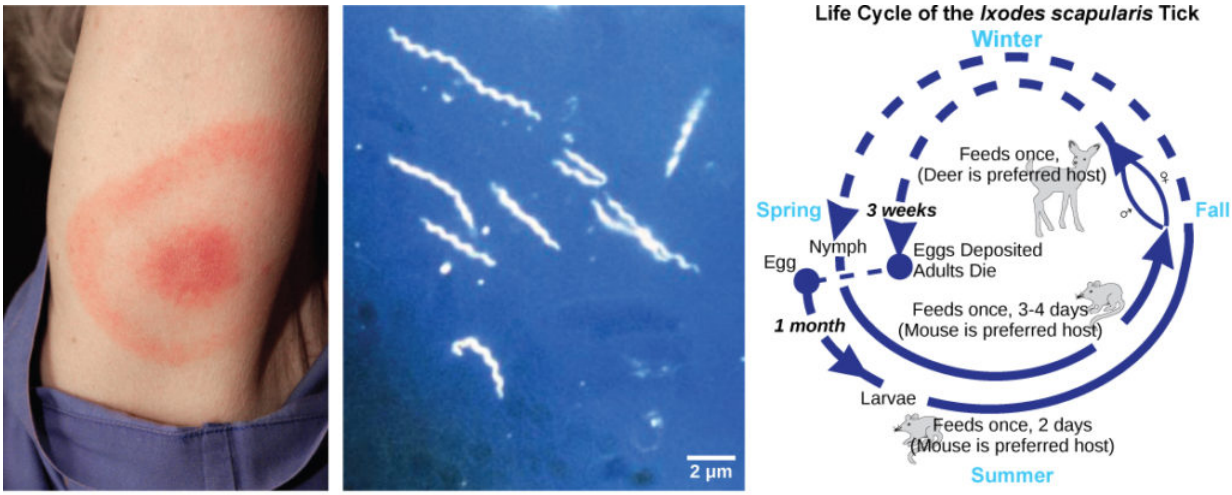


Figure 4. Lyme disease often, but not always, results in (a) a characteristic bullseye rash. The disease is caused by a (b) Gram-negative spirochete bacterium of the genus *Borrelia*. The bacteria (c) infect ticks, which in turns infect mice. Deer are the preferred secondary host, but the ticks also 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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6.15: Antibiotic Resistance

Learning Objectives

- Explain how overuse of antibiotics may be creating “superbugs”

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.

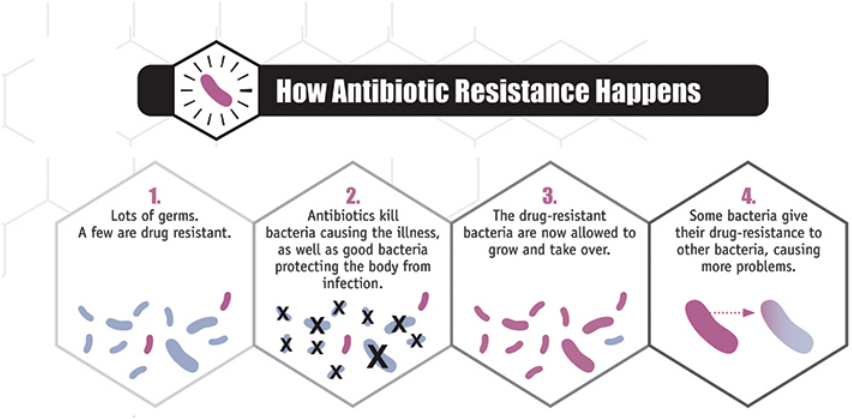
Watch a recent news report on the problem of routine antibiotic administration to livestock and antibiotic-resistant bacteria.

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 of different species 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



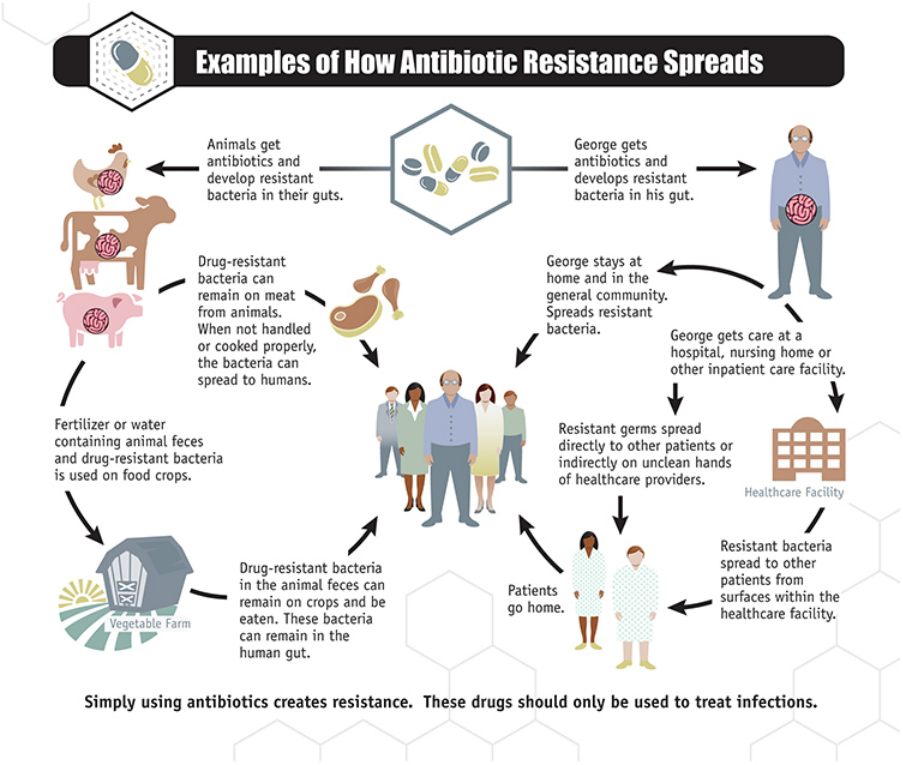
How Resistance Spreads

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

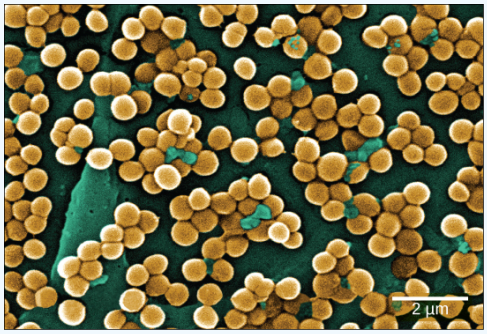


Figure 1. This scanning electron micrograph shows methicillin-resistant *Staphylococcus aureus* bacteria, commonly known as MRSA. *S. aureus* is not always pathogenic, but can cause diseases such as food poisoning and skin and respiratory infections. (credit: modification of work by Janice Haney Carr; 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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6.16: Introduction to Beneficial Prokaryotes

What you'll learn to do: 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. Prokaryotes and other microscopic organisms also play important direct roles in human lives, including processing food, breaking down environmental contaminants, and influencing human health.

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6.17: Food from Bacteria

Learning Outcomes

- Identify foods in which prokaryotes are used in the processing

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).

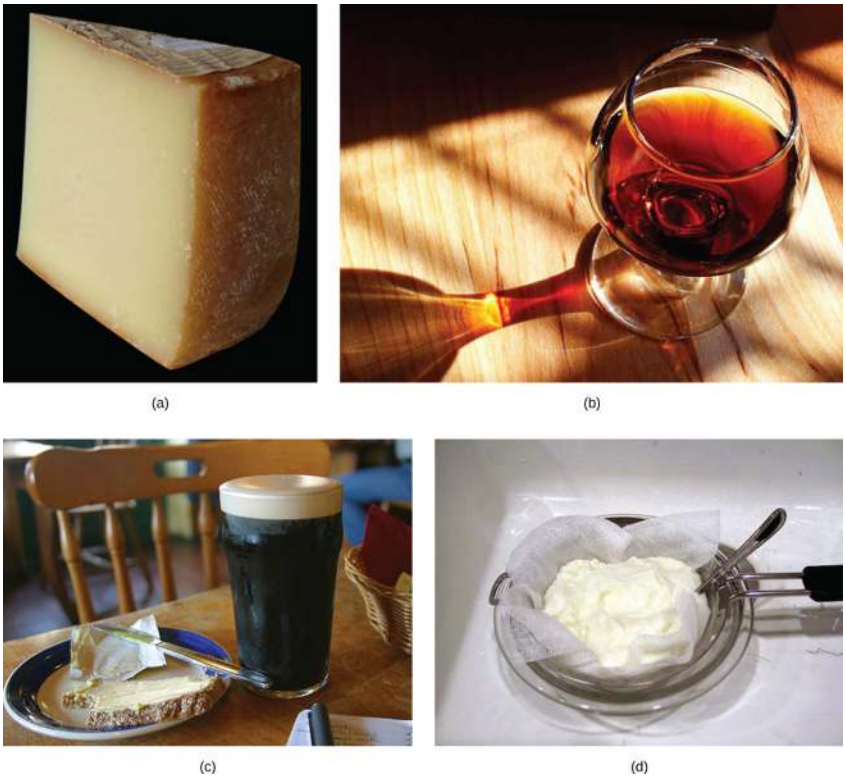


Figure 1. Some of the products derived from the use of prokaryotes in early biotechnology include (a) cheese, (b) wine, (c) beer and bread, and (d) yogurt. (credit bread: modification of work by F. Rodrigo/Wikimedia Commons; credit wine: modification of work by Jon Sullivan; credit beer and bread: modification 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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6.18: Bioremediation

Learning Outcomes

- Describe the use of prokaryotes in 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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6.19: Microbes and the Human Body

Learning Outcomes

- Describe the beneficial effects of bacteria that colonize our skin and digestive tracts

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.

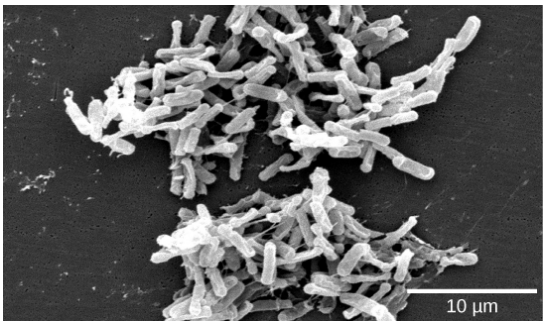


Figure 1. This scanning electron micrograph shows *Clostridium difficile*, a Gram-positive, rod-shaped bacterium that causes severe diarrhea. Infection commonly occurs after the normal gut fauna is eradicated by antibiotics. (credit: modification of work by CDC, HHS; scale-bar data from Matt Russell)

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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6.20: 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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CHAPTER OVERVIEW

7: Module 4- Protists

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7.2: Introduction to the Characteristics of Protists
7.3: Cell Structure and Motility
7.4: Metabolism
7.5: Life Cycles and Habitats
7.6: Groups of Protists
7.7: Introduction to the Ecology of Protists
7.8: Primary Producers
7.9: Protists as Decomposers
7.10: Pathogenic Protists
7.11: Putting It Together- Protists

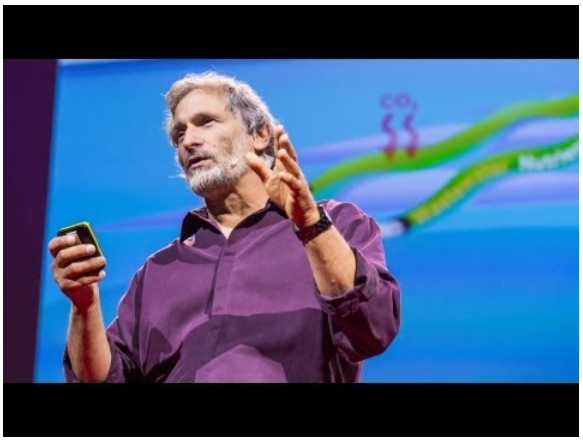
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7.1: Why It Matters- Protists

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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- 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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7.2: Introduction to the Characteristics of Protists

What you'll learn to do: 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.

Traditionally, protists were classified due to their size, shape and color. When Robert Whittaker proposed original Kingdom, he recognized that some members did not fit an easily identifiable mold. With the advent of genetic testing, the entire classification and description of this group has changed, resulting in new species and new genealogy.

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7.3: Cell Structure and Motility

Learning Objectives

- Describe the cell structure of protists
- Describe the motility of protists

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**.

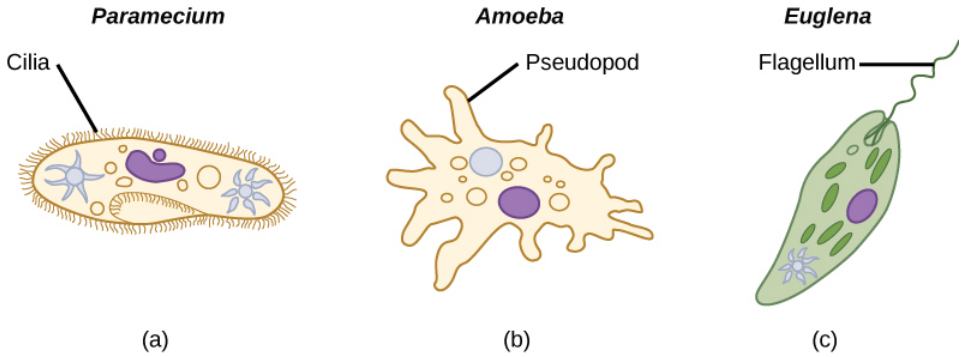


Figure 1. Protists use various methods for transportation. (a) *Paramecium* waves hair-like appendages called cilia to propel itself. (b) *Amoeba* uses lobe-like pseudopodia to anchor itself to a solid surface and pull itself forward. (c) *Euglena* uses a whip-like tail called a flagellum to propel itself.

Some protists can move toward or away from a stimulus, a movement referred to as taxis. For example, 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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7.4: Metabolism

Learning Outcomes

- Describe the metabolic diversity of protists

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.

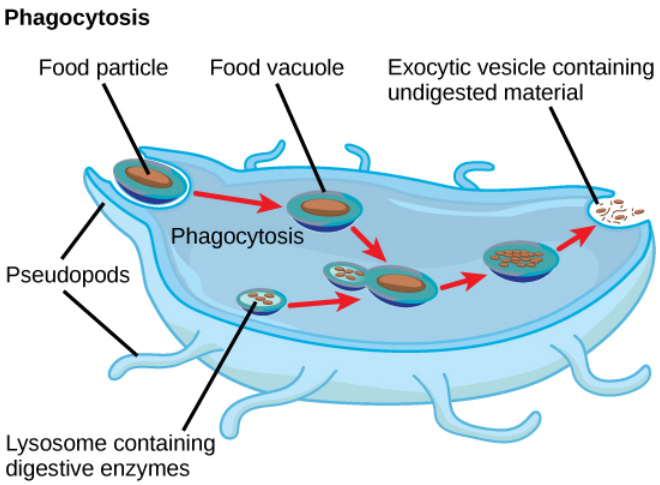


Figure 1. The stages of phagocytosis include the engulfment of a food particle, the digestion of the particle using hydrolytic enzymes contained within a lysosome, and the expulsion of undigested materials from the cell.

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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7.5: Life Cycles and Habitats

Learning Objectives

- Describe the life cycle and habitat diversity of protists

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* exhibit 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 protists 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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7.6: Groups of Protists

Learning Objectives

- Differentiate between groups of protists

In the span of several decades, the Kingdom Protista has been disassembled because sequence analyses have revealed new genetic (and therefore evolutionary) relationships among these eukaryotes. Moreover, protists that exhibit similar morphological features may have evolved analogous structures because of similar selective pressures—rather than because of recent common ancestry. This phenomenon, called convergent evolution, is one reason why protist classification is so challenging. 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.

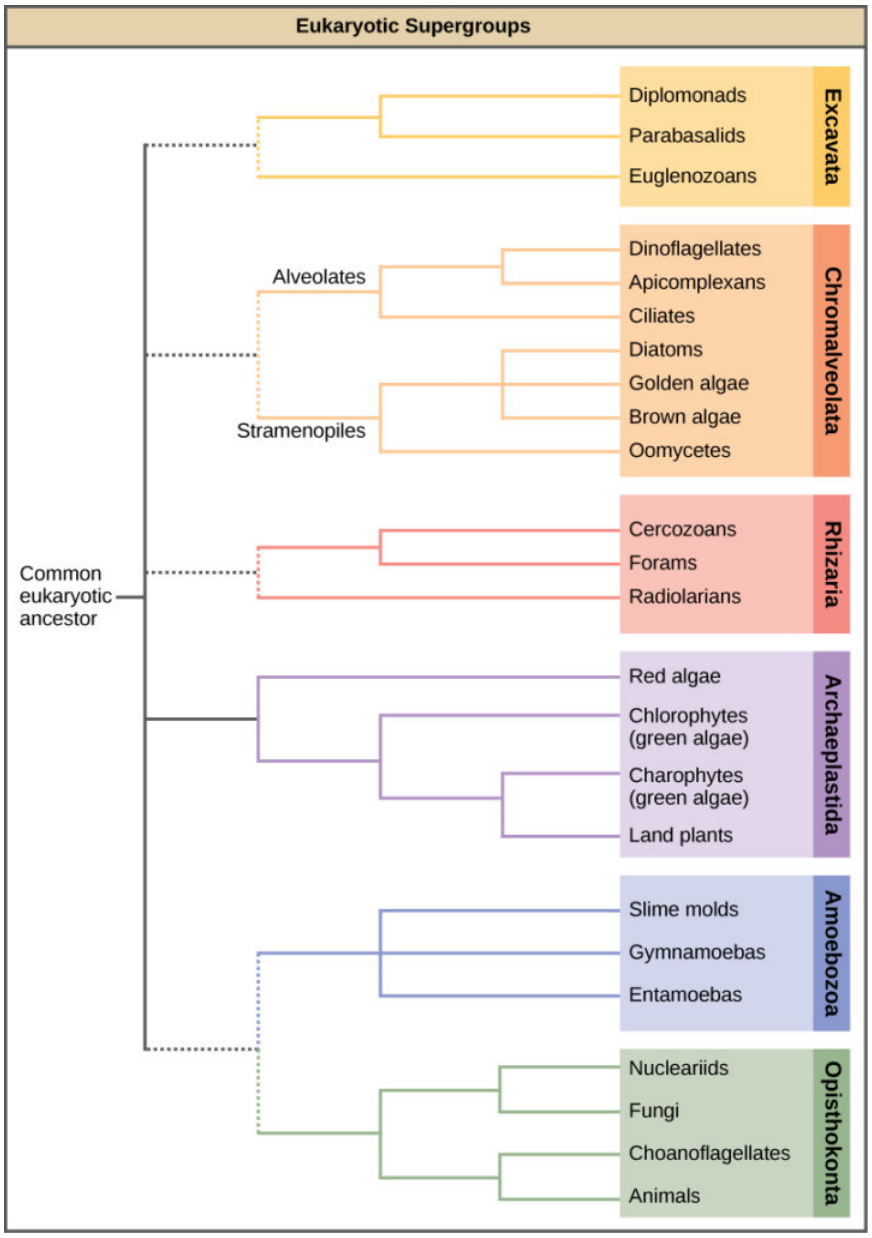


Figure 1. This diagram shows a proposed classification of the domain Eukarya. Currently, the domain Eukarya is divided into six supergroups. Within each supergroup are multiple kingdoms. Dotted lines indicate suggested evolutionary relationships that remain under debate.

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.

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 2. 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 2). 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.

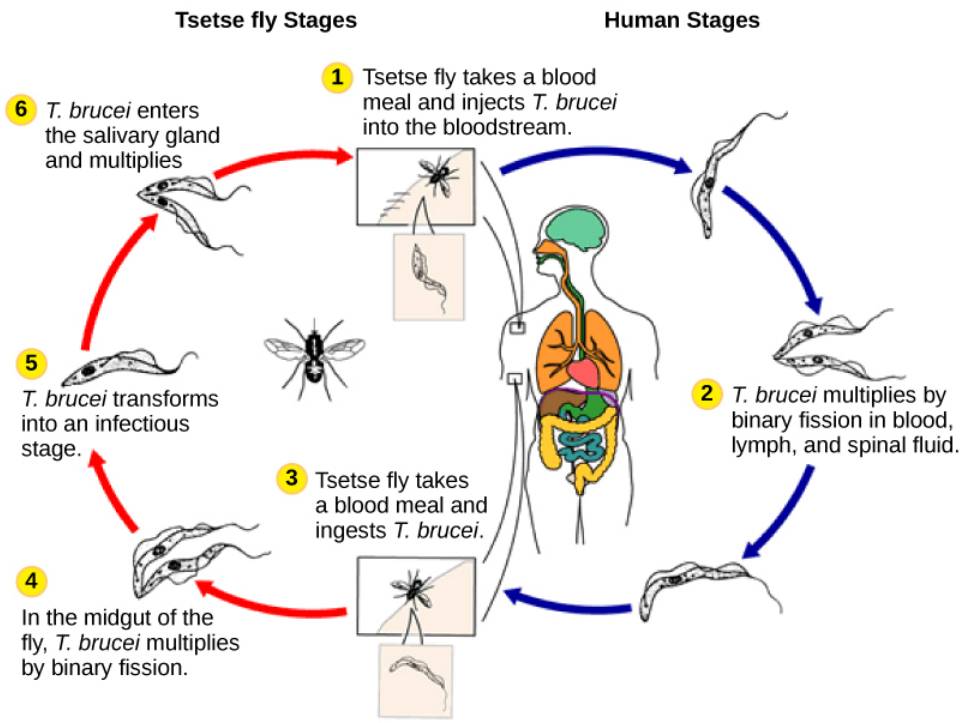


Figure 3. *Trypanosoma brucei*, the causative agent of sleeping sickness, spends part of its life cycle in the tsetse fly and part in humans. (credit: modification of work by CDC)

Watch this video to see *T. brucei* swimming. Note that there is no audio in this video.



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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.

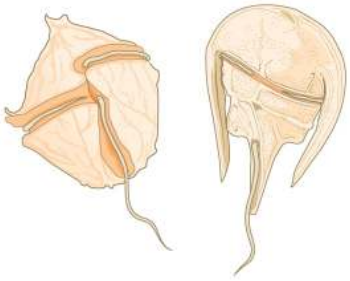


Figure 4. The dinoflagellates exhibit great diversity in shape. Many are encased in cellulose armor and have two flagella that fit in grooves between the plates. Movement of these two perpendicular flagella causes a spinning motion.

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 4). 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 5). 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 5. 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 6). 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.

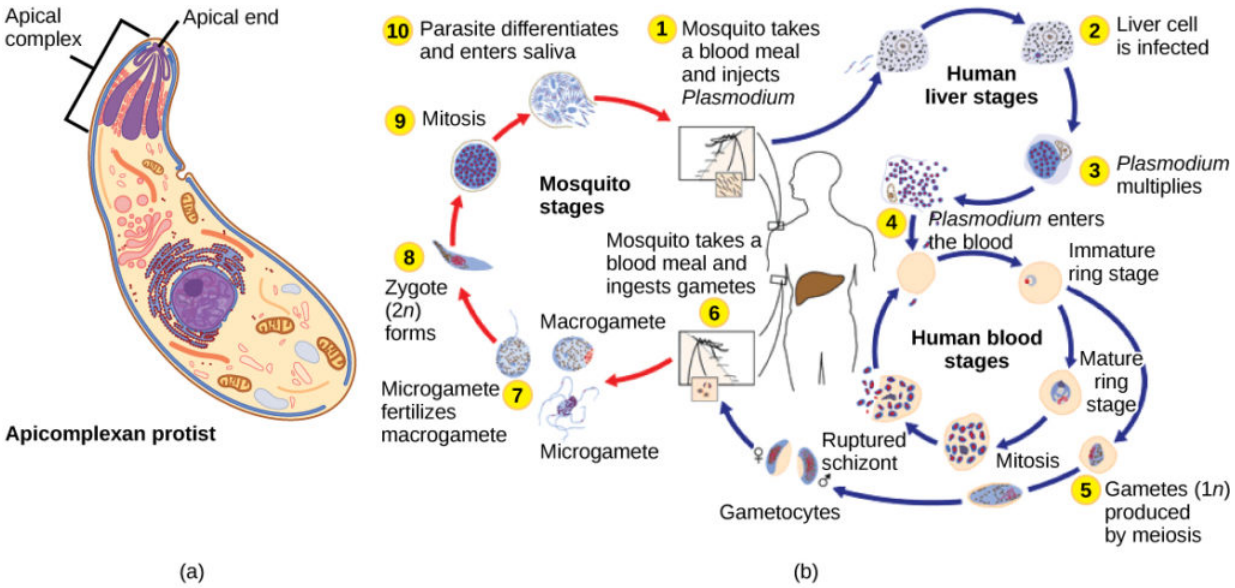


Figure 6. (a) Apicomplexans are parasitic protists. They have a characteristic apical complex that enables them to infect host cells. (b) Plasmodium, the causative agent of malaria, has a complex life cycle typical of apicomplexans. (credit b: modification of work by CDC)

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 7). 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.

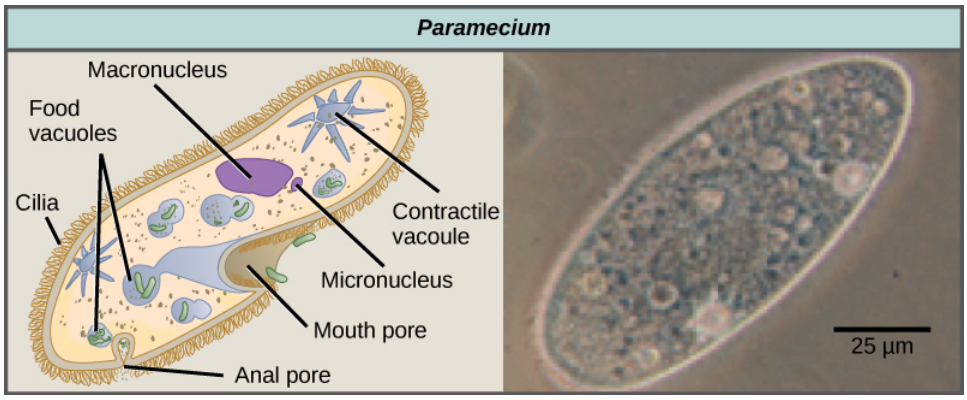


Figure 7. *Paramecium* has a primitive mouth (called an oral groove) to ingest food, and an anal pore to excrete it. Contractile vacuoles allow the organism to excrete excess water. Cilia enable the organism to move. (credit "paramecium micrograph": modification of work by NIH; scale-bar data from Matt 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 8). 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.

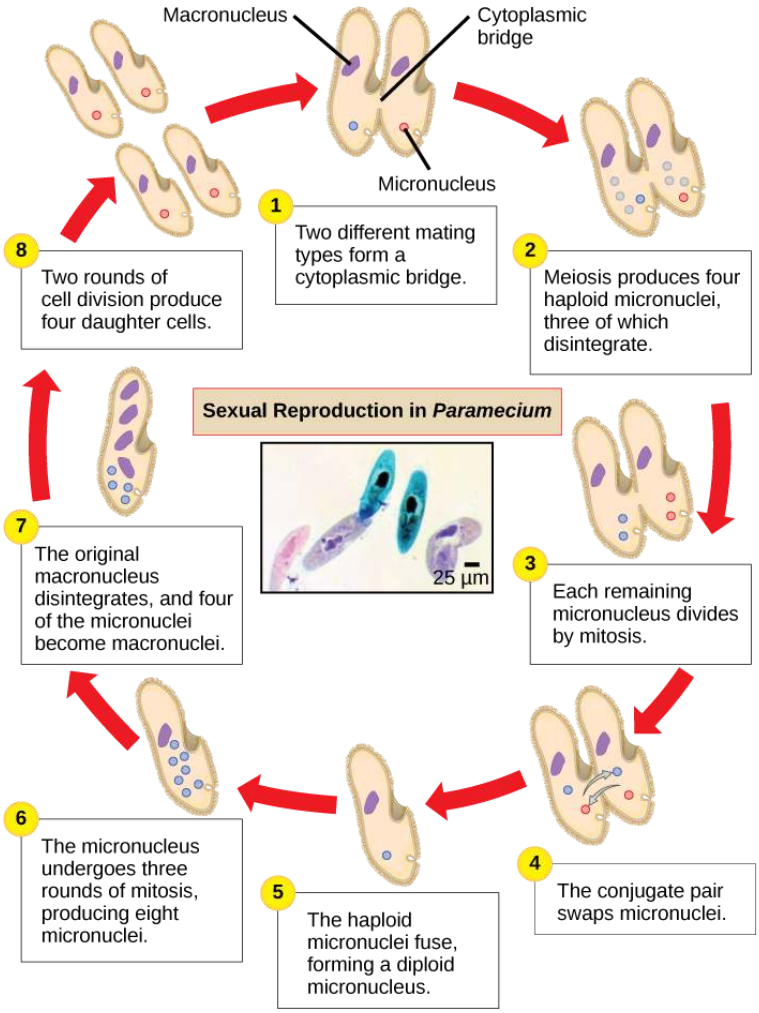


Figure 8. The complex process of sexual reproduction in *Paramecium* creates eight daughter cells from two original cells. Each cell has a macronucleus and a micronucleus. During sexual reproduction, the macronucleus dissolves and is replaced by a micronucleus. (credit "micrograph": modification of work 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]

Stramenopiles: Diatoms, Brown Algae, Golden Algae and Oomycetes

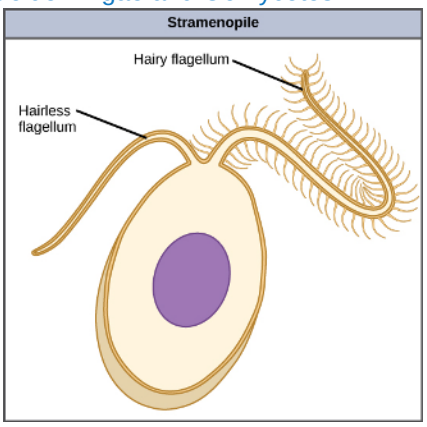


Figure 9. This stramenopile cell has a single hairy flagellum and a secondary smooth flagellum.

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 9). 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 10). 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.

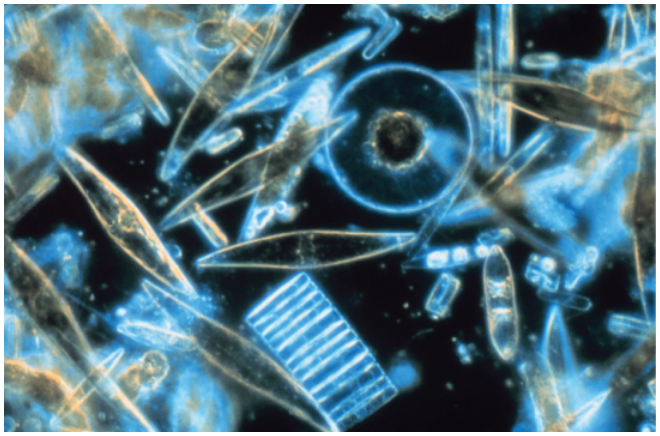


Figure 10. Assorted diatoms, visualized here using light microscopy, live among annual sea ice in McMurdo Sound, Antarctica. Diatoms range in size from 2 to 200 µm. (credit: Prof. Gordon T. Taylor, Stony Brook University, NSF, NOAA)

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 11). Certain other organisms perform alternation of generations in which both the haploid and diploid forms look the same.

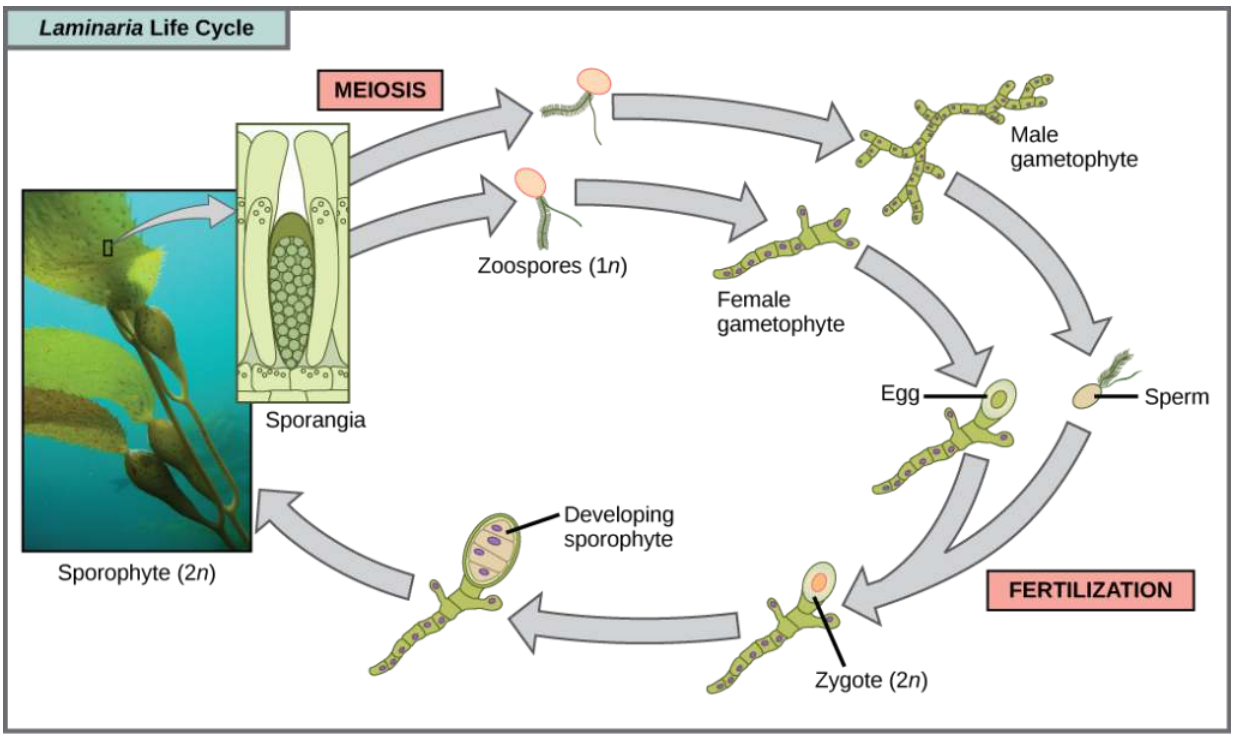


Figure 11. Several species of brown algae, such as the Laminaria shown here, have evolved life cycles in which both the haploid (gametophyte) and diploid (sporophyte) forms are multicellular. The gametophyte is different in structure than the sporophyte. (credit “laminaria photograph”: modification of 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 12. 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 12).

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.

Rhizaria

The Rhizaria supergroup includes many of the amoebas, most of which have threadlike or needle-like pseudopodia (*Ammoniatepida*, a Rhizaria species, can be seen in Figure 13).

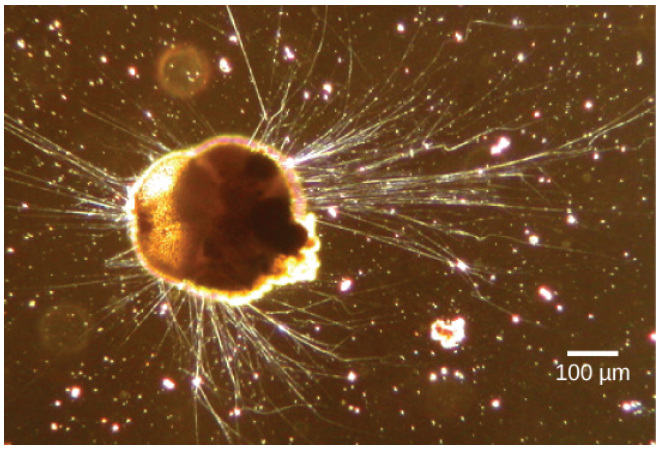
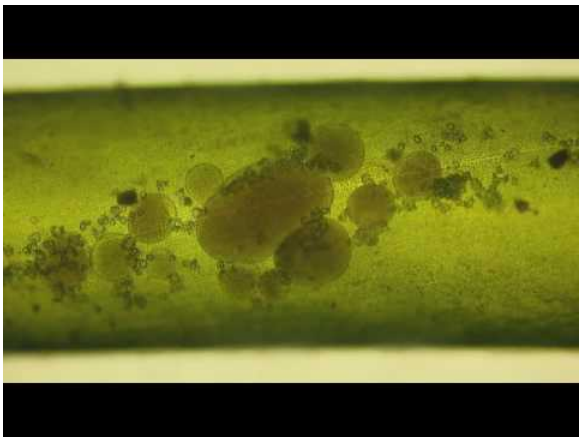


Figure 13. *Ammonia tepida*, under a phase contrast light microscope (credit: modification of work by Scott Fay, UC Berkeley; scale-bar data from Matt Russell)

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 14. 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 14).

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

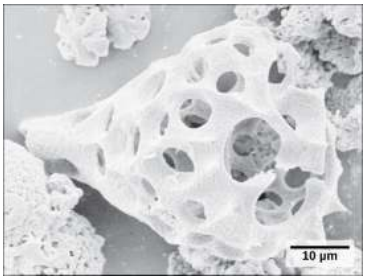


Figure 15. This fossilized radiolarian shell was imaged using a scanning electron microscope. (credit: modification of work by Hannes Grobe, Alfred Wegener Institute; scale-bar data from Matt Russell)

A second subtype of Rhizaria, the radiolarians, exhibit intricate exteriors of glassy silica with radial or bilateral symmetry (Figure 15). Needle-like pseudopods supported by microtubules radiate outward from the cell bodies of these protists and function to catch food particles. The shells of dead radiolarians sink to the ocean floor, where they may accumulate in 100 meter-thick depths. Preserved, sedimented radiolarians are very common in the fossil record.

Archaeplastida

Red algae and green algae are included in the supergroup Archaeplastida. It was from a common ancestor of these protists that the land plants evolved, since their closest relatives are found in this group. Molecular evidence supports that all Archaeplastida are

descendents of an endosymbiotic relationship between a heterotrophic protist and a cyanobacterium. The red and green algae include unicellular, multicellular, and colonial forms.

Red Algae

Red algae, or rhodophytes, are primarily multicellular, lack flagella, and range in size from microscopic, unicellular protists to large, multicellular forms grouped into the informal seaweed category. The red algae life cycle is an alternation of generations. Some species of red algae contain phycoerythrins, photosynthetic accessory pigments that are red in color and outcompete the green tint of chlorophyll, making these species appear as varying shades of red. Other protists classified as red algae lack phycoerythrins and are parasites. Red algae are common in tropical waters where they have been detected at depths of 260 meters. Other red algae exist in terrestrial or freshwater environments.

Green Algae: Chlorophytes and Charophytes

The most abundant group of algae is the green algae. The green algae exhibit similar features to the land plants, particularly in terms of chloroplast structure. That this group of protists shared a relatively recent common ancestor with land plants is well supported. The green algae are subdivided into the chlorophytes and the charophytes. The charophytes are the closest living relatives to land plants and resemble them in morphology and reproductive strategies. Charophytes are common in wet habitats, and their presence often signals a healthy ecosystem.

The chlorophytes exhibit great diversity of form and function. Chlorophytes primarily inhabit freshwater and damp soil, and are a common component of plankton. *Chlamydomonas* is a simple, unicellular chlorophyte with a pear-shaped morphology and two opposing, anterior flagella that guide this protist toward light sensed by its eyespot. More complex chlorophyte species exhibit haploid gametes and spores that resemble *Chlamydomonas*.

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 16). *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 *Volvox* cells 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.



Figure 16. *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 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 17). *Caulerpa* species undergo nuclear division, but their cells do not complete cytokinesis, remaining instead as massive and elaborate single cells.



Figure 17. *Caulerpa taxifolia* is a chlorophyte consisting of a single cell containing potentially thousands of nuclei. (credit: NOAA)

Amoebozoa

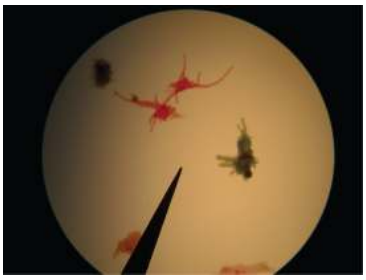


Figure 18. Amoebae with tubular and lobe-shaped pseudopodia are seen under a microscope. These isolates would be morphologically classified as amoebozoans.

The amoebozoans characteristically exhibit pseudopodia that extend like tubes or flat lobes, rather than the hair-like pseudopodia of rhizarian amoeba (Figure 18). 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 19). Food particles are lifted and engulfed into the slime mold as it glides along. Upon maturation, the plasmodium takes on a net-like appearance with the ability to form fruiting bodies, or sporangia, during times of stress. Haploid spores are produced by meiosis within the sporangia, and spores can be disseminated through the air or water to potentially land in more favorable environments. If this occurs, the spores germinate to form ameboid or flagellate haploid cells that can combine with each other and produce a diploid zygotic slime mold to complete the life cycle.

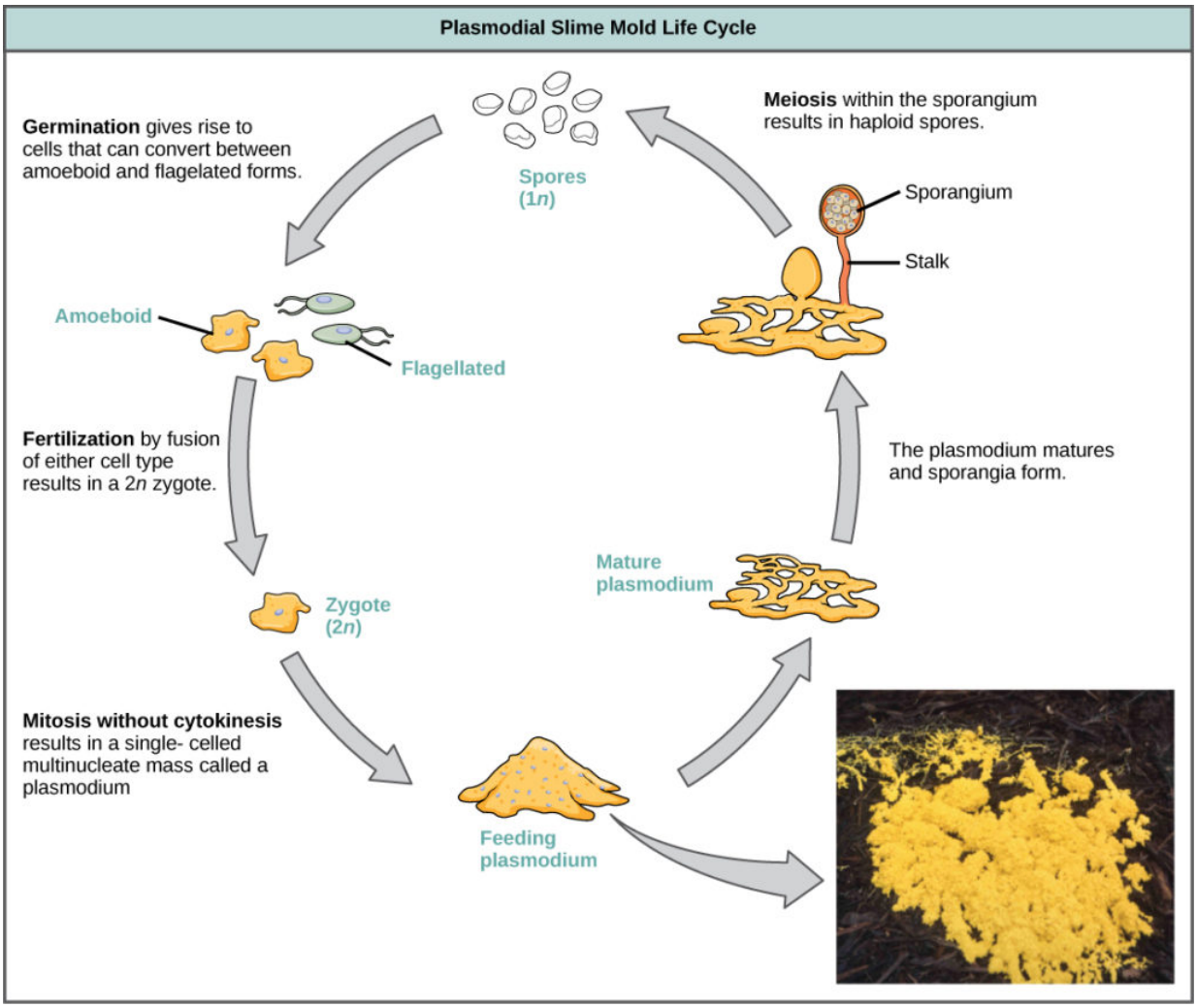


Figure 19. The life cycle of the plasmodial slime mold is shown. The brightly colored plasmodium in the inset photo is a single-celled, multinucleate mass. (credit: modification of work by Dr. Jonatha Gott and the Center for RNA Molecular Biology, Case Western Reserve University)

The cellular slime molds function as independent amoeboid cells when nutrients are abundant (Figure 20). 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.

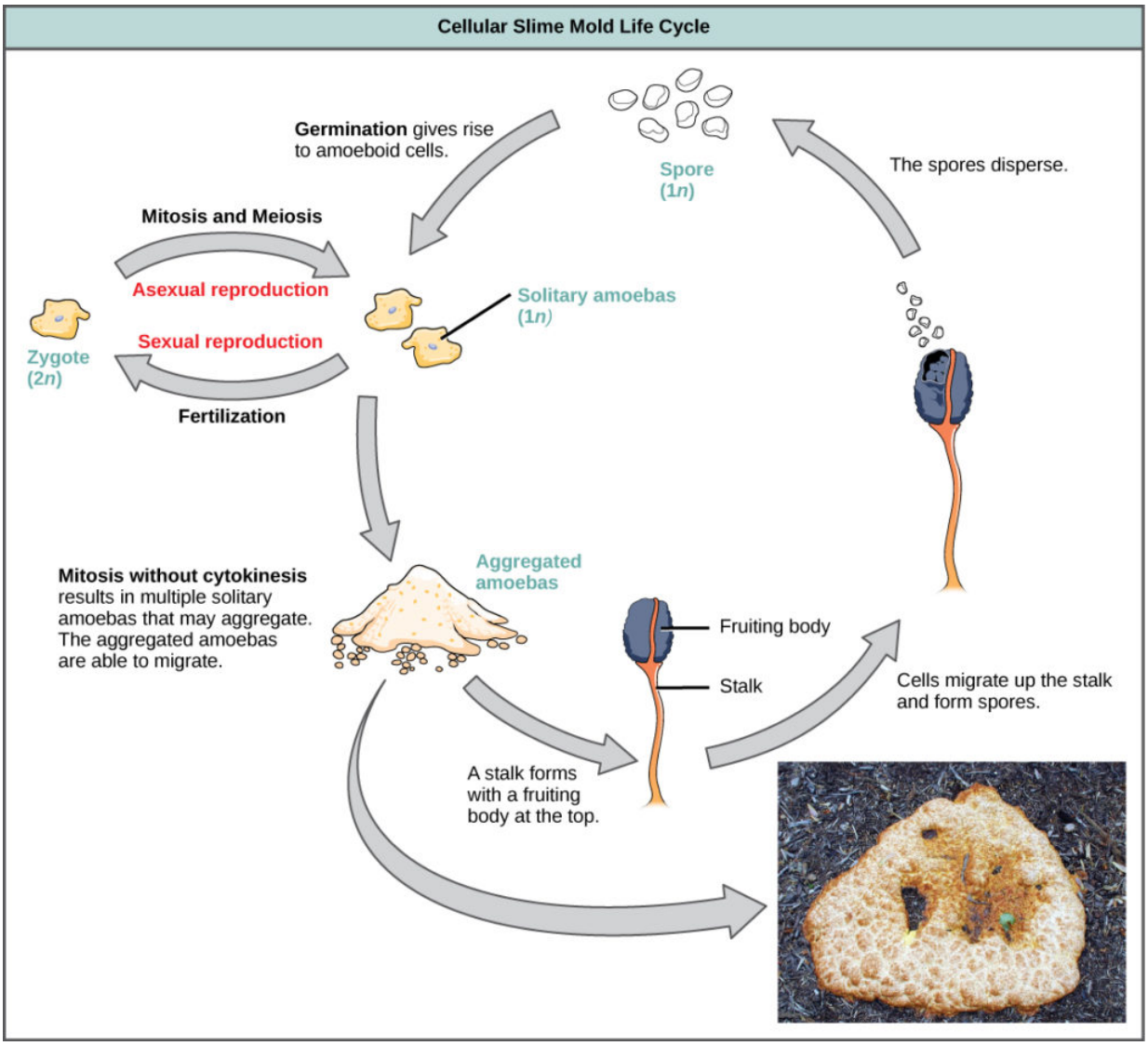
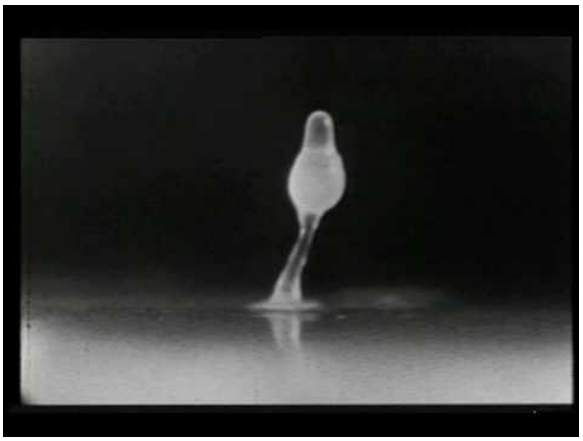


Figure 20. Cellular slime molds may exist as solitary or aggregated amoebas. (credit: modification of work by "thatredhead4"/Flickr)

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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Opisthokonta



Figure 21. 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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7.7: Introduction to the Ecology of Protists

What you'll learn to do: 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.

The key point to remember is that protists have a wide impact on the ecosystem as well at the biosphere as well. Oxygen levels on the planet wouldn't be where they are without plant-like protists going through photosynthesis. There are protists vital to the nitrogen cycle as well as decomposition and recycling of dead organic matter. Science is only now learning the true impact of the group Protista.

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7.8: Primary Producers

Learning Outcomes

- Identify protists that act as 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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7.9: Protists as Decomposers

Learning Outcomes

- Provide examples of the protists' important roles in decomposition

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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7.10: Pathogenic Protists

Learning Objectives

- Describe important pathogenic species of protists with a focus on human impacts

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

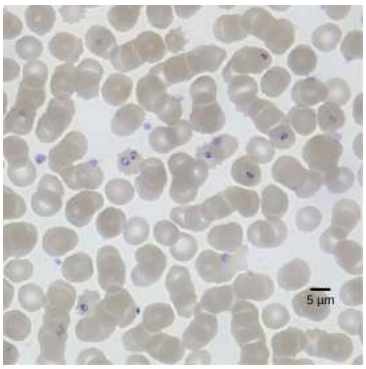


Figure 1. Red blood cells are shown to be infected with *P. falciparum.* In this light microscopic image, the ring-shaped *P. falciparum* stains purple. (credit: modification of work by Michael Zahniser; scale-bar data from Matt Russell)

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.

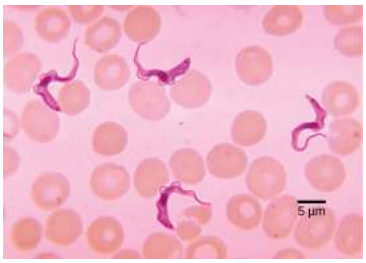


Figure 2. Trypanosomes are shown among red blood cells. (credit: modification of work by Dr. Myron G. Shultz; scale-bar data from Matt Russell)

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.

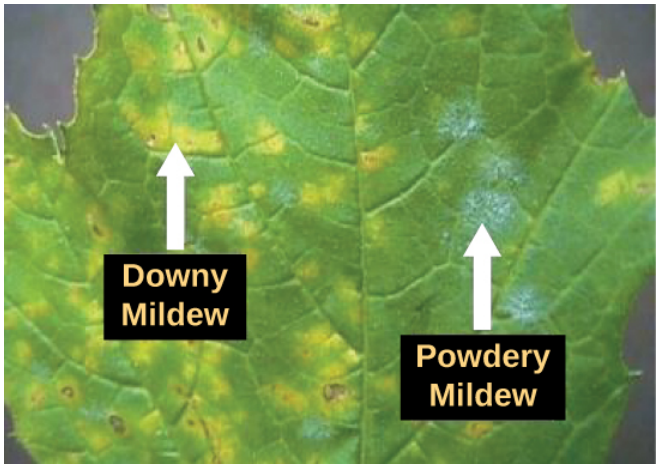


Figure 3. Both downy and powdery mildews on this grape leaf are caused by an infection of *P. viticola*. (credit: modification of work by USDA)



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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7.11: 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, or a fungus. If the organism isn't any of those, then it is 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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CHAPTER OVERVIEW

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8.1: 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.

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8.2: Introduction to the Characteristics of Fungi

What you'll learn to do: 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.

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8.3: Fungal Structure and Habitats

Learning Objectives

- Describe the common structures of fungi
- Identify common habitats of fungi

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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8.4: Nutrition and Growth

Learning Objectives

- Describe the mode of nutrition and growth in fungi

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

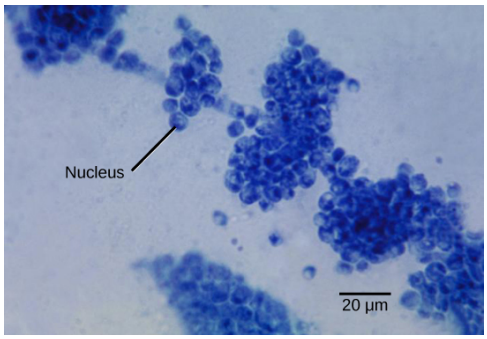


Figure 1. *Candida albicans*. (credit: modification of work by Dr. Godon Roberstad, CDC; scale-bar data from Matt Russell)

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).

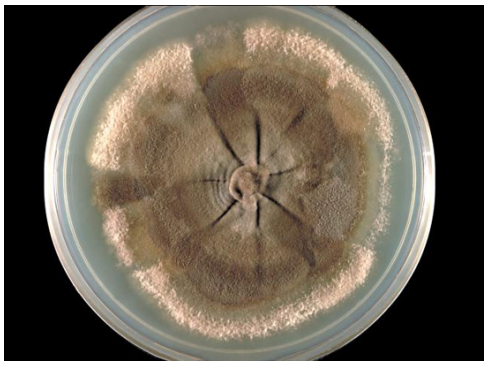


Figure 2. The mycelium of the fungus *Neotestudina rosati* can be pathogenic to humans. The fungus enters through a cut or scrape and develops a mycetoma, a chronic subcutaneous infection. (credit: CDC)

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).

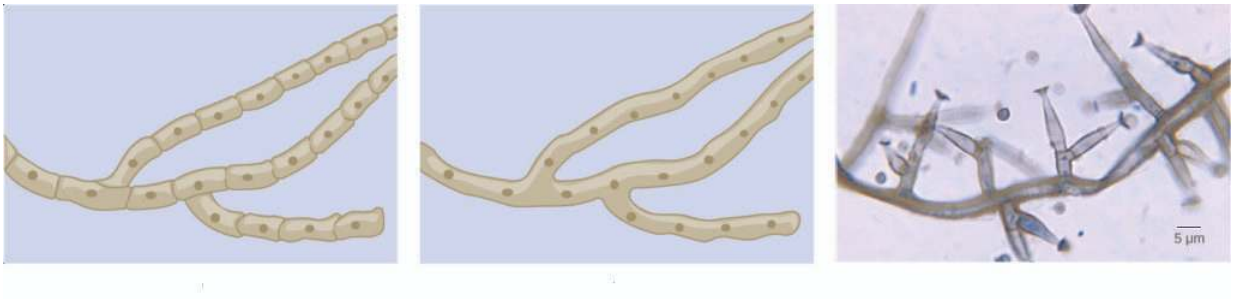


Figure 3. Fungal hyphae may be (a) septated or (b) coenocytic (coeno- = "common"; -cytic = "cell") with many nuclei present in a single hypha. A bright field light micrograph of (c) *Phialophora richardsiae* shows septa that divide the hyphae. (credit c: modification of work by Dr. Lucille Georg, CDC; 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 **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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8.5: Reproduction

Learning Objectives

- Explain sexual and asexual reproduction in fungi

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 shown below illustrates dispersing spores on the wind when it 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

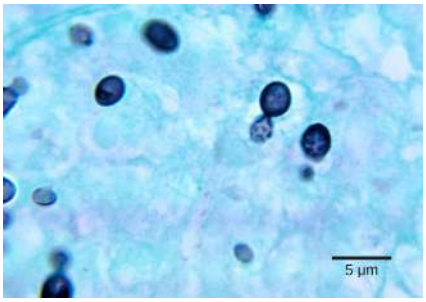


Figure 2. The dark cells in this bright field light micrograph are the pathogenic yeast *Histoplasma capsulatum*, seen against a backdrop of light blue tissue. (credit: modification of work by Dr. Libero Ajello, CDC; scale-bar data from Matt Russell)

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* shown in Figure 2 shows this type of reproduction; it 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.

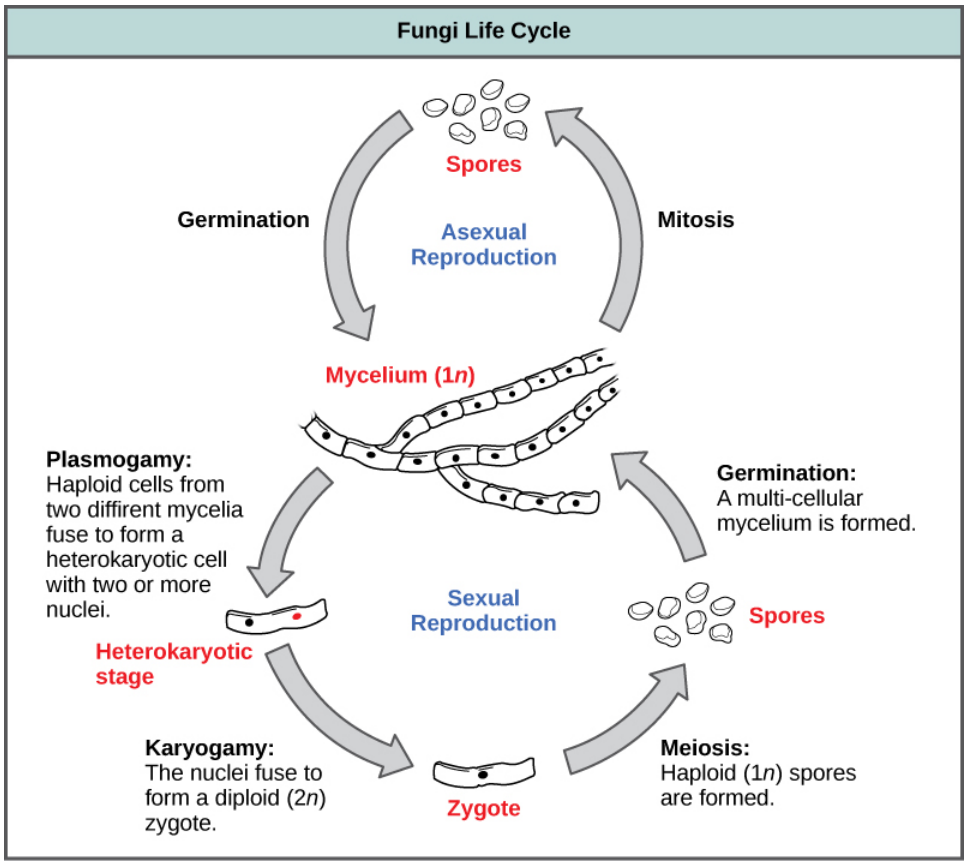


Figure 3. Fungi may have both asexual and sexual stages of reproduction.

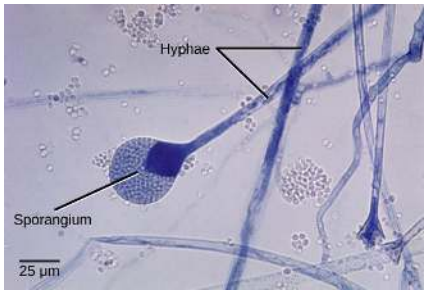


Figure 4. This bright field light micrograph shows the release of spores from a sporangium at the end of a hypha called a sporangiophore. The organism is a *Mucor sp.* fungus, a mold often found indoors. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

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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8.6: Classifications of Fungi

Learning Objectives

- Differentiate among the five phylum of fungi and the informal group Deuteromycota

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.

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.

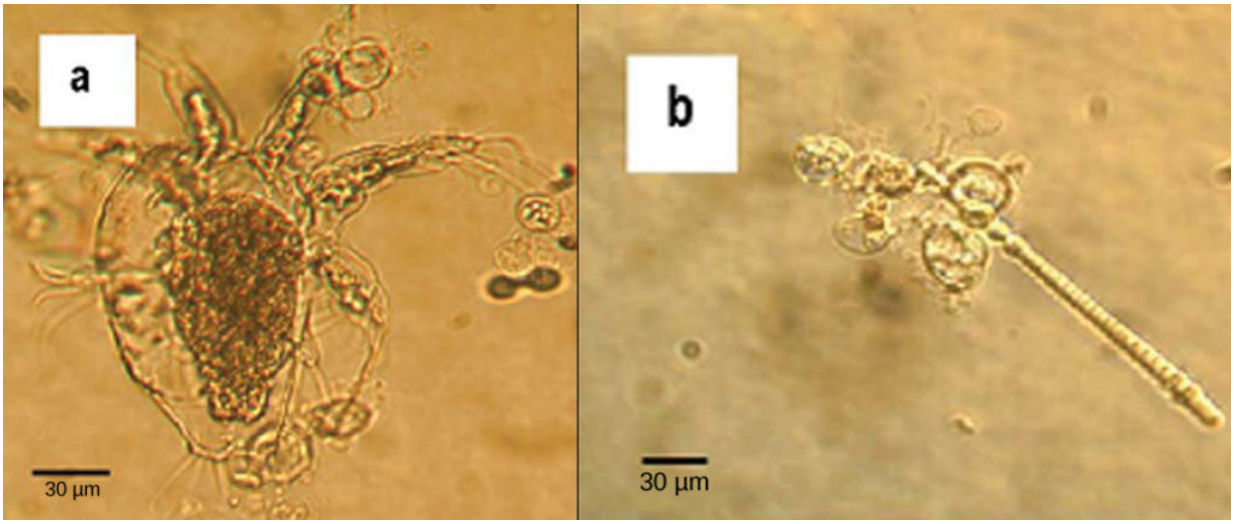


Figure 1. The chytrid *Batrachochytrium dendrobatidis* is seen in these light micrographs as transparent spheres growing on (a) a freshwater arthropod and (b) algae. This chytrid causes skin diseases in many species of amphibians, resulting in species decline and extinction. (credit: modification of work by Johnson ML, Speare R., CDC)

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 2).

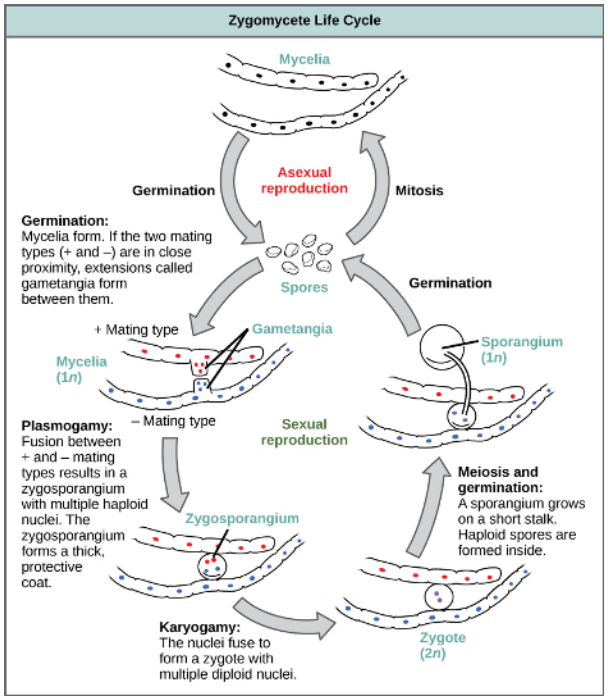


Figure 2. Zygomycetes have asexual and asexual life cycles. In the sexual life cycle, plus and minus mating types conjugate to form a zygosporangium.

The black tips of bread mold are the swollen sporangia packed with black spores (Figure 3). 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.”



Figure 3. 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)

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.

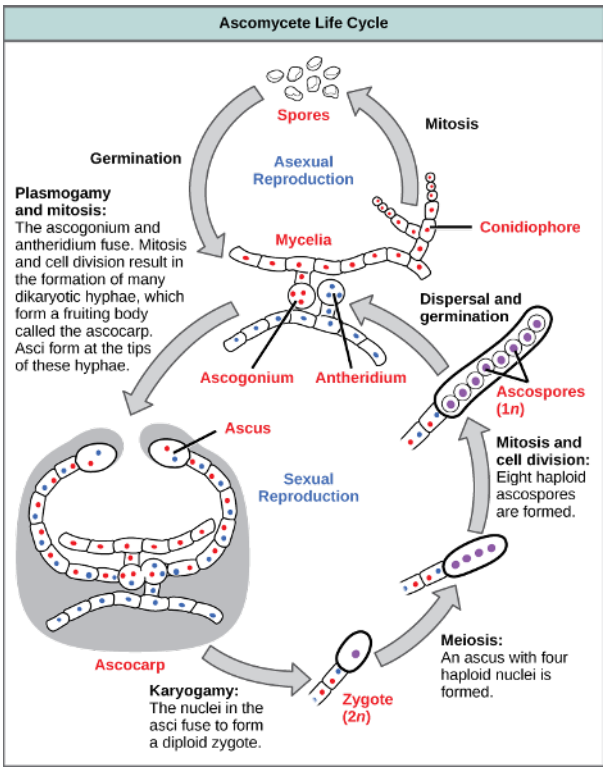


Figure 4. Click for a larger image. The lifecycle of an ascomycete is characterized by the production of asci during the sexual phase. The haploid phase is the predominant phase of the life cycle.

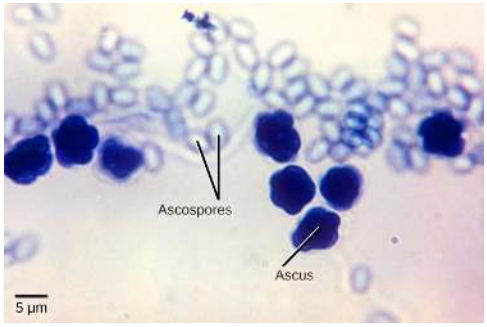


Figure 5. The bright field light micrograph shows ascospores being released from asci in the fungus *Talaromyces flavus* var. *flavus*. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

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 4).

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 5).

? 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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[hidden-answer a=”34326″]Statement a is true.[/hidden-answer]

Basidiomycota: The Club Fungi



Figure 6. 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 6). 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 7). 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.

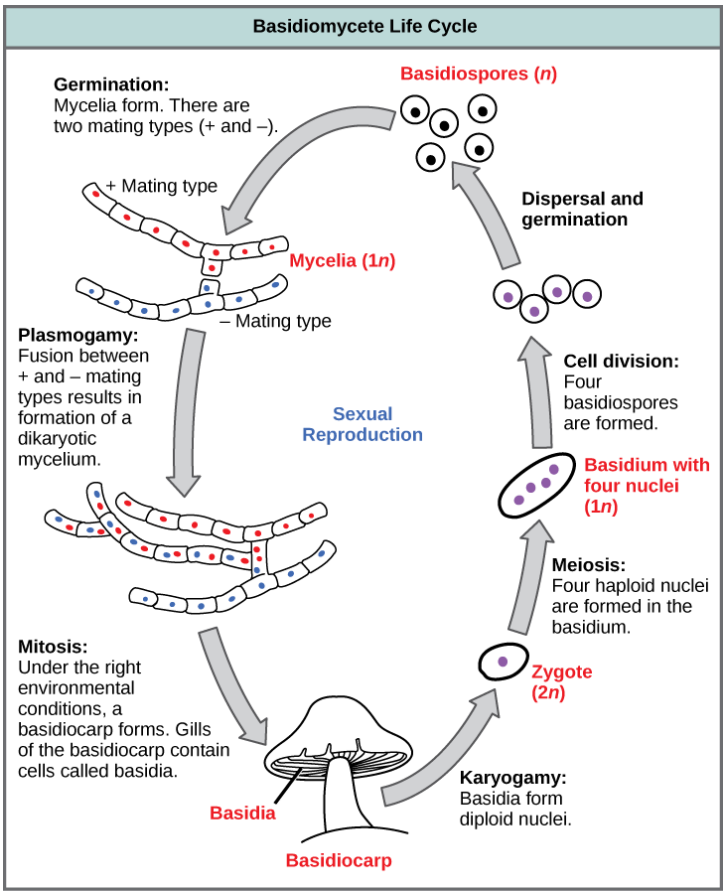


Figure 7. The lifecycle of a basidiomycete alternates generation with a prolonged stage in which two nuclei (dikaryon) are present in the hyphae.

? 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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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.

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.

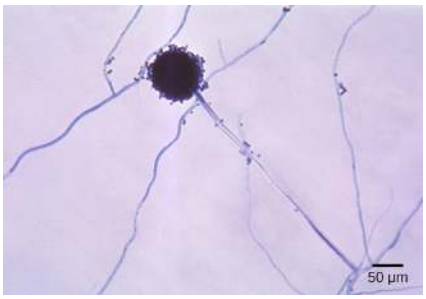


Figure 8. *Aspergillus niger* is an imperfect fungus commonly found as a food contaminant. The spherical structure in this light micrograph is a conidiophore. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Reproduction of Deuteromycota is strictly asexual and occurs mostly by production of asexual conidiospores (Figure 8). 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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8.7: 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.

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8.8: Decomposers and Recyclers

Learning Objectives

- Describe the importance of fungi to the balance of the environment



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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8.9: Mutualistic Relationships

Learning Objectives

- Identify some mutualistic relationships of fungi with other organisms

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).

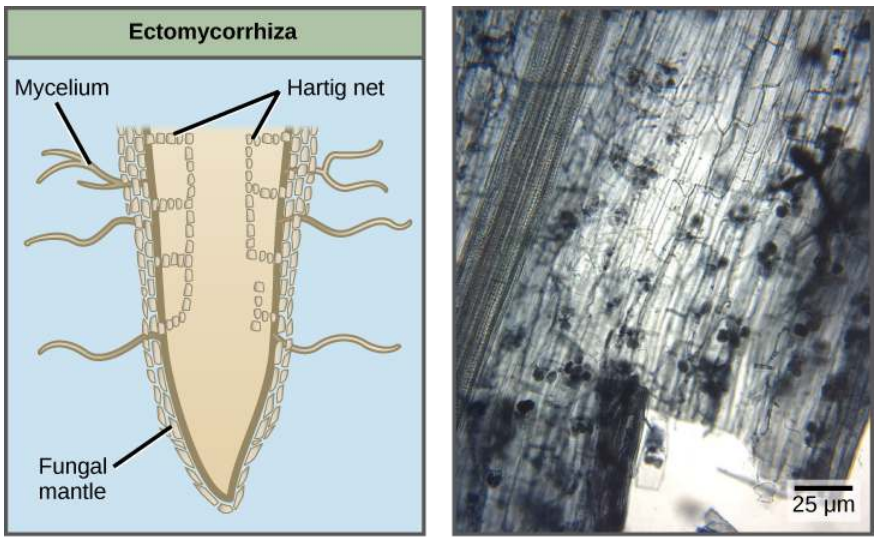
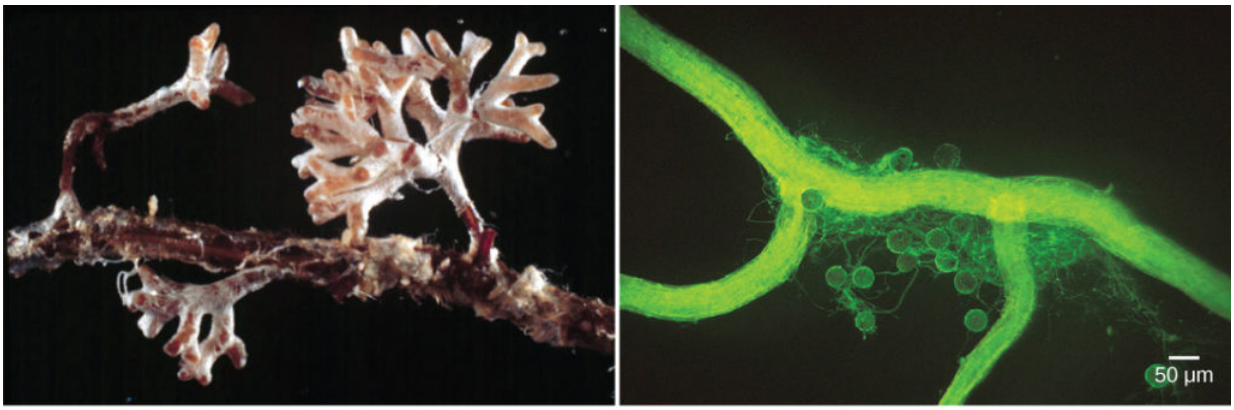


Figure 1. (a) Ectomycorrhiza and (b) arbuscular mycorrhiza have different mechanisms for interacting with the roots of plants. (credit b: MS Turmel, University of Manitoba, Plant Science Department)

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.

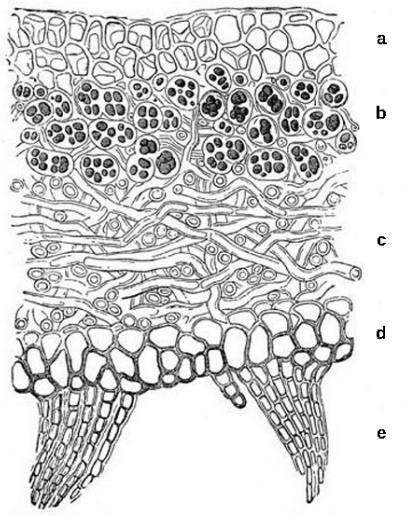


Figure 4. This cross-section of a lichen thallus shows the (a) upper cortex of fungal hyphae, which provides protection; the (b) algal zone where photosynthesis occurs, the (c) medulla of fungal hyphae, and the (d) lower cortex, which also provides protection and may have (e) rhizines to anchor the thallus 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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8.10: Introduction to Fungal Parasites and Pathogens

What you'll learn to do: Identify common fungal parasites and pathogens

Fungi are everywhere. There are millions of different fungal species on Earth, but only about 300 of those are known to make people sick. Fungal diseases are often caused by fungi that are common in the environment. Fungi live outdoors in soil and on plants and trees as well as on many indoor surfaces and on human skin. Most fungi are not dangerous, but some types can be harmful to health.

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.

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8.11: Infections in Plants

Learning Outcomes

- Describe fungal parasites and pathogens of 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.

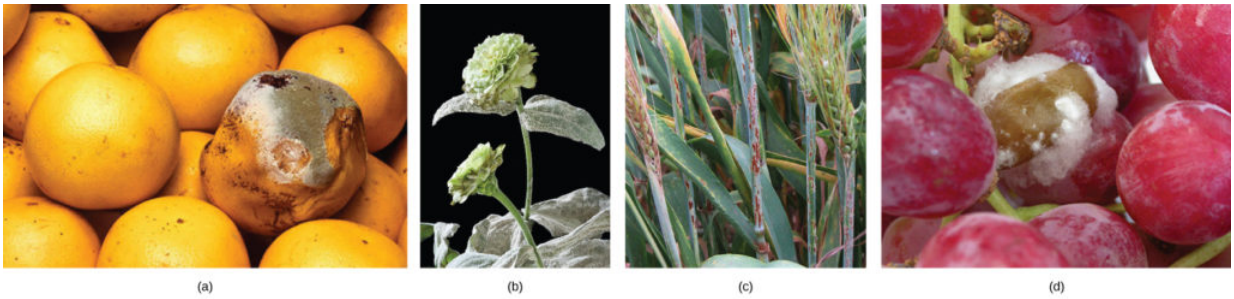


Figure 1. Some fungal pathogens include (a) green mold on grapefruit, (b) powdery mildew on a zinnia, (c) stem rust on a sheaf of barley, and (d) grey rot on grapes. In wet conditions *Botrytis cinerea*, the fungus that causes grey rot, can destroy a grape crop. However, controlled infection of grapes 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	[practice-area rows="1"][/practice-area]
Fungicide	[practice-area rows="1"][/practice-area]
Tissue from Susceptible Elm #1	[practice-area rows="1"][/practice-area]
Tissue from Susceptible Elm #2	[practice-area rows="1"][/practice-area]
Tissue from Resistant Elm #1	[practice-area rows="1"][/practice-area]
Tissue from Resistant Elm #2	[practice-area rows="1"][/practice-area]

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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8.12: Infections in Animals

Learning Outcomes

- Describe the different types of fungal infections in animals

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.

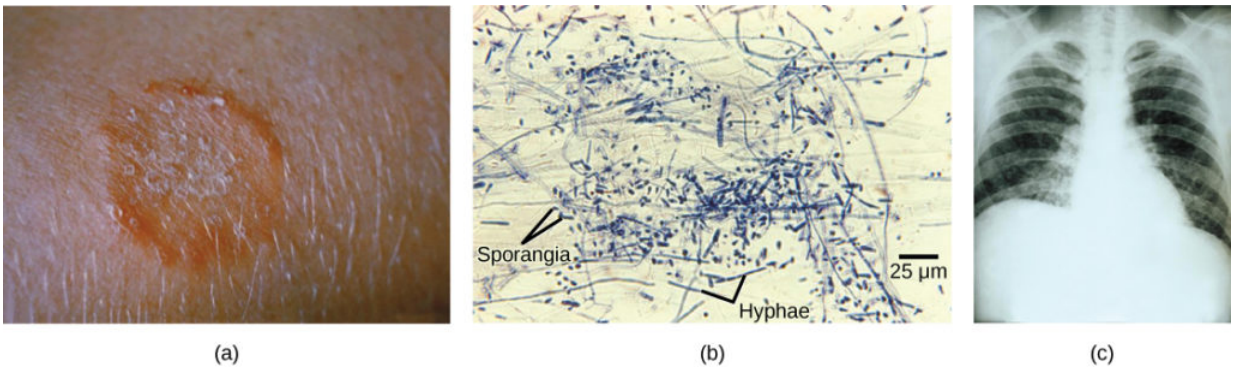


Figure 1. (a) Ringworm presents as a red ring on skin; (b) *Trichophyton violaceum*, shown in this bright field light micrograph, causes superficial mycoses on the scalp; (c) *Histoplasma capsulatum* is an ascomycete that infects airways and causes symptoms similar to influenza. (credit a: modification 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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8.13: Antifungal Therapy

Learning Objectives

- Explain why antifungal therapy is becoming less successful in public health

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

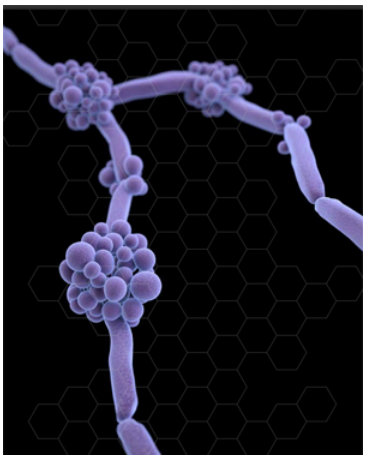


Figure 1. Medical illustration of fluconazole-resistant *Candida*

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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8.14: Introduction to Human Usage of Fungi

What you'll learn to do: Discuss common human usage of fungi

Humans are nothing if not resourceful; we've found ways to use most substances we come across in one way or another (even if that use is causing harm).

In this section we'll focus on our use of fungi as food and as medicine, but, as you can see in this video, there may be even more use of fungi in our future.



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/bionm2/?p=234

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8.15: Fungi as Food

Learning Objectives

- Identify fungi that serve as food

Humans have collected and used fungi for thousands of years. Going out to dinner, you find fungi everywhere. It can be found in the Bleu Cheese used with your chicken wings or burger, to the yeast in the dough for your mushroom pizza.



Figure 1. A selection of edible mushrooms eaten in Asia

Edible mushrooms include commercially raised and wild-harvested fungi. *Agaricus bisporus*, sold as button mushrooms when small or Portobello mushrooms when larger, is the most widely cultivated species in the West, used in salads, soups, and many other dishes. Many Asian fungi are commercially grown and have increased in popularity in the West. They are often available fresh in grocery stores and markets, including straw mushrooms (*Volvariella volvacea*), oyster mushrooms (*Pleurotus ostreatus*), shiitakes (*Lentinula edodes*), and enokitake (*Flammulina* spp.).

Many other mushroom species are harvested from the wild for personal consumption or commercial sale. Milk mushrooms, morels, chanterelles, truffles, black trumpets, and *porcini* mushrooms (*Boletus edulis*), also known as king boletes, demand a high price on the market. They are often used in gourmet dishes.



Figure 2. Stilton cheese veined with *Penicillium roqueforti*

Certain types of cheeses require inoculation of milk curds with fungal species that impart a unique flavor and texture to the cheese. Examples include the blue color in cheeses such as Stilton or Roquefort, which are made by inoculation with *Penicillium roqueforti*. Molds used in cheese production are non-toxic and are thus safe for human consumption; however, mycotoxins (e.g., aflatoxins, roquefortine C, patulin, or others) may accumulate because of growth of other fungi during cheese ripening or storage.

Cultured foods

Baker's yeast or *Saccharomyces cerevisiae*, a unicellular fungus, is used to make bread and other wheat-based products, such as pizza dough and dumplings. Yeast species of the genus *Saccharomyces* are also used to produce alcoholic beverages through fermentation. Shoyu koji mold (*Aspergillus oryzae*) is an essential ingredient in brewing Shoyu (soy sauce) and sake, and the preparation of miso, while *Rhizopus* species are used for making tempeh. Several of these fungi are domesticated species that were bred or selected according to their capacity to ferment food without producing harmful mycotoxins (see below), which are produced by very closely related *Aspergilli*. Quorn, a meat substitute, is made from *Fusarium venenatum*.

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8.16: Fungi as Antibiotics

Learning Outcomes

- Discuss fungi that act as antibiotics

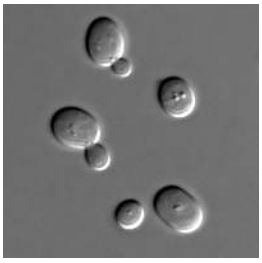


Figure 1. The yeast *Saccharomyces cerevisiae* is approximately 5 µm in diameter and is important for the production of wine, beer, and bread. The yeast also has many applications in medical research.

Many secondary metabolites of fungi are of great commercial importance. Fungi naturally produce antibiotics to kill or inhibit the growth of bacteria, limiting their competition in the natural environment. Important antibiotics, such as penicillin and the cephalosporins, can be 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.

At the start of the 21st century, fungi were engaged in the development of more than 10 of the 20 most money-making products utilized in human medicine. Two anti-cholesterol statins, the antibiotic penicillin and the immunosuppressant cyclosporin A are amidst the peak 10. Each of these has a turnover in surplus of $1 billion annually. As pharmaceutical breakthrough extends, the following have lately been accepted for human use: micafungin is an antifungal agent; mycophenolate is used to avert tissue rejection; rosuvastatin is used to decrease cholesterol; and cefditoren as an antibiotic.

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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8.17: Fungi as Fuel

Learning Outcomes

- Discuss the use of fungi as alternative fuels

While the use of fungi as food or medicine is fairly well known, people often is overlook are the other uses for fungi. One of the newest uses of fungus is to make fuel.

For thousands of years, we have used yeast to make alcohol. In many countries around the world, ethanol is used to power cars. Since the 1970s Brazil has pioneered the use of ethanol or ethanol / gasoline mixes in their cars. It is just as common to fill up with gasoline as it is with ethanol.



Figure 1. Ethanol and Gasoline pump in Brazil

New research has also looked at the use of fungi to produce **mycodiesel**. Gary Strobel at Live Science gave the following explanation of mycodiesel:

“Mycodiesel” is a novel name applied to the volatile organic products made by fungi that have fuel potential. The latest discovery is that of an endophytic Hypoxylon/Nodulosporium species, or one that lives within a plant, that makes the compound cineole along with a number of other cyclohexanes (colorless, flammable liquids found in petroleum crude oil and volcanic gases) and compounds with enormous fuel potential.[1]

The compound cineole is particularly interesting, as it can be mixed with gasoline (eight parts cineole to one part gasoline) and create a fuel that has an octane rating of 95.[2] For reference, the average “regular” gasoline in the United States has an octane rating of 87.

While the use of fungi is still a new idea, it could prove to be an exciting and eco-friendly alternative to the current fuels we use today.

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1. Strobel, Gary. "Fungi that Make Fuel Discovered," Live Science, 25 Feb 2011. Web. 26 June 2018. ↵
2. Ibid. ↵

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8.18: 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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CHAPTER OVERVIEW

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9.1: 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.

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9.2: Introduction to Seedless Plants

What you'll learn to do: 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.

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9.3: Early Plant Life

Learning Objectives

- Describe the timeline of plant evolution and the impact of land plants on other living things

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. Most biologists also consider 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 **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 in other types of algae.

Try It

Some scientists consider all algae to be plants, while others assert that only the Charophytes belong in the kingdom Plantae. These divergent opinions are related to the different evolutionary paths to photosynthesis selected for in different types of algae. While all algae are photosynthetic—that is, they contain some form of a chloroplast—they didn't all become photosynthetic via the same path.

The ancestors to the green algae became photosynthetic by endosymbiosing a green, photosynthetic bacterium about 1.65 billion years ago. That algal line evolved into the Charophytes, and eventually into the modern mosses, ferns, gymnosperms, and angiosperms. Their evolutionary trajectory was relatively straight and monophyletic. In contrast, the other algae—red, brown, golden, stramenopiles, and so on—all became photosynthetic by secondary, or even tertiary, endosymbiotic events; that is, they endosymbiosed cells that had already endosymbiosed a cyanobacterium. These latecomers to photosynthesis are parallels to the Charophytes in terms of autotrophy, but they did not expand to the same extent as the Charophytes, nor did they colonize the land.

The different views on whether all algae are Plantae arise from how these evolutionary paths are viewed. Scientists who solely track evolutionary straight lines (that is, monophyly), consider only the Charophytes as plants. To biologists who cast a broad net over living things that share a common characteristic (in this case, photosynthetic eukaryotes), all algae are plants.

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 watery soup: in this medium, most small molecules dissolve and diffuse, and the majority of the chemical reactions of metabolism take place. Desiccation, or drying out, is a constant danger for an organism 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 are found in all terrestrial plants: the alternation of generations, a sporangium in which the spores are formed, a gametangium that produces haploid cells, and apical meristem tissue in roots and shoots. The evolution of a waxy cuticle and a cell wall with lignin also contributed to the success of land plants. These adaptations are noticeably lacking in the closely related green algae—another reason for the debate over their placement in the plant kingdom.

Alternation of Generations

Alternation of generations describes a life cycle in which an organism has both haploid and diploid multicellular stages (Figure 1).

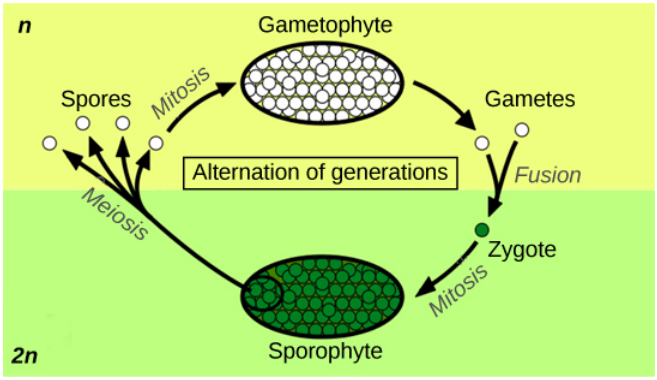


Figure 1. Alternation of generations between the 1n gametophyte and 2n sporophyte is shown. (credit: Peter Coxhead)

Haplontic refers to a lifecycle in which there is a dominant haploid stage, and **diplontic** refers to a lifecycle in which the diploid is the dominant life stage. Humans are diplontic. Most plants exhibit alternation of generations, which is described as **haplodiplodontic:** the haploid multicellular form, known as a gametophyte, is followed in the development sequence by a multicellular diploid organism: the sporophyte. The gametophyte gives rise to the gametes (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 higher plants (a common collective term for the vascular plants). The sporophyte stage is barely noticeable in lower plants (the collective term for the plant groups of mosses, liverworts, and lichens). Towering trees are the diplontic phase in the lifecycles of plants such as 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 generation of sporophyte. This distinguishing feature of land plants gave the group its alternate name of **embryophytes**.

Sporangia in Seedless Plants



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): organs that first appeared in the land plants. The term “sporangia” literally means “spore in a vessel,” as it is a reproductive sac that contains spores Figure 2. Inside the multicellular sporangia, the diploid **sporocytes**, or mother cells, produce haploid spores by meiosis, where the 2*n* chromosome number is reduced to 1*n* (note that many plant sporophytes are polyploid: 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. Two different types of spores are produced in land plants, resulting in the separation of sexes at different points in the lifecycle. **Seedless non-vascular plants** produce only one kind of spore and are called **homosporous**. The gametophyte phase is dominant in these plants. After germinating from a spore, the resulting gametophyte produces both male and female gametangia, usually on the same individual. In contrast, **heterosporous** plants produce two morphologically different types of spores. The male spores are called **microspores**, because of their smaller size, and develop into the male gametophyte; the comparatively larger **megaspores** develop into the female gametophyte. Heterospory is observed in a few **seedless vascular plants** and in all seed plants.

When the haploid spore germinates in a hospitable environment, it generates a multicellular gametophyte by mitosis. The gametophyte supports the zygote formed from the fusion of gametes and the resulting young sporophyte (vegetative form). The cycle then begins anew.

The spores of seedless plants are surrounded by thick cell walls containing a tough polymer known as **sporopollenin**. 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, which use pollen to transfer the male sperm to the female egg, 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 green algae *Coleochaetes* 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.

Apical Meristems

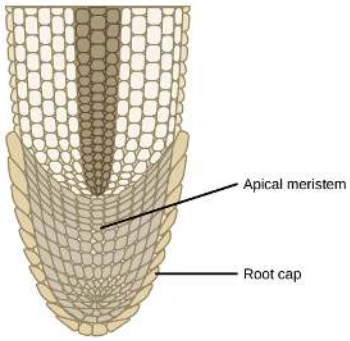


Figure 3. Addition of new cells in a root occurs at the apical meristem. Subsequent enlargement of these cells causes the organ to grow and elongate. The root cap protects the fragile apical meristem as the root tip is pushed through the soil by cell elongation.

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.

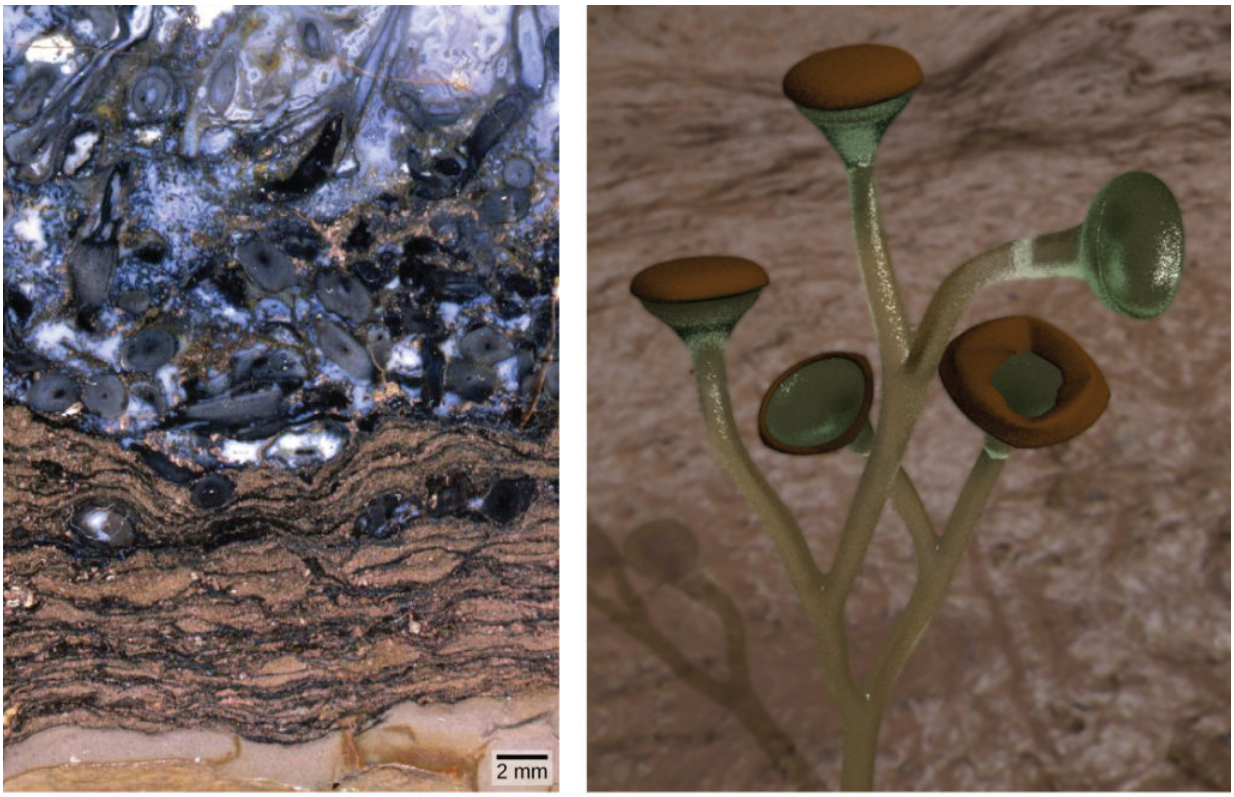


Figure 4. This Rhynie chert contains fossilized material from vascular plants. The area inside the circle contains bulbous underground stems called corms, and root-like structures called rhizoids. (credit b: modification of work by Peter Coxhead based on original image by "Smith609"/Wikimedia Commons; 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="9">STREPTOPHYTES: THE GREEN PLANTS</th></tr>
<tr><td rowspan="5">Charophytes</td><td colspan="8">Embryophytes: The Land Plants</td></tr>
<tr><td colspan="3">Non Vascular</td><td colspan="5">Vascular</td></tr>
<tr><td colspan="3" rowspan="2">Seedless Plants
Bryophytes</td><td colspan="3">Seedless Plants</td><td colspan="2" rowspan="2">Seed Plants
Spermatophytes</td></tr>
<tr><td>Lycophytes</td><td>Pterophytes</td></tr>
<tr><td>Liver-worts</td><td>Horn-worts</td><td>Mosses</td><td>Club Mosses</td><td>Whisk Ferns</td><td rowspan="3">Gymno-sperms</td><td rowspan="3">Angio-sperms</td></tr>
<tr><td colspan="3"></td><td>Quillworts</td><td>Horsetails</td></tr>
<tr><td colspan="3"></td><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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9.4: Green Algae- Precursors of Land Plants

Learning Objectives

- Describe the traits shared by green algae and 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).

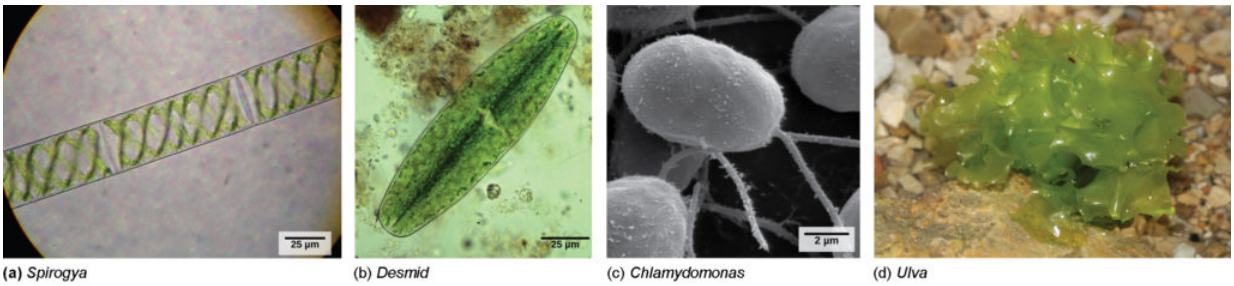


Figure 1. Chlorophyta include (a) *Spirogyra*, (b) desmids, (c) *Chlamydomonas*, and (d) *Ulva*. Desmids and *Chlamydomonas* are single-celled organisms, *Spirogyra* forms chains of cells, and *Ulva* forms colonies resembling leaves (credit b: modification of work by Derek Keats; credit c: modification 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. 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)

Green algae in the order Charales, and the coleochaetes (microscopic green algae that enclose their spores in sporopollenin), are considered the closest living relatives of embryophytes. The Charales can be traced back 420 million years. They live in a range of fresh water habitats and vary in size from a few millimeters to a meter in length. The representative species is *Chara* (Figure 2), 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. Unlike land plants, Charales do not undergo alternation of generations in their lifecycle. Charales exhibit a number of traits that are significant in their adaptation to land life. They produce the compounds lignin and sporopollenin, and form plasmodesmata that connect the cytoplasm of adjacent cells. The egg, and later, the zygote, form in a protected chamber on the parent plant.

New information from recent, extensive DNA sequence analysis of green algae indicates that the Zygnematales are more closely related to the embryophytes than the Charales. The Zygnematales include the familiar genus *Spirogyra*. As techniques in DNA analysis improve and new information on comparative genomics arises, the phylogenetic connections between species will change. Clearly, plant biologists have not yet solved the mystery of the origin of land plants.

Learning Objectives

Green algae share more traits with land plants than other algae, according to structure and DNA analysis. Charales form sporopollenin and precursors of lignin, phragmoplasts, and have flagellated sperm. They do not exhibit alternation of generations.

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9.5: Bryophytes

Learning Objectives

- Identify the main characteristics of 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.

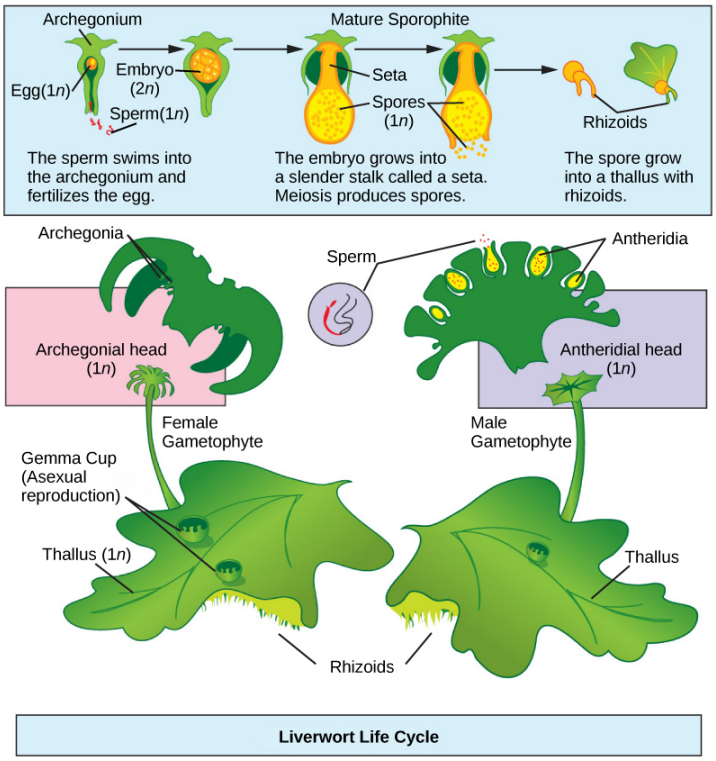


Figure 3. The life cycle of a typical liverwort is shown. (credit: modification of work by Mariana Ruiz Villareal)

Hornworts



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, and gives the group its name. 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.

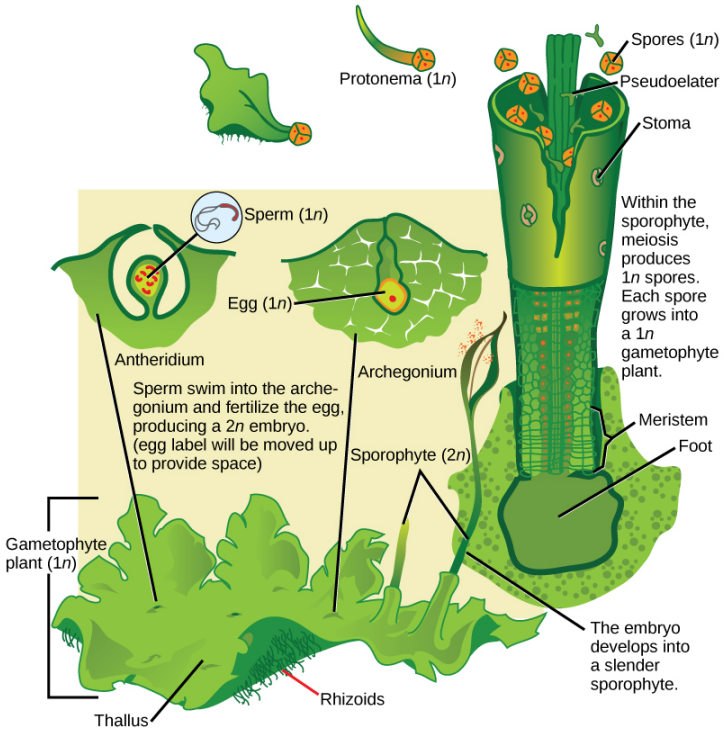


Figure 5. The alternation of generation in hornworts is shown. (credit: modification of work by “Smith609”/Wikimedia Commons based on original work by Mariana Ruiz Villareal)

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.

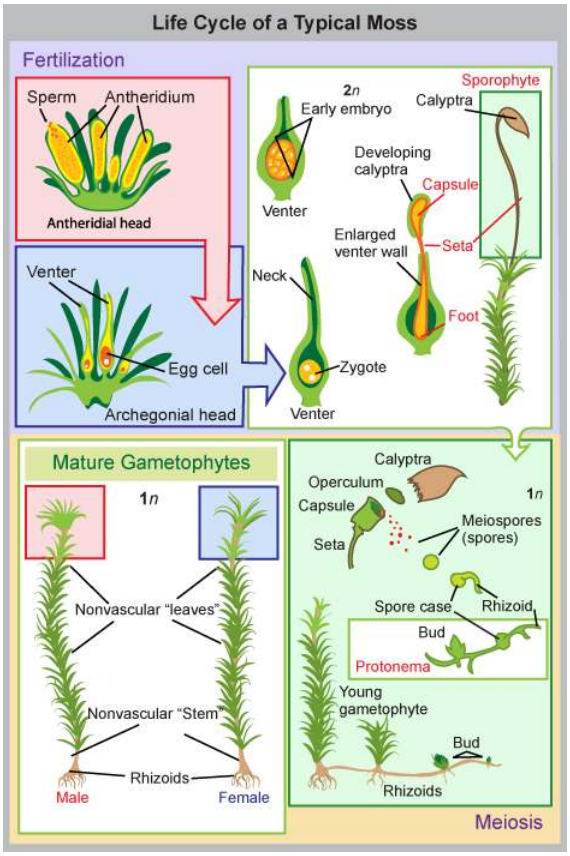


Figure 6. This illustration shows the life cycle of mosses. (credit: modification of work by Mariana Ruiz Villareal)



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.

[reveal-answer q="646233"]Show Answer[/reveal-answer]
[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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9.6: Seedless Vascular Plants

Learning Objectives

- Differentiate between vascular and non-vascular plants
- Identify the main characteristics of 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.

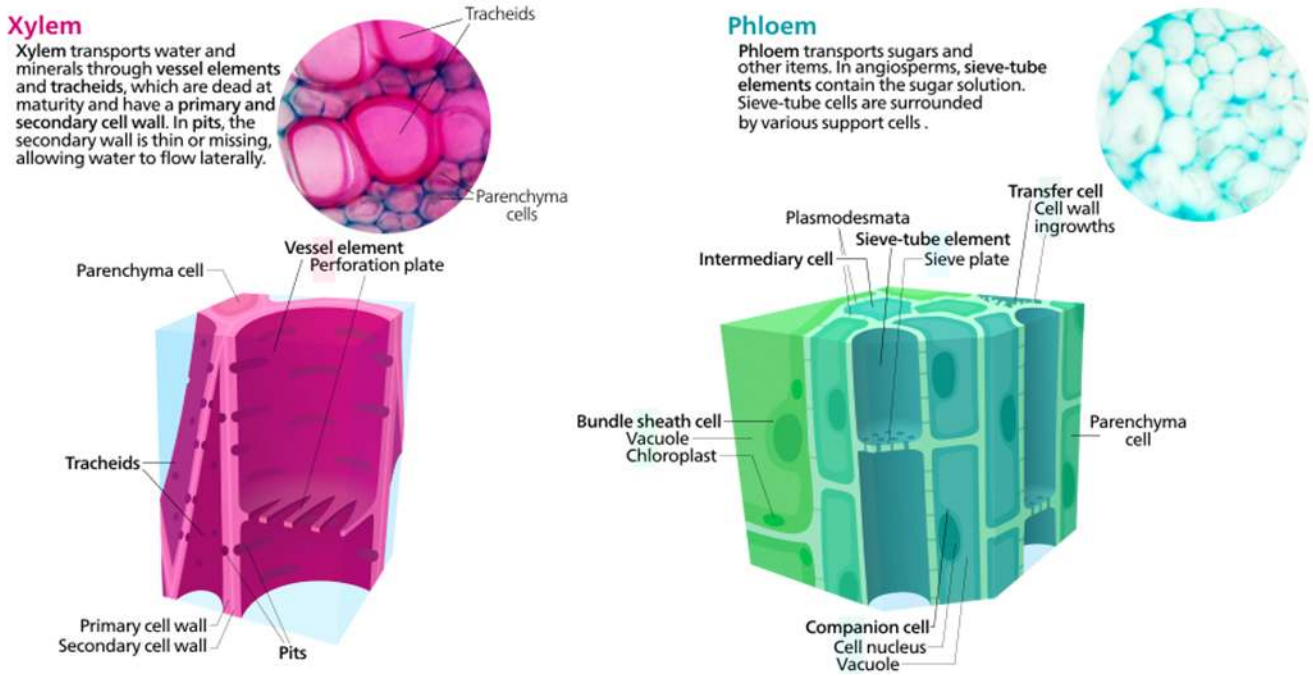


Figure 1. Diagrams of xylem and phloem tissues

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.

Phylum Monilophyta: Class Psilotopsida (Ferns)

With their large fronds, **ferns** are the most readily recognizable seedless vascular plants. They are considered 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 tropics to temperate forests.



Figure 6. Some specimens of this short tree-fern species can grow very tall. (credit: Adrian Pingstone)

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 and expanded during the Carboniferous.

The dominant stage of the lifecycle of a fern is the sporophyte, which consists of large compound leaves called fronds. 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 6). **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.

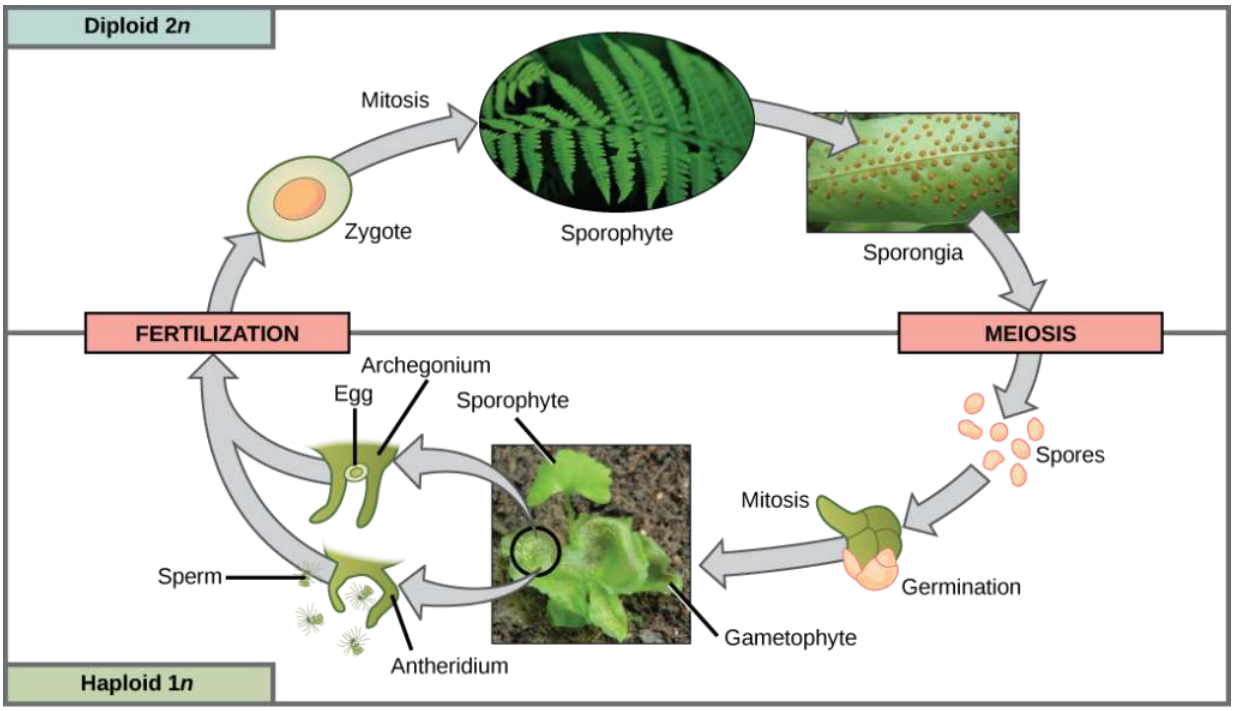


Figure 8. This life cycle of a fern shows alternation of generations with a dominant sporophyte stage. (credit “fern”: modification of work by Cory Zanker; credit “gametophyte”: modification of work by “Vlmastra”/Wikimedia Commons)

? 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]



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.

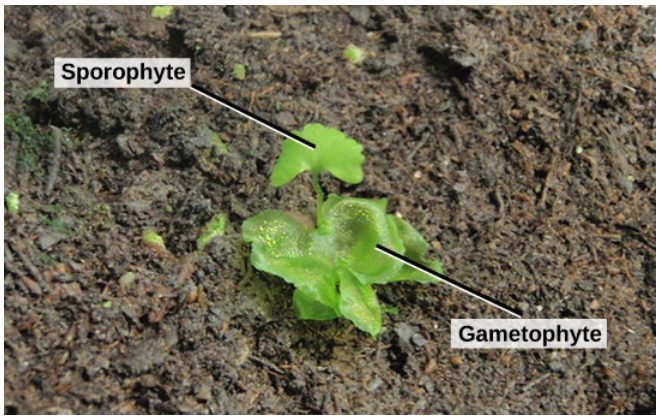


Figure 10. Shown here are a young sporophyte (upper part of image) and a heart-shaped gametophyte (bottom part of image). (credit: modification of work by “Vlmastra”/Wikimedia Commons)

? 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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9.7: Introduction to Seed Plants

What you'll learn to do: 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)

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9.8: Evolution of Seed Plants

Learning Objectives

- Describe the evolutionary history 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 *Ginkgo 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. Ginkgoales 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

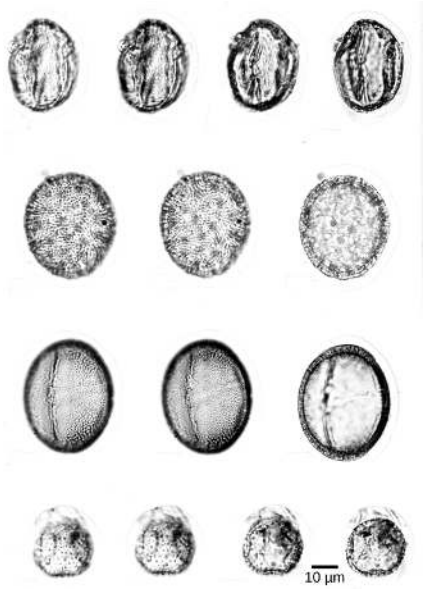


Figure 3. This fossilized pollen is from a Buckbean fen core found in Yellowstone National Park, Wyoming. The pollen is magnified 1,054 times. (credit: R.G. Baker, USGS; scale-bar data from Matt Russell)

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.

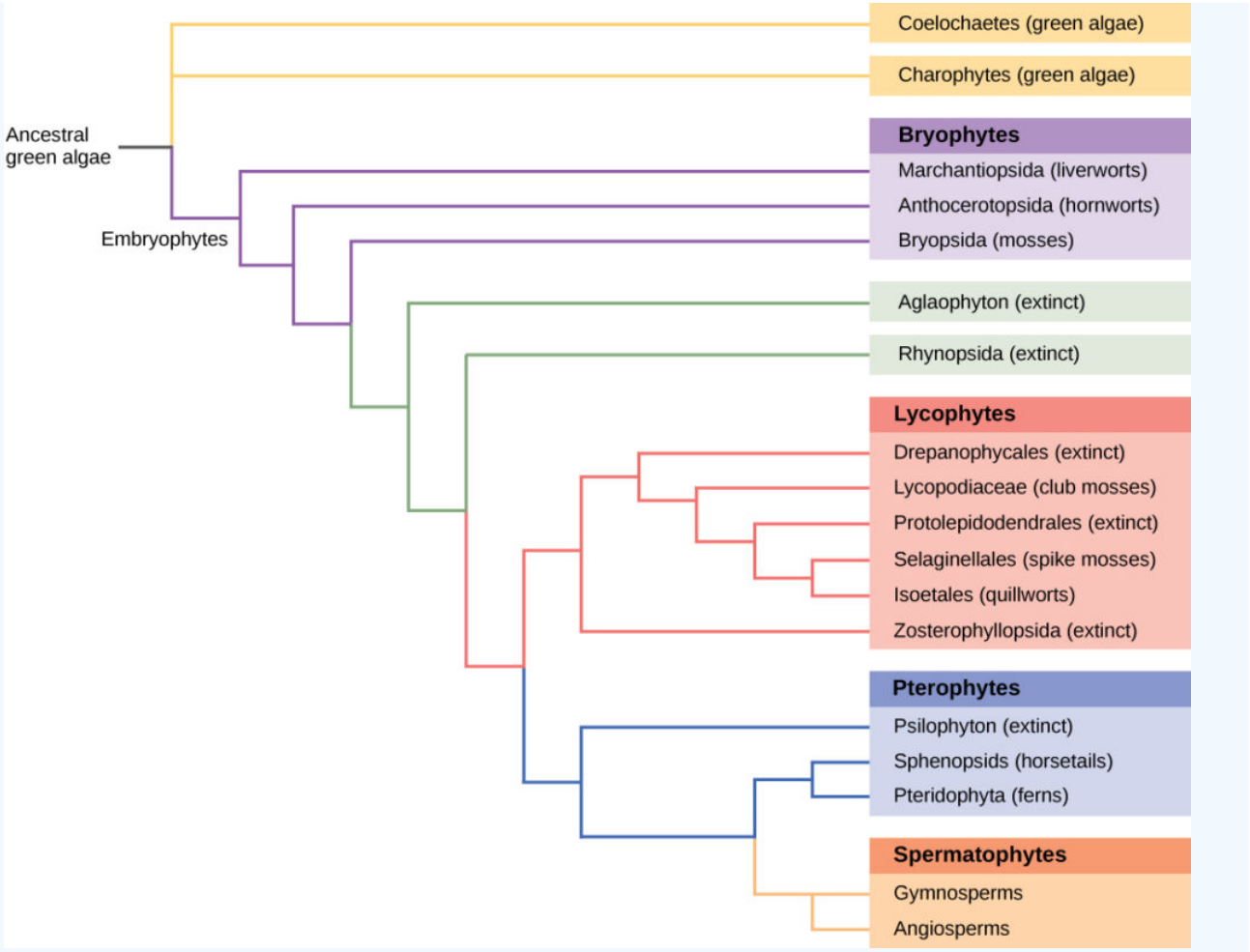


Figure 5. This phylogenetic tree shows the evolutionary relationships of plants.

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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9.9: Gymnosperms

Learning Objectives

- Identify the main characteristics of 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 ($1n$).

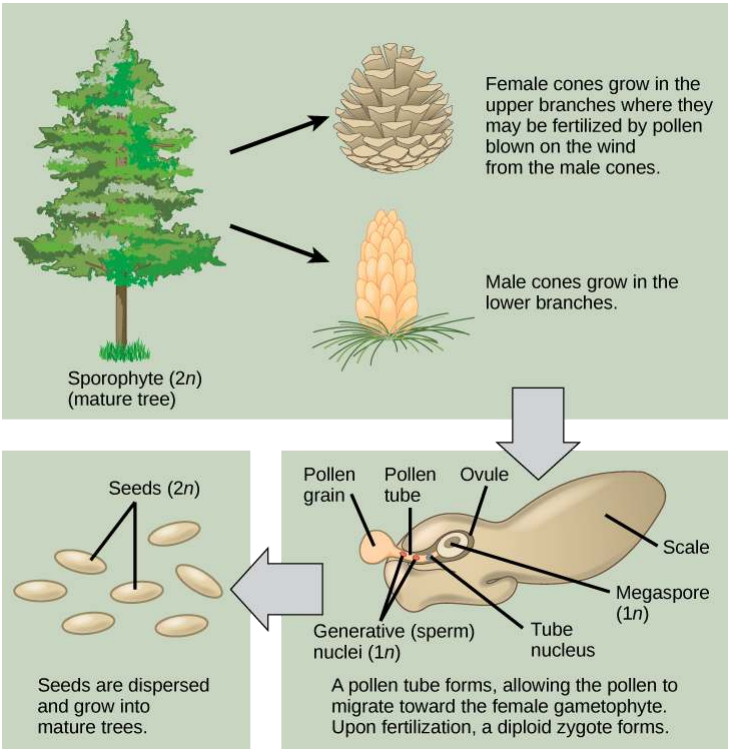


Figure 1. This image shows the life cycle of a conifer. Pollen from male cones blows up into upper branches, where it fertilizes female cones.

? 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.”

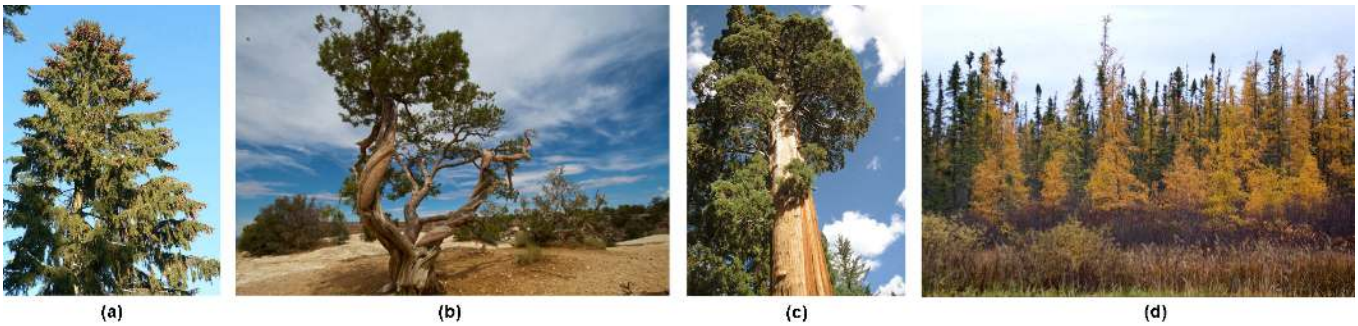


Figure 2. Conifers are the dominant form of vegetation in cold or arid environments and at high altitudes. Shown here are the (a) evergreen spruce *Picea sp*., (b) juniper *Juniperus sp*., (c) sequoia *Sequoia Semervirens*, which is a deciduous gymnosperm, and (d) the tamarack *Larix larcinia*. Notice 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.

Ginkgophytes

The single surviving species of the **ginkgophytes** group is the *Ginkgo 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 *Ginkgo 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. *Ginkgo biloba* is the only representative of the phylum Ginkgophyta. The last phylum, Gnetophyta, is a diverse group of shrubs that produce vessel elements in their wood.

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9.10: Angiosperms

Learning Objectives

- Identify the main characteristics of 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. All angiosperms have seeds that are covered or protected: this feature separates them from the 'naked seeds' of gymnosperms.

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.

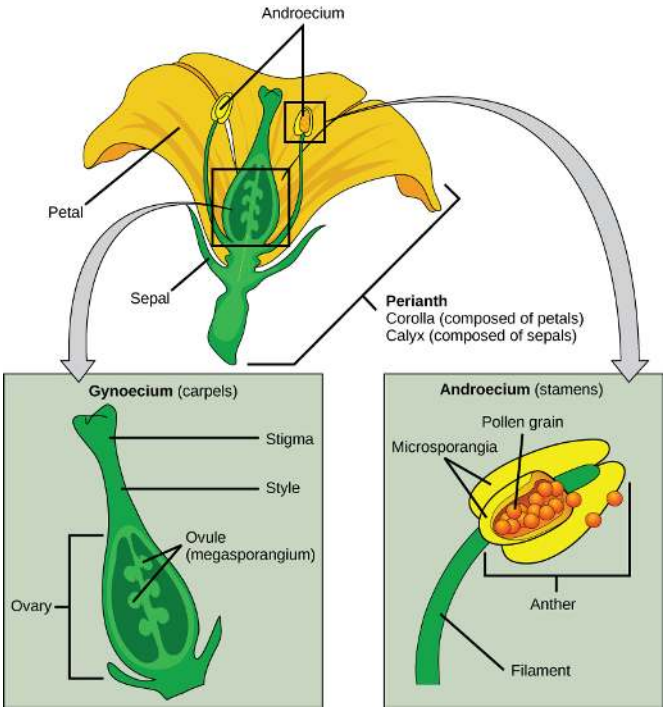


Figure 2. This image depicts the structure of a perfect flower. Perfect flowers produce both male and female floral organs. The flower shown has only one carpel, but some flowers have a cluster of carpels. Together, all the carpels make up the gynoecium. (credit: modification of work by Mariana Ruiz 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.

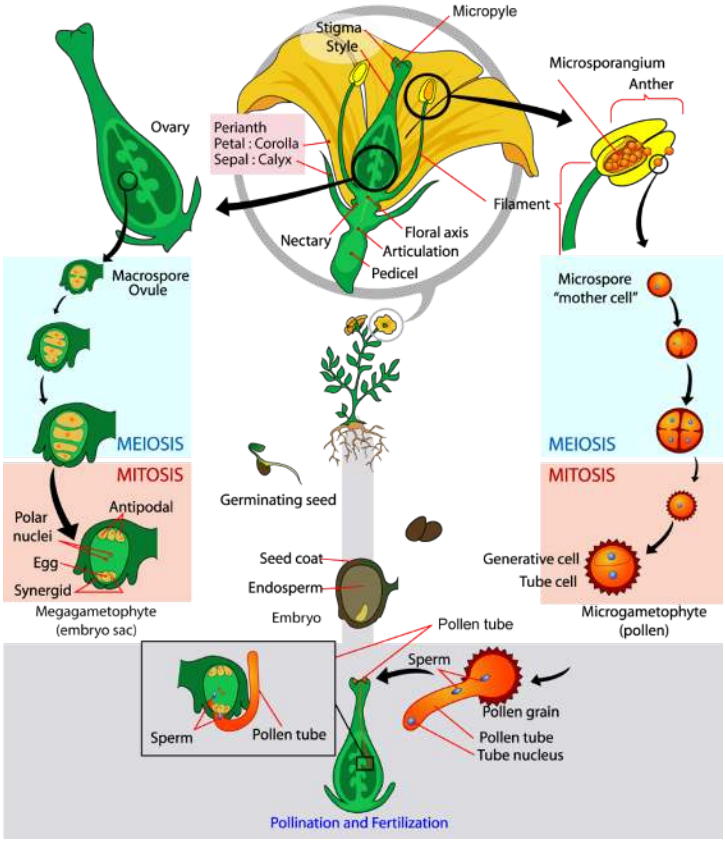


Figure 3. The life cycle of an angiosperm is shown. Anthers and carpels are structures that shelter the actual gametophytes: the pollen grain and embryo sac. Double fertilization is a process unique to angiosperms. (credit: modification of work by Mariana Ruiz Villareal)

? Practice Question

If a flower lacked a megasporangium, what type of gamete would not form?

[practice-area rows="2"][/practice-area]
[reveal-answer q="366526"]Show Answer[/reveal-answer]
[hidden-answer a="366526"]Without a megasporangium, an egg would not form

[/hidden-answer]

If the flower lacked a microsporangium, what type of gamete would not form?

[practice-area rows="2"][/practice-area]
[reveal-answer q="773905"]Show Answer[/reveal-answer]
[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.

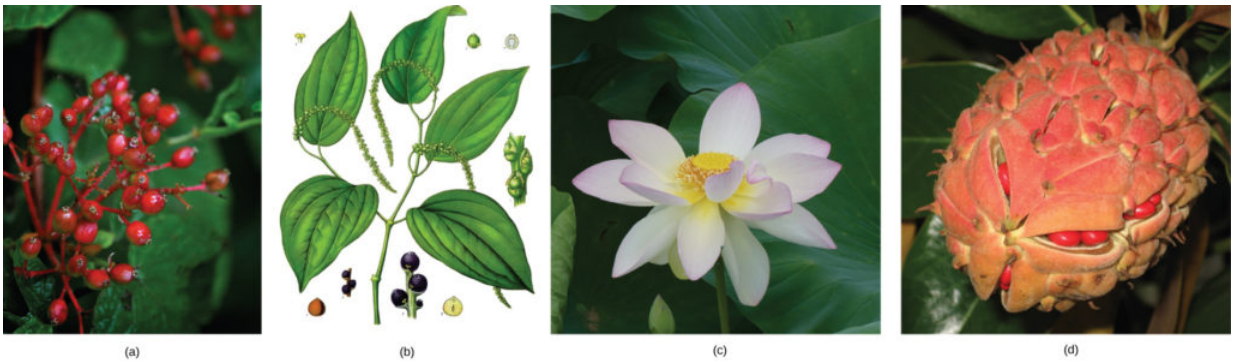


Figure 4. The (a) common spicebush belongs to the *Laurales*, the same family as cinnamon and bay laurel. The fruit of (b) the *Piper nigrumplant* is black pepper, the main product that was traded along spice routes. Notice the small, unobtrusive, clustered flowers. (c) Lotus flowers, *Nelumbo nucifera*, 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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9.11: The Role of Seed Plants

Learning Objectives

- Discuss the roles that plants play in ecosystems

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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9.12: 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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CHAPTER OVERVIEW

10: Module 7- Plant Structure and Function

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10.1: 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?

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10.2: Introduction to Plant Structures

What you'll learn to do: 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. Deeper than this, all plants have the same type of cells (remember plant cells are different from animal cells!), which allow for the rigid structures found in plants.

In this section we'll learn just how these different structures come together to form unique plants.

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10.3: Plant Cells

Learning Objectives

- Discuss features of plant cells

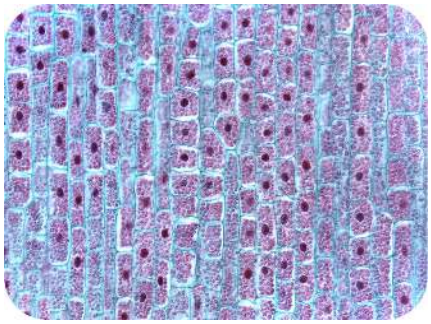


Figure 1. A section of a pine embryo.

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.

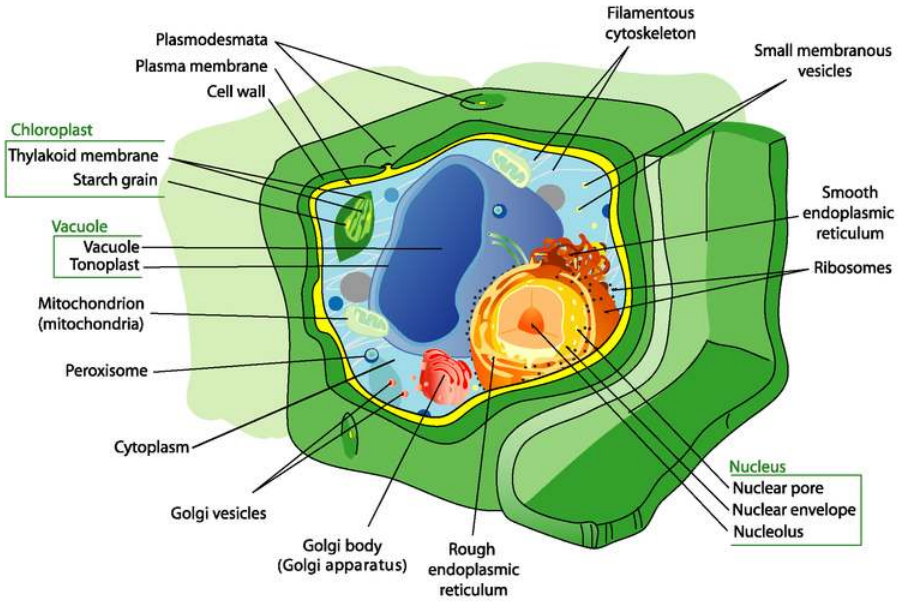


Figure 2. Plant cells have all the same structures as animal cells, plus some additional structures. Can you identify the unique plant structures in the diagram?

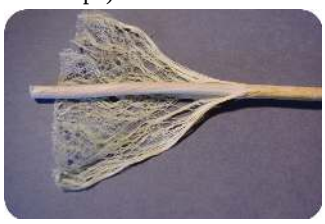
Plant Cell Structures

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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10.4: Plant Tissues and Organs

Learning Objectives

- Identify the different tissue types and organ systems in plants

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.

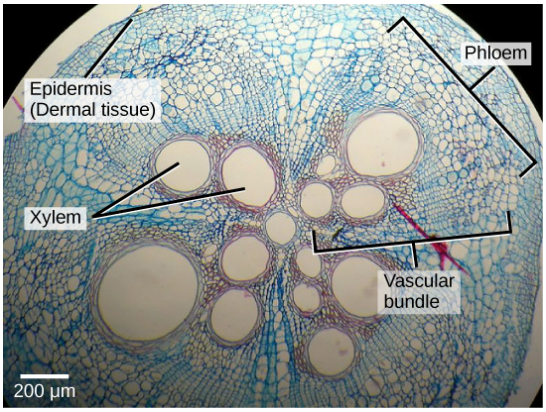


Figure 1. This light micrograph shows a cross section of a squash (*Curcurbita maxima*) stem. Each teardrop-shaped vascular bundle consists of large xylem vessels toward the inside and smaller phloem cells toward the outside. Xylem cells, which transport water and nutrients from the roots to the rest 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.

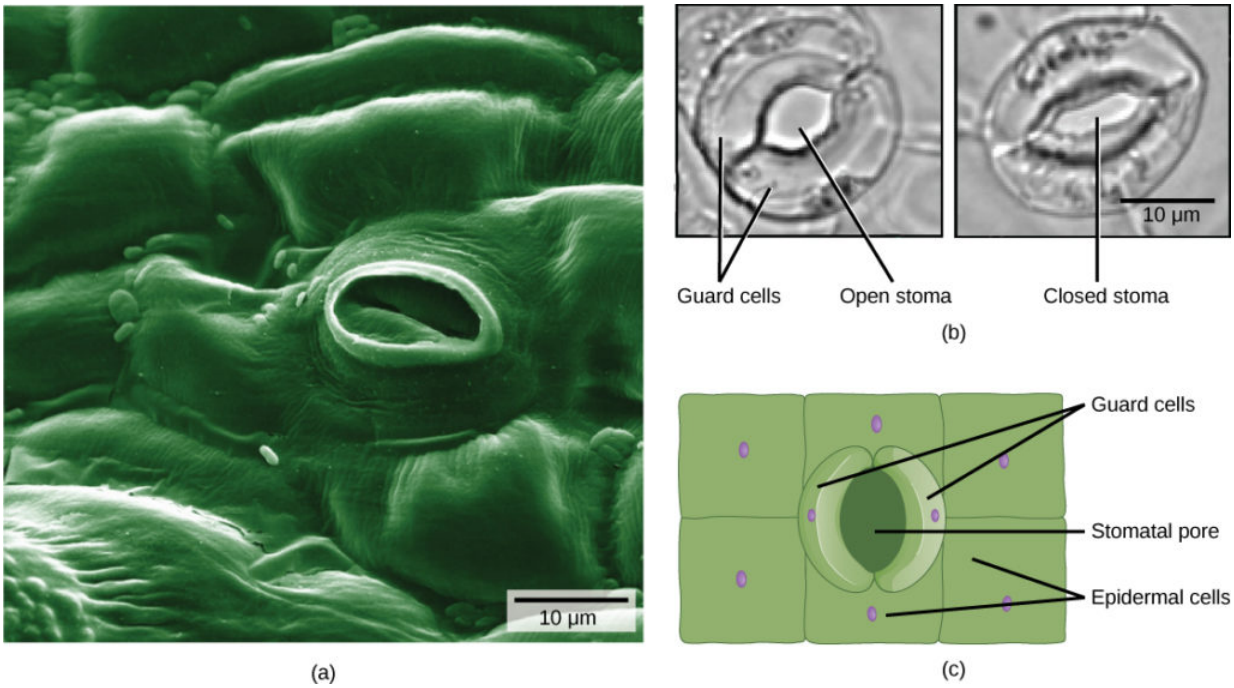


Figure 2. Openings called stomata (singular: stoma) allow a plant to take up carbon dioxide and release oxygen and water vapor. The (a) colorized scanning-electron micrograph shows a closed stoma of a dicot. Each stoma is flanked by two guard cells that regulate its (b) opening and closing. The (c) guard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

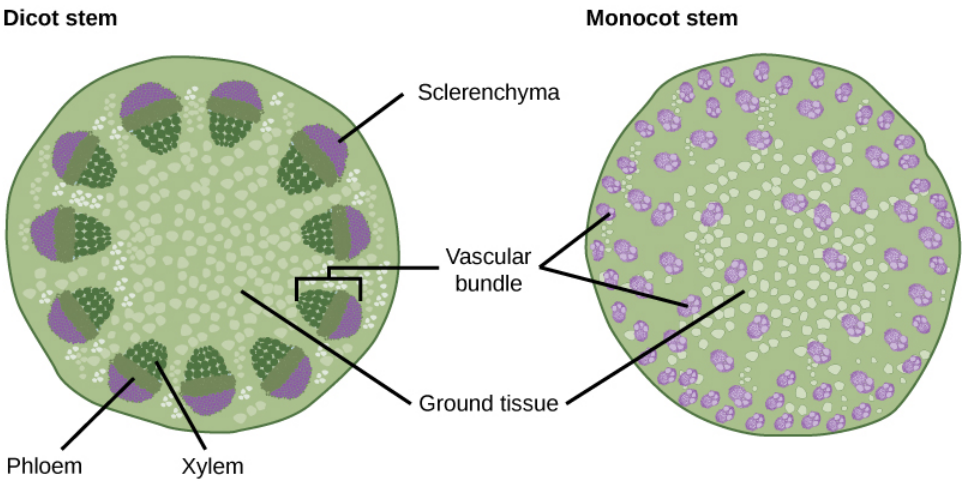


Figure 3. In (a) dicot stems, vascular bundles are arranged around the periphery of the ground tissue. The xylem tissue is located toward the interior of the vascular bundle, and phloem is located toward the exterior. Sclerenchyma fibers cap the vascular bundles. In (b) monocot stems, vascular bundles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

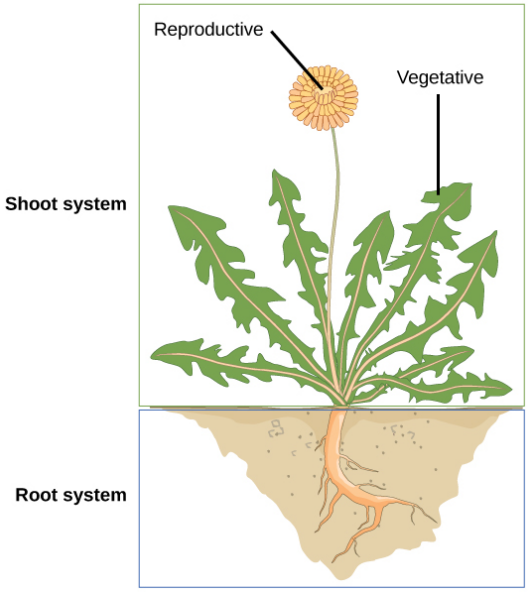


Figure 4. The shoot system of a plant consists of leaves, stems, flowers, and fruits. The root system anchors the plant while absorbing water and minerals from the soil.

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10.5: Stems

Learning Objectives

- Describe the main function and basic structure of stems

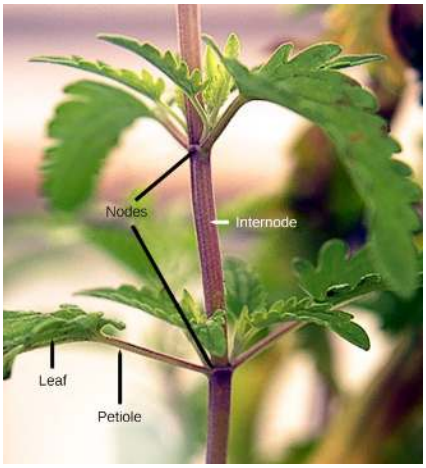


Figure 1. Leaves are attached to the plant stem at areas called nodes. An internode is the stem region between two nodes. The petiole is the stalk connecting the leaf to the stem. The leaves just above the nodes arose from axillary buds.

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

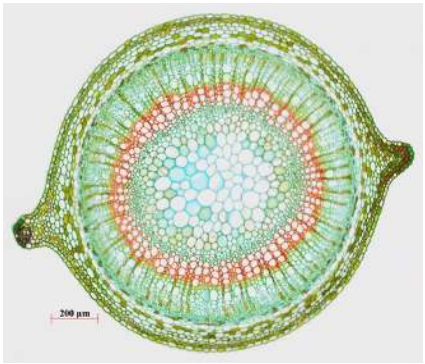


Figure 2. The stem of common St John's Wort (*Hypericum perforatum*) is shown in cross section in this light micrograph. (credit: Rolf-Dieter Mueller)

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.

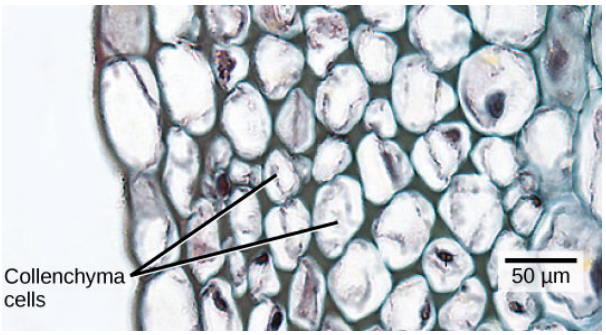


Figure 3. Collenchyma cell walls are uneven in thickness, as seen in this light micrograph. They provide support to plant structures. (credit: modification of work by Carl Szczerski; scale-bar data from Matt Russell)

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).

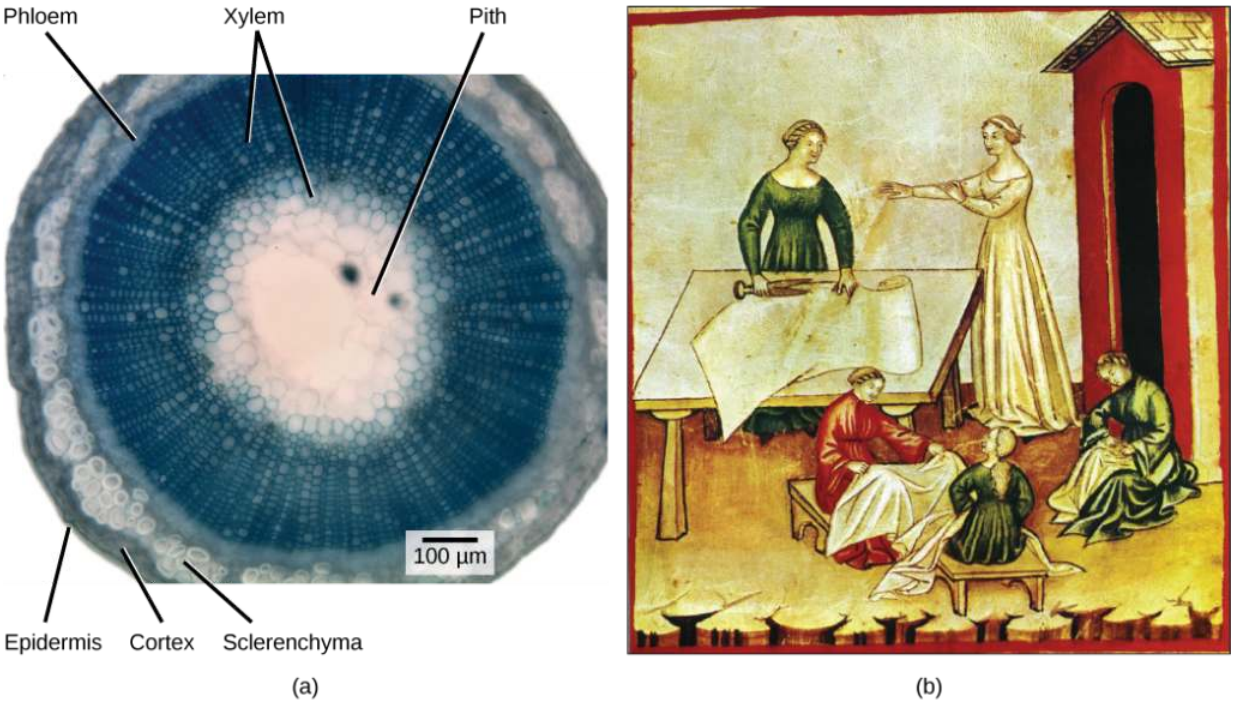


Figure 4. The central pith and outer cortex of the (a) flax stem are made up of parenchyma cells. Inside the cortex is a layer of sclerenchyma cells, which make up the fibers in flax rope and clothing. Humans have grown and harvested flax for thousands of years. In (b) this drawing, fourteenth-century 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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10.6: Leaves

Learning Objectives

- Identify the structure and function of a typical leaf

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

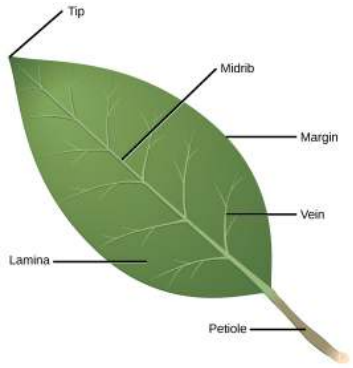


Figure 1. Deceptively simple in appearance, a leaf is a highly efficient structure.

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.

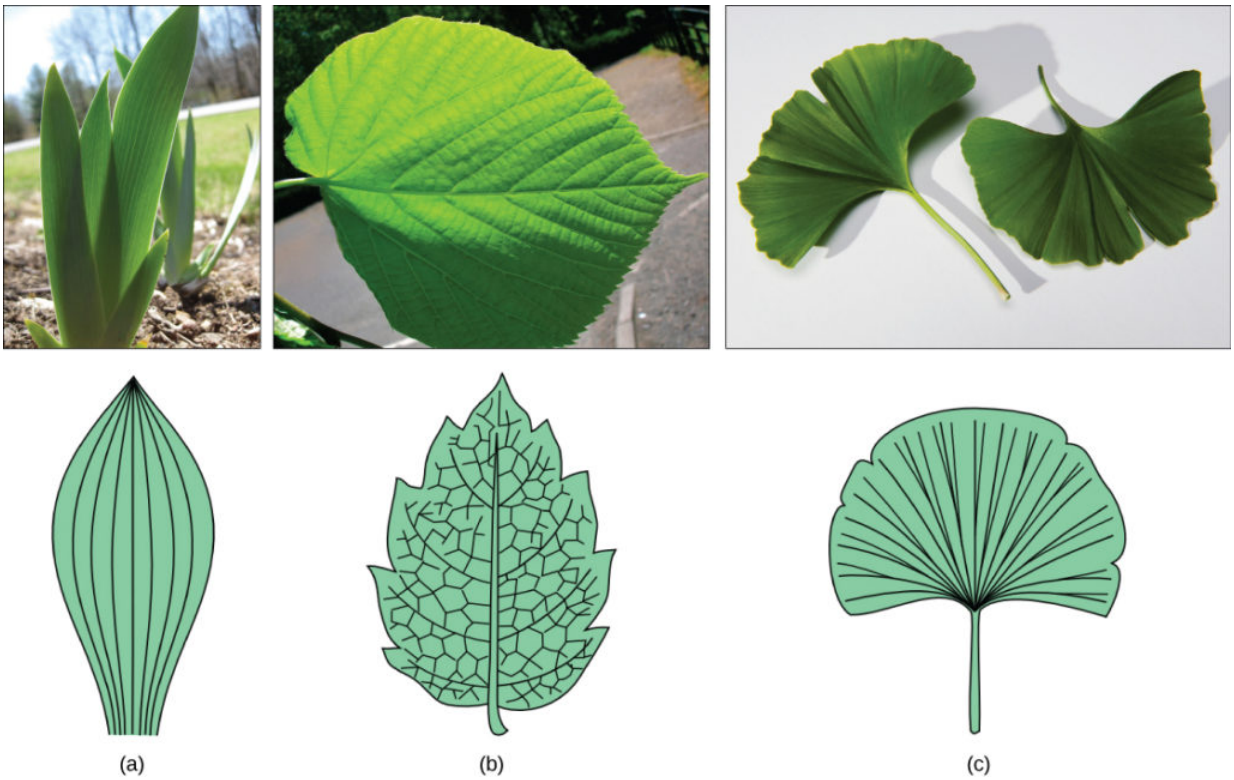


Figure 2. (a) Tulip (*Tulipa*), a monocot, has leaves with parallel venation. The netlike venation in this (b) linden (*Tilia cordata*) leaf distinguishes it as a dicot. The (c) *Ginkgo biloba* tree has dichotomous venation. (credit a photo: modification of work by "Drewboy64"/Wikimedia Commons; credit 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.

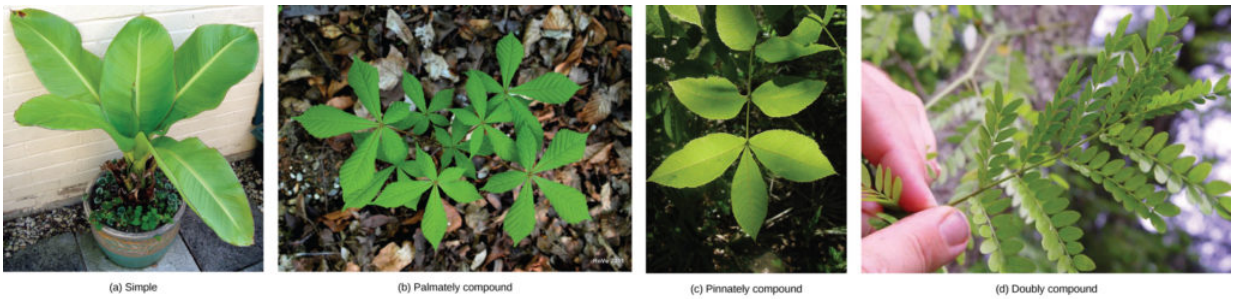


Figure 3. Leaves may be simple or compound. In simple leaves, the lamina is continuous. The (a) banana plant (*Musa* sp.) has simple leaves. In compound leaves, the lamina is separated into leaflets. Compound leaves may be palmate or pinnate. In (b) palmately compound leaves, such as those of the horse 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.

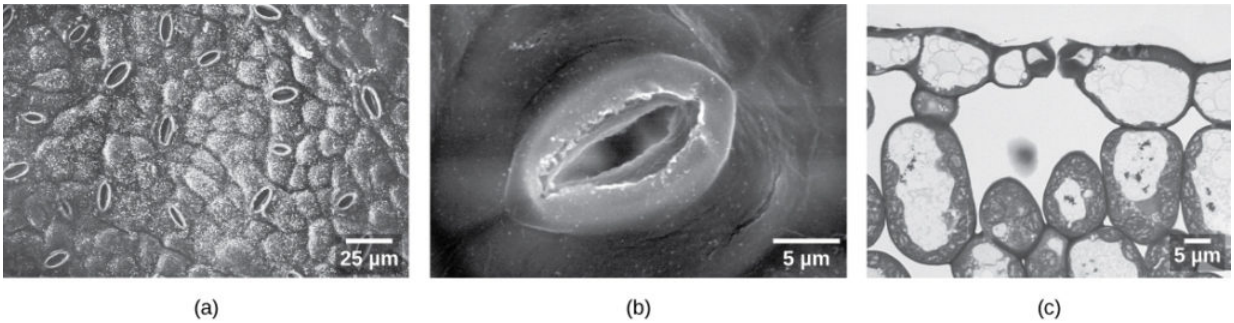


Figure 4. Visualized at 500x with a scanning electron microscope, several stomata are clearly visible on (a) the surface of this sumac (*Rhus glabra*) leaf. At 5,000x magnification, the guard cells of (b) a single stoma from lyre-leaved sand cress (*Arabidopsis lyrata)* have the appearance of lips that 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).

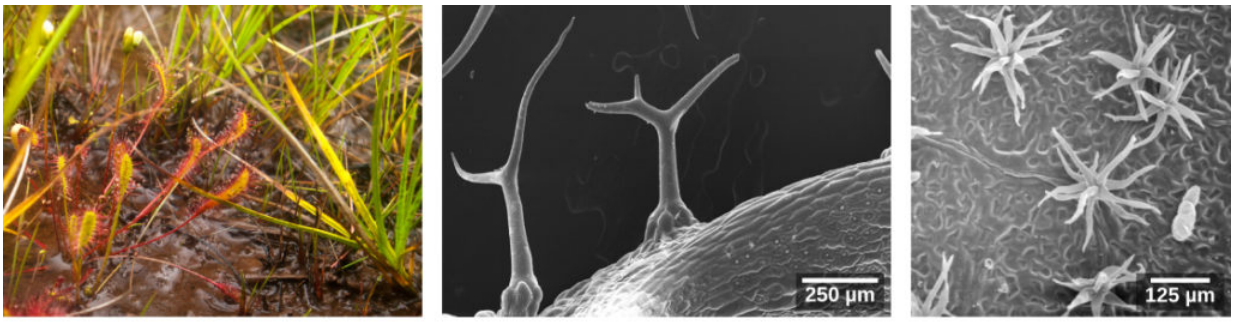


Figure 5. Trichomes give leaves a fuzzy appearance as in this (a) sundew (*Drosera* sp.). Leaf trichomes include (b) branched trichomes on the leaf of *Arabidopsis lyrata* and (c) multibranched trichomes on a mature *Quercus marilandica* leaf. (credit a: John Freeland; credit b, c: modification of work 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.

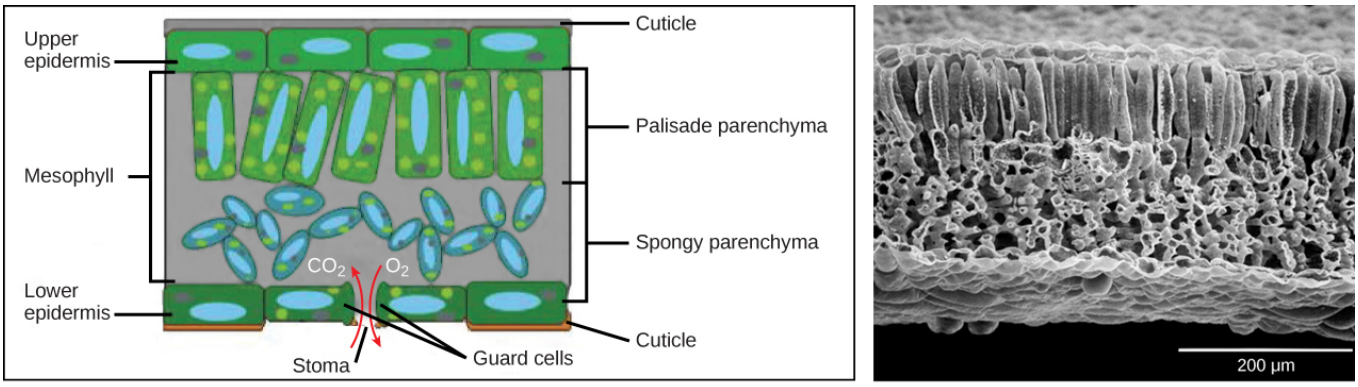


Figure 6. (a) Leaf drawing (b) Scanning electron micrograph of a leaf. (credit b: modification of work by Robert R. Wise)

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.

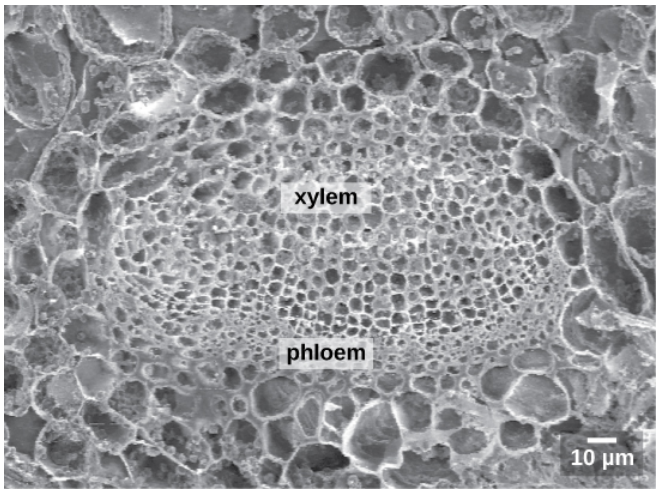


Figure 7. This scanning electron micrograph shows xylem and phloem in the leaf vascular bundle from the lyre-leaved sand cress (Arabidopsis lyrata). (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

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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10.7: Roots

Learning Objectives

- Identify the two types of root systems

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)

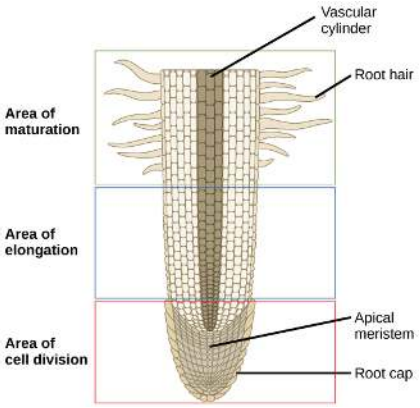


Figure 2. A longitudinal view of the root reveals the zones of cell division, elongation, and maturation. Cell division occurs in the apical meristem.

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.

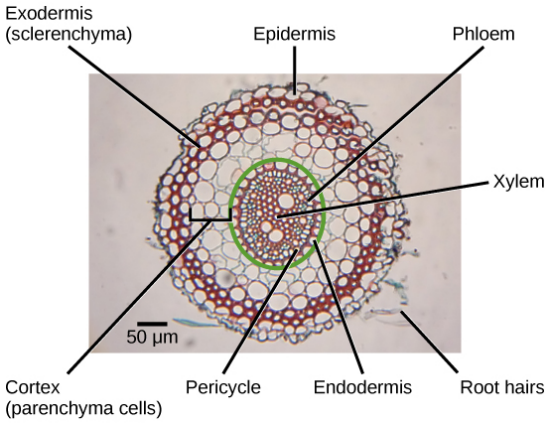


Figure 3. Staining reveals different cell types in this light micrograph of a wheat (*Triticum*) root cross section. Sclerenchyma cells of the exodermis and xylem cells stain red, and phloem cells stain blue. Other cell types stain black. The stele, or vascular tissue, is the area inside endodermis (indicated 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.

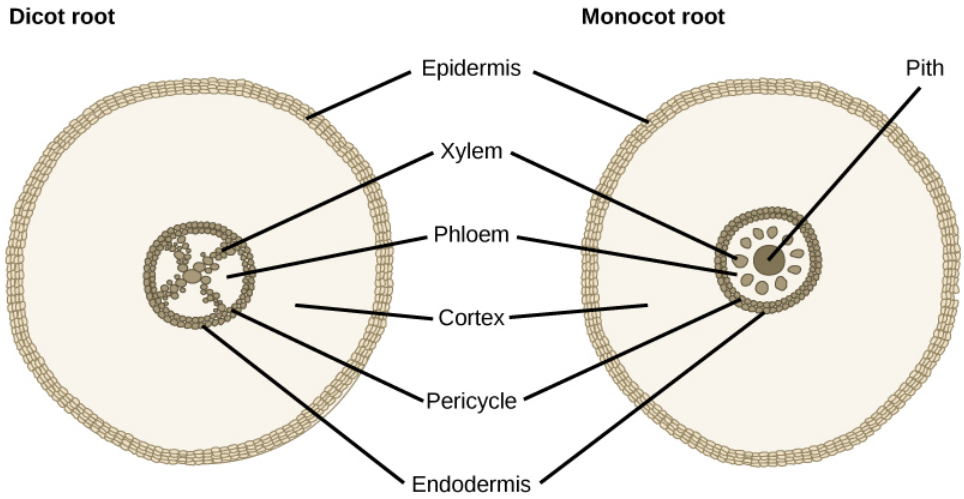


Figure 4. In (left) typical dicots, the vascular tissue forms an X shape in the center of the root. In (right) typical monocots, the phloem cells and the larger xylem cells form a characteristic ring around the central pith.

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?

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[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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10.8: Introduction to Plant Functionality

What you'll learn to do: Discuss common functions of plants

You may have heard the common phrase "form follows function"; this phrase simply means that the form of anything is created or designed (or evolved!) to allow the function that thing needs. As we've learned previously, plants share several common structures: stems, roots, and leaves. As you may have guessed, these common structures allow for the common functions of plants.

All plants 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.

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10.9: Transport of Water and Solutes in Plants

Learning Objectives

- 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.

Transpiration

Transpiration is the loss of water from the plant through evaporation at the leaf surface. It is the main driver of water movement in the xylem. Transpiration is caused by the evaporation of water at the leaf–atmosphere interface; it creates negative pressure (tension) at the leaf surface. 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.

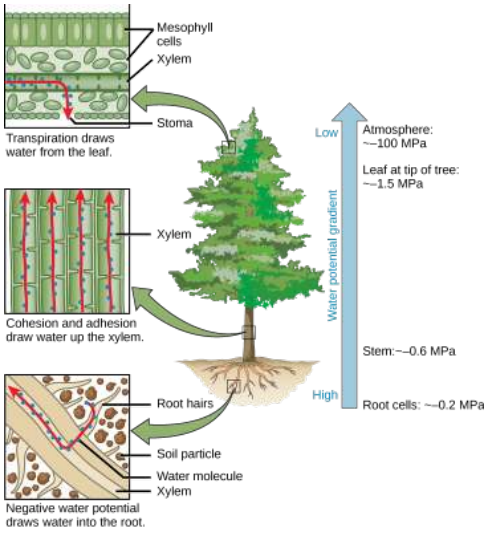


Figure 1. The cohesion–tension theory of sap ascent is shown. Evaporation from the mesophyll cells produces a negative water potential gradient that causes water to move upwards from the roots through the xylem.

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. Transpiration 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.

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 3a).

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. This causes the bulk flow of phloem from source to sink (Figure 3b). 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.

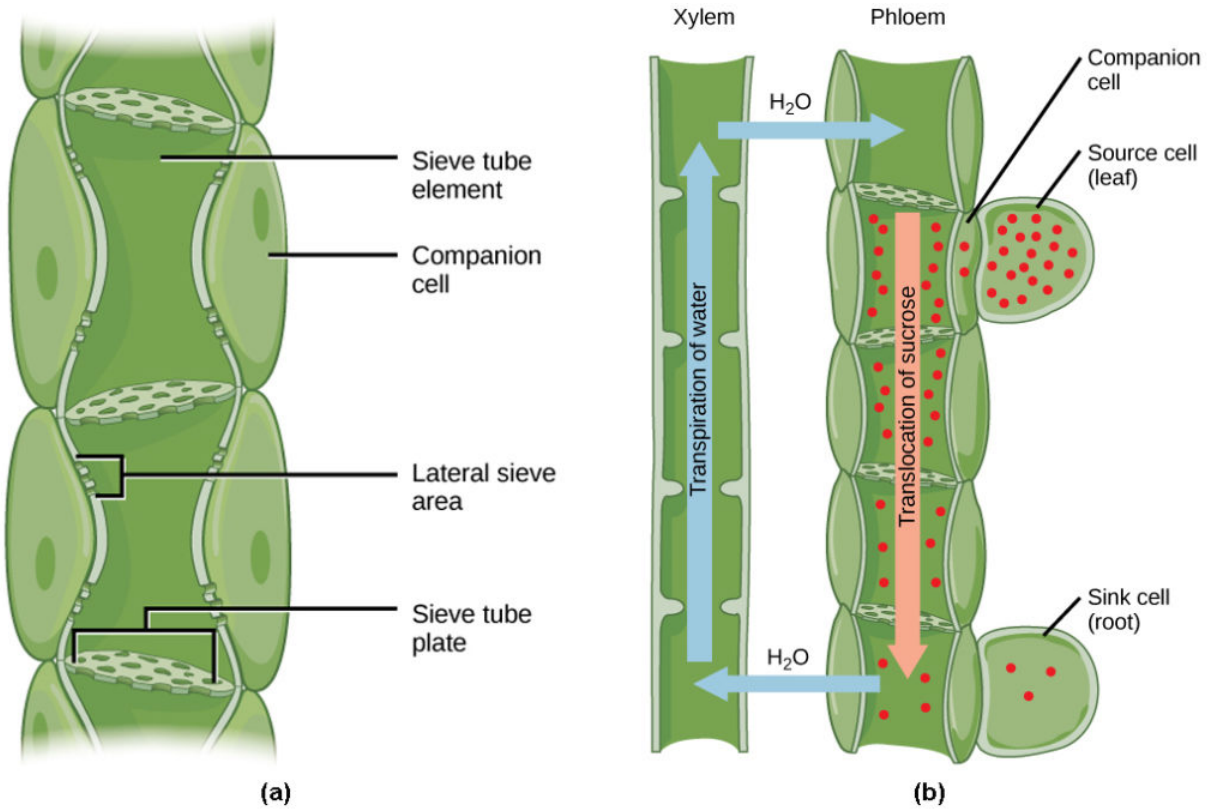


Figure 3. (a) Phloem is comprised of cells called sieve-tube elements. Phloem sap travels through perforations called sieve tube plates. Neighboring companion cells carry out metabolic functions for the sieve-tube elements and provide them with energy. Lateral sieve areas connect the sieve-tube elements 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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10.10: Plant Sensory Systems and Responses

Learning Objectives

- 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.

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. Positive phototropism is growth towards a light source (Figure 1), while negative phototropism (also called skototropism) is growth away from light.



Figure 1. Azure bluets (*Houstonia caerulea*) display a phototropic response by bending toward the light. (credit: Cory Zanker)

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.

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.

Use the navigation menu in the left panel of this website to view images of plants in motion.

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.

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.

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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10.11: Plant Growth

Learning Objectives

- 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.

How Plants Grow

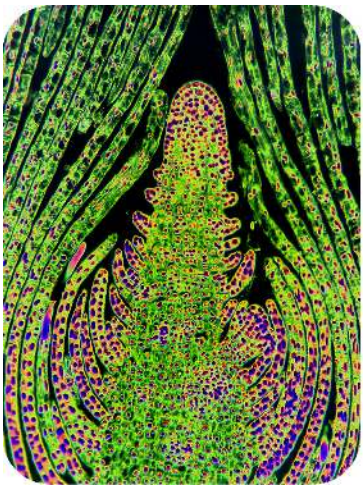


Figure 1. There must be an area of growth, similar to how the bones in your fingers, arms, and legs grow longer. There is, and it is called the apical meristem, which is shown here.

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**.

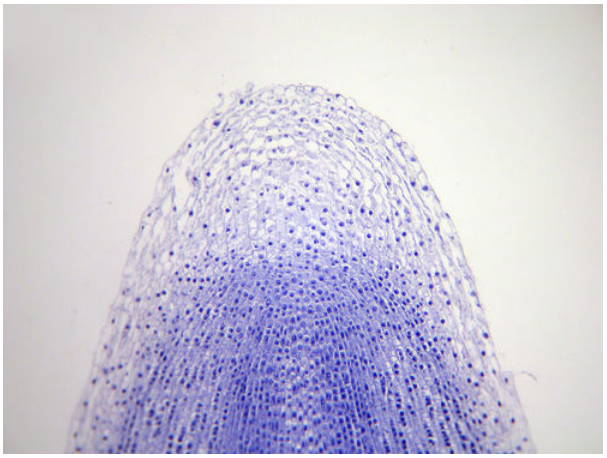


Figure 2. Microphotograph of the root tip of a broad bean show rapidly dividing apical meristem tissue just behind the root cap. Numerous cells in various stages of mitosis can be observed.

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.

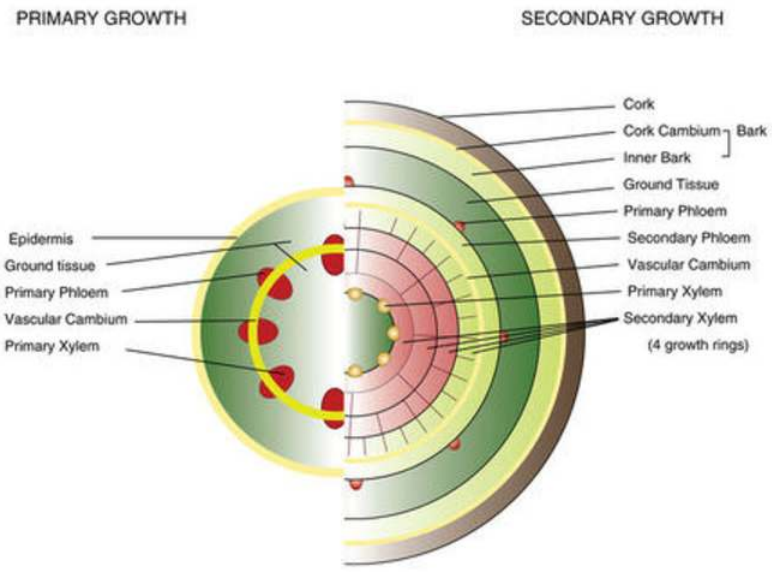


Figure 3. Primary and secondary growth

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/bionm2/?p=292

Learning Objectives

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).

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 4 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.

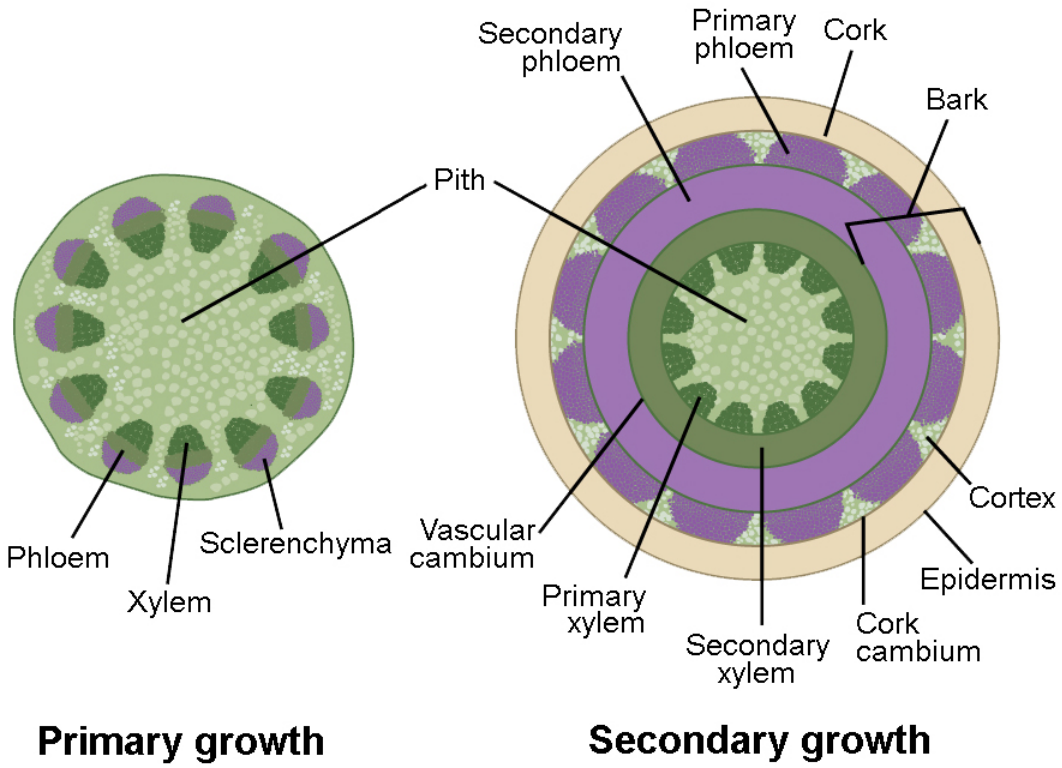


Figure 4. In woody plants, primary growth is followed by secondary growth, which allows the plant stem to increase in thickness or girth. Secondary vascular tissue is added as the plant grows, as well as a cork layer. The bark of a tree extends from the vascular cambium to the epidermis.

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 4).



Figure 5. 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 5). This supplies oxygen to the living and metabolically active cells of the cortex, xylem and phloem.

Annual Rings



Figure 6. 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 6). 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.

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 7. 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 7).

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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10.12: Plant Nutrition

Learning Objectives

- 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.

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

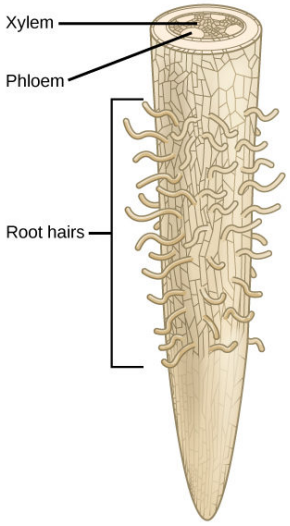


Figure 1. Water is absorbed through the root hairs and moves up the xylem to the leaves.

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.

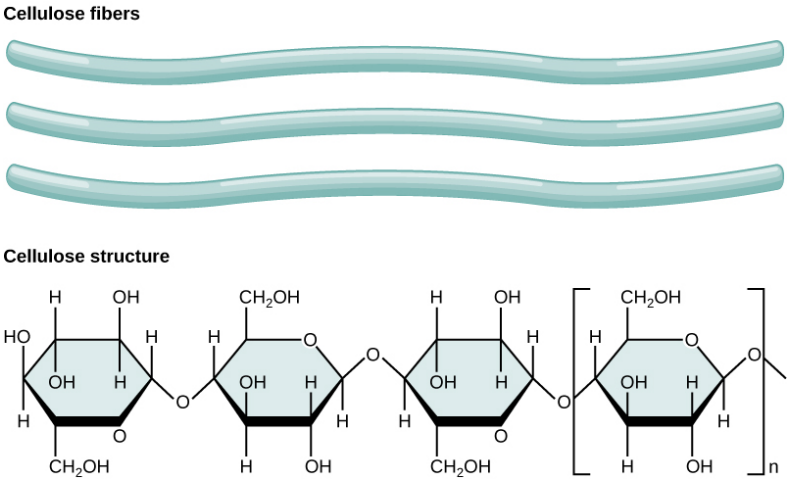


Figure 2. Cellulose, the main structural component of the plant cell wall, makes up over thirty percent of plant matter. It is the most abundant organic compound on earth.

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).



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)

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.

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.

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. 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 most important source of BNF is the symbiotic interaction between soil bacteria and legume plants, including many crops important to humans (Figure 4). The NH_3 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 4. 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?

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[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 5).



Figure 5. 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 6. 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 6). 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.

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 7a), 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 7b). 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 7. (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 8a). 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 8b). 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 8. (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 9. 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 9).

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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10.13: Plant Photorespiration

Learning Objectives

- Differentiate between C_3, C_4, and CAM plant approaches to photorespiration

High crop yields are pretty important—for keeping people fed, and also for keeping economies running. If you heard there was a single factor that reduced the yield of wheat by 20 percent and the yield of soybeans by 36 percent in the United States, for instance, you might be curious to know what it was[1].

As it turns out, the factor behind those (real-life) numbers is photorespiration. This wasteful metabolic pathway begins when rubisco, the carbon-fixing enzyme of the Calvin cycle, grabs O_2 rather than CO_2. It uses up fixed carbon, wastes energy, and tends to happens when plants close their stomata (leaf pores) to reduce water loss. High temperatures make it even worse.

Some plants, unlike wheat and soybean, can escape the worst effects of photorespiration. The C_4 and CAM pathways are two adaptations—beneficial features arising by natural selection—that allow certain species to minimize photorespiration. These pathways work by ensuring that Rubisco always encounters high concentrations of CO_2 making it unlikely to bind to O_2.

Now, let's take a closer look at the C_3, C_4 and CAM pathways and see how they do (or don't!) reduce photorespiration.

C_3 plants

A "normal" plant—one that doesn't have photosynthetic adaptations to reduce photorespiration—is called a C_3 plant. The first step of the Calvin cycle is the fixation of carbon dioxide by rubisco, and plants that use only this "standard" mechanism of carbon fixation are called C_3 plants, for the three-carbon compound (3-PGA) the reaction produces[2]. About 85 percent of the plant species on the planet are C_3 plants, including rice, wheat, soybeans and all trees.

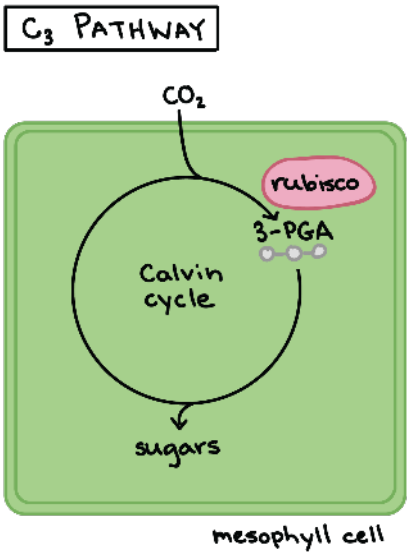


Figure 1. The C_3 Pathway

C_4 plants

In C_4 plants, the light-dependent reactions and the Calvin cycle are physically separated, with the light-dependent reactions occurring in the mesophyll cells (spongy tissue in the middle of the leaf) and the Calvin cycle occurring in special cells around the leaf veins. These cells are called **bundle-sheath** cells.

To see how this division helps, let's look at an example of C_4 photosynthesis in action. First, atmospheric CO_2 is fixed in the mesophyll cells to form a simple, 4-carbon organic acid (oxaloacetate). This step is carried out by a non-rubisco enzyme, PEP carboxylase, that has no tendency to bind O_2. Oxaloacetate is then converted to a similar molecule, malate, that can be transported

in to the bundle-sheath cells. Inside the bundle sheath, malate breaks down, releasing a molecule of CO_2. The CO_2 is then fixed by rubisco and made into sugars via the Calvin cycle, exactly as in C_3 photosynthesis.

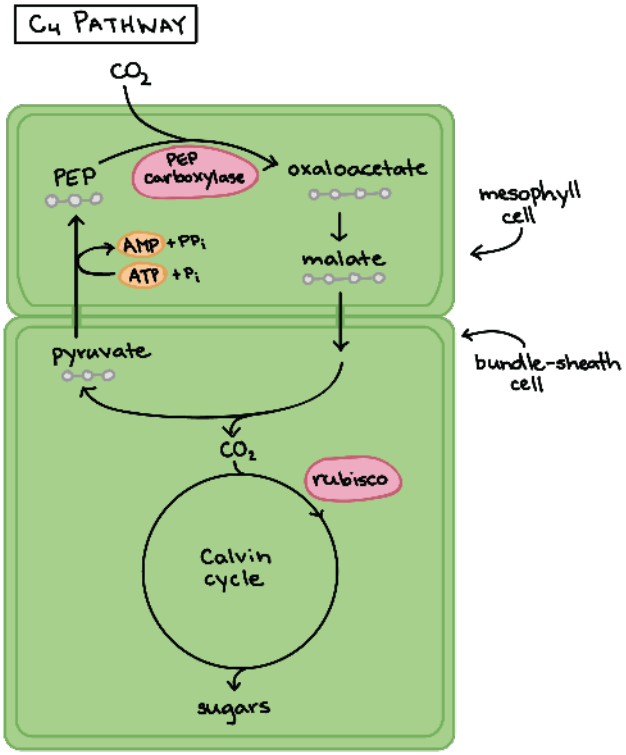


Figure 2. The C_4 Pathway

This process isn't without its energetic price: ATP must be expended to return the three-carbon "ferry" molecule from the bundle sheath cell and get it ready to pick up another molecule of atmospheric CO_2. However, because the mesophyll cells constantly pump CO_2 into neighboring bundle-sheath cells in the form of malate, there's always a high concentration of CO_2 relative to O_2 right around rubisco. This strategy minimizes photorespiration.

The C_4 pathway is used in about 3 percent of all vascular plants; some examples are crabgrass, sugarcane and corn. C_4 plants are common in habitats that are hot, but are less abundant in areas that are cooler. In hot conditions, the benefits of reduced photorespiration likely exceed the ATP cost of moving CO_2 from the mesophyll cell to the bundle-sheath cell.

CAM plants



Figure 3. Crassulaceae

Some plants that are adapted to dry environments, such as cacti and pineapples, use the crassulacean acid metabolism (CAM) pathway to minimize photorespiration. This name comes from the family of plants, the Crassulaceae, in which scientists first discovered the pathway.

Instead of separating the light-dependent reactions and the use of CO_2 in the Calvin cycle in space, CAM plants separate these processes in time. At night, CAM plants open their stomata, allowing CO_2 to diffuse into the leaves. This CO_2 is fixed into oxaloacetate by PEP carboxylase (the same step used by C_4 plants), then converted to malate or another type of organic acid[3].

The organic acid is stored inside vacuoles until the next day. In the daylight, the CAM plants do not open their stomata, but they can still photosynthesis. That's because the organic acids are transported out of the vacuole and broken down to release CO_2, which enters the Calvin cycle. This controlled release maintains a high concentration of CO_2 around rubisco[4].

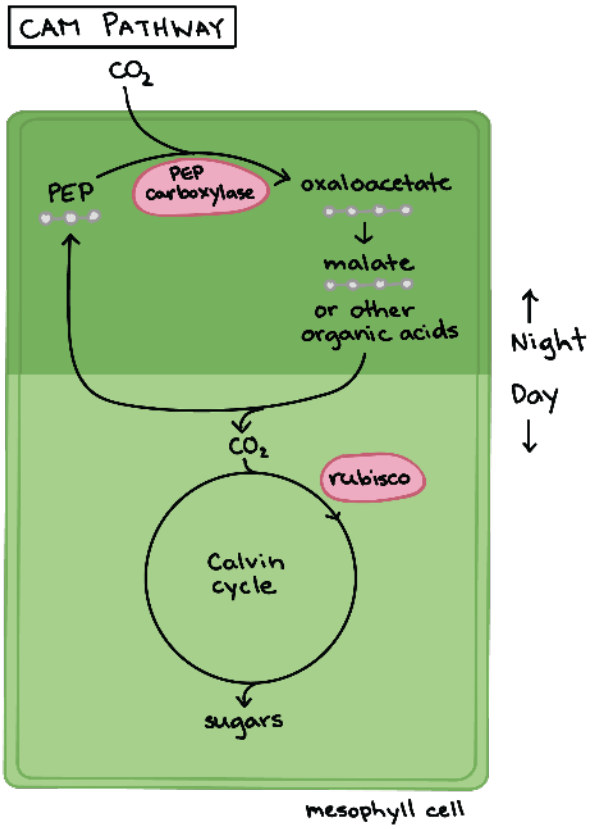


Figure 4. The CAM Pathway

The CAM pathway requires ATP at multiple steps (not shown above), so like C_4 photosynthesis, it is not an energetic "freebie."[5] However, plant species that use CAM photosynthesis not only avoid photorespiration, but are also very water-efficient. Their stomata only open at night, when humidity tends to be higher and temperatures are cooler, both factors that reduce water loss from leaves. CAM plants are typically dominant in very hot, dry areas, like deserts.

Comparisons of C_3, C_4, and CAM plants

C_3, C_4, and CAM plants all use the Calvin cycle to make sugars from CO_2. These pathways for fixing CO_2 have different advantages and disadvantages and make plants suited for different habitats. The C_3 mechanism works well in cool environments, while C_4 and CAM plants are adapted to hot, dry areas.

Both the C_4 and CAM pathways have evolved independently over two dozen times, which suggests they may give plant species in hot climates a significant evolutionary advantage[6].

Type	Separation of initial CO_2 fixation and Calvin cycle	Stomata open	Best adapted to
C_3	No separation	Day	Cool, wet environments
C_4	Between mesophyll and bundle-sheath cells (in space)	Day	Hot, sunny environments
CAM	Between night and day (in time)	Night	Very hot, dry environments

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6. Guralnick, Lonnie J., Amanda Cline, Monica Smith, and Rowan F. Sage. (2008). Evolutionary physiology: the extent of C_4 and CAM photosynthesis in the genera Anacampseros and Grahamia of the Portulacaceae. *Journal of Experimental Botany*, 59(7), 1735–1742. http://dx.doi.org/10.1093/jxb/ern081. ↵

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10.14: 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.

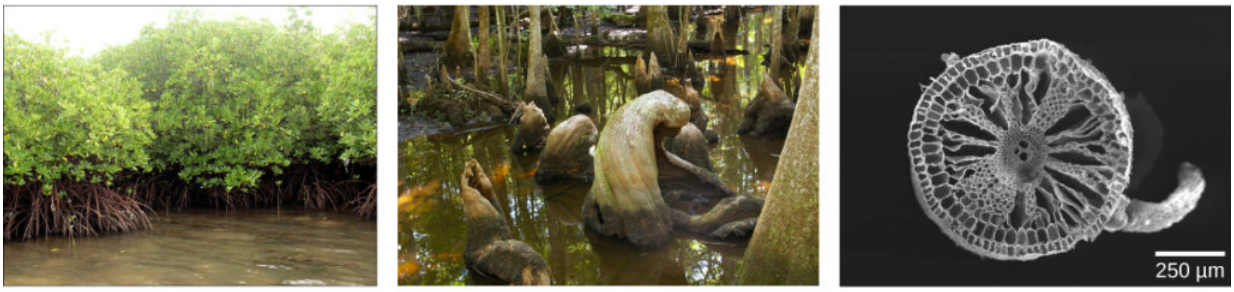


(a) (b)

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)

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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CHAPTER OVERVIEW

11: Module 8- Plant Reproduction

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11.2: Introduction to Reproductive Development and Structure
11.3: Stages of a Plant’s Life Cycle
11.4: Sexual Reproduction in Gymnosperms
11.5: Sexual Reproduction in Angiosperms
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11.10: Natural and Artificial Asexual Reproduction
11.11: Plant Life Cycles
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11.1: 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 post-nasal 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 life cycle.

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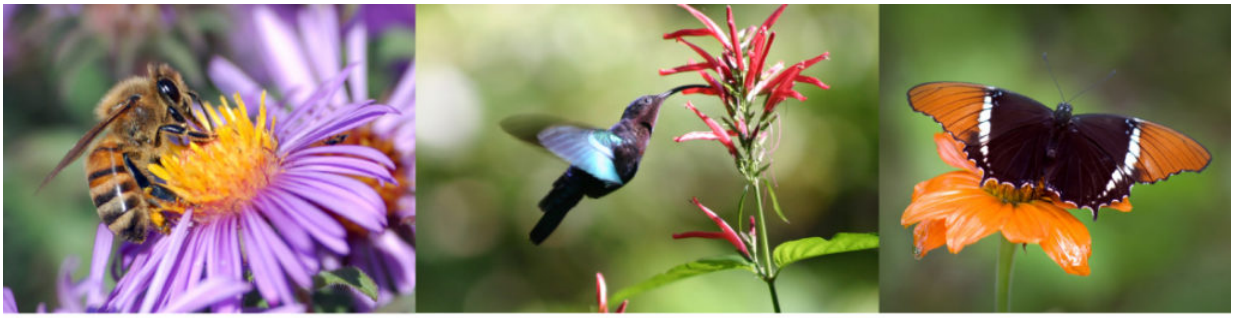
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11.2: Introduction to Reproductive Development and Structure

What you'll learn to do: 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)

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11.3: Stages of a Plant's Life Cycle

Learning Outcomes

- Describe the two stages of a plant's lifecycle

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).

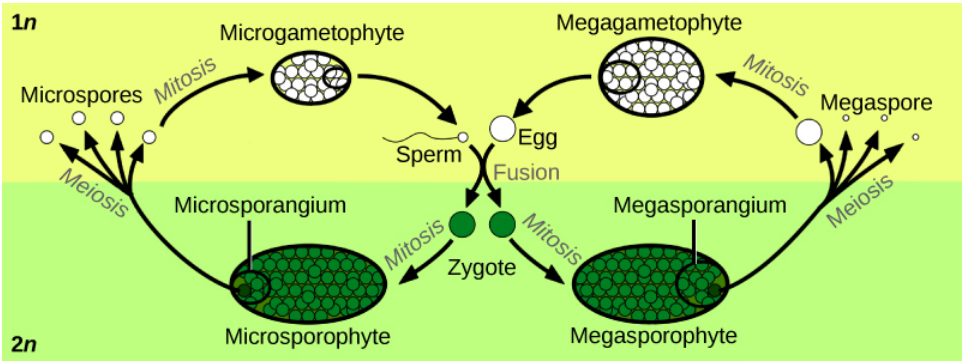


Figure 1. The alternation of generations in angiosperms is depicted in this diagram. (credit: modification of work by Peter Coxhead)

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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11.4: Sexual Reproduction in Gymnosperms

Learning Objectives

- Identify the structures involved in reproduction of gymnosperms

The life cycle of a gymnosperm is 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.

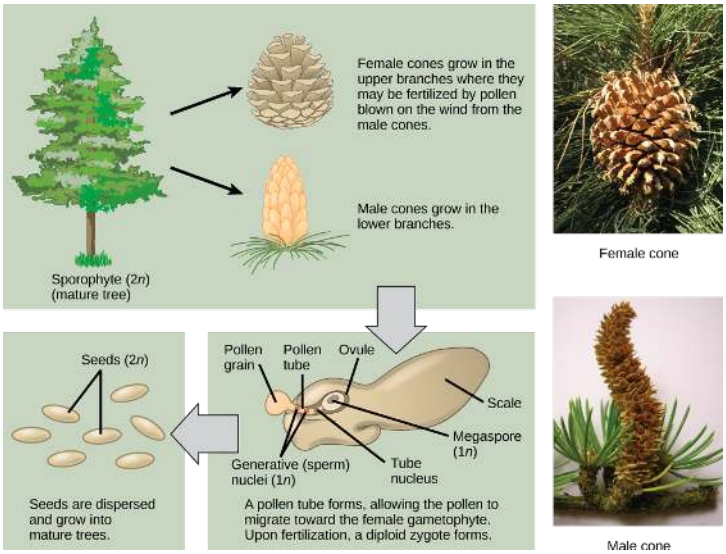


Figure 1. This image shows the life cycle of a conifer. Pollen from male cones blows up into upper branches, where it fertilizes female cones. Examples are shown of female and male cones. (credit “female”: modification of work by “Geographer”/Wikimedia Commons; credit “male”: modification of work by 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.

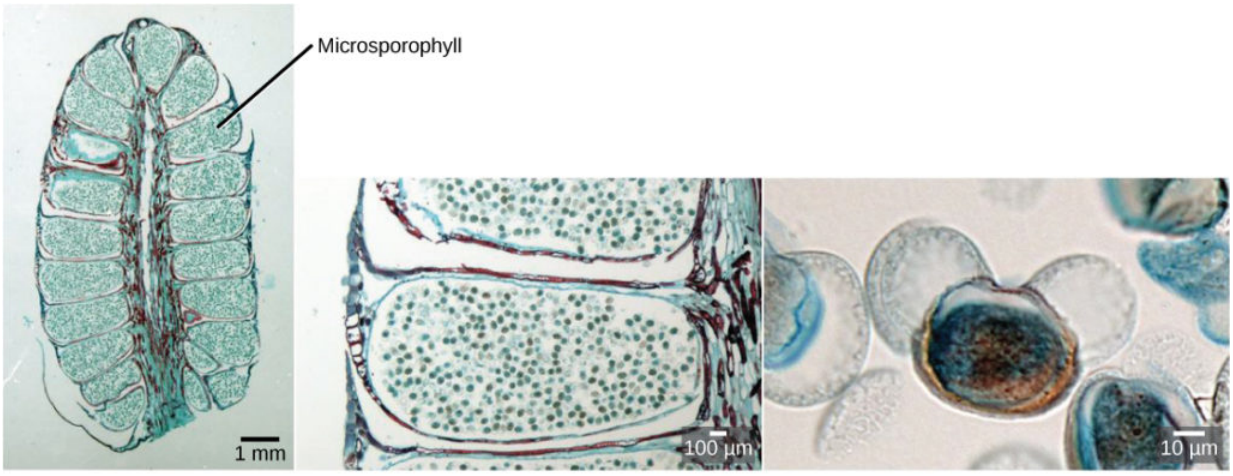


Figure 2. These series of micrographs shows a male gymnosperm gametophyte. (a) This male cone, shown in cross section, has approximately 20 microsporophylls, each of which produces hundreds of male gametophytes (pollen grains). (b) Pollen grains are visible in this single microsporophyll. (c) This micrograph 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/bionm2/?p=308

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.

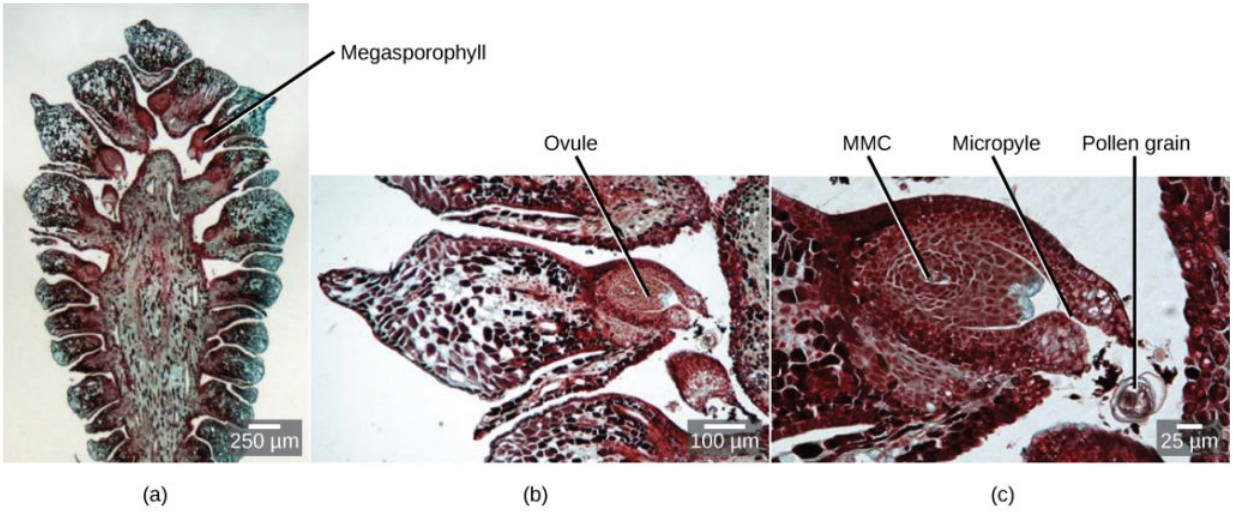


Figure 3. These series of micrographs shows a female gymnosperm gametophyte. (a) This cross section of a female cone shows portions of about 15 megasporophylls. (b) The ovule can be seen in this single megasporophyll. (c) Within this single ovule are the megaspore mother cell (MMC), micropyle, and a 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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11.5: Sexual Reproduction in Angiosperms

Learning Objectives

- Identify the structures involved in reproduction of 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.

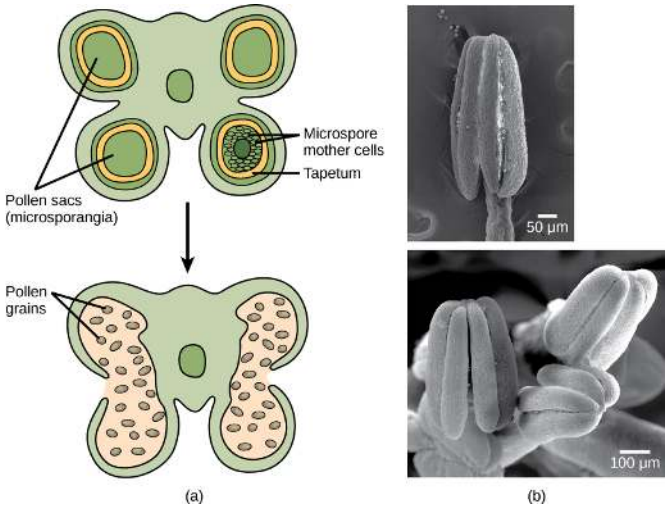


Figure 1. Shown is (a) a cross section of an anther at two developmental stages. The immature anther (top) contains four microsporangia, or pollen sacs. Each microsporangium contains hundreds of microspore mother cells that will each give rise to four pollen grains. The tapetum supports the development 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.

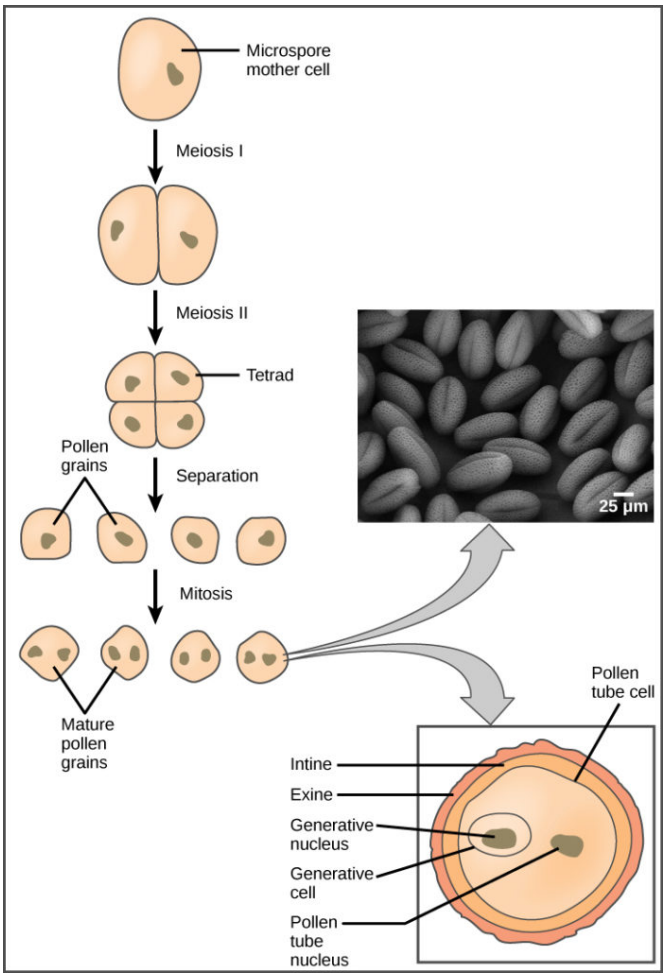


Figure 2. Pollen develops from the microspore mother cells. The mature pollen grain is composed of two cells: the pollen tube cell and the generative cell, which is inside the tube cell. The pollen grain has two coverings: an inner layer (intine) and an outer layer (exine). The inset scanning electron 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

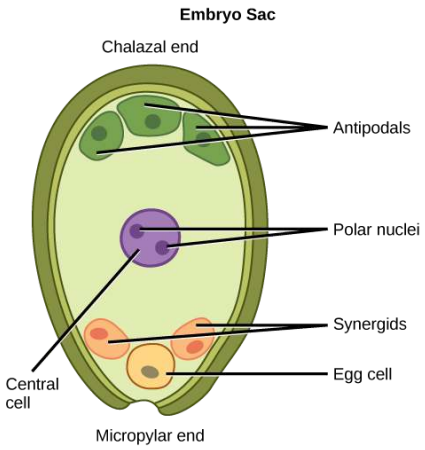


Figure 3. As shown in this diagram of the embryo sac in angiosperms, the ovule is covered by integuments and has an opening called a micropyle. Inside the embryo sac are three antipodal cells, two synergids, a central cell, and the egg cell.

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.

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[hidden-answer a="673553"]Statement b should be expected.[/hidden-answer]

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11.6: Flower Structure

Learning Outcomes

- Describe the components of a complete flower

Flowers contain angiosperm reproductive structures. A typical flower has four main parts—or whorls—known as the calyx, corolla, androecium, and gynoecium (Figure 1).

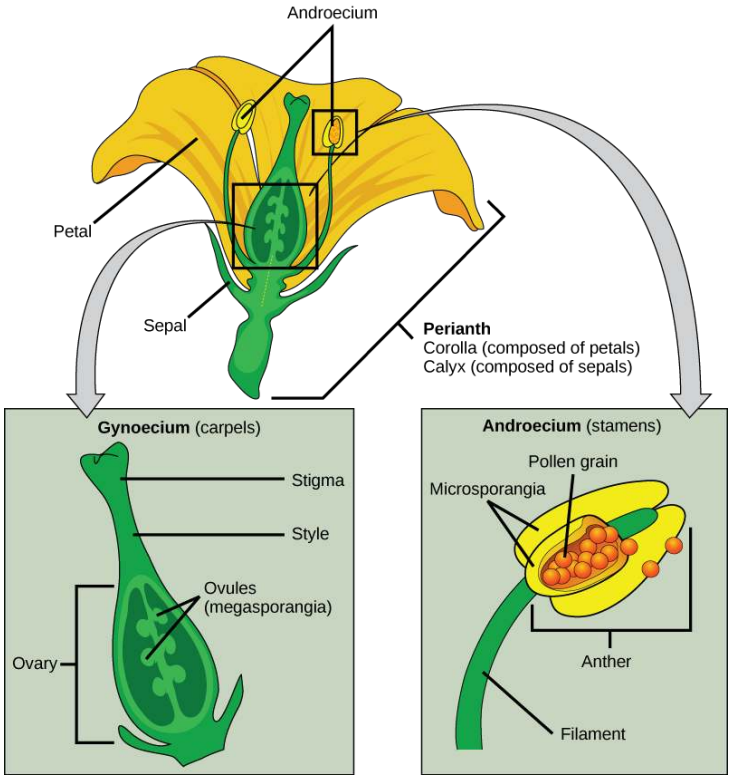


Figure 1. The four main parts of the flower are the calyx, corolla, androecium, and gynoecium. The androecium is the sum of all the male reproductive organs, and the gynoecium is the sum of the female reproductive organs. (credit: modification of work by Mariana Ruiz Villareal)

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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[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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[hidden-answer a="261988"]Carpellate

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What term describes an incomplete flower lacking a gynoecium?

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[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).

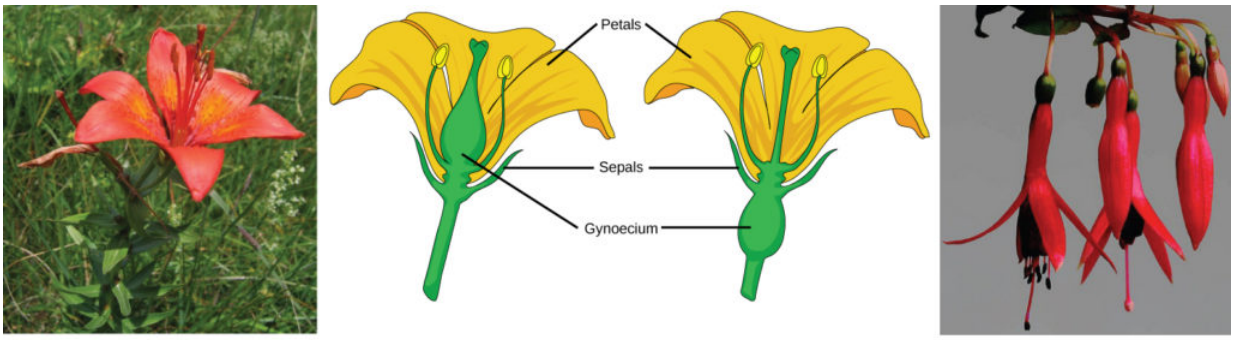


Figure 3. The (a) lily is a superior flower, which has the ovary above the other flower parts. (b) Fuchsia is an inferior flower, which has the ovary beneath other flower parts. (credit a photo: modification of work by Benjamin Zwittnig; credit b photo: modification of work by “Koshy Koshy”/Flickr)

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11.7: Angiosperms versus Gymnosperms

Learning Outcomes

- Identify the structures involved in reproduction of gymnosperms
- Identify the structures involved in reproduction of angiosperms



(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.

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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11.8: Introduction to Asexual Reproduction in Plants

What you'll learn to do: 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.

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11.9: Asexual Plants

Learning Outcomes

- Describe characteristics of plants that reproduce asexually

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.

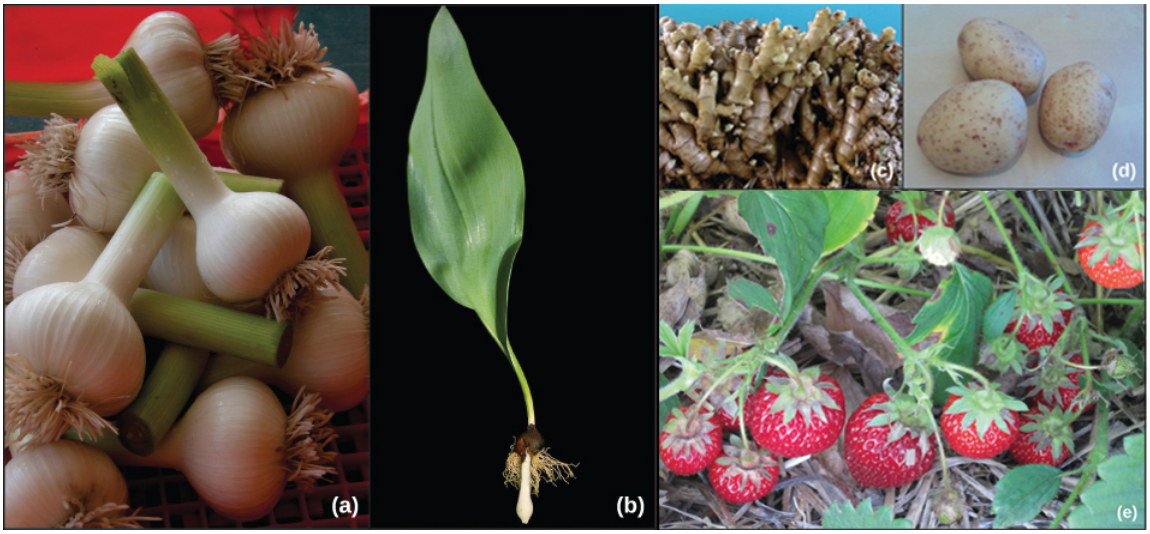


Figure 1. Different types of stems allow for asexual reproduction. (a) The corm of a garlic plant looks similar to (b) a tulip bulb, but the corm is solid tissue, while the bulb consists of layers of modified leaves that surround an underground stem. Both corms and bulbs can self-propagate, giving rise 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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11.10: Natural and Artificial Asexual Reproduction

Learning Objectives

- Discuss the mechanisms, advantages, and disadvantages of 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.

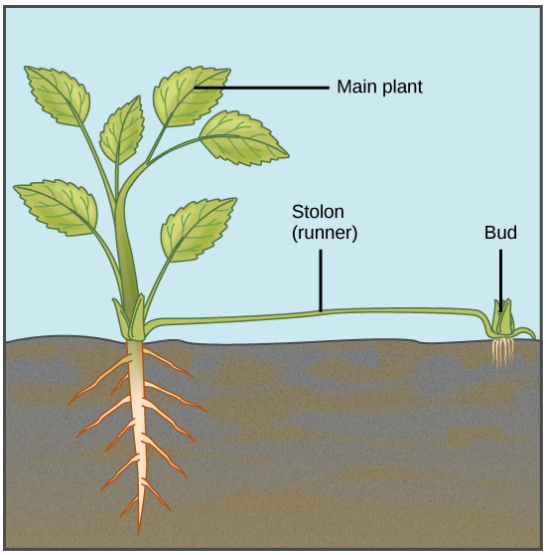


Figure 1. A stolon, or runner, is a stem that runs along the ground. At the nodes, it forms adventitious roots and buds that grow into a new plant.

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

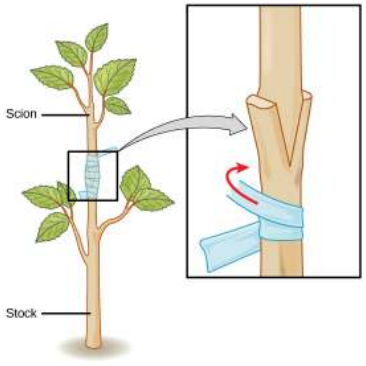


Figure 2. Grafting is an artificial method of asexual reproduction used to produce plants combining favorable stem characteristics with favorable root characteristics. The stem of the plant to be grafted is known as the scion, and the root is called the stock.

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

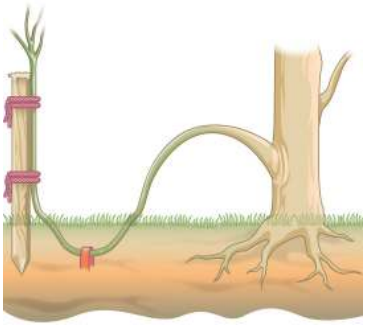


Figure 3. In layering, a part of the stem is buried so that it forms a new plant.

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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11.11: Plant Life Cycles

Learning Outcomes

- Discuss plant life cycles



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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11.12: Putting It Together- Plant Reproduction

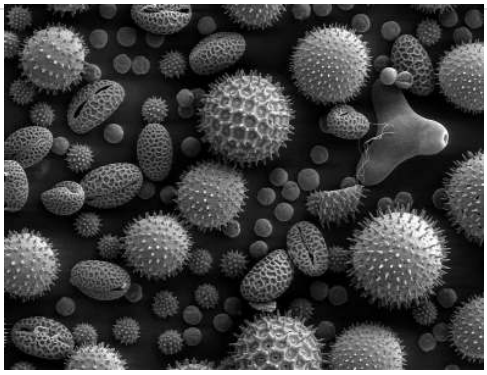


Figure 1. A micrograph of miscellaneous pollen

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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CHAPTER OVERVIEW

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12.1: 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 did 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.

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12.2: Introduction to the Evolutionary History of the Animal Kingdom

What you'll learn to do: 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.

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12.3: Pre-Cambrian Animal Life

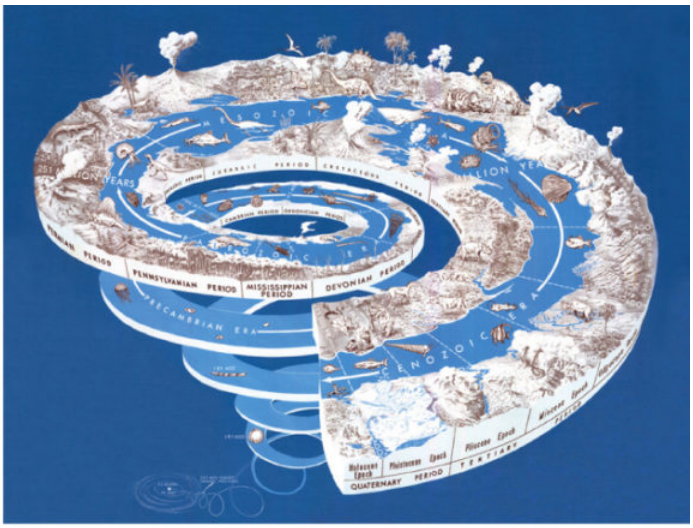
Learning Outcomes

- Describe the features that characterized the earliest animals and when they appeared on earth

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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12.4: The Cambrian Explosion

Learning Outcomes

- Explain the significance of the Cambrian period for animal evolution and the changes in animal diversity that took place during that time

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).

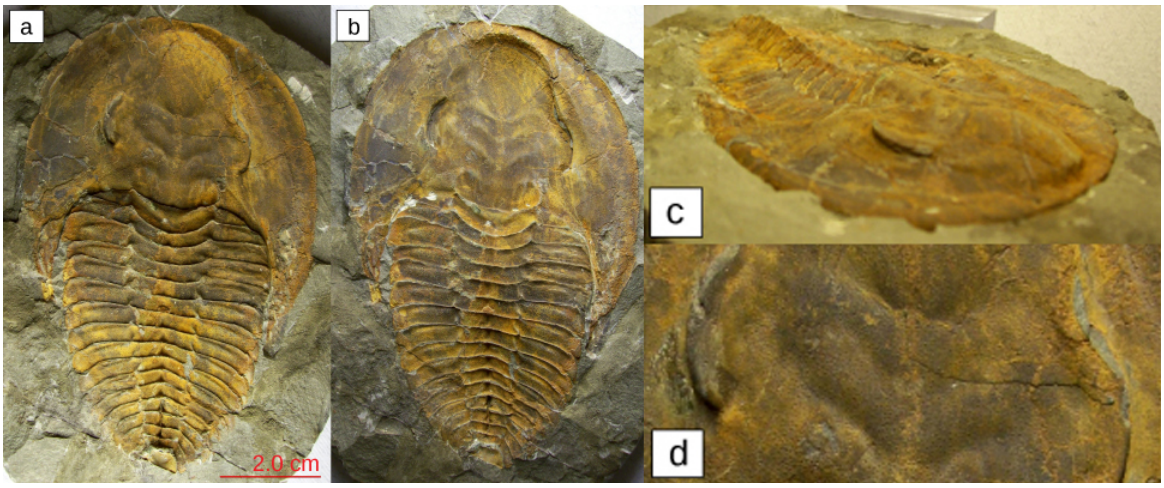


Figure 1. These fossils (a–d) belong to trilobites, extinct arthropods that appeared in the early Cambrian period, 525 million years ago, and disappeared from the fossil record during a mass extinction at the end of the Permian period, about 250 million years ago.

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).

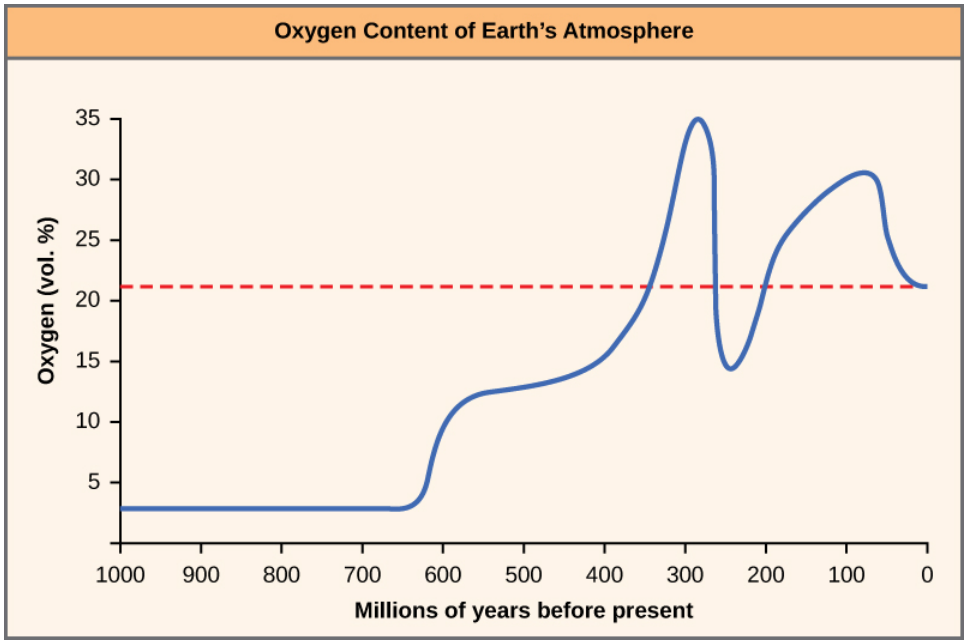


Figure 2. The oxygen concentration in Earth's atmosphere rose sharply around 300 million years ago.

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.



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12.5: Post-Cambrian Evolution

Learning Outcomes

- Discuss the implications of mass animal extinctions that have occurred in evolutionary history

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.

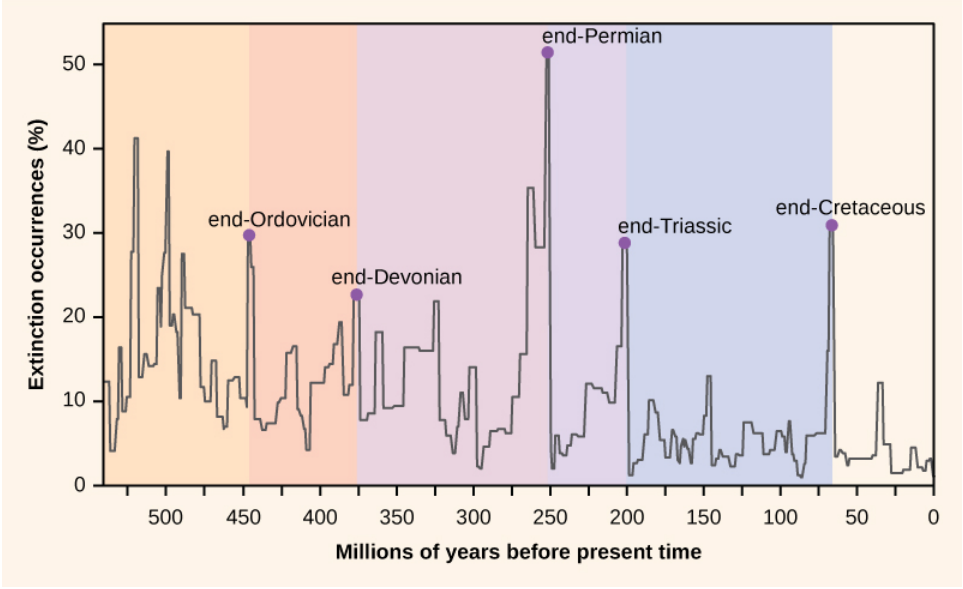


Figure 1. Mass extinctions have occurred repeatedly over geological time.

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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12.6: Introduction to Animal Phylogeny

What you'll learn to do: 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.

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12.7: Classifying Animals

Learning Outcomes

- Identify key features scientists use to classify 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.

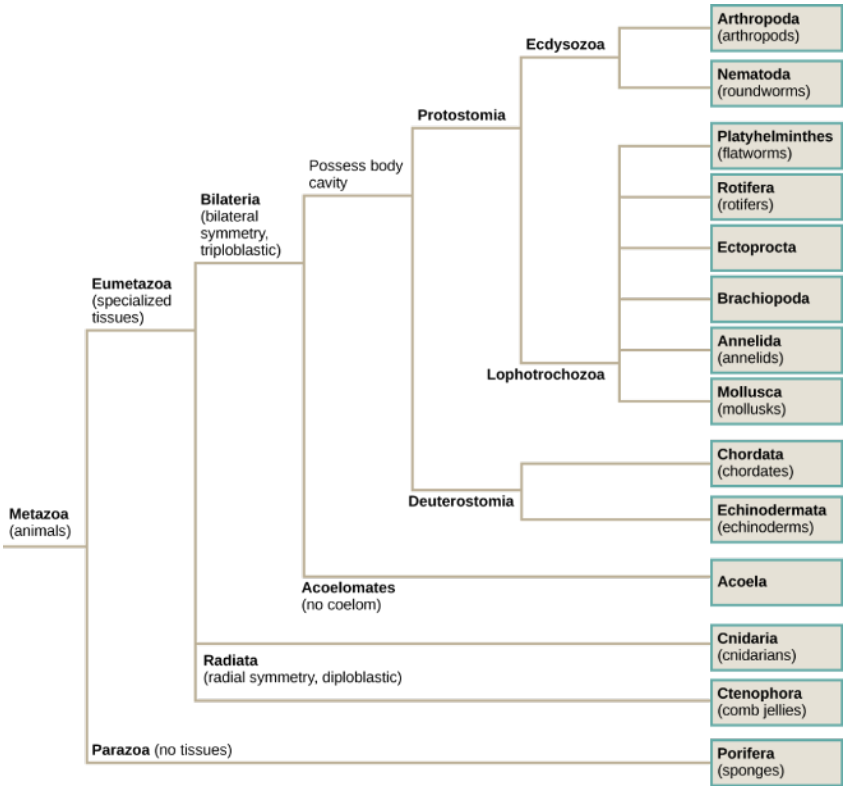


Figure 1. The phylogenetic tree of animals is based on morphological, fossil, and genetic evidence.

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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12.8: Constructing an Animal Phylogenetic Tree

Learning Outcomes

- Interpret the metazoan 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).

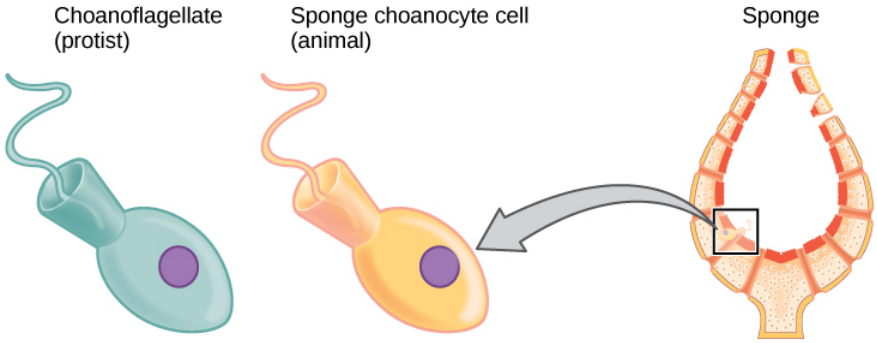


Figure 1. Cells of the protist choanoflagellate resemble sponge choanocyte cells. Beating of choanocyte flagella draws water through the sponge so that nutrients can be extracted and waste removed.

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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12.9: Modern Revisions of Phylogeny

Learning Outcomes

- List some of the relationships within the modern phylogenetic tree that have been discovered as a result of modern molecular data

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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12.10: 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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CHAPTER OVERVIEW

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13.1: Why It Matters- Features of the Animal Kingdom

Why learn about the Animal Kingdom?

Sea sponges and corals may look like plants, but they actually belong to the animal kingdom. Let's take a look at these interesting animals!



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/bionm2/?p=350

So just why do sponges "count" as animals? In this module we'll learn about the shared characteristics of animals, and learn just how sponges fit into this kingdom.

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13.2: Introduction to Animal Form and Function

What you'll learn to do: 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)

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13.3: Body Plans

Learning Objectives

- Describe the various types of body plans that occur in animals

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). These 'beside animals' are considered animals because they lack the ability to make their own food.

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.

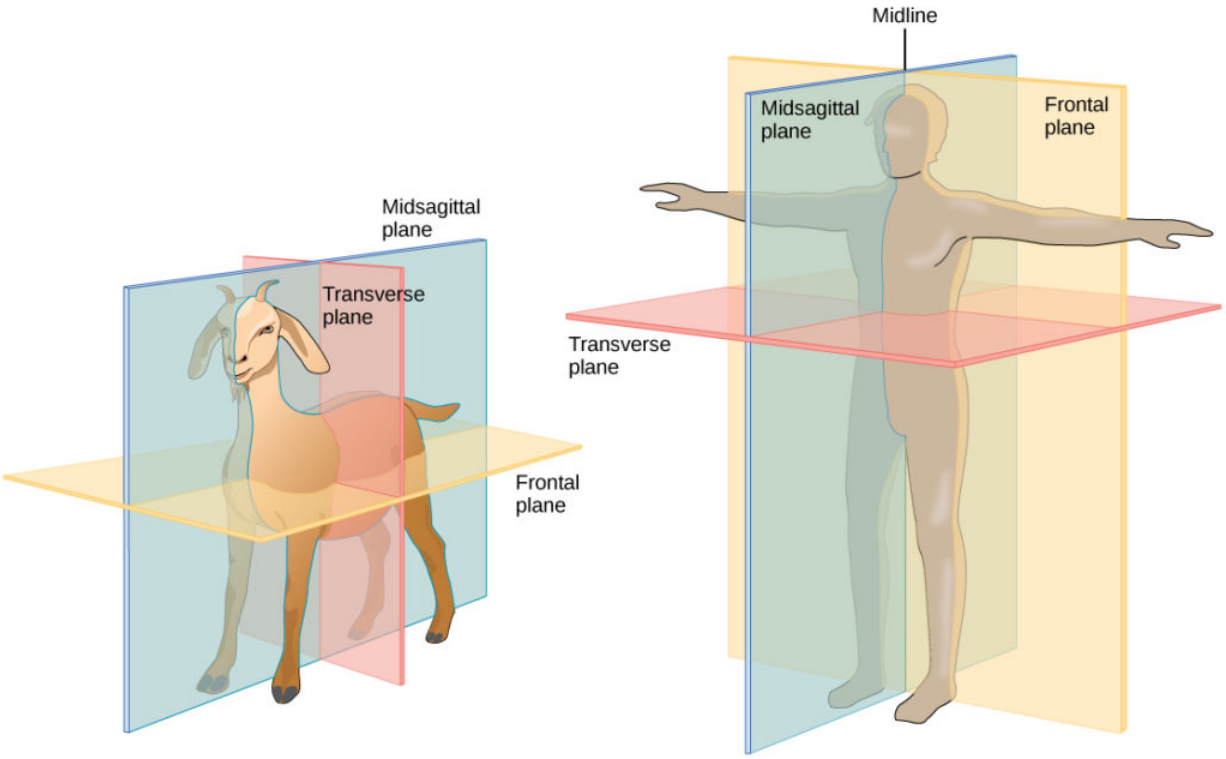


Figure 4. Shown are the planes of a quadruped goat and a bipedal human. The midsagittal plane divides the body exactly in half, into right and left portions. The frontal plane divides the front and back, and the transverse plane divides the body into upper and lower portions.

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.

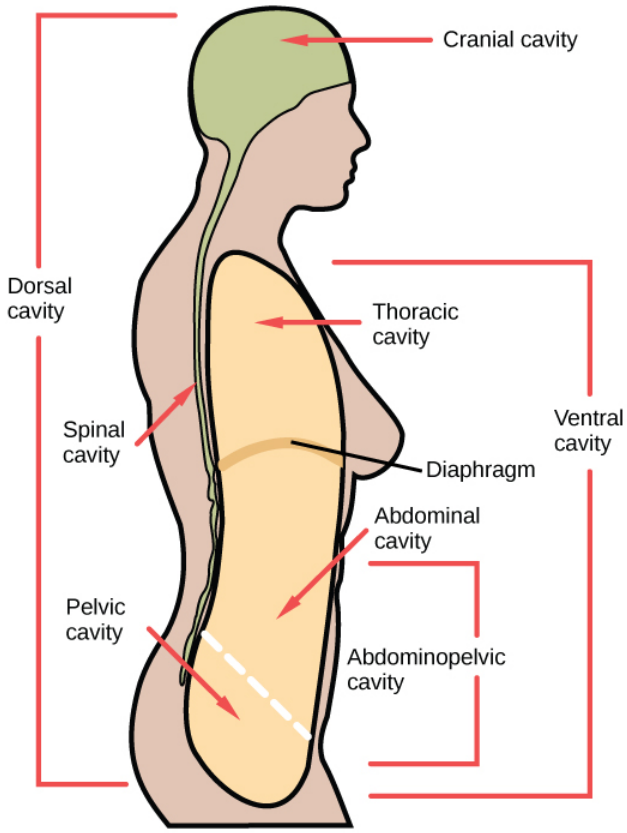


Figure 5. Vertebrate animals have two major body cavities. The dorsal cavity, indicated in green, contains the cranial and the spinal cavity. The ventral cavity, indicated in yellow, contains the thoracic cavity and the abdominopelvic cavity. The thoracic cavity is separated from the abdominopelvic cavity 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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13.4: Limits on Animal Size and Shape

Learning Objectives

- Describe limits on animal size and shape

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.

Bilateral symmetry is found in both land-based and aquatic animals; it enables a high level of mobility. 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).

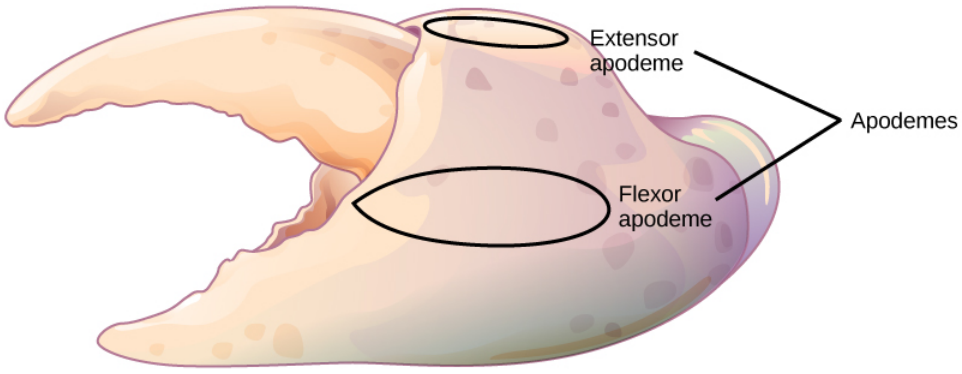


Figure 1. Apodemes are ingrowths on arthropod exoskeletons to which muscles attach. The apodemes on this crab leg are located above and below the fulcrum of the claw. Contraction of muscles attached to the apodemes pulls the claw closed.

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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13.5: Introduction to Animal Primary Tissues

What you'll learn to do: Discuss the tissue structures found in animals

The tissues of multicellular, complex animals are four primary types: epithelial, connective, muscle, and nervous. Recall that tissues are groups of similar cells carrying out related functions. These tissues combine to form organs—like the skin or kidney—that have specific, specialized functions within the body. Organs are organized into organ systems to perform functions; examples include the circulatory system, which consists of the heart and blood vessels, and the digestive system, consisting of several organs, including the stomach, intestines, liver, and pancreas. Organ systems come together to create an entire organism.

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13.6: Complex Tissue Structure

Learning Outcomes

- Discuss the complex tissue structure found in animals

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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13.7: Epithelial Tissues

Learning Objectives

- Describe 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.

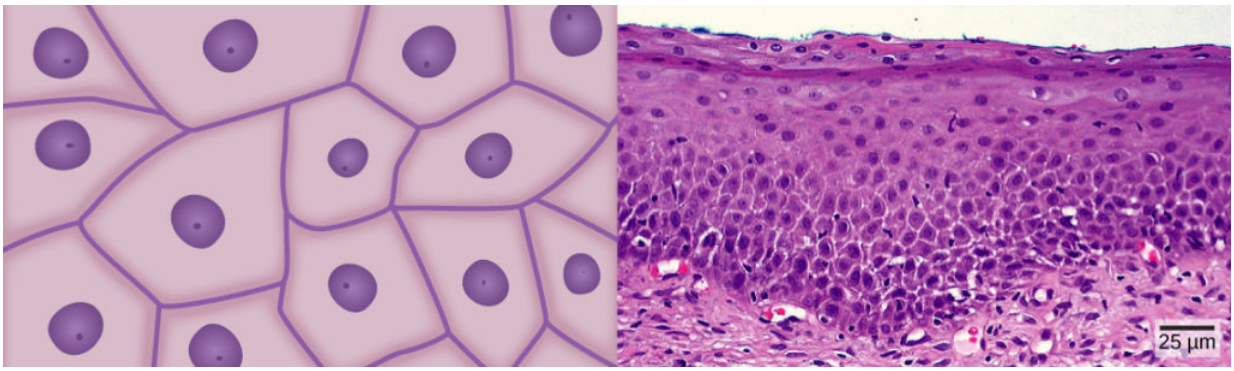


Figure 1. Squamous epithelia cells (a) have a slightly irregular shape, and a small, centrally located nucleus. These cells can be stratified into layers, as in (b) this human cervix specimen. (credit b: modification of work by Ed Uthman; scale-bar data from Matt Russell)

Figure 1a illustrates a layer of squamous cells with their membranes joined together to form an epithelium. 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.

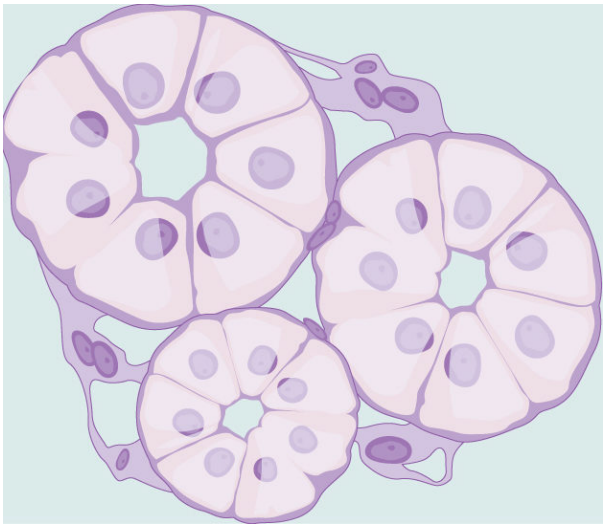


Figure 2. Simple cuboidal epithelial cells line tubules in the mammalian kidney, where they are involved in filtering the blood.

Columnar Epithelia

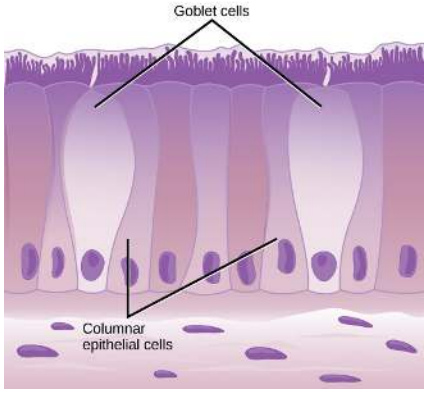


Figure 3. Simple columnar epithelial cells absorb material from the digestive tract. Goblet cells secret mucous into the digestive tract lumen.

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.

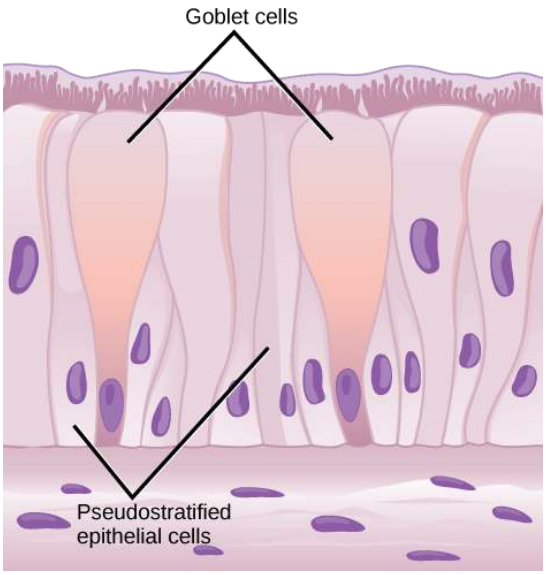


Figure 4. Pseudostratified columnar epithelia line the respiratory tract. They exist in one layer, but the arrangement of nuclei at different levels makes it appear that there is more than one layer. Goblet cells interspersed between the columnar epithelial cells secrete mucous into the respiratory tract.

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.

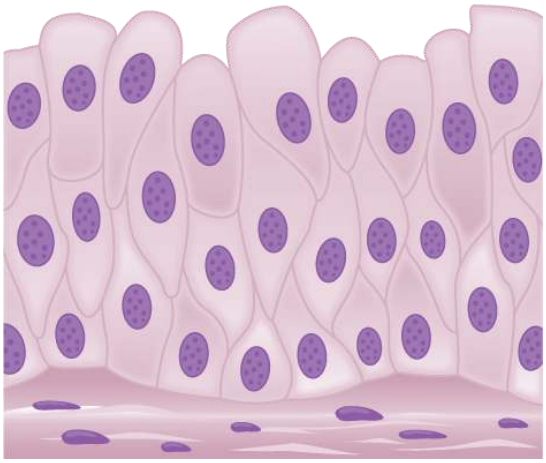


Figure 5. Transitional epithelia of the urinary bladder undergo changes in thickness depending on how full the bladder is.

? 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.

[reveal-answer q="277616"]Show Answer[/reveal-answer]
[hidden-answer a="277616"]Statement d is false. The transitional epithelia itself does not change thickness: the layer simply unfolds.[/hidden-answer]

Click through the interactive review to learn more about epithelial tissues.

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13.8: Connective Tissues

Learning Objectives

- Discuss the different types of connective tissues in animals

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

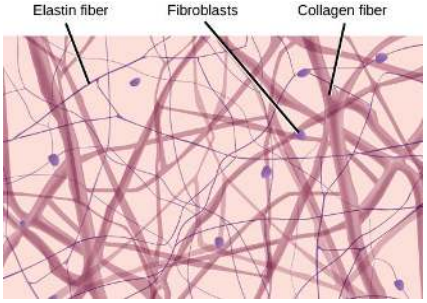


Figure 1. Loose connective tissue is composed of loosely woven collagen and elastic fibers. The fibers and other components of the connective tissue matrix are secreted by fibroblasts.

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).

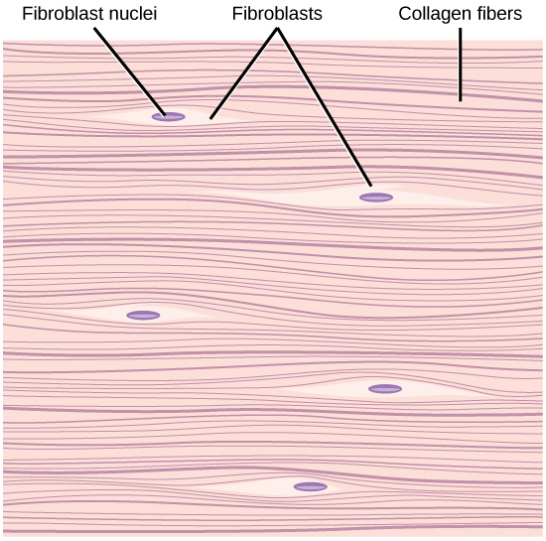


Figure 2. Fibrous connective tissue from the tendon has strands of collagen fibers lined up in parallel.

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**.

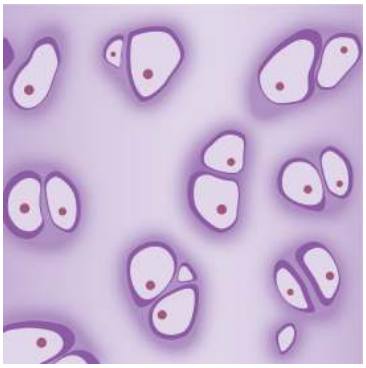


Figure 3. Hyaline cartilage consists of a matrix with cells called chondrocytes embedded in it. The chondrocytes exist in cavities in the matrix called lacunae.

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.

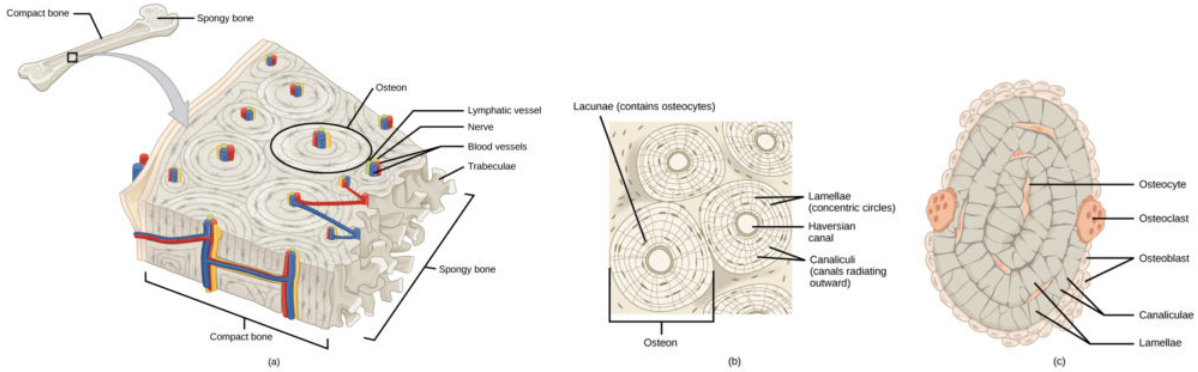


Figure 4. (a) Compact bone is a dense matrix on the outer surface of bone. Spongy bone, inside the compact bone, is porous with web-like trabeculae. (b) Compact bone is organized into rings called osteons. Blood vessels, nerves, and lymphatic vessels are found in the central Haversian canal. Rings of 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

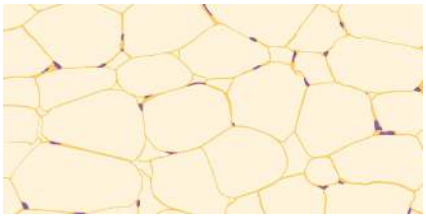


Figure 5. Adipose is a connective tissue is made up of cells called adipocytes. Adipocytes have small nuclei localized at the cell edge.

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.

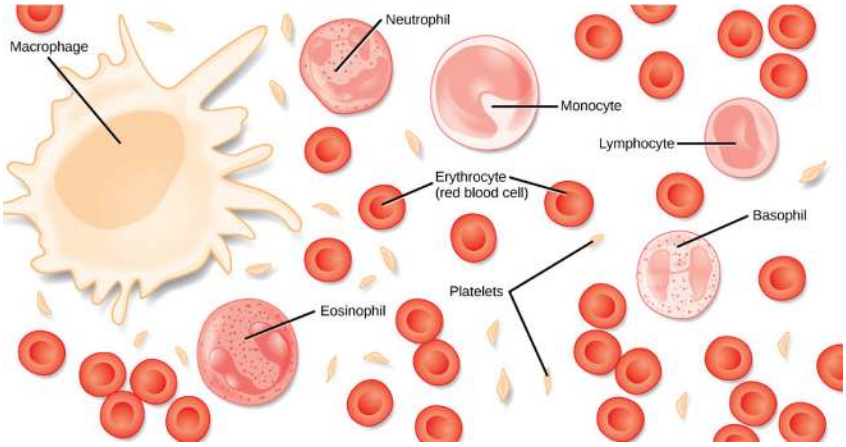


Figure 6. Blood is a connective tissue that has a fluid matrix, called plasma, and no fibers. Erythrocytes (red blood cells), the predominant cell type, are involved in the transport of oxygen and carbon dioxide. Also present are various leukocytes (white blood cells) involved in immune response.

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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13.9: Muscle and Nervous Tissues

Learning Objectives

- Describe three types of muscle tissues
- Describe nervous tissue

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.

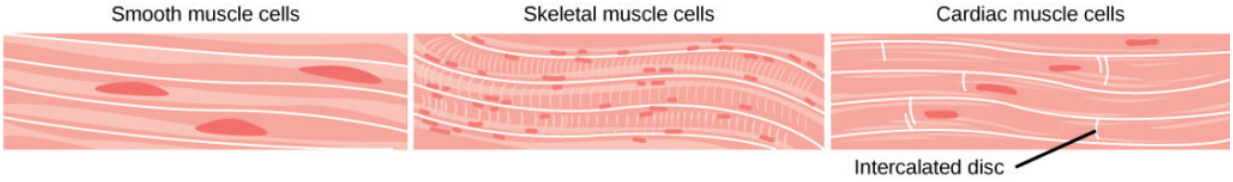


Figure 1. Smooth muscle cells do not have striations, while skeletal muscle cells do. Cardiac muscle cells have striations, but, unlike the multinucleate skeletal cells, they have only one nucleus. Cardiac muscle tissue also has intercalated discs, specialized regions running along the plasma membrane that join adjacent cardiac muscle cells and assist in passing an electrical impulse from cell to cell.

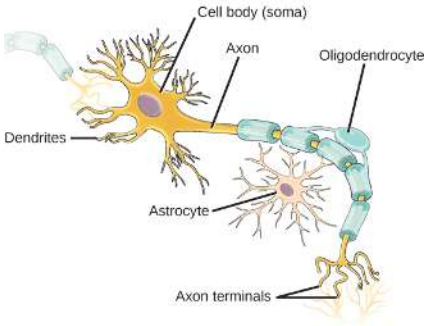


Figure 2. Diagram of a neuron

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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13.10: Introduction to Animal Reproduction

What you'll learn to do: 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.

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13.11: Processes of Animal Reproduction and Development

Learning Outcomes

- Explain the processes of animal reproduction and embryonic development

During sexual reproduction, the haploid gametes of the male and female individuals of a species combine in a process called fertilization. Typically, the small, motile male sperm fertilizes the much larger, sessile female egg. This process produces a diploid fertilized egg called a zygote.

Some animal species—including sea stars and sea anemones, as well as some insects, reptiles, and fish—are capable of asexual reproduction. The most common forms of asexual reproduction for stationary aquatic animals include budding and fragmentation, where part of a parent individual can separate and grow into a new individual. In contrast, a form of asexual reproduction found in certain insects and vertebrates is called parthenogenesis (or “virgin beginning”), where unfertilized eggs can develop into new male offspring. This type of parthenogenesis is called haplodiploidy. These types of asexual reproduction produce genetically identical offspring, which is disadvantageous from the perspective of evolutionary adaptability because of the potential buildup of deleterious mutations. However, for animals that are limited in their capacity to attract mates, asexual reproduction can ensure genetic propagation.

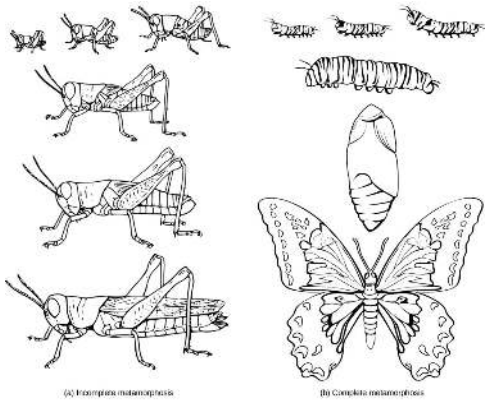


Figure 1. (a) The grasshopper undergoes incomplete metamorphosis. (b) The butterfly undergoes complete metamorphosis. (credit: S.E. Snodgrass, USDA)

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**.

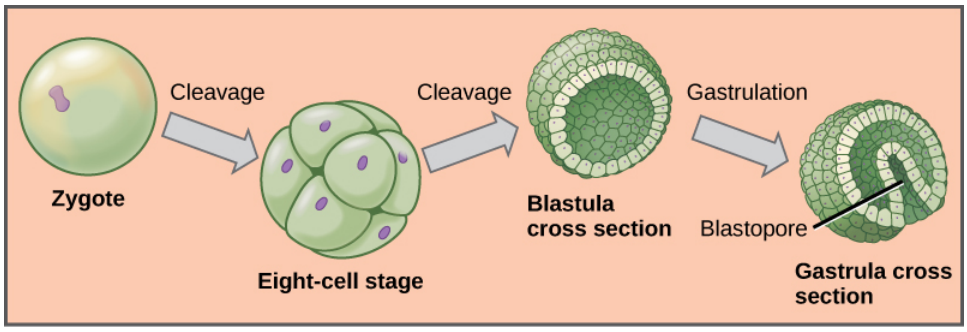


Figure 2. During embryonic development, the zygote undergoes a series of mitotic cell divisions, or cleavages, to form an eight-cell stage, then a hollow blastula. During a process called gastrulation, the blastula folds inward to form a cavity in the gastrula.

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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13.12: Embryological Development

Learning Objectives

- Compare and contrast the embryonic development of diploblasts and triploblasts, and protostomes and deuterostomes

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**.

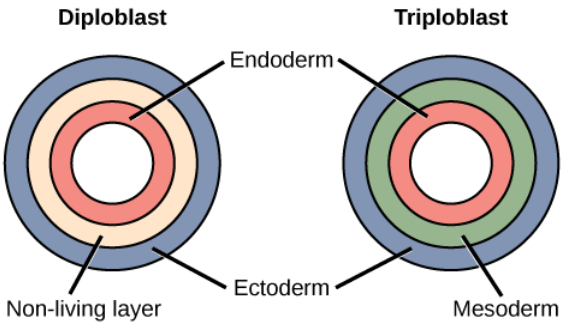


Figure 1. During embryogenesis, diploblasts develop two embryonic germ layers: an ectoderm and an endoderm. Triploblasts develop a third layer—the mesoderm—between the endoderm and ectoderm.

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]
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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.

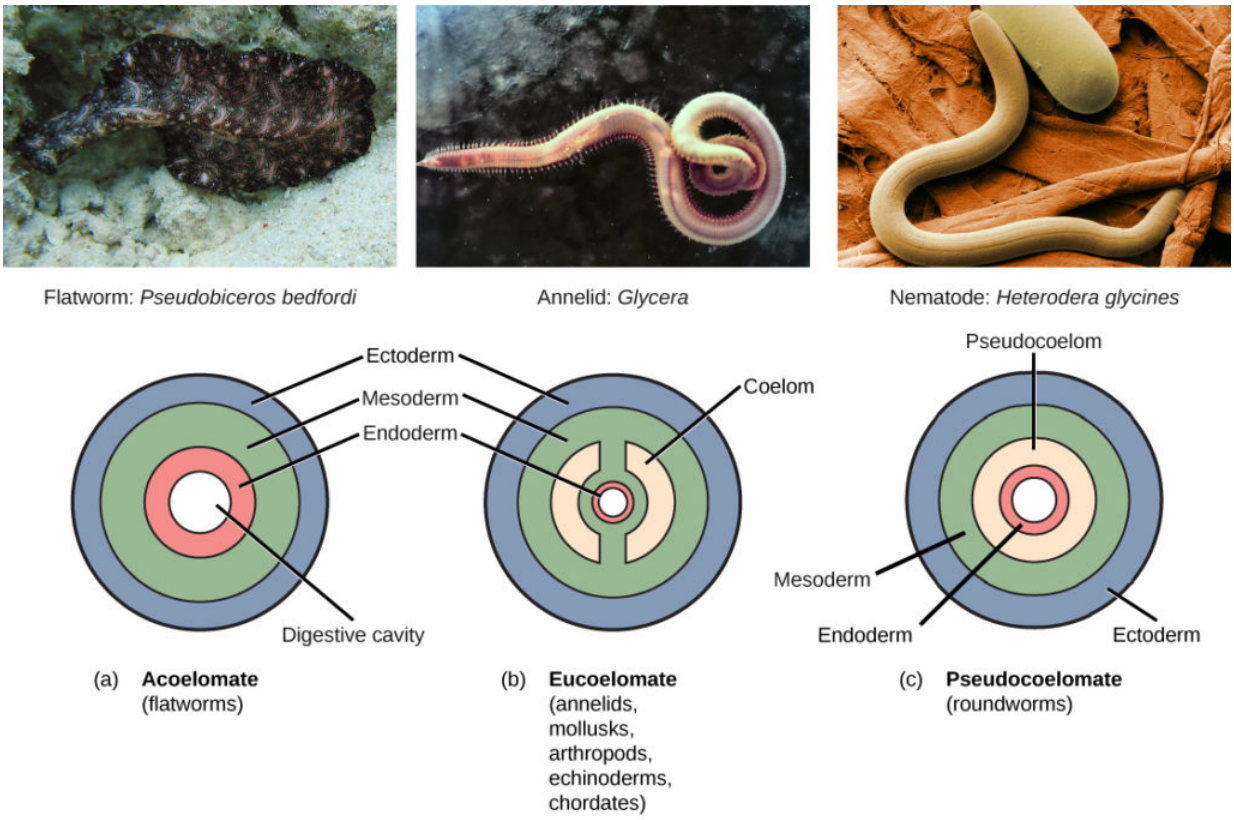


Figure 2. Triploblasts may be (a) acoelomates, (b) eucoelomates, or (c) pseudocoelomates. Acoelomates have no body cavity. Eucoelomates have a body cavity within the mesoderm, called a coelom, which is lined with mesoderm. Pseudocoelomates also have a body cavity, but it is sandwiched between the endoderm 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)

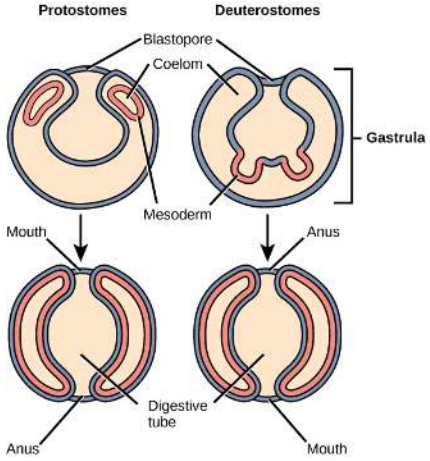


Figure 3. Eucoelomates can be divided into two groups based on their early embryonic development. In protostomes, part of the mesoderm separates to form the coelom in a process called schizocoely. In deuterostomes, the mesoderm pinches off to form the coelom in a process called enterocoely. It was long 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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13.13: Introduction to Homeostasis

What you'll learn to do: 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.

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13.14: What is Homeostasis?

Learning Outcomes

- Define 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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13.15: Control of Homeostasis

Learning Objectives

- Describe the factors affecting 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.

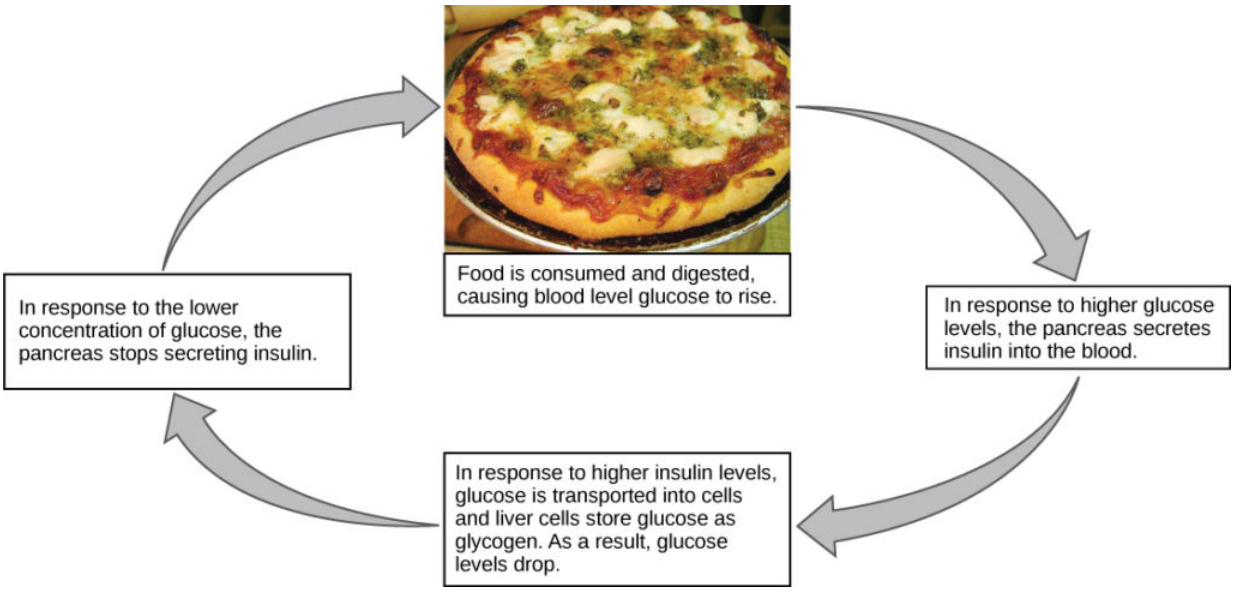


Figure 1. Blood sugar levels are controlled by a negative feedback loop. (credit: modification of work by Jon Sullivan)

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.

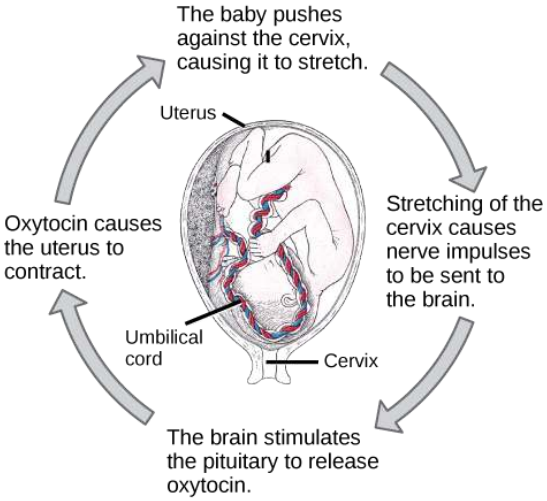


Figure 2. The birth of a human infant is the result of positive feedback.

? 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.

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

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13.16: Thermoregulation

Learning Objectives

- Describe the process of thermoregulation
- Describe thermoregulation of endothermic and ectothermic animals

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 regulation of body temperature. The processes of homeostasis and temperature control are centered in the hypothalamus of the advanced animal brain. 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 is important to note that not all changes in body temperature are necessarily bad. For example, a fever can be part of the body's natural response to invasion by bacteria.

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, since the hypothalamus will respond to chemical as well as environmental signals. 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.

Practice Question

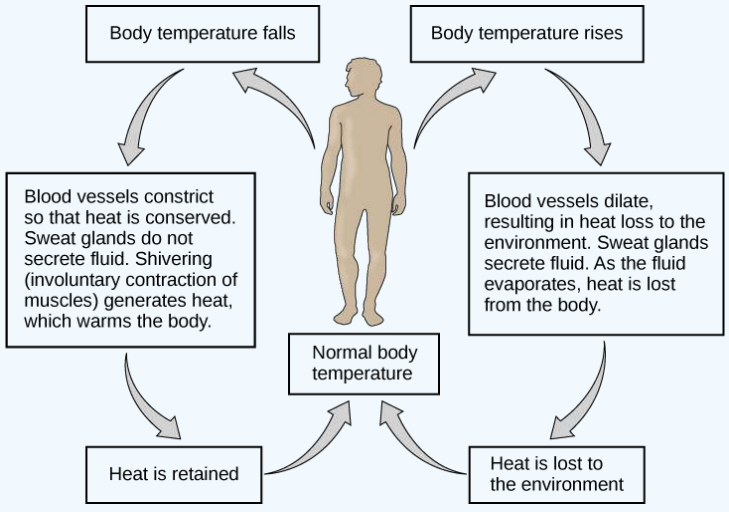


Figure 1. The body is able to regulate temperature in response to signals from the nervous system.

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]

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.

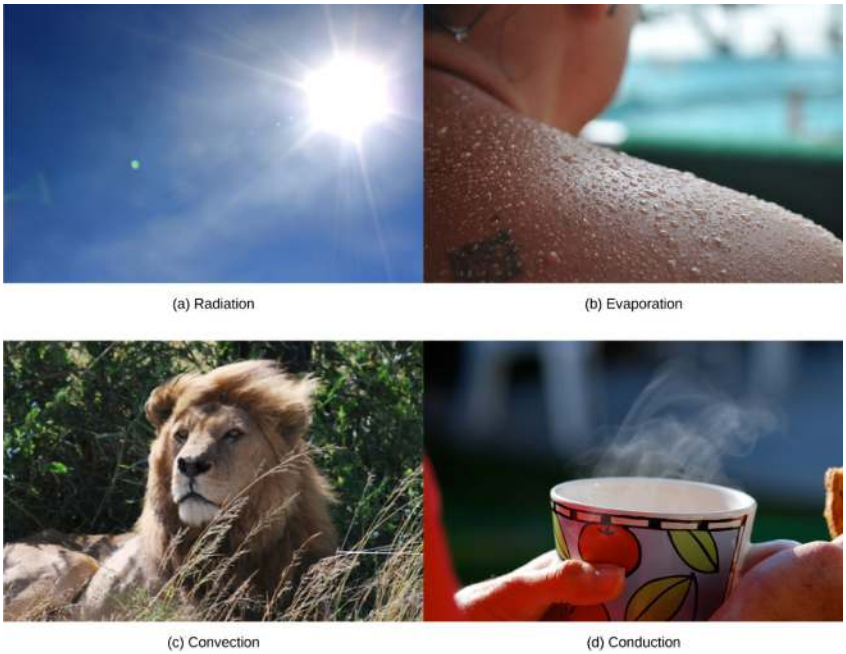


Figure 2. Heat can be exchanged by four mechanisms: (a) radiation, (b) evaporation, (c) convection, or (d) conduction. (credit b: modification of work by "Kullez"/Flickr; credit c: modification of work by Chad Rosenthal; credit d: modification of work by "stacey.d"/Flickr)

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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13.17: Putting It Together- Features of the Animal Kingdom

At the beginning of this module, we looked at the sea sponge, which isn't exactly the first thing that comes to mind when you hear the word *animal*, which may be due to the fact that sponges were the first to branch away from the rest of the Animal Kingdom on the evolutionary tree. Despite their early divergence from other animals, they still have several shared characteristics with rest of the Animal Kingdom:

- All animal species are multicellular
- All animal species are heterotrophic
- All animal species lack cell walls
- All animal species produce sperm cells

Most animals share these other notable features that sponges lack:

- Most animal species have tissues
- Most animal species have organs
- Most animals have body symmetry

While these shared characteristics serve as foundational similarities, there is incredible diversity among animals (as we learned in Module 9: Animal Diversity)—all you have to do is look at the differences between yourself and a sponge to see the range of features within the Animal Kingdom.

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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.

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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

What you'll learn to do: 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.

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14.3: Morphology of Sponges

Learning Outcomes

- Describe the organizational features of the simplest multicellular organisms

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.

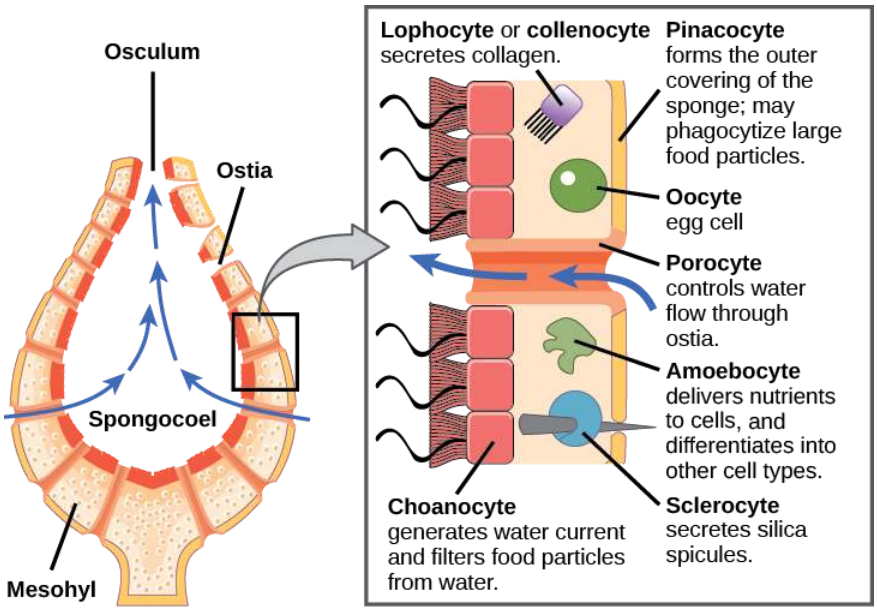
Watch this video to see the movement of water through the sponge body.



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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.



(a) Basic sponge body plan (b) Some sponge cell types

Figure 1. The sponge's (a) basic body plan and (b) some of the specialized cell types found in sponges are shown.

Practice Question

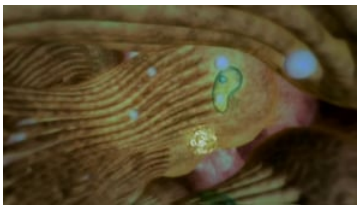
Which of the following statements is false?

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.

Take an up-close tour through the sponge and its cells:



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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.

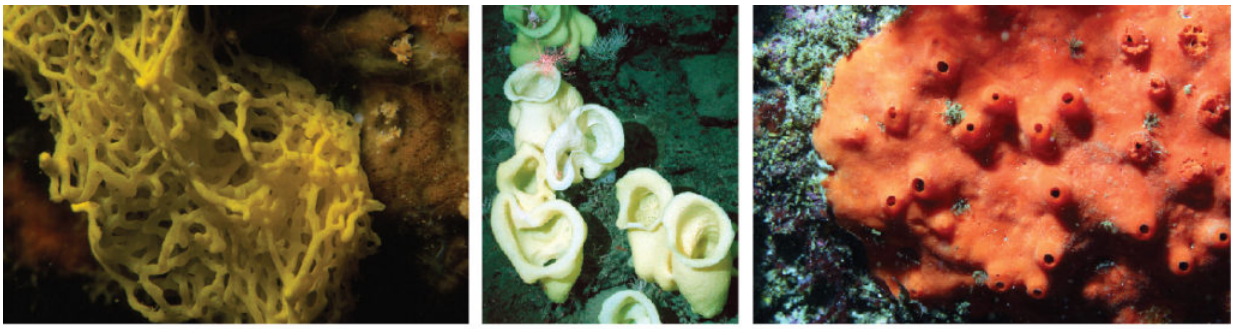


Figure 3. (a) *Clathrina clathrus* belongs to class Calcarea, (b) *Staurocalyptus spp*. (common name: yellow Picasso sponge) belongs to class Hexactinellida, and (c) *Acarnus erithacus* belongs to class Demospongia. (credit a: modification of work by Parent Géry; credit b: modification of work by Monterey 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

Learning Objectives

- Explain the various body forms and bodily functions of 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

What you'll learn to do: 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.

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14.6: Characteristics of Phylum Cnidaria

Learning Outcomes

- Identify common structural and organizational characteristics of the 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.

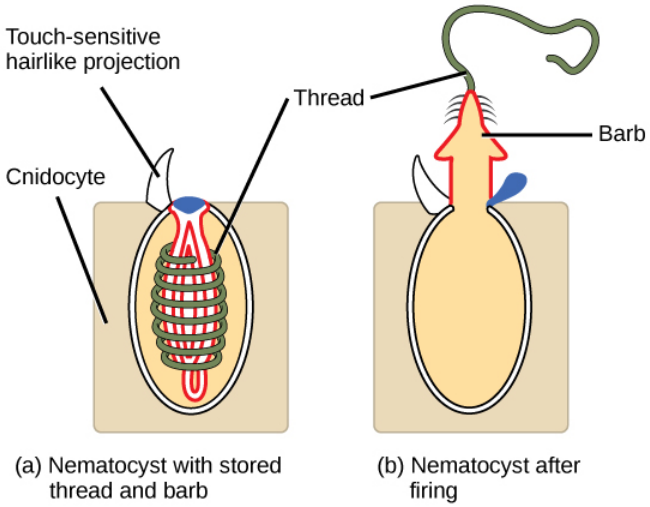


Figure 1. Animals from the phylum Cnidaria have stinging cells called cnidocytes. Cnidocytes contain large organelles called (a) nematocysts that store a coiled thread and barb. When hairlike projections on the cell surface are touched, (b) the thread, barb, and a toxin are fired from the organelle.

View this video animation showing two anemones engaged in a battle.



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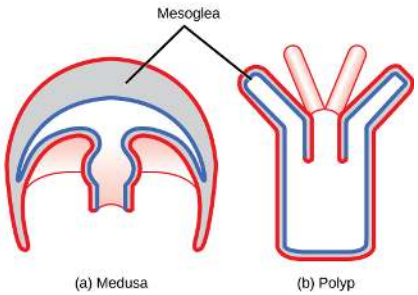


Figure 2. Cnidarians have two distinct body plans, the medusa (a) and the polyp (b). All cnidarians have two membrane layers, with a jelly-like mesoglea between them.

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.

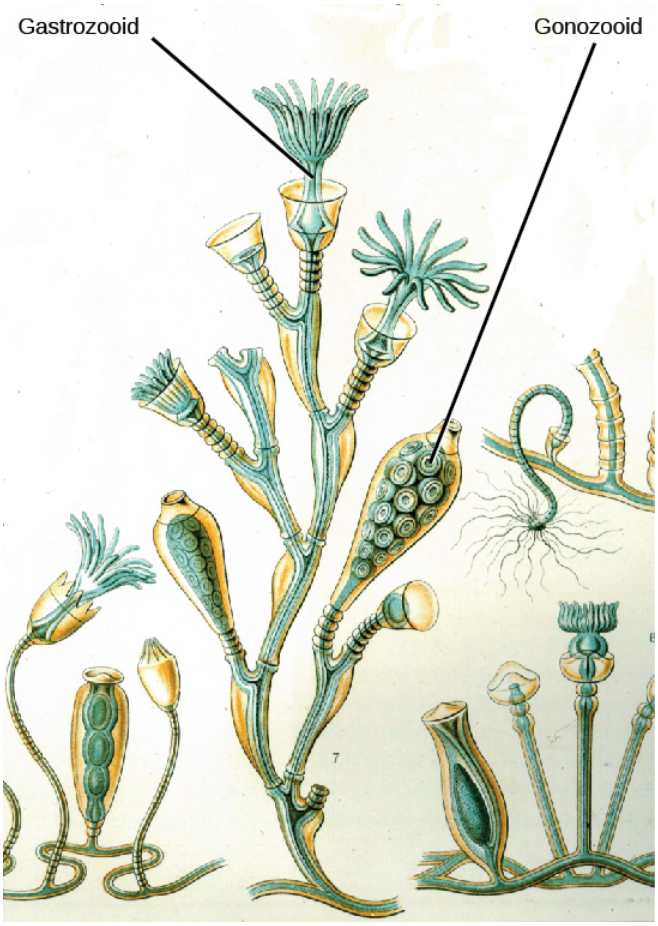


Figure 3. The sessile form of Obelia geniculate has two types of polyps: gastrozooids, which are adapted for capturing prey, and gonozooids, which bud to produce medusae asexually.

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

Learning Objectives

- 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

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.

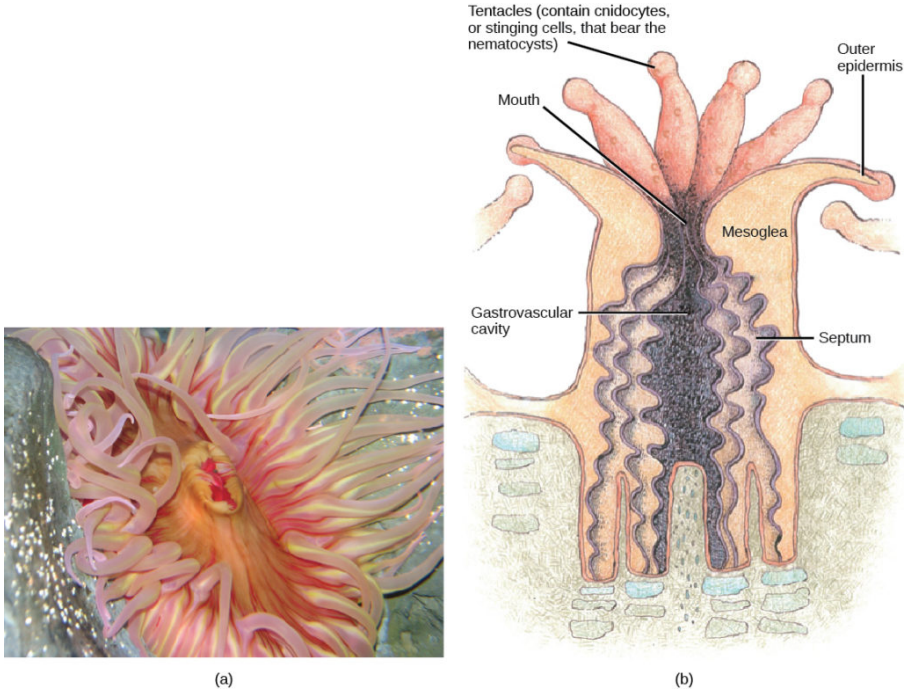


Figure 1. The sea anemone is shown (a) photographed and (b) in a diagram illustrating its morphology. (credit a: modification of work by “Dancing With Ghosts”/Flickr; credit b: modification of work by NOAA)

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).

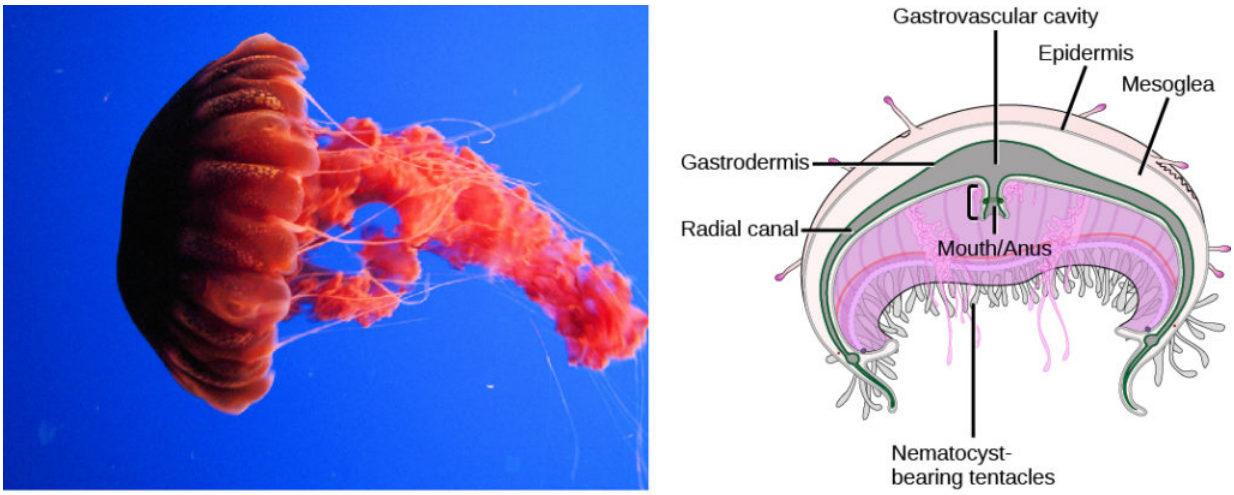


Figure 2. A jelly is shown (a) photographed and (b) in a diagram illustrating its morphology. (credit a: modification of work by "Jimg944"/Flickr; credit b: modification of work by Mariana Ruiz Villareal)

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.

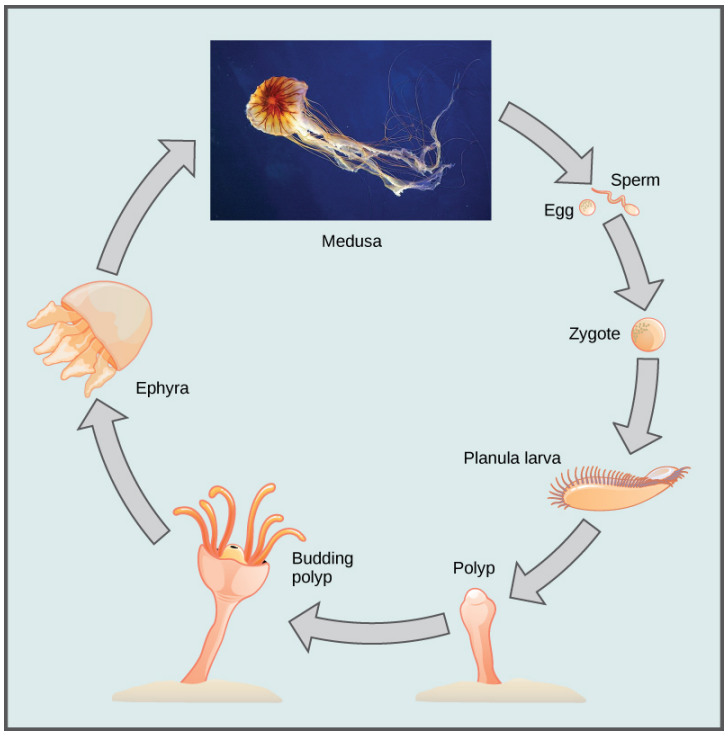


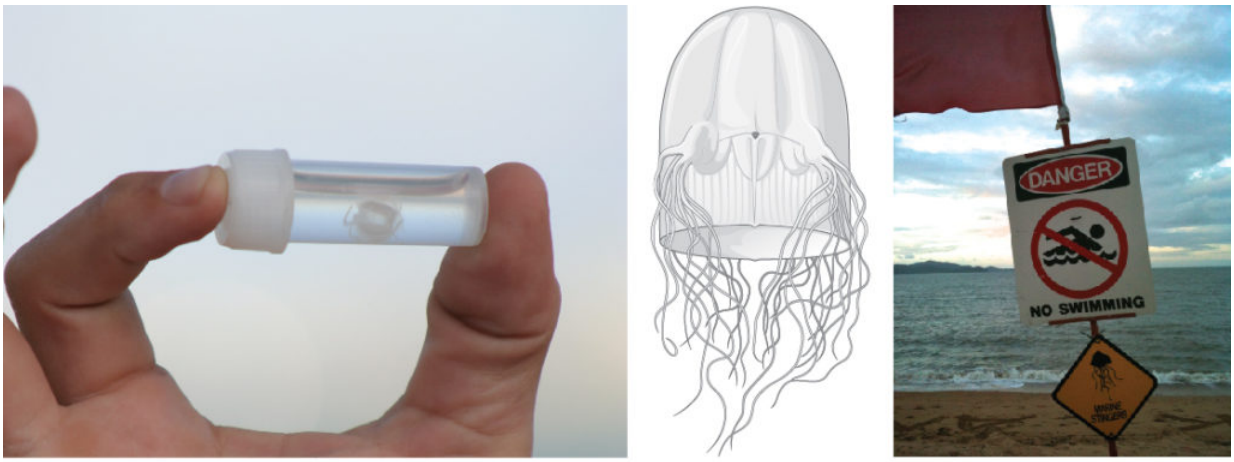
Figure 3. The life cycle of a jellyfish includes two stages: the medusa stage and the polyp stage. The polyp reproduces asexually by budding, and the medusa reproduces sexually. (credit “medusa”: modification of work by Francesco Crippa)

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.



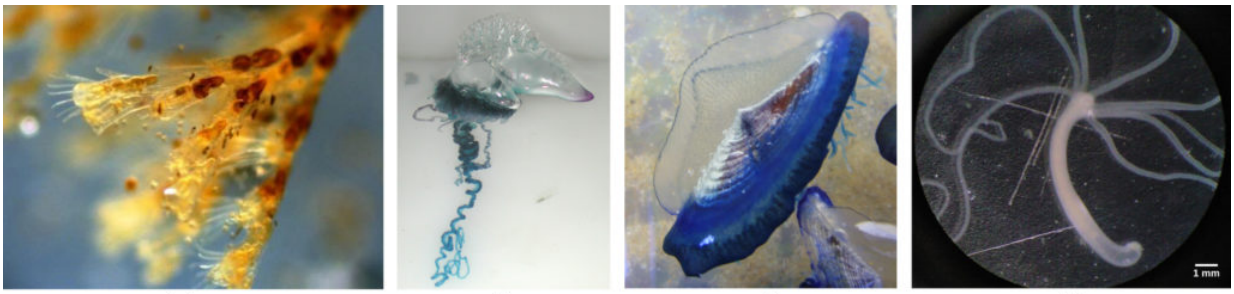
(a) (b) (c)

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 life cycle, 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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14.7: Classes in the Phylum Cnidaria is shared under a not declared license and was authored, remixed, and/or curated by LibreTexts.

14.8: Introduction to Superphylum Lophotrochozoa

What you'll learn to do: 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.

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14.9: Characteristics of Superphylum Lophotrochozoa

Learning Outcomes

- Identify common structural and organizational characteristics of the superphylum Lophotrochozoa

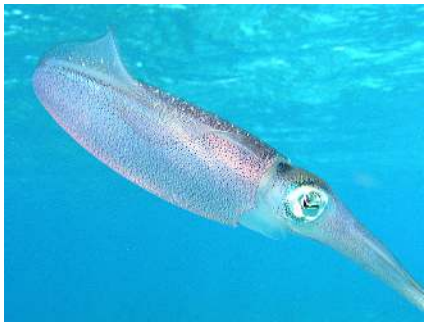


Figure 1. The Caribbean reef squid (*Sepioteuthis sepioidea*) is a complex lophotrochozoan.

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

Learning Objectives

- Describe the unique anatomical and morphological features of flatworms

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.

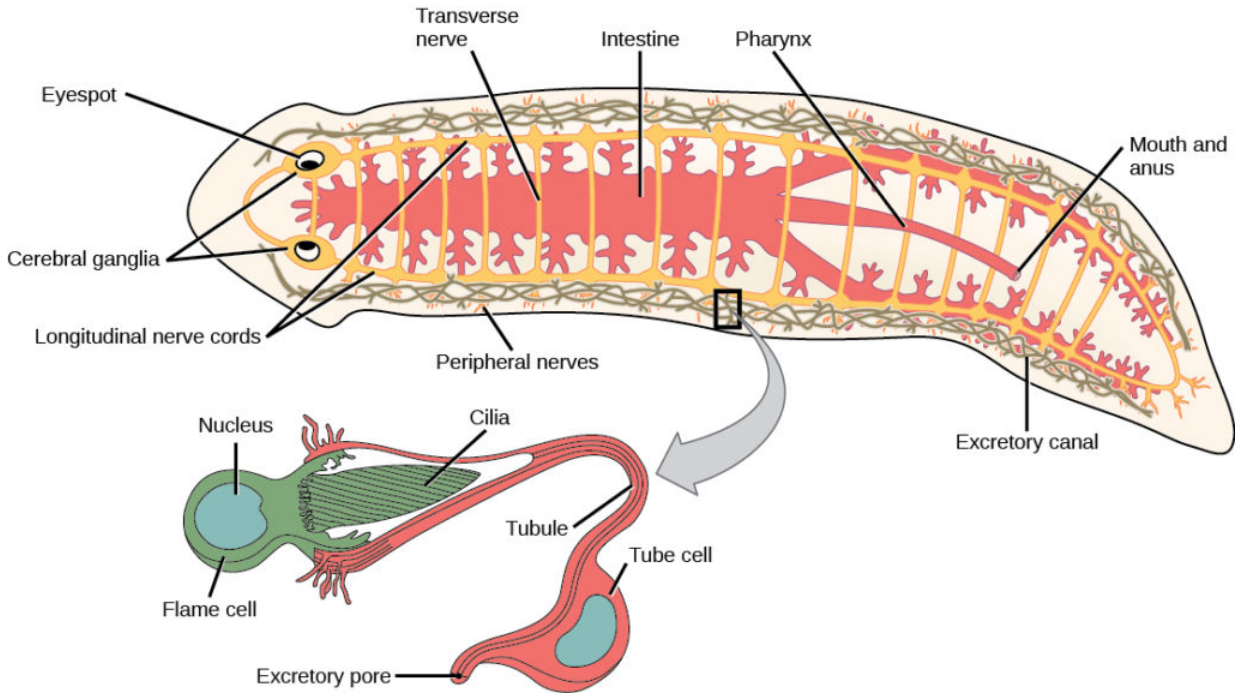


Figure 1. The planarian is a flatworm that has a gastrovascular cavity with one opening that serves as both mouth and anus. The excretory system is made up of tubules connected to excretory pores on both sides of the body. The nervous system is composed of two interconnected nerve cords running the length 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.

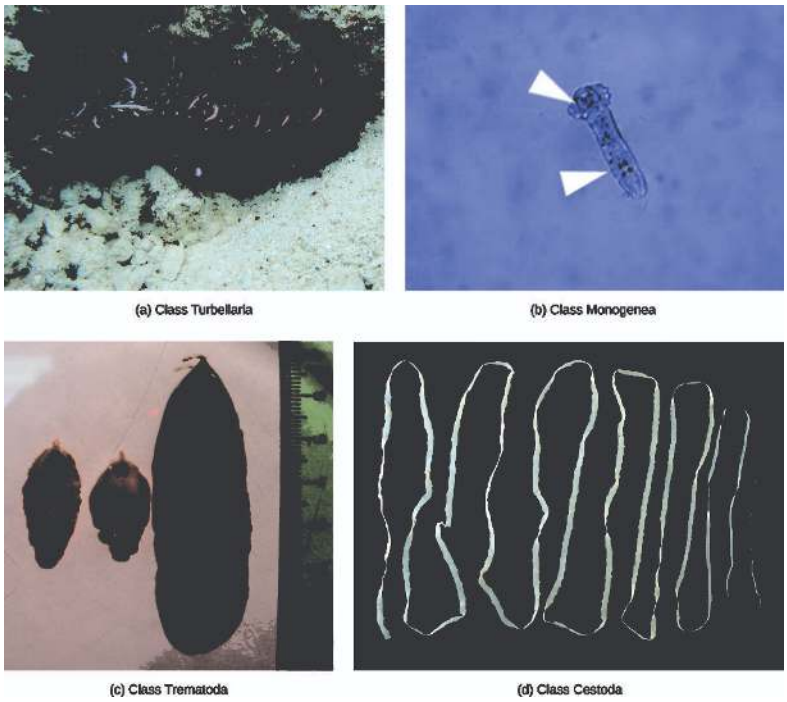


Figure 2. Phylum Platyhelminthes is divided into four classes. (a) Class Turbellaria includes the Bedford's flatworm (*Pseudobiceros bedfordi*), which is about 8–10 cm in length. (b) The parasitic class Monogenea includes *Dactylogyrus spp. Dactylogyrus*, commonly called a gill fluke, is about 0.2 mm 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.

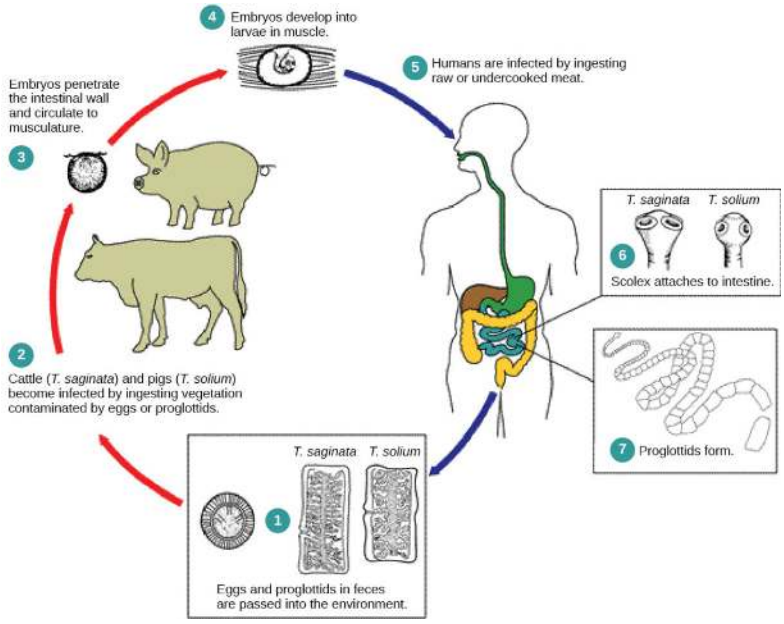


Figure 3. Tapeworm (*Taenia spp.*) infections occur when humans consume raw or undercooked infected meat. (credit: modification of work by CDC)

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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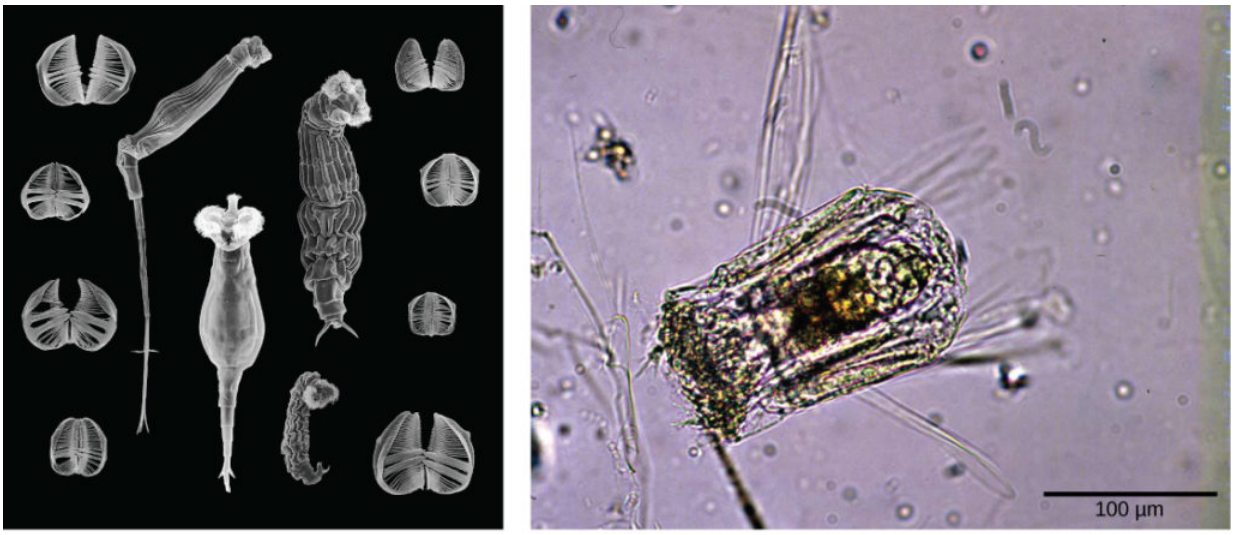
14.11: Phylum Rotifera

Learning Outcomes

- Describe the unique anatomical and morphological features of rotifers

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/bionm2/?p=406

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.

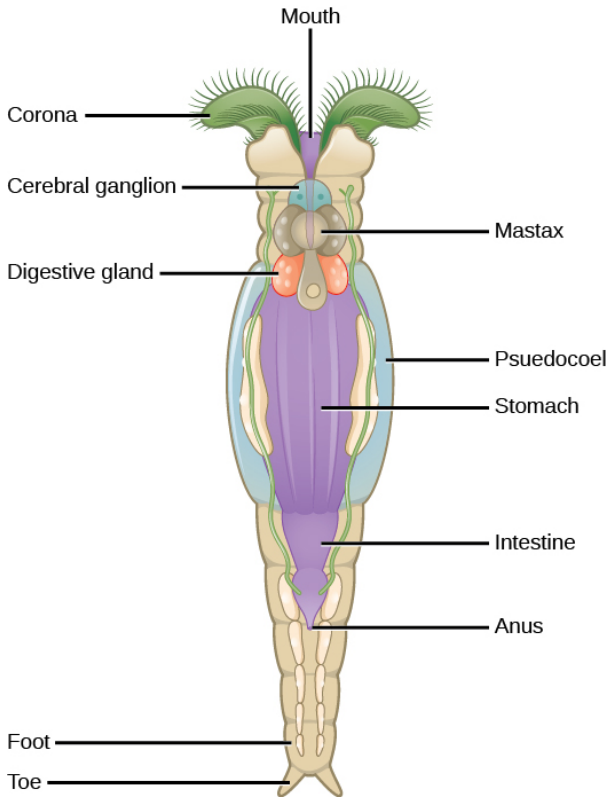


Figure 2. This illustration shows the anatomy of a bdelloid rotifer.

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

Learning Objectives

- Describe the unique anatomical and morphological features of 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.

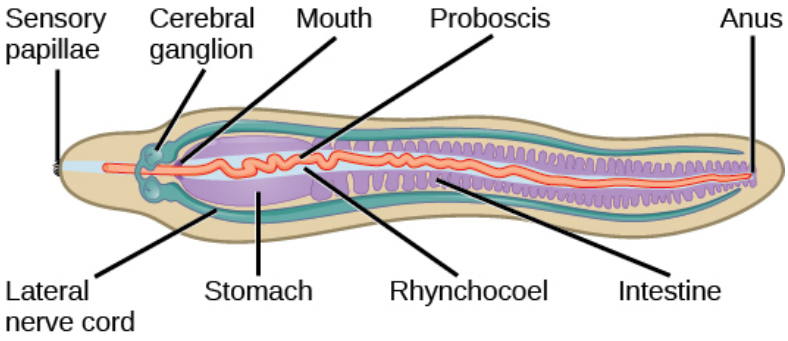


Figure 2. The anatomy of a Nemertean is shown.

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

Learning Objectives

- Describe the unique anatomical and morphological features of mollusks

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).

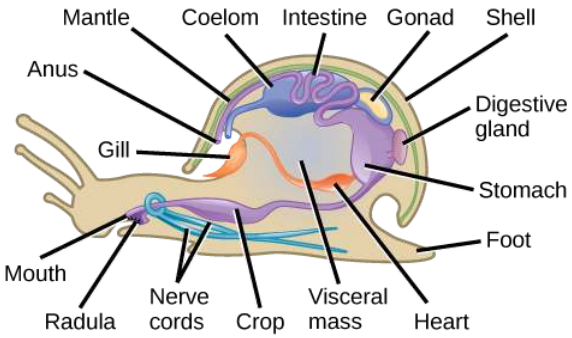


Figure 1. There are many species and variations of mollusks; this illustration shows the anatomy of an aquatic gastropod.

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.

[reveal-answer q=”848589″]Show Answer[/reveal-answer]
[hidden-answer a=”848589″]Statement d is false[/hidden-answer]

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.

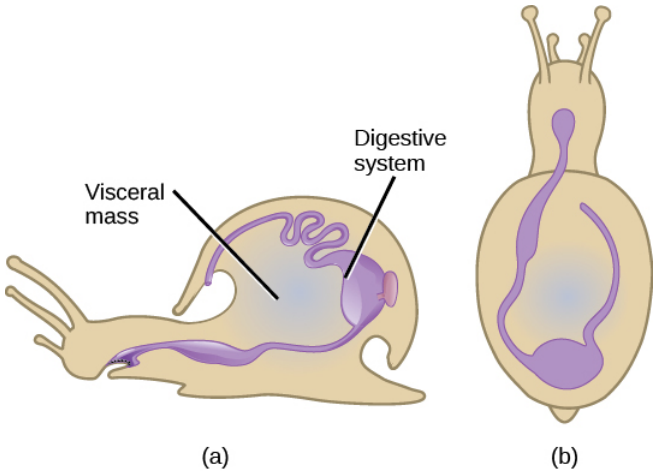


Figure 5. During embryonic development of gastropods, the visceral mass undergoes torsion, or counterclockwise rotation of anatomical features. As a result, the anus of the adult animal is located over the head. Torsion is an independent process from coiling of the shell.

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 octopi, 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 octopi, 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 octopi 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 octopi 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.

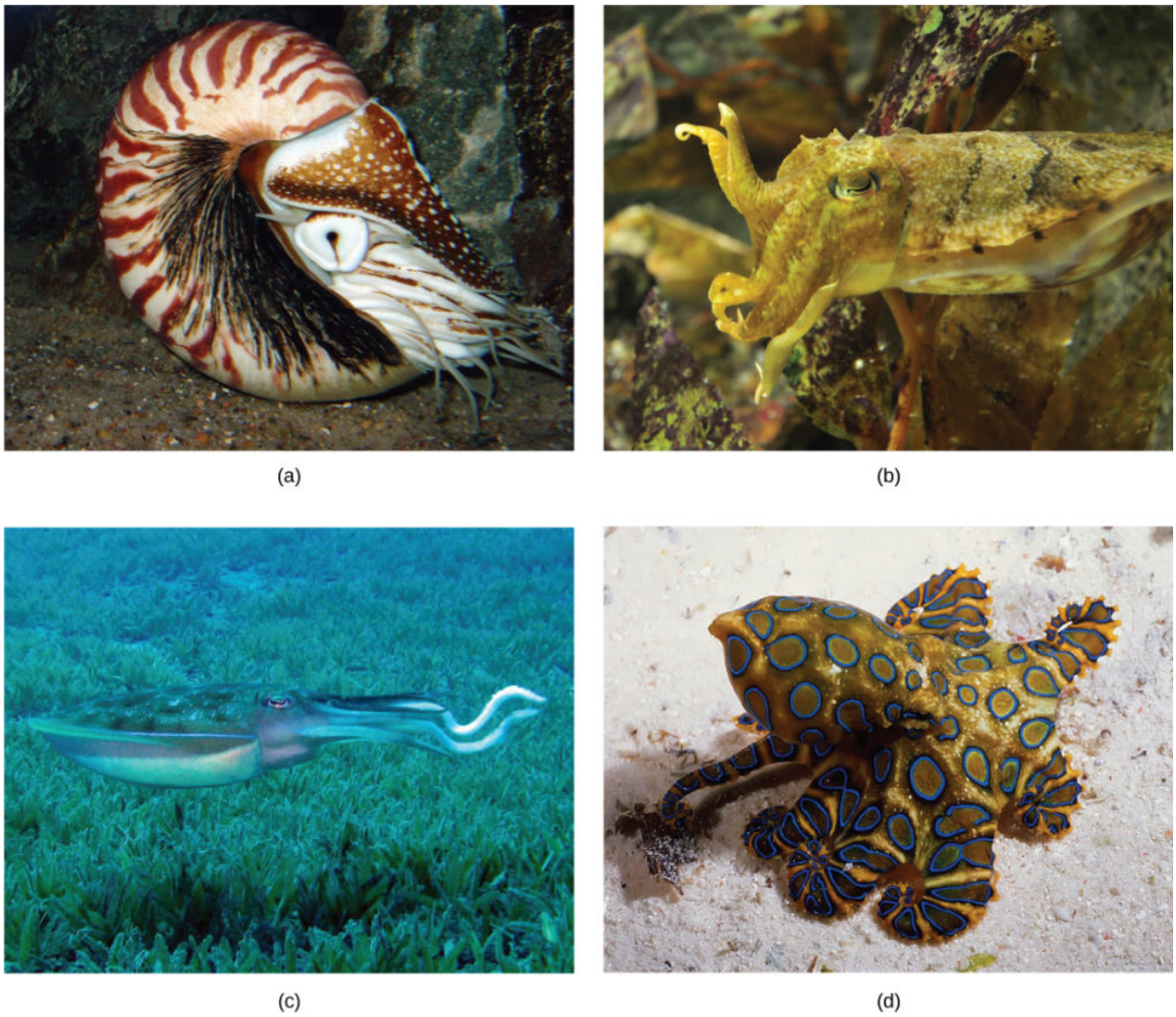


Figure 7. The (a) nautilus, (b) giant cuttlefish, (c) reef squid, and (d) blue-ring octopus are all members of the class Cephalopoda. (credit a: modification of work by J. Baecker; credit b: modification of work by Adrian Mohedano; credit c: modification of work by Silke Baron; credit d: modification 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

Learning Objectives

- Describe the features of animals classified in 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.

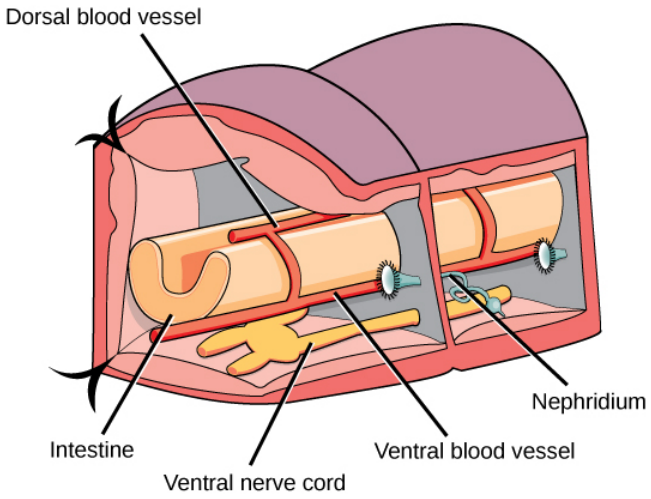


Figure 2. This schematic drawing shows the basic anatomy of annelids in a cross-sectional view.

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

What you'll learn to do: 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 that 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.

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14.16: Phylum Nematoda

Learning Objectives

- Describe the features of animals classified in 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] 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.

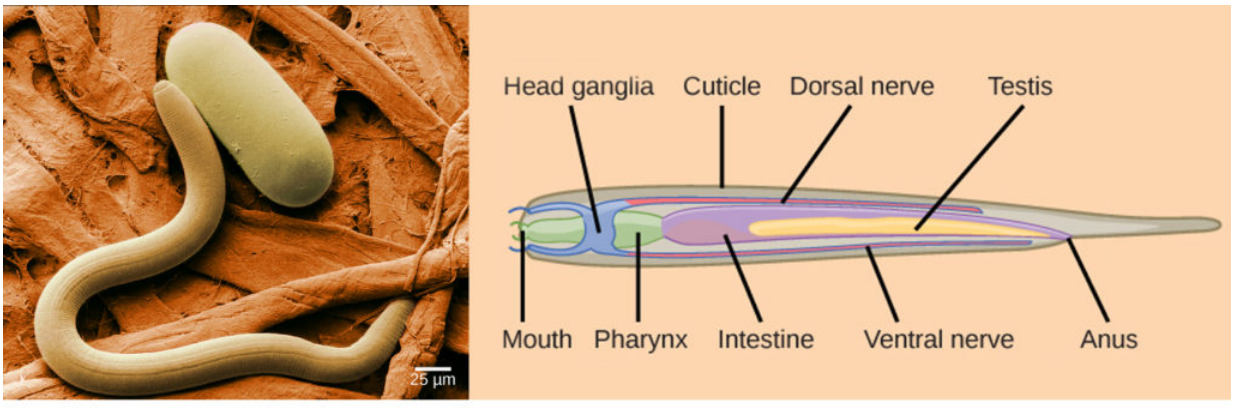


Figure 1. Scanning electron micrograph shows (a) the soybean cyst nematode (*Heterodera glycines*) and a nematode egg. (b) A schematic representation shows the anatomy of a typical nematode. (credit a: modification of work by USDA ARS; scale-bar data from Matt Russell)

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: Phylum Arthropoda

Learning Objectives

- Describe the features of animals classified in 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).

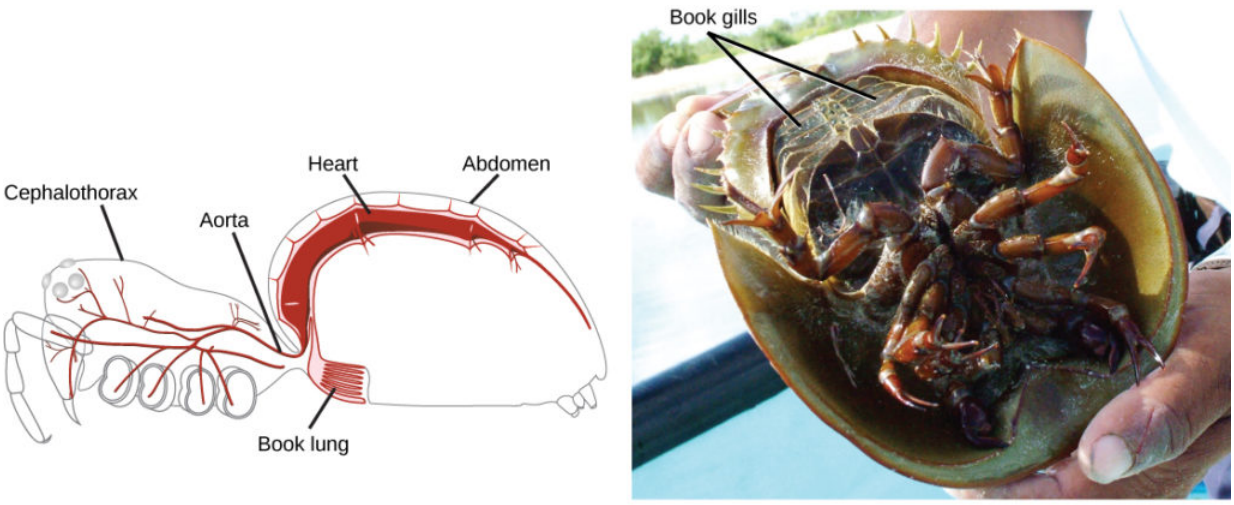


Figure 2. The book lungs of (a) arachnids are made up of alternating air pockets and hemocoel tissue shaped like a stack of books. The book gills of (b) crustaceans are similar to book lungs but are external so that gas exchange can occur with the surrounding water. (credit a: modification of work by 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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14.18: Subphylums of Arthropoda

Learning Objectives

- Identify the different subphylums in phylum 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).

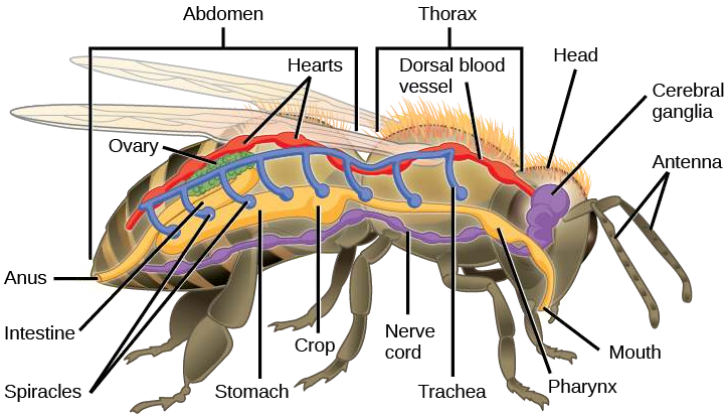


Figure 1. In this basic anatomy of a hexapod insect, note that insects have a developed digestive system (yellow), a respiratory system (blue), a circulatory system (red), and a nervous system (red).

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).

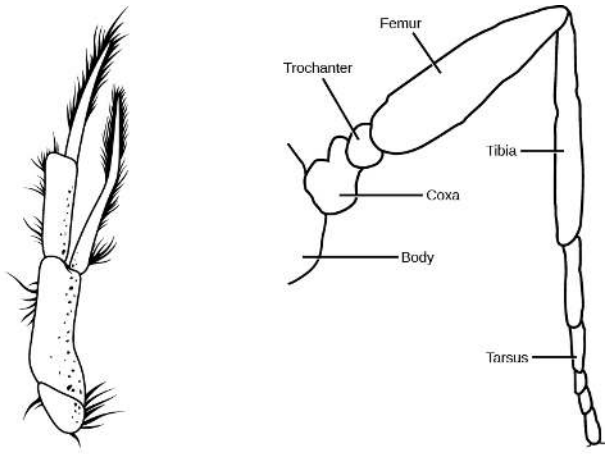


Figure 4. Arthropods may have (a) biramous (two-branched) appendages or (b) uniramous (one-branched) appendages. (credit b: modification of work by Nicholas W. Beeson)

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.

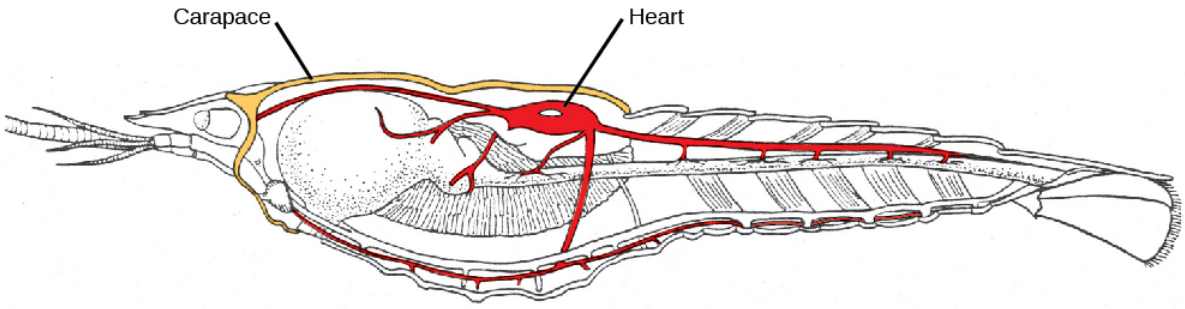
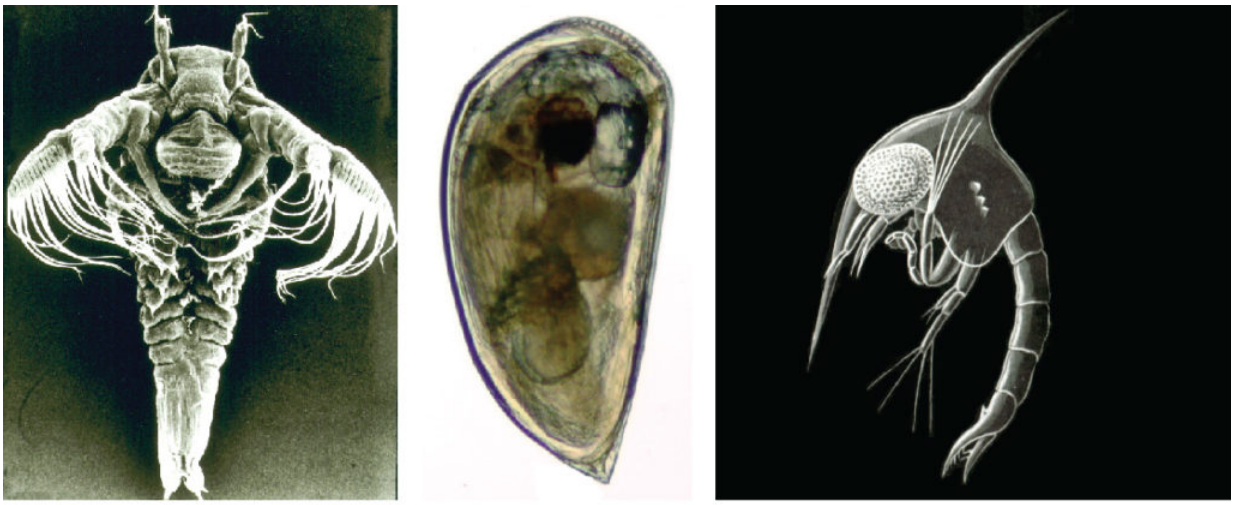


Figure 5. The crayfish is an example of a crustacean. It has a carapace around the cephalothorax and the heart in the dorsal thorax area. (credit: Jane Whitney)

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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14.19: Introduction to Superphylum Deuterostomia

What you'll learn to do: 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).

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14.20: Characteristics of Superphylum Deuterostomia

Learning Objectives

- Identify the common characteristics of superphylum Deuterostomia
- Describe the distinguishing characteristics of chordates

The phyla Echinodermata and Chordata (the phylum in which humans are placed) both belong to the superphylum Deuterostomia. Recall that protostomes 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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14.21: Phylum Echinodermata

Learning Objectives

- Describe the distinguishing characteristics of echinoderms
- Identify the different classes in 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.

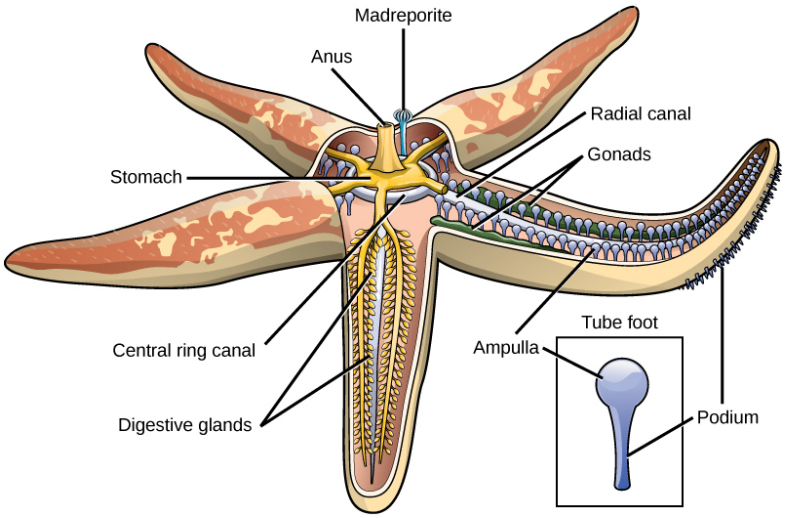


Figure 1. This diagram shows the anatomy of a sea star.

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).

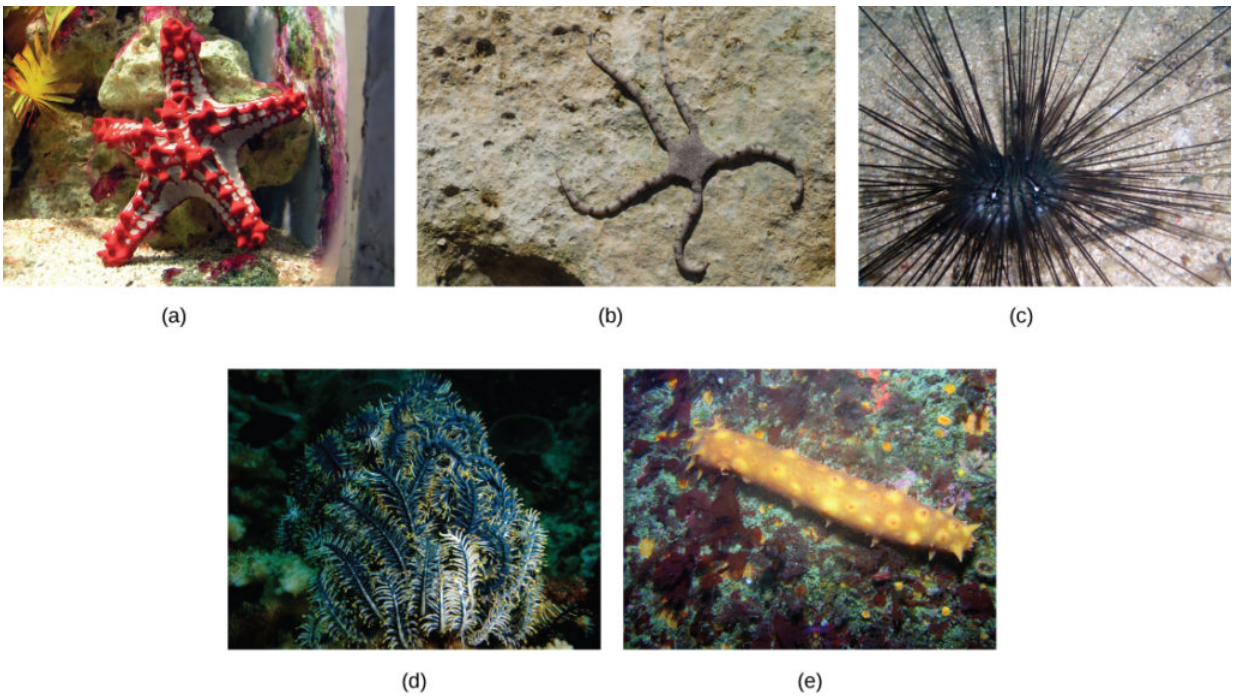


Figure 2. Different members of Echinodermata include the (a) sea star of class Asteroidea, (b) the brittle star of class Ophiuroidea, (c) the sea urchins of class Echinoidea, (d) the sea lilies belonging to class Crinoidea, and (d) sea cucumbers, representing class Holothuroidea. (credit a: modification 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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14.22: 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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CHAPTER OVERVIEW

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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.

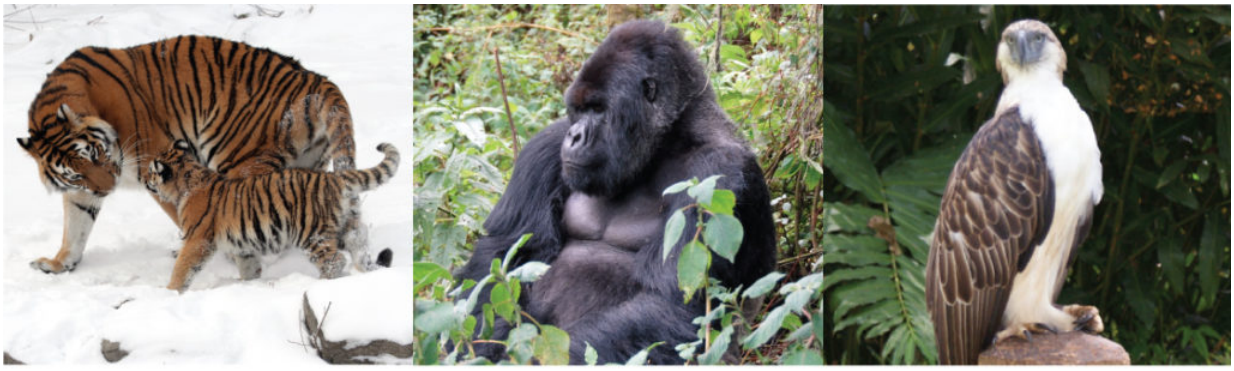


Figure 1. Examples of critically endangered vertebrate species include (a) the Siberian tiger (*Panthera tigris*), (b) the mountain gorilla (*Gorilla beringei*), and (c) the Philippine eagle (*Pithecophega jefferyi*). (credit a: modification of work by Dave Pape; credit b: modification of work by Dave 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.

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15.2: Introduction to Chordates

What you'll learn to do: 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.

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15.3: Characteristics of Chordates

Learning Objectives

- Describe the distinguishing 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.

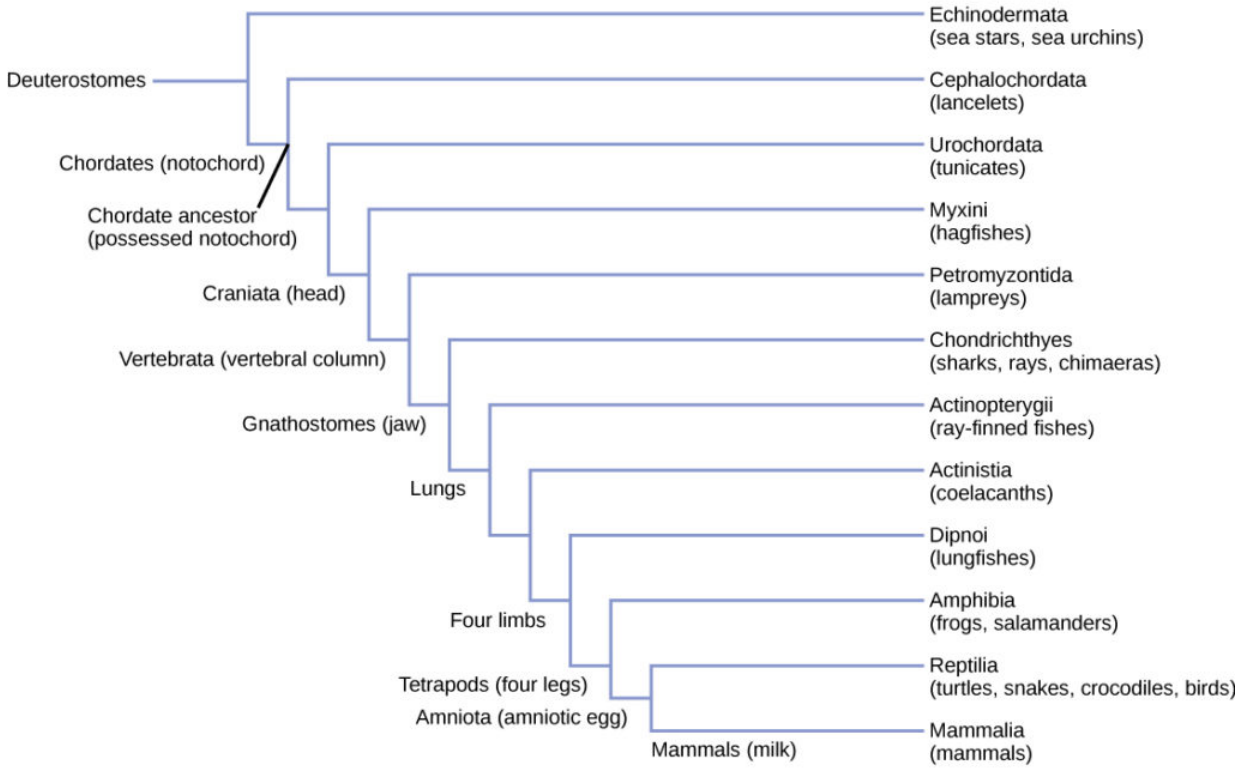


Figure 1. All chordates are deuterostomes possessing a notochord.

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).

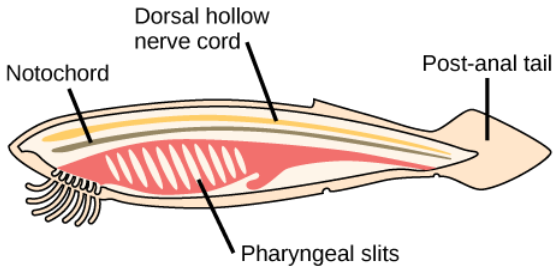


Figure 2. In chordates, four common features appear at some point during development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail.

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.

? 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]

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

Learning Objectives

- Discuss the invertebrate chordate lineages

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.

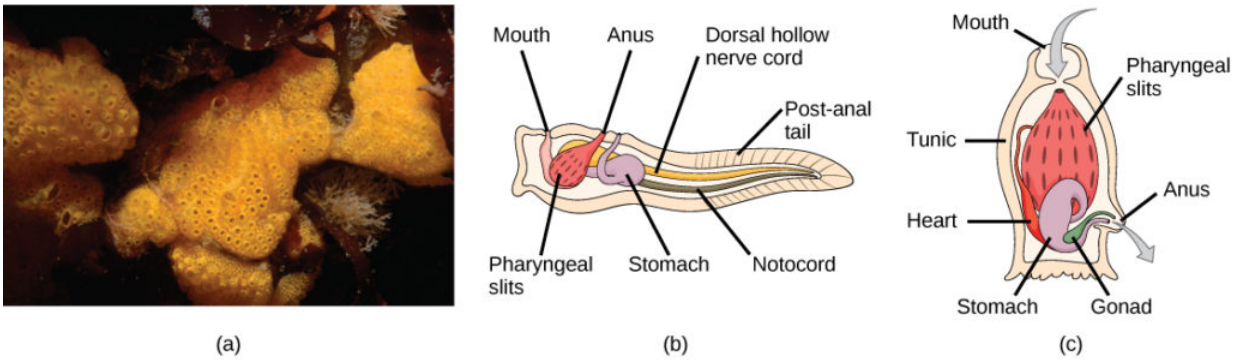


Figure 1. (a) This photograph shows a colony of the tunicate *Botrylloides violaceus*. (b) The larval stage of the tunicate possesses all of the features characteristic of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. (c) In the adult stage, the notochord, 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.

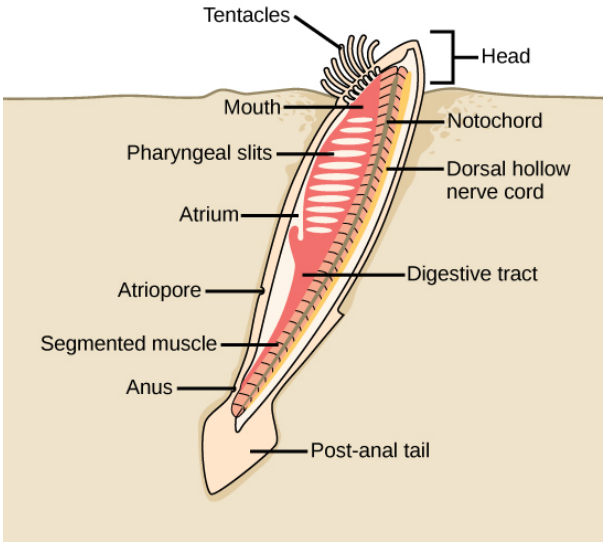


Figure 2. The lancelet, like all cephalochordates, has a head. Adult lancelets retain the four key features of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Water from the mouth enters the pharyngeal slits, which filter out food particles. The filtered water then collects in the atrium and exits through the atriopore.

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15.5: Craniates

Learning Outcomes

- Identify the derived character of craniates that sets them apart from other chordates

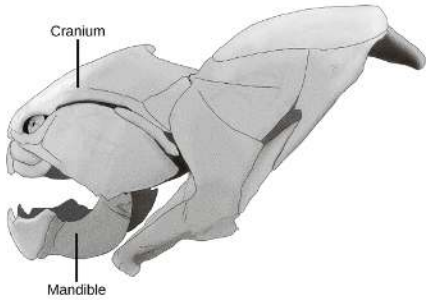


Figure 1. Craniata, including this fish (*Dunkleosteus sp.*), are characterized by the presence of a cranium, mandible, and other facial bones. (credit: “Steveoc 86”/Wikimedia Commons)

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.

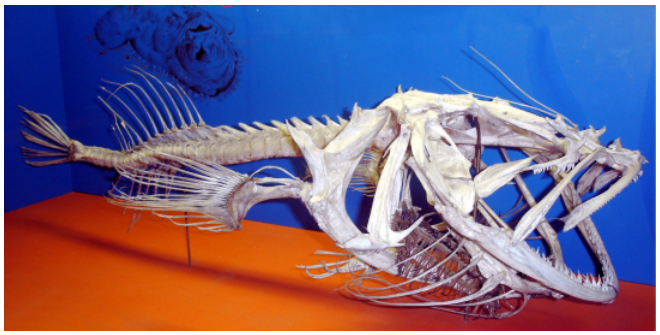


Figure 2. Vertebrata are characterized by the presence of a backbone, such as the one that runs through the middle of this fish. All vertebrates are in the Craniata clade and have a cranium. (credit: Ernest V. More; taken at Smithsonian Museum of Natural History, Washington, D.C.)

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

What you'll learn to do: 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.

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15.7: Jawless Fishes

Learning Objectives

- Identify the common characteristics of 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

Learning Objectives

- Identify the common characteristics of jawed fishes
- Identify the common characteristics of bony fishes
- Identify the common characteristics of sharks and other cartilaginous 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.

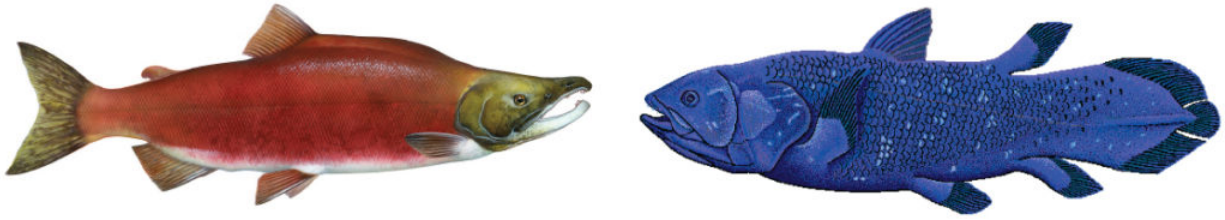


Figure 5. The (a) sockeye salmon and (b) coelacanth are both bony fishes of the Osteichthyes clade. The coelacanth, sometimes called a lobe-finned fish, was thought to have gone extinct in the Late Cretaceous period, 100 million years ago, until one was discovered in 1938 near the Comoros Islands between 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

What you'll learn to do: 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.

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15.10: Amphibians

Learning Objectives

- Identify characteristics of amphibians
- Describe the evolutionary history of 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 damp; 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 that will 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.

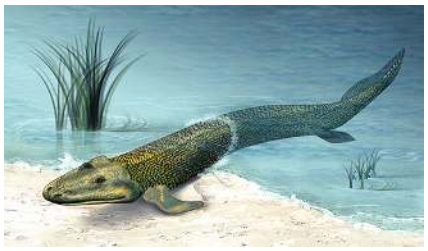


Figure 1. The recent fossil discovery of *Tiktaalik roseae* suggests evidence for an animal intermediate to finned fish and legged tetrapods. (credit: Zina Deretsky, National Science Foundation)

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.

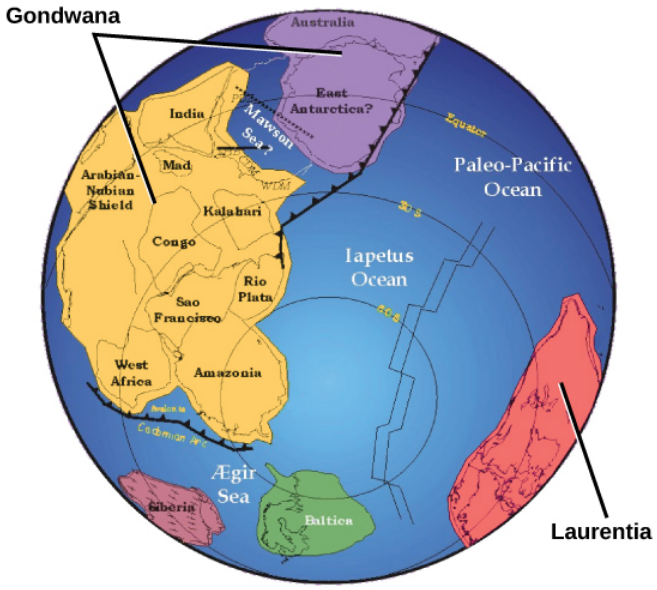


Figure 2. During the Paleozoic Era, around 550 million years ago, the continent Gondwana formed. Both Gondwana and the continent Laurentia were located near the equator.

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

Learning Objectives

- Describe the important difference between the life cycle of amphibians and the life cycles of other vertebrates

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.

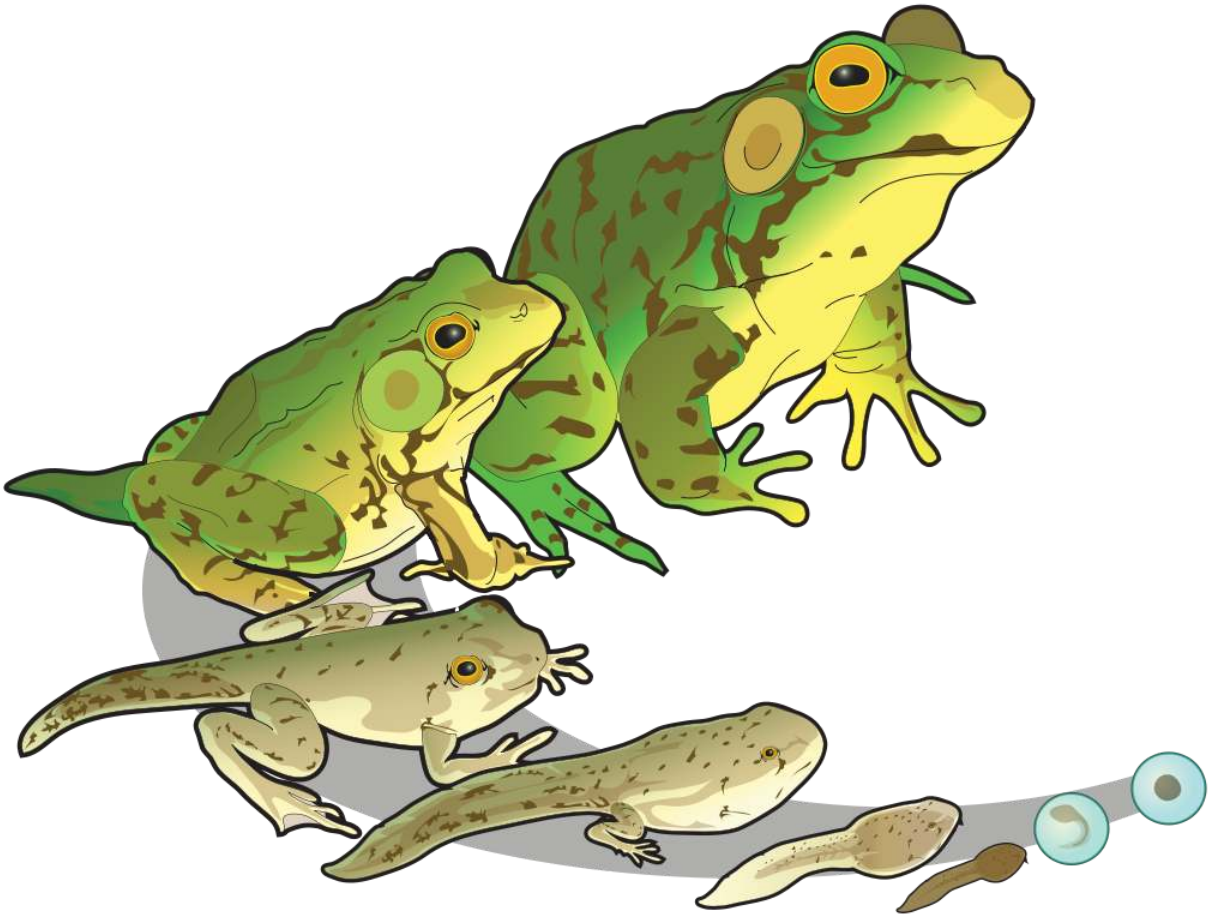


Figure 1. The life cycle of a green frog.

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.

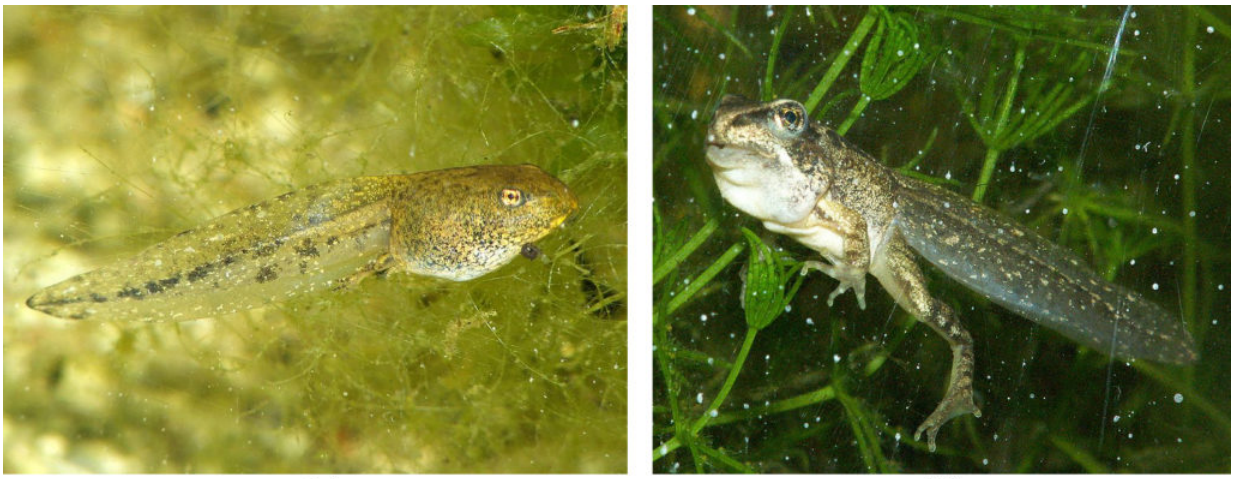


Figure 2. (a) Just before metamorphosis, only 24 hours are needed to reach the stage in part b. (b) Almost functional common frog with some remains of the gill sac and a not fully developed jaw

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

Learning Objectives

- Distinguish between the characteristics of Urodela, Anura, and Apoda

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.



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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15.13: Introduction to Amniotes

What you'll learn to do: 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.

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15.14: Amniotic Animals

Learning Objectives

- Identify the classes of animals that are amniotes
- Describe the main characteristics of amniotes

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

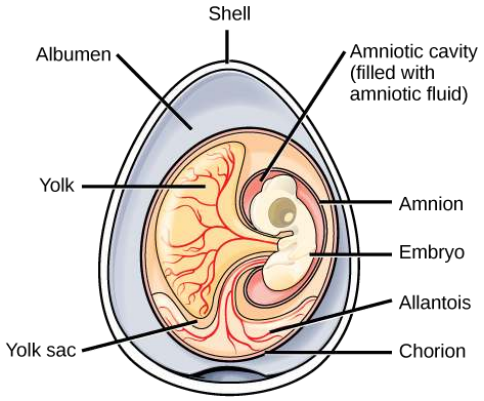


Figure 1. The key features of an amniotic egg are shown.

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).

Extraembryonic 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.

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[hidden-answer a="428004"]Statement d is false.[/hidden-answer]

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15.15: Evolution of Amniotes

Learning Outcomes

- Discuss the 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).

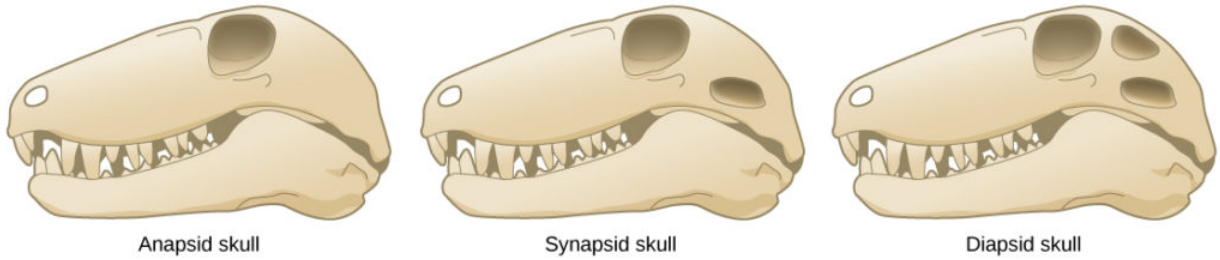


Figure 1. Compare the skulls and temporal fenestrae of anapsids, synapsids, and diapsids. Anapsids have no openings, synapsids have one opening, and diapsids have two openings.

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.

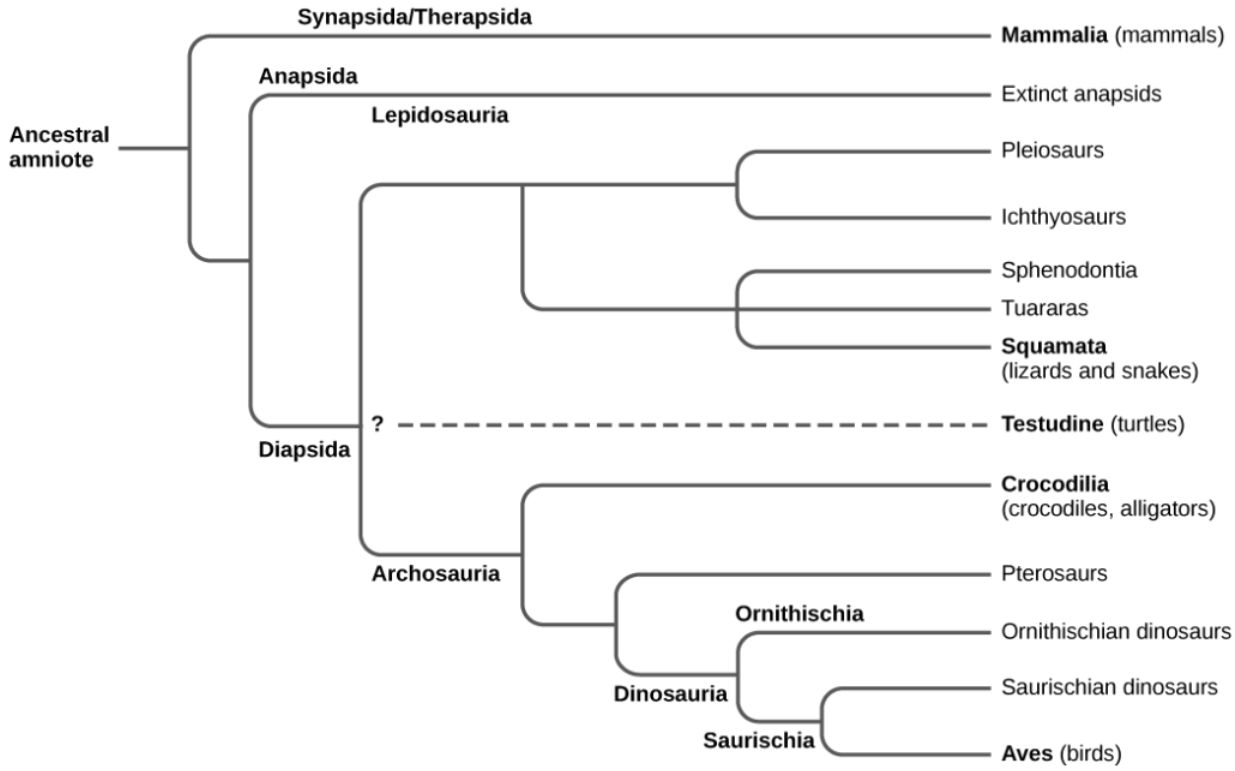


Figure 2. This chart shows the evolution of amniotes. The placement of Testudines (turtles) is currently still debated.

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?

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[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

What you'll learn to do: 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. In this course, we will study them separately.

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15.17: Characteristics of Reptiles

Learning Outcomes

- Identify the 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

Learning Objectives

- Explain the difference between the clades 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 about 325 species of the Testudines.

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

Learning Outcomes

- Discuss the evolution of reptiles

Reptiles originated approximately 300 million years ago during the Carboniferous period. One of the oldest known amniotes is **Casineria**, which had both amphibian and reptilian characteristics. One of the earliest undisputed reptiles was **Hylonomus**. Soon after the first amniotes appeared, they diverged into three groups—synapsids, anapsids, and diapsids—during the Permian period.

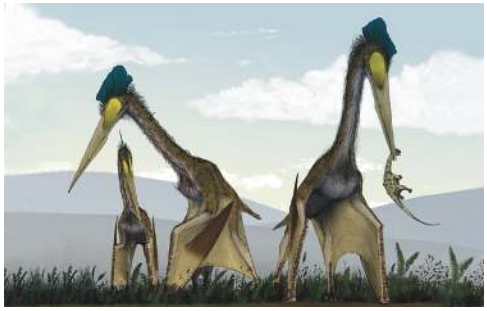


Figure 1. Pterosaurs, which existed from the late Triassic to the Cretaceous period (210 to 65.5 million years ago), possessed wings but are not believed to have been capable of powered flight. Instead, they may have been able to soar after launching from cliffs. (credit: Mark Witton, Darren Naish)

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.

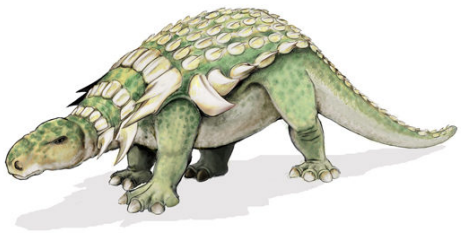


Figure 2. Edmontonia was an armored dinosaur that lived in the late Cretaceous period, 145.5 to 65.6 million years ago. (credit: Mariana Ruiz Villareal)

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

What you'll learn to do: 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.

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15.21: Characteristics of Birds

Learning Outcomes

- Identify characteristics of birds
- Describe the derived characteristics in birds that facilitate flight

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.

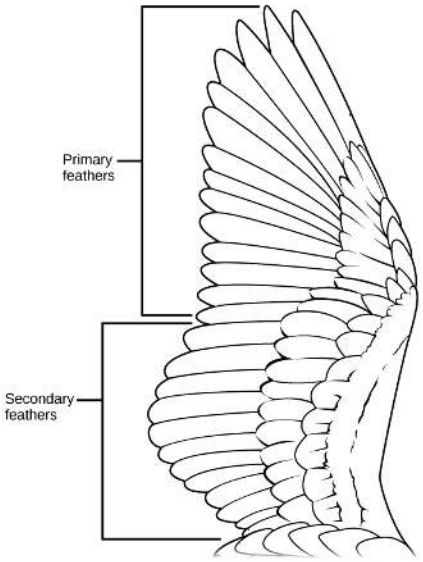


Figure 1. Primary feathers are located at the wing tip and provide thrust; secondary feathers are located close to the body and provide lift.

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.

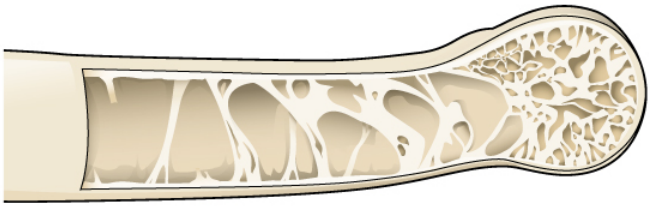


Figure 2. Many birds have hollow, pneumatic bones, which make flight easier.

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.

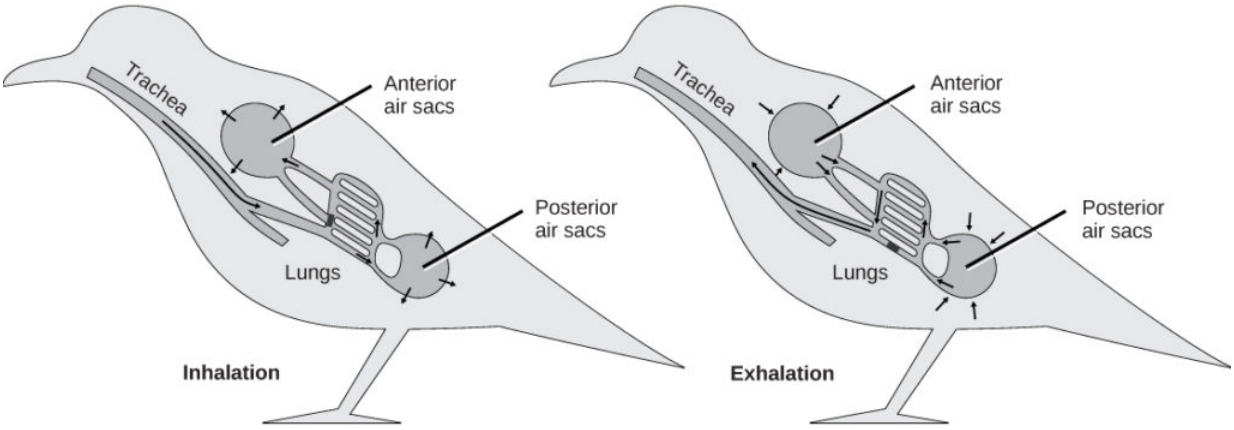


Figure 3. Avian respiration is an efficient system of gas exchange with air flowing unidirectionally. During inhalation, air passes from the trachea into posterior air sacs, then through the lungs to anterior air sacs. The air sacs are connected to the hollow interior of bones. During exhalation, air from air sacs passes into the lungs and out the trachea. (credit: modification of work by L. Shyamal)

To help supply blood to the tissues, Birds have also evolved a four cambered heart, similar to that found in mammals. The heart, with two atria and two ventricles, directs deoxygenated blood to the lungs while the oxygenated blood can travel to the rest of the body.

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.

- Warm blooded (endothermic)
- Insulated Covering (feathers)
- No Urinary bladder
- Pneumatic Bones

- Modified Lungs
- Four chambered heart

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15.22: Evolution and Diversity of Birds

Learning Objectives

- Describe the evolutionary history of birds
- Discuss the diversity of birds

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.

Diversity of Birds

Bird diversity is much greater than that of reptiles, amphibians and mammals respectively. Presently, there are 10,711 extant species and 158 extinct species of birds of the world. The diversity is astounding, with birds existing almost everywhere in the world.

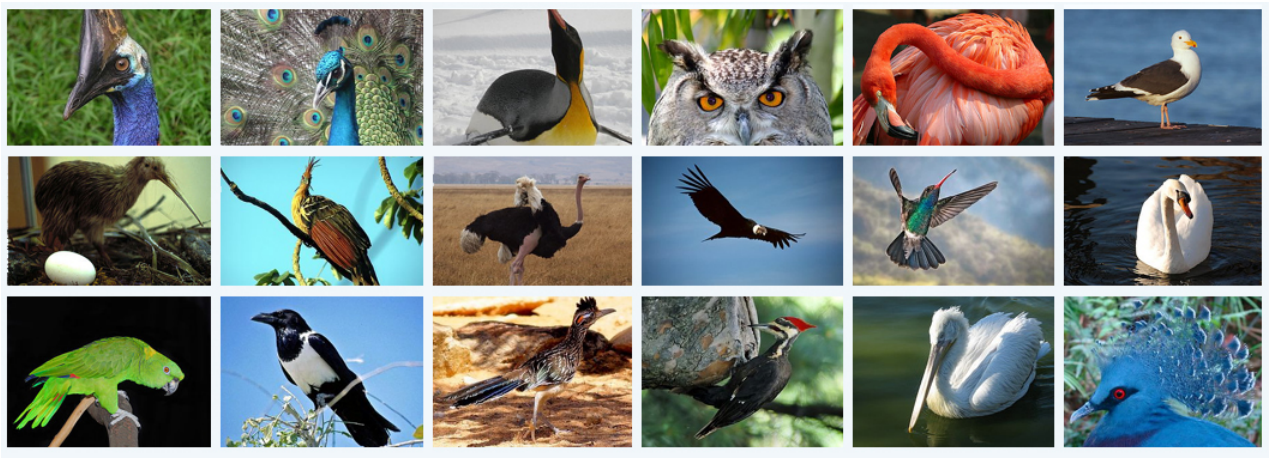


Figure 3. Diversity of Birds

Birds live all over the world. They range in size from the two-inch bee hummingbird to the nine-foot ostrich. More than half of the known birds on earth are perching birds. As we just learned, birds first appeared during the Cretaceous, about 100 million years ago. Birds diversified dramatically round about the time of the Cretaceous–Palaeogene extinction event 66 million years ago, which killed off all the non-avian dinosaur lines. Birds, especially those in the southern continents, survived this event and then migrated to other parts of the world.

Modern birds have wings which are more or less developed depending on the species; the only known groups without wings are the extinct moa and elephant birds. Wings, which evolved from forelimbs, gave birds the ability to fly. Later many groups evolved with reduced wings, such as ratites, penguins, and many island species of birds. The digestive and respiratory systems of birds are also adapted for flight. Some bird species in aquatic environments, particularly seabirds and some waterbirds, have evolved as good swimmers.

Some birds, especially crows and parrots, are among the most intelligent animals. Several bird species make and use tools. Many social species pass on knowledge across generations, a form of culture. Many species annually migrate great distances. Birds are social. They communicate with visual signals, calls, and bird songs. They have social behaviours such as cooperative breeding and hunting, flocking, and mobbing of predators.

Most bird species are socially monogamous, usually for one breeding season at a time, sometimes for years, but rarely for life. Other species are polygynous (one male with many females) or, rarely, polyandrous (one female with many males). Birds produce offspring by laying eggs which are fertilised by sexual reproduction. They are often laid in a nest and incubated by the parents. Most birds have an extended period of parental care after hatching. Some birds, such as hens, lay eggs even when not fertilised, though unfertilised eggs do not produce offspring.

? Try It

Birds are a beautifully diverse class of animal; however, many species are at risk. As of 2009, 1,223 species of birds were marked as endangered by IUCN's 2009 Red List. In the United States alone, about 74species of birds were at risk.

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15.23: Introduction to Mammals

What you'll learn to do: 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).

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15.24: Mammals

Learning Objectives

- Identify characteristics of mammals
- Name and describe the distinguishing features of the three main groups of mammals
- Describe the evolutionary history of 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.

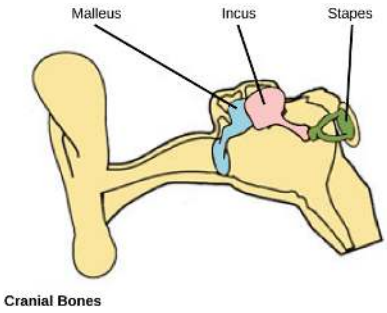


Figure 1. Bones of the mammalian inner ear are modified from bones of the jaw and skull. (credit: NCI)

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 (334 extant species), while roughly 100 extant species can be found in the Americas. The North American opossum is the only marsupial found north of Mexico, 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 are the most widespread of the mammals, occurring throughout the world. There are 18 to 20 orders of placental mammals. Some examples are Insectivora, the insect eaters; Edentata, the toothless anteaters; Rodentia, the rodents; Cetacea, the aquatic mammals including whales; Carnivora, carnivorous mammals including dogs, cats, and bears; and Primates, which includes humans. **Eutherian mammals** are sometimes called placental mammals because all species possess a complex placenta that connects a fetus to the mother, allowing for gas, fluid, and nutrient exchange. While other mammals possess a less complex placenta or briefly have a placenta, all eutherians possess a complex placenta during gestation.

Monotremes

There are three living species of **monotremes**: the platypus and four 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

Learning Objectives

- Identify characteristics of primates
- Describe the evolutionary history of 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.

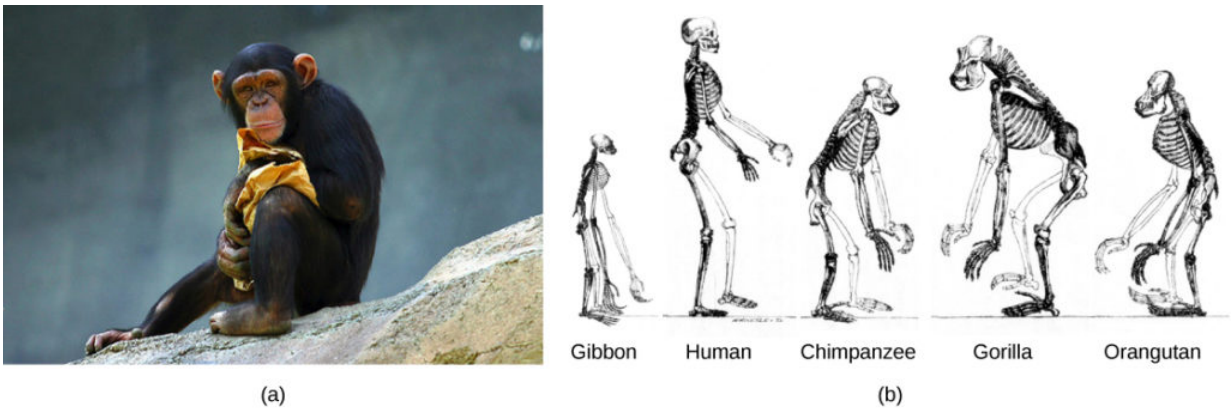


Figure 2. The (a) chimpanzee is one of the great apes. It possesses a relatively large brain and has no tail. (b) All great apes have a similar skeletal structure. (credit a: modification of work by Aaron Logan; credit b: modification of work by Tim Vickers)

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15.26: Evolution of Humans

Learning Objectives

- Describe the evolutionary history 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.

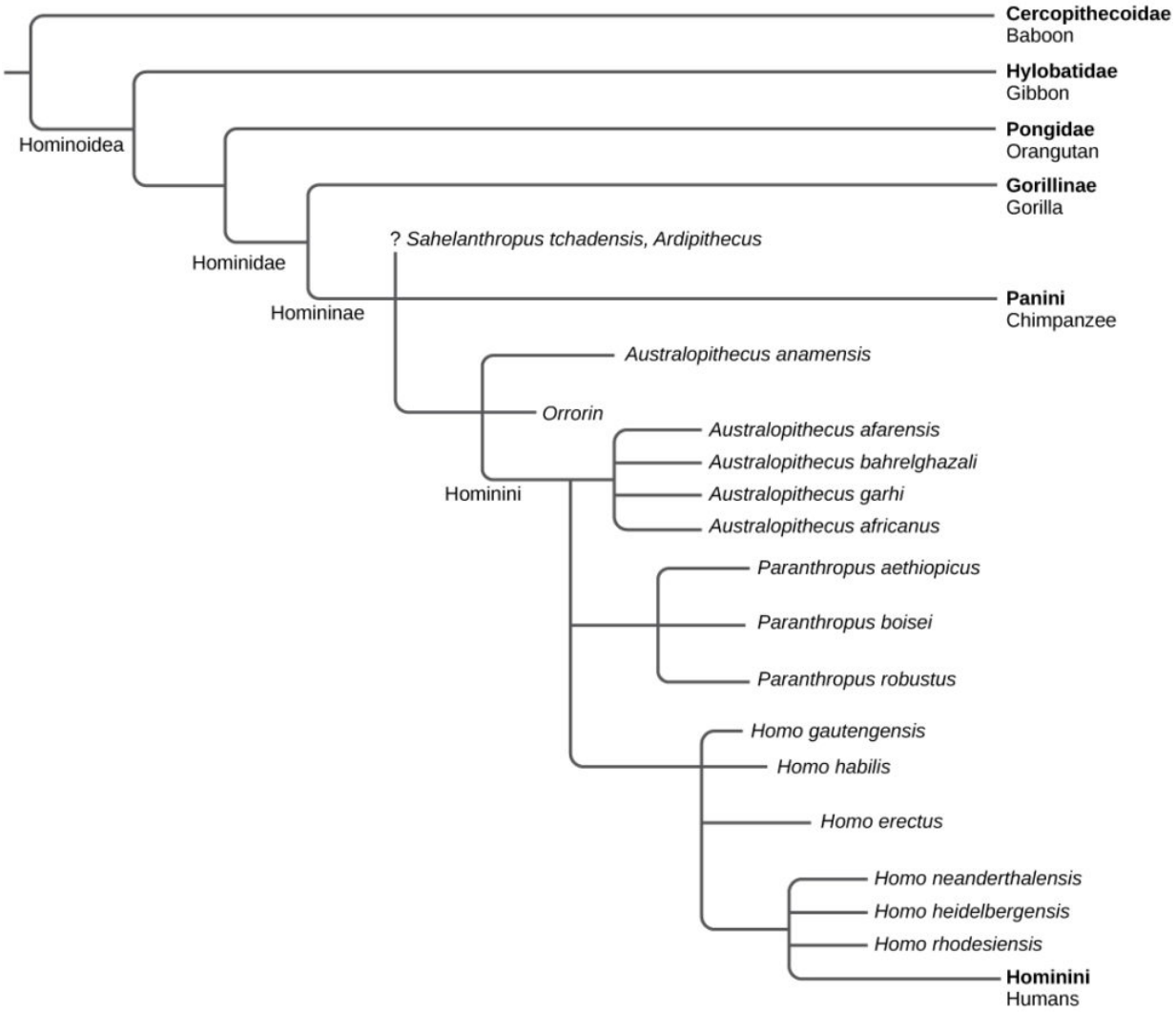


Figure 1. This chart shows the evolution of modern humans.

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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CHAPTER OVERVIEW

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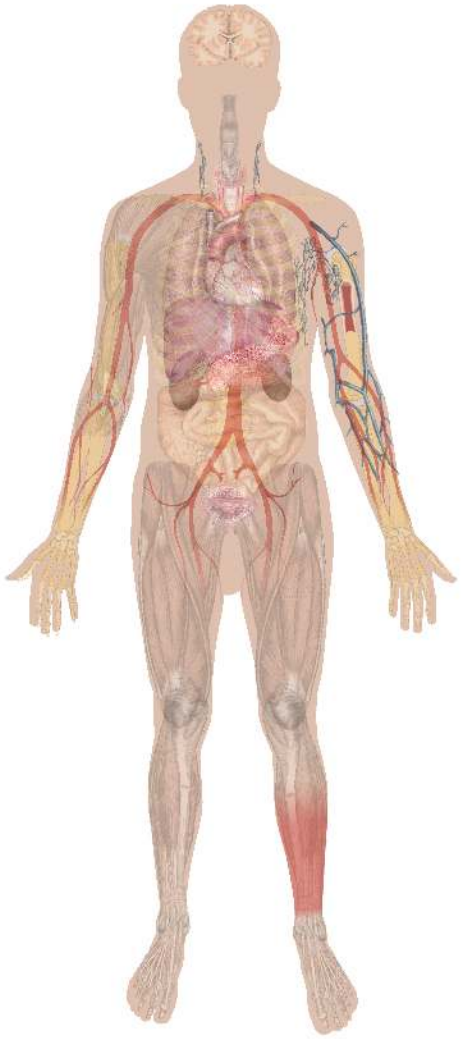
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16.1: Why It Matters- Overview of Body Systems

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:



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16.2: Introduction to Integration of Systems

What you'll learn to do: 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.

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16.3: How Bodies Work

Learning Objectives

- Discuss how different body systems interact with one another

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.

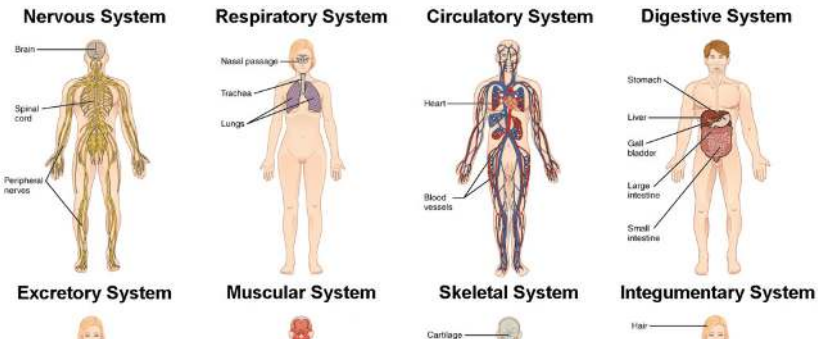


Figure 1. Click for a larger image. Organs that work together are grouped into organ systems.

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16.4: Maintaining Homeostasis

Learning Objectives

- Explain how different organ systems relate to one another to maintain 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.

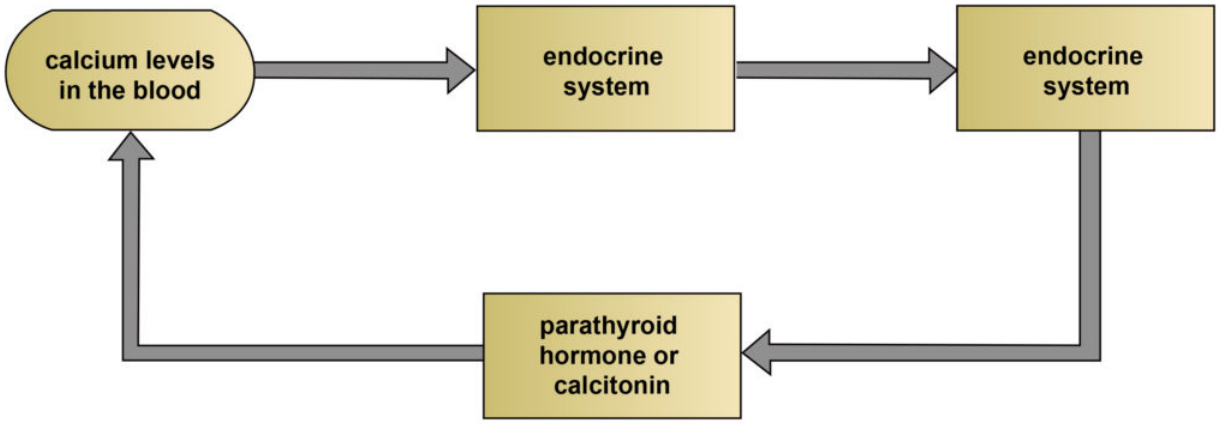
Osteoclasts in bones reabsorb bone tissue and release calcium.

- 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

Learning Objectives

- Explain how different organ systems work together to maintain blood solute 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

What you'll learn to do: 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.

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16.7: Nervous System

Learning Objectives

- Identify the structure and function of the 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.

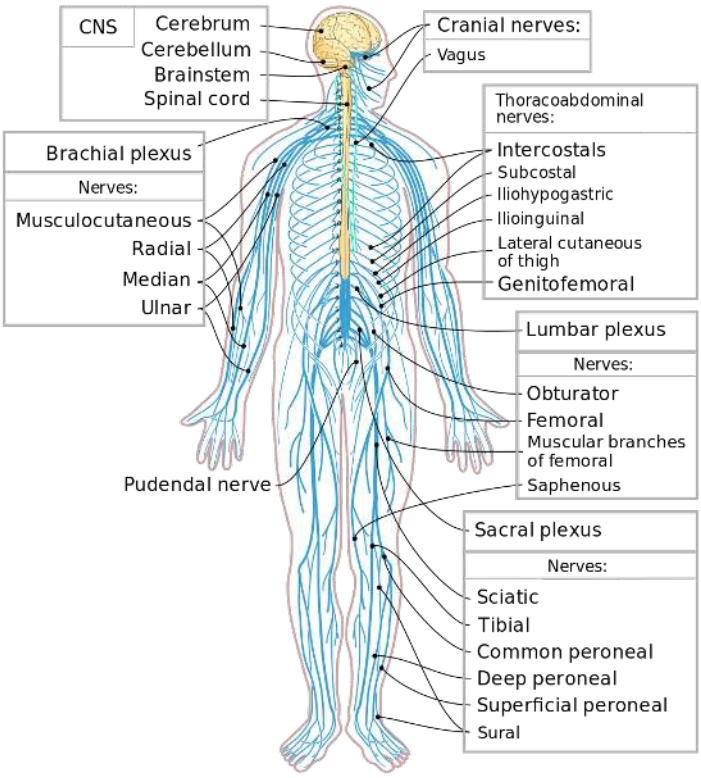


Figure 1. The nervous system.

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

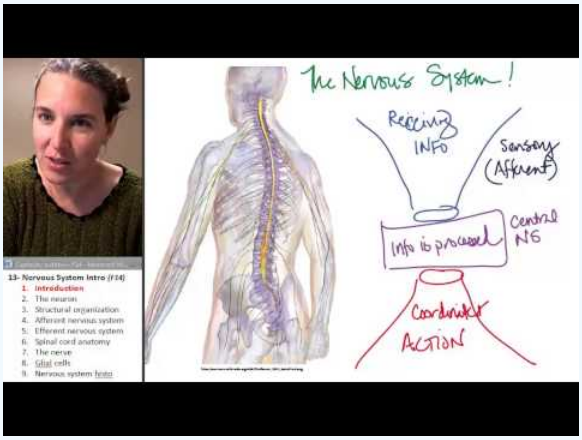
Sensory afferent neurons convey information from tissues and organs into the central nervous system. Efferent neurons transmit signals from the central nervous system to the effector cells and are sometimes called motor neurons. Interneurons connect neurons within specific regions of the central nervous 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

Learning Objectives

- Identify the structure and function of the 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.

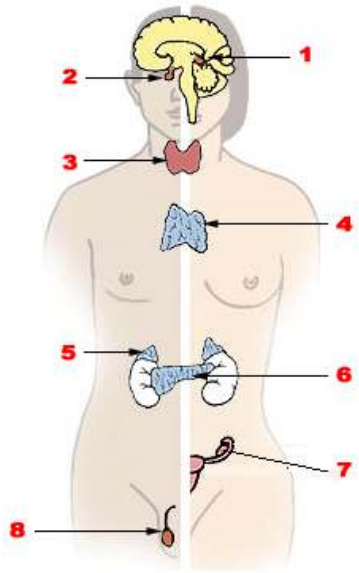


Figure 1. Major endocrine glands. (Male left, female on the right.) 1. Pineal gland 2. Pituitary gland 3. Thyroid gland 4. Thymus 5. Adrenal gland 6. Pancreas 7. Ovary 8. Testis

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

Learning Objectives

- Identify the structure and function of the 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.

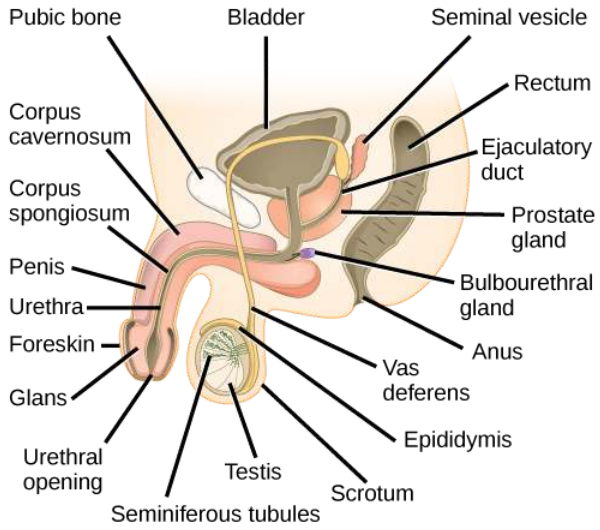


Figure 1. The reproductive structures of the human male are shown.

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.

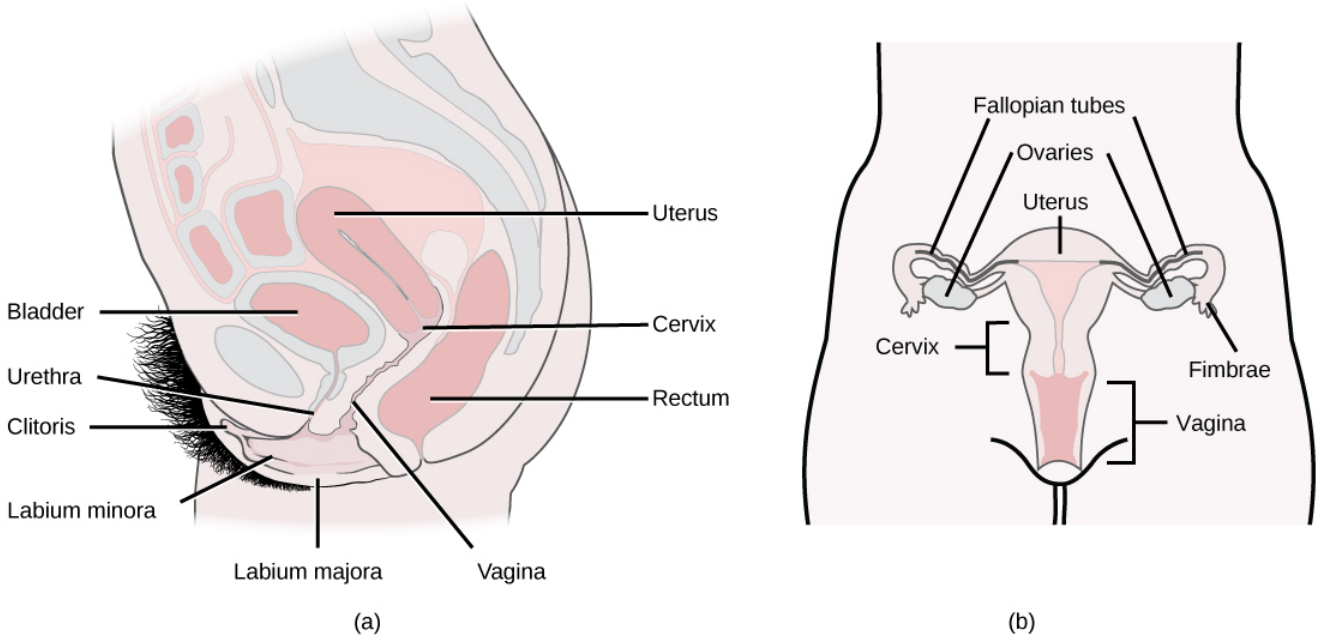


Figure 2. The reproductive structures of the human female are shown. (credit a: modification of work by Gray's Anatomy; credit b: modification of work by CDC)

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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16.10: Sensory Systems

Learning Objectives

- Identify the structure and function of the 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

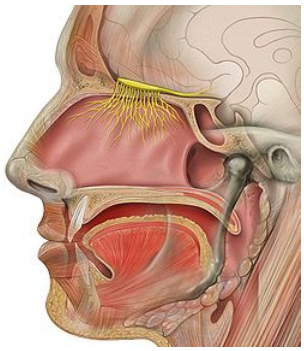


Figure 1. The Olfactory Nerve leading to the brain.

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).

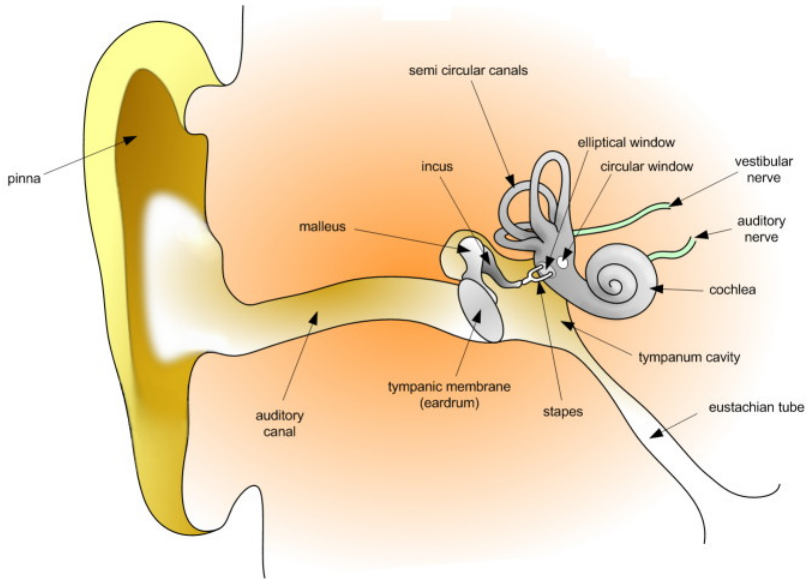


Figure 3. Anatomy of the human ear.

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

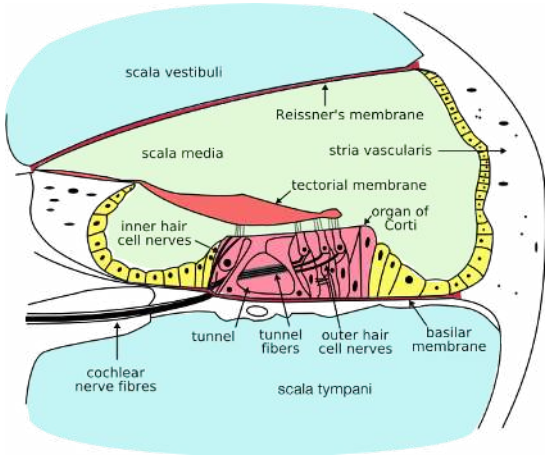


Figure 4. Cross section of the cochlea

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

What you'll learn to do: 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.

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16.12: Circulatory System

Learning Objectives

- Identify the structure and function of the 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

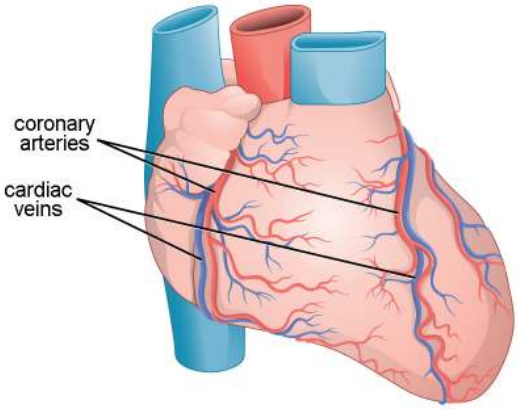


Figure 1. Blood vessels of the coronary system, including the coronary arteries and veins, keep the heart musculature oxygenated.

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

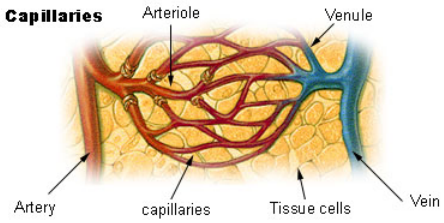


Figure 2. Capillaries

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

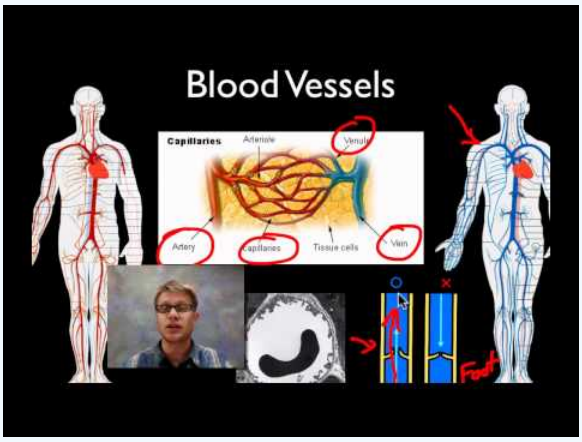
Veins carry blood to the heart. The pulmonary veins will carry oxygenated blood to the heart awhile the systemic veins will carry deoxygenated to the heart. Most of the blood volume is found in the venous system; about 70% at any given time. The veins outer walls have the same three layers as the arteries, 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

Learning Objectives

- Identify the structure and function of the 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.

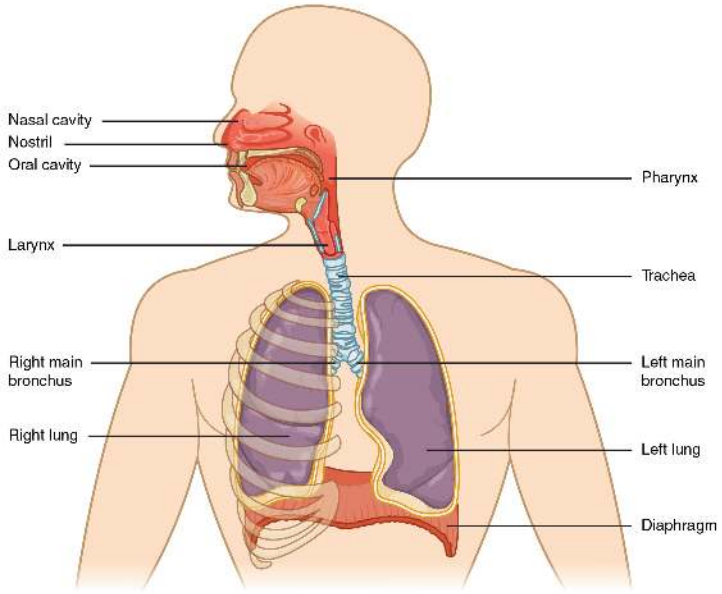


Figure 1. Click for a larger image. The major respiratory structures span the nasal cavity to the diaphragm.

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

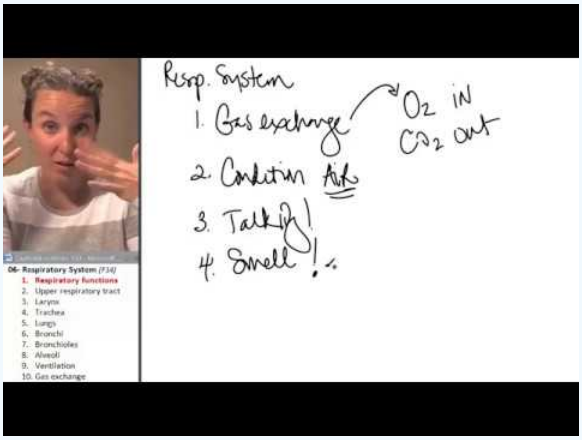
allows for gas exchange. The cells of the simple squamous epithelium are called Type I pneumocytes. The alveoli also contain other cells known as type II pneumocytes. These cells secrete a substance known as surfactant that helps to decrease the surface tension in the alveoli. The lungs contain about 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

Learning Objectives

- Identify the structure and function of the 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

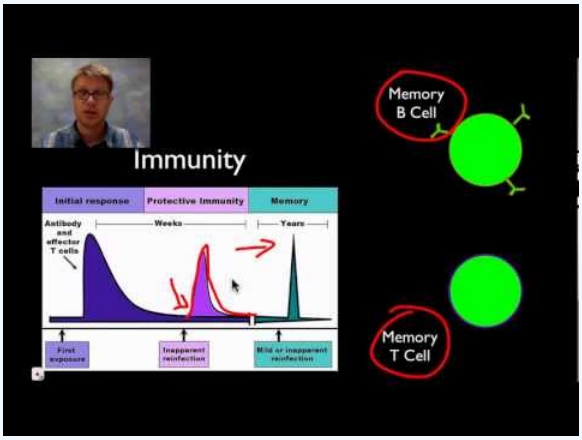
Specific glycoproteins can activate T-cells. These glycoproteins are called major histocompatibility complex molecules (MHC molecules). MHC molecules reside on cell membranes and contain a variable region. The variable region is the portion of the molecule that allows for binding to antigens.

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

Learning Objectives

- Identify the structure and function of the 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

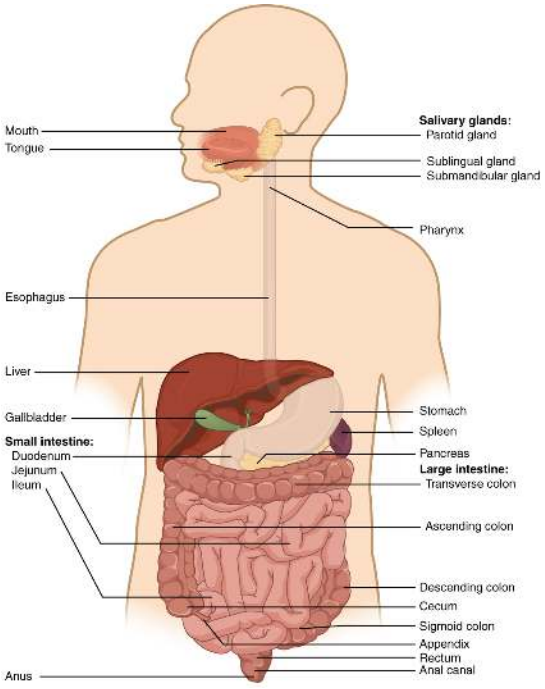


Figure 1. All digestive organs play integral roles in the life-sustaining process of digestion.

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:

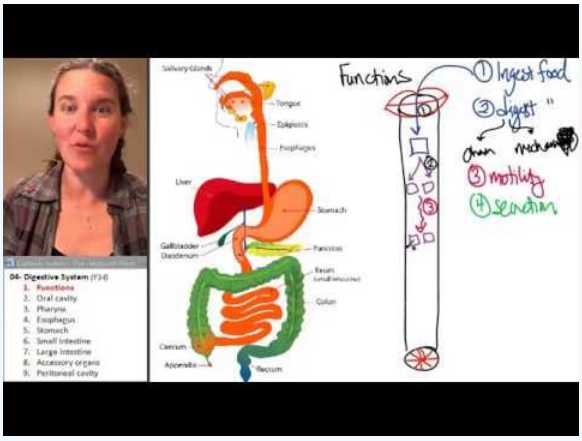
- **Mechanical Digestion**: larger pieces of food get broken down into smaller pieces while being prepared for chemical digestion. Mechanical digestion starts in the mouth and continues in to the stomach.
- **Chemical Digestion**: several different enzymes break down macromolecules into smaller molecules 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

What you'll learn to do: 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.

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16.17: The Muscular System

Learning Objectives

- Identify the structure and function of 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.

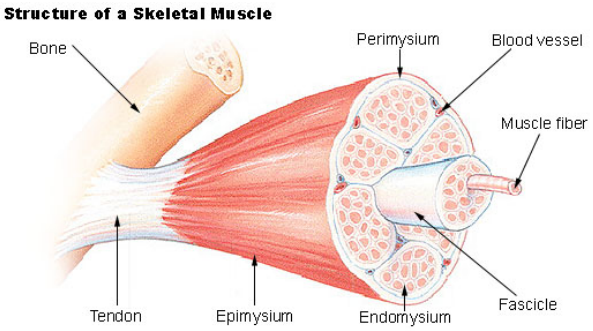


Figure 1. Muscle structure

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

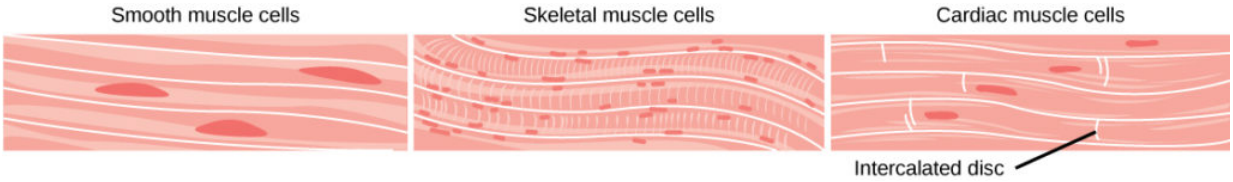


Figure 2. Smooth muscle cells do not have striations, while skeletal muscle cells do. Cardiac muscle cells have striations, but, unlike the multinucleate skeletal cells, they have only one nucleus. Cardiac muscle tissue also has intercalated discs, specialized regions running along the plasma membrane 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

Learning Objectives

- Identify the structure and function of the skeletal system

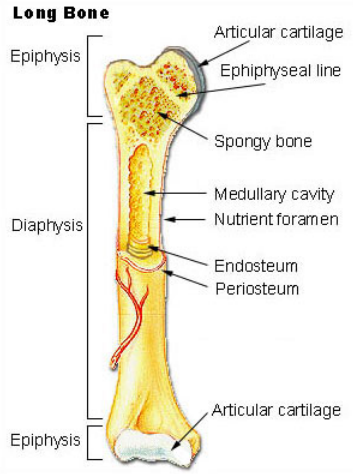


Figure 1. Parts of a long bone.

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).

Bone Structure

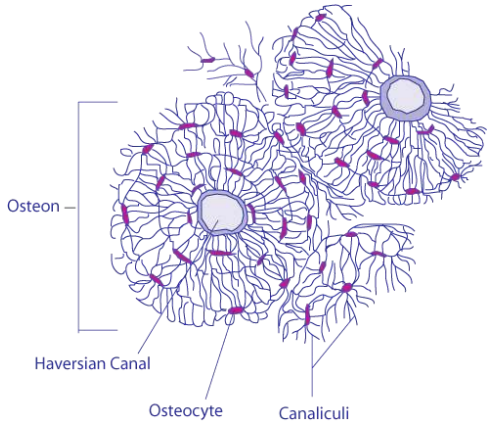


Figure 3. Haversian system.

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).

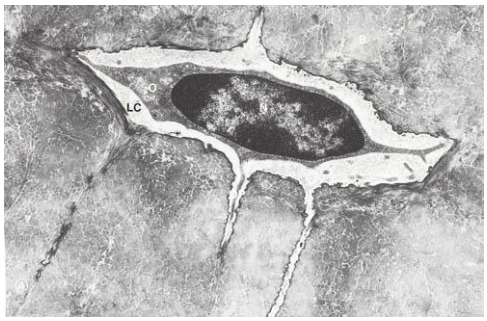


Figure 4. Osteocytes are mature osteoblasts that reside in a lacuna. They are surrounded by bony matrix.

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.

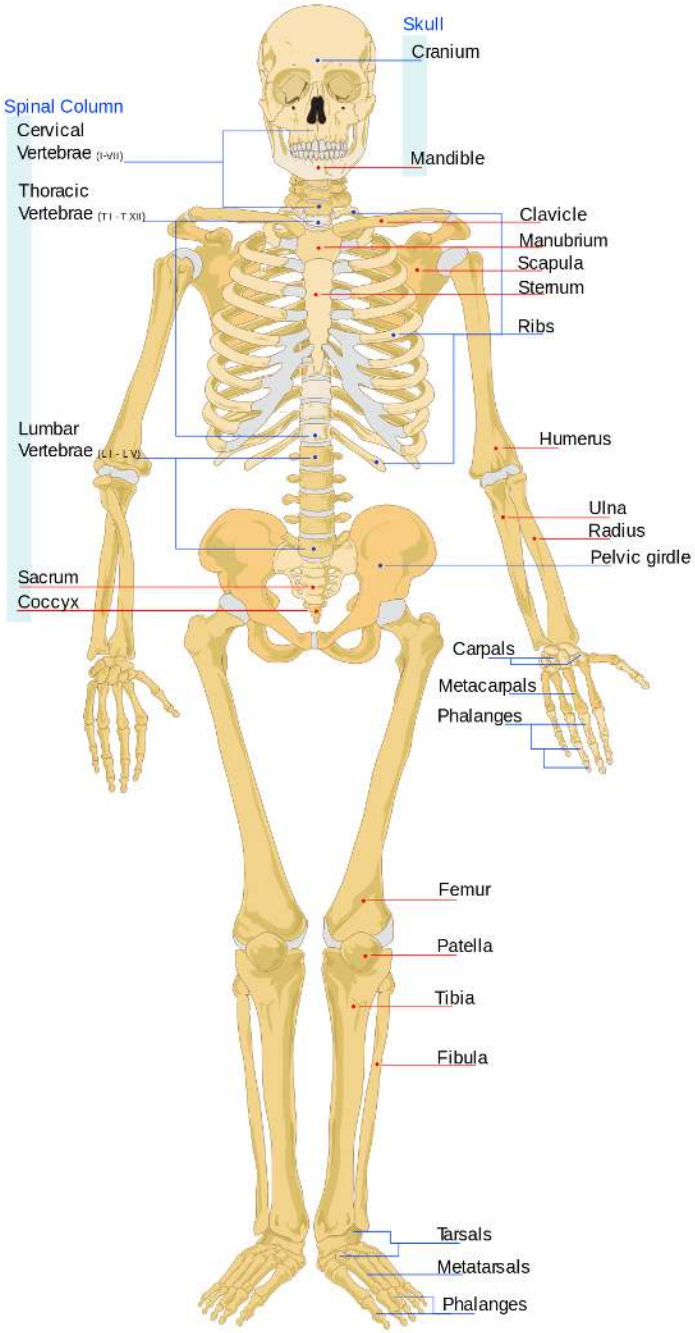


Figure 5. The skeleton.

Learning Objectives

This video provides another introduction to the skeletal system:



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16.19: Integumentary System

Learning Objectives

- Identify the structure and function of the 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.

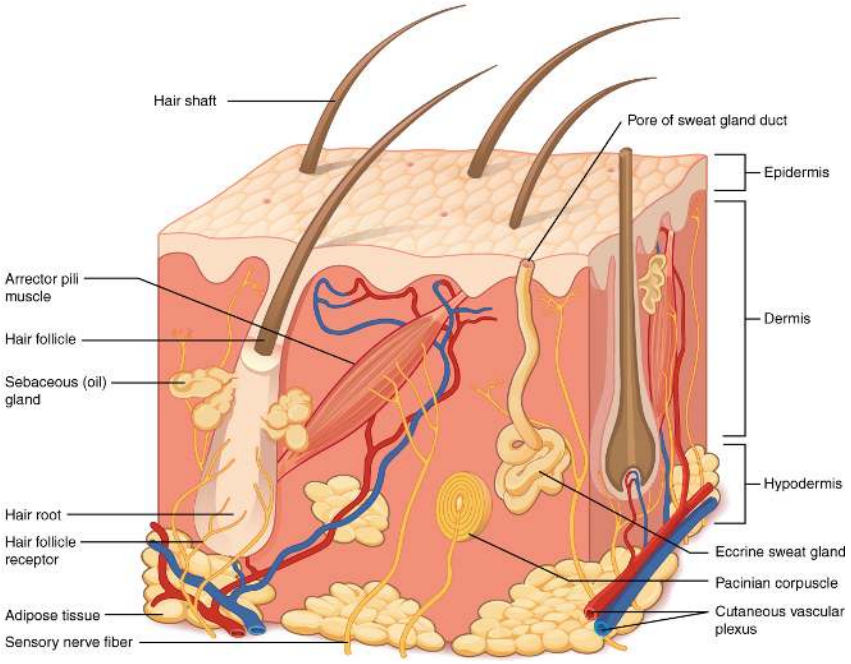


Figure 1. The skin is composed of two main layers: the epidermis, made of closely packed epithelial cells, and the dermis, made of dense, irregular connective tissue that houses blood vessels, hair follicles, sweat glands, and other structures. Beneath the dermis lies the hypodermis, which is composed 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

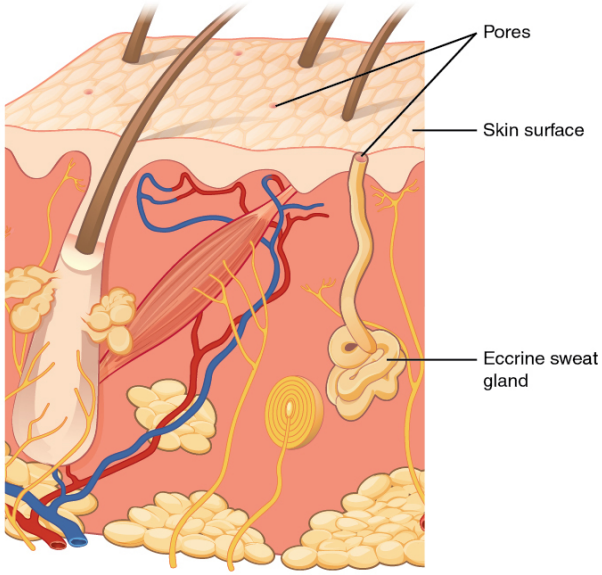


Figure 3. Eccrine glands are coiled glands in the dermis that release sweat that is mostly water.

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

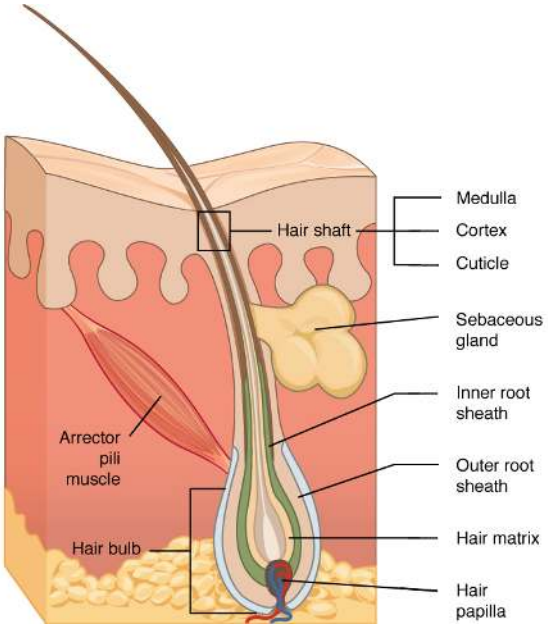


Figure 4. Hair follicles originate in the epidermis and have many different parts.

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.

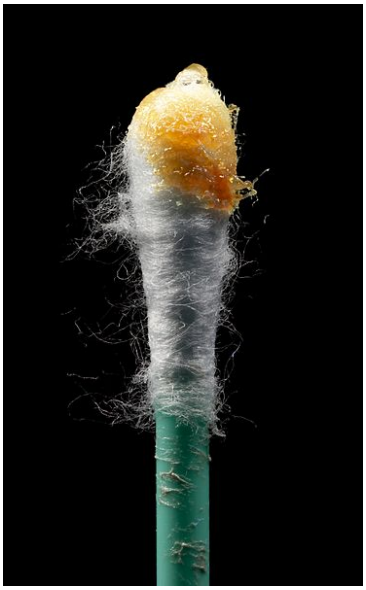


Figure 5. Wet-type human earwax on a cotton swab.

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

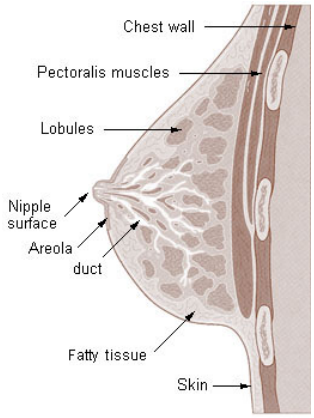


Figure 7. Cross section of the breast of a human female.

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 medical 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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CHAPTER OVERVIEW

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17.1: Why It Matters- Ecology of Living Things

Why define the scope and components of ecology?



You've probably heard the word *ecology* before, but how easily do you think you could define the term? Put simply, ecology is the study of the way living things interact with each other and with the nonliving influences around them. By studying ecology, you're improving your knowledge of the ways the world works, and the ways that it sustains life.

Like all sciences, ecology has different branches that different individuals focus on. Imagine that you've decided to become an ecologist, but you can't decide what facet of ecology you want to focus on. Perhaps you are interested in learning about the natural world and how living things interact with each other as they compete for resources.

It's also important for other professionals to understand ecology: perhaps you're a future physician seeking to understand the connection between human health and ecology. Regardless of your profession though, ecology is the world around us and it is important we understand the cycle between human and ecological impacts.

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17.2: Introduction to the Scope of Ecology

What you'll learn to do: Identify the scope of ecology

Ecology is the study of the interactions of living organisms with their environment. One core goal of ecology is to understand the distribution and abundance of living things in the physical environment. Attainment of this goal requires the integration of scientific disciplines inside and outside of biology, such as biochemistry, physiology, evolution, biodiversity, molecular biology, geology, and climatology. Some ecological research also applies aspects of chemistry and physics, and it frequently uses mathematical models.

Climate change can alter where organisms live, which can sometimes directly affect human health. Watch the PBS video "Feeling the Effects of Climate Change" in which researchers discover a pathogenic organism living far outside of its normal range.

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17.3: What Is Ecology?

Learning Objectives

- Define the science of ecology

Ecology is the study of the interactions of living things with their environment. Ecologists ask questions across four levels of biological organization—organismal, population, community, and ecosystem. At the organismal level, ecologists study individual organisms and how they interact with their environments. At the population and community levels, ecologists explore, respectively, how a population of organisms changes over time and the ways in which that population interacts with other species in the community. Ecologists studying an ecosystem examine the living species (the biotic components) of the ecosystem as well as the nonliving portions (the abiotic components), such as air, water, and soil, of the environment.

Ecology

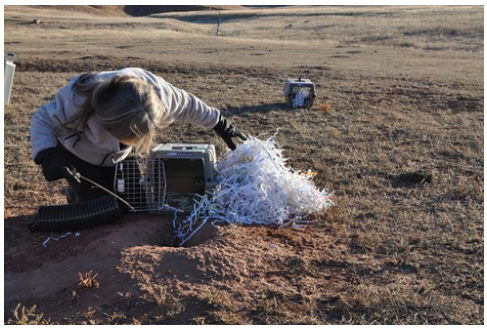


Figure 1. This landscape ecologist is releasing a black-footed ferret into its native habitat as part of a study. (credit: USFWS Mountain Prairie Region, NPS)

A career in ecology contributes to many facets of human society. Understanding ecological issues can help society meet the basic human needs of food, shelter, and health care. Ecologists can conduct their research in the laboratory and outside in natural environments. These natural environments can be as close to home as the stream running through your campus or as far away as the hydrothermal vents at the bottom of the Pacific Ocean. Ecologists manage natural resources such as white-tailed deer populations (*Odocoileus virginianus*) for hunting or aspen (*Populus* spp.) timber stands for paper production. Ecologists also work as educators who teach children and adults at various institutions including universities, high schools, museums, and nature centers. Ecologists may also work in advisory positions assisting local, state, and federal policymakers to develop laws that are ecologically sound, or they may develop those policies and legislation themselves. To become an ecologist requires an undergraduate degree, usually in a natural science. The undergraduate degree is often followed by specialized training or an advanced degree, depending on the area of ecology selected. Ecologists should also have a broad background in the physical sciences, as well as a sound foundation in mathematics and statistics.

Visit this site to see Stephen Wing, a marine ecologist from the University of Otago, discuss the role of an ecologist and the types of issues ecologists explore.

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17.4: Levels of Ecological Research

Learning Objectives

- Define ecology and the four levels of ecological research

When a discipline such as biology is studied, it is often helpful to subdivide it into smaller, related areas. For instance, cell biologists interested in cell signaling need to understand the chemistry of the signal molecules (which are usually proteins) as well as the result of cell signaling. The same subdivisions occur in ecology. Ecologists interested in the factors that influence the survival of an endangered species might use mathematical models to predict how current conservation efforts affect endangered organisms. To produce a sound set of management options, a conservation biologist needs to collect accurate data, including current population size, factors affecting reproduction (like physiology and behavior), habitat requirements (such as plants and soils), and potential human influences on the endangered population and its habitat (which might be derived through studies in sociology and urban ecology). Within the discipline of ecology, researchers work at four specific levels, sometimes discretely and sometimes with overlap: organism, population, community, and ecosystem (Figure 1).

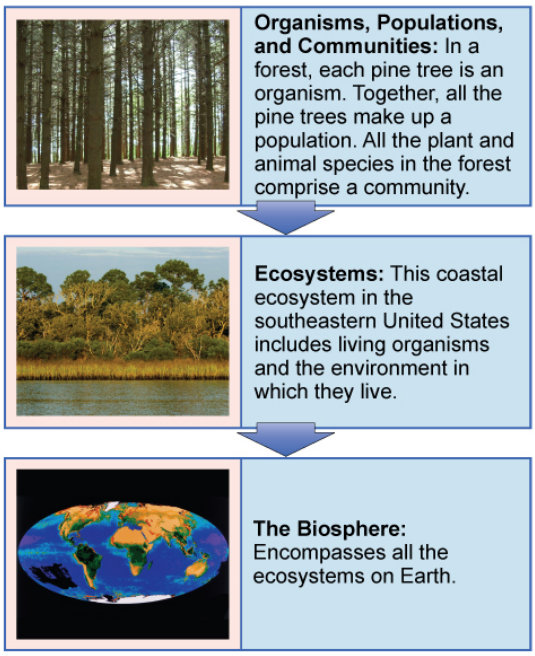


Figure 1. Ecologists study within several biological levels of organization. (credit “organisms”: modification of work by “Crystl”/Flickr; credit “ecosystems”: modification of work by Tom Carlisle, US Fish and Wildlife Service Headquarters; credit “biosphere”: NASA)

Organismal Ecology

Researchers studying ecology at the organismal level are interested in the adaptations that enable individuals to live in specific habitats. These adaptations can be morphological, physiological, and behavioral. For instance, the Karner blue butterfly (*Lycaeides melissa samuelis*) is a rare butterfly that lives only in open areas with few trees or shrubs, such as pine barrens and oak savannas. It is considered a specialist because the females preferentially oviposit (that is, lay eggs) on wild lupine (Figure 2). This preferential adaptation means that the Karner blue butterfly is highly dependent on the presence of wild lupine plants for its continued survival.



Figure 2. (a) The Karner blue butterfly (*Lycaeides melissa samuelis*). (b) The wild lupine (*Lupinus perennis*) is the host plant for the Karner blue butterfly (credit a: modification of work by J & K Hollingsworth, USFWS; credit b: Joel Trick, USFWS)

After hatching, the larval caterpillars emerge and spend four to six weeks feeding solely on wild lupine. The caterpillars pupate (undergo metamorphosis) and emerge as butterflies after about four weeks. The adult butterflies feed on the nectar of flowers of wild lupine and other plant species. A researcher interested in studying Karner blue butterflies at the organismal level might, in addition to asking questions about egg laying, ask questions about the butterflies' preferred temperature (a physiological question) or the behavior of the caterpillars when they are at different larval stages (a behavioral question).

Population Ecology

A population is a group of interbreeding organisms that are members of the same species living in the same area at the same time. (Organisms that are all members of the same species are called **conspecifics**.) A population is identified, in part, by where it lives, and its area of population may have natural or artificial boundaries: natural boundaries might be rivers, mountains, or deserts, while examples of artificial boundaries include mowed grass, manmade structures, or roads. The study of population ecology focuses on the number of individuals in an area and how and why population size changes over time. Population ecologists are particularly interested in counting the Karner blue butterfly, for example, because it is classified as federally endangered. However, the distribution and density of this species is highly influenced by the distribution and abundance of wild lupine. Researchers might ask questions about the factors leading to the decline of wild lupine and how these affect Karner blue butterflies. For example, ecologists know that wild lupine thrives in open areas where trees and shrubs are largely absent. In natural settings, intermittent wildfires regularly remove trees and shrubs, helping to maintain the open areas that wild lupine requires. Mathematical models can be used to understand how wildfire suppression by humans has led to the decline of this important plant for the Karner blue butterfly.

Community Ecology

A biological community consists of the different species within an area, typically a three-dimensional space, and the interactions within and among these species. Community ecologists are interested in the processes driving these interactions and their consequences. Questions about conspecific interactions often focus on competition among members of the same species for a limited resource. Ecologists also study interactions among various species; members of different species are called **heterospecifics**. Examples of heterospecific interactions include predation, parasitism, herbivory, competition, and pollination. These interactions can have regulating effects on population sizes and can impact ecological and evolutionary processes affecting diversity.

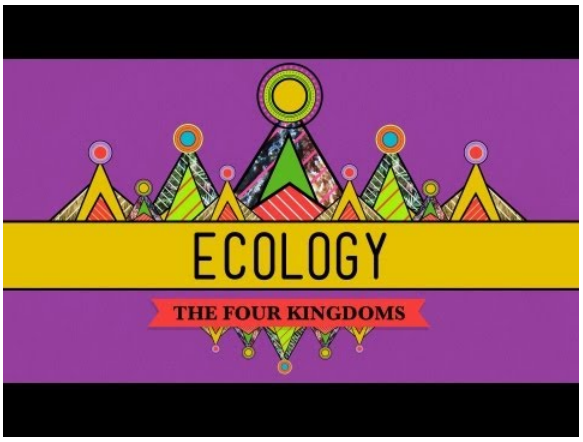
For example, Karner blue butterfly larvae form mutualistic relationships with ants. Mutualism is a form of a long-term relationship that has coevolved between two species and from which each species benefits. For mutualism to exist between individual organisms, each species must receive some benefit from the other as a consequence of the relationship. Researchers have shown that there is an increase in the probability of survival when Karner blue butterfly larvae (caterpillars) are tended by ants. This might be because the larvae spend less time in each life stage when tended by ants, which provides an advantage for the larvae. Meanwhile, the Karner blue butterfly larvae secrete a carbohydrate-rich substance that is an important energy source for the ants. Both the Karner blue larvae and the ants benefit from their interaction.

Ecosystem Ecology

Ecosystem ecology is an extension of organismal, population, and community ecology. The ecosystem is composed of all the **biotic** components (living things) in an area along with the **abiotic** components (non-living things) of that area. Some of the abiotic components include air, water, and soil. Ecosystem biologists ask questions about how nutrients and energy are stored and how they move among organisms and the surrounding atmosphere, soil, and water.

The Karner blue butterflies and the wild lupine live in an oak-pine barren habitat. This habitat is characterized by natural disturbance and nutrient-poor soils that are low in nitrogen. The availability of nutrients is an important factor in the distribution of the plants that live in this habitat. Researchers interested in ecosystem ecology could ask questions about the importance of limited resources and the movement of resources, such as nutrients, though the biotic and abiotic portions of the ecosystem.

Watch this video for another introduction to ecology:



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? Try It

Ecology can also be classified on the basis of:

- the primary kinds of organism under study (e.g. animal ecology, plant ecology, insect ecology)
- the biomes principally studied (e.g. forest ecology, grassland ecology, desert ecology, benthic ecology, marine ecology, urban ecology)
- the geographic or climatic area (e.g. arctic ecology, tropical ecology)
- the spatial scale under consideration (e.g. macroecology, landscape ecology)
- the philosophical approach (e.g. systems ecology which adopts a holistic approach)
- the methods used (e.g. molecular ecology)

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17.5: Branches of Ecology

Learning Objectives

- Identify common branches of ecology

Ecology can be divided into many sub-disciplines using various criteria. Many of these fields overlap, complement and inform each other, and few of these disciplines exist in isolation. For example, methods from molecular ecology might inform the study of the population, and all kinds of data are modeled and analyzed using quantitative ecology techniques. Specialized branches of ecology include, among many others:

- applied ecology, the practice of employing ecological principles and understanding to solve real world problems (includes agroecology and conservation biology)
- biogeochemistry, effect of biota on global chemistry, and the cycles of matter and energy that transport the Earth's chemical components in time and space
- biogeography, the study of the geographic distributions of species
- conservation ecology, which studies how to reduce the risk of species extinction
- ecological succession, which focuses on understanding directed vegetation change
- evolutionary ecology or ecoevolution which looks at evolutionary changes in the context of the populations and communities in which the organisms exist
- functional ecology, the study of the roles, or functions, that certain species (or groups thereof) play in an ecosystem
- global ecology, which examines ecological phenomena at the largest possible scale, addressing macroecological questions
- marine ecology, and aquatic ecology, where the dominant environmental milieu is water
- microbial ecology, the ecology of micro-organisms
- paleoecology, which seeks to understand the relationships between species in fossil assemblages
- restoration ecology, which attempts to understand the ecological basis needed to restore impaired or damaged ecosystems
- soil ecology, the ecology of the pedosphere
- urban ecology, the study of ecosystems in urban areas

Interdisciplinary Fields

Ecology also plays important roles in many inter-disciplinary fields:

- ecological design and ecological engineering
- ecological economics
- festive ecology
- human ecology and ecological anthropology
- social ecology, ecological health and environmental psychology

Ecology has also inspired (and lent its name to) other non-biological disciplines such as

- industrial ecology
- media ecology
- software ecology and information ecology

Finally, ecology is used to describe several philosophies or ideologies, such as

- deep ecology
- social ecology

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17.6: Introduction to Biotic and Abiotic Factors

What you'll learn to do: Distinguish between abiotic and biotic components of the environment

Many forces influence the communities of living organisms present in different parts of the biosphere (all of the parts of Earth inhabited by life). The biosphere extends into the atmosphere (several kilometers above Earth) and into the depths of the oceans. Despite its apparent vastness to an individual human, the biosphere occupies only a minute space when compared to the known universe. Many abiotic forces influence where life can exist and the types of organisms found in different parts of the biosphere. The abiotic factors influence the distribution of climates, flora, and fauna.

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17.7: Biogeography and Species Distribution

Learning Objectives

- Define the term biogeography and the abiotic factors that impact it
- Discuss how abiotic factors affect species distribution

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Abiotic factors such as temperature and rainfall vary based mainly on latitude and elevation. As these abiotic factors change, the composition of plant and animal communities also changes. For example, if you were to begin a journey at the equator and walk north, you would notice gradual changes in plant communities. At the beginning of your journey, you would see tropical wet forests with broad-leaved evergreen trees, which are characteristic of plant communities found near the equator. As you continued to travel north, you would see these broad-leaved evergreen plants eventually give rise to seasonally dry forests with scattered trees. You would also begin to notice changes in temperature and moisture. At about 30 degrees north, these forests would give way to deserts, which are characterized by low precipitation.

Moving farther north, you would see that deserts are replaced by grasslands or prairies. Eventually, grasslands are replaced by deciduous temperate forests. These deciduous forests give way to the boreal forests found in the subarctic, the area south of the Arctic Circle. Finally, you would reach the Arctic tundra, which is found at the most northern latitudes. This trek north reveals gradual changes in both climate and the types of organisms that have adapted to environmental factors associated with ecosystems found at different latitudes. However, different ecosystems exist at the same latitude due in part to abiotic factors such as jet streams, the Gulf Stream, and ocean currents. If you were to hike up a mountain, the changes you would see in the vegetation would parallel those as you move to higher latitudes.

Species Distribution

Ecologists who study biogeography examine patterns of species distribution. No species exists everywhere; for example, the Venus flytrap is endemic to a small area in North and South Carolina. An **endemic** species is one which is naturally found only in a specific geographic area that is usually restricted in size. Other species are generalists: species which live in a wide variety of geographic areas; the raccoon, for example, is native to most of North and Central America.

Species distribution patterns are based on biotic and abiotic factors and their influences during the very long periods of time required for species evolution; therefore, early studies of biogeography were closely linked to the emergence of evolutionary thinking in the eighteenth century. Some of the most distinctive assemblages of plants and animals occur in regions that have been physically separated for millions of years by geographic barriers. Biologists estimate that Australia, for example, has between 600,000 and 700,000 species of plants and animals. Approximately 3/4 of living plant and mammal species are endemic species found solely in Australia (Figure 1).



(a) (b)

Figure 1. Australia is home to many endemic species. The (a) wallaby (Wallabia bicolor), a medium-sized member of the kangaroo family, is a pouched mammal, or marsupial. The (b) echidna (Tachyglossus aculeatus) is an egg-laying mammal. (credit a: modification of work by Derrick Coetzee; credit b: modification of work by Allan Whittome)

Sometimes ecologists discover unique patterns of species distribution by determining where species are *not* found. Hawaii, for example, has no native land species of reptiles or amphibians, and has only one native terrestrial mammal, the hoary bat. Most of New Guinea, as another example, lacks placental mammals.

Check out this video to observe a platypus swimming in its natural habitat in New South Wales, Australia. Note that this video has no narration.

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Plants can be endemic or generalists: endemic plants are found only on specific regions of the Earth, while generalists are found on many regions. Isolated land masses—such as Australia, Hawaii, and Madagascar—often have large numbers of endemic plant species. Some of these plants are endangered due to human activity. The forest gardenia (*Gardenia brighamii*), for instance, is endemic to Hawaii; only an estimated 15–20 trees are thought to exist.

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17.8: Energy Sources

Learning Outcomes

- Identify ways energy sources impact the biotic factors of biogeography



Figure 1. The spring beauty is an ephemeral spring plant that flowers early in the spring to avoid competing with larger forest trees for sunlight. (credit: John Beetham)

Energy from the sun is captured by green plants, algae, cyanobacteria, and photosynthetic protists. These organisms convert solar energy into the chemical energy needed by all living things. Light availability can be an important force directly affecting the evolution of adaptations in photosynthesizers. For instance, plants in the understory of a temperate forest are shaded when the trees above them in the canopy completely leaf out in the late spring. Not surprisingly, understory plants have adaptations to successfully capture available light. One such adaptation is the rapid growth of spring ephemeral plants such as the spring beauty (Figure 1). These spring flowers achieve much of their growth and finish their life cycle (reproduce) early in the season before the trees in the canopy develop leaves.

In aquatic ecosystems, the availability of light may be limited because sunlight is absorbed by water, plants, suspended particles, and resident microorganisms. Toward the bottom of a lake, pond, or ocean, there is a zone that light cannot reach. Photosynthesis cannot take place there and, as a result, a number of adaptations have evolved that enable living things to survive without light. For instance, aquatic plants have photosynthetic tissue near the surface of the water; for example, think of the broad, floating leaves of a water lily—water lilies cannot survive without light. In environments such as hydrothermal vents, some bacteria extract energy from inorganic chemicals because there is no light for photosynthesis.

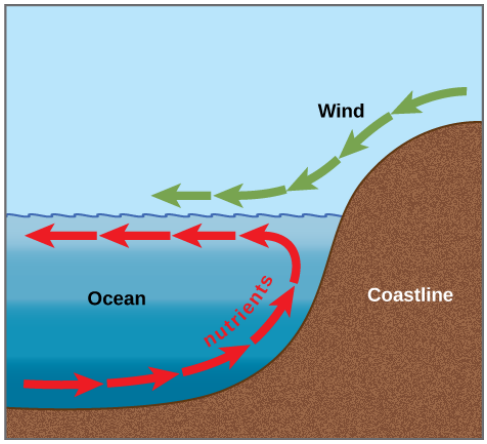


Figure 2. Ocean upwelling is an important process that recycles nutrients and energy in the ocean. As wind (green arrows) pushes offshore, it causes water from the ocean bottom (red arrows) to move to the surface, bringing up nutrients from the ocean depths.

The availability of nutrients in aquatic systems is also an important aspect of energy or photosynthesis. Many organisms sink to the bottom of the ocean when they die in the open water; when this occurs, the energy found in that living organism is sequestered for some time unless ocean upwelling occurs. **Ocean upwelling** is the rising of deep ocean waters that occurs when prevailing winds blow along surface waters near a coastline (Figure 2). As the wind pushes ocean waters offshore, water from the bottom of the

ocean moves up to replace this water. As a result, the nutrients once contained in dead organisms become available for reuse by other living organisms.

In freshwater systems, the recycling of nutrients occurs in response to air temperature changes. The nutrients at the bottom of lakes are recycled twice each year: in the spring and fall turnover. The **spring and fall turnover** is a seasonal process that recycles nutrients and oxygen from the bottom of a freshwater ecosystem to the top of a body of water (Figure 3). These turnovers are caused by the formation of a **thermocline**: a layer of water with a temperature that is significantly different from that of the surrounding layers. In wintertime, the surface of lakes found in many northern regions is frozen. However, the water under the ice is slightly warmer, and the water at the bottom of the lake is warmer yet at 4 °C to 5 °C (39.2 °F to 41 °F). Water is densest at 4 °C; therefore, the deepest water is also the densest. The deepest water is oxygen poor because the decomposition of organic material at the bottom of the lake uses up available oxygen that cannot be replaced by means of oxygen diffusion into the water due to the surface ice layer.

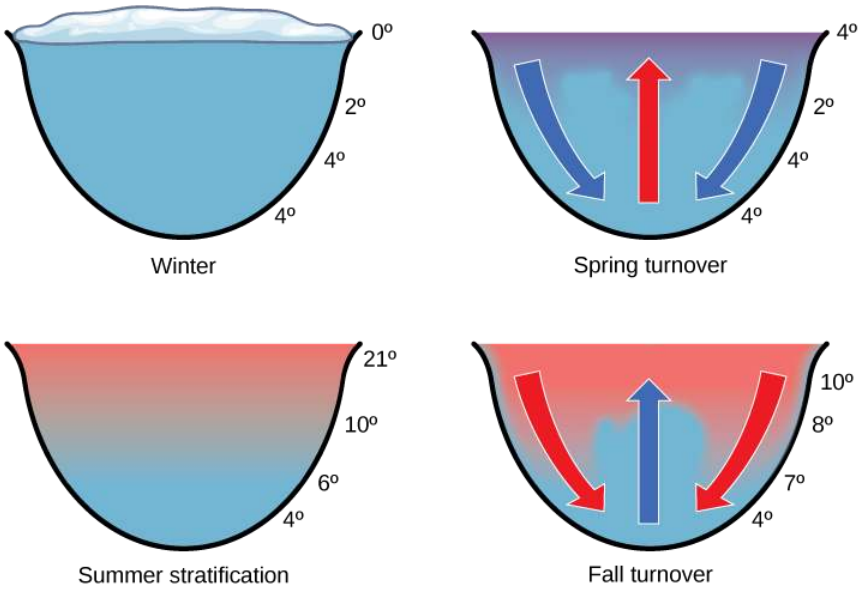


Figure 3. The spring and fall turnovers are important processes in freshwater lakes that act to move the nutrients and oxygen at the bottom of deep lakes to the top. Turnover occurs because water has a maximum density at 4 °C. Surface water temperature changes as the seasons progress, and denser water sinks.

Practice Question

How might turnover in tropical lakes differ from turnover in lakes that exist in temperate regions?

[practice-area rows="2"][/practice-area]
[reveal-answer q="236527"]Show Answer[/reveal-answer]
[hidden-answer a="236527"]Tropical lakes don't freeze, so they don't undergo spring turnover in the same way temperate lakes do. However, stratification does occur, as well as seasonal turnover.[/hidden-answer]

In springtime, air temperatures increase and surface ice melts. When the temperature of the surface water begins to reach 4 °C, the water becomes heavier and sinks to the bottom. The water at the bottom of the lake is then displaced by the heavier surface water and, thus, rises to the top. As that water rises to the top, the sediments and nutrients from the lake bottom are brought along with it. During the summer months, the lake water **stratifies**, or forms layers of temperature, with the warmest water at the lake surface.

As air temperatures drop in the fall, the temperature of the lake water cools to 4 °C; therefore, this causes fall turnover as the heavy cold water sinks and displaces the water at the bottom. The oxygen-rich water at the surface of the lake then moves to the bottom of the lake, while the nutrients at the bottom of the lake rise to the surface. During the winter, the oxygen at the bottom of the lake is used by decomposers and other organisms requiring oxygen, such as fish.

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17.9: Temperature

Learning Outcomes

- Identify ways temperature impacts the biotic factors of biogeography



Figure 1. This colorful hot spring in Yellowstone National Park, located in Midway Geyser Basin, is the largest hot spring in the United States and the third largest in the world. Its rich color is the result of thermophilic organisms living along the edges of the hot spring,

Temperature affects the physiology of living things as well as the density and state of water. Temperature exerts an important influence on living things because few living things can survive at temperatures below 0 °C (32 °F) due to metabolic constraints. It is also rare for living things to survive at temperatures exceeding 45 °C (113 °F); this is a reflection of evolutionary response to typical temperatures. Enzymes are most efficient within a narrow and specific range of temperatures; enzyme degradation can occur at higher temperatures. Therefore, organisms either must maintain an internal temperature or they must inhabit an environment that will keep the body within a temperature range that supports metabolism. Some animals have adapted to enable their bodies to survive significant temperature fluctuations, such as seen in hibernation or reptilian torpor. Similarly, some bacteria are adapted to surviving in extremely hot temperatures such as geysers. Such bacteria are examples of extremophiles: organisms that thrive in extreme environments.

Temperature can limit the distribution of living things. Animals faced with temperature fluctuations may respond with adaptations, such as migration, in order to survive. **Migration**, the movement from one place to another, is an adaptation found in many animals, including many that inhabit seasonally cold climates. Migration solves problems related to temperature, locating food, and finding a mate. In migration, for instance, the Arctic Tern (*Sterna paradisaea*) makes a 40,000 km (24,000 mi) round trip flight each year between its feeding grounds in the southern hemisphere and its breeding grounds in the Arctic Ocean. Monarch butterflies (*Danaus plexippus*) live in the eastern United States in the warmer months and migrate to Mexico and the southern United States in the wintertime. Some species of mammals also make migratory forays. Reindeer (*Rangifer tarandus*) travel about 5,000 km (3,100 mi) each year to find food. Amphibians and reptiles are more limited in their distribution because they lack migratory ability. Not all animals that can migrate do so: migration carries risk and comes at a high energy cost.



Figure 2. Chipmunks hibernate for the winter, but they come out of sleep every few days to eat.

Some animals hibernate or estivate to survive hostile temperatures. **Hibernation** enables animals to survive cold conditions, and **estivation** allows animals to survive the hostile conditions of a hot, dry climate. Animals that hibernate or estivate enter a state known as **torpor**: a condition in which their metabolic rate is significantly lowered. This enables the animal to wait until its environment better supports its survival. Some amphibians, such as the wood frog (*Rana sylvatica*), have an antifreeze-like chemical in their cells, which retains the cells' integrity and prevents them from bursting.

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17.10: Abiotic Factors Influencing Plant Growth

Learning Objectives

- Identify abiotic factors that impact plant growth

Temperature and moisture are important influences on plant production (primary productivity) and the amount of organic matter available as food (net primary productivity). **Net primary productivity** is an estimation of all of the organic matter available as food; it is calculated as the total amount of carbon fixed per year minus the amount that is oxidized during cellular respiration. In terrestrial environments, net primary productivity is estimated by measuring the **aboveground biomass** per unit area, which is the total mass of living plants, excluding roots. This means that a large percentage of plant biomass which exists underground is not included in this measurement. Net primary productivity is an important variable when considering differences in biomes. Very productive biomes have a high level of aboveground biomass.

Annual biomass production is directly related to the abiotic components of the environment. Environments with the greatest amount of biomass have conditions in which photosynthesis, plant growth, and the resulting net primary productivity are optimized. The climate of these areas is warm and wet. Photosynthesis can proceed at a high rate, enzymes can work most efficiently, and stomata can remain open without the risk of excessive transpiration; together, these factors lead to the maximal amount of carbon dioxide (CO_2) moving into the plant, resulting in high biomass production. The aboveground biomass produces several important resources for other living things, including habitat and food. Conversely, dry and cold environments have lower photosynthetic rates and therefore less biomass. The animal communities living there will also be affected by the decrease in available food.

Inorganic Nutrients and Soil

Inorganic nutrients, such as nitrogen and phosphorus, are important in the distribution and the abundance of living things. Plants obtain these inorganic nutrients from the soil when water moves into the plant through the roots. Therefore, soil structure (particle size of soil components), soil pH, and soil nutrient content play an important role in the distribution of plants. Animals obtain inorganic nutrients from the food they consume. Therefore, animal distributions are related to the distribution of what they eat. In some cases, animals will follow their food resource as it moves through the environment.

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17.11: Water and Other Factors

Learning Objectives

- Identify other abiotic factors that impact the biogeography of our world

Water

Water is required by all living things because it is critical for cellular processes. Since terrestrial organisms lose water to the environment by simple diffusion, they have evolved many adaptations to retain water.

- Animals will be covered in an oily or waxy skin or cuticle to retain moisture.
- Plants have a number of interesting features on their leaves, such as leaf hairs and a waxy cuticle, that serve to decrease the rate of water loss via transpiration.

Organisms surrounded by water are not immune to water imbalance; they too have unique adaptations to manage water inside and out of cells.

- Freshwater organisms are surrounded by water and are constantly in danger of having water rush into their cells because of osmosis. Many adaptations of organisms living in freshwater environments have evolved to ensure that solute concentrations in their bodies remain within appropriate levels. One such adaptation is the excretion of dilute urine.
- Marine organisms are surrounded by water with a higher solute concentration than the organism and, thus, are in danger of losing water to the environment because of osmosis. These organisms have morphological and physiological adaptations to retain water and release solutes into the environment. For example, Marine iguanas (*Amblyrhynchus cristatus*), sneeze out water vapor that is high in salt in order to maintain solute concentrations within an acceptable range while swimming in the ocean and eating marine plants.

Other Aquatic Factors

Some abiotic factors, such as oxygen, are important in aquatic ecosystems as well as terrestrial environments. Terrestrial animals obtain oxygen from the air they breathe. Oxygen availability can be an issue for organisms living at very high elevations, however, where there are fewer molecules of oxygen in the air. In aquatic systems, the concentration of dissolved oxygen is related to water temperature and the speed at which the water moves. Cold water has more dissolved oxygen than warmer water. In addition, salinity, current, and tide can be important abiotic factors in aquatic ecosystems.

Other Terrestrial Factors



Figure 1. The mature cones of the jack pine open only when exposed to high temperatures, such as during a forest fire. (credit: USDA)

Wind can be an important abiotic factor because it influences the rate of evaporation and transpiration. The physical force of wind is also important because it can move soil, water, or other abiotic factors, as well as an ecosystem's organisms.

Fire is another terrestrial factor that can be an important agent of disturbance in terrestrial ecosystems. Some organisms are adapted to fire and, thus, require the high heat associated with fire to complete a part of their life cycle. For example, the jack pine (*Pinus banksiana*)—a coniferous tree—requires heat from fire for its seed cones to open. A fire is likely to kill most vegetation, so a

seedling that germinates after a fire is more likely to receive ample sunlight than one that germinates under normal conditions. Through the burning of pine needles, fire adds nitrogen to the soil and limits competition by destroying undergrowth.

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17.12: Introduction to Biomes

What you'll learn to do: Identify different biomes of our world

The Earth's biomes are categorized into two major groups: terrestrial and aquatic. Terrestrial biomes are based on land, while aquatic biomes include both ocean and freshwater biomes.

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17.13: Characteristics of Terrestrial Biomes

Learning Outcomes

- Identify the two major abiotic factors that determine terrestrial biomes

Terrestrial ecosystems are known for their diversity; they are grouped into large categories called biomes. Grouping these ecosystems into just a few biome categories obscures the great diversity of the individual ecosystems within them. For example, there is great variation in desert vegetation: the saguaro cacti and other plant life in the Sonoran Desert, in the United States, are relatively abundant compared to the desolate rocky desert of Boa Vista, an island off the coast of Western Africa (Figure 1).



(a) (b)

Figure 1. Desert ecosystems, like all ecosystems, can vary greatly. The desert in (a) Saguaro National Park, Arizona, has abundant plant life, while the rocky desert of (b) Boa Vista island, Cape Verde, Africa, is devoid of plant life. (credit a: modification of work by Jay Galvin; credit b: modification of work by Ingo Wölbern)

There are eight major terrestrial biomes: tropical wet forests, savannas, subtropical deserts, chaparral, temperate grasslands, temperate forests, boreal forests, and Arctic tundra. Temperature and precipitation, and variations in both, are key abiotic factors that shape the composition of animal and plant communities in terrestrial biomes. Comparing the annual totals of precipitation and fluctuations in precipitation from one biome to another provides clues as to the importance of abiotic factors in the distribution of biomes. Temperature variation on a daily and seasonal basis is also important for predicting the geographic distribution of the biome and the vegetation type in the biome. The distribution of these biomes shows that the same biome can occur in geographically distinct areas with similar climates (Figure 2).

Some biomes, such as temperate grasslands and temperate forests, have distinct seasons, with cold weather and hot weather alternating throughout the year. In warm, moist biomes, such as the tropical wet forest, net primary productivity is high, as warm temperatures, abundant water, and a year-round growing season fuel plant growth. Other biomes, such as deserts and tundra, have low primary productivity due to extreme temperatures and a shortage of available water. Terrestrial biomes on Earth are each distinguished by characteristic temperatures and amount of precipitation.

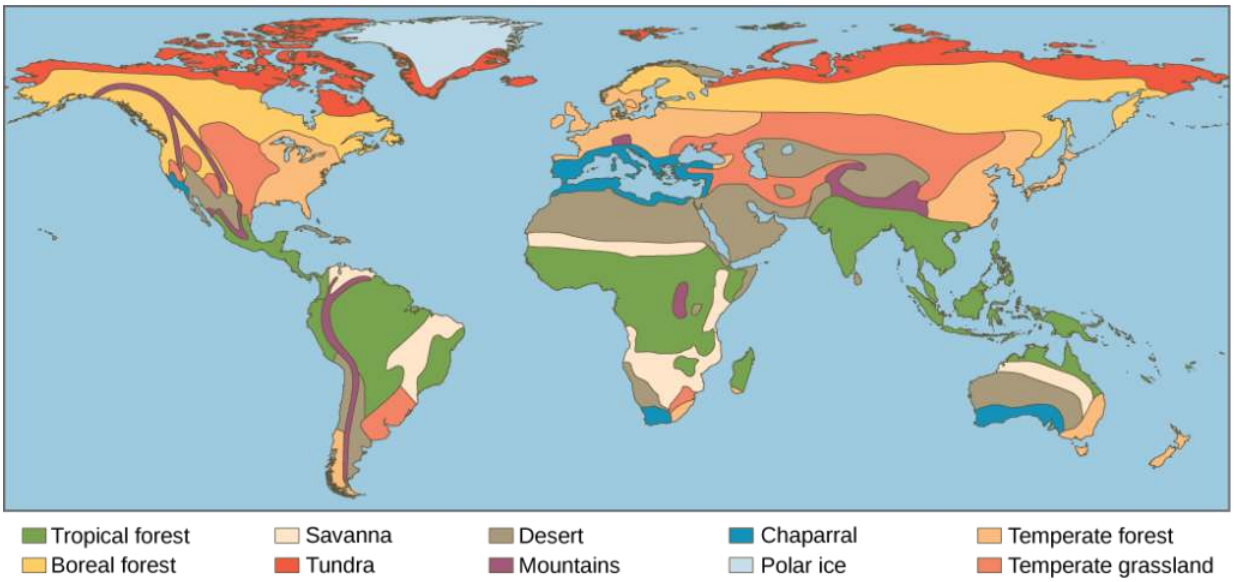


Figure 2. Each of the world's major biomes is distinguished by characteristic temperatures and amounts of precipitation. Polar ice and mountains are also shown.

Watch this *Assignment Discovery: Biomes* video for an overview of biomes. To explore further, select one of the biomes on the extended playlist: desert, savanna, temperate forest, temperate grassland, tropic, tundra.

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17.14: Major Terrestrial Biomes

Learning Objectives

- Recognize distinguishing characteristics of each of the eight major terrestrial biomes

Tropical Wet Forest

Tropical wet forests are also referred to as tropical rainforests. This biome is found in equatorial regions. The vegetation is characterized by plants with broad leaves that fall off throughout the year. Unlike the trees of deciduous forests, the trees in this biome do not have a seasonal loss of leaves associated with variations in temperature and sunlight; these forests are “evergreen” year-round.

The temperature and sunlight profiles of tropical wet forests are very stable in comparison to that of other terrestrial biomes, with the temperatures ranging from 20 °C to 34 °C (68 °F to 93 °F). When one compares the annual temperature variation of tropical wet forests with that of other forest biomes, the lack of seasonal temperature variation in the tropical wet forest becomes apparent. This lack of seasonality leads to year-round plant growth, rather than the seasonal (spring, summer, and fall) growth seen in other biomes. In contrast to other ecosystems, tropical ecosystems do not have long days and short days during the yearly cycle. Instead, a constant daily amount of sunlight (11–12 hrs per day) provides more solar radiation, thereby, a longer period of time for plant growth.

The annual rainfall in tropical wet forests ranges from 125 to 660 cm (50–200 in) with some monthly variation. While sunlight and temperature remain fairly consistent, annual rainfall is highly variable. Tropical wet forests have wet months in which there can be more than 30 cm (11–12 in) of precipitation, as well as dry months in which there are fewer than 10 cm (3.5 in) of rainfall. However, the driest month of a tropical wet forest still exceeds the *annual* rainfall of some other biomes, such as deserts.



Figure 1. Tropical wet forests, such as these forests of Madre de Dios, Peru, near the Amazon River, have high species diversity. (credit: Roosevelt Garcia)

Tropical wet forests have high net primary productivity because the annual temperatures and precipitation values in these areas are ideal for plant growth. Therefore, the extensive biomass present in the tropical wet forest leads to plant communities with very high species diversities (Figure 1). Tropical wet forests have more species of trees than any other biome; on average between 100 and 300 species of trees are present in a single hectare (2.5 acres) of South America. One way to visualize this is to compare the distinctive horizontal layers within the tropical wet forest biome. On the forest floor is a sparse layer of plants and decaying plant matter. Above that is an understory of short shrubby foliage. A layer of trees rises above this understory and is topped by a closed upper **canopy**—the uppermost overhead layer of branches and leaves. Some additional trees emerge through this closed upper canopy. These layers provide diverse and complex habitats for the variety of plants, fungi, animals, and other organisms within the tropical wet forests. For instance, epiphytes are plants that grow on other plants, which typically are not harmed. Epiphytes are found throughout tropical wet forest biomes. Many species of animals use the variety of plants and the complex structure of the tropical wet forests for food and shelter. Some organisms live several meters above ground and have adapted to this arboreal lifestyle.

Savannas



Figure 2. Savannas, like this one in Taita Hills Wildlife Sanctuary in Kenya, are dominated by grasses. (credit: Christopher T. Cooper)

Savannas are grasslands with scattered trees, and they are located in Africa, South America, and northern Australia (Figure 2). Savannas are hot, tropical areas with temperatures averaging from 24 °C to 29 °C (75 °F to 84 °F) and an annual rainfall of 10–40 cm (3.9–15.7 in). Savannas have an extensive dry season; for this reason, forest trees do not grow as well as they do in the tropical wet forest (or other forest biomes). As a result, within the grasses and forbs (herbaceous flowering plants) that dominate the savanna, there are relatively few trees (Figure 2). Since fire is an important source of disturbance in this biome, plants have evolved well-developed root systems that allow them to quickly re-sprout after a fire.

Subtropical Deserts



Figure 3. To reduce water loss, many desert plants have tiny leaves or no leaves at all. The leaves of ocotillo (Fouquieria splendens), shown here in the Sonora Desert near Gila Bend, Arizona, appear only after rainfall, and then are shed.

Subtropical deserts exist between 15 ° and 30 ° north and south latitude and are centered on the Tropics of Cancer and Capricorn (Figure 3). This biome is very dry; in some years, evaporation exceeds precipitation. Subtropical hot deserts can have daytime soil surface temperatures above 60 °C (140 °F) and nighttime temperatures approaching 0 °C (32 °F). In cold deserts, temperatures can be as high as 25 °C and can drop below −30 °C (−22 °F). Subtropical deserts are characterized by low annual precipitation of fewer than 30 cm (12 in) with little monthly variation and lack of predictability in rainfall. In some cases, the annual rainfall can be as low as 2 cm (0.8 in) in subtropical deserts located in central Australia (“the Outback”) and northern Africa.

The vegetation and low animal diversity of this biome is closely related to this low and unpredictable precipitation. Very dry deserts lack perennial vegetation that lives from one year to the next; instead, many plants are annuals that grow quickly and reproduce when rainfall does occur, then they die. Many other plants in these areas are characterized by having a number of adaptations that conserve water, such as deep roots, reduced foliage, and water-storing stems (Figure 3). Seed plants in the desert produce seeds that can be in dormancy for extended periods between rains. Adaptations in desert animals include nocturnal behavior and burrowing.

Chaparral



Figure 4. The chaparral is dominated by shrubs. (credit: Miguel Vieira)

The chaparral is also called the scrub forest and is found in California, along the Mediterranean Sea, and along the southern coast of Australia (Figure 4). The annual rainfall in this biome ranges from 65 cm to 75 cm (25.6–29.5 in), and the majority of the rain falls in the winter. Summers are very dry and many chaparral plants are dormant during the summertime. The chaparral vegetation, shown in Figure 4, is dominated by shrubs and is adapted to periodic fires, with some plants producing seeds that only germinate after a hot fire. The ashes left behind after a fire are rich in nutrients like nitrogen that fertilize the soil and promote plant regrowth.

Temperate Grasslands

Temperate grasslands are found throughout central North America, where they are also known as prairies; they are also in Eurasia, where they are known as steppes (Figure 5). Temperate grasslands have pronounced annual fluctuations in temperature with hot summers and cold winters. The annual temperature variation produces specific growing seasons for plants. Plant growth is possible when temperatures are warm enough to sustain plant growth and when ample water is available, which occurs in the spring, summer, and fall. During much of the winter, temperatures are low, and water, which is stored in the form of ice, is not available for plant growth.



Figure 5. The American bison (*Bison bison*), more commonly called the buffalo, is a grazing mammal that once populated American prairies in huge numbers. (credit: Jack Dykinga, USDA Agricultural Research Service)

Annual precipitation ranges from 25 cm to 75 cm (9.8–29.5 in). Because of relatively lower annual precipitation in temperate grasslands, there are few trees except for those found growing along rivers or streams. The dominant vegetation tends to consist of grasses and some prairies sustain populations of grazing animals Figure 5. The vegetation is very dense and the soils are fertile because the subsurface of the soil is packed with the roots and rhizomes (underground stems) of these grasses. The roots and rhizomes act to anchor plants into the ground and replenish the organic material (humus) in the soil when they die and decay.

Fires, mainly caused by lightning, are a natural disturbance in temperate grasslands. When fire is suppressed in temperate grasslands, the vegetation eventually converts to scrub and dense forests. Often, the restoration or management of temperate grasslands requires the use of controlled burns to suppress the growth of trees and maintain the grasses.

Temperate Forests



Figure 6. Deciduous trees are the dominant plant in the temperate forest. (credit: Oliver Herold)

Temperate forests are the most common biome in eastern North America, Western Europe, Eastern Asia, Chile, and New Zealand (Figure 6). This biome is found throughout mid-latitude regions. Temperatures range between −30 °C and 30 °C (−22 °F to 86 °F) and drop to below freezing on an annual basis. These temperatures mean that temperate forests have defined growing seasons during the spring, summer, and early fall. Precipitation is relatively constant throughout the year and ranges between 75 cm and 150 cm (29.5–59 in).

Because of the moderate annual rainfall and temperatures, deciduous trees are the dominant plant in this biome (Figure 6). Deciduous trees lose their leaves each fall and remain leafless in the winter. Thus, no photosynthesis occurs in the deciduous trees during the dormant winter period. Each spring, new leaves appear as the temperature increases. Because of the dormant period, the net primary productivity of temperate forests is less than that of tropical wet forests. In addition, temperate forests show less diversity of tree species than tropical wet forest biomes.

The trees of the temperate forests leaf out and shade much of the ground; however, this biome is more open than tropical wet forests because trees in the temperate forests do not grow as tall as the trees in tropical wet forests. The soils of the temperate forests are rich in inorganic and organic nutrients. This is due to the thick layer of leaf litter on forest floors. As this leaf litter decays, nutrients are returned to the soil. The leaf litter also protects soil from erosion, insulates the ground, and provides habitats for invertebrates (such as the pill bug or roly-poly, *Armadillidium vulgare*) and their predators, such as the red-backed salamander (*Plethodon cinereus*).

Boreal Forests

The boreal forest, also known as taiga or coniferous forest, is found south of the Arctic Circle and across most of Canada, Alaska, Russia, and northern Europe (Figure 7). This biome has cold, dry winters and short, cool, wet summers. The annual precipitation is from 40 cm to 100 cm (15.7–39 in) and usually takes the form of snow. Little evaporation occurs because of the cold temperatures.



Figure 7. The boreal forest (taiga) has low lying plants and conifer trees. (credit: L.B. Brubaker)

The long and cold winters in the boreal forest have led to the predominance of cold-tolerant cone-bearing plants. These are evergreen coniferous trees like pines, spruce, and fir, which retain their needle-shaped leaves year-round. Evergreen trees can photosynthesize earlier in the spring than deciduous trees because less energy from the sun is required to warm a needle-like leaf than a broad leaf. This benefits evergreen trees, which grow faster than deciduous trees in the boreal forest. In addition, soils in boreal forest regions tend to be acidic with little available nitrogen. Leaves are a nitrogen-rich structure and deciduous trees must

produce a new set of these nitrogen-rich structures each year. Therefore, coniferous trees that retain nitrogen-rich needles may have a competitive advantage over the broad-leafed deciduous trees.

The net primary productivity of boreal forests is lower than that of temperate forests and tropical wet forests. The aboveground biomass of boreal forests is high because these slow-growing tree species are long lived and accumulate standing biomass over time. Plant species diversity is less than that seen in temperate forests and tropical wet forests. Boreal forests lack the pronounced elements of the layered forest structure seen in tropical wet forests. The structure of a boreal forest is often only a tree layer and a ground layer (Figure 7). When conifer needles are dropped, they decompose more slowly than broad leaves; therefore, fewer nutrients are returned to the soil to fuel plant growth.

Arctic Tundra



Figure 8. Low-growing plants such as shrub willow dominate the tundra landscape, shown here in the Arctic National Wildlife Refuge. (credit: USFWS Arctic National Wildlife Refuge)

The Arctic tundra lies north of the subarctic boreal forest and is located throughout the Arctic regions of the northern hemisphere (Figure 8). The average winter temperature is −34 °C (−34 °F) and the average summer temperature is from 3 °C to 12 °C (37 °F–52 °F). Plants in the arctic tundra have a very short growing season of approximately 10–12 weeks. However, during this time, there are almost 24 hours of daylight and plant growth is rapid. The annual precipitation of the Arctic tundra is very low with little annual variation in precipitation. And, as in the boreal forests, there is little evaporation due to the cold temperatures.

Plants in the Arctic tundra are generally low to the ground (Figure 8). There is little species diversity, low net primary productivity, and low aboveground biomass. The soils of the Arctic tundra may remain in a perennially frozen state referred to as **permafrost**. The permafrost makes it impossible for roots to penetrate deep into the soil and slows the decay of organic matter, which inhibits the release of nutrients from organic matter. During the growing season, the ground of the Arctic tundra can be completely covered with plants or lichens.

? Practice Question

Which of the following statements about biomes is false?

a. Chaparral is dominated by shrubs.
b. Savannas and temperate grasslands are dominated by grasses.
c. Boreal forests are dominated by deciduous trees.
d. Lichens are common in the arctic tundra.

[reveal-answer q=”451629″]Show Answer[/reveal-answer]
[hidden-answer a=”451629″]Statement c is false. Boreal forests are not dominated by deciduous trees.[/hidden-answer]

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17.15: Characteristics of Aquatic Biomes

Learning Outcomes

- Describe the effects of abiotic factors on the composition of plant and animal communities in aquatic biomes

Aquatic ecosystems include both saltwater and freshwater biomes. The abiotic factors important for the structuring of aquatic ecosystems can be different than those seen in terrestrial systems. Sunlight is a driving force behind the structure of forests and also is an important factor in bodies of water, especially those that are very deep, because of the role of photosynthesis in sustaining certain organisms.

Like terrestrial biomes, aquatic biomes are influenced by a series of abiotic factors. The aquatic medium—water— has different physical and chemical properties than air, however. Even if the water in a pond or other body of water is perfectly clear (there are no suspended particles), water, on its own, absorbs light. As one descends into a deep body of water, there will eventually be a depth which the sunlight cannot reach. While there are some abiotic and biotic factors in a terrestrial ecosystem that might obscure light (like fog, dust, or insect swarms), usually these are not permanent features of the environment. The importance of light in aquatic biomes is central to the communities of organisms found in both freshwater and marine ecosystems. In freshwater systems, stratification due to differences in density is perhaps the most critical abiotic factor and is related to the energy aspects of light. The thermal properties of water (rates of heating and cooling) are significant to the function of marine systems and have major impacts on global climate and weather patterns. Marine systems are also influenced by large-scale physical water movements, such as currents; these are less important in most freshwater lakes.

The ocean is categorized by several areas or zones (Figure 1). All of the ocean's open water is referred to as the **pelagic realm** (or zone). The **benthic realm** (or zone) extends along the ocean bottom from the shoreline to the deepest parts of the ocean floor. Within the pelagic realm is the **photic zone**, which is the portion of the ocean that light can penetrate (approximately 200 m or 650 ft). At depths greater than 200 m, light cannot penetrate; thus, this is referred to as the **aphotic zone**. The majority of the ocean is aphotic and lacks sufficient light for photosynthesis. The deepest part of the ocean, the Challenger Deep (in the Mariana Trench, located in the western Pacific Ocean), is about 11,000 m (about 6.8 mi) deep. To give some perspective on the depth of this trench, the ocean is, on average, 4267 m or 14,000 ft deep. These realms and zones are relevant to freshwater lakes as well.

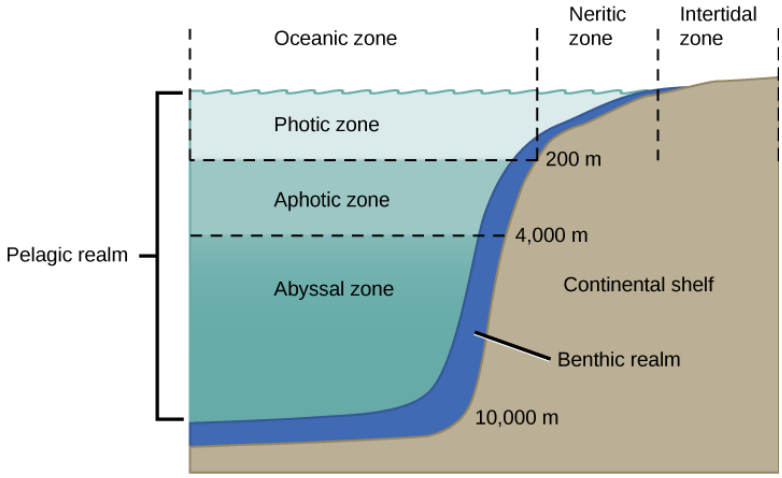


Figure 1. The ocean is divided into different zones based on water depth and distance from the shoreline.

Practice Question

In which of the following regions would you expect to find photosynthetic organisms?

a. the aphotic zone, the neritic zone, the oceanic zone, and the benthic realm
b. the photic zone, the intertidal zone, the neritic zone, and the oceanic zone
c. the photic zone, the abyssal zone, the neritic zone, and the oceanic zone
d. the pelagic realm, the aphotic zone, the neritic zone, and the oceanic zone

[reveal-answer q="953127"]Show Answer[/reveal-answer]
[hidden-answer a="953127"]Option c: Photosynthetic organisms would be found in the photic, abyssal, neritic, and oceanic zones.[/hidden-answer]

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17.16: Major Oceanic Biomes

Learning Objectives

- Compare and contrast the characteristics of the ocean zones

The ocean is the largest marine biome. It is a continuous body of salt water that is relatively uniform in chemical composition; it is a weak solution of mineral salts and decayed biological matter. Within the ocean, coral reefs are a second kind of marine biome. Estuaries, coastal areas where salt water and fresh water mix, form a third unique marine biome.

Ocean

The physical diversity of the ocean is a significant influence on plants, animals, and other organisms. The ocean is categorized into different zones based on how far light reaches into the water. Each zone has a distinct group of species adapted to the biotic and abiotic conditions particular to that zone.



Figure 1. Sea urchins, mussel shells, and starfish are often found in the intertidal zone, shown here in Kachemak Bay, Alaska. (credit: NOAA)

The **intertidal zone**, which is the zone between high and low tide, is the oceanic region that is closest to land (Figure 1). Generally, most people think of this portion of the ocean as a sandy beach. In some cases, the intertidal zone is indeed a sandy beach, but it can also be rocky or muddy. The intertidal zone is an extremely variable environment because of tides. Organisms are exposed to air and sunlight at low tide and are underwater most of the time, especially during high tide. Therefore, living things that thrive in the intertidal zone are adapted to being dry for long periods of time. The shore of the intertidal zone is also repeatedly struck by waves, and the organisms found there are adapted to withstand damage from the pounding action of the waves (Figure 1). The exoskeletons of shoreline crustaceans (such as the shore crab, *Carcinus maenas*) are tough and protect them from desiccation (drying out) and wave damage. Another consequence of the pounding waves is that few algae and plants establish themselves in the constantly moving rocks, sand, or mud.

The **neritic zone** extends from the intertidal zone to depths of about 200 m (or 650 ft) at the edge of the continental shelf. Since light can penetrate this depth, photosynthesis can occur in the neritic zone. The water here contains silt and is well-oxygenated, low in pressure, and stable in temperature. Phytoplankton and floating ***Sargassum*** (a type of free-floating marine seaweed) provide a habitat for some sea life found in the neritic zone. Zooplankton, protists, small fishes, and shrimp are found in the neritic zone and are the base of the food chain for most of the world's fisheries.

Beyond the neritic zone is the open ocean area known as the **oceanic zone**. Within the oceanic zone there is thermal stratification where warm and cold waters mix because of ocean currents. Abundant plankton serve as the base of the food chain for larger animals such as whales and dolphins. Nutrients are scarce and this is a relatively less productive part of the marine biome. When photosynthetic organisms and the protists and animals that feed on them die, their bodies fall to the bottom of the ocean where they remain; unlike freshwater lakes, the open ocean lacks a process for bringing the organic nutrients back up to the surface. The majority of organisms in the aphotic zone include sea cucumbers (phylum Echinodermata) and other organisms that survive on the nutrients contained in the dead bodies of organisms in the photic zone.

Beneath the pelagic zone is the benthic realm, the deepwater region beyond the continental shelf. The bottom of the benthic realm is comprised of sand, silt, and dead organisms. Temperature decreases, remaining above freezing, as water depth increases. This is

a nutrient-rich portion of the ocean because of the dead organisms that fall from the upper layers of the ocean. Because of this high level of nutrients, a diversity of fungi, sponges, sea anemones, marine worms, sea stars, fishes, and bacteria exist.

The deepest part of the ocean is the **abyssal zone**, which is at depths of 4000 m or greater. The abyssal zone is very cold and has very high pressure, high oxygen content, and low nutrient content. There are a variety of invertebrates and fishes found in this zone, but the abyssal zone does not have plants because of the lack of light. Hydrothermal vents are found primarily in the abyssal zone; chemosynthetic bacteria utilize the hydrogen sulfide and other minerals emitted from the vents. These chemosynthetic bacteria use the hydrogen sulfide as an energy source and serve as the base of the food chain found in the abyssal zone.

Coral Reefs



Figure 2. Coral reefs are formed by the calcium carbonate skeletons of coral organisms, which are marine invertebrates in the phylum Cnidaria. (credit: Terry Hughes)

Coral reefs are ocean ridges formed by marine invertebrates living in warm shallow waters within the photic zone of the ocean. They are found within 30˚ north and south of the equator. The Great Barrier Reef is a well-known reef system located several miles off the northeastern coast of Australia. Other coral reef systems are fringing islands, which are directly adjacent to land, or atolls, which are circular reef systems surrounding a former landmass that is now underwater. The coral organisms (members of phylum Cnidaria) are colonies of saltwater polyps that secrete a calcium carbonate skeleton. These calcium-rich skeletons slowly accumulate, forming the underwater reef.

Corals found in shallower waters (at a depth of approximately 60 m or about 200 ft) have a mutualistic relationship with photosynthetic unicellular algae. The relationship provides corals with the majority of the nutrition and the energy they require. The waters in which these corals live are nutritionally poor and, without this mutualism, it would not be possible for large corals to grow. Some corals living in deeper and colder water do not have a mutualistic relationship with algae; these corals attain energy and nutrients using stinging cells on their tentacles to capture prey.

It is estimated that more than 4,000 fish species inhabit coral reefs. These fishes can feed on coral, the **cryptofauna** (invertebrates found within the calcium carbonate substrate of the coral reefs), or the seaweed and algae that are associated with the coral. In addition, some fish species inhabit the boundaries of a coral reef; these species include **predators**, herbivores, or **planktivores**. Predators are animal species that hunt and are carnivores or “flesh eaters.” Herbivores eat plant material, and planktivores eat plankton.

Watch this National Oceanic and Atmospheric Administration (NOAA) video to see marine ecologist Dr. Peter Etnoyer discusses his research on coral organisms.

? Try It

It takes a long time to build a coral reef. The animals that create coral reefs have evolved over millions of years, continuing to slowly deposit the calcium carbonate that forms their characteristic ocean homes. Bathed in warm tropical waters, the coral animals and their symbiotic algal partners evolved to survive at the upper limit of ocean water temperature.

Together, climate change and human activity pose dual threats to the long-term survival of the world's coral reefs. As global warming due to fossil fuel emissions raises ocean temperatures, coral reefs are suffering. The excessive warmth causes the reefs to expel their symbiotic, food-producing algae, resulting in a phenomenon known as bleaching. When bleaching occurs, the reefs lose much of their characteristic color as the algae and the coral animals die if loss of the symbiotic zooxanthellae is prolonged.

Rising levels of atmospheric carbon dioxide further threaten the corals in other ways; as CO_2 dissolves in ocean waters, it lowers the pH and increases ocean acidity. As acidity increases, it interferes with the calcification that normally occurs as coral animals build their calcium carbonate homes.

When a coral reef begins to die, species diversity plummets as animals lose food and shelter. Coral reefs are also economically important tourist destinations, so the decline of coral reefs poses a serious threat to coastal economies.

Human population growth has damaged corals in other ways, too. As human coastal populations increase, the runoff of sediment and agricultural chemicals has increased, too, causing some of the once-clear tropical waters to become cloudy. At the same time, overfishing of popular fish species has allowed the predator species that eat corals to go unchecked.

Although a rise in global temperatures of 1–2˚C (a conservative scientific projection) in the coming decades may not seem large, it is very significant to this biome. When change occurs rapidly, species can become extinct before evolution leads to new adaptations. Many scientists believe that global warming, with its rapid (in terms of evolutionary time) and inexorable increases in temperature, is tipping the balance beyond the point at which many of the world's coral reefs can recover.

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17.17: Major Freshwater Biomes

Learning Objectives

- Summarize the characteristics of standing water and flowing water freshwater biomes

Freshwater biomes include lakes and ponds (standing water) as well as rivers and streams (flowing water). They also include wetlands. Humans rely on freshwater biomes to provide aquatic resources for drinking water, crop irrigation, sanitation, and industry. These various roles and human benefits are referred to as **ecosystem services**. Lakes and ponds are found in terrestrial landscapes and are, therefore, connected with abiotic and biotic factors influencing these terrestrial biomes.

Lakes and Ponds

Lakes and ponds can range in area from a few square meters to thousands of square kilometers. Temperature is an important abiotic factor affecting living things found in lakes and ponds. In the summer, thermal stratification of lakes and ponds occurs when the upper layer of water is warmed by the sun and does not mix with deeper, cooler water. Light can penetrate within the photic zone of the lake or pond. Phytoplankton (algae and cyanobacteria) are found here and carry out photosynthesis, providing the base of the food web of lakes and ponds. Zooplankton, such as rotifers and small crustaceans, consume these phytoplankton. At the bottom of lakes and ponds, bacteria in the aphotic zone break down dead organisms that sink to the bottom.



Figure 1. The uncontrolled growth of algae in this lake has resulted in an algal bloom. (credit: Jeremy Nettleton)

Nitrogen and phosphorus are important limiting nutrients in lakes and ponds. Because of this, they are determining factors in the amount of phytoplankton growth in lakes and ponds. When there is a large input of nitrogen and phosphorus (from sewage and runoff from fertilized lawns and farms, for example), the growth of algae skyrockets, resulting in a large accumulation of algae called an **algal bloom**. Algal blooms (Figure 1) can become so extensive that they reduce light penetration in water. As a result, the lake or pond becomes aphotic and photosynthetic plants cannot survive. When the algae die and decompose, severe oxygen depletion of the water occurs. Fishes and other organisms that require oxygen are then more likely to die, and resulting dead zones are found across the globe. Lake Erie and the Gulf of Mexico represent freshwater and marine habitats where phosphorus control and storm water runoff pose significant environmental challenges.

Rivers and Streams

Rivers and streams are continuously moving bodies of water that carry large amounts of water from the source, or headwater, to a lake or ocean. The largest rivers include the Nile River in Africa, the Amazon River in South America, and the Mississippi River in North America.

Abiotic features of rivers and streams vary along the length of the river or stream. Streams begin at a point of origin referred to as **source water**. The source water is usually cold, low in nutrients, and clear. The **channel** (the width of the river or stream) is narrower than at any other place along the length of the river or stream. Because of this, the current is often faster here than at any other point of the river or stream.

The fast-moving water results in minimal silt accumulation at the bottom of the river or stream; therefore, the water is clear. Photosynthesis here is mostly attributed to algae that are growing on rocks; the swift current inhibits the growth of phytoplankton.

An additional input of energy can come from leaves or other organic material that falls into the river or stream from trees and other plants that border the water. When the leaves decompose, the organic material and nutrients in the leaves are returned to the water. Plants and animals have adapted to this fast-moving water. For instance, leeches (phylum Annelida) have elongated bodies and suckers on both ends. These suckers attach to the substrate, keeping the leech anchored in place. Freshwater trout species (phylum Chordata) are an important predator in these fast-moving rivers and streams.

As the river or stream flows away from the source, the width of the channel gradually widens and the current slows. This slow-moving water, caused by the gradient decrease and the volume increase as tributaries unite, has more sedimentation. Phytoplankton can also be suspended in slow-moving water. Therefore, the water will not be as clear as it is near the source. The water is also warmer. Worms (phylum Annelida) and insects (phylum Arthropoda) can be found burrowing into the mud. The higher order predator vertebrates (phylum Chordata) include waterfowl, frogs, and fishes. These predators must find food in these slow moving, sometimes murky, waters and, unlike the trout in the waters at the source, these vertebrates may not be able to use vision as their primary sense to find food. Instead, they are more likely to use taste or chemical cues to find prey.

Wetlands

Wetlands are environments in which the soil is either permanently or periodically saturated with water. Wetlands are different from lakes because wetlands are shallow bodies of water whereas lakes vary in depth. **Emergent vegetation** consists of wetland plants that are rooted in the soil but have portions of leaves, stems, and flowers extending above the water's surface. There are several types of wetlands including marshes, swamps, bogs, mudflats, and salt marshes (Figure 2). The three shared characteristics among these types—what makes them wetlands—are their hydrology, hydrophytic vegetation, and hydric soils.



Figure 2. Located in southern Florida, Everglades National Park is vast array of wetland environments, including sawgrass marshes, cypress swamps, and estuarine mangrove forests. Here, a great egret walks among cypress trees. (credit: NPS)

Freshwater marshes and swamps are characterized by slow and steady water flow. Bogs develop in depressions where water flow is low or nonexistent. Bogs usually occur in areas where there is a clay bottom with poor percolation. Percolation is the movement of water through the pores in the soil or rocks. The water found in a bog is stagnant and oxygen depleted because the oxygen that is used during the decomposition of organic matter is not replaced. As the oxygen in the water is depleted, decomposition slows. This leads to organic acids and other acids building up and lowering the pH of the water. At a lower pH, nitrogen becomes unavailable to plants. This creates a challenge for plants because nitrogen is an important limiting resource. Some types of bog plants (such as sundews, pitcher plants, and Venus flytraps) capture insects and extract the nitrogen from their bodies. Bogs have low net primary productivity because the water found in bogs has low levels of nitrogen and oxygen.

Estuaries: Where the Ocean Meets Fresh Water

Estuaries are biomes that occur where a source of fresh water, such as a river, meets the ocean. Therefore, both fresh water and salt water are found in the same vicinity; mixing results in a diluted (brackish) saltwater. Estuaries form protected areas where many of the young offspring of crustaceans, mollusks, and fish begin their lives. Salinity is a very important factor that influences the organisms and the adaptations of the organisms found in estuaries. The salinity of estuaries varies and is based on the rate of flow of its freshwater sources. Once or twice a day, high tides bring salt water into the estuary. Low tides occurring at the same frequency reverse the current of salt water.

The short-term and rapid variation in salinity due to the mixing of fresh water and salt water is a difficult physiological challenge for the plants and animals that inhabit estuaries. Many estuarine plant species are halophytes: plants that can tolerate salty conditions. Halophytic plants are adapted to deal with the salinity resulting from saltwater on their roots or from sea spray. In some

halophytes, filters in the roots remove the salt from the water that the plant absorbs. Other plants are able to pump oxygen into their roots. Animals, such as mussels and clams (phylum Mollusca), have developed behavioral adaptations that expend a lot of energy to function in this rapidly changing environment. When these animals are exposed to low salinity, they stop feeding, close their shells, and switch from aerobic respiration (in which they use gills) to anaerobic respiration (a process that does not require oxygen). When high tide returns to the estuary, the salinity and oxygen content of the water increases, and these animals open their shells, begin feeding, and return to aerobic respiration.

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17.18: Introduction to Population Ecology

What you'll learn to do: Discuss the scope and study of population ecology

Imagine sailing down a river in a small motorboat on a weekend afternoon; the water is smooth and you are enjoying the warm sunshine and cool breeze when suddenly you are hit in the head by a 20-pound silver carp. This is a risk now on many rivers and canal systems in Illinois and Missouri because of the presence of Asian carp.



Figure 1. Asian carp jump out of the water in response to electrofishing. The Asian carp in the inset photograph were harvested from the Little Calumet River in Illinois in May, 2010, using rotenone, a toxin often used as an insecticide, in an effort to learn more about the population of the species. (credit main image: modification of work by USGS; credit inset: modification of work by Lt. David French, USCG)

This fish—actually a group of species including the silver, black, grass, and big head carp—has been farmed and eaten in China for over 1000 years. It is one of the most important aquaculture food resources worldwide. In the United States, however, Asian carp is considered a dangerous invasive species that disrupts community structure and composition to the point of threatening native species.

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17.19: Population Demography

Learning Objectives

- Describe how ecologists measure population size and density
- Identify methods used to study population changes over time

Populations are dynamic entities. Populations consist all of the species living within a specific area, and populations fluctuate based on a number of factors: seasonal and yearly changes in the environment, natural disasters such as forest fires and volcanic eruptions, and competition for resources between and within species. The statistical study of population dynamics, demography, uses a series of mathematical tools to investigate how populations respond to changes in their biotic and abiotic environments. Many of these tools were originally designed to study human populations. For example, life tables, which detail the life expectancy of individuals within a population, were initially developed by life insurance companies to set insurance rates. In fact, while the term “demographics” is commonly used when discussing humans, all living populations can be studied using this approach.

Population Size and Density

The study of any population usually begins by determining how many individuals of a particular species exist, and how closely associated they are with each other. Within a particular habitat, a population can be characterized by its population size (*N*), the total number of individuals, and its population density, the number of individuals within a specific area or volume. Population size and density are the two main characteristics used to describe and understand populations. For example, populations with more individuals may be more stable than smaller populations based on their genetic variability, and thus their potential to adapt to the environment. Alternatively, a member of a population with low population density (more spread out in the habitat), might have more difficulty finding a mate to reproduce compared to a population of higher density. As is shown in the Figure 1 below, smaller organisms tend to be more densely distributed than larger organisms.

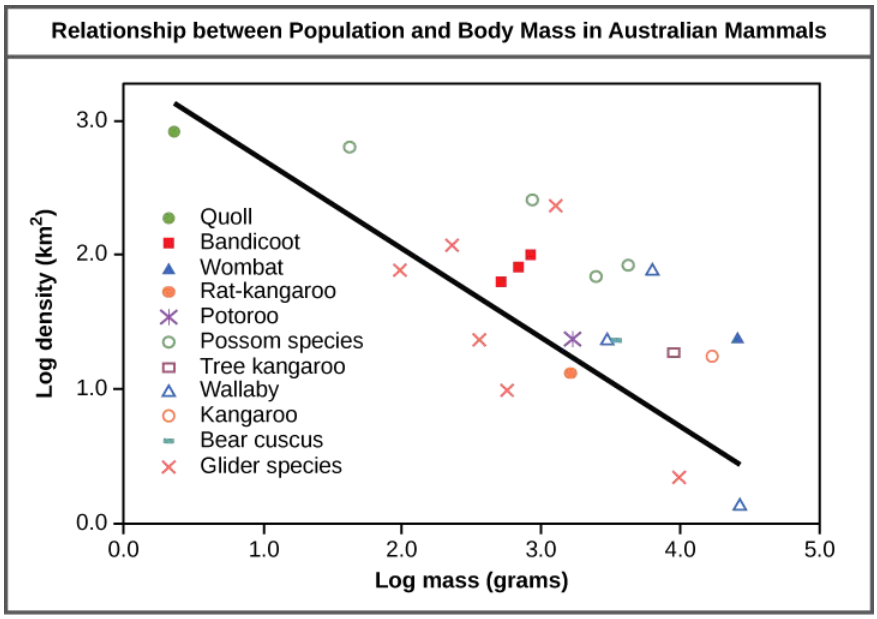


Figure 1. Australian mammals show a typical inverse relationship between population density and body size.

Practice Question

As this graph shows, population density typically decreases with increasing body size. Why do you think this is the case?

[practice-area rows=”2″][/practice-area]
[reveal-answer q=”808454″]Show Answer[/reveal-answer]

[hidden-answer a=”808454″]Smaller animals require less food and other resources, so the environment can support more of them.[/hidden-answer]

Population Research Methods

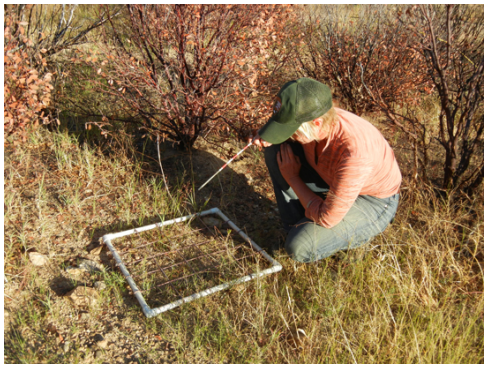
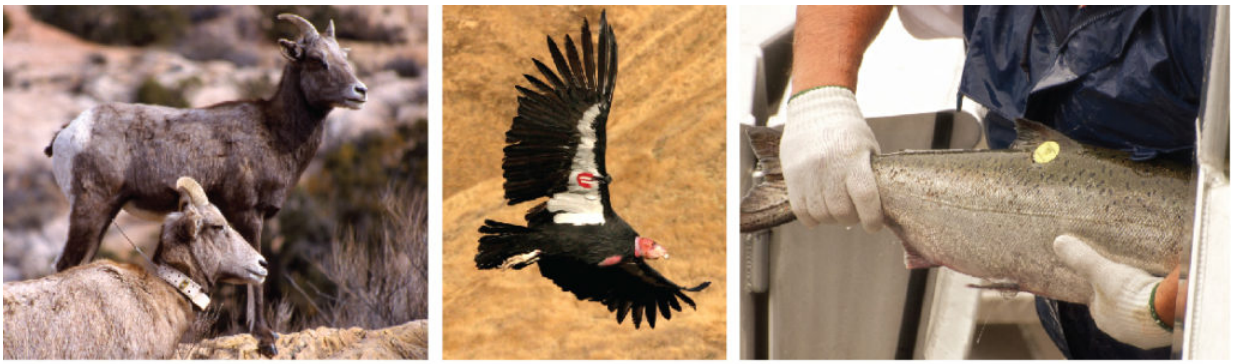


Figure 2. A scientist uses a quadrat to measure population size and density. (credit: NPS Sonoran Desert Network)

The most accurate way to determine population size is to simply count all of the individuals within the habitat. However, this method is often not logistically or economically feasible, especially when studying large habitats. Thus, scientists usually study populations by sampling a representative portion of each habitat and using this data to make inferences about the habitat as a whole. A variety of methods can be used to sample populations to determine their size and density. For immobile organisms such as plants, or for very small and slow-moving organisms, a quadrat may be used. A quadrat is a way of marking off square areas within a habitat, either by staking out an area with sticks and string, or by the use of a wood, plastic, or metal square placed on the ground. After setting the quadrats, researchers then count the number of individuals that lie within their boundaries. Multiple quadrat samples are performed throughout the habitat at several random locations. All of this data can then be used to estimate the population size and population density within the entire habitat. The number and size of quadrat samples depends on the type of organisms under study and other factors, including the density of the organism. For example, if sampling daffodils, a 1 m^2 quadrat might be used whereas with giant redwoods, which are larger and live much further apart from each other, a larger quadrat of 100 m^2 might be employed. This ensures that enough individuals of the species are counted to get an accurate sample that correlates with the habitat, including areas not sampled.

For mobile organisms, such as mammals, birds, or fish, a technique called mark and recapture is often used. This method involves marking a sample of captured animals in some way (such as tags, bands, paint, or other body markings), and then releasing them back into the environment to allow them to mix with the rest of the population; later, a new sample is collected, including some individuals that are marked (recaptures) and some individuals that are unmarked.



(a) (b) (c)

Figure 3. Mark and recapture is used to measure the population size of mobile animals such as (a) bighorn sheep, (b) the California condor, and (c) salmon. (credit a: modification of work by Neal Herbert, NPS; credit b: modification of work by Pacific Southwest Region USFWS; credit c: modification of work by Ingrid Taylar)

Using the ratio of marked and unmarked individuals, scientists determine how many individuals are in the sample. From this, calculations are used to estimate the total population size. This method assumes that the larger the population, the lower the percentage of tagged organisms that will be recaptured since they will have mixed with more untagged individuals. There are some

limitations to the mark and recapture method. Some animals from the first catch may learn to avoid capture in the second round, thus inflating population estimates. Alternatively, animals may preferentially be retrapped (especially if a food reward is offered), resulting in an underestimate of population size. Also, some species may be harmed by the marking technique, reducing their survival. A variety of other techniques have been developed, including the electronic tracking of animals tagged with radio transmitters and the use of data from commercial fishing and trapping operations to estimate the size and health of populations and communities.

Species Distribution

In addition to measuring simple density, further information about a population can be obtained by looking at the distribution of the individuals. Species dispersion patterns (or distribution patterns) show the spatial relationship between members of a population within a habitat at a particular point in time. In other words, they show whether members of the species live close together or far apart, and what patterns are evident when they are spaced apart.

Individuals in a population can be more or less equally spaced apart, dispersed randomly with no predictable pattern, or clustered in groups. These are known as uniform, random, and clumped dispersion patterns, respectively. Uniform dispersion is observed in plants that secrete substances inhibiting the growth of nearby individuals (such as the release of toxic chemicals by the sage plant*Salvia leucophylla*, a phenomenon called allelopathy) and in animals like the penguin that maintain a defined territory. An example of random dispersion occurs with dandelion and other plants that have wind-dispersed seeds that germinate wherever they happen to fall in a favorable environment. A clumped dispersion may be seen in plants that drop their seeds straight to the ground, such as oak trees, or animals that live in groups (schools of fish or herds of elephants). Clumped dispersions may also be a function of habitat heterogeneity. Thus, the dispersion of the individuals within a population provides more information about how they interact with each other than does a simple density measurement. Just as lower density species might have more difficulty finding a mate, solitary species with a random distribution might have a similar difficulty when compared to social species clumped together in groups.

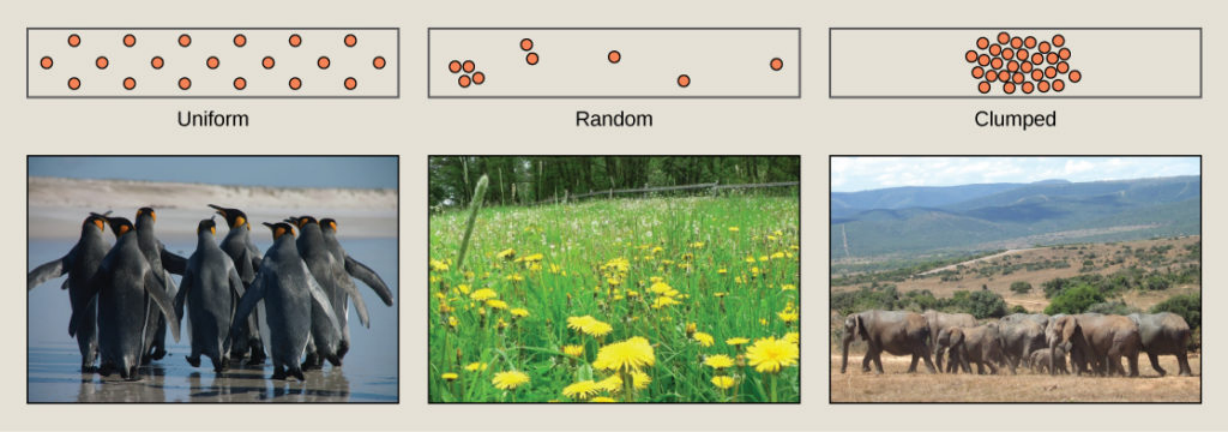


Figure 4. Species may have uniform, random, or clumped distribution. Territorial birds such as penguins tend to have uniform distribution. Plants such as dandelions with wind-dispersed seeds tend to be randomly distributed. Animals such as elephants that travel in groups exhibit clumped distribution. (credit a: modification of work by Ben Tubby; credit b: modification of work by Rosendahl; credit c: modification of work by Rebecca Wood)

Demography

While population size and density describe a population at one particular point in time, scientists must use demography to study the dynamics of a population. Demography is the statistical study of population changes over time: birth rates, death rates, and life expectancies. Each of these measures, especially birth rates, may be affected by the population characteristics described above. For example, a large population size results in a higher birth rate because more potentially reproductive individuals are present. In contrast, a large population size can also result in a higher death rate because of competition, disease, and the accumulation of waste. Similarly, a higher population density or a clumped dispersion pattern results in more potential reproductive encounters between individuals, which can increase birth rate. Lastly, a female-biased sex ratio (the ratio of males to females) or age structure (the proportion of population members at specific age ranges) composed of many individuals of reproductive age can increase birth rates.

In addition, the demographic characteristics of a population can influence how the population grows or declines over time. If birth and death rates are equal, the population remains stable. However, the population size will increase if birth rates exceed death rates; the population will decrease if birth rates are less than death rates. Life expectancy is another important factor; the length of time individuals remain in the population impacts local resources, reproduction, and the overall health of the population. These demographic characteristics are often displayed in the form of a life table.

Life Tables

Life tables provide important information about the life history of an organism. Life tables divide the population into age groups and often sexes, and show how long a member of that group is likely to live. They are modeled after actuarial tables used by the insurance industry for estimating human life expectancy. Life tables may include the probability of individuals dying before their next birthday (i.e., their **mortality rate**), the percentage of surviving individuals dying at a particular age interval, and their life expectancy at each interval. An example of a life table is shown in the Table below from a study of Dall mountain sheep, a species native to northwestern North America. Notice that the population is divided into age intervals (column A). The mortality rate (per 1000), shown in column D, is based on the number of individuals dying during the age interval (column B) divided by the number of individuals surviving at the beginning of the interval (Column C), multiplied by 1000.

For example, between ages three and four, 12 individuals die out of the 776 that were remaining from the original 1000 sheep. This number is then multiplied by 1000 to get the mortality rate per thousand. As can be seen from the mortality rate data (column D), a high death rate occurred when the sheep were between 6 and 12 months old, and then increased even more from 8 to 12 years old, after which there were few survivors. The data indicate that if a sheep in this population were to survive to age one, it could be expected to live another 7.7 years on average, as shown by the life expectancy numbers in column E.

Table 1. Life Table of Dall Mountain Sheep[1]

Age interval (years)	Number dying in age interval out of 1000 born	Number surviving at beginning of age interval out of 1000 born	Mortality rate per 1000 alive at beginning of age interval	Life expectancy or mean lifetime remaining to those attaining age interval
0–0.5	54	1000	54.0	7.06
0.5–1	145	946	153.3	—
1–2	12	801	15.0	7.7
2–3	13	789	16.5	6.8
3–4	12	776	15.5	5.9
4–5	30	764	39.3	5.0
5–6	46	734	62.7	4.2
6–7	48	688	69.8	3.4
7–8	69	640	107.8	2.6
8–9	132	571	231.2	1.9
9–10	187	439	426.0	1.3
10–11	156	252	619.0	0.9
11–12	90	96	937.5	0.6
12–13	3	6	500.0	1.2
13–14	3	3	1000	0.7

Survivorship Curves

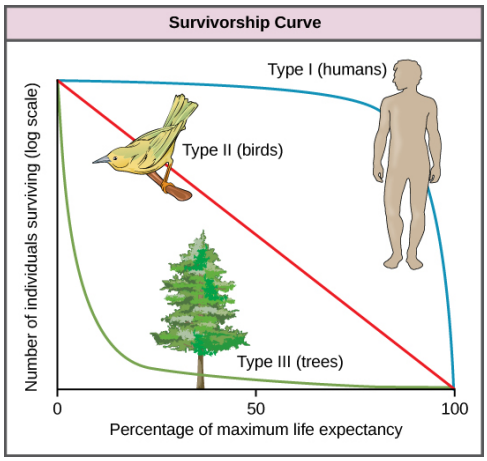


Figure 5. Survivorship curves show the distribution of individuals in a population according to age. Humans and most mammals have a Type I survivorship curve because death primarily occurs in the older years. Birds have a Type II survivorship curve, as death at any age is equally probable. Trees have a Type III survivorship curve because very few survive the younger years, but after a certain age, individuals are much more likely to survive.

Another tool used by population ecologists is a **survivorship curve**, which is a graph of the number of individuals surviving at each age interval plotted versus time (usually with data compiled from a life table). These curves allow us to compare the life histories of different populations. Humans and most primates exhibit a Type I survivorship curve because a high percentage of offspring survive their early and middle years—death occurs predominantly in older individuals. These types of species usually have small numbers of offspring at one time, and they give a high amount of parental care to them to ensure their survival. Birds are an example of an intermediate or Type II survivorship curve because birds die more or less equally at each age interval. These organisms also may have relatively few offspring and provide significant parental care. Trees, marine invertebrates, and most fishes exhibit a Type III survivorship curve because very few of these organisms survive their younger years; however, those that make it to an old age are more likely to survive for a relatively long period of time. Organisms in this category usually have a very large number of offspring, but once they are born, little parental care is provided. Thus these offspring are “on their own” and vulnerable to predation, but their sheer numbers assure the survival of enough individuals to perpetuate the species.

1. Data Adapted from Edward S. Deevey, Jr., “Life Tables for Natural Populations of Animals,” *The Quarterly Review of Biology* 22, no. 4 (December 1947): 283–314. ↵

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17.20: Life Histories and Natural Selection

Learning Objectives

- Describe how life history patterns are influenced by natural selection

A species' **life history** describes the series of events over its lifetime, such as how resources are allocated for growth, maintenance, and reproduction. Life history traits affect the life table of an organism. A species' life history is genetically determined and shaped by the environment and natural selection.

Life History Patterns and Energy Budgets

Energy is required by all living organisms for their growth, maintenance, and reproduction; at the same time, energy is often a major limiting factor in determining an organism's survival. Plants, for example, acquire energy from the sun via photosynthesis, but must expend this energy to grow, maintain health, and produce energy-rich seeds to produce the next generation. Animals have the additional burden of using some of their energy reserves to acquire food. Furthermore, some animals must expend energy caring for their offspring. Thus, all species have an **energy budget**: they must balance energy intake with their use of energy for metabolism, reproduction, parental care, and energy storage (such as bears building up body fat for winter hibernation).

Parental Care and Fecundity

Fecundity is the potential reproductive capacity of an individual within a population. In other words, fecundity describes how many offspring could ideally be produced if an individual has as many offspring as possible, repeating the reproductive cycle as soon as possible after the birth of the offspring. In animals, fecundity is inversely related to the amount of parental care given to an individual offspring. Species, such as many marine invertebrates, that produce many offspring usually provide little if any care for the offspring (they would not have the energy or the ability to do so anyway). Most of their energy budget is used to produce many tiny offspring. Animals with this strategy are often self-sufficient at a very early age. This is because of the energy tradeoff these organisms have made to maximize their evolutionary fitness. Because their energy is used for producing offspring instead of parental care, it makes sense that these offspring have some ability to be able to move within their environment and find food and perhaps shelter. Even with these abilities, their small size makes them extremely vulnerable to predation, so the production of many offspring allows enough of them to survive to maintain the species.

Animal species that have few offspring during a reproductive event usually give extensive parental care, devoting much of their energy budget to these activities, sometimes at the expense of their own health. This is the case with many mammals, such as humans, kangaroos, and pandas. The offspring of these species are relatively helpless at birth and need to develop before they achieve self-sufficiency.

Plants with low fecundity produce few energy-rich seeds (such as coconuts and chestnuts) with each having a good chance to germinate into a new organism; plants with high fecundity usually have many small, energy-poor seeds (like orchids) that have a relatively poor chance of surviving. Although it may seem that coconuts and chestnuts have a better chance of surviving, the energy tradeoff of the orchid is also very effective. It is a matter of where the energy is used, for large numbers of seeds or for fewer seeds with more energy.

Early versus Late Reproduction

The timing of reproduction in a life history also affects species survival. Organisms that reproduce at an early age have a greater chance of producing offspring, but this is usually at the expense of their growth and the maintenance of their health. Conversely, organisms that start reproducing later in life often have greater fecundity or are better able to provide parental care, but they risk that they will not survive to reproductive age. Examples of this can be seen in fishes. Small fish like guppies use their energy to reproduce rapidly, but never attain the size that would give them defense against some predators. Larger fish, like the bluegill or shark, use their energy to attain a large size, but do so with the risk that they will die before they can reproduce or at least reproduce to their maximum. These different energy strategies and tradeoffs are key to understanding the evolution of each species as it maximizes its fitness and fills its niche. In terms of energy budgeting, some species "blow it all" and use up most of their energy

reserves to reproduce early before they die. Other species delay having reproduction to become stronger, more experienced individuals and to make sure that they are strong enough to provide parental care if necessary.

Single versus Multiple Reproductive Events

Some life history traits, such as fecundity, timing of reproduction, and parental care, can be grouped together into general strategies that are used by multiple species. **Semelparity** occurs when a species reproduces only once during its lifetime and then dies. Such species use most of their resource budget during a single reproductive event, sacrificing their health to the point that they do not survive. Examples of semelparity are bamboo, which flowers once and then dies, and the Chinook salmon (Figure 1a), which uses most of its energy reserves to migrate from the ocean to its freshwater nesting area, where it reproduces and then dies. Scientists have posited alternate explanations for the evolutionary advantage of the Chinook's post-reproduction death: a programmed suicide caused by a massive release of corticosteroid hormones, presumably so the parents can become food for the offspring, or simple exhaustion caused by the energy demands of reproduction; these are still being debated.

Iteroparity describes species that reproduce repeatedly during their lives. Some animals are able to mate only once per year, but survive multiple mating seasons. The pronghorn antelope is an example of an animal that goes into a seasonal estrus cycle ("heat"): a hormonally induced physiological condition preparing the body for successful mating (Figure 1b). Females of these species mate only during the estrus phase of the cycle. A different pattern is observed in primates, including humans and chimpanzees, which may attempt reproduction at any time during their reproductive years, even though their menstrual cycles make pregnancy likely only a few days per month during ovulation (Figure 1c).



Figure 1. The (a) Chinook salmon mates once and dies. The (b) pronghorn antelope mates during specific times of the year during its reproductive life. Primates, such as humans and (c) chimpanzees, may mate on any day, independent of ovulation. (credit a: modification of work by Roger Tabor, USFWS; credit b: modification of work by Mark Gocke, USDA; credit c: modification of work by "Shiny Things"/Flickr)

? Try It

Research into how animals allocate their energy resources for growth, maintenance, and reproduction has used a variety of experimental animal models. Some of this work has been done using the common fruit fly, *Drosophila melanogaster*. Studies have shown that not only does reproduction have a cost as far as how long male fruit flies live, but also fruit flies that have already mated several times have limited sperm remaining for reproduction. Fruit flies maximize their last chances at reproduction by selecting optimal mates.

In a 1981 study, male fruit flies were placed in enclosures with either virgin or inseminated females. The males that mated with virgin females had shorter life spans than those in contact with the same number of inseminated females with which they were unable to mate. This effect occurred regardless of how large (indicative of their age) the males were. Thus, males that did not mate lived longer, allowing them more opportunities to find mates in the future.

More recent studies, performed in 2006, show how males select the female with which they will mate and how this is affected by previous matings (Table 1).[1] Males were allowed to select between smaller and larger females. Findings showed that larger females had greater fecundity, producing twice as many offspring per mating as the smaller females did. Males that had previously mated, and thus had lower supplies of sperm, were termed "resource-depleted," while males that had not mated were termed "non-resource-depleted." The study showed that although non-resource-depleted males preferentially mated with larger females, this selection of partners was more pronounced in the resource-depleted males. Thus, males with depleted

sperm supplies, which were limited in the number of times that they could mate before they replenished their sperm supply, selected larger, more fecund females, thus maximizing their chances for offspring. This study was one of the first to show that the physiological state of the male affected its mating behavior in a way that clearly maximizes its use of limited reproductive resources.

Table 1

	Ratio large/small females mated
Non sperm-depleted	8 ± 5
Sperm-depleted	15 ± 5

Male fruit flies that had previously mated (sperm-depleted) picked larger, more fecund females more often than those that had not mated (non-sperm-depleted). This change in behavior causes an increase in the efficiency of a limited reproductive resource: sperm.

These studies demonstrate two ways in which the energy budget is a factor in reproduction. First, energy expended on mating may reduce an animal's lifespan, but by this time they have already reproduced, so in the context of natural selection this early death is not of much evolutionary importance. Second, when resources such as sperm (and the energy needed to replenish it) are low, an organism's behavior can change to give them the best chance of passing their genes on to the next generation. These changes in behavior, so important to evolution, are studied in a discipline known as behavioral biology, or ethology, at the interface between population biology and psychology.

Learning Objectives

All species have evolved a pattern of living, called a life history strategy, in which they partition energy for growth, maintenance, and reproduction. These patterns evolve through natural selection; they allow species to adapt to their environment to obtain the resources they need to successfully reproduce. There is an inverse relationship between fecundity and parental care. A species may reproduce early in life to ensure surviving to a reproductive age or reproduce later in life to become larger and healthier and better able to give parental care. A species may reproduce once (semelparity) or many times (iteroparity) in its life.

1. Adapted from Phillip G. Byrne and William R. Rice, "Evidence for adaptive male mate choice in the fruit fly *Drosophila melanogaster*," Proc Biol Sci. 273, no. 1589 (2006): 917–922, doi: 10.1098/rspb.2005.3372. ↵

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17.21: Human Population Growth

Learning Objectives

- Discuss how the human population has changed over time

Concepts of animal population dynamics can be applied to human population growth. Humans are not unique in their ability to alter their environment. For example, beaver dams alter the stream environment where they are built. Humans, however, have the ability to alter their environment to increase its carrying capacity sometimes to the detriment of other species (e.g., via artificial selection for crops that have a higher yield). Earth's human population is growing rapidly, to the extent that some worry about the ability of the earth's environment to sustain this population, as long-term exponential growth carries the potential risks of famine, disease, and large-scale death.

Although humans have increased the carrying capacity of their environment, the technologies used to achieve this transformation have caused unprecedented changes to Earth's environment, altering ecosystems to the point where some may be in danger of collapse. The depletion of the ozone layer, erosion due to acid rain, and damage from global climate change are caused by human activities. The ultimate effect of these changes on our carrying capacity is unknown. As some point out, it is likely that the negative effects of increasing carrying capacity will outweigh the positive ones—the carrying capacity of the world for human beings might actually decrease.

The world's human population is currently experiencing exponential growth even though human reproduction is far below its biotic potential (Figure 1). To reach its biotic potential, all females would have to become pregnant every nine months or so during their reproductive years. Also, resources would have to be such that the environment would support such growth. Neither of these two conditions exists. In spite of this fact, human population is still growing exponentially.

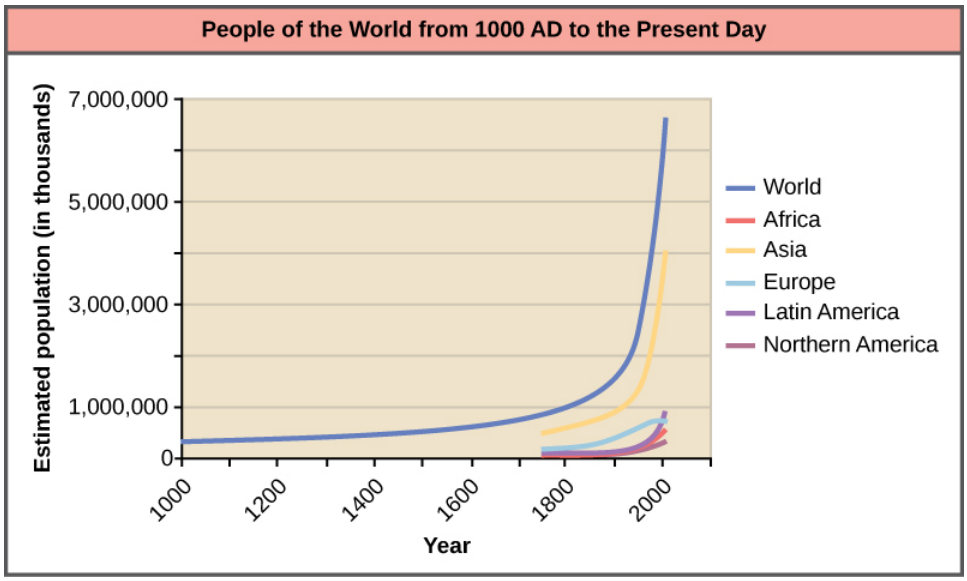


Figure 1. Human population growth since 1000 AD is exponential (dark blue line). Notice that while the population in Asia (yellow line), which has many economically underdeveloped countries, is increasing exponentially, the population in Europe (light blue line), where most of the countries are economically developed, is growing much more slowly.

A consequence of exponential human population growth is the time that it takes to add a particular number of humans to the Earth is becoming shorter. Figure 2 shows that 123 years were necessary to add 1 billion humans in 1930, but it only took 24 years to add two billion people between 1975 and 1999. As already discussed, at some point it would appear that our ability to increase our carrying capacity indefinitely on a finite world is uncertain. Without new technological advances, the human growth rate has been predicted to slow in the coming decades. However, the population will still be increasing and the threat of overpopulation remains.

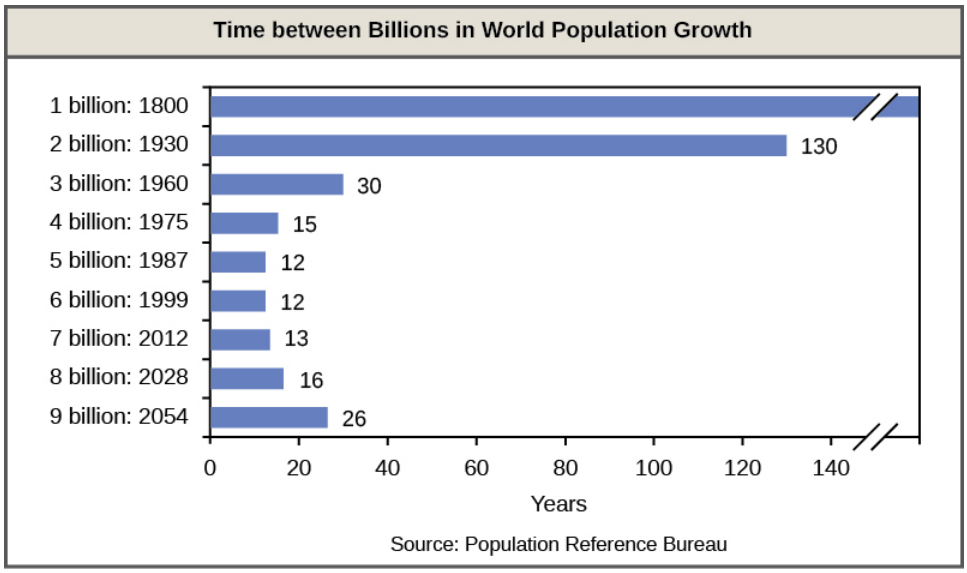


Figure 2. The time between the addition of each billion human beings to Earth decreases over time. (credit: modification of work by Ryan T. Cragun)

Click through this interactive view of how human populations have changed over time.

Overcoming Density-Dependent Regulation

Humans are unique in their ability to alter their environment with the conscious purpose of increasing its carrying capacity. This ability is a major factor responsible for human population growth and a way of overcoming density-dependent growth regulation. Much of this ability is related to human intelligence, society, and communication. Humans can construct shelter to protect them from the elements and have developed agriculture and domesticated animals to increase their food supplies. In addition, humans use language to communicate this technology to new generations, allowing them to improve upon previous accomplishments.

Other factors in human population growth are migration and public health. Humans originated in Africa, but have since migrated to nearly all inhabitable land on the Earth. Public health, sanitation, and the use of antibiotics and vaccines have decreased the ability of infectious disease to limit human population growth. In the past, diseases such as the bubonic plaque of the fourteenth century killed between 30 and 60 percent of Europe's population and reduced the overall world population by as many as 100 million people. Today, the threat of infectious disease, while not gone, is certainly less severe. According to the World Health Organization, global death from infectious disease declined from 16.4 million in 1993 to 14.7 million in 1992. To compare to some of the epidemics of the past, the percentage of the world's population killed between 1993 and 2002 decreased from 0.30 percent of the world's population to 0.24 percent. Thus, it appears that the influence of infectious disease on human population growth is becoming less significant.

Age Structure, Population Growth, and Economic Development

The age structure of a population is an important factor in population dynamics. **Age structure** is the proportion of a population at different age ranges. Age structure allows better prediction of population growth, plus the ability to associate this growth with the level of economic development in the region. Countries with rapid growth have a pyramidal shape in their age structure diagrams, showing a preponderance of younger individuals, many of whom are of reproductive age or will be soon (Figure 3). This pattern is most often observed in underdeveloped countries where individuals do not live to old age because of less-than-optimal living conditions. Age structures of areas with slow growth, including developed countries such as the United States, still have a pyramidal structure, but with many fewer young and reproductive-aged individuals and a greater proportion of older individuals. Other developed countries, such as Italy, have zero population growth. The age structure of these populations is more conical, with an even greater percentage of middle-aged and older individuals. The actual growth rates in different countries are shown in Figure 4, with the highest rates tending to be in the less economically developed countries of Africa and Asia.

? Practice Question

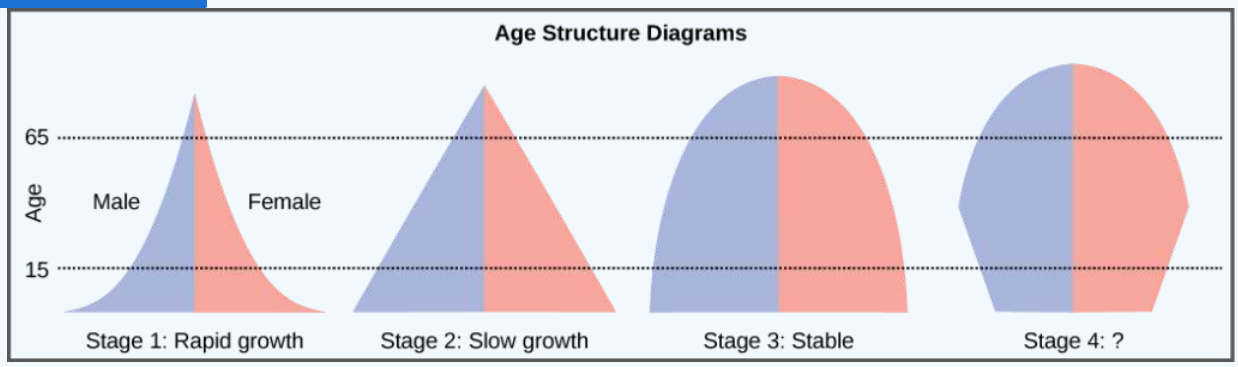


Figure 3. Typical age structure diagrams are shown. The rapid growth diagram narrows to a point, indicating that the number of individuals decreases rapidly with age. In the slow growth model, the number of individuals decreases steadily with age. Stable population diagrams are rounded on the top, showing that the number of individuals per age group decreases gradually, and then increases for the older part of the population.

Age structure diagrams for rapidly growing, slow growing and stable populations are shown in stages 1 through 3. What type of population change do you think stage 4 represents?

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[reveal-answer q="115181"]Show Answer[/reveal-answer]
[hidden-answer a="115181"]Stage 4 represents a population that is decreasing.[/hidden-answer]

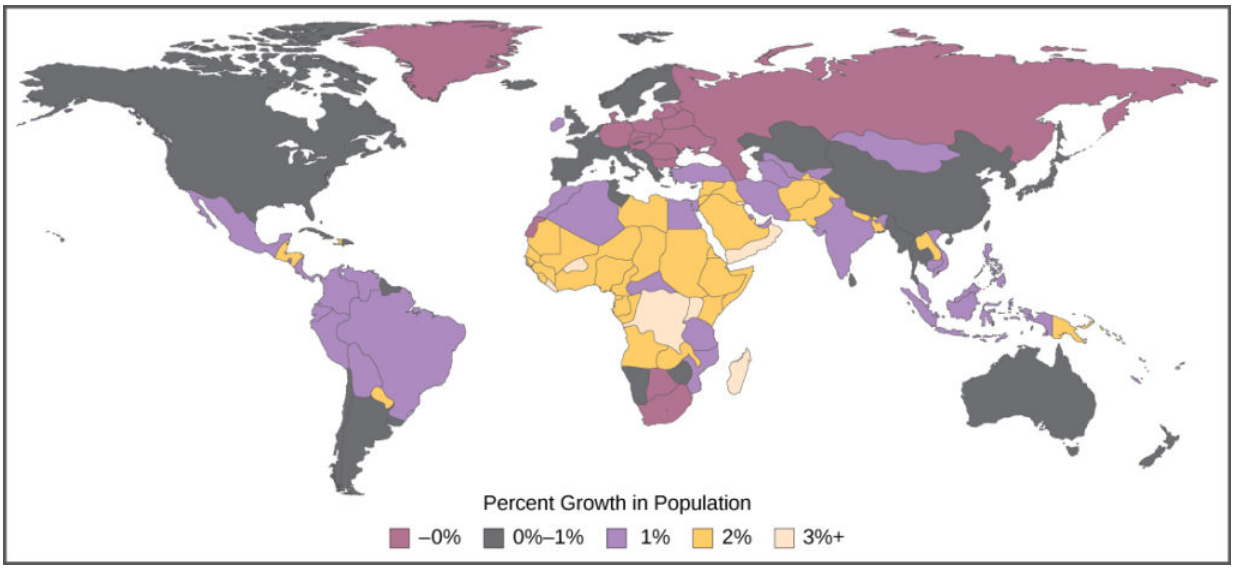


Figure 4. The percent growth rate of population in different countries is shown. Notice that the highest growth is occurring in less economically developed countries in Africa and Asia.

Long-Term Consequences of Exponential Human Population Growth

Many dire predictions have been made about the world's population leading to a major crisis called the "population explosion." In the 1968 book *The Population Bomb*, biologist Dr. Paul R. Ehrlich wrote, "The battle to feed all of humanity is over. In the 1970s hundreds of millions of people will starve to death in spite of any crash programs embarked upon now. At this late date nothing can prevent a substantial increase in the world death rate." While many critics view this statement as an exaggeration, the laws of exponential population growth are still in effect, and unchecked human population growth cannot continue indefinitely.

Efforts to control population growth led to the **one-child policy** in China, which used to include more severe consequences, but now imposes fines on urban couples who have more than one child. Due to the fact that some couples wish to have a male heir, many Chinese couples continue to have more than one child. The policy itself, its social impacts, and the effectiveness of limiting overall population growth are controversial. In spite of population control policies, the human population continues to grow. At

some point the food supply may run out because of the subsequent need to produce more and more food to feed our population. The United Nations estimates that future world population growth may vary from 6 billion (a decrease) to 16 billion people by the year 2100. There is no way to know whether human population growth will moderate to the point where the crisis described by Dr. Ehrlich will be averted.

Another result of population growth is the endangerment of the natural environment. Many countries have attempted to reduce the human impact on climate change by reducing their emission of the greenhouse gas carbon dioxide. However, these treaties have not been ratified by every country, and many underdeveloped countries trying to improve their economic condition may be less likely to agree with such provisions if it means slower economic development. Furthermore, the role of human activity in causing climate change has become a hotly debated socio-political issue in some developed countries, including the United States. Thus, we enter the future with considerable uncertainty about our ability to curb human population growth and protect our environment.

Visit this website and select “Launch movie” for an animation discussing the global impacts of human population growth.

Learning Objectives

The world’s human population is growing at an exponential rate. Humans have increased the world’s carrying capacity through migration, agriculture, medical advances, and communication. The age structure of a population allows us to predict population growth. Unchecked human population growth could have dire long-term effects on our environment.

This video tells us the specifics of why and how human population growth has happened over the past hundred and fifty years or so, and how those specifics relate to ecology.



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17.22: Introduction to Community Ecology

What you'll learn to do: Discuss the scope and study of community ecology

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

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17.23: Predation and Herbivory

Learning Objectives

- Discuss the importance of predation and herbivory in the ecosystem, including how organisms defend against these

Perhaps the classical example of species interaction is predation: the hunting of prey by its predator. Nature shows on television highlight the drama of one living organism killing another. Populations of predators and prey in a community are not constant over time: in most cases, they vary in cycles that appear to be related. The most often cited example of predator-prey dynamics is seen in the cycling of the lynx (predator) and the snowshoe hare (prey), using nearly 200 year-old trapping data from North American forests (Figure 1). This cycle of predator and prey lasts approximately 10 years, with the predator population lagging 1–2 years behind that of the prey population. As the hare numbers increase, there is more food available for the lynx, allowing the lynx population to increase as well. When the lynx population grows to a threshold level, however, they kill so many hares that hare population begins to decline, followed by a decline in the lynx population because of scarcity of food. When the lynx population is low, the hare population size begins to increase due, at least in part, to low predation pressure, starting the cycle anew.

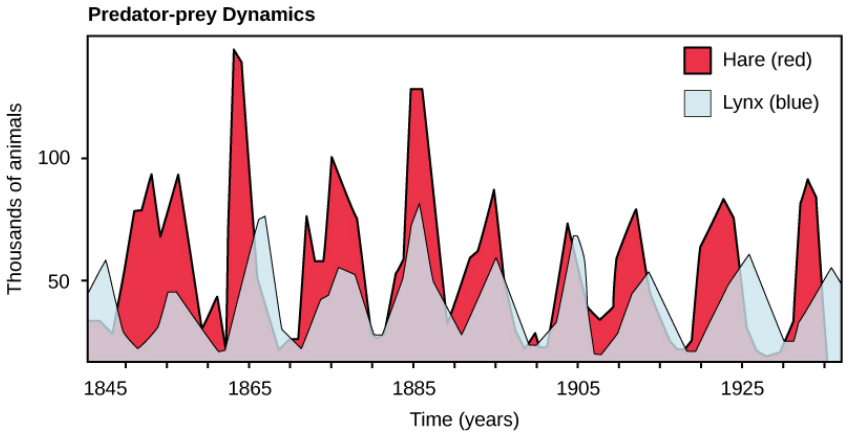


Figure 1. The cycling of lynx and snowshoe hare populations in Northern Ontario is an example of predator-prey dynamics.

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

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

Defense Mechanisms against Predation and Herbivory

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

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

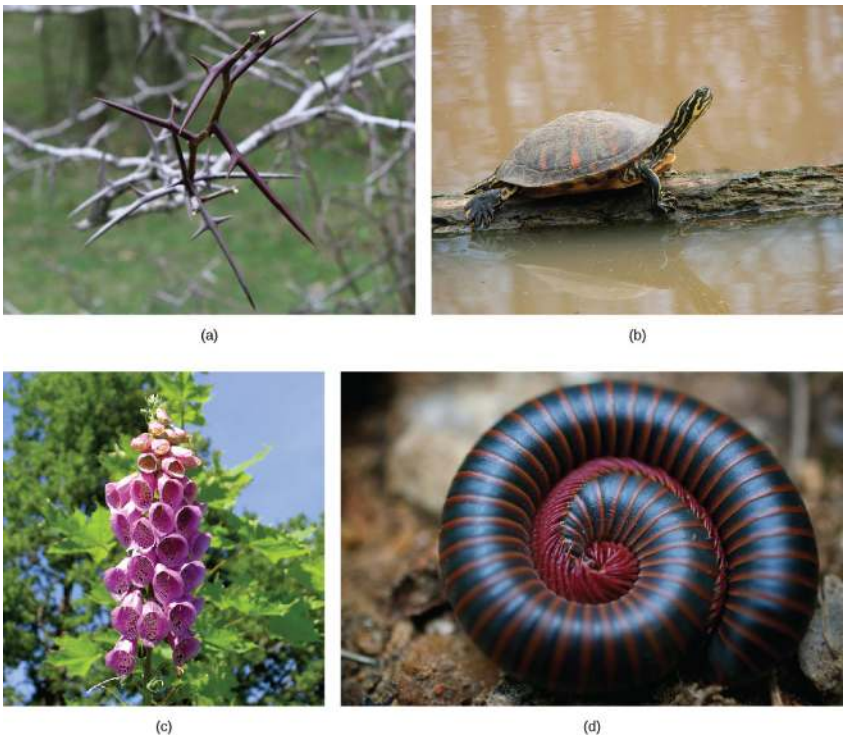


Figure 2. The (a) honey locust tree (Gleditsia triacanthos) uses thorns, a mechanical defense, against herbivores, while the (b) Florida red-bellied turtle (Pseudemys nelsoni) uses its shell as a mechanical defense against predators. (c) Foxglove (Digitalis sp.) uses a chemical defense: toxins produced by the plant can cause nausea, vomiting, hallucinations, convulsions, or death when consumed. (d) The North American millipede (Narceus americanus) uses both mechanical and chemical defenses: when threatened, the millipede curls into a defensive ball and produces a noxious substance that irritates eyes and skin. (credit a: modification of work by Huw Williams; credit b: modification of work by "JamieS93"/Flickr; credit c: modification of work by Philip Jägenstedt; credit d: modification of work by Cory Zanker)

Many species use their body shape and coloration to avoid being detected by predators. The tropical walking stick is an insect with the coloration and body shape of a twig which makes it very hard to see when stationary against a background of real twigs (Figure 3a). In another example, the chameleon can change its color to match its surroundings (Figure 3b). Both of these are examples of **camouflage**, or avoiding detection by blending in with the background.



Figure 3. (a) The tropical walking stick and (b) the chameleon use body shape and/or coloration to prevent detection by predators. (credit a: modification of work by Linda Tanner; credit b: modification of work by Frank Vassen)

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



Figure 4. (a) The strawberry poison dart frog (*Oophaga pumilio*) uses aposematic coloration to warn predators that it is toxic, while the (b) striped skunk (*Mephitis mephitis*) uses aposematic coloration to warn predators of the unpleasant odor it produces. (credit a: modification of work by Jay Iwasaki; credit b: modification of work by Dan Dzurisin)

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



Figure 5. Batesian mimicry occurs when a harmless species mimics the coloration of a harmful species, as is seen with the (a) bumblebee and (b) bee-like robber fly. (credit a, b: modification of work by Cory Zanker)



Figure 6. Several unpleasant-tasting Heliconius butterfly species share a similar color pattern with better-tasting varieties. (credit: Joron M, Papa R, Beltrán M, Chamberlain N, Mavárez J, et al.)

In **Müllerian mimicry**, multiple species share the same warning coloration, but all of them actually have defenses. Figure 6 shows a variety of foul-tasting butterflies with similar coloration.

In **Emsleyan/Mertensian mimicry**, a deadly prey mimics a less dangerous one, such as the venomous coral snake mimicking the non-venomous milk snake. This type of mimicry is extremely rare and more difficult to understand than the previous two types. For this type of mimicry to work, it is essential that eating the milk snake has unpleasant, but not fatal, consequences. Then, these predators learn not to eat snakes with this coloration, protecting the coral snake as well. If the snake were fatal to the predator, there would be no opportunity for the predator to learn not to eat it, and the benefit for the less toxic species would disappear.

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17.24: Competition

Learning Objectives

- Define the competitive exclusion principle

Resources are often limited within a habitat and multiple species may compete to obtain them. All species have an ecological **niche** in the ecosystem, which describes how they acquire the resources they need and how they interact with other species in the community. The **competitive exclusion principle** states that two species cannot occupy the same niche in a habitat. In other words, different species cannot coexist in a community if they are competing for all the same resources. An example of this principle is shown in Figure 1, with two protozoan species, *Paramecium aurelia* and *Paramecium caudatum*. When grown individually in the laboratory, they both thrive. But when they are placed together in the same test tube (habitat), *P. aurelia* outcompetes *P. caudatum* for food, leading to the latter's eventual extinction.

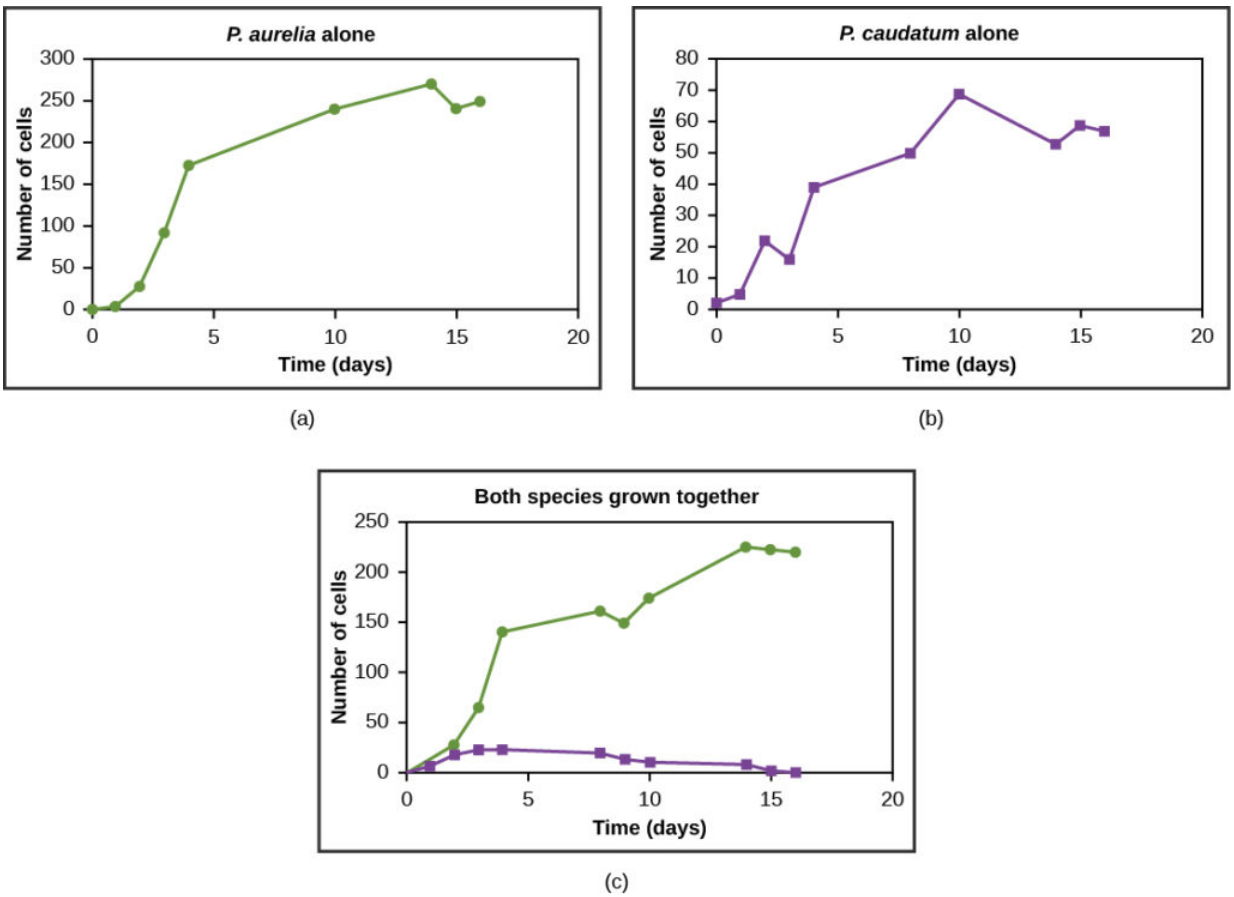


Figure 1. *Paramecium aurelia* and *Paramecium caudatum* grow well individually, but when they compete for the same resources, the *P. aurelia* outcompetes the *P. caudatum*.

Resource Partitioning

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

The anole lizards found on the island of Puerto Rico are a good example of resource partitioning. In this group, natural selection has led to the evolution of different species that make use of different resources. The figure below shows resource partitioning

among 11 species of anole lizards. Each species lives in its own preferred habitat, which is defined by type and height of vegetation (trees, shrubs, cactus, etc.), sunlight, and moisture, among other factors.

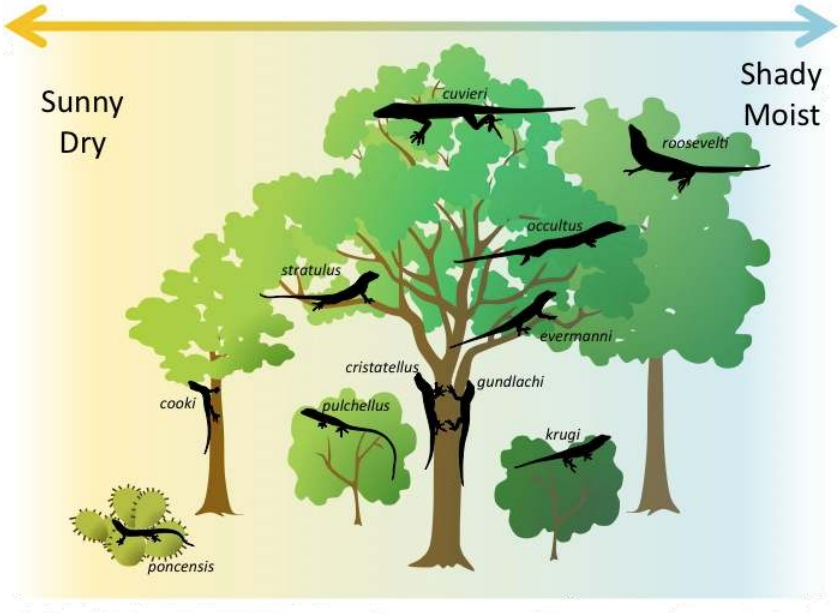


Figure 2. Resource partitioning among anole lizards

Learning Objectives

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



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17.25: Symbiosis

Learning Objectives

- Compare and contrast the three different types of symbiotic relationships

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

Commensalism



Figure 1. The southern masked-weaver bird is starting to make a nest in a tree in Zambezi Valley, Zambia. This is an example of a commensal relationship, in which one species (the bird) benefits, while the other (the tree) neither benefits nor is harmed. (credit: "Hanay"/Wikimedia Commons)

A **commensal** relationship occurs when one species benefits from the close, prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship (Figure 1). The tree is not harmed by the presence of the nest among its branches. The nests are light and produce little strain on the structural integrity of the branch, and most of the leaves, which the tree uses to get energy by photosynthesis, are above the nest so they are unaffected. The bird, on the other hand, benefits greatly. If the bird had to nest in the open, its eggs and young would be vulnerable to predators. Another example of a commensal relationship is the clown fish and the sea anemone. The sea anemone is not harmed by the fish, and the fish benefits with protection from predators who would be stung upon nearing the sea anemone.

Mutualism

A second type of symbiotic relationship is called **mutualism**, where two species benefit from their interaction. Some scientists believe that these are the only true examples of symbiosis. For example, termites have a mutualistic relationship with protozoa that live in the insect's gut (Figure 2a). The termite benefits from the ability of bacterial symbionts within the protozoa to digest cellulose. The termite itself cannot do this, and without the protozoa, it would not be able to obtain energy from its food (cellulose from the wood it chews and eats). The protozoa and the bacterial symbionts benefit by having a protective environment and a constant supply of food from the wood chewing actions of the termite. Lichens have a mutualistic relationship between fungus and photosynthetic algae or bacteria (Figure 2b). As these symbionts grow together, the glucose produced by the algae provides nourishment for both organisms, whereas the physical structure of the lichen protects the algae from the elements and makes certain nutrients in the atmosphere more available to the algae.



Figure 2. (a) Termites form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living inside its cells. (credit a: modification of work by Scott Bauer, USDA; credit b: modification of work by Cory Zanker)

Parasitism

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

The reproductive cycles of parasites are often very complex, sometimes requiring more than one host species. A tapeworm is a parasite that causes disease in humans when contaminated, undercooked meat such as pork, fish, or beef is consumed (Figure 3). The tapeworm can live inside the intestine of the host for several years, benefiting from the food the host is bringing into its gut by eating, and may grow to be over 50 ft long by adding segments. The parasite moves from species to species in a cycle, making two hosts necessary to complete its life cycle. Another common parasite is *Plasmodium falciparum*, the protozoan cause of malaria, a significant disease in many parts of the world. Living in human liver and red blood cells, the organism reproduces asexually in the gut of blood-feeding mosquitoes to complete its life cycle. Thus malaria is spread from human to human by mosquitoes, one of many arthropod-borne infectious diseases.

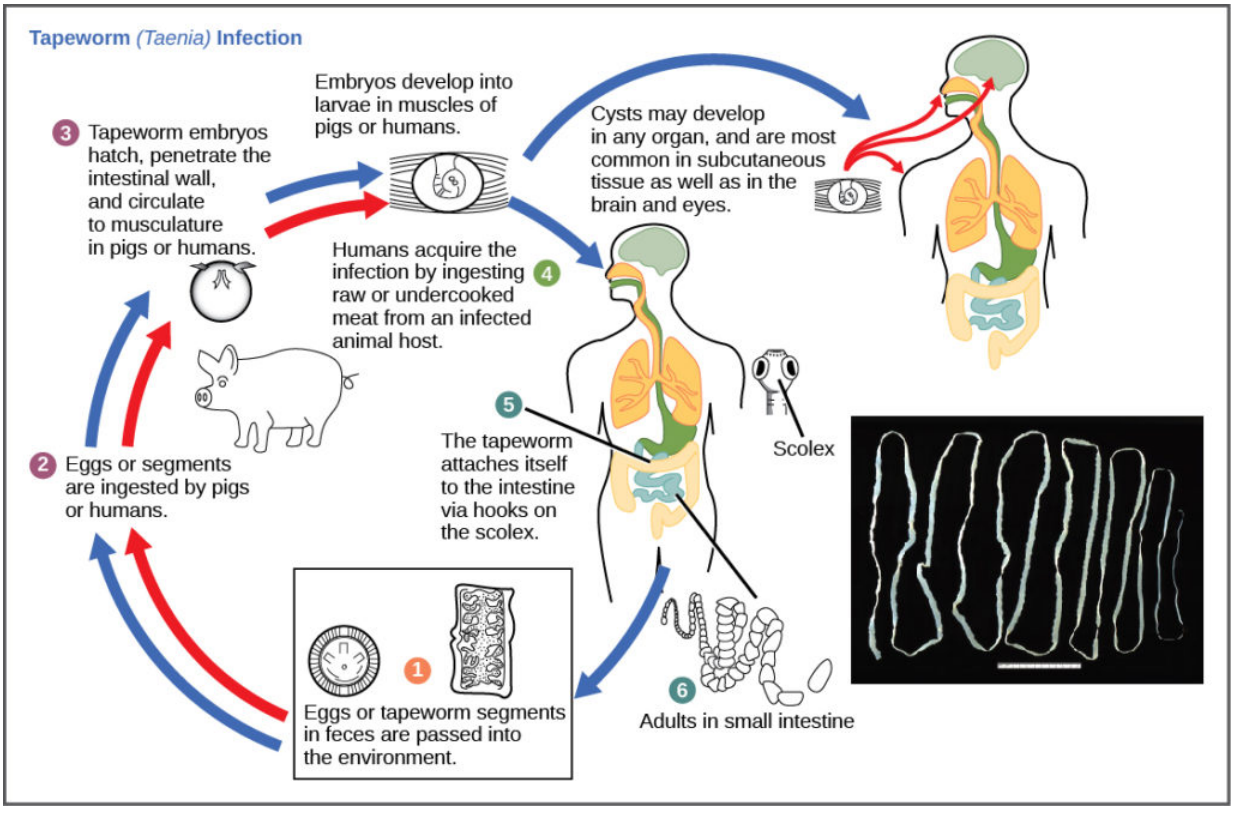


Figure 3. This diagram shows the life cycle of a pork tapeworm (*Taenia solium*), a human worm parasite. (credit: modification of work by CDC)

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17.26: Community Structure and Dynamics

Learning Objectives

- Identify different species roles that structure communities
- Describe community dynamics as the changes in community structure that take place over time

Community Structure

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

Foundation Species

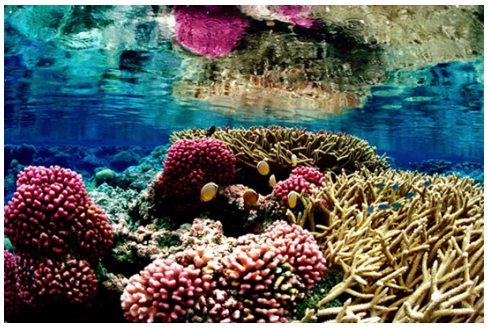


Figure 1. Coral is the foundation species of coral reef ecosystems. (credit: Jim E. Maragos, USFWS)

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

Foundation species may physically modify the environment to produce and maintain habitats that benefit the other organisms that use them. An example is the photosynthetic corals of the coral reef (Figure 1). Corals themselves are not photosynthetic, but harbor symbionts within their body tissues (dinoflagellates called zooxanthellae) that perform photosynthesis; this is another example of a mutualism. The exoskeletons of living and dead coral make up most of the reef structure, which protects many other species from waves and ocean currents.

Biodiversity, Species Richness, and Relative Species Abundance

Biodiversity describes a community’s biological complexity: it is measured by the number of different species (species richness) in a particular area and their relative abundance (species evenness). The area in question could be a habitat, a biome, or the entire biosphere. **Species richness** is the term that is used to describe the number of species living in a habitat or biome. Species richness varies across the globe (Figure 2). One factor in determining species richness is latitude, with the greatest species richness occurring in ecosystems near the equator, which often have warmer temperatures, large amounts of rainfall, and low seasonality. The lowest species richness occurs near the poles, which are much colder, drier, and thus less conducive to life in Geologic time (time since glaciations). The predictability of climate or productivity is also an important factor. Other factors influence species richness as well. For example, the study of **island biogeography** attempts to explain the relatively high species richness found in certain isolated island chains, including the Galápagos Islands that inspired the young Darwin. **Relative species abundance** is the number of individuals in a species relative to the total number of individuals in all species within a habitat, ecosystem, or biome. Foundation species often have the highest relative abundance of species.

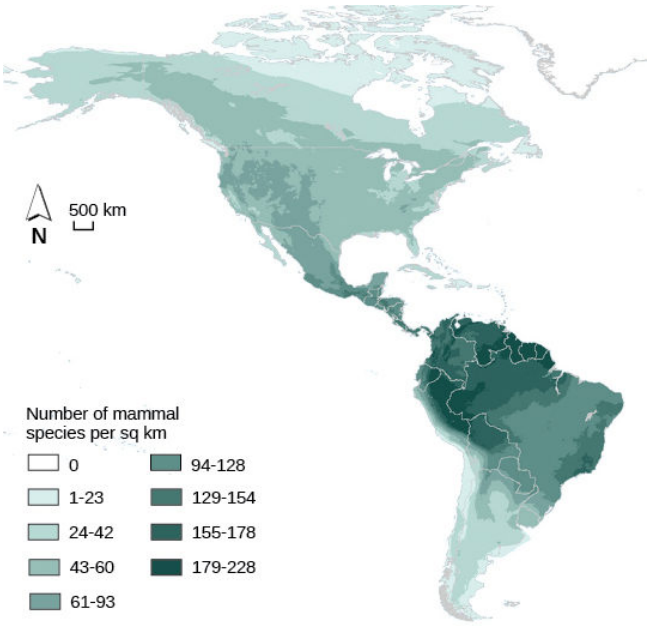


Figure 2. The greatest species richness for mammals in North and South America is associated with the equatorial latitudes. (credit: modification of work by NASA, CIESIN, Columbia University)

Keystone Species



Figure 3. The *Pisaster ochraceus* sea star is a keystone species. (credit: Jerry Kirkhart)

A **keystone species** is one whose presence is key to maintaining biodiversity within an ecosystem and to upholding an ecological community's structure. The intertidal sea star, *Pisaster ochraceus*, of the northwestern United States is a keystone species (Figure 3).

Studies have shown that when this organism is removed from communities, populations of their natural prey (mussels) increase, completely altering the species composition and reducing biodiversity. Another keystone species is the banded tetra, a fish in tropical streams, which supplies nearly all of the phosphorus, a necessary inorganic nutrient, to the rest of the community. If these fish were to become extinct, the community would be greatly affected.

Invasive Species



Figure 4. Aquatic invasive species in the United States: (a) purple loosestrife and (b) zebra mussel. (credit a: modification of work by Liz West; credit b: modification of work by M. McCormick, NOAA)

Invasive species are non-native organisms that, when introduced to an area out of their native range, threaten the ecosystem balance of that habitat. Many such species exist in the United States, as shown in Figures 4–6. Whether enjoying a forest hike, taking a summer boat trip, or simply walking down an urban street, you have likely encountered an invasive species.

Invasive species like purple loosestrife (*Lythrum salicaria*) and the zebra mussel (*Dreissena polymorpha*) threaten certain aquatic ecosystems (Figure 4).

Some forests are threatened by the spread of common buckthorn (*Rhamnus cathartica*), garlic mustard (*Alliaria petiolata*), and the emerald ash borer (*Agrilus planipennis*) (Figure 5).

The European starling (*Sturnus vulgaris*) may compete with native bird species for nest holes.



Figure 5. Invasive species in US forests: (a) common buckthorn, (b) garlic mustard, and (c) the emerald ash borer. (credit a: modification of work by E. Dronkert; credit b: modification of work by Dan Davison; credit c: modification of work by USDA)

Community Dynamics

Community dynamics are the changes in community structure and composition over time. Sometimes these changes are induced by **environmental disturbances** such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a stable structure are said to be at equilibrium. Following a disturbance, the community may or may not return to the equilibrium state.

Succession describes the sequential appearance and disappearance of species in a community over time. In **primary succession**, newly exposed or newly formed land is colonized by living things; in **secondary succession**, part of an ecosystem is disturbed and remnants of the previous community remain.

Primary Succession and Pioneer Species



Figure 6. During primary succession in lava on Maui, Hawaii, succulent plants are the pioneer species. (credit: Forest and Kim Starr)

Primary succession occurs when new land is formed or rock is exposed: for example, following the eruption of volcanoes, such as those on the Big Island of Hawaii. As lava flows into the ocean, new land is continually being formed. On the Big Island, approximately 32 acres of land is added each year. First, weathering and other natural forces break down the substrate enough for the establishment of certain hearty plants and lichens with few soil requirements, known as **pioneer species** (Figure 6). These species help to further break down the mineral rich lava into soil where other, less hardy species will grow and eventually replace the pioneer species. In addition, as these early species grow and die, they add to an ever-growing layer of decomposing organic material and contribute to soil formation. Over time the area will reach an equilibrium state, with a set of organisms quite different from the pioneer species.

Secondary Succession

A classic example of secondary succession occurs in oak and hickory forests cleared by wildfire (Figure 7). Wildfires will burn most vegetation and kill those animals unable to flee the area. Their nutrients, however, are returned to the ground in the form of ash. Thus, even when areas are devoid of life due to severe fires, the area will soon be ready for new life to take hold.

Before the fire, the vegetation was dominated by tall trees with access to the major plant energy resource: sunlight. Their height gave them access to sunlight while also shading the ground and other low-lying species. After the fire, though, these trees are no longer dominant. Thus, the first plants to grow back are usually annual plants followed within a few years by quickly growing and spreading grasses and other pioneer species. Due to, at least in part, changes in the environment brought on by the growth of the grasses and other species, over many years, shrubs will emerge along with small pine, oak, and hickory trees. These organisms are called intermediate species. Eventually, over 150 years, the forest will reach its equilibrium point where species composition is no longer changing and resembles the community before the fire. This equilibrium state is referred to as the **climax community**, which will remain stable until the next disturbance.

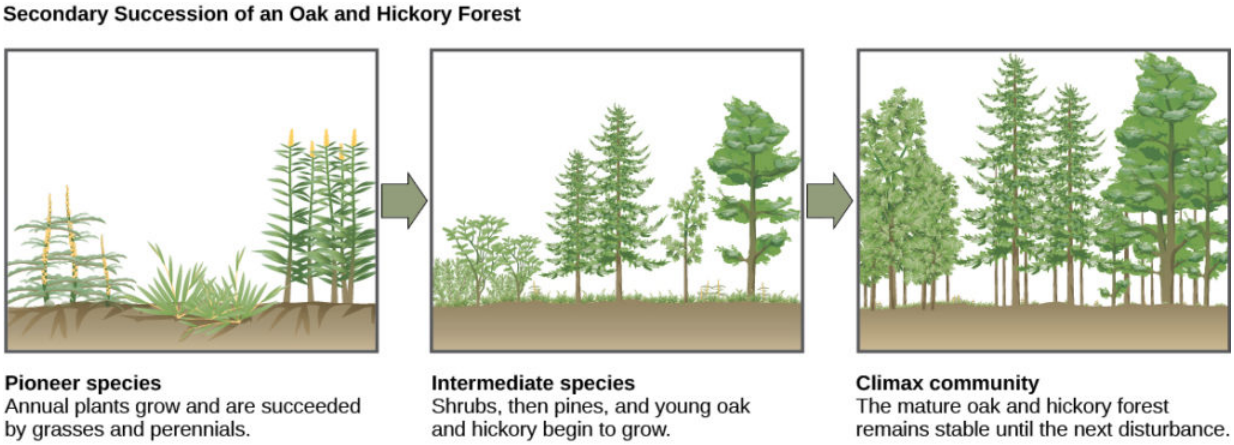


Figure 7. Secondary succession is shown in an oak and hickory forest after a forest fire.

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17.27: Putting It Together- Ecology of Living Things

Now that we've learned about the ecology of living things, let's return to the two examples we brought up at the beginning of the module.

Ecologist

We first had you imagine that you were an ecologist interested in learning about the natural world and how living things interact with each other as they compete for resources. This type of study would fall under population or community ecology, depending on if you're studying members of the same species or not. Remember: populations are made up of a single species, and communities are made up of all living things in a specified area.



Figure 1. The invasive Asian carp

One example of community ecology is the study of invasive species. One of the many recent proliferations of an invasive species concerns the growth of Asian carp populations (Figure 1). Asian carp were introduced to the United States in the 1970s by fisheries and sewage treatment facilities that used the fish's excellent filter feeding capabilities to clean their ponds of excess plankton. Some of the fish escaped, however, and by the 1980s they had colonized many waterways of the Mississippi River basin, including the Illinois and Missouri Rivers.

Voracious eaters and rapid reproducers, Asian carp may outcompete native species for food, potentially leading to their extinction. For example, black carp are voracious eaters of native mussels and snails, limiting this food source for native fish species. Silver carp eat plankton that native mussels and snails feed on, reducing this food source by a different alteration of the food web. In some areas of the Mississippi River, Asian carp species have become the most predominant, effectively outcompeting native fishes for habitat. In some parts of the Illinois River, Asian carp constitute 95 percent of the community's biomass. Although edible, the fish is bony and not a desired food in the United States. Moreover, their presence threatens the native fish and fisheries of the Great Lakes, which are important to local economies and recreational anglers. Asian carp have even injured humans. The fish, frightened by the sound of approaching motorboats, thrust themselves into the air, often landing in the boat or directly hitting the boaters.

The Great Lakes and their prized salmon and lake trout fisheries are also being threatened by these invasive fish. Asian carp have already colonized rivers and canals that lead into Lake Michigan. One infested waterway of particular importance is the Chicago Sanitary and Ship Channel, the major supply waterway linking the Great Lakes to the Mississippi River. To prevent the Asian carp from leaving the canal, a series of electric barriers have been successfully used to discourage their migration; however, the threat is significant enough that several states and Canada have sued to have the Chicago channel permanently cut off from Lake Michigan. Local and national politicians have weighed in on how to solve the problem, but no one knows whether the Asian carp will ultimately be considered a nuisance, like other invasive species such as the water hyacinth and zebra mussel, or whether it will be the destroyer of the largest freshwater fishery of the world.

The issues associated with Asian carp show how population and community ecology, fisheries management, and politics intersect on issues of vital importance to the human food supply and economy. Socio-political issues like this make extensive use of the sciences of population ecology (the study of members of a particular species occupying a particular area known as a habitat) and community ecology (the study of the interaction of all species within a habitat).

Physician

We then had you imagine being a future physician seeking to understand the connection between human health and ecology. Humans are a part of the ecological landscape, and human health is one important part of human interaction with our physical and living environment. Lyme disease, for instance, serves as one modern-day example of the connection between our health and the natural world (Figure 2).



(a) (b) (c)

Figure 2. The (a) deer tick carries the bacterium that produces Lyme disease in humans, often evident in (b) a symptomatic bull's eye rash. The (c) white-footed mouse is one well-known host to deer ticks carrying the Lyme disease bacterium. (credit a: modification of work by Scott Bauer, USDA ARS; credit b: modification of work by James Gathany, CDC; credit c: modification of work by Rob Ireton)

More formally known as Lyme borreliosis, Lyme disease is a bacterial infection that can be transmitted to humans when they are bitten by the deer tick (*Ixodes scapularis*), which is the primary vector for this disease. However, not all deer ticks carry the bacteria that will cause Lyme disease in humans, and *I. scapularis* can have other hosts besides deer. In fact, it turns out that the probability of infection depends on the type of host upon which the tick develops: a higher proportion of ticks that live on white-footed mice carry the bacterium than do ticks that live on deer. Knowledge about the environments and population densities in which the host species is abundant would help a physician or an epidemiologist better understand how Lyme disease is transmitted and how its incidence could be reduced.

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18.1: Why It Matters- Ecology and the Environment

Why discuss ecology as it relates to the environment?

We all live on the same world, and we all affect the ecosystem as we use resources and release waste products every day. As a whole, people are becoming more and more aware of the impact that they have on the earth, and what they can do to mitigate the damage they might cause. There is a multitude of eco-friendly organizations that are working to improve our world and increase the sustainability of our lives.

Two of the most prevalent concerns in our world today are climate change and decreasing biodiversity. We've all heard about these concerns on the news: the melting polar ice caps, now-extinct species, loss of habitat, etc. As we go through this module and learn more about these concerns, think about how you can act in simple ways to help preserve and restore our environment.

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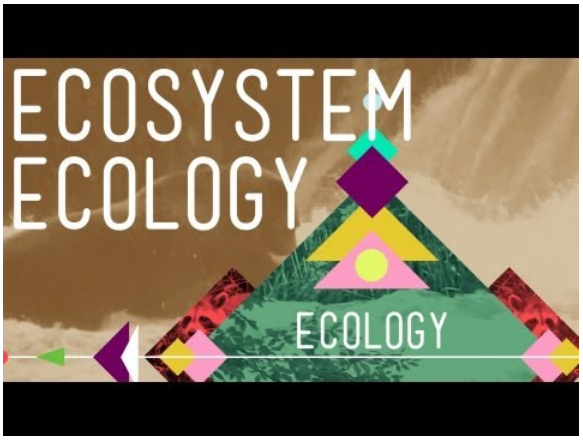
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18.2: Introduction to Energy in the Environment

What you'll learn to do: Describe how organisms acquire energy

Ecosystem is a term that you've probably heard before—but just what is an ecosystem? In this section, we'll learn about ecosystems and how energy moves within a system. This video provides a quick introduction to the concepts we'll discuss.



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18.3: Ecology of Ecosystems

Learning Objectives

- Explain the methods that ecologists use to study ecosystem structure and dynamics

Life in an ecosystem is often about competition for limited resources, a characteristic of the theory of natural selection. Competition in communities (all living things within specific habitats) is observed both within species and among different species. The resources for which organisms compete include organic material from living or previously living organisms, sunlight, and mineral nutrients, which provide the energy for living processes and the matter to make up organisms' physical structures. Other critical factors influencing community dynamics are the components of its physical and geographic environment: a habitat's latitude, amount of rainfall, topography (elevation), and available species. These are all important environmental variables that determine which organisms can exist within a particular area.

An **ecosystem** is a community of living organisms and their interactions with their abiotic (non-living) environment. Ecosystems can be small, such as the tide pools found near the rocky shores of many oceans, or large, such as the Amazon Rainforest in Brazil (Figure 1).



(a) (b)

Figure 1. A (a) tidal pool ecosystem in Matinicus Island in Maine is a small ecosystem, while the (b) Amazon Rainforest in Brazil is a large ecosystem. (credit a: modification of work by "takomabibelot"/Flickr; credit b: modification of work by Ivan Mlinaric)

Ecosystems are complex with many interacting parts. They are routinely exposed to various disturbances, or changes in the environment that effect their compositions: yearly variations in rainfall and temperature and the slower processes of plant growth, which may take several years. Many of these disturbances are a result of natural processes. For example, when lightning causes a forest fire and destroys part of a forest ecosystem, the ground is eventually populated by grasses, then by bushes and shrubs, and later by mature trees, restoring the forest to its former state. The impact of environmental disturbances caused by human activities is as important as the changes wrought by natural processes. Human agricultural practices, air pollution, acid rain, global deforestation, overfishing, eutrophication, oil spills, and illegal dumping on land and into the ocean are all issues of concern to conservationists.

Equilibrium is the steady state of an ecosystem where all organisms are in balance with their environment and with each other. In ecology, two parameters are used to measure changes in ecosystems: resistance and resilience. The ability of an ecosystem to remain at equilibrium in spite of disturbances is called **resistance**. The speed at which an ecosystem recovers equilibrium after being disturbed, called its **resilience**. Ecosystem resistance and resilience are especially important when considering human impact. The nature of an ecosystem may change to such a degree that it can lose its resilience entirely. This process can lead to the complete destruction or irreversible altering of the ecosystem.

? Try It

It is well established by the theory of natural selection that changes in the environment play a major role in the evolution of species within an ecosystem. However, little is known about how the evolution of species within an ecosystem can alter the ecosystem environment. In 2009, Dr. Luke Harmon, from the University of Idaho in Moscow, published a paper that for the first time showed that the evolution of organisms into subspecies can have direct effects on their ecosystem environment.



Figure 2. The three-spined stickleback evolved from a saltwater fish to freshwater fish. (credit: Barrett Paul, USFWS)

The three-spines stickleback (*Gasterosteus aculeatus*) is a freshwater fish that evolved from a saltwater fish to live in freshwater lakes about 10,000 years ago, which is considered a recent development in evolutionary time. Over the last 10,000 years, these freshwater fish then became isolated from each other in different lakes. Depending on which lake population was studied, findings showed that these sticklebacks then either remained as one species or evolved into two species. The divergence of species was made possible by their use of different areas of the pond for feeding called micro niches.

Dr. Harmon and his team created artificial pond microcosms in 250-gallon tanks and added muck from freshwater ponds as a source of zooplankton and other invertebrates to sustain the fish. In different experimental tanks they introduced one species of stickleback from either a single-species or double-species lake.

Over time, the team observed that some of the tanks bloomed with algae while others did not. This puzzled the scientists, and they decided to measure the water's dissolved organic carbon (DOC), which consists of mostly large molecules of decaying organic matter that give pond-water its slightly brownish color. It turned out that the water from the tanks with two-species fish contained larger particles of DOC (and hence darker water) than water with single-species fish. This increase in DOC blocked the sunlight and prevented algal blooming. Conversely, the water from the single-species tank contained smaller DOC particles, allowing more sunlight penetration to fuel the algal blooms.

This change in the environment, which is due to the different feeding habits of the stickleback species in each lake type, probably has a great impact on the survival of other species in these ecosystems, especially other photosynthetic organisms. Thus, the study shows that, at least in these ecosystems, the environment and the evolution of populations have reciprocal effects that may now be factored into simulation models.

Research into Ecosystem Dynamics

The study of the changes in ecosystem structure caused by changes in the environment (disturbances) or by internal forces is called **ecosystem dynamics**. Ecosystems are characterized using a variety of research methodologies. Some ecologists study ecosystems using controlled experimental systems, while some study entire ecosystems in their natural state, and others use both approaches.

A **holistic ecosystem model** attempts to quantify the composition, interaction, and dynamics of entire ecosystems; it is the most representative of the ecosystem in its natural state. A food web is an example of a holistic ecosystem model. However, this type of study is limited by time and expense, as well as the fact that it is neither feasible nor ethical to do experiments on large natural ecosystems. To quantify all different species in an ecosystem and the dynamics in their habitat is difficult, especially when studying large habitats such as the Amazon Rainforest, which covers 1.4 billion acres (5.5 million km^2) of the Earth's surface.

For these reasons, scientists study ecosystems under more controlled conditions. Experimental systems usually involve either partitioning a part of a natural ecosystem that can be used for experiments, termed a **mesocosm**, or by re-creating an ecosystem entirely in an indoor or outdoor laboratory environment, which is referred to as a **microcosm**. A major limitation to these

approaches is that removing individual organisms from their natural ecosystem or altering a natural ecosystem through partitioning may change the dynamics of the ecosystem. These changes are often due to differences in species numbers and diversity and also to environment alterations caused by partitioning (mesocosm) or re-creating (microcosm) the natural habitat. Thus, these types of experiments are not totally predictive of changes that would occur in the ecosystem from which they were gathered.

As both of these approaches have their limitations, some ecologists suggest that results from these experimental systems should be used only in conjunction with holistic ecosystem studies to obtain the most representative data about ecosystem structure, function, and dynamics.

Scientists use the data generated by these experimental studies to develop ecosystem models that demonstrate the structure and dynamics of ecosystems. Three basic types of ecosystem modeling are routinely used in research and ecosystem management: a conceptual model, an analytical model, and a simulation model. A **conceptual model** is an ecosystem model that consists of flow charts to show interactions of different compartments of the living and nonliving components of the ecosystem. A conceptual model describes ecosystem structure and dynamics and shows how environmental disturbances affect the ecosystem; however, its ability to predict the effects of these disturbances is limited. Analytical and simulation models, in contrast, are mathematical methods of describing ecosystems that are indeed capable of predicting the effects of potential environmental changes without direct experimentation, although with some limitations as to accuracy. An **analytical model** is an ecosystem model that is created using simple mathematical formulas to predict the effects of environmental disturbances on ecosystem structure and dynamics. A **simulation model** is an ecosystem model that is created using complex computer algorithms to holistically model ecosystems and to predict the effects of environmental disturbances on ecosystem structure and dynamics. Ideally, these models are accurate enough to determine which components of the ecosystem are particularly sensitive to disturbances, and they can serve as a guide to ecosystem managers (such as conservation ecologists or fisheries biologists) in the practical maintenance of ecosystem health.

Conceptual Models

Conceptual models are useful for describing ecosystem structure and dynamics and for demonstrating the relationships between different organisms in a community and their environment. Conceptual models are usually depicted graphically as flow charts. The organisms and their resources are grouped into specific compartments with arrows showing the relationship and transfer of energy or nutrients between them. Thus, these diagrams are sometimes called compartment models.

To model the cycling of mineral nutrients, organic and inorganic nutrients are subdivided into those that are bioavailable (ready to be incorporated into biological macromolecules) and those that are not. For example, in a terrestrial ecosystem near a deposit of coal, carbon will be available to the plants of this ecosystem as carbon dioxide gas in a short-term period, not from the carbon-rich coal itself. However, over a longer period, microorganisms capable of digesting coal will incorporate its carbon or release it as natural gas (methane, CH_4), changing this unavailable organic source into an available one. This conversion is greatly accelerated by the combustion of fossil fuels by humans, which releases large amounts of carbon dioxide into the atmosphere. This is thought to be a major factor in the rise of the atmospheric carbon dioxide levels in the industrial age. The carbon dioxide released from burning fossil fuels is produced faster than photosynthetic organisms can use it. This process is intensified by the reduction of photosynthetic trees because of worldwide deforestation. Most scientists agree that high atmospheric carbon dioxide is a major cause of global climate change.

Analytical and Simulation Models

The major limitation of conceptual models is their inability to predict the consequences of changes in ecosystem species and/or environment. Ecosystems are dynamic entities and subject to a variety of abiotic and biotic disturbances caused by natural forces and/or human activity. Ecosystems altered from their initial equilibrium state can often recover from such disturbances and return to a state of equilibrium. As most ecosystems are subject to periodic disturbances and are often in a state of change, they are usually either moving toward or away from their equilibrium state. There are many of these equilibrium states among the various components of an ecosystem, which affects the ecosystem overall. Furthermore, as humans have the ability to greatly and rapidly alter the species content and habitat of an ecosystem, the need for predictive models that enable understanding of how ecosystems respond to these changes becomes more crucial.

Analytical models often use simple, linear components of ecosystems, such as food chains, and are known to be complex mathematically; therefore, they require a significant amount of mathematical knowledge and expertise. Although analytical models

have great potential, their simplification of complex ecosystems is thought to limit their accuracy. Simulation models that use computer programs are better able to deal with the complexities of ecosystem structure.

A recent development in simulation modeling uses supercomputers to create and run individual-based simulations, which accounts for the behavior of individual organisms and their effects on the ecosystem as a whole. These simulations are considered to be the most accurate and predictive of the complex responses of ecosystems to disturbances.

Visit The Darwin Project to view a variety of ecosystem models.

Learning Objectives

Ecosystems exist on land, at sea, in the air, and underground. Different ways of modeling ecosystems are necessary to understand how environmental disturbances will affect ecosystem structure and dynamics. Conceptual models are useful to show the general relationships between organisms and the flow of materials or energy between them. Analytical models are used to describe linear food chains, and simulation models work best with holistic food webs.

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18.4: Food Chains and Food Webs

Learning Objectives

- Differentiate between food chains and food webs and recognize the importance of each

The term “food chain” is sometimes used metaphorically to describe human social situations. In this sense, food chains are thought of as a competition for survival, such as “who eats whom?” Someone eats and someone is eaten. Therefore, it is not surprising that in our competitive “dog-eat-dog” society, individuals who are considered successful are seen as being at the top of the food chain, consuming all others for their benefit, whereas the less successful are seen as being at the bottom.

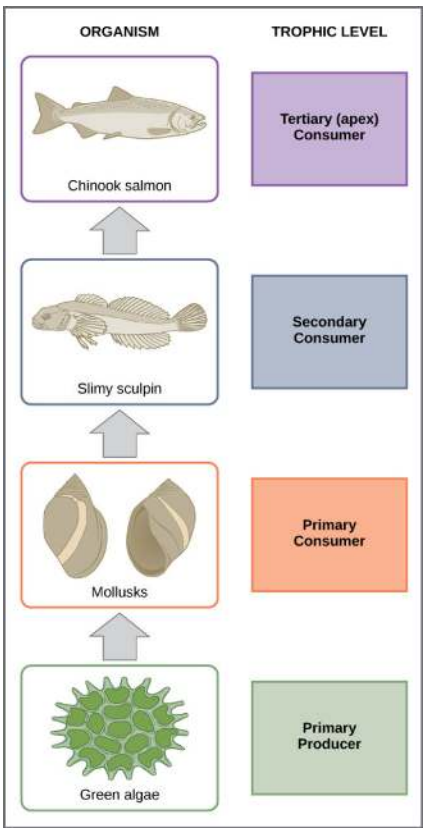


Figure 1. These are the trophic levels of a food chain in Lake Ontario at the United States-Canada border. Energy and nutrients flow from photosynthetic green algae at the bottom to the top of the food chain: the Chinook salmon.

The scientific understanding of a food chain is more precise than in its everyday usage. In ecology, a **food chain** is a linear sequence of organisms through which nutrients and energy pass: primary producers, primary consumers, and higher-level consumers are used to describe ecosystem structure and dynamics. There is a single path through the chain. Each organism in a food chain occupies what is called a **trophic level**. Depending on their role as producers or consumers, species or groups of species can be assigned to various trophic levels.

In many ecosystems, the bottom of the food chain consists of photosynthetic organisms (plants and/or phytoplankton), which are called **primary producers**. The organisms that consume the primary producers are herbivores: the **primary consumers**. **Secondary consumers** are usually carnivores that eat the primary consumers. **Tertiary consumers** are carnivores that eat other carnivores. Higher-level consumers feed on the next lower tropic levels, and so on, up to the organisms at the top of the food chain: the **apex consumers**. In the Lake Ontario food chain shown in Figure 1, the Chinook salmon is the apex consumer at the top of this food chain.

One major factor that limits the length of food chains is energy. Energy is lost as heat between each trophic level due to the second law of thermodynamics. Thus, after a limited number of trophic energy transfers, the amount of energy remaining in the food chain may not be great enough to support viable populations at yet a higher trophic level.

The loss of energy between trophic levels is illustrated by the pioneering studies of Howard T. Odum in the Silver Springs, Florida, ecosystem in the 1940s (Figure 2). The primary producers generated 20,819 kcal/m^2/yr (kilocalories per square meter per year), the primary consumers generated 3368 kcal/m^2/yr, the secondary consumers generated 383 kcal/m^2/yr, and the tertiary consumers only generated 21 kcal/m^2/yr. Thus, there is little energy remaining for another level of consumers in this ecosystem.

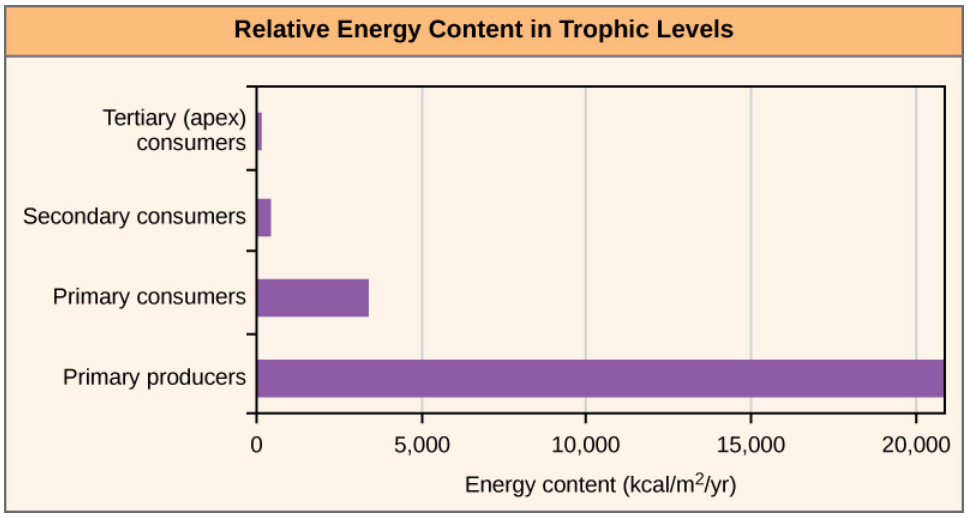


Figure 2. The relative energy in trophic levels in a Silver Springs, Florida, ecosystem is shown. Each trophic level has less energy available and supports fewer organisms at the next level.

There is a one problem when using food chains to accurately describe most ecosystems. Even when all organisms are grouped into appropriate trophic levels, some of these organisms can feed on species from more than one trophic level; likewise, some of these organisms can be eaten by species from multiple trophic levels. In other words, the linear model of ecosystems, the food chain, is not completely descriptive of ecosystem structure. A holistic model—which accounts for all the interactions between different species and their complex interconnected relationships with each other and with the environment—is a more accurate and descriptive model for ecosystems. A **food web** is a graphic representation of a holistic, non-linear web of primary producers, primary consumers, and higher-level consumers used to describe ecosystem structure and dynamics (Figure 3).

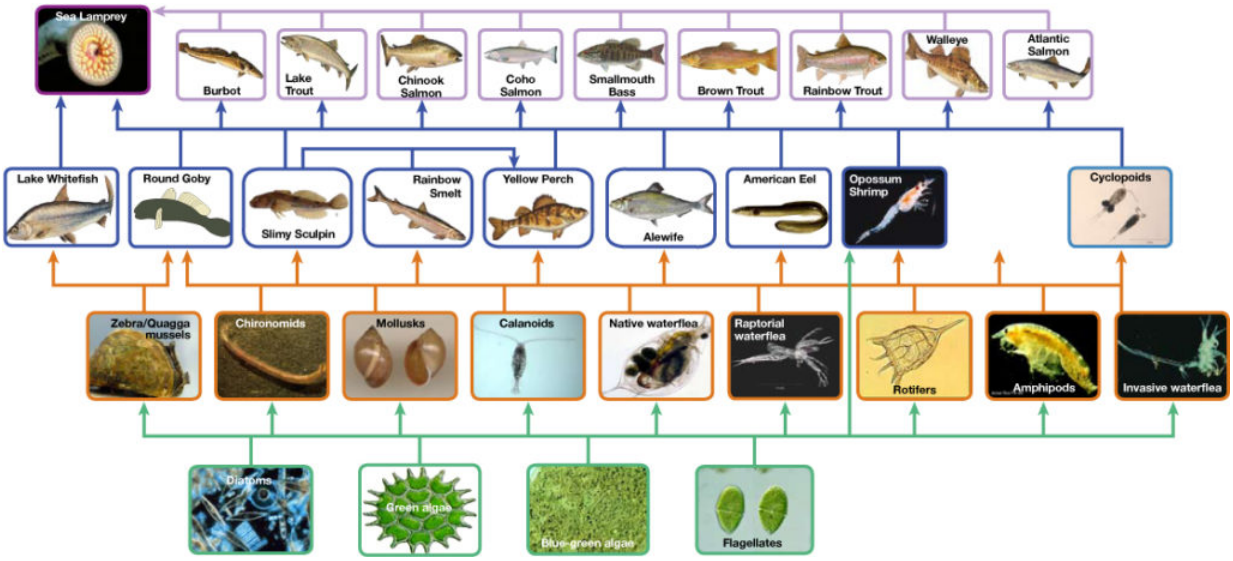


Figure 3. This food web shows the interactions between organisms across trophic levels in the Lake Ontario ecosystem. Primary producers are outlined in green, primary consumers in orange, secondary consumers in blue, and tertiary (apex) consumers in purple. Arrows point from an organism that is consumed to the organism that consumes it. Notice how some lines point to more than one trophic level. For example, the opossum shrimp eats both primary producers and primary consumers. (credit: NOAA, GLERL)

A comparison of the two types of structural ecosystem models shows strength in both. Food chains are more flexible for analytical modeling, are easier to follow, and are easier to experiment with, whereas food web models more accurately represent ecosystem

structure and dynamics, and data can be directly used as input for simulation modeling.

Head to this online interactive simulator to investigate food web function. In the *Interactive Labs* box, under **Food Web**, click **Step 1**. Read the instructions first, and then click **Step 2** for additional instructions. When you are ready to create a simulation, in the upper-right corner of the *Interactive Labs* box, click **OPEN SIMULATOR**.

Two general types of food webs are often shown interacting within a single ecosystem. A **grazing food web** (such as the Lake Ontario food web in Figure 3) has plants or other photosynthetic organisms at its base, followed by herbivores and various carnivores. A **detrital food web** consists of a base of organisms that feed on decaying organic matter (dead organisms), called decomposers or detritivores. These organisms are usually bacteria or fungi that recycle organic material back into the biotic part of the ecosystem as they themselves are consumed by other organisms. As all ecosystems require a method to recycle material from dead organisms, most grazing food webs have an associated detrital food web. For example, in a meadow ecosystem, plants may support a grazing food web of different organisms, primary and other levels of consumers, while at the same time supporting a detrital food web of bacteria, fungi, and detrivorous invertebrates feeding off dead plants and animals.

Consequences of Food Webs: Biological Magnification

One of the most important environmental consequences of ecosystem dynamics is biomagnification. **Biomagnification** is the increasing concentration of persistent, toxic substances in organisms at each trophic level, from the primary producers to the apex consumers. Many substances have been shown to bioaccumulate, including classical studies with the pesticide **d**ichloro**d**iphenyl**t**richloroethane (DDT), which was published in the 1960s bestseller, *Silent Spring*, by Rachel Carson. DDT was a commonly used pesticide before its dangers became known. In some aquatic ecosystems, organisms from each trophic level consumed many organisms of the lower level, which caused DDT to increase in birds (apex consumers) that ate fish. Thus, the birds accumulated sufficient amounts of DDT to cause fragility in their eggshells. This effect increased egg breakage during nesting and was shown to have adverse effects on these bird populations. The use of DDT was banned in the United States in the 1970s.

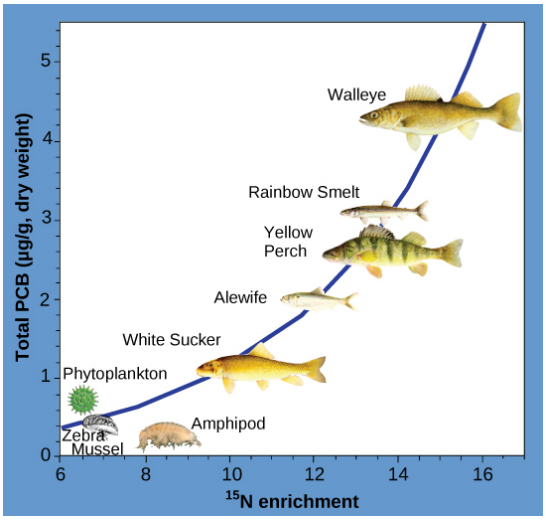


Figure 4. This chart shows the PCB concentrations found at the various trophic levels in the Saginaw Bay ecosystem of Lake Huron. Numbers on the *x*-axis reflect enrichment with heavy isotopes of nitrogen (15N), which is a marker for increasing trophic level. Notice that the fish in the higher trophic levels accumulate more PCBs than those in lower trophic levels. (credit: Patricia Van Hoof, NOAA, GLERL)

Other substances that biomagnify are polychlorinated biphenyls (PCBs), which were used in coolant liquids in the United States until their use was banned in 1979, and heavy metals, such as mercury, lead, and cadmium. These substances were best studied in aquatic ecosystems, where fish species at different trophic levels accumulate toxic substances brought through the ecosystem by the primary producers. As illustrated in a study performed by the National Oceanic and Atmospheric Administration (NOAA) in the Saginaw Bay of Lake Huron (Figure 4), PCB concentrations increased from the ecosystem's primary producers (phytoplankton) through the different trophic levels of fish species. The apex consumer (walleye) has more than four times the amount of PCBs compared to phytoplankton. Also, based on results from other studies, birds that eat these fish may have PCB levels at least one order of magnitude higher than those found in the lake fish.

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

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18.5: Energy Flow through Ecosystems

Learning Objectives

- Describe how energy flows through ecosystems

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

It is important to understand how organisms acquire energy and how that energy is passed from one organism to another through food webs and their constituent food chains. Food webs illustrate how energy flows directionally through ecosystems, including how efficiently organisms acquire it, use it, and how much remains for use by other organisms of the food web.

How Organisms Acquire Energy in a Food Web

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

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



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

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

Chemoautotrophs are primarily bacteria that are found in rare ecosystems where sunlight is not available, such as in those associated with dark caves or hydrothermal vents at the bottom of the ocean (Figure 1). Many chemoautotrophs in hydrothermal vents use hydrogen sulfide (H_2S), which is released from the vents as a source of chemical energy. This allows chemoautotrophs to synthesize complex organic molecules, such as glucose, for their own energy and in turn supplies energy to the rest of the ecosystem.

Productivity within Trophic Levels

Productivity within an ecosystem can be defined as the percentage of energy entering the ecosystem incorporated into biomass in a particular trophic level. **Biomass** is the total mass, in a unit area at the time of measurement, of living or previously living organisms within a trophic level. Ecosystems have characteristic amounts of biomass at each trophic level. For example, in the

English Channel ecosystem the primary producers account for a biomass of 4 g/m^2 (grams per meter squared), while the primary consumers exhibit a biomass of 21 g/m^2.

The productivity of the primary producers is especially important in any ecosystem because these organisms bring energy to other living organisms by photoautotrophy or chemoautotrophy. The rate at which photosynthetic primary producers incorporate energy from the sun is called **gross primary productivity**. An example of gross primary productivity is shown in the compartment diagram of energy flow in Howard T. Odum's classical study of the Silver Springs, Florida, holistic ecosystem in the mid-twentieth century (Figure 2). This study shows the energy content and transfer between various ecosystem compartments. In this ecosystem, the total energy accumulated by the primary producers (gross primary productivity) was shown to be 20,810 kcal/m^2/yr.

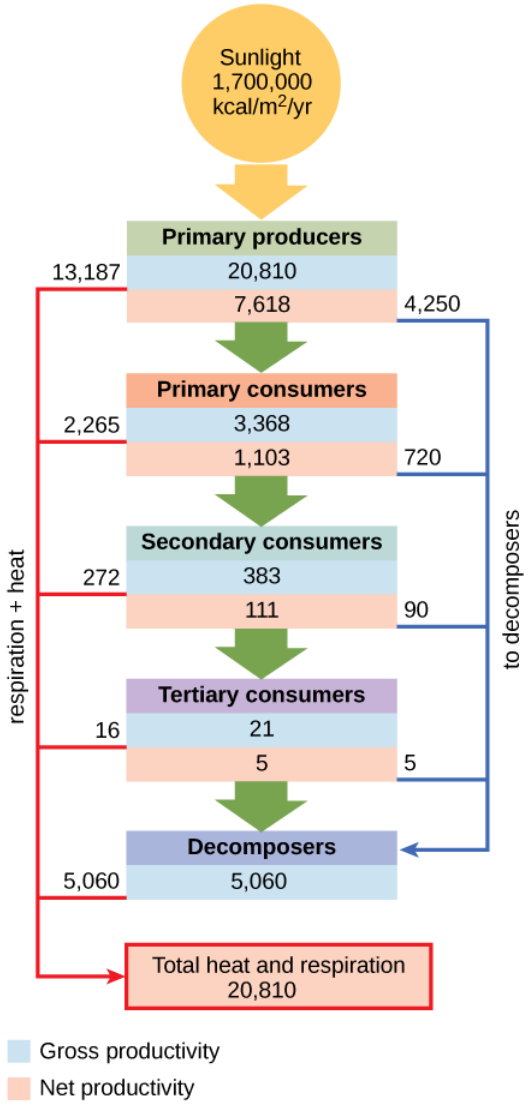


Figure 2. This conceptual model shows the flow of energy through a spring ecosystem in Silver Springs, Florida. Notice that the energy decreases with each increase in trophic level.

? Practice Question

Why do you think the value for gross productivity of the primary producers is the same as the value for total heat and respiration (20,810 kcal/m^2/yr)?

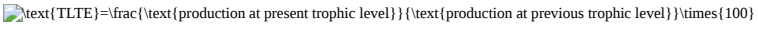
[practice-area rows="2"][/practice-area]
[reveal-answer q="439384"]Show Answer[/reveal-answer]
[hidden-answer a="439384"]According to the first law of thermodynamics, energy can neither be created nor destroyed.

Eventually, all energy consumed by living systems is lost as heat or used for respiration, and the total energy output of the system must equal the energy that went into it.[/hidden-answer]

Because all organisms need to use some of this energy for their own functions (like respiration and resulting metabolic heat loss) scientists often refer to the net primary productivity of an ecosystem. **Net primary productivity** is the energy that remains in the primary producers after accounting for the organisms' respiration and heat loss. The net productivity is then available to the primary consumers at the next trophic level. In our Silver Spring example, 13,187 of the 20,810 kcal/m^2/yr were used for respiration or were lost as heat, leaving 7,632 kcal/m^2/yr of energy for use by the primary consumers.

Ecological Efficiency

As illustrated in Figure 2, large amounts of energy are lost from the ecosystem from one trophic level to the next level as energy flows from the primary producers through the various trophic levels of consumers and decomposers. The main reason for this loss is the second law of thermodynamics, which states that whenever energy is converted from one form to another, there is a tendency toward disorder (entropy) in the system. In biologic systems, this means a great deal of energy is lost as metabolic heat when the organisms from one trophic level consume the next level. In the Silver Springs ecosystem example (Figure 2), we see that the primary consumers produced 1103 kcal/m^2/yr from the 7618 kcal/m^2/yr of energy available to them from the primary producers. The measurement of energy transfer efficiency between two successive trophic levels is termed the **trophic level transfer efficiency (TLTE)** and is defined by the formula:



In Silver Springs, the TLTE between the first two trophic levels was approximately 14.8 percent. The low efficiency of energy transfer between trophic levels is usually the major factor that limits the length of food chains observed in a food web. The fact is, after four to six energy transfers, there is not enough energy left to support another trophic level. Returning to the Lake Ontario example (shown in Figure 3), only three energy transfers occurred between the primary producer, (green algae), and the apex consumer (Chinook salmon).

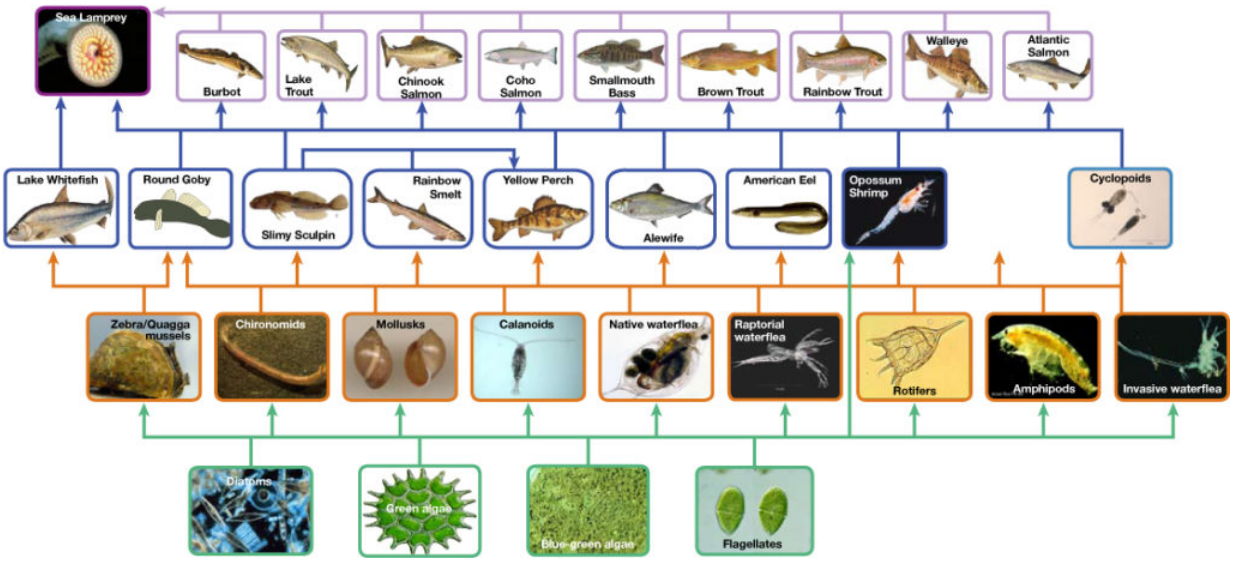
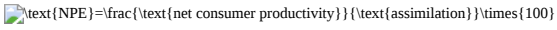


Figure 3. This food web shows the interactions between organisms across trophic levels in the Lake Ontario ecosystem. Primary producers are outlined in green, primary consumers in orange, secondary consumers in blue, and tertiary (apex) consumers in purple. Arrows point from an organism that is consumed to the organism that consumes it. Notice how some lines point to more than one trophic level. For example, the opossum shrimp eats both primary producers and primary consumers. (credit: NOAA, GLERL)

Ecologists have many different methods of measuring energy transfers within ecosystems. Some transfers are easier or more difficult to measure depending on the complexity of the ecosystem and how much access scientists have to observe the ecosystem. In other words, some ecosystems are more difficult to study than others, and sometimes the quantification of energy transfers has to be estimated.

Another main parameter that is important in characterizing energy flow within an ecosystem is the net production efficiency. **Net production efficiency (NPE)** allows ecologists to quantify how efficiently organisms of a particular trophic level incorporate the energy they receive into biomass; it is calculated using the following formula:



Net consumer productivity is the energy content available to the organisms of the next trophic level. **Assimilation** is the biomass (energy content generated per unit area) of the present trophic level after accounting for the energy lost due to incomplete ingestion of food, energy used for respiration, and energy lost as waste. Incomplete ingestion refers to the fact that some consumers eat only a part of their food. For example, when a lion kills an antelope, it will eat everything except the hide and bones. The lion is missing the energy-rich bone marrow inside the bone, so the lion does not make use of all the calories its prey could provide.

Thus, NPE measures how efficiently each trophic level uses and incorporates the energy from its food into biomass to fuel the next trophic level. In general, cold-blooded animals (ectotherms), such as invertebrates, fish, amphibians, and reptiles, use less of the energy they obtain for respiration and heat than warm-blooded animals (endotherms), such as birds and mammals. The extra heat generated in endotherms, although an advantage in terms of the activity of these organisms in colder environments, is a major disadvantage in terms of NPE. Therefore, many endotherms have to eat more often than ectotherms to get the energy they need for survival. In general, NPE for ectotherms is an order of magnitude (10x) higher than for endotherms. For example, the NPE for a caterpillar eating leaves has been measured at 18 percent, whereas the NPE for a squirrel eating acorns may be as low as 1.6 percent.

The inefficiency of energy use by warm-blooded animals has broad implications for the world's food supply. It is widely accepted that the meat industry uses large amounts of crops to feed livestock, and because the NPE is low, much of the energy from animal feed is lost. For example, it costs about 1¢ to produce 1000 dietary calories (kcal) of corn or soybeans, but approximately $0.19 to produce a similar number of calories growing cattle for beef consumption. The same energy content of milk from cattle is also costly, at approximately $0.16 per 1000 kcal. Much of this difference is due to the low NPE of cattle. Thus, there has been a growing movement worldwide to promote the consumption of non-meat and non-dairy foods so that less energy is wasted feeding animals for the meat industry.

Ecological Pyramids

The structure of ecosystems can be visualized with ecological pyramids, which were first described by the pioneering studies of Charles Elton in the 1920s. **Ecological pyramids** show the relative amounts of various parameters (such as number of organisms, energy, and biomass) across trophic levels.

Pyramids of numbers can be either upright or inverted, depending on the ecosystem. As shown in Figure 4, typical grassland during the summer has a base of many plants and the numbers of organisms decrease at each trophic level. However, during the summer in a temperate forest, the base of the pyramid consists of few trees compared with the number of primary consumers, mostly insects. Because trees are large, they have great photosynthetic capability, and dominate other plants in this ecosystem to obtain sunlight. Even in smaller numbers, primary producers in forests are still capable of supporting other trophic levels.

Another way to visualize ecosystem structure is with pyramids of biomass. This pyramid measures the amount of energy converted into living tissue at the different trophic levels. Using the Silver Springs ecosystem example, this data exhibits an upright biomass pyramid (Figure 4), whereas the pyramid from the English Channel example is inverted. The plants (primary producers) of the Silver Springs ecosystem make up a large percentage of the biomass found there. However, the phytoplankton in the English Channel example make up less biomass than the primary consumers, the zooplankton. As with inverted pyramids of numbers, this inverted pyramid is not due to a lack of productivity from the primary producers, but results from the high turnover rate of the phytoplankton. The phytoplankton are consumed rapidly by the primary consumers, thus, minimizing their biomass at any particular point in time. However, phytoplankton reproduce quickly, thus they are able to support the rest of the ecosystem.

Pyramid ecosystem modeling can also be used to show energy flow through the trophic levels. Notice that these numbers are the same as those used in the energy flow compartment diagram in Figure 2. Pyramids of energy are always upright, and an ecosystem without sufficient primary productivity cannot be supported. All types of ecological pyramids are useful for characterizing ecosystem structure. However, in the study of energy flow through the ecosystem, pyramids of energy are the most consistent and representative models of ecosystem structure (Figure 4).

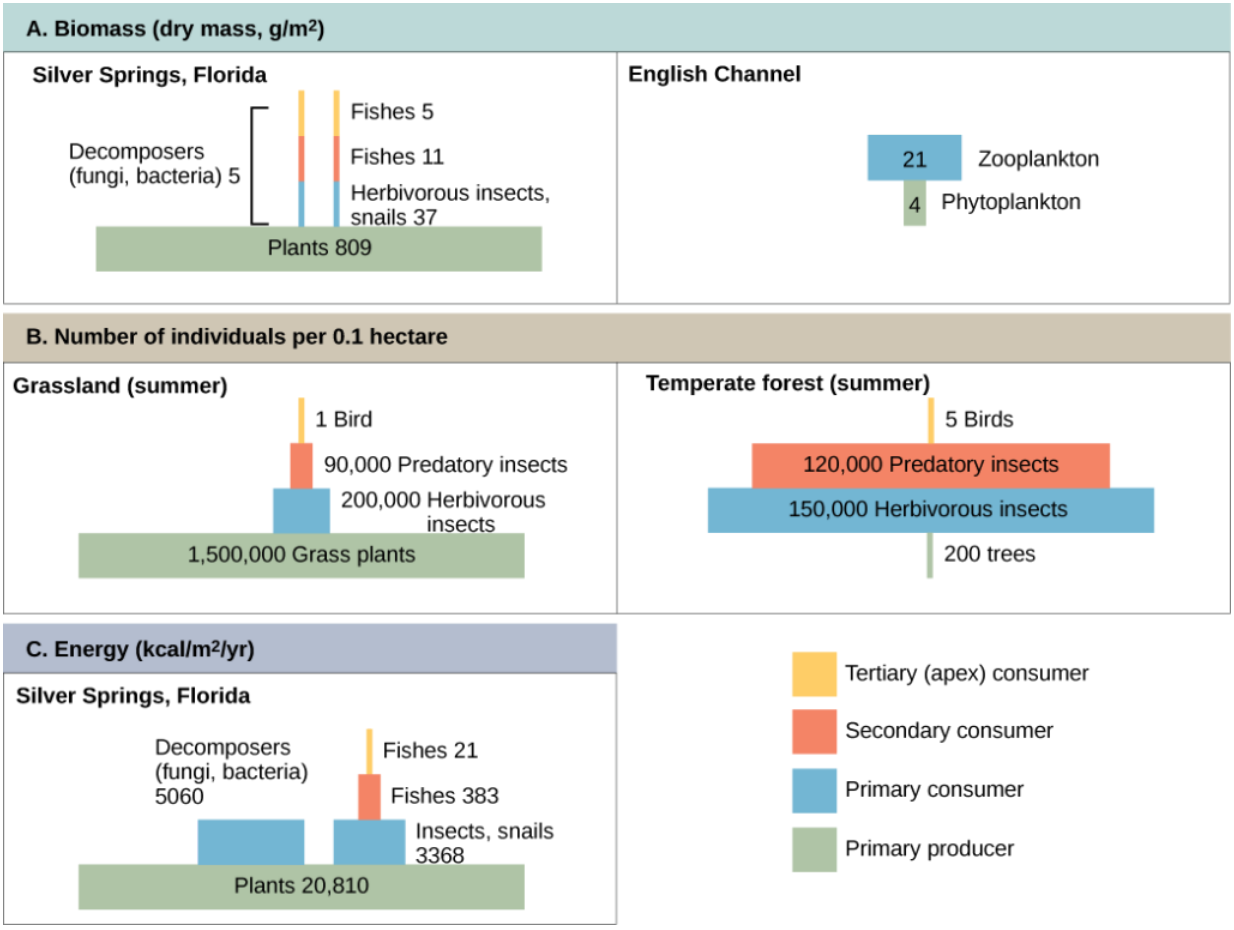


Figure 4. Ecological pyramids depict the (a) biomass, (b) number of organisms, and (c) energy in each trophic level.

? Practice Question

Pyramids depicting the number of organisms or biomass may be inverted, upright, or even diamond-shaped. Energy pyramids, however, are always upright. Why?

[practice-area rows="2"][/practice-area]
[reveal-answer q="924780"]Show Answer[/reveal-answer]
[hidden-answer a="924780"]Pyramids of organisms may be inverted or diamond-shaped because a large organism, such as a tree, can sustain many smaller organisms. Likewise, a low biomass of organisms can sustain a larger biomass at the next trophic level because the organisms reproduce rapidly and thus supply continuous nourishment. Energy pyramids, however, must always be upright because of the laws of thermodynamics. The first law of thermodynamics states that energy can neither be created nor destroyed; thus, each trophic level must acquire energy from the trophic level below. The second law of thermodynamics states that, during the transfer of energy, some energy is always lost as heat; thus, less energy is available at each higher trophic level.[/hidden-answer]

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Learning Objectives

Organisms in an ecosystem acquire energy in a variety of ways, which is transferred between trophic levels as the energy flows from the bottom to the top of the food web, with energy being lost at each transfer. The efficiency of these transfers is important for understanding the different behaviors and eating habits of warm-blooded versus cold-blooded animals. Modeling of ecosystem energy is best done with ecological pyramids of energy, although other ecological pyramids provide other vital information about ecosystem structure.

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18.6: Introduction to Biogeochemical Cycles

What you'll learn to do: Discuss the biogeochemical cycles of water, carbon, nitrogen, phosphorus, and sulfur

Energy flows directionally through ecosystems, entering as sunlight (or inorganic molecules for chemoautotrophs) and leaving as heat during the many transfers between trophic levels. However, the matter that makes up living organisms is conserved and recycled. The six most common elements associated with organic molecules—carbon, nitrogen, hydrogen, oxygen, phosphorus, and sulfur—take a variety of chemical forms and may exist for long periods in the atmosphere, on land, in water, or beneath the Earth's surface. Geologic processes, such as weathering, erosion, water drainage, and the subduction of the continental plates, all play a role in this recycling of materials. Because geology and chemistry have major roles in the study of this process, the recycling of inorganic matter between living organisms and their environment is called a **biogeochemical cycle**.

The cycling of these elements is interconnected. For example, the movement of water is critical for the leaching of nitrogen and phosphate into rivers, lakes, and oceans. Furthermore, the ocean itself is a major reservoir for carbon. Thus, mineral nutrients are cycled, either rapidly or slowly, through the entire biosphere, from one living organism to another, and between the biotic and abiotic world.

Head to this website to learn more about biogeochemical cycles.

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18.7: The Hydrologic Cycle

Learning Outcomes

- Discuss the hydrologic cycle and why it is essential for all life on Earth

Water contains hydrogen and oxygen, which is essential to all living processes. The **hydrosphere** is the area of the Earth where water movement and storage occurs: as liquid water on the surface and beneath the surface or frozen (rivers, lakes, oceans, groundwater, polar ice caps, and glaciers), and as water vapor in the atmosphere.

Water is the basis of all living processes. The human body is more than 1/2 water and human cells are more than 70 percent water. Thus, most land animals need a supply of fresh water to survive. However, when examining the stores of water on Earth, 97.5 percent of it is non-potable salt water (Figure 1). Of the remaining water, 99 percent is locked underground as water or as ice. Thus, less than 1 percent of fresh water is easily accessible from lakes and rivers. Many living things, such as plants, animals, and fungi, are dependent on the small amount of fresh surface water supply, a lack of which can have massive effects on ecosystem dynamics. Humans, of course, have developed technologies to increase water availability, such as digging wells to harvest groundwater, storing rainwater, and using desalination to obtain drinkable water from the ocean. Although this pursuit of drinkable water has been ongoing throughout human history, the supply of fresh water is still a major issue in modern times.

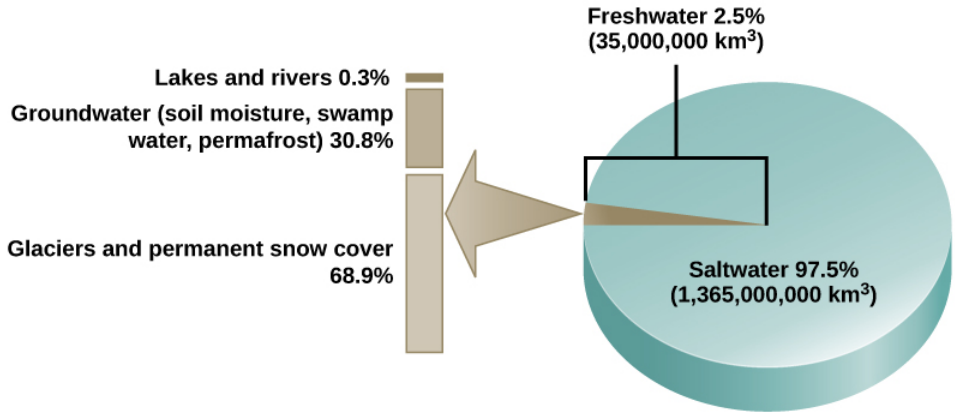


Figure 1. Only 2.5 percent of water on Earth is fresh water, and less than 1 percent of fresh water is easily accessible to living things.

Water cycling is extremely important to ecosystem dynamics. Water has a major influence on climate and, thus, on the environments of ecosystems, some located on distant parts of the Earth. Most of the water on Earth is stored for long periods in the oceans, underground, and as ice. Figure 2 illustrates the average time that an individual water molecule may spend in the Earth's major water reservoirs. **Residence time** is a measure of the average time an individual water molecule stays in a particular reservoir. A large amount of the Earth's water is locked in place in these reservoirs as ice, beneath the ground, and in the ocean, and, thus, is unavailable for short-term cycling (only surface water can evaporate).

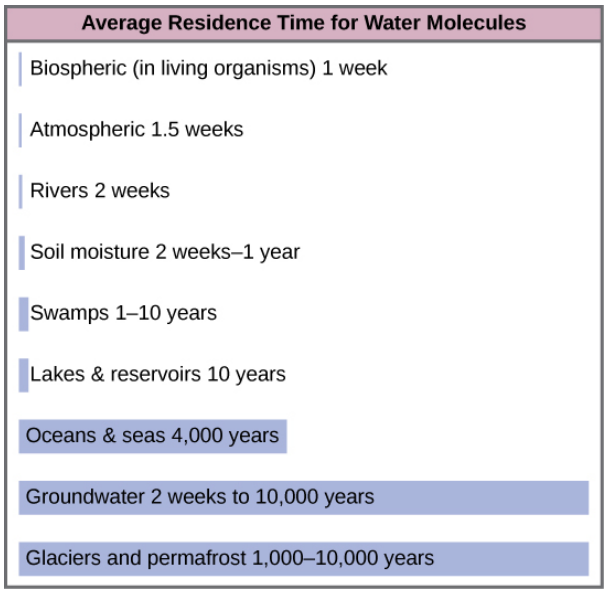


Figure 2. This graph shows the average residence time for water molecules in the Earth's water reservoirs.

There are various processes that occur during the cycling of water, shown in Figure 3. These processes include the following:

- evaporation/sublimation
- condensation/precipitation
- subsurface water flow
- surface runoff/snowmelt
- streamflow

The water cycle is driven by the sun's energy as it warms the oceans and other surface waters. This leads to the **evaporation** (water to water vapor) of liquid surface water and the **sublimation** (ice to water vapor) of frozen water, which deposits large amounts of water vapor into the atmosphere. Over time, this water vapor condenses into clouds as liquid or frozen droplets and is eventually followed by **precipitation** (rain or snow), which returns water to the Earth's surface. Rain eventually permeates into the ground, where it may evaporate again if it is near the surface, flow beneath the surface, or be stored for long periods. More easily observed is **surface runoff**: the flow of fresh water either from rain or melting ice. Runoff can then make its way through streams and lakes to the oceans or flow directly to the oceans themselves.

Rain and surface runoff are major ways in which minerals, including carbon, nitrogen, phosphorus, and sulfur, are cycled from land to water. The environmental effects of runoff will be discussed later as these cycles are described.

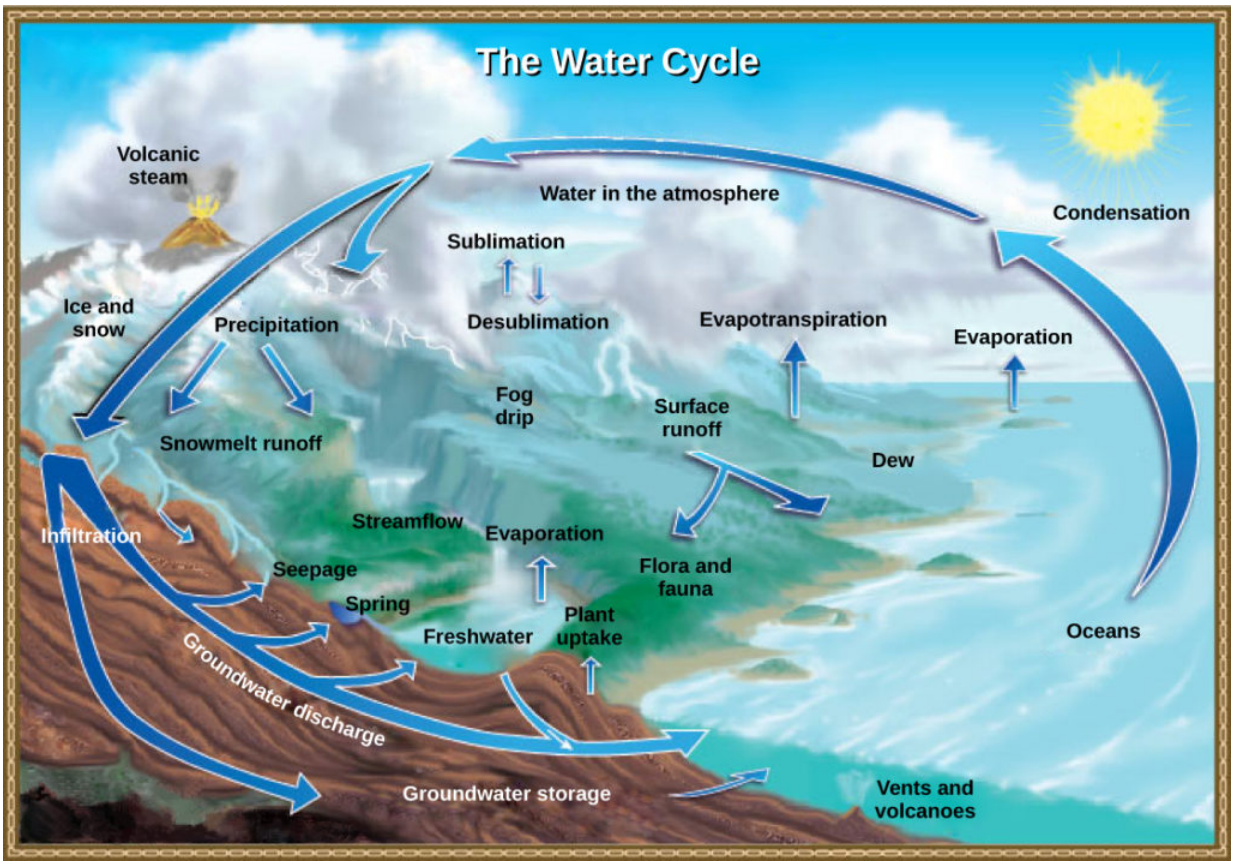


Figure 3. Water from the land and oceans enters the atmosphere by evaporation or sublimation, where it condenses into clouds and falls as rain or snow. Precipitated water may enter freshwater bodies or infiltrate the soil. The cycle is complete when surface or groundwater reenters the ocean. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

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18.8: The Carbon Cycle

Learning Objectives

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

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

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

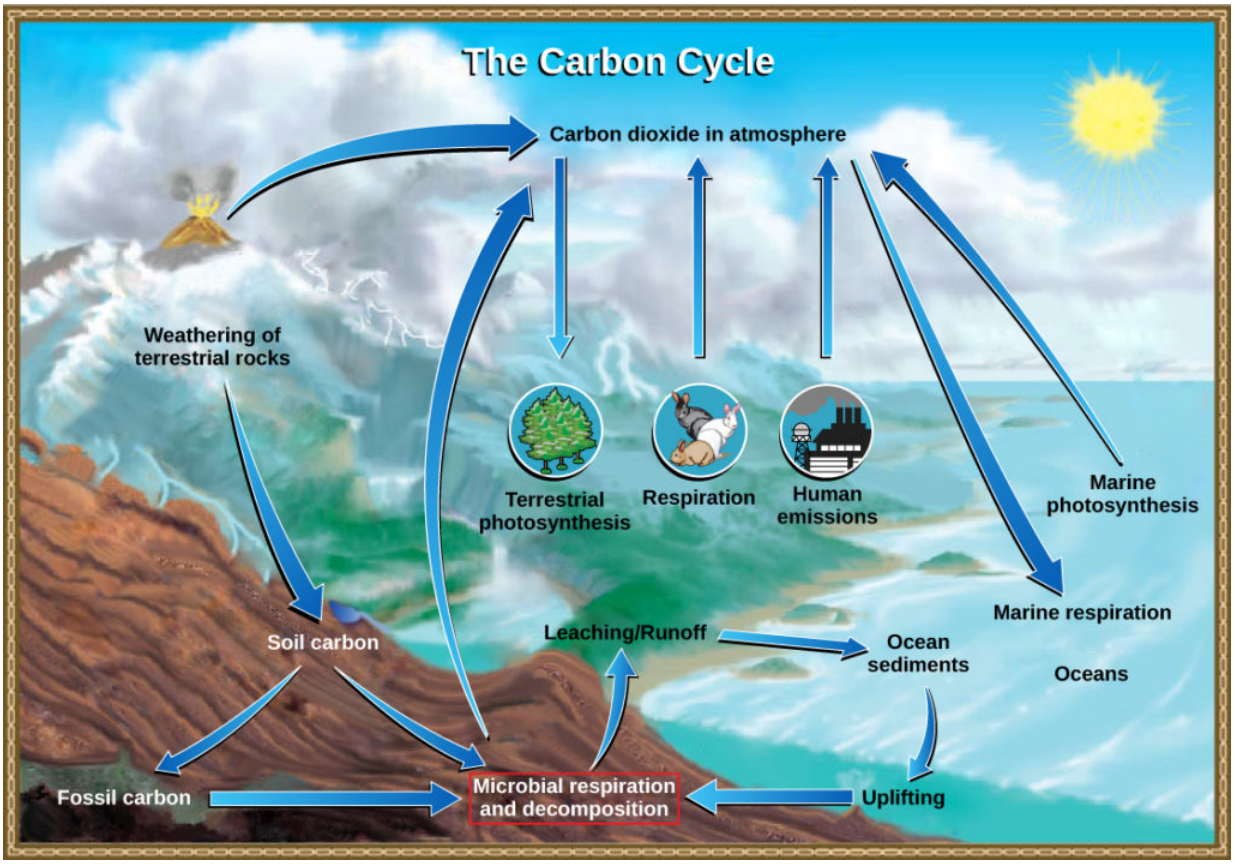


Figure 1. Carbon dioxide gas exists in the atmosphere and is dissolved in water. Photosynthesis converts carbon dioxide gas to organic carbon, and respiration cycles the organic carbon back into carbon dioxide gas. Long-term storage of organic carbon occurs when matter from living organisms is buried deep underground and becomes fossilized. Volcanic activity and, more recently, human emissions, bring this stored carbon back into the carbon cycle. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

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

The Biological Carbon Cycle

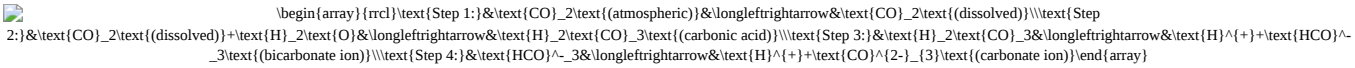
Living organisms are connected in many ways, even between ecosystems. A good example of this connection is the exchange of carbon between autotrophs and heterotrophs within and between ecosystems by way of atmospheric carbon dioxide. Carbon dioxide is the basic building block that most autotrophs use to build multi-carbon, high energy compounds, such as glucose. The energy harnessed from the sun is used by these organisms to form the covalent bonds that link carbon atoms together. These chemical bonds thereby store this energy for later use in the process of respiration. Most terrestrial autotrophs obtain their carbon dioxide directly from the atmosphere, while marine autotrophs acquire it in the dissolved form (carbonic acid, $H_2CO_3^-$). However carbon dioxide is acquired, a by-product of the process is oxygen. The photosynthetic organisms are responsible for depositing approximately 21 percent oxygen content of the atmosphere that we observe today.

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

The Biogeochemical Carbon Cycle

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

As stated, the atmosphere is a major reservoir of carbon in the form of carbon dioxide and is essential to the process of photosynthesis. The level of carbon dioxide in the atmosphere is greatly influenced by the reservoir of carbon in the oceans. The exchange of carbon between the atmosphere and water reservoirs influences how much carbon is found in each location, and each one affects the other reciprocally. Carbon dioxide (CO_2) from the atmosphere dissolves in water and combines with water molecules to form carbonic acid, and then it ionizes to carbonate and bicarbonate ions:



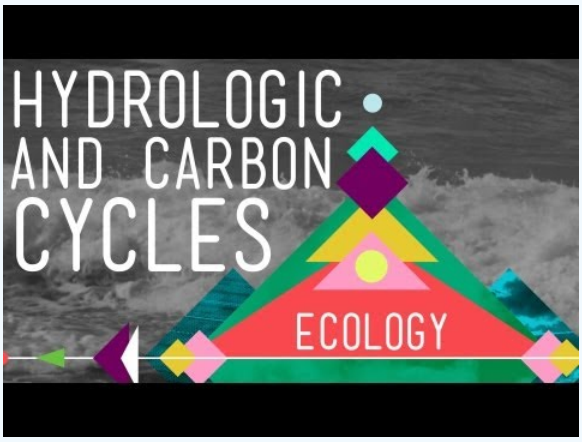
The equilibrium coefficients are such that more than 90 percent of the carbon in the ocean is found as bicarbonate ions. Some of these ions combine with seawater calcium to form calcium carbonate ($CaCO_3$), a major component of marine organism shells. These organisms eventually form sediments on the ocean floor. Over geologic time, the calcium carbonate forms limestone, which comprises the largest carbon reservoir on Earth.

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

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

Learning Objectives

This video talks about two of the biogeochemical cycles: carbon and water. The hydrologic cycle describes how water moves on, above, and below the surface of the Earth, driven by energy supplied by the sun and wind. The carbon cycle does the same . . . for carbon!



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18.9: The Nitrogen Cycle

Learning Outcomes

- Discuss the nitrogen cycle and nitrogen's role on Earth

Nitrogen is a major component of our nucleic acids and proteins and is critical to human agriculture. Getting nitrogen into the living world is difficult. Plants and phytoplankton are not equipped to incorporate nitrogen from the atmosphere (which exists as tightly bonded, triple covalent N_2) even though this molecule comprises approximately 78 percent of the atmosphere. Nitrogen enters the living world via free-living and symbiotic bacteria, which incorporate nitrogen into their macromolecules through nitrogen fixation (conversion of N_2). Cyanobacteria live in most aquatic ecosystems where sunlight is present; they play a key role in nitrogen fixation. Cyanobacteria are able to use inorganic sources of nitrogen to "fix" nitrogen. *Rhizobium* bacteria live symbiotically in the root nodules of legumes (such as peas, beans, and peanuts) and provide them with the organic nitrogen they need. Free-living bacteria, such as *Azotobacter*, are also important nitrogen fixers.

Organic nitrogen is especially important to the study of ecosystem dynamics since many ecosystem processes, such as primary production and decomposition, are limited by the available supply of nitrogen. As shown in Figure 1, the nitrogen that enters living systems by nitrogen fixation is successively converted from organic nitrogen back into nitrogen gas by bacteria. This process occurs in three steps in terrestrial systems: ammonification, nitrification, and denitrification. First, the ammonification process converts nitrogenous waste from living animals or from the remains of dead animals into ammonium (NH_4^+) by certain bacteria and fungi. Second, the ammonium is converted to nitrites (NO_2^-) by nitrifying bacteria, such as *Nitrosomonas*, through nitrification. Subsequently, nitrites are converted to nitrates (NO_3^-) by similar organisms. Third, the process of denitrification occurs, whereby bacteria, such as *Pseudomonas* and *Clostridium*, convert the nitrates into nitrogen gas, allowing it to re-enter the atmosphere.

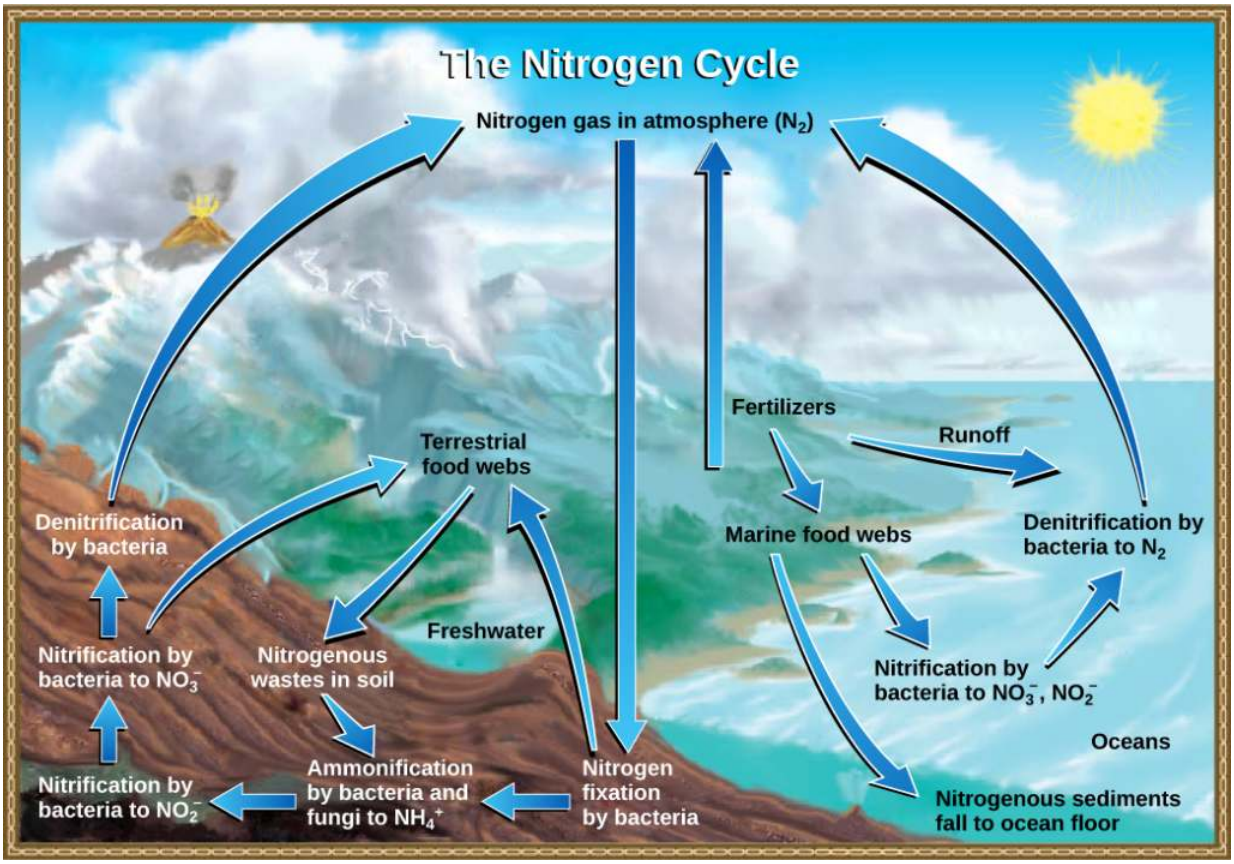


Figure 1. Nitrogen enters the living world from the atmosphere via nitrogen-fixing bacteria. This nitrogen and nitrogenous waste from animals is then processed back into gaseous nitrogen by soil bacteria, which also supply terrestrial food webs with the organic nitrogen they need. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Practice Question

Which of the following statements about the nitrogen cycle is false?

a. Ammonification converts organic nitrogenous matter from living organisms into ammonium (NH_4^+).
b. Denitrification by bacteria converts nitrates (NO_3^-) to nitrogen gas (N_2).
c. Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).
d. Nitrogen fixing bacteria convert nitrogen gas (N_2) into organic compounds.

[reveal-answer q="404642"]Show Answer[/reveal-answer]
[hidden-answer a="404642"]Statement c is false.[/hidden-answer]

Human activity can release nitrogen into the environment by two primary means: the combustion of fossil fuels, which releases different nitrogen oxides, and by the use of artificial fertilizers in agriculture, which are then washed into lakes, streams, and rivers by surface runoff. Atmospheric nitrogen is associated with several effects on Earth's ecosystems including the production of acid rain (as nitric acid, HNO_3) and greenhouse gas (as nitrous oxide, N_2O) potentially causing climate change. A major effect from fertilizer runoff is saltwater and freshwater **eutrophication**, a process whereby nutrient runoff causes the excess growth of microorganisms, depleting dissolved oxygen levels and killing ecosystem fauna.

A similar process occurs in the marine nitrogen cycle, where the ammonification, nitrification, and denitrification processes are performed by marine bacteria. Some of this nitrogen falls to the ocean floor as sediment, which can then be moved to land in geologic time by uplift of the Earth's surface and thereby incorporated into terrestrial rock. Although the movement of nitrogen from rock directly into living systems has been traditionally seen as insignificant compared with nitrogen fixed from the atmosphere, a recent study showed that this process may indeed be significant and should be included in any study of the global nitrogen cycle.

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18.10: The Phosphorus Cycle

Learning Outcomes

- Discuss the phosphorus cycle and phosphorus's role on Earth

Phosphorus, a major component of nucleic acid (along with nitrogen), is an essential nutrient for living processes; it is also a major component of phospholipids, and, as calcium phosphate, makes up the supportive components of our bones. Phosphorus is often the limiting nutrient (necessary for growth) in aquatic ecosystems (Figure 1).

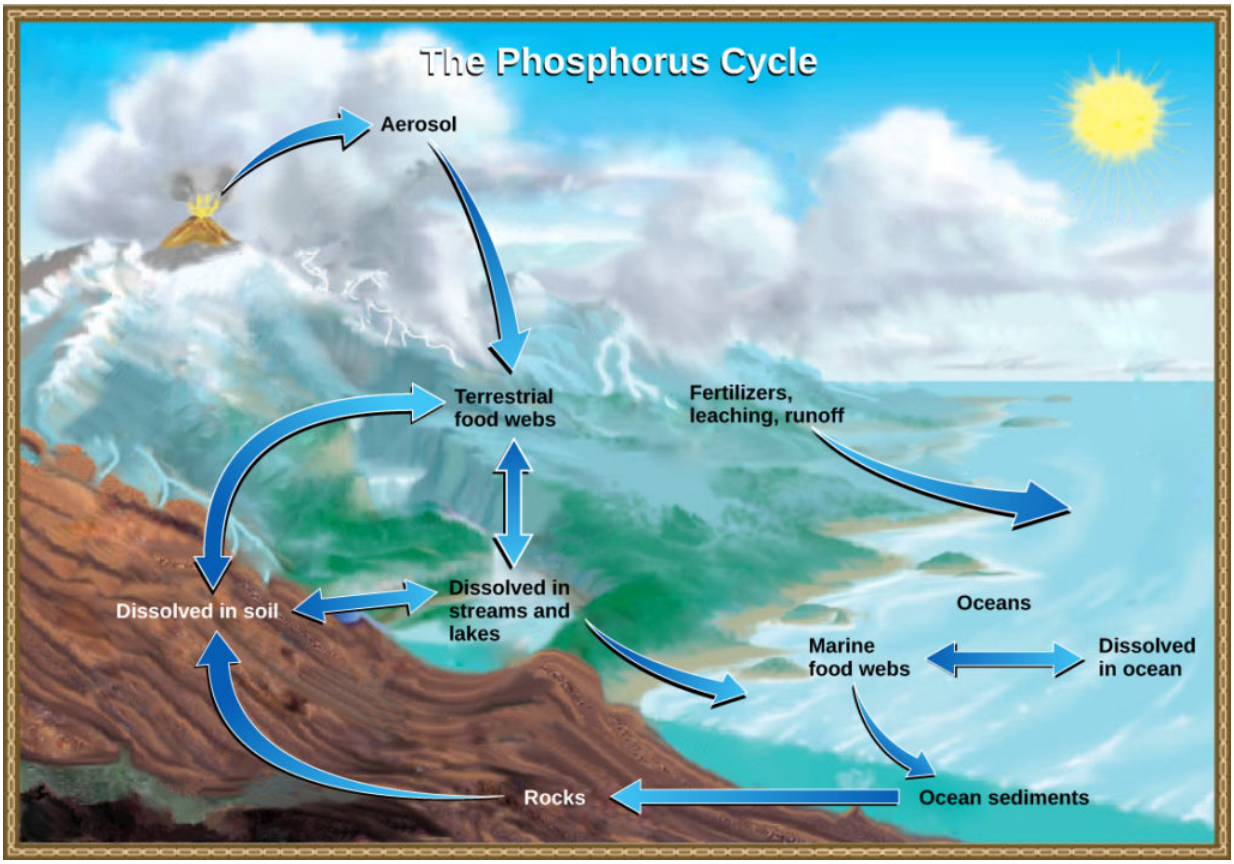


Figure 1. In nature, phosphorus exists as the phosphate ion (PO_4^{3-}). Weathering of rocks and volcanic activity releases phosphate into the soil, water, and air, where it becomes available to terrestrial food webs. Phosphate enters the oceans via surface runoff, groundwater flow, and river flow. Phosphate dissolved in ocean water cycles into marine food webs. Some phosphate from the marine food webs falls to the ocean floor, where it forms sediment. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Phosphorus occurs in nature as the phosphate ion (PO_4^{3-}). In addition to phosphate runoff as a result of human activity, natural surface runoff occurs when it is leached from phosphate-containing rock by weathering, thus sending phosphates into rivers, lakes, and the ocean. This rock has its origins in the ocean. Phosphate-containing ocean sediments form primarily from the bodies of ocean organisms and from their excretions. However, in remote regions, volcanic ash, aerosols, and mineral dust may also be significant phosphate sources. This sediment then is moved to land over geologic time by the uplifting of areas of the Earth's surface.

Phosphorus is also reciprocally exchanged between phosphate dissolved in the ocean and marine ecosystems. The movement of phosphate from the ocean to the land and through the soil is extremely slow, with the average phosphate ion having an oceanic residence time between 20,000 and 100,000 years.

Phosphorus is one of the main ingredients in artificial fertilizers used in agriculture and their associated environmental impacts on our surface water. Excess phosphorus and nitrogen that enters these ecosystems from fertilizer runoff and from sewage causes

excessive growth of microorganisms and depletes the dissolved oxygen, which leads to the death of many ecosystem fauna, such as shellfish and finfish. This process is responsible for dead zones in lakes and at the mouths of many major rivers (Figure 2).

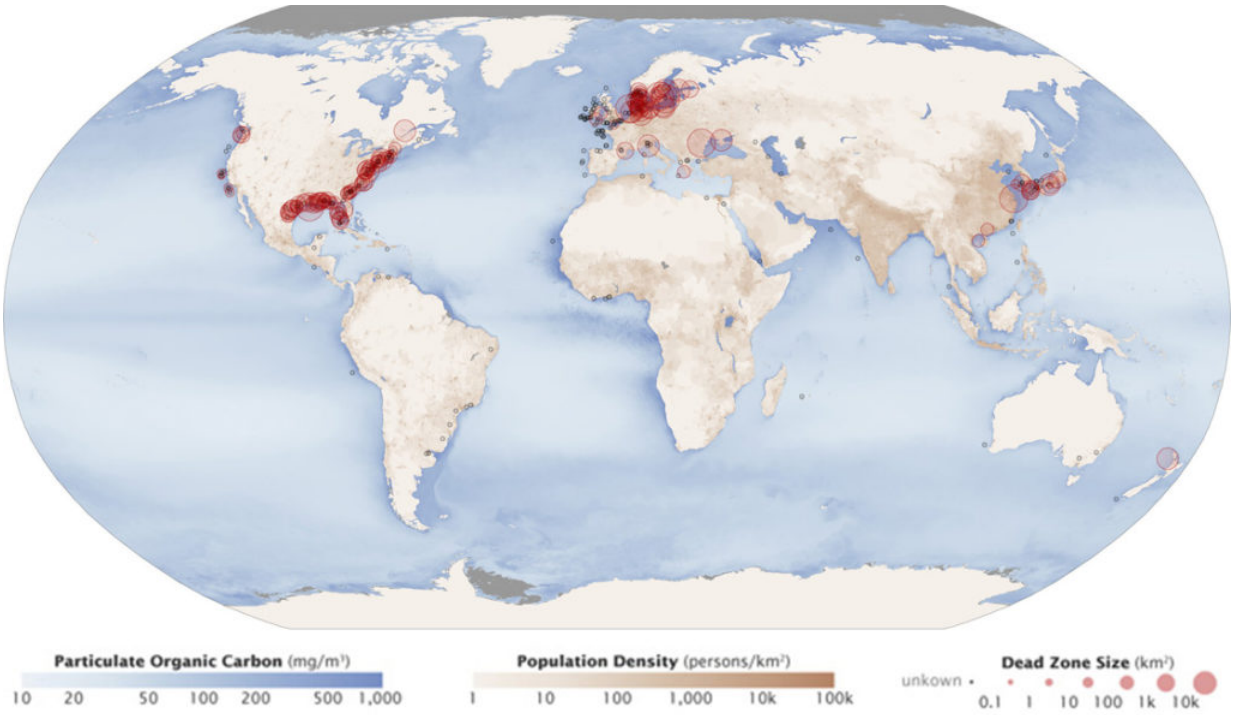


Figure 2. Dead zones occur when phosphorus and nitrogen from fertilizers cause excessive growth of microorganisms, which depletes oxygen and kills fauna. Worldwide, large dead zones are found in coastal areas of high population density. (credit: NASA Earth Observatory)

A **dead zone** is an area within a freshwater or marine ecosystem where large areas are depleted of their normal flora and fauna; these zones can be caused by eutrophication, oil spills, dumping of toxic chemicals, and other human activities. The number of dead zones has been increasing for several years, and more than 400 of these zones were present as of 2008. One of the worst dead zones is off the coast of the United States in the Gulf of Mexico, where fertilizer runoff from the Mississippi River basin has created a dead zone of over 8463 square miles. Phosphate and nitrate runoff from fertilizers also negatively affect several lake and bay ecosystems including the Chesapeake Bay in the eastern United States.

Chesapeake Bay



Figure 3. This (a) satellite image shows the Chesapeake Bay, an ecosystem affected by phosphate and nitrate runoff. A (b) member of the Army Corps of Engineers holds a clump of oysters being used as a part of the oyster restoration effort in the bay. (credit a: modification of work by NASA/MODIS; credit b: modification of work by U.S. Army)

The Chesapeake Bay has long been valued as one of the most scenic areas on Earth; it is now in distress and is recognized as a declining ecosystem. In the 1970s, the Chesapeake Bay was one of the first ecosystems to have identified dead zones, which continue to kill many fish and bottom-dwelling species, such as clams, oysters, and worms. Several species have declined in the Chesapeake Bay due to surface water runoff containing excess nutrients from artificial fertilizer used on land. The source of the

fertilizers (with high nitrogen and phosphate content) is not limited to agricultural practices. There are many nearby urban areas and more than 150 rivers and streams empty into the bay that are carrying fertilizer runoff from lawns and gardens. Thus, the decline of the Chesapeake Bay is a complex issue and requires the cooperation of industry, agriculture, and everyday homeowners.

Of particular interest to conservationists is the oyster population; it is estimated that more than 200,000 acres of oyster reefs existed in the bay in the 1700s, but that number has now declined to only 36,000 acres. Oyster harvesting was once a major industry for Chesapeake Bay, but it declined 88 percent between 1982 and 2007. This decline was due not only to fertilizer runoff and dead zones but also to overharvesting. Oysters require a certain minimum population density because they must be in close proximity to reproduce. Human activity has altered the oyster population and locations, greatly disrupting the ecosystem.

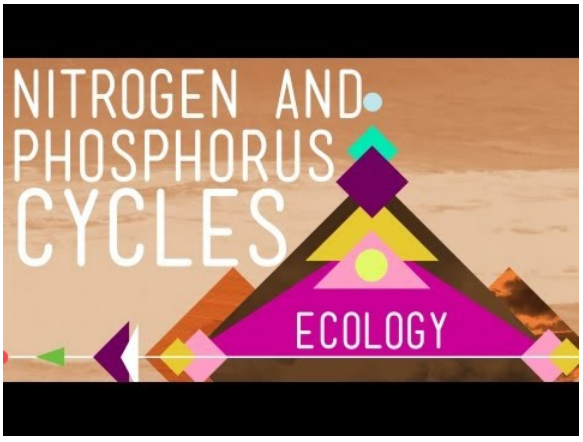
The restoration of the oyster population in the Chesapeake Bay has been ongoing for several years with mixed success. Not only do many people find oysters good to eat, but they also clean up the bay. Oysters are filter feeders, and as they eat, they clean the water around them. In the 1700s, it was estimated that it took only a few days for the oyster population to filter the entire volume of the bay. Today, with changed water conditions, it is estimated that the present population would take nearly a year to do the same job.

Restoration efforts have been ongoing for several years by non-profit organizations, such as the Chesapeake Bay Foundation. The restoration goal is to find a way to increase population density so the oysters can reproduce more efficiently. Many disease-resistant varieties (developed at the Virginia Institute of Marine Science for the College of William and Mary) are now available and have been used in the construction of experimental oyster reefs. Efforts to clean and restore the bay by Virginia and Delaware have been hampered because much of the pollution entering the bay comes from other states, which stresses the need for inter-state cooperation to gain successful restoration.

The new, hearty oyster strains have also spawned a new and economically viable industry—oyster aquaculture—which not only supplies oysters for food and profit, but also has the added benefit of cleaning the bay.

Video Review

Many organisms require nitrogen and phosphorus. This video explains just how they go about getting them via the nitrogen and phosphorus cycles.



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18.11: The Sulfur Cycle

Learning Outcomes

- Discuss the sulfur cycle and sulfur's role on Earth

Sulfur, an essential element for the macromolecules of living things, is released into the atmosphere by the burning of fossil fuels, such as coal. As a part of the amino acid cysteine, it is involved in the formation of disulfide bonds within proteins, which help to determine their 3-D folding patterns, and hence their functions. As shown in Figure 1, sulfur cycles between the oceans, land, and atmosphere. Atmospheric sulfur is found in the form of sulfur dioxide (SO_2) and enters the atmosphere in three ways: from the decomposition of organic molecules, from volcanic activity and geothermal vents, and from the burning of fossil fuels by humans.

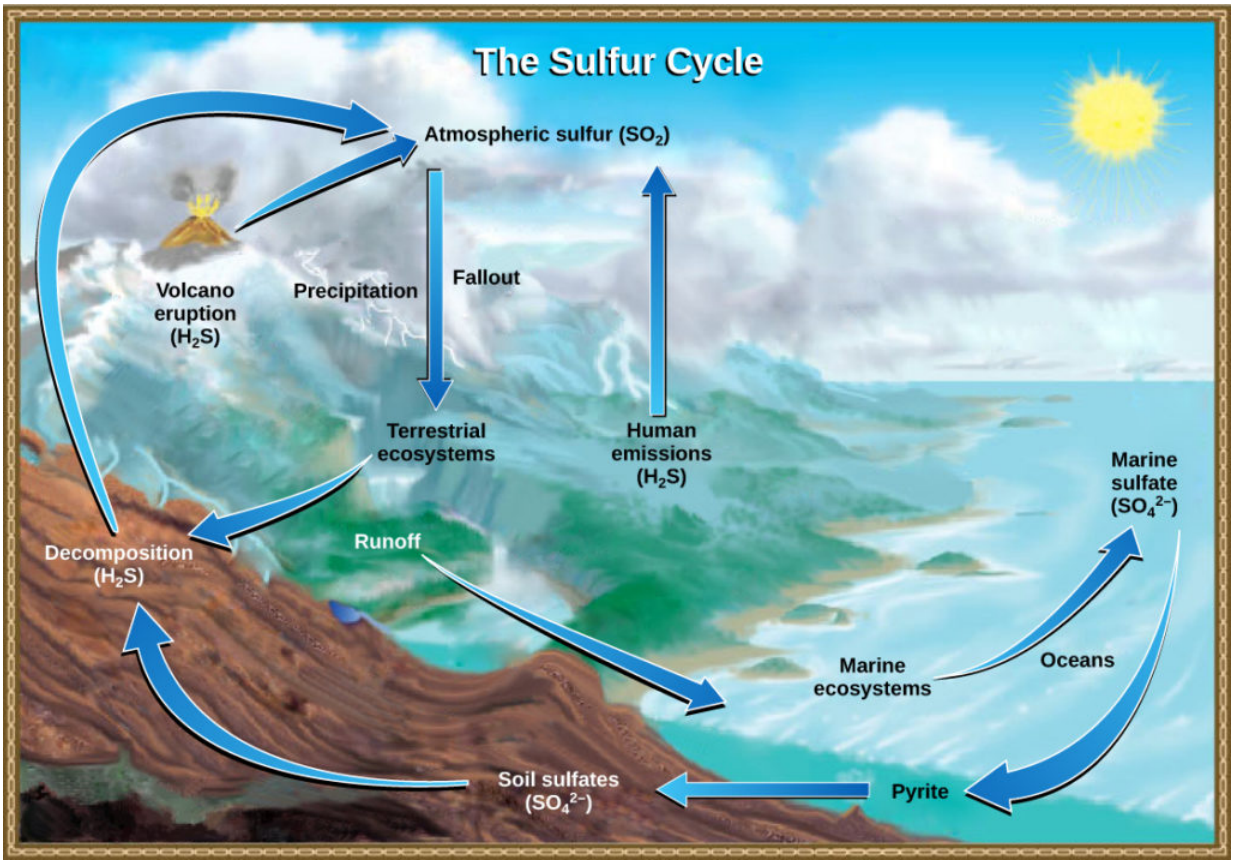


Figure 1. Sulfur dioxide from the atmosphere becomes available to terrestrial and marine ecosystems when it is dissolved in precipitation as weak sulfuric acid or when it falls directly to the Earth as fallout. Weathering of rocks also makes sulfates available to terrestrial ecosystems. Decomposition of living organisms returns sulfates to the ocean, soil and atmosphere. (credit: modification of work by John M. Evans and Howard Perlman, USGS)



Figure 2. At this sulfur vent in Lassen Volcanic National Park in northeastern California, the yellowish sulfur deposits are visible near the mouth of the vent.

On land, sulfur is deposited in four major ways: precipitation, direct fallout from the atmosphere, rock weathering, and geothermal vents (Figure 2). Atmospheric sulfur is found in the form of sulfur dioxide (SO_2), and as rain falls through the atmosphere, sulfur is dissolved in the form of weak sulfuric acid (H_2SO_4). Sulfur can also fall directly from the atmosphere in a process called **fallout**. Also, the weathering of sulfur-containing rocks releases sulfur into the soil. These rocks originate from ocean sediments that are moved to land by the geologic uplifting of ocean sediments. Terrestrial ecosystems can then make use of these soil sulfates (SO_4^-), and upon the death and decomposition of these organisms, release the sulfur back into the atmosphere as hydrogen sulfide (H_2S) gas.

Sulfur enters the ocean via runoff from land, from atmospheric fallout, and from underwater geothermal vents. Some ecosystems rely on chemoautotrophs using sulfur as a biological energy source. This sulfur then supports marine ecosystems in the form of sulfates.

Human activities have played a major role in altering the balance of the global sulfur cycle. The burning of large quantities of fossil fuels, especially from coal, releases larger amounts of hydrogen sulfide gas into the atmosphere. As rain falls through this gas, it creates the phenomenon known as acid rain. **Acid rain** is corrosive rain caused by rainwater falling to the ground through sulfur dioxide gas, turning it into weak sulfuric acid, which causes damage to aquatic ecosystems. Acid rain damages the natural environment by lowering the pH of lakes, which kills many of the resident fauna; it also affects the man-made environment through the chemical degradation of buildings. For example, many marble monuments, such as the Lincoln Memorial in Washington, DC, have suffered significant damage from acid rain over the years. These examples show the wide-ranging effects of human activities on our environment and the challenges that remain for our future.

Click this link to learn more about global climate change.

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18.12: Introduction to Climate Change

What you'll learn to do: Identify evidence of climate change

All biomes are universally affected by global conditions, such as climate, that ultimately shape each biome's environment. Scientists who study climate have noted a series of marked changes that have gradually become increasingly evident during the last sixty years. Global climate change is the term used to describe altered global weather patterns, including a worldwide increase in temperature, due largely to rising levels of atmospheric carbon dioxide.

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18.13: What is Climate Change?

Learning Objectives

- Define global climate change

A common misconception about global climate change is that a specific weather event occurring in a particular region (for example, a very cool week in June in central Indiana) is evidence of global climate change. However, a cold week in June is a weather-related event and not a climate-related one. These misconceptions often arise because of confusion over the terms climate and weather.

Climate refers to the long-term, predictable atmospheric conditions of a specific area. The climate of a biome is characterized by having consistent temperature and annual rainfall ranges. Climate does not address the amount of rain that fell on one particular day in a biome or the colder-than-average temperatures that occurred on one day. In contrast, **weather** refers to the conditions of the atmosphere during a short period of time. Weather forecasts are usually made for 48-hour cycles. Long-range weather forecasts are available but can be unreliable.

To better understand the difference between climate and weather, imagine that you are planning an outdoor event in northern Wisconsin. You would be thinking about *climate* when you plan the event in the summer rather than the winter because you have long-term knowledge that any given Saturday in the months of May to August would be a better choice for an outdoor event in Wisconsin than any given Saturday in January. However, you cannot determine the specific day that the event should be held on because it is difficult to accurately predict the weather on a specific day. Climate can be considered “average” weather.

Climate change can be understood by approaching three areas of study:

- current and past global climate change
- causes of past and present-day global climate change
- ancient and current results of climate change

It is helpful to keep these three different aspects of climate change clearly separated when consuming media reports about global climate change. It is common for reports and discussions about global climate change to confuse the data showing that Earth’s climate is changing with the factors that drive this climate change.

Climate Change

Climate change, and specifically the anthropogenic (meaning, caused by humans) warming trend presently underway, is recognized as a major extinction threat, particularly when combined with other threats such as habitat loss. Scientists disagree about the likely magnitude of the effects, with extinction rate estimates ranging from 15 percent to 40 percent of species committed to extinction by 2050. Scientists do agree, however, that climate change will alter regional climates, including rainfall and snowfall patterns, making habitats less hospitable to the species living in them. The warming trend will shift colder climates toward the north and south poles, forcing species to move with their adapted climate norms while facing habitat gaps along the way. The shifting ranges will impose new competitive regimes on species as they find themselves in contact with other species not present in their historic range. One such unexpected species contact is between polar bears and grizzly bears. Previously, these two species had separate ranges. Now, their ranges are overlapping and there are documented cases of these two species mating and producing viable offspring. Changing climates also throw off species’ delicate timing adaptations to seasonal food resources and breeding times. Many contemporary mismatches to shifts in resource availability and timing have already been documented.



Figure 1. Since 2008, grizzly bears (*Ursus arctos horribilis*) have been spotted farther north than their historic range, a possible consequence of climate change. As a result, grizzly bear habitat now overlaps polar bear (*Ursus maritimus*) habitat. The two kinds of bears, which are capable of mating and producing viable offspring, are considered separate species as historically they lived in different habitats and never met. However, in 2006 a hunter shot a wild grizzly-polar bear hybrid known as a grolar bear, the first wild hybrid ever found.

Range shifts are already being observed: for example, some European bird species ranges have moved 91 km northward. The same study suggested that the optimal shift based on warming trends was double that distance, suggesting that the populations are not moving quickly enough. Range shifts have also been observed in plants, butterflies, other insects, freshwater fishes, reptiles, and mammals.

Climate gradients will also move up mountains, eventually crowding species higher in altitude and eliminating the habitat for those species adapted to the highest elevations. Some climates will completely disappear. The rate of warming appears to be accelerated in the arctic, which is recognized as a serious threat to polar bear populations that require sea ice to hunt seals during the winter months: seals are the only source of protein available to polar bears. A trend to decreasing sea ice coverage has occurred since observations began in the mid-twentieth century. The rate of decline observed in recent years is far greater than previously predicted by climate models.

Finally, global warming will raise ocean levels due to melt water from glaciers and the greater volume of warmer water. Shorelines will be inundated, reducing island size, which will have an effect on some species, and a number of islands will disappear entirely. Additionally, the gradual melting and subsequent refreezing of the poles, glaciers, and higher elevation mountains—a cycle that has provided freshwater to environments for centuries—will also be jeopardized. This could result in an overabundance of salt water and a shortage of fresh water.

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18.14: Evidence for Global Climate Change

Learning Outcomes

- Identify evidence for global climate change

Since scientists cannot go back in time to directly measure climatic variables, such as average temperature and precipitation, they must instead indirectly measure temperature. To do this, scientists rely on historical evidence of Earth's past climate.

Antarctic ice cores are a key example of such evidence. These ice cores are samples of polar ice obtained by means of drills that reach thousands of meters into ice sheets or high mountain glaciers. Viewing the ice cores is like traveling backwards through time; the deeper the sample, the earlier the time period. Trapped within the ice are bubbles of air and other biological evidence that can reveal temperature and carbon dioxide data. Antarctic ice cores have been collected and analyzed to indirectly estimate the temperature of the Earth over the past 400,000 years (Figure 1a). The 0 °C on this graph refers to the long-term average. Temperatures that are greater than 0 °C exceed Earth's long-term average temperature. Conversely, temperatures that are less than 0 °C are less than Earth's average temperature. This figure shows that there have been periodic cycles of increasing and decreasing temperature.

Before the late 1800s, the Earth has been as much as 9 °C cooler and about 3 °C warmer. Note that the graph in Figure 1b shows that the atmospheric concentration of carbon dioxide has also risen and fallen in periodic cycles; note the relationship between carbon dioxide concentration and temperature. Figure 1b shows that carbon dioxide levels in the atmosphere have historically cycled between 180 and 300 parts per million (ppm) by volume.

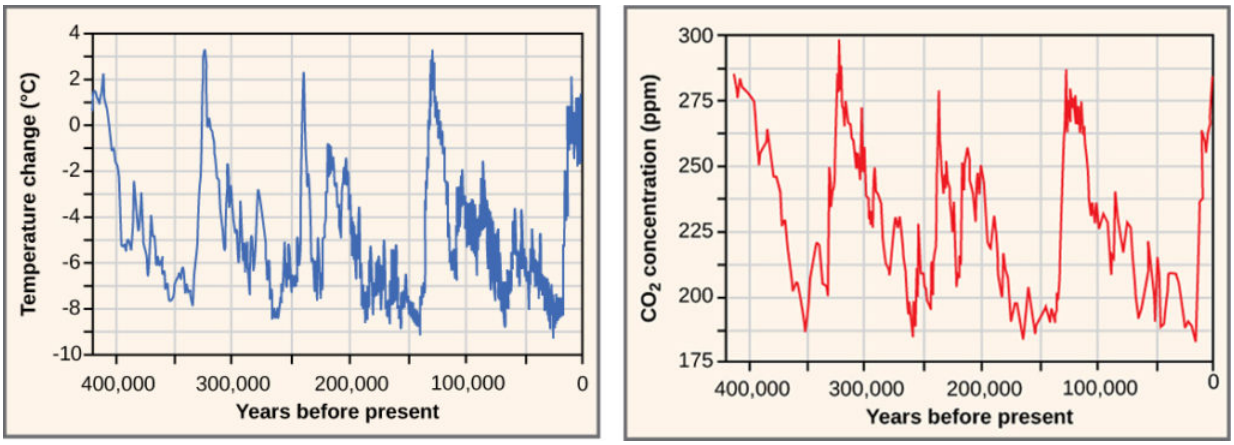


Figure 1. Ice at the Russian Vostok station in East Antarctica was laid down over the course 420,000 years and reached a depth of over 3,000 m. By measuring the amount of CO_2 trapped in the ice, scientists have determined past atmospheric CO_2 concentrations. Temperatures relative to modern day were determined from the amount of deuterium (an isotope of hydrogen) present.

Figure 1a does not show the last 2,000 years with enough detail to compare the changes of Earth's temperature during the last 400,000 years with the temperature change that has occurred in the more recent past. Two significant temperature anomalies, or irregularities, have occurred in the last 2000 years. These are the Medieval Climate Anomaly (or the Medieval Warm Period) and the Little Ice Age. A third temperature anomaly aligns with the Industrial Era. The Medieval Climate Anomaly occurred between 900 and 1300 AD. During this time period, many climate scientists think that slightly warmer weather conditions prevailed in many parts of the world; the higher-than-average temperature changes varied between 0.10 °C and 0.20 °C above the norm. Although 0.10 °C does not seem large enough to produce any noticeable change, it did free seas of ice. Because of this warming, the Vikings were able to colonize Greenland.

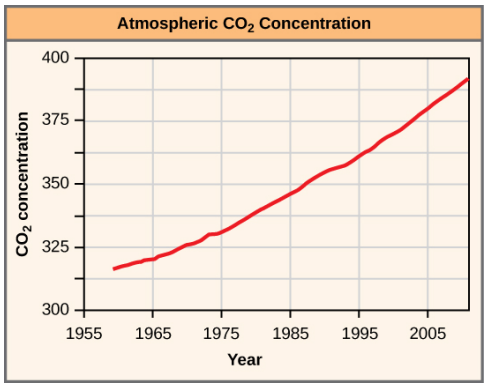


Figure 2. The atmospheric concentration of CO_2 has risen steadily since the beginning of industrialization.

The Little Ice Age was a cold period that occurred between 1550 AD and 1850 AD. During this time, a slight cooling of a little less than 1 °C was observed in North America, Europe, and possibly other areas of the Earth. This 1 °C change in global temperature is a seemingly small deviation in temperature (as was observed during the Medieval Climate Anomaly); however, it also resulted in noticeable changes. Historical accounts reveal a time of exceptionally harsh winters with much snow and frost.

The Industrial Revolution, which began around 1750, was characterized by changes in much of human society. Advances in agriculture increased the food supply, which improved the standard of living for people in Europe and the United States. New technologies were invented and provided jobs and cheaper goods. These new technologies were powered using fossil fuels, especially coal. The Industrial Revolution starting in the early nineteenth century ushered in the beginning of the Industrial Era. When a fossil fuel is burned, carbon dioxide is released. With the beginning of the Industrial Era, atmospheric carbon dioxide began to rise (Figure 2).

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18.15: Drivers of Global Climate Change

Learning Outcomes

- Identify different drivers of global climate change

Since it is not possible to go back in time to directly observe and measure climate, scientists use indirect evidence to determine the drivers, or factors, that may be responsible for climate change. The indirect evidence includes data collected using ice cores, boreholes (a narrow shaft bored into the ground), tree rings, glacier lengths, pollen remains, and ocean sediments. The data shows a correlation between the timing of temperature changes and drivers of climate change: before the Industrial Era (pre-1780), there were three drivers of climate change that were not related to human activity or atmospheric gases. The first of these is the Milankovitch cycles. The **Milankovitch cycles** describe the effects of slight changes in the Earth's orbit on Earth's climate. The length of the Milankovitch cycles ranges between 19,000 and 100,000 years. In other words, one could expect to see some predictable changes in the Earth's climate associated with changes in the Earth's orbit at a minimum of every 19,000 years.

The variation in the sun's intensity is the second natural factor responsible for climate change. **Solar intensity** is the amount of solar power or energy the sun emits in a given amount of time. There is a direct relationship between solar intensity and temperature. As solar intensity increases (or decreases), the Earth's temperature correspondingly increases (or decreases). Changes in solar intensity have been proposed as one of several possible explanations for the Little Ice Age.

Finally, volcanic eruptions are a third natural driver of climate change. Volcanic eruptions can last a few days, but the solids and gases released during an eruption can influence the climate over a period of a few years, causing short-term climate changes. The gases and solids released by volcanic eruptions can include carbon dioxide, water vapor, sulfur dioxide, hydrogen sulfide, hydrogen, and carbon monoxide. Generally, volcanic eruptions cool the climate. This occurred in 1783 when volcanos in Iceland erupted and caused the release of large volumes of sulfuric oxide. This led to **haze-effect cooling**, a global phenomenon that occurs when dust, ash, or other suspended particles block out sunlight and trigger lower global temperatures as a result; haze-effect cooling usually extends for one or more years. In Europe and North America, haze-effect cooling produced some of the lowest average winter temperatures on record in 1783 and 1784.

Greenhouse gases are probably the most significant drivers of the climate. When heat energy from the sun strikes the Earth, gases known as **greenhouse gases** trap the heat in the atmosphere, as do the glass panes of a greenhouse keep heat from escaping. The greenhouse gases that affect Earth include carbon dioxide, methane, water vapor, nitrous oxide, and ozone. Approximately half of the radiation from the sun passes through these gases in the atmosphere and strikes the Earth. This radiation is converted into thermal radiation on the Earth's surface, and then a portion of that energy is re-radiated back into the atmosphere. Greenhouse gases, however, reflect much of the thermal energy back to the Earth's surface. The more greenhouse gases there are in the atmosphere, the more thermal energy is reflected back to the Earth's surface. Greenhouse gases absorb and emit radiation and are an important factor in the **greenhouse effect**: the warming of Earth due to carbon dioxide and other greenhouse gases in the atmosphere.

Evidence supports the relationship between atmospheric concentrations of carbon dioxide and temperature: as carbon dioxide rises, global temperature rises. Since 1950, the concentration of atmospheric carbon dioxide has increased from about 280 ppm to 382 ppm in 2006. In 2011, the atmospheric carbon dioxide concentration was 392 ppm. However, the planet would not be inhabitable by current life forms if water vapor did not produce its drastic greenhouse warming effect.

Scientists look at patterns in data and try to explain differences or deviations from these patterns. The atmospheric carbon dioxide data reveal a historical pattern of carbon dioxide increasing and decreasing, cycling between a low of 180 ppm and a high of 300 ppm. Scientists have concluded that it took around 50,000 years for the atmospheric carbon dioxide level to increase from its low minimum concentration to its higher maximum concentration. However, starting recently, atmospheric carbon dioxide concentrations have increased beyond the historical maximum of 300 ppm. The current increases in atmospheric carbon dioxide have happened very quickly—in a matter of hundreds of years rather than thousands of years. What is the reason for this difference in the rate of change and the amount of increase in carbon dioxide? A key factor that must be recognized when comparing the historical data and the current data is the presence of modern human society; no other driver of climate change has yielded changes in atmospheric carbon dioxide levels at this rate or to this magnitude.



Figure 1. The burning of fossil fuels in industry and by vehicles releases carbon dioxide and other greenhouse gases into the atmosphere. (credit: “Pöllö”/Wikimedia Commons)

Human activity releases carbon dioxide and methane, two of the most important greenhouse gases, into the atmosphere in several ways. The primary mechanism that releases carbon dioxide is the burning of fossil fuels, such as gasoline, coal, and natural gas (Figure 1).

Deforestation, cement manufacture, animal agriculture, the clearing of land, and the burning of forests are other human activities that release carbon dioxide. Methane (CH_4) is produced when bacteria break down organic matter under anaerobic conditions. Anaerobic conditions can happen when organic matter is trapped underwater (such as in rice paddies) or in the intestines of herbivores. Methane can also be released from natural gas fields and the decomposition that occurs in landfills. Another source of methane is the melting of clathrates.

Clathrates are frozen chunks of ice and methane found at the bottom of the ocean. When water warms, these chunks of ice melt and methane is released. As the ocean’s water temperature increases, the rate at which clathrates melt is increasing, releasing even more methane. This leads to increased levels of methane in the atmosphere, which further accelerates the rate of global warming. This is an example of the positive feedback loop that is leading to the rapid rate of increase of global temperatures.

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18.16: Documented Results of Climate Change

Learning Objectives

- Discuss the results of climate change in our world

Scientists have geological evidence of the consequences of long-ago climate change. Modern-day phenomena such as retreating glaciers and melting polar ice cause a continual rise in sea level. Meanwhile, changes in climate can negatively affect organisms.

Geological Climate Change

Global warming has been associated with at least one planet-wide extinction event during the geological past. The Permian extinction event occurred about 251 million years ago toward the end of the roughly 50-million-year-long geological time span known as the Permian period. This geologic time period was one of the three warmest periods in Earth's geologic history. Scientists estimate that approximately 70 percent of the terrestrial plant and animal species and 84 percent of marine species became extinct, vanishing forever near the end of the Permian period. Organisms that had adapted to wet and warm climatic conditions, such as annual rainfall of 300–400 cm (118–157 in) and 20 °C–30 °C (68 °F–86 °F) in the tropical wet forest, may not have been able to survive the Permian climate change.

Watch this NASA video to discover the mixed effects of global warming on plant growth. While scientists found that warmer temperatures in the 1980s and 1990s caused an increase in plant productivity, this advantage has since been counteracted by more frequent droughts.

Present Climate Change

A number of global events have occurred that may be attributed to climate change during our lifetimes. Glacier National Park in Montana is undergoing the retreat of many of its glaciers, a phenomenon known as glacier recession. In 1850, the area contained approximately 150 glaciers. By 2010, however, the park contained only about 24 glaciers greater than 25 acres in size. One of these glaciers is the Grinnell Glacier (Figure 1) at Mount Gould. Between 1966 and 2005, the size of Grinnell Glacier shrank by 40 percent. Similarly, the mass of the ice sheets in Greenland and the Antarctic is decreasing: Greenland lost 150–250 km^3 of ice per year between 2002 and 2006. In addition, the size and thickness of the Arctic sea ice is decreasing.



Figure 1. The effect of global warming can be seen in the continuing retreat of Grinnel Glacier. The mean annual temperature in the park has increased 1.33 °C since 1900. The loss of a glacier results in the loss of summer meltwaters, sharply reducing seasonal water supplies and severely affecting local ecosystems. (credit: modification of work by USGS)

This loss of ice is leading to increases in the global sea level. On average, the sea is rising at a rate of 1.8 mm per year. However, between 1993 and 2010 the rate of sea level increase ranged between 2.9 and 3.4 mm per year. A variety of factors affect the volume of water in the ocean, including the temperature of the water (the density of water is related to its temperature) and the amount of water found in rivers, lakes, glaciers, polar ice caps, and sea ice. As glaciers and polar ice caps melt, there is a significant contribution of liquid water that was previously frozen.

In addition to some abiotic conditions changing in response to climate change, many organisms are also being affected by the changes in temperature. Temperature and precipitation play key roles in determining the geographic distribution and phenology of plants and animals. (Phenology is the study of the effects of climatic conditions on the timing of periodic lifecycle events, such as flowering in plants or migration in birds.) Researchers have shown that 385 plant species in Great Britain are flowering 4.5 days sooner than was recorded earlier during the previous 40 years. In addition, insect-pollinated species were more likely to flower earlier than wind-pollinated species. The impact of changes in flowering date would be mitigated if the insect pollinators emerged earlier. This mismatched timing of plants and pollinators could result in injurious ecosystem effects because, for continued survival, insect-pollinated plants must flower when their pollinators are present.

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18.17: Human Impact on the Environment

Learning Objectives

- Discuss the impact humans have had on climate change



Figure 1. The ecosystem of public parks often includes humans feeding the wildlife.

Human impact on the environment includes impacts on biophysical environments, biodiversity, and other resources. The term is sometimes used in the context of pollution emissions that are produced as a result of human activities but applies broadly to all major human impacts on the environment.

Technology

Environmental impacts caused by the application of technology are often perceived as unavoidable for several reasons. First, the purpose of many technologies is to exploit, control, or otherwise "improve" upon nature for the perceived benefit of humanity. At the same time, the myriad of processes in nature have been optimized, and are continually adjusted, by evolution: any disturbance of these natural processes by technology is likely to result in negative environmental consequences. Second, the conservation of mass principle and the first law of thermodynamics (i.e., conservation of energy) dictate that whenever material resources or energy are moved around or manipulated by technology, environmental consequences are inescapable. Third, according to the second law of thermodynamics, order can be increased within a system (such as the human economy) only by increasing disorder or entropy outside the system (i.e., the environment). Thus, technologies can create "order" in the human economy (i.e., order as manifested in buildings, factories, transportation networks, communication systems, etc.) only at the expense of increasing "disorder" in the environment. According to a number of studies, increased entropy is likely to be correlated to negative environmental impacts.

Agriculture

The environmental impact of agriculture can vary widely—ultimately, environmental impact of agriculture depends on the production practices of the system used by farmers. There are two types of indicators of environmental impact: **means-based**, which is based on the farmer's production methods, and **effect-based**, which is the impact that farming methods have on the farming system or on emissions to the environment. An example of a means-based indicator would be the quality of groundwater, that is effected by the amount of nitrogen applied to the soil. An indicator reflecting the loss of nitrate to groundwater would be effect-based.

The environmental impact of agriculture involves a variety of factors from the soil, to water, the air, animal and soil diversity, plants, and the food itself. Some of the environmental issues that are related to agriculture are climate change, deforestation, genetic engineering, irrigation problems, pollutants, soil degradation, and waste.



Figure 2. Water pollution in a rural stream due to runoff from farming activity in New Zealand.

The environmental impact of irrigation includes the changes in quantity and quality of soil and water as a result of irrigation and the ensuing effects on natural and social conditions at the tail-end and downstream of the irrigation scheme. The impacts stem from the changed hydrological conditions owing to the installation and operation of the scheme. An irrigation scheme often draws water from the river and distributes it over the irrigated area. As a hydrological result it is found that:

- the downstream river discharge is reduced
- the evaporation in the scheme is increased
- the groundwater recharge in the scheme is increased
- the level of the water table rises
- the drainage flow is increased

Land Loss and Soil Erosion

Lal and Stewart estimated global loss of agricultural land by degradation and abandonment at 12 million hectares per year.[1] In contrast, according to Scherr, GLASOD (Global Assessment of Human-Induced Soil Degradation, under the UN Environment Programme) estimated that 6 million hectares of agricultural land per year had been lost to soil degradation since the mid-1940s, and she noted that this magnitude is similar to earlier estimates by Dudal and by Rozanov et al.[2] Such losses are attributable not only to soil erosion, but also to salinization, loss of nutrients and organic matter, acidification, compaction, water logging and subsidence. Human-induced land degradation tends to be particularly serious in dry regions.

Energy Industry

The environmental impact of energy harvesting and consumption is diverse. In the real world, consumption of fossil fuel resources leads to global warming and climate change. However, little change is being made in many parts of the world. If the peak oil theory proves true, more explorations of viable alternative energy sources could minimize the environmental impact of human energy demands, leading to a more ‘environmentally friend’ resource consumption.

In recent years there has been a trend towards the increased commercialization of various renewable energy sources. Rapidly advancing technologies can achieve a transition of energy generation, water and waste management, and food production towards better environmental and energy usage practices using methods of systems ecology and industrial ecology.

Invasive Species

Introductions of species, particularly plants into new areas, by whatever means and for whatever reasons have brought about major and permanent changes to the environment over large areas. Examples include the introduction of *Caulerpa taxifolia* into the Mediterranean, the introduction of oat species into the California grasslands, and the introduction of privet, kudzu, and purple loosestrife to North America. Rats, cats, and goats have radically altered biodiversity in many islands. Additionally, introductions have resulted in genetic changes to native fauna where interbreeding has taken place, as with buffalo with domestic cattle, and wolves with domestic dogs.

Transport

The environmental impact of transport is significant because it is a major user of energy, and burns most of the world's petroleum. This creates air pollution, including nitrous oxides and particulates, and is a significant contributor to global warming through emission of carbon dioxide, for which transport is the fastest-growing emission sector. By subsector, road transport is the largest contributor to global warming.



Figure 3. Interstate 10 and Interstate 45 near downtown Houston, Texas in the United States.

Environmental regulations in developed countries have reduced the individual vehicles emission; however, this has been offset by an increase in the number of vehicles, and more use of each vehicle. Some pathways to reduce the carbon emissions of road vehicles considerably have been studied. Energy use and emissions vary largely between modes, causing environmentalists to call for a transition from air and road to rail and human-powered transport, and increase transport electrification and energy efficiency.

Other environmental impacts of transport systems include traffic congestion and automobile-oriented urban sprawl, which can consume natural habitat and agricultural lands. By reducing transportation emissions globally, it is predicted that there will be significant positive effects on Earth's air quality, acid rain, smog and climate change.

5 Human Impacts on the Environment

In this video, we'll learn about the important services the ecosystem provides (including biogeochemical cycles and food) as well as the top five negative impact humans have had on the environment: deforestation, desertification, global warming, invasive species, and overharvesting.



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/bionm2/?p=618

1. Lal, R. and B. A. Stewart. 1990. Soil degradation. Springer-Verlag, New York. ↵
2. Scherr, S. J. 1999. Soil degradation: a threat to developing country food security by 2020? International Food Policy Research Institute. Washington, D. C. ↵

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18.18: Introduction to Conservation Biology and Biodiversity

What you'll learn to do: Explain why conservation biology and biodiversity are important

In the 1980s, biologists working in Lake Victoria in Africa discovered one of the most extraordinary products of evolution on the planet. Located in the Great Rift Valley, Lake Victoria is a large lake about 68,900 km^2 in area (larger than Lake Huron, the second largest of North America's Great Lakes). Biologists were studying species of a family of fish called cichlids. They found that as they sampled for fish in different locations of the lake, they never stopped finding new species, and they identified nearly 500 evolved types of cichlids. But while studying these variations, they quickly discovered that the invasive Nile Perch was destroying the lake's cichlid population, bringing hundreds of cichlid species to extinction with devastating rapidity.

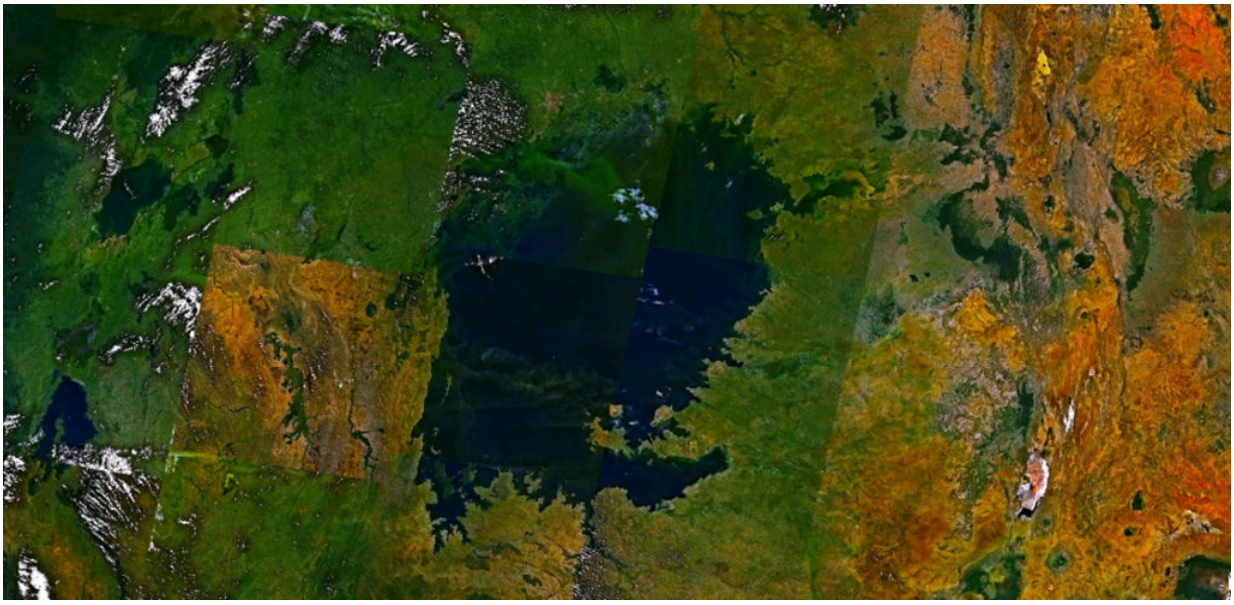


Figure 1. Lake Victoria in Africa, shown in this satellite image, was the site of one of the most extraordinary evolutionary findings on the planet, as well as a casualty of devastating biodiversity loss. (credit: modification of work by Rishabh Tatiraju, using NASA World Wind software

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18.19: Biodiversity

Learning Objectives

- Describe biodiversity and the different ways it may be assessed

Traditionally, ecologists have measured **biodiversity**, a general term for the variety present in the biosphere, by taking into account both the number of species and their commonness. Biodiversity can be estimated at a number of levels of organization of living things. These estimation indexes, which came from information theory, are most useful as a first step in quantifying biodiversity between and within ecosystems; they are less useful when the main concern among conservation biologists is simply the loss of biodiversity. However, biologists recognize that measures of biodiversity, in terms of species diversity, may help focus efforts to preserve the biologically or technologically important elements of biodiversity.

The Lake Victoria cichlids (Figure 1) provide an example through which we can begin to understand biodiversity. The biologists studying cichlids in the 1980s discovered hundreds of cichlid species representing a variety of specializations to particular habitat types and specific feeding strategies: eating plankton floating in the water, scraping and then eating algae from rocks, eating insect larvae from the bottom, and eating the eggs of other species of cichlid. The cichlids of Lake Victoria are the product of an **adaptive radiation**. An adaptive radiation is a rapid (less than three million years in the case of the Lake Victoria cichlids) branching through speciation of a phylogenetic tree into many closely related species; typically, the species "radiate" into different habitats and niches. The Galápagos finches are an example of a modest adaptive radiation with 15 species. The cichlids of Lake Victoria are an example of a spectacular adaptive radiation that includes about 500 species.



Figure 1. Both (a) *Haplochromis nyererei* and (b) *Haplochromis vonlinnei* are cichlids endemic to Lake Victoria. *Haplochromis vonlinnei* has not been seen in the lake for over two decades, and has likely gone extinct due to the presence of invasive species.

At the time biologists were making this discovery, some species began to quickly disappear. A culprit in these declines was a species of large fish that was introduced to Lake Victoria by fisheries to feed the people living around the lake. The Nile perch was introduced in 1963, but lay low until the 1980s when its populations began to surge. The Nile perch population grew by consuming cichlids, driving species after species to the point of **extinction** (the disappearance of a species). In fact, there were several factors that played a role in the extinction of perhaps 200 cichlid species in Lake Victoria: the Nile perch, declining lake water quality due to agriculture and land clearing on the shores of Lake Victoria, and increased fishing pressure. Scientists had not even catalogued all of the species present—so many were lost that were never named. The diversity is now a shadow of what it once was.

The cichlids of Lake Victoria are a thumbnail sketch of contemporary rapid species loss that occurs all over Earth and is caused by human activity. Extinction is a natural process of macroevolution that occurs at the rate of about one out of 1 million species becoming extinct per year. The fossil record reveals that there have been five periods of mass extinction in history with much higher rates of species loss, and the rate of species loss today is comparable to those periods of mass extinction. However, there is a major difference between the previous mass extinctions and the current extinction we are experiencing: human activity. Specifically, three human activities have a major impact: destruction of habitat, introduction of exotic species, and over-harvesting. Predictions of species loss within the next century, a tiny amount of time on geological timescales, range from 10 percent to 50

percent. Extinctions on this scale have only happened five other times in the history of the planet, and they have been caused by cataclysmic events that changed the course of the history of life in each instance. Earth is now in one of those times.

Types of Biodiversity

Scientists generally accept that the term biodiversity describes the number and kinds of species in a location or on the planet. Species can be difficult to define, but most biologists still feel comfortable with the concept and are able to identify and count eukaryotic species in most contexts. Biologists have also identified alternate measures of biodiversity, some of which are important for planning how to preserve biodiversity.

Genetic diversity is one of those alternate concepts. Genetic diversity or variation is the raw material for adaptation in a species. A species' future potential for adaptation depends on the genetic diversity held in the genomes of the individuals in populations that make up the species. The same is true for higher taxonomic categories. A genus with very different types of species will have more genetic diversity than a genus with species that look alike and have similar ecologies. If there were a choice between one of these genera of species being preserved, the one with the greatest potential for subsequent evolution is the most genetically diverse one. It would be ideal not to have to make such choices, but increasingly this may be the norm.

Many genes code for proteins, which in turn carry out the metabolic processes that keep organisms alive and reproducing. Genetic diversity can be measured as **chemical diversity** in that different species produce a variety of chemicals in their cells, both the proteins as well as the products and byproducts of metabolism. This chemical diversity has potential benefit for humans as a source of pharmaceuticals, so it provides one way to measure diversity that is important to human health and welfare.

Humans have generated diversity in domestic animals, plants, and fungi. This diversity is also suffering losses because of migration, market forces, and increasing globalism in agriculture, especially in heavily populated regions such as China, India, and Japan. The human population directly depends on this diversity as a stable food source, and its decline is troubling biologists and agricultural scientists.

It is also useful to define **ecosystem diversity**, meaning the number of different ecosystems on the planet or in a given geographic area (Figure 2). Whole ecosystems can disappear even if some of the species might survive by adapting to other ecosystems. The loss of an ecosystem means the loss of interactions between species, the loss of unique features of coadaptation, and the loss of biological productivity that an ecosystem is able to create. An example of a largely extinct ecosystem in North America is the prairie ecosystem. Prairies once spanned central North America from the boreal forest in northern Canada down into Mexico. They are now all but gone, replaced by crop fields, pasture lands, and suburban sprawl. Many of the species survive, but the hugely productive ecosystem that was responsible for creating the most productive agricultural soils is now gone. As a consequence, soils are disappearing or must be maintained at greater expense.



(a) (b)

Figure 2. The variety of ecosystems on Earth—from (a) coral reef to (b) prairie—enables a great diversity of species to exist. (credit a: modification of work by Jim Maragos, USFWS; credit b: modification of work by Jim Minnerath, USFWS)

Patterns of Biodiversity

Biodiversity is not evenly distributed on Earth. Lake Victoria contained almost 500 species of cichlids alone, ignoring the other fish families present in the lake. All of these species were found only in Lake Victoria; therefore, the 500 species of cichlids were endemic. **Endemic species** are found in only one location. Endemics with highly restricted distributions are particularly vulnerable to extinction. Higher taxonomic levels, such as genera and families, can also be endemic. Lake Huron contains about 79 species of fish, all of which are found in many other lakes in North America. What accounts for the difference in fish diversity in these two lakes? Lake Victoria is a tropical lake, while Lake Huron is a temperate lake. Lake Huron in its present form is only about 7,000 years old, while Lake Victoria in its present form is about 15,000 years old. Biogeographers have suggested these two factors, latitude and age, are two of several hypotheses to explain biodiversity patterns on the planet.

? Try It

Biogeography is the study of the distribution of the world's species—both in the past and in the present. The work of biogeographers is critical to understanding our physical environment, how the environment affects species, and how environmental changes impact the distribution of a species; it has also been critical to developing evolutionary theory. Biogeographers need to understand both biology and ecology. They also need to be well-versed in evolutionary studies, soil science, and climatology.

There are three main fields of study under the heading of biogeography: ecological biogeography, historical biogeography (called paleobiogeography), and conservation biogeography. Ecological biogeography studies the current factors affecting the distribution of plants and animals. Historical biogeography, as the name implies, studies the past distribution of species. Conservation biogeography, on the other hand, is focused on the protection and restoration of species based upon known historical and current ecological information. Each of these fields considers both zoogeography and phytogeography—the past and present distribution of animals and plants.

One of the oldest observed patterns in ecology is that species biodiversity in almost every taxonomic group increases as latitude declines. In other words, biodiversity increases closer to the equator (Figure 3).

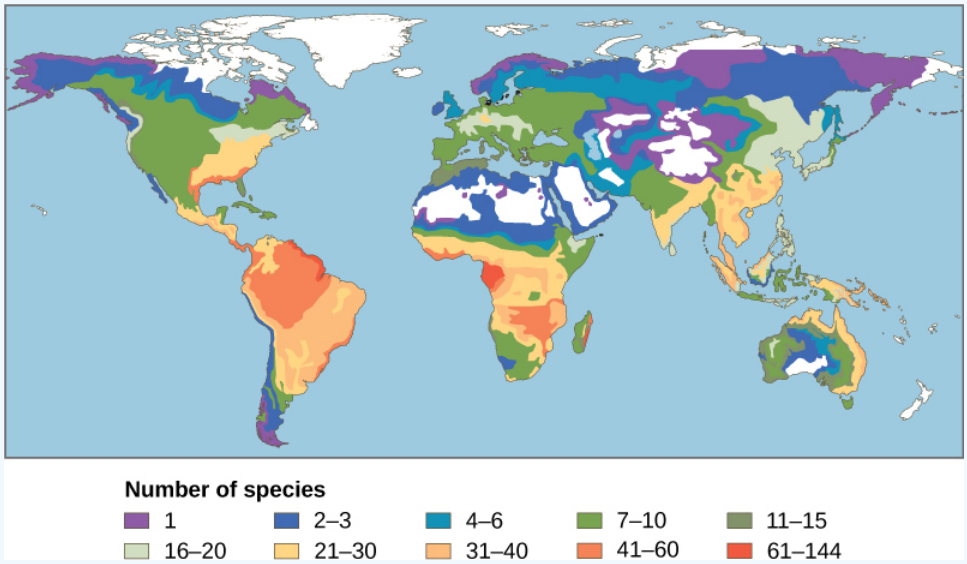


Figure 3. This map illustrates the number of amphibian species across the globe and shows the trend toward higher biodiversity at lower latitudes. A similar pattern is observed for most taxonomic groups.

It is not yet clear why biodiversity increases closer to the equator, but hypotheses include the greater age of the ecosystems in the tropics versus temperate regions that were largely devoid of life or drastically impoverished during the last glaciation. The idea is that greater age provides more time for speciation. Another possible explanation is the increased energy the tropics receive from the sun versus the decreased energy that temperate and polar regions receive. It is not entirely clear how greater energy input could translate into more species. The complexity of tropical ecosystems may promote speciation by increasing the **heterogeneity**, or number of ecological niches, in the tropics relative to higher latitudes. The greater heterogeneity provides more opportunities for

coevolution, specialization, and perhaps greater selection pressures leading to population differentiation. However, this hypothesis suffers from some circularity—ecosystems with more species encourage speciation, but how did they get more species to begin with? The tropics have been perceived as being more stable than temperate regions, which have a pronounced climate and day-length seasonality. The tropics have their own forms of seasonality, such as rainfall, but they are generally assumed to be more stable environments and this stability might promote speciation.

Regardless of the mechanisms, it is certainly true that all levels of biodiversity are greatest in the tropics. Additionally, the rate of endemism is highest, and there are more biodiversity hotspots. However, this richness of diversity also means that knowledge of species is lowest, and there is a high potential for biodiversity loss.

Learning Objectives

Biodiversity exists at multiple levels of organization and is measured in different ways depending on the goals of those taking the measurements. These measurements include numbers of species, genetic diversity, chemical diversity, and ecosystem diversity. The number of described species is estimated to be 1.5 million with about 17,000 new species being described each year. Estimates for the total number of species on Earth vary but are on the order of 10 million. Biodiversity is negatively correlated with latitude for most taxa, meaning that biodiversity is higher in the tropics. The mechanism for this pattern is not known with certainty, but several plausible hypotheses have been advanced.

Five mass extinctions with losses of more than 50 percent of extant species are observable in the fossil record. Biodiversity recovery times after mass extinctions vary, but have been up to 30 million years. Recent extinctions are recorded in written history and are the basis for one method of estimating contemporary extinction rates. The other method uses measures of habitat loss and species-area relationships. Estimates of contemporary extinction rates vary, but some rates are as high as 500 times the background rate, as determined from the fossil record, and are predicted to rise.

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18.20: Mass Extinctions

Learning Objectives

- Identify historical and potential causes of high extinction rates

The number of species on the planet, or in any geographical area, is the result of an equilibrium of two evolutionary processes that are ongoing: speciation and extinction. Both are natural “birth” and “death” processes of macroevolution. When speciation rates begin to outstrip extinction rates, the number of species will increase; likewise, the number of species will decrease when extinction rates begin to overtake speciation rates. Throughout Earth’s history, these two processes have fluctuated—sometimes leading to dramatic changes in the number of species on Earth as reflected in the fossil record (Figure 1).

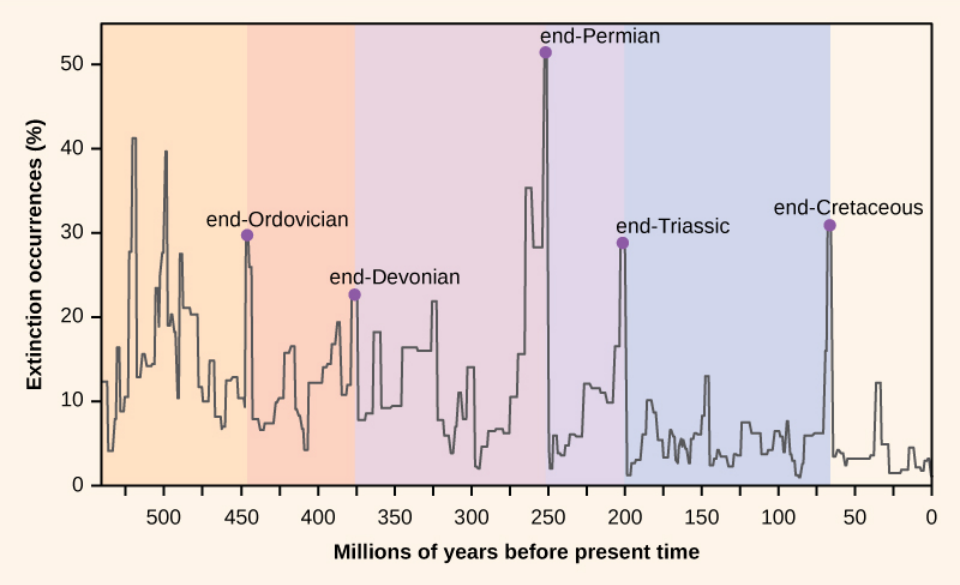


Figure 1. Percent extinction occurrences as reflected in the fossil record have fluctuated throughout Earth’s history. Sudden and dramatic losses of biodiversity, called mass extinctions, have occurred five times.

Paleontologists have identified five strata in the fossil record that appear to show sudden and dramatic (greater than half of all extant species disappearing from the fossil record) losses in biodiversity. These are called mass extinctions. There are many lesser, yet still dramatic, extinction events, but the five mass extinctions have attracted the most research. An argument can be made that the five mass extinctions are only the five most extreme events in a continuous series of large extinction events throughout the Phanerozoic (since 542 million years ago). In most cases, the hypothesized causes are still controversial; however, the most recent event seems clear.

Recorded Mass Extinctions

The fossil record of the mass extinctions was the basis for defining periods of geological history, so they typically occur at the transition point between geological periods. The transition in fossils from one period to another reflects the dramatic loss of species and the gradual origin of new species. These transitions can be seen in the rock strata. Table 1 provides data on the five mass extinctions.

Table 1. Mass Extinctions

Geological Period	Mass Extinction Name	Time (millions of years ago)
Ordovician–Silurian	end-Ordovician O–S	450–440
Late Devonian	end-Devonian	375–360
Permian–Triassic	end-Permian	251
Triassic–Jurassic	end-Triassic	205
Cretaceous–Paleogene	end-Cretaceous K–Pg (K–T)	65.5

The Ordovician-Silurian extinction event is the first recorded mass extinction and the second largest. During this period, about 85 percent of marine species (few species lived outside the oceans) became extinct. The main hypothesis for its cause is a period of glaciation and then warming. The extinction event actually consists of two extinction events separated by about 1 million years. The first event was caused by cooling, and the second event was due to the subsequent warming. The climate changes affected temperatures and sea levels. Some researchers have suggested that a gamma-ray burst, caused by a nearby supernova, is a possible cause of the Ordovician-Silurian extinction. The gamma-ray burst would have stripped away the Earth's ozone layer causing intense ultraviolet radiation from the sun and may account for climate changes observed at the time. The hypothesis is speculative, but extraterrestrial influences on Earth's history are an active line of research. Recovery of biodiversity after the mass extinction took from 5 to 20 million years, depending on the location.

The late Devonian extinction may have occurred over a relatively long period of time. It appears to have affected marine species and not the plants or animals inhabiting terrestrial habitats. The causes of this extinction are poorly understood.

The end-Permian extinction was the largest in the history of life. Indeed, an argument could be made that Earth nearly became devoid of life during this extinction event. The planet looked very different before and after this event. Estimates are that 96 percent of all marine species and 70 percent of all terrestrial species were lost. It was at this time, for example, that the trilobites, a group that survived the Ordovician–Silurian extinction, became extinct. The causes for this mass extinction are not clear, but the leading suspect is extended and widespread volcanic activity that led to a runaway global-warming event. The oceans became largely anoxic, suffocating marine life. Terrestrial tetrapod diversity took 30 million years to recover after the end-Permian extinction. The Permian extinction dramatically altered Earth's biodiversity makeup and the course of evolution.

The causes of the Triassic–Jurassic extinction event are not clear and hypotheses of climate change, asteroid impact, and volcanic eruptions have been argued. The extinction event occurred just before the breakup of the supercontinent Pangaea, although recent scholarship suggests that the extinctions may have occurred more gradually throughout the Triassic.

The causes of the end-Cretaceous extinction event are the ones that are best understood. It was during this extinction event about 65 million years ago that the dinosaurs, the dominant vertebrate group for millions of years, disappeared from the planet (with the exception of a theropod clade that gave rise to birds). Indeed, every land animal that weighed more then 25 kg became extinct. The cause of this extinction is now understood to be the result of a cataclysmic impact of a large meteorite, or asteroid, off the coast of what is now the Yucatán Peninsula. This hypothesis, proposed first in 1980, was a radical explanation based on a sharp spike in the levels of iridium (which rains down from space in meteors at a fairly constant rate but is otherwise absent on Earth's surface) at the rock stratum that marks the boundary between the Cretaceous and Paleogene periods (Figure 2). This boundary marked the disappearance of the dinosaurs in fossils as well as many other taxa. The researchers who discovered the iridium spike interpreted it as a rapid influx of iridium from space to the atmosphere (in the form of a large asteroid) rather than a slowing in the deposition of sediments during that period. It was a radical explanation, but the report of an appropriately aged and sized impact crater in 1991 made the hypothesis more believable. Now an abundance of geological evidence supports the theory. Recovery times for biodiversity after the end-Cretaceous extinction are shorter, in geological time, than for the end-Permian extinction, on the order of 10 million years.

? Practice Question



Figure 2. Iridium band (credit: USGS)

In 1980, Luis and Walter Alvarez, Frank Asaro, and Helen Michels discovered, across the world, a spike in the concentration of iridium within the sedimentary layer at the K–Pg boundary. These researchers hypothesized that this iridium spike was caused by an asteroid impact that resulted in the K–Pg mass extinction. In Figure 2, the iridium layer is the light band.

Scientists measured the relative abundance of fern spores above and below the K–Pg boundary in this rock sample. Which of the following statements most likely represents their findings?

a. An abundance of fern spores from several species was found below the K–Pg boundary, but none was found above.
b. An abundance of fern spores from several species was found above the K–Pg boundary, but none was found below.
c. An abundance of fern spores was found both above and below the K–Pg boundary, but only one species was found below the boundary, and many species were found above the boundary.
d. Many species of fern spores were found both above and below the boundary, but the total number of spores was greater below the boundary.

[reveal-answer q="553713″]Show Answer[/reveal-answer]
[hidden-answer a="553713″]Answer a: An abundance of fern spores from several species was found below the K-Pg boundary, but none was found above.[/hidden-answer]

Explore this interactive website about mass extinctions.

The Pleistocene Extinction

The Pleistocene Extinction is one of the lesser extinctions, and a recent one. It is well known that the North American, and to some degree Eurasian, **megafauna**, or large animals, disappeared toward the end of the last glaciation period. The extinction appears to have happened in a relatively restricted time period of 10,000–12,000 years ago. In North America, the losses were quite dramatic and included the woolly mammoths (last dated about 4,000 years ago in an isolated population), mastodon, giant beavers, giant ground sloths, saber-toothed cats, and the North American camel, just to name a few. The possibility that the rapid extinction of these large animals was caused by over-hunting was first suggested in the 1900s. Research into this hypothesis continues today. It seems likely that over-hunting caused many pre-written history extinctions in many regions of the world.

In general, the timing of the Pleistocene extinctions correlated with the arrival of humans and not with climate-change events, which is the main competing hypothesis for these extinctions. The extinctions began in Australia about 40,000 to 50,000 years ago, just after the arrival of humans in the area: a marsupial lion, a giant one-ton wombat, and several giant kangaroo species disappeared. In North America, the extinctions of almost all of the large mammals occurred 10,000–12,000 years ago. All that are left are the smaller mammals such as bears, elk, moose, and cougars. Finally, on many remote oceanic islands, the extinctions of many species occurred coincident with human arrivals. Not all of the islands had large animals, but when there were large animals, they were lost. Madagascar was colonized about 2,000 years ago and the large mammals that lived there became extinct. Eurasia and Africa do not show this pattern, but they also did not experience a recent arrival of humans. Humans arrived in Eurasia hundreds of thousands of years ago after the origin of the species in Africa. This topic remains an area of active research and hypothesizing. It seems clear that even if climate played a role, in most cases human hunting precipitated the extinctions.

Present-Time Extinctions

The sixth, or Holocene, mass extinction appears to have begun earlier than previously believed and has mostly to do with the activities of *Homo sapiens*. Since the beginning of the Holocene period, there are numerous recent extinctions of individual species that are recorded in human writings. Most of these are coincident with the expansion of the European colonies since the 1500s.

One of the earlier and popularly known examples is the dodo bird. The dodo bird lived in the forests of Mauritius, an island in the Indian Ocean. The dodo bird became extinct around 1662. It was hunted for its meat by sailors and was easy prey because the dodo, which did not evolve with humans, would approach people without fear. Introduced pigs, rats, and dogs brought to the island by European ships also killed dodo young and eggs.

Steller's sea cow became extinct in 1768; it was related to the manatee and probably once lived along the northwest coast of North America. Steller's sea cow was first discovered by Europeans in 1741 and was hunted for meat and oil. The last sea cow was killed in 1768. That amounts to 27 years between the sea cow's first contact with Europeans and extinction of the species.

In 1914, the last living passenger pigeon died in a zoo in Cincinnati, Ohio. This species had once darkened the skies of North America during its migrations, but it was hunted and suffered from habitat loss through the clearing of forests for farmland. In 1918, the last living Carolina parakeet died in captivity. This species was once common in the eastern United States, but it suffered from habitat loss. The species was also hunted because it ate orchard fruit when its native foods were destroyed to make way for farmland. The Japanese sea lion, which inhabited a broad area around Japan and the coast of Korea, became extinct in the 1950s due to fishermen. The Caribbean monk seal was distributed throughout the Caribbean Sea but was driven to extinction via hunting by 1952.

These are only a few of the recorded extinctions in the past 500 years. The International Union for Conservation of Nature (IUCN) keeps a list of extinct and endangered species called the Red List. The list is not complete, but it describes 380 extinct species of vertebrates after 1500 AD, 86 of which were driven extinct by overhunting or overfishing.

Estimates of Present-Time Extinction Rates

Estimates of **extinction rates** are hampered by the fact that most extinctions are probably happening without observation. The extinction of a bird or mammal is likely to be noticed by humans, especially if it has been hunted or used in some other way. But there are many organisms that are of less interest to humans (not necessarily of less value) and many that are undescribed.

The background extinction rate is estimated to be about one per million species per year (E/MSY). For example, assuming there are about ten million species in existence, the expectation is that ten species would become extinct each year (each year represents ten million species per year).

One contemporary extinction rate estimate uses the extinctions in the written record since the year 1500. For birds alone this method yields an estimate of 26 E/MSY. However, this value may be underestimated for three reasons. First, many species would not have been described until much later in the time period, so their loss would have gone unnoticed. Second, the number of recently extinct species is increasing because extinct species now are being described from skeletal remains. And third, some species are probably already extinct even though conservationists are reluctant to name them as such. Taking these factors into account raises the estimated extinction rate closer to 100 E/MSY. The predicted rate by the end of the century is 1500 E/MSY.

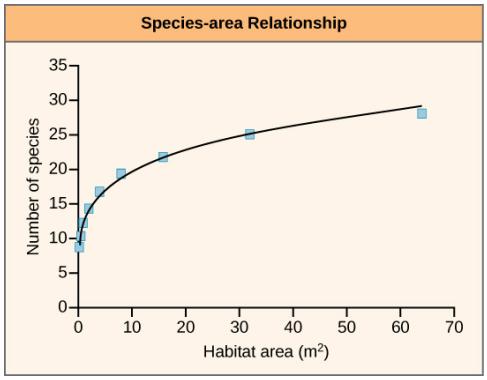


Figure 3. Studies have shown that the number of species present increases with the size of the habitat. (credit: modification of work by Adam B. Smith)

A second approach to estimating present-time extinction rates is to correlate species loss with habitat loss by measuring forest-area loss and understanding species-area relationships. The **species-area relationship** is the rate at which new species are seen when the area surveyed is increased. Studies have shown that the number of species present increases as the size of the island increases. This phenomenon has also been shown to hold true in other habitats as well. Turning this relationship around, if the habitat area is reduced, the number of species living there will also decline. Estimates of extinction rates based on habitat loss and species-area relationships have suggested that with about 90 percent habitat loss an expected 50 percent of species would become extinct. Species-area estimates have led to species extinction rate calculations of about 1000 E/MSY and higher. In general, actual observations do not show this amount of loss and suggestions have been made that there is a delay in extinction. Recent work has also called into question the applicability of the species-area relationship when estimating the loss of species. This work argues that the species-area relationship leads to an overestimate of extinction rates. A better relationship to use may be the endemics-area relationship. Using this method would bring estimates down to around 500 E/MSY in the coming century. Note that this value is still 500 times the background rate.

Check out this interactive exploration of endangered and extinct species, their ecosystems, and the causes of the endangerment or extinction.

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18.21: The Importance of Biodiversity to Human Life

Learning Objectives

- Identify biodiversity components that support human life

It may not be clear why biologists are concerned about biodiversity loss. When biodiversity loss is thought of as the extinction of the passenger pigeon, the dodo bird, and even the woolly mammoth, the loss may appear to be an emotional one. But is the loss practically important for the welfare of the human species? From the perspective of evolution and ecology, the loss of a particular individual species is unimportant (however, the loss of a keystone species can lead to ecological disaster). Extinction is a normal part of macroevolution. But the accelerated extinction rate means the loss of tens of thousands of species within our lifetimes, and it is likely to have dramatic effects on human welfare through the collapse of ecosystems and in added costs to maintain food production, clean air and water, and human health.

Agriculture began after early hunter-gatherer societies first settled in one place and heavily modified their immediate environment. This cultural transition has made it difficult for humans to recognize their dependence on undomesticated living things on the planet. Biologists recognize the human species is embedded in ecosystems and is dependent on them, just as every other species on the planet is dependent. Technology smoothes out the extremes of existence, but ultimately the human species cannot exist without its ecosystem.

Human Health

Contemporary societies that live close to the land often have a broad knowledge of the medicinal uses of plants growing in their area. Most plants produce **secondary plant compounds**, which are toxins used to protect the plant from insects and other animals that eat them, but some of which also work as medication. For centuries in Europe, older knowledge about the medical uses of plants was compiled in herbals—books that identified plants and their uses. Humans are not the only species to use plants for medicinal reasons: the great apes, orangutans, chimpanzees, bonobos, and gorillas have all been observed self-medicating with plants.



Figure 1. *Catharanthus roseus*, the Madagascar periwinkle, has various medicinal properties. Among other uses, it is a source of vincristine, a drug used in the treatment of lymphomas. (credit: Forest and Kim Starr)

Modern pharmaceutical science also recognizes the importance of these plant compounds. Examples of significant medicines derived from plant compounds include aspirin, codeine, digoxin, atropine, and vincristine (Figure 1). Many medicines were once derived from plant extracts but are now synthesized. It is estimated that, at one time, 25 percent of modern drugs contained at least one plant extract. That number has probably decreased to about 10 percent as natural plant ingredients are replaced by synthetic versions. Antibiotics, which are responsible for extraordinary improvements in health and lifespans in developed countries, are compounds largely derived from fungi and bacteria.

In recent years, animal venoms and poisons have excited intense research for their medicinal potential. By 2007, the FDA had approved five drugs based on animal toxins to treat diseases such as hypertension, chronic pain, and diabetes. Another five drugs are undergoing clinical trials, and at least six drugs are being used in other countries. Other toxins under investigation come from mammals, snakes, lizards, various amphibians, fish, snails, octopuses, and scorpions.

Aside from representing billions of dollars in profits, these medicines improve people's lives. Pharmaceutical companies are actively looking for new compounds synthesized by living organisms that can function as medicine. It is estimated that 1/3 of pharmaceutical research and development is spent on natural compounds and that about 35 percent of new drugs brought to market between 1981 and 2002 were from natural compounds. The opportunities for new medications will be reduced in direct proportion to the disappearance of species.

Agricultural Diversity

Since the beginning of human agriculture more than 10,000 years ago, human groups have been breeding and selecting crop varieties. This crop diversity matched the cultural diversity of highly subdivided populations of humans. For example, potatoes were domesticated beginning around 7,000 years ago in the central Andes of Peru and Bolivia. The potatoes grown in that region belong to seven species and the number of varieties likely is in the thousands. Each variety has been bred to thrive at particular elevations and soil and climate conditions. The diversity is driven by the diverse demands of the topography, the limited movement of people, and the demands created by crop rotation for different varieties that will do well in different fields.

Potatoes are only one example of human-generated diversity. Every plant, animal, and fungus that has been cultivated by humans has been bred from original wild ancestor species into diverse varieties arising from the demands for food value, adaptation to growing conditions, and resistance to pests. The potato demonstrates a well-known example of the risks of low crop diversity: the tragic Irish potato famine when the single variety grown in Ireland became susceptible to a potato blight, wiping out the crop. The loss of the crop led to famine, death, and mass emigration. Resistance to disease is a chief benefit to maintaining crop biodiversity, and lack of diversity in contemporary crop species carries similar risks. Seed companies, which are the source of most crop varieties in developed countries, must continually breed new varieties to keep up with evolving pest organisms. These same seed companies, however, have participated in the decline of the number of varieties available as they focus on selling fewer varieties in more areas of the world.



Figure 2. The Svalbard Global Seed Vault is a storage facility for seeds of Earth's diverse crops. (credit: Mari Tefre, Svalbard Global Seed Vault)

The ability to create new crop varieties relies on the diversity of varieties available and the accessibility of wild forms related to the crop plant. These wild forms are often the source of new gene variants that can be bred with existing varieties to create varieties with new attributes. Loss of wild species related to a crop will mean the loss of potential in crop improvement. Maintaining the genetic diversity of wild species related to domesticated species ensures our continued food supply.

Since the 1920s, government agriculture departments have maintained seed banks of crop varieties as a way to maintain crop diversity. This system has flaws because, over time, seed banks are lost through accidents, and there is no way to replace them. In 2008, the Svalbard Global Seed Vault (Figure 2) began storing seeds from around the world as a backup system to the regional seed banks. If a regional seed bank stores varieties in Svalbard, losses can be replaced from Svalbard.

The seed vault is located deep into the rock of an arctic island. Conditions within the vault are maintained at ideal temperature and humidity for seed survival, but the deep underground location of the vault in the arctic means that failure of the vault's systems will not compromise the climatic conditions inside the vault.

? Practice Question

The Svalbard Global Seed Vault is located on Spitsbergen island in Norway, which has an arctic climate. Why might an arctic climate be good for seed storage?

[practice-area rows="2"][/practice-area]
[reveal-answer q="338511"]Show Answer[/reveal-answer]
[hidden-answer a="338511"]The ground is permanently frozen so the seeds will keep even if the electricity fails.[/hidden-answer]

Crop success s is largely dependent on the quality of the soil. Although some agricultural soils are rendered sterile using controversial cultivation and chemical treatments, most contain a huge diversity of organisms that maintain nutrient cycles—breaking down organic matter into nutrient compounds that crops need for growth. These organisms also maintain soil texture that affects water and oxygen dynamics in the soil that are necessary for plant growth. If farmers had to maintain arable soil using alternate means, the cost of food would be much higher than it is now. These kinds of processes are called ecosystem services. They occur within ecosystems, such as soil ecosystems, as a result of the diverse metabolic activities of the organisms living there, but they provide benefits to human food production, drinking water availability, and breathable air.

Other key ecosystem services related to food production are plant pollination and crop pest control. Over 150 crops in the United States require pollination to produce. One estimate of the benefit of honeybee pollination within the United States is $1.6 billion per year; other pollinators contribute up to $6.7 billion more.

Many honeybee populations are managed by apiarists who rent out their hives' services to farmers. Honeybee populations in North America have been suffering large losses caused by a syndrome known as colony collapse disorder, whose cause is unclear. Other pollinators include a diverse array of other bee species and various insects and birds. Loss of these species would make growing crops requiring pollination impossible, increasing dependence on other crops.

Finally, humans compete for their food with crop pests, most of which are insects. Pesticides control these competitors; however, pesticides are costly and lose their effectiveness over time as pest populations adapt. They also lead to collateral damage by killing non-pest species and risking the health of consumers and agricultural workers. Ecologists believe that the bulk of the work in removing pests is actually done by predators and parasites of those pests, but the impact has not been well studied. A review found that in 74 percent of studies that looked for an effect of landscape complexity on natural enemies of pests, the greater the complexity, the greater the effect of pest-suppressing organisms. An experimental study found that introducing multiple enemies of pea aphids (an important alfalfa pest) increased the yield of alfalfa significantly. This study shows the importance of landscape diversity via the question of whether a diversity of pests is more effective at control than one single pest; the results showed this to be the case. Loss of diversity in pest enemies will inevitably make it more difficult and costly to grow food.

Wild Food Sources

In addition to growing crops and raising animals for food, humans obtain food resources from wild populations, primarily fish populations. For approximately 1 billion people, aquatic resources provide the main source of animal protein. But since 1990, global fish production has declined. Despite considerable effort, few fisheries on the planet are managed for sustainability.

Fishery extinctions rarely lead to complete extinction of the harvested species, but rather to a radical restructuring of the marine ecosystem in which a dominant species is so over-harvested that it becomes a minor player, ecologically. In addition to humans losing the food source, these alterations affect many other species in ways that are difficult or impossible to predict. The collapse of fisheries has dramatic and long-lasting effects on local populations that work in the fishery. In addition, the loss of an inexpensive protein source to populations that cannot afford to replace it will increase the cost of living and limit societies in other ways. In general, the fish taken from fisheries have shifted to smaller species as larger species are fished to extinction. The ultimate outcome could clearly be the loss of aquatic systems as food sources.

View a brief video discussing declining fish stocks.

Psychological and Moral Value

Finally, it has been argued that humans benefit psychologically from living in a biodiverse world. A chief proponent of this idea is entomologist E. O. Wilson. He argues that human evolutionary history has adapted us to live in a natural environment and that built environments generate stressors that affect human health and well-being. There is considerable research into the psychological regenerative benefits of natural landscapes that suggests the hypothesis may hold some truth. In addition, there is a moral argument that humans have a responsibility to inflict as little harm as possible on other species.

Learning Objectives

Humans use many compounds that were first discovered or derived from living organisms as medicines: secondary plant compounds, animal toxins, and antibiotics produced by bacteria and fungi. More medicines are expected to be discovered in nature. Loss of biodiversity will impact the number of pharmaceuticals available to humans.

Crop diversity is a requirement for food security, and it is being lost. The loss of wild relatives to crops also threatens breeders' abilities to create new varieties. Ecosystems provide ecosystem services that support human agriculture: pollination, nutrient cycling, pest control, and soil development and maintenance. Loss of biodiversity threatens these ecosystem services and risks making food production more expensive or impossible. Wild food sources are mainly aquatic, but few are being managed for sustainability. Fisheries' ability to provide protein to human populations is threatened when extinction occurs.

Biodiversity may provide important psychological benefits to humans. Additionally, there are moral arguments for the maintenance of biodiversity.

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18.22: Threats to Biodiversity

Learning Objectives

- Identify significant threats to biodiversity

The core threat to biodiversity on the planet, and therefore a threat to human welfare, is the combination of human population growth and resource exploitation. The human population requires resources to survive and grow, and those resources are being removed unsustainably from the environment. The three greatest proximate threats to biodiversity are habitat loss, overharvesting, and introduction of exotic species. The first two of these are a direct result of human population growth and resource use. The third results from increased mobility and trade. A fourth major cause of extinction, anthropogenic climate change, has not yet had a large impact, but it is predicted to become significant during this century. Global climate change is also a consequence of human population needs for energy and the use of fossil fuels to meet those needs (Figure 1). Environmental issues, such as toxic pollution, have specific targeted effects on species, but they are not generally seen as threats at the magnitude of the others.

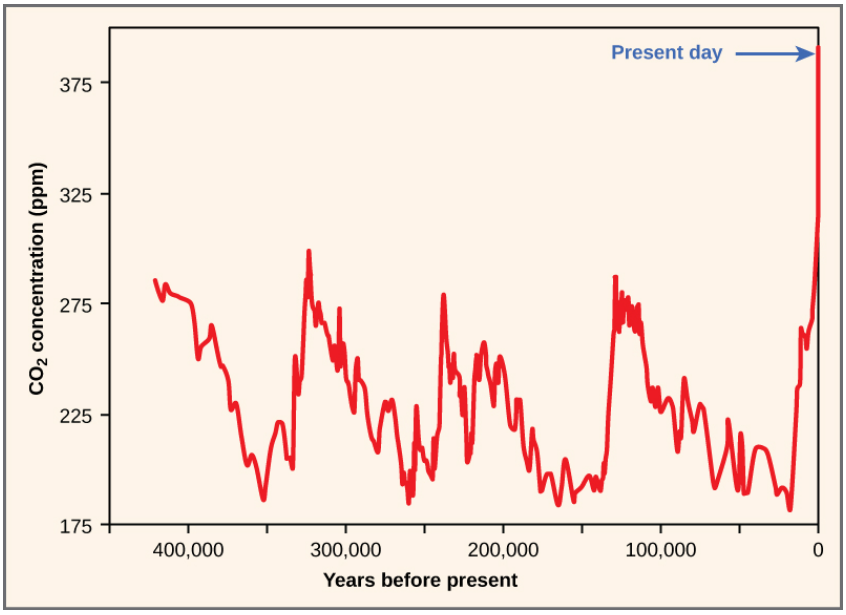


Figure 1. Atmospheric carbon dioxide levels fluctuate in a cyclical manner. However, the burning of fossil fuels in recent history has caused a dramatic increase in the levels of carbon dioxide in the Earth's atmosphere, which have now reached levels never before seen in human history. Scientists predict that the addition of this "greenhouse gas" to the atmosphere is resulting in climate change that will significantly impact biodiversity in the coming century.

Habitat Loss

Humans rely on technology to modify their environment and replace certain functions that were once performed by the natural ecosystem. Other species cannot do this. Elimination of their ecosystem—whether it is a forest, a desert, a grassland, a freshwater estuarine, or a marine environment—will kill the individuals in the species. Remove the entire habitat within the range of a species and, unless they are one of the few species that do well in human-built environments, the species will become extinct. Human destruction of habitats accelerated in the latter half of the twentieth century. Consider the exceptional biodiversity of Sumatra: it is home to one species of orangutan, a species of critically endangered elephant, and the Sumatran tiger, but half of Sumatra's forest is now gone. The neighboring island of Borneo, home to the other species of orangutan, has lost a similar area of forest. Forest loss continues in protected areas of Borneo. The orangutan in Borneo is listed as endangered by the International Union for Conservation of Nature (IUCN), but it is simply the most visible of thousands of species that will not survive the disappearance of the forests of Borneo. The forests are removed for timber and to plant palm oil plantations (Figure 2). Palm oil is used in many products including food products, cosmetics, and biodiesel in Europe. A five-year estimate of global forest cover loss for the years 2000–2005 was 3.1 percent. In the humid tropics where forest loss is primarily from timber extraction, 272,000 km^2 was lost out of

a global total of 11,564,000 km^2 (or 2.4 percent). In the tropics, these losses certainly also represent the extinction of species because of high levels of endemism.

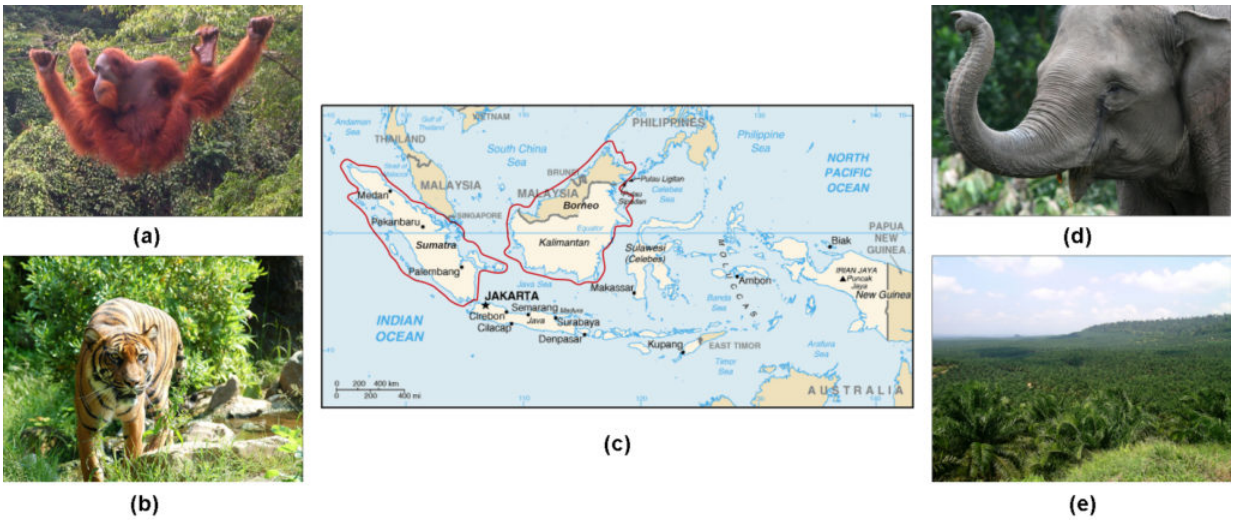


Figure 2. (a) One species of orangutan, *Pongo pygmaeus*, is found only in the rainforests of Borneo, and the other species of orangutan (*Pongo abelii*) is found only in the rainforests of Sumatra. These animals are examples of the exceptional biodiversity of (c) the islands of Sumatra and Borneo. Other species include the (b) Sumatran tiger (*Panthera tigris sumatrae*) and the (d) Sumatran elephant (*Elephas maximus sumatranus*), both critically endangered species. Rainforest habitat is being removed to make way for (e) oil palm plantations such as this one in Borneo's Sabah Province. (credit a: modification of work by Thorsten Bachner; credit b: modification of work by Dick Mudde; credit c: modification of work by U.S. CIA World Factbook; credit d: modification of work by "Nonprofit Organizations"/Flickr; credit e: modification of work by Dr. Lian Pin Koh)

? Try It

Most consumers do not imagine that the home improvement products they buy might be contributing to habitat loss and species extinctions. Yet the market for illegally harvested tropical timber is huge, and the wood products often find themselves in building supply stores in the United States. One estimate is that 10 percent of the imported timber stream in the United States, which is the world's largest consumer of wood products, is potentially illegally logged. In 2006, this amounted to $3.6 billion in wood products. Most of the illegal products are imported from countries that act as intermediaries and are not the originators of the wood.

How is it possible to determine if a wood product, such as flooring, was harvested sustainably or even legally? The Forest Stewardship Council (FSC) certifies sustainably harvested forest products, therefore, looking for their certification on flooring and other hardwood products is one way to ensure that the wood has not been taken illegally from a tropical forest. Certification applies to specific products, not to a producer; some producers' products may not have certification while other products are certified. While there are other industry-backed certifications other than the FSC, these are unreliable due to lack of independence from the industry. Another approach is to buy domestic wood species. While it would be great if there was a list of legal versus illegal wood products, it is not that simple. Logging and forest management laws vary from country to country; what is illegal in one country may be legal in another. Where and how a product is harvested and whether the forest from which it comes is being maintained sustainably all factor into whether a wood product will be certified by the FSC. It is always a good idea to ask questions about where a wood product came from and how the supplier knows that it was harvested legally.

Habitat destruction can affect ecosystems other than forests. Rivers and streams are important ecosystems and are frequently modified through land development and from damming or water removal. Damming of rivers affects the water flow and access to all parts of a river. Differing flow regimes can reduce or eliminate populations that are adapted to these changes in flow patterns. For example, an estimated 91percent of river lengths in the United States have been developed: they have modifications like dams, to create energy or store water; levees, to prevent flooding; or dredging or rerouting, to create land that is more suitable for human development. Many fish species in the United States, especially rare species or species with restricted distributions, have seen

declines caused by river damming and habitat loss. Research has confirmed that species of amphibians that must carry out parts of their life cycles in both aquatic and terrestrial habitats have a greater chance of suffering population declines and extinction because of the increased likelihood that one of their habitats or access between them will be lost.

Overharvesting

Overharvesting is a serious threat to many species, but particularly to aquatic species. There are many examples of regulated commercial fisheries monitored by fisheries scientists that have nevertheless collapsed. The western Atlantic cod fishery is the most spectacular recent collapse. While it was a hugely productive fishery for 400 years, the introduction of modern factory trawlers in the 1980s and the pressure on the fishery led to it becoming unsustainable. The causes of fishery collapse are both economic and political in nature. Most fisheries are managed as a common (shared) resource even when the fishing territory lies within a country's territorial waters. Common resources are subject to an economic pressure known as the **tragedy of the commons** in which essentially no fisher has a motivation to exercise restraint in harvesting a fishery when it is not owned by that fisher. The natural outcome of harvests of resources held in common is their overexploitation. While large fisheries are regulated to attempt to avoid this pressure, it still exists in the background. This overexploitation is exacerbated when access to the fishery is open and unregulated and when technology gives fishers the ability to overfish. In a few fisheries, the biological growth of the resource is less than the potential growth of the profits made from fishing if that time and money were invested elsewhere. In these cases—whales are an example—economic forces will always drive toward fishing the population to extinction.

Explore a U.S. Fish & Wildlife Service interactive map of critical habitat for endangered and threatened species in the United States. To begin, select "Visit the online mapper."

For the most part, fishery extinction is not equivalent to biological extinction—the last fish of a species is rarely fished out of the ocean. At the same time, fishery extinction is still harmful to fish species and their ecosystems. There are some instances in which true extinction is a possibility. Whales have slow-growing populations and are at risk of complete extinction through hunting. There are some species of sharks with restricted distributions that are at risk of extinction. The groupers are another population of generally slow-growing fishes that, in the Caribbean, includes a number of species that are at risk of extinction from overfishing.

Coral reefs are extremely diverse marine ecosystems that face peril from several processes. Reefs are home to 1/3 of the world's marine fish species—about 4,000 species—despite making up only 1 percent of marine habitat. Most home marine aquaria are stocked with wild-caught organisms, not cultured organisms. Although no species is known to have been driven extinct by the pet trade in marine species, there are studies showing that populations of some species have declined in response to harvesting, indicating that the harvest is not sustainable at those levels. There are concerns about the effect of the pet trade on some terrestrial species such as turtles, amphibians, birds, plants, and even the orangutan.

View a brief video discussing the role of marine ecosystems in supporting human welfare and the decline of ocean ecosystems.

Bush meat is the generic term used for wild animals killed for food. Hunting is practiced throughout the world, but hunting practices, particularly in equatorial Africa and parts of Asia, are believed to threaten several species with extinction. Traditionally, bush meat in Africa was hunted to feed families directly; however, recent commercialization of the practice now has bush meat available in grocery stores, which has increased harvest rates to the level of unsustainability. Additionally, human population growth has increased the need for protein foods that are not being met from agriculture. Species threatened by the bush meat trade are mostly mammals including many primates living in the Congo basin.

Exotic Species

Exotic species are species that have been intentionally or unintentionally introduced by humans into an ecosystem in which they did not evolve. Such introductions likely occur frequently as natural phenomena. For example, Kudzu (*Pueraria lobata*), which is native to Japan, was introduced in the United States in 1876. It was later planted for soil conservation. Problematically, it grows too well in the southeastern United States—up to a foot a day. It is now a pest species and covers over 7 million acres in the southeastern United States. If an introduced species is able to survive in its new habitat, that introduction is now reflected in the observed range of the species. Human transportation of people and goods, including the intentional transport of organisms for trade, has dramatically increased the introduction of species into new ecosystems, sometimes at distances that are well beyond the capacity of the species to ever travel itself and outside the range of the species' natural predators.

Most exotic species introductions probably fail because of the low number of individuals introduced or poor adaptation to the ecosystem they enter. Some species, however, possess preadaptations that can make them especially successful in a new ecosystem. These exotic species often undergo dramatic population increases in their new habitat and reset the ecological conditions in the new environment, threatening the species that exist there. For this reason, exotic species are also called invasive species. Exotic species can threaten other species through competition for resources, predation, or disease.

Explore an interactive global database of exotic or invasive species.

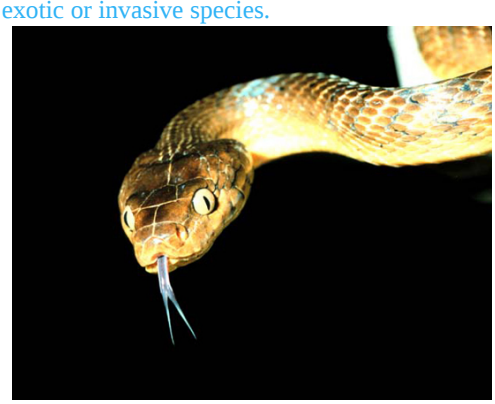


Figure 3. The brown tree snake, *Boiga irregularis*, is an exotic species that has caused numerous extinctions on the island of Guam since its accidental introduction in 1950. (credit: NPS)

Lakes and islands are particularly vulnerable to extinction threats from introduced species. In Lake Victoria, as mentioned earlier, the intentional introduction of the Nile perch was largely responsible for the extinction of about 200 species of cichlids. The accidental introduction of the brown tree snake via aircraft (Figure 3) from the Solomon Islands to Guam in 1950 has led to the extinction of three species of birds and three to five species of reptiles endemic to the island. Several other species are still threatened.

The brown tree snake is adept at exploiting human transportation as a means to migrate; one was even found on an aircraft arriving in Corpus Christi, Texas. Constant vigilance on the part of airport, military, and commercial aircraft personnel is required to prevent the snake from moving from Guam to other islands in the Pacific, especially Hawaii. Islands do not make up a large area of land on the globe, but they do contain a disproportionate number of endemic species because of their isolation from mainland ancestors.



Figure 4. This Limosa Harlequin Frog (*Atelopus limosus*), an endangered species from Panama, died from a fungal disease called chytridiomycosis. The red lesions are symptomatic of the disease. (credit: Brian Gratwicke)

It now appears that the global decline in amphibian species recognized in the 1990s is, in some part, caused by the fungus *Batrachochytrium dendrobatidis*, which causes the disease **chytridiomycosis** (Figure 4). There is evidence that the fungus is native to Africa and may have been spread throughout the world by transport of a commonly used laboratory and pet species: the African clawed toad (*Xenopus laevis*). It may well be that biologists themselves are responsible for spreading this disease worldwide. The North American bullfrog, *Rana catesbeiana*, which has also been widely introduced as a food animal but which easily escapes captivity, survives most infections of *Batrachochytriumdendrobatidis* and can act as a reservoir for the disease.

Early evidence suggests that another fungal pathogen, *Geomyces destructans*, introduced from Europe is responsible for **white-nose syndrome**, which infects cave-hibernating bats in eastern North America and has spread from a point of origin in western

New York State (Figure 5). The disease has decimated bat populations and threatens extinction of species already listed as endangered: the Indiana bat, *Myotis sodalis*, and potentially the Virginia big-eared bat, *Corynorhinus townsendii virginianus*. How the fungus was introduced is unclear, but one logical presumption would be that recreational cavers unintentionally brought the fungus on clothes or equipment from Europe.



Figure 5. This little brown bat in Greeley Mine, Vermont, March 26, 2009, was found to have white-nose syndrome. (credit: Marvin Moriarty, USFWS)

Learning Objectives

The core threats to biodiversity are human population growth and unsustainable resource use. To date, the most significant causes of extinctions are habitat loss, introduction of exotic species, and overharvesting. Climate change is predicted to be a significant cause of extinctions in the coming century. Habitat loss occurs through deforestation, damming of rivers, and other activities. Overharvesting is a threat particularly to aquatic species, while the taking of bush meat in the humid tropics threatens many species in Asia, Africa, and the Americas. Exotic species have been the cause of a number of extinctions and are especially damaging to islands and lakes. Exotic species' introductions are increasing because of the increased mobility of human populations and growing global trade and transportation. Climate change is forcing range changes that may lead to extinction. It is also affecting adaptations to the timing of resource availability that negatively affects species in seasonal environments. The impacts of climate change are greatest in the arctic. Global warming will also raise sea levels, eliminating some islands and reducing the area of all others.

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18.23: Current Biodiversity

Learning Objectives

- Describe current biodiversity estimates

Despite considerable effort, knowledge of the species that inhabit the planet is limited. A recent estimate suggests that the eukaryote species for which science has names, about 1.5 million species, account for less than 20 percent of the total number of eukaryote species present on the planet (8.7 million species, by one estimate). Estimates of numbers of prokaryotic species are largely guesses, but biologists agree that science has only begun to catalog their diversity. Even with what is known, there is no central repository of names or samples of the described species; therefore, there is no way to be sure that the 1.5 million descriptions is an accurate number. It is a best guess based on the opinions of experts in different taxonomic groups. Given that Earth is losing species at an accelerating pace, science is very much in the place it was with the Lake Victoria cichlids: knowing little about what is being lost. Table 1 presents recent estimates of biodiversity in different groups.

Table 1. Estimates of the Numbers of Described and Predicted Species by Taxonomic Group

	Mora et al. 2011[1]		Chapman 2009[2]		Groombridge & Jenkins 2002[3]	
	Described	Predicted	Described	Predicted	Described	Predicted
Animalia	1,124,516	9,920,000	1,424,153	6,836,330	1,225,500	10,820,000
Chromista	17,892	34,900	25,044	200,500	—	—
Fungi	44,368	616,320	98,998	1,500,000	72,000	1,500,000
Plantae	224,244	314,600	310,129	390,800	270,000	320,000
Protozoa	16,236	72,800	28,871	1,000,000	80,000	600,000
Prokaryotes	—	—	10,307	1,000,000	10,175	—
Total	1,438,769	10,960,000	1,897,502	10,897,630	1,657,675	13,240,000

There are various initiatives to catalog described species in accessible ways, and the internet is facilitating that effort. Nevertheless, it has been pointed out that at the current rate of species description, which according to the State of Observed Species Report is 17,000 to 20,000 new species per year, it will take close to 500 years to finish describing life on this planet.[4] Over time, the task becomes both increasingly impossible and increasingly easier as extinction removes species from the planet.

Naming and counting species may seem an unimportant pursuit given the other needs of humanity, but it is not simply an accounting. Describing species is a complex process by which biologists determine an organism's unique characteristics and whether or not that organism belongs to any other described species. It allows biologists to find and recognize the species after the initial discovery, and allows them to follow up on questions about its biology. In addition, the unique characteristics of each species make it potentially valuable to humans or other species on which humans depend. Understanding these characteristics is the value of finding and naming species.

In 1988, British environmentalist Norman Myers developed a conservation concept to identify areas rich in species and at significant risk for species loss: biodiversity hotspots. **Biodiversity hotspots** are geographical areas that contain high numbers of endemic species. The purpose of the concept was to identify important locations on the planet for conservation efforts, a kind of conservation triage. By protecting hotspots, governments are able to protect a larger number of species. The original criteria for a hotspot included the presence of 1500 or more endemic plant species and 70 percent of the area disturbed by human activity. There are now 34 biodiversity hotspots (Figure 3) containing large numbers of endemic species, which include half of Earth's endemic plants.

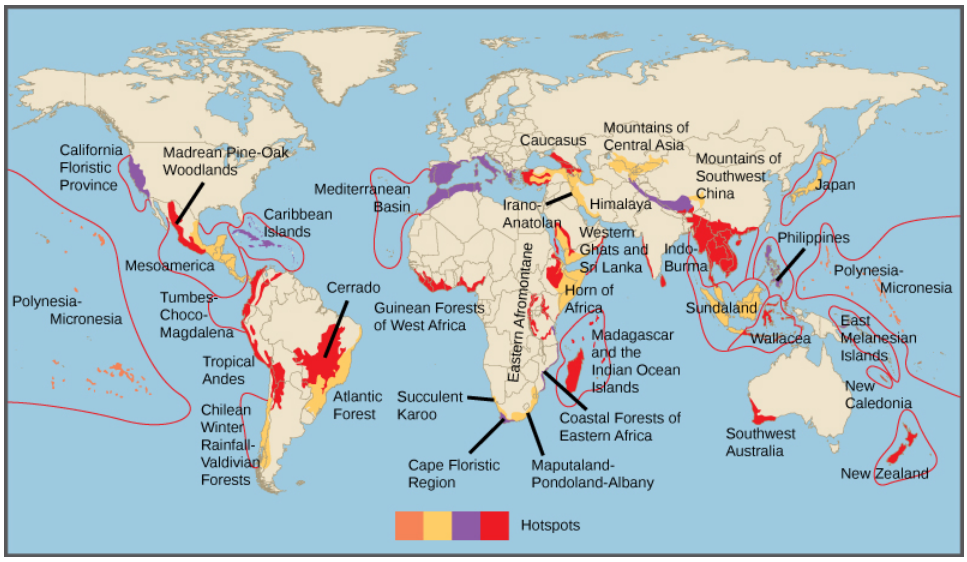


Figure 3. Conservation International has identified 34 biodiversity hotspots, which cover only 2.3 percent of the Earth's surface but have endemic to them 42 percent of the terrestrial vertebrate species and 50 percent of the world's plants.

Conservation and Restoration

This video takes a look at the growing fields of conservation biology and restoration ecology, which apply ecological principles to protecting ecosystems and to cleaning up the messes that we've already made.



A YouTube element has been excluded from this version of the text. You can view it online here: pb.libretexts.org/bionm2/?p=630

1. Mora Camilo et al., "How Many Species Are There on Earth and in the Ocean?" *PLoS Biology* (2011), doi:10.1371/journal.pbio.1001127. ↵
2. Arthur D. Chapman, *Numbers of Living Species in Australia and the World*, 2nd ed. (Canberra, AU: Australian Biological Resources Study, 2009). www.environment.gov.au/biodiversity/abrs/publications/other/species-numbers/2009/pubs/nlsaw-2nd-complete.pdf. ↵
3. Brian Groombridge and Martin D. Jenkins. *World Atlas of Biodiversity: Earth's Living Resources in the 21st Century*. Berkeley: University of California Press, 2002. ↵
4. International Institute for Species Exploration (IISE), *2011 State of Observed Species (SOS)*. Tempe, AZ: IISE, 2011. Accessed May, 20, 2012. species.asu.edu/SOS. ↵

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18.24: Preserving Biodiversity

Learning Objectives

- Identify modern methods for preserving biodiversity

Preserving biodiversity is an extraordinary challenge that must be met by greater understanding of biodiversity itself, changes in human behavior and beliefs, and various preservation strategies.

Measuring Biodiversity

The technology of molecular genetics and data processing and storage are maturing to the point where cataloguing the planet's species in an accessible way is close to feasible. **DNA barcoding** is one molecular genetic method, which takes advantage of rapid evolution in a mitochondrial gene present in eukaryotes, excepting the plants, to identify species using the sequence of portions of the gene. Plants may be barcoded using a combination of chloroplast genes. Rapid mass sequencing machines make the molecular genetics portion of the work relatively inexpensive and quick. Computer resources store and make available the large volumes of data. Projects are currently underway to use DNA barcoding to catalog museum specimens, which have already been named and studied, as well as testing the method on less studied groups. As of mid 2012, close to 150,000 named species had been barcoded. Early studies suggest there are significant numbers of undescribed species that looked too much like sibling species to previously be recognized as different. These now can be identified with DNA barcoding.

Numerous computer databases now provide information about named species and a framework for adding new species. However, as already noted, at the present rate of description of new species, it will take close to 500 years before the complete catalog of life is known. Many, perhaps most, species on the planet do not have that much time.

There is also the problem of understanding which species known to science are threatened and to what degree they are threatened. This task is carried out by the non-profit IUCN which, as previously mentioned, maintains the Red List—an online listing of endangered species categorized by taxonomy, type of threat, and other criteria (Figure 1). The Red List is supported by scientific research. In 2011, the list contained 61,000 species, all with supporting documentation.

Practice Question

Which of the following statements is not supported by this graph?

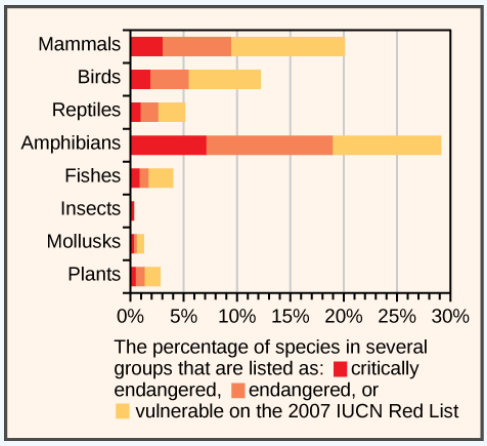


Figure 1. This chart shows the percentage of various animal species, by group, on the IUCN Red List as of 2007.

a. There are more vulnerable fishes than critically endangered and endangered fishes combined.
b. There are more critically endangered amphibians than vulnerable, endangered and critically endangered reptiles combined.
c. Within each group, there are more critically endangered species than vulnerable species.
d. A greater percentage of bird species are critically endangered than mollusk species.

[reveal-answer q="687830"]Show Answer[/reveal-answer]
[hidden-answer a="687830"]Statement c is not supported by the graph.[/hidden-answer]

Changing Human Behavior

Legislation throughout the world has been enacted to protect species. The legislation includes international treaties as well as national and state laws. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) treaty came into force in 1975. The treaty, and the national legislation that supports it, provides a legal framework for preventing approximately 33,000 listed species from being transported across nations' borders, thus protecting them from being caught or killed when international trade is involved. The treaty is limited in its reach because it only deals with international movement of organisms or their parts. It is also limited by various countries' ability or willingness to enforce the treaty and supporting legislation. The illegal trade in organisms and their parts is probably a market in the hundreds of millions of dollars. Illegal wildlife trade is monitored by another non-profit: Trade Records Analysis of Flora and Fauna in Commerce (TRAFFIC).

Within many countries there are laws that protect endangered species and regulate hunting and fishing. In the United States, the Endangered Species Act (ESA) was enacted in 1973. Species at risk are listed by the Act; the U.S. Fish & Wildlife Service is required by law to develop management plans that protect the listed species and bring them back to sustainable numbers. The Act, and others like it in other countries, is a useful tool, but it suffers because it is often difficult to get a species listed, or to get an effective management plan in place once it is listed. Additionally, species may be controversially taken off the list without necessarily having had a change in their situation. More fundamentally, the approach to protecting individual species rather than entire ecosystems is both inefficient and focuses efforts on a few highly visible and often charismatic species, perhaps at the expense of other species that go unprotected. At the same time, the Act has a critical habitat provision outlined in the recovery mechanism that may benefit species other than the one targeted for management.

The Migratory Bird Treaty Act (MBTA) is an agreement between the United States and Canada that was signed into law in 1918 in response to declines in North American bird species caused by hunting. The Act now lists over 800 protected species. It makes it illegal to disturb or kill the protected species or distribute their parts (much of the hunting of birds in the past was for their feathers).

The international response to global warming has been mixed. The Kyoto Protocol, an international agreement that came out of the United Nations Framework Convention on Climate Change that committed countries to reducing greenhouse gas emissions by 2012, was ratified by some countries, but spurned by others. Two important countries in terms of their potential impact that did not ratify the Kyoto Protocol were the United States and China. The United States rejected it as a result of a powerful fossil fuel industry and China because of a concern it would stifle the nation's growth. Some goals for reduction in greenhouse gasses were met and exceeded by individual countries, but worldwide, the effort to limit greenhouse gas production is not succeeding. The intended replacement for the Kyoto Protocol has not materialized because governments cannot agree on timelines and benchmarks. Meanwhile, climate scientists predict the resulting costs to human societies and biodiversity will be high.

As already mentioned, the private non-profit sector plays a large role in the conservation effort both in North America and around the world. The approaches range from species-specific organizations to the broadly focused IUCN and TRAFFIC. The Nature Conservancy takes a novel approach. It purchases land and protects it in an attempt to set up preserves for ecosystems. Ultimately, human behavior will change when human values change. At present, the growing urbanization of the human population is a force that poses challenges to the valuing of biodiversity.

Conservation in Preserves

Establishment of wildlife and ecosystem preserves is one of the key tools in conservation efforts. A preserve is an area of land set aside with varying degrees of protection for the organisms that exist within the boundaries of the preserve. Preserves can be effective in the short term for protecting both species and ecosystems, but they face challenges that scientists are still exploring to strengthen their viability as long-term solutions.

How Much Area to Preserve?

Due to the way protected lands are allocated (they tend to contain less economically valuable resources rather than being set aside specifically for the species or ecosystems at risk) and the way biodiversity is distributed, determining a target percentage of land or

marine habitat that should be protected to maintain biodiversity levels is challenging. The IUCN World Parks Congress estimated that 11.5 percent of Earth's land surface was covered by preserves of various kinds in 2003. This area is greater than previous goals; however, it only represents 9 out of 14 recognized major biomes. Research has shown that 12 percent of all species live only outside preserves; these percentages are much higher when only threatened species and high quality preserves are considered. For example, high quality preserves include only about 50 percent of threatened amphibian species. The conclusion must be that either the percentage of area protected must increase, or the percentage of high quality preserves must increase, or preserves must be targeted with greater attention to biodiversity protection. Researchers argue that more attention to the latter solution is required.

Preserve Design

There has been extensive research into optimal preserve designs for maintaining biodiversity. The fundamental principle behind much of the research has been the seminal theoretical work of Robert H. MacArthur and Edward O. Wilson published in 1967 on island biogeography.[1] This work sought to understand the factors affecting biodiversity on islands. The fundamental conclusion was that biodiversity on an island was a function of the origin of species through migration, speciation, and extinction on that island. Islands farther from a mainland are harder to get to, so migration is lower and the equilibrium number of species is lower. Within island populations, evidence suggests that the number of species gradually increases to a level similar to the numbers on the mainland from which the species is suspected to have migrated. In addition, smaller islands are harder to find, so their immigration rates for new species are lower. Smaller islands are also less geographically diverse so there are fewer niches to promote speciation. And finally, smaller islands support smaller populations, so the probability of extinction is higher.

As islands get larger, the number of species accelerates, although the effect of island area on species numbers is not a direct correlation. Conservation preserves can be seen as "islands" of habitat within "an ocean" of non-habitat. For a species to persist in a preserve, the preserve must be large enough. The critical size depends, in part, on the home range that is characteristic of the species. A preserve for wolves, which range hundreds of kilometers, must be much larger than a preserve for butterflies, which might range within ten kilometers during its lifetime. But larger preserves have more core area of optimal habitat for individual species, they have more niches to support more species, and they attract more species because they can be found and reached more easily.

Preserves perform better when there are buffer zones around them of suboptimal habitat. The buffer allows organisms to exit the boundaries of the preserve without immediate negative consequences from predation or lack of resources. One large preserve is better than the same area of several smaller preserves because there is more core habitat unaffected by edges. For this same reason, preserves in the shape of a square or circle will be better than a preserve with many thin "arms." If preserves must be smaller, then providing wildlife corridors between them so that individuals and their genes can move between the preserves, for example along rivers and streams, will make the smaller preserves behave more like a large one. All of these factors are taken into consideration when planning the nature of a preserve before the land is set aside.

In addition to the physical, biological, and ecological specifications of a preserve, there are a variety of policy, legislative, and enforcement specifications related to uses of the preserve for functions other than protection of species. These can include anything from timber extraction, mineral extraction, regulated hunting, human habitation, and nondestructive human recreation. Many of these policy decisions are made based on political pressures rather than conservation considerations. In some cases, wildlife protection policies have been so strict that subsistence-living indigenous populations have been forced from ancestral lands that fell within a preserve. In other cases, even if a preserve is designed to protect wildlife, if the protections are not or cannot be enforced, the preserve status will have little meaning in the face of illegal poaching and timber extraction. This is a widespread problem with preserves in areas of the tropics.

Limitations on Preserves

Some of the limitations on preserves as conservation tools are evident from the discussion of preserve design. Political and economic pressures typically make preserves smaller, never larger, so setting aside areas that are large enough is difficult. If the area set aside is sufficiently large, there may not be sufficient area to create a buffer around the preserve. In this case, an area on the outer edges of the preserve inevitably becomes a riskier suboptimal habitat for the species in the preserve. Enforcement of protections is also a significant issue in countries without the resources or political will to prevent poaching and illegal resource extraction.

Climate change will create inevitable problems with the location of preserves. The species within them will migrate to higher latitudes as the habitat of the preserve becomes less favorable. Scientists are planning for the effects of global warming on future preserves and striving to predict the need for new preserves to accommodate anticipated changes to habitats; however, the end effectiveness is tenuous since these efforts are prediction based.

Finally, an argument can be made that conservation preserves reinforce the cultural perception that humans are separate from nature, can exist outside of it, and can only operate in ways that do damage to biodiversity. Creating preserves reduces the pressure on human activities outside the preserves to be sustainable and non-damaging to biodiversity. Ultimately, the political, economic, and human demographic pressures will degrade and reduce the size of conservation preserves if the activities outside them are not altered to be less damaging to biodiversity.

An interactive global data system of protected areas can be found at website. Review data about individual protected areas by location or study statistics on protected areas by country or region.

Habitat Restoration

Habitat restoration holds considerable promise as a mechanism for restoring and maintaining biodiversity. Of course once a species has become extinct, its restoration is impossible. However, restoration can improve the biodiversity of degraded ecosystems. Reintroducing wolves, a top predator, to Yellowstone National Park in 1995 led to dramatic changes in the ecosystem that increased biodiversity. The wolves (Figure 2) function to suppress elk and coyote populations and provide more abundant resources to the guild of carrion eaters. Reducing elk populations has allowed revegetation of riparian areas, which has increased the diversity of species in that habitat. Decreasing the coyote population has increased the populations of species that were previously suppressed by this predator. The number of species of carrion eaters has increased because of the predatory activities of the wolves. In this habitat, the wolf is a keystone species, meaning a species that is instrumental in maintaining diversity in an ecosystem. Removing a keystone species from an ecological community may cause a collapse in diversity. The results from the Yellowstone experiment suggest that restoring a keystone species can have the effect of restoring biodiversity in the community. Ecologists have argued for the identification of keystone species where possible and for focusing protection efforts on those species; likewise, it also makes sense to attempt to return them to their ecosystem if they have been removed.

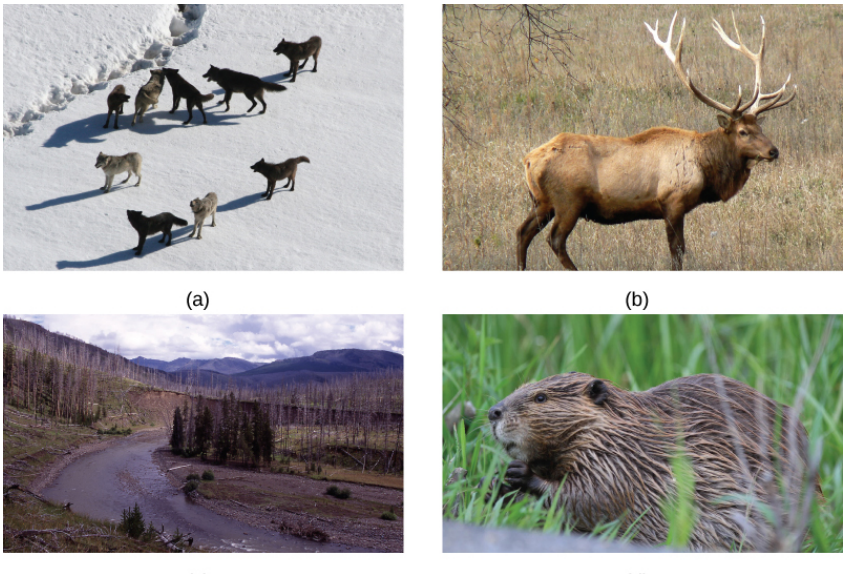


Figure 2. (a) The Gibbon wolf pack in Yellowstone National Park, March 1, 2007, represents a keystone species. The reintroduction of wolves into Yellowstone National Park in 1995 led to a change in the grazing behavior of (b) elk. To avoid predation, the elk no longer grazed exposed stream and riverbeds, such as (c) the Lamar Riverbed in Yellowstone. This allowed willow and cottonwood seedlings to grow. The seedlings decreased erosion and provided shading to the creek, which improved fish habitat. A new colony of (d) beaver may also have benefited from the habitat change. (credit a: modification of work by Doug Smith, NPS; credit c: modification of work by Jim Peaco, NPS; credit d: modification of work by “Shiny Things”/Flickr.

Other large-scale restoration experiments underway involve dam removal. In the United States, since the mid-1980s, many aging dams are being considered for removal rather than replacement because of shifting beliefs about the ecological value of free-

flowing rivers and because many dams no longer provide the benefit and functions that they did when they were first built. The measured benefits of dam removal include restoration of naturally fluctuating water levels (the purpose of dams is frequently to reduce variation in river flows), which leads to increased fish diversity and improved water quality. In the Pacific Northwest, dam removal projects are expected to increase populations of salmon, which is considered a keystone species because it transports key nutrients to inland ecosystems during its annual spawning migrations. In other regions such as the Atlantic coast, dam removal has allowed the return of spawning anadromous fish species (species that are born in fresh water, live most of their lives in salt water, and return to fresh water to spawn). Some of the largest dam removal projects have yet to occur or have happened too recently for the consequences to be measured. The large-scale ecological experiments that these removal projects constitute will provide valuable data for other dam projects slated either for removal or construction.

The Role of Captive Breeding

Zoos have sought to play a role in conservation efforts both through captive breeding programs and education. The transformation of the missions of zoos from collection and exhibition facilities to organizations that are dedicated to conservation is ongoing. In general, it has been recognized that, except in some specific targeted cases, captive breeding programs for endangered species are inefficient and often prone to failure when the species are reintroduced to the wild. Zoo facilities are far too limited to contemplate captive breeding programs for the numbers of species that are now at risk. Education is another potential positive impact of zoos on conservation efforts, particularly given the global trend to urbanization and the consequent reduction in contacts between people and wildlife. A number of studies have been performed to look at the effectiveness of zoos on people's attitudes and actions regarding conservation; at present, the results tend to be mixed.

Learning Objectives

New technological methods such as DNA barcoding and information processing and accessibility are facilitating the cataloging of the planet's biodiversity. There is also a legislative framework for biodiversity protection. International treaties such as CITES regulate the transportation of endangered species across international borders. Legislation within individual countries protecting species and agreements on global warming have had limited success; there is at present no international agreement on targets for greenhouse gas emissions. In the United States, the Endangered Species Act protects listed species but is hampered by procedural difficulties and a focus on individual species. The Migratory Bird Act is an agreement between Canada and the United States to protect migratory birds. The non-profit sector is also very active in conservation efforts in a variety of ways.

Conservation preserves are a major tool in biodiversity protection. Presently, 11percent of Earth's land surface is protected in some way. The science of island biogeography has informed the optimal design of preserves; however, preserves have limitations imposed by political and economic forces. In addition, climate change will limit the effectiveness of preserves in the future. A downside of preserves is that they may lessen the pressure on human societies to function more sustainably outside the preserves.

Habitat restoration has the potential to restore ecosystems to previous biodiversity levels before species become extinct. Examples of restoration include reintroduction of keystone species and removal of dams on rivers. Zoos have attempted to take a more active role in conservation and can have a limited role in captive breeding programs. Zoos also may have a useful role in education.

1. Robert H. MacArthur and Edward O. Wilson, E. O., *The Theory of Island Biogeography* (Princeton, N.J.: Princeton University Press, 1967). ↵

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18.25: Putting It Together- Ecology and the Environment

At the beginning of this module, we talked about our environment, calling out climate change and loss of biodiversity as two major concerns in our world today. Now that we've learned more about these topics, what do you think you can do to help the environment?

Think about It

How can you combat climate change?

[practice-area rows="4"][/practice-area]
[reveal-answer q="69791"]See Our Thoughts[/reveal-answer]
[hidden-answer a="69791"]The most important thing to do is to be aware of your actions and the impact they may have on the environment. While it's not possible to completely remove your influence on the world around you, you can take steps to be cautious about the waste materials you put out in the world.

[/hidden-answer]

How can you help preserve and restore biodiversity?

[practice-area rows="4"][/practice-area]
[reveal-answer q="69792"]See Our Thoughts[/reveal-answer]
[hidden-answer a="69792"]Look in your local neighborhood for opportunities to volunteer. You may find wildlife or nature preserves that need volunteers. Again, the most important thing to do is to pay attention. [/hidden-answer]

We also mentioned eco-friendly organizations at the start of this module. One of these is the **Intergovernmental Panel on Climate Change** (IPCC), established by the United Nations in 1988.

The IPCC is responsible for reviewing the scientific literature on climate change and issuing periodic reports on several topics, including the scientific basis for understanding climate change, our vulnerability to observed and predicted climate changes, and what we can do to limit climate change and minimize its impacts.

The biggest anthropogenic contributor to warming is the emission of CO_2, which accounts for 50 percent of positive forcing. CH_4 and its atmospheric derivatives (CO_2, H_2O, and O_3) account for 29%, and the halocarbon gases (mostly leaked from air-conditioning appliances) and nitrous oxide (N_2O) (from burning fossils fuels) account for 5 percent each. Carbon monoxide (CO) (also produced by burning fossil fuels) accounts for 7%, and the volatile organic compounds other than methane (NMVOC) account for 3%.

CO_2 emissions come mostly from coal- and gas-fired power stations, motorized vehicles (cars, trucks, and aircraft), and industrial operations (e.g., smelting), and indirectly from forestry. CH_4 emissions come from production of fossil fuels (escape from coal mining and from gas and oil production), livestock farming (mostly beef), landfills, and wetland rice farming. N_2O and CO come mostly from the combustion of fossil fuels. In summary, close to 70 percent of our current GHG emissions come from fossil fuel production and use, while most of the rest comes from agriculture and landfills.

With the information provided by the IPCC and other organizations, we can act to help preserve and protect the world we live in.

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