VCU BIOL 152: Introduction to Biological Sciences II

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Contents

This textbook has been modified from OpenStax Biology by faculty at Virginia Commonwealth University. We endeavoured on this project with the goal of providing students a complete textbook with interactive features (reading quizzes, videos, links) that was highly engaging and, of course, at no cost to the students. Moreover, we recognize that this textbook will need to be constantly updated as our understanding of the world around us continues to grow. On that note, we encourage any person using this textbook to inform us when we've missed an opportunity to update the knowledge presented here. We would like to thank the Virtual Library of Virginia for providing the funding to create this body of work as well as the numerous student and former student artists from the Department of Communication Arts at VCU School of the Arts that helped to provide some of the figures in this book.

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1.

Learning Goals

By the end of this reading you should be able to:

- Explain how natural selection can result in adaptive evolution
- Identify sources of genetic variations in populations
- Define adaptation as it relates to natural selection
- Distinguish between convergent and divergent evolution

Introduction

Evolution by natural selection describes a mechanism for how species change over time. Scientists, philosophers, researchers, and others had made suggestions and debated this topic well before Darwin began to explore this idea. In the eighteenth century, naturalist Georges-Louis Leclerc Comte de Buffon reintroduced ideas about the evolution of animals and noted that various geographic regions have different plant and animal populations, even when the environments are similar. Also, during the eighteenth century, James Hutton, a Scottish geologist and naturalist, proposed that geological change occurred gradually by accumulating small changes from processes operating like they are today over long periods of time. Nineteenth-century geologist Charles Lyell popularized Hutton's view and Lyell's notion of the greater age of Earth gave more time for gradual change in species, and the process of change provided an analogy for this change. In the early nineteenth century, Jean-Baptiste Lamarck published a book that detailed a mechanism for evolutionary change. We now refer to this mechanism as an inheritance of acquired characteristics by which the use or disuse of a structure during an organism's lifetime could bring about long-term changes in traits in species. While many discredited this mechanism for evolutionary change, Lamarck's ideas were an important influence on evolutionary thought.

Darwin, Wallace and Natural Selection

In the mid-nineteenth century, two naturalists, Charles Darwin and Alfred Russel Wallace, independently conceived and described the actual mechanism for evolution. On the ship H.M.S. Beagle, Darwin traveled around the world, including stops in South America, Australia, and the southern tip of Africa. Darwin's journey, like Wallace's later journeys to the Malay Archipelago, included stops at several island chains. Darwin's 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.

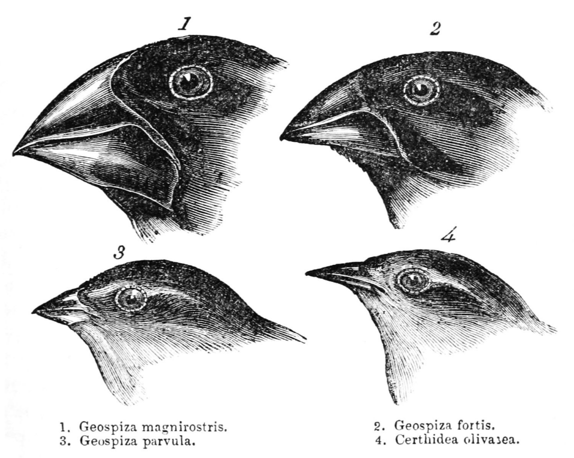

Figure 1. A representative example of Finch beaks on Galapagos islands. Darwin postulated that these differences were the result of adaptations over generations

For example, the ground finches inhabiting the Galápagos Islands comprised several species with a unique beak shape (Fig. 1). What Darwin noted was that the species on the islands had a graded series of beak sizes (small to large) and shapes (width and depth). In addition, between the most similar species, there were very small differences. Darwin also observed that these finches closely resembled another finch species on the South American mainland. As a result of his observations, Darwin hypothesized that the island species might be the result of modifications of one original mainland species. Upon further study, he realized that each finch's varied beaks helped the birds acquire a specific type of food. For example, seed-eating finches had stronger, thicker beaks that helped break seeds. Insect-eating finches had spear-like beaks, allowing them to stab their prey.

Over their travels, Wallace and Darwin both observed similar patterns to those seen in the finches in other organisms. Based on their observations they each independently developed the same explanation (natural selection) for how and why such changes could take place. Natural selection, or **"survival of the fittest"** is the increased reproductive success of individuals with traits that enhance survival and reproduction. This differential reproduction in individuals within a population can lead to evolutionary change.

Review Question:

How did Darwin explain the differences in beak shape among Galapagos finches? (multiple answers)
A) as differences in the original colonizing species
B) as inheritable acquired characteristics
C) as adaptations over generations to eating different foods
D) as inherited characteristics that impacted survival and reproduction

Natural Selection

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, though neither Darwin nor Wallace (or anyone else) knew exactly how this happened at the time. ***Second***, more offspring are produced than are able to survive, because 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. ***Third***, offspring vary in regard to their characteristics and those variations are inherited. Darwin and Wallace reasoned that offspring with inherited characteristics that allow them to best compete for limited resources are more likely to survive and thus likely to produce more offspring than individuals with variations that are less able to compete. Since the characteristics that allow one individual to reproduce more successfully are inherited, and those individuals produce more offspring, thus their traits will be better represented in the next generation as a result of having more offspring. Over generations, this can lead to changes in traits in populations, a process that Darwin called "descent with modification". Ultimately, natural selection can lead to greater adaptation of the population to its local environment. Natural selection is the only mechanism that will necessarily result in adaptive evolution.

Variation in Populations

Natural selection can only take place if there is variation, or differences, among individuals in a population (Fig. 2). Importantly, these differences must have some genetic basis; otherwise, the selection will not lead to change in the next generation. This is critical because nongenetic reasons can cause variation among individuals such as an individual's height because of better nutrition rather than different genes.

Figure 2. Individuals in the mollusk species Donax variabilis show diverse coloration and patterning in their phenotypes.

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 that mutation causes can have one of three outcomes on the phenotype.

(1) A mutation affects the organism's phenotype in a way that

gives it reduced fitness—the lower likelihood of survival or fewer offspring.

(2) A mutation may produce a phenotype with a beneficial effect on fitness.

(3) A mutation may also have no effect on the phenotype or the organism's fitness.

Most mutations do not affect the phenotype of the organism. Sexual reproduction can also lead to changes genetic diversity: when two parents reproduce, unique combinations of alleles assemble to produce the unique genotypes and thus phenotypes in each offspring.

Adaptations

A heritable trait that helps an organism survive and/or reproduce in its present environment is often referred to as an adaptation. A platypus's webbed feet are an adaptation for swimming. A snow leopard's thick fur is an adaptation for living in the cold. A cheetah's fast speed is an adaptation for catching prey. Whether or not a trait is favorable depends on the current environmental conditions. The same traits are not always selected because environmental conditions can change. For example, consider a plant species 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.

Review Question:

Whether or not a trait is favorable depends on the environmental conditions at the time and thus the same traits are not always selected.

A) True

B) False

Divergent and Convergent Processes

The evolution of species has resulted in enormous variation in form and function. Sometimes, evolution gives rise to groups of organisms that become tremendously different from each other. We call the process by which two species evolve in diverse directions from a common point divergent evolution (Fig. 3).

Figure 3. Flowering plants share a common ancestor, however, natural selection can result in divergent phenotypes.

We can see such divergent evolution in the forms of the reproductive organs of flowering plants. The flowers share the same basic anatomies that may include sepals, petals, pistils, and stamen. However, the individual shapes of the structures can result in very different appearances. This is often the result of selection in different physical environments and adaptations to different kinds of pollinators.

In other cases, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have structures we refer to as wings, which are adaptations to flight. However, bat and insect wings evolved from very different original structures.

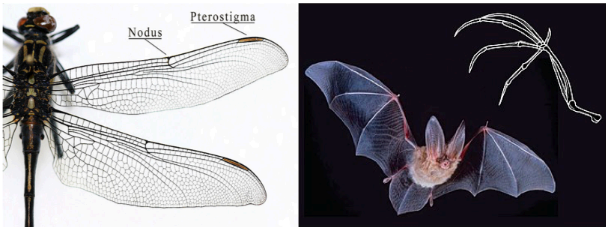

Figure 4. Insects and bats both have wings for flight. However, the basic structure is very different, indicating that the traits evolved independently of each other.

We call this phenomenon **convergent evolution**, where similar traits evolve independently in species that do not share a recent common ancestor. The wings in the two species came to the same function, flying, but did so separately from each other (Fig. 4).

The white feathers of arctic birds and the white fur of arctic mammals are other examples of convergent evolution. These similarities occur not because of common ancestry, but because of similar selection pressures. These physical changes occur over enormous time spans and help explain how evolution occurs. Natural selection acts on individual organisms, which can then shape an entire species. Although natural selection may work in a single generation on an individual, it can take thousands or even millions of years for an entire species' genotype to evolve. It is over these large time spans that life on earth has changed and continues to change.

Summary

For living organisms to adapt to changing environmental pressures, genetic variation must be present. This variation can be the result of mutations in individuals as well as sexual reproduction in the population. As a result of this genetic variation, individuals have differences in form and function that allow some to survive certain conditions better than others. Those organisms that have increased survival, and thus are more likely to reproduce, pass their favorable traits to their offspring. This differential reproductive success can result in changes in the frequencies of traits in populations, and over time increased adaptation to environmental conditions. However most natural environments are not static (often change), and what was once an advantageous trait may no longer be as advantageous. This alters the survival and reproduction of individuals within the population and can result in different adaptions over time. Evolution is a continuously ongoing process. When similar traits evolve in unrelated species, such as wings in birds, bats, and insects, it is called convergent evolution. Divergent evolution occurs when diverse traits evolve in multiple species that came from a common ancestor.

End of Section Review Questions:

Review: Principles of Natural Selection

1) **What must be true in order for individuals best suited for growth and reproduction in a particular environment to contribute disproportionately to the next generation? (multiple answers)**

A) There must be visible differences between organisms in the population

B) There must be favorable traits that can be inherited

C) There must be genetic variation within the population

D) There must be differential survival and reproduction amongst the individuals

Review: Evolutionary Patterns
2) **___________evolution occurs when organisms that are NOT closely related become more similar over long periods of time.**

Review: Components of Natural Selection
3) **What inherent characteristics of populations did both Darwin and Wallace propose were needed for natural selection to lead to adaptation? (multiple answers)**
A) population had to have variability within traits
B) organisms often overproduce resulting in competition for resources among offspring
C) some individuals within a population are more successful at reproduction
D) some individuals in a population acquire traits that allow them to be more fit

Review: Addressing a common misconception
4) Explain why it is populations that become more adapted to environments and not individuals.

References

Modification of OpenStax Biology 2nd Edition, Biology 2e. OpenStax CNX. Nov 26, 2018 18.1 Understanding Evolution. https://cnx.org/contents/jVCgr5SL@15.1:zE5eDZcY@10/18-1-Understanding-Evolution

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2.

Learning Goals

By the end of this reading you should be able to:

- Describe how comparative anatomy and embryology support the theory of evolution
- Explain how information can be gathered from the fossil record
- Discuss the contributions of biogeography and vestigial structures to evolutionary theory
- Define and give examples of homologous traits

Introduction

When Charles Darwin finally published his pinnacle work "On The Origin of Species", it was the culmination of years of observations on his part and the works of other scientists that came before. People had observed changes in populations of organisms over time before Charles Darwin and his contemporary Alfred Russell Wallace put pen to paper. What the works of both Darwin and Wallace did was bring together ideas in a new way to formulate a theory that provides an explanation of how organisms over time became more adapted to their environments. Like other scientific theories, the theory of evolution identifies a pattern that exists in the natural world and a process that is responsible for that pattern. The questions that evolutionary biology addresses are where do living things come from, how and why do living things change over time, and, ultimately, what is the source of the diversity that is seen in living organisms. The theory of evolution contends that organisms are related by common ancestry and that species have changed over time, what Darwin referred to as “common descent with modification”. Like other scientific theories, the theory of evolution is based on evidence and is supported by research.

Comparative Anatomy and Embryology

As humans studied the anatomy of the organisms around them they noticed that there were some key structural similarities across groups of organisms. The term homology was used to refer to having the same or similar relation, relative position, and/or structure. Let’s examine at some of the evidence of evolution that comparative anatomy provides. A comparison of the fore and hind limbs of animals reveals that there is significant homology in structure (Fig. 1), specifically the arrangement and some cases the number of bones in the limbs.

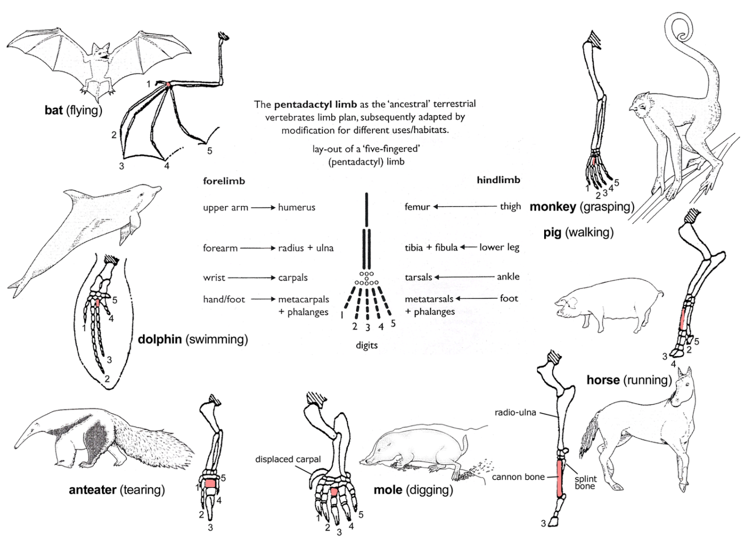

Figure 1. Comparative anatomy of the forelimbs of different mammals

For example, the forelimb of the dolphin and the bat, two limbs that are used for very different purposes – flying in the bat and swimming in the dolphin. However, if you look at the organization and structure of the limbs you can see that each has one bone in the upper part of the limb, then two bones, and finally five digits. The same comparison can be made between other vertebrate animals.

In addition to the homology that is seen in the limbs of some animals, there is also evidence of homology in the embryological development across a widely diverse group of vertebrate animals. In vertebrate embryos, including humans, there is a stage in which gill slits and tails are present. These structures are absent in the adults of terrestrial groups but adult forms of aquatic groups such as fish and some amphibians maintain them. This commonality of structures at some stage of embryo development suggests a shared common ancestry among these groups.

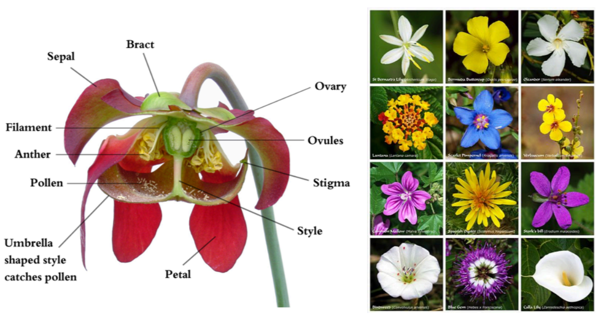

Figure 2. Comparative anatomy of floral structures

We can expand this idea of homology of structure to other groups of organisms as well. For example, flowers in plants are all composed of the same set of parts with different modifications. While each flower may not have all of the exact same structures, there are some parts that are found in common in all flowers (Fig. 2). Thus, there is a similarity in the structural design of each type of flower but the appearance of each flower is uniquely different.

It is possible to make a connection between the homologous features that occur later in the development of organisms with homologous groups of cells that are present in their embryos. Thus, the similarity that is seen later in development is one that happens as a result of shared developmental pathways. Why do some organisms share the same pathways then? Because they have a shared common ancestor. We now know that with only a few minor exceptions, all organisms use the same codons (triplets of mRNA nucleotides) to specify the same amino acid carrying tRNAs and that all organisms use the same nucleotides (DNA) to store the genetic information within each cell. Thus, not only are the similar structures found within groups of organisms the result of genetic programs within the organism, they are often the result of similar genes.

Review Question:

What do shared structural features of organisms often indicate? (multiple answers)
A) Homologous developmental pathways
B) Homologous embryonic cell groups
C) Homologous gene sequences
D) A shared common ancestor

Evidence of change over time

Vestigial structures: Some structures exist in organisms that have no apparent function at all, and appear to be residual parts from a past common ancestor. For example, the presence of eye sockets in blind cave salamanders reduced wings on flightless birds (penguins, ostriches), and in some snakes the presence of highly reduced hip and rear leg bones. Thus, vestigial traits are ones that appear to be functionless or rudimentary structural, developmental, or genetic features in one group of organisms that have a function in a closely related species.

Fossils: Fossils provide evidence that organisms from the past are not the same as those today, the vast majority of fossils that have been discovered are unlike the species that are present today. It was through the study of available fossils that George Cuvier first proposed that some organisms that once existed had become extinct. While this may not seem like earth-shattering news to you, at the time he proposed this theory it was. Through the use of radiometric dating, scientists can now determine the relative age of fossils. This allows them to determine where organisms lived in the past relative to other organisms of the same age as well as the place changes in groups of similar fossils in chronological sequence. These records can show the evolution of form over millions of years. In addition, some fossils show transitional forms that show characteristics with an ancestral organism as well as a current species. Lastly, fossils demonstrate changes in the environment over time, for example, the presence of fossils of aquatic organisms in areas where there is currently no water.

Geology: Some of the information that we currently have about the relative age of fossils comes from work done in geology. Geologists can determine the relative age of strata (layers of rocks) based on their relative position. The lower strata were typically formed first and thus based on the principle of superposition determined to be older.

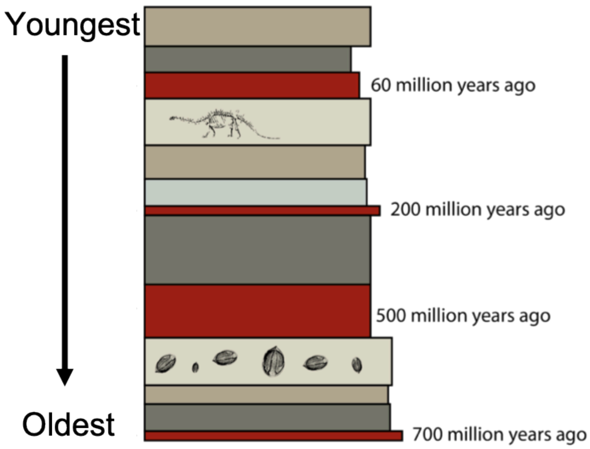

Figure 3. Relative dating of strata based on the location of the layer in the rock profile

Thus, fossils found in lower strata are older than those in the upper layers (Fig. 3). In some areas, however, the rocks were either not deposited in horizontal layers or have been somehow overturned. In these cases, geologists can use the decay of radioactive elements, such as uranium, potassium, rubidium, and carbon to help determine the relative ages of the layers and the fossils within them.

Biogeography: Biogeography is the study of the geographic distribution of organisms both living and fossil on the planet. It reveals patterns of distribution that can be explained by evolution in conjunction with tectonic plate movement over geological time. Some groups of organisms are broadly distributed across the current continents, and thus are likely to have evolved before the supercontinent Pangaea broke up (about 200 million years ago).

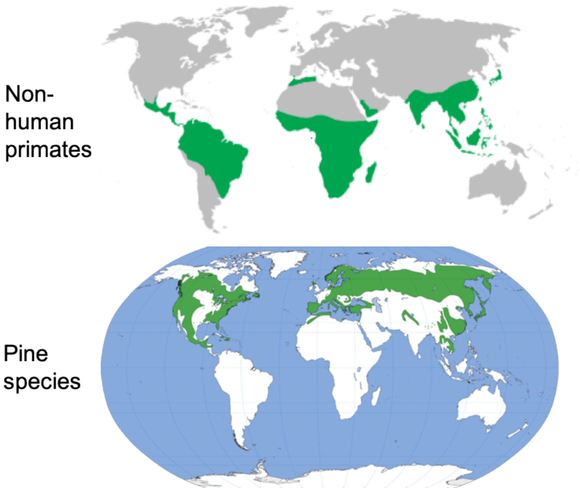

Figure 4. Biogeographic distributions of non-human primates and Pinus species. Patterns of distribution can be used to determine the evolutionary relationships of species.

Other groups of organisms are unique to specific regions of the planet. Non- human primates are found in the southern hemisphere and Pine tree species are distributed in the northern hemisphere (Fig. 4). As another example, Australia has an abundance of endemic marsupial species—species found nowhere else— and no other native mammals. This type of distribution is typical of islands that are isolated by expanses of water. This isolation creates a barrier that prevents most species from migrating to or from the island. In Australia, over time, these ancestral marsupial species though evolutionary processes diverged into new species that look very different from marsupial species found anywhere else in the world.

Review Question:

Which of the following contributes to the evidence for the theory of evolution? (multiple answers)

A) There are patterns in the fossil record that suggest other species

have diverged from a single ancestor species.
B) Anatomical structures in different groups appear to be modified versions of structures that might have been present in a common ancestor
C) There are biogeographic patterns in the distribution of species that suggest a common ancestor.

Summary

Comparative anatomy and embryology revealed to scientists that there are shared structural features in some groups of organisms. We now know that these features are often the result of shared development pathways and ultimately similar sequences of nucleotides in genes. Thus, homologous structures are indicators of a shared common ancestry. Vestigial structures can also be an indicator of shared ancestry. Changes in organisms over time is sometimes captured within the fossil record, and the dating of the rock strata can give a timeline of the appearance, disappearance, and sometimes the transitional states of groups of organisms. Finally, the geographical distribution of organisms and fossils can provide an indication of shared ancestry as well as the changes that have occurred environmentally over time.

End of Section Review Questions:

Review: Homologous Structures
1) **The wing of the bat and the fore-limb of the dog are said to be homologous structures. What does this mean?**
A) Bats evolved from the lineage of dogs
B) They are structures that are similar due to common ancestry
C) These structures have the same function
D) They have a different ancestry but a common function

Review: Shared Ancestry

2) **Which of these provides support for shared ancestry?**

A) Genetic material that is composed of the same nucleic acids

B) Similar nucleotide coding for amino acids

C) Similar patterns of development in embryos (in vertebrates)

D) Similar floral structure components in flowering plants

Review: Explaining the evidence

3) How do vestigial structures support the theory of evolution?

References

OpenStax Biology 2nd Edition, Biology 2e. OpenStax CNX. Nov 26, 2018 http://cnx.org/contents/8d50a0af-948b-4204-a71d-4826cba765b8@15.1.

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3.

Learning Goals

By the end of this reading you should be able to:

- Describe the different types of point mutations
- Differentiate between different chromosomal mutations
- Explain how mutations play a role in evolutionary processes
- Discuss factors that can influence the rate of mutations

Introduction

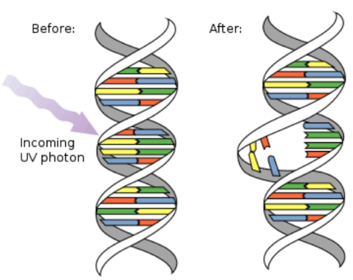


Figure 1. UV radiation can cause a break in the DNA double-stranded resulting in a mutation

A cell's DNA is the repository of all the information needed to not only make the cell but to enable it to function. In addition, the chromosome(s) also contain the information to make any cell in the organism. Mutations are variations that occur in the DNA sequence which alter the genetic code and can be passed on through cell division (Fig. 1). It is the genetic variation within cells and within individuals that account in part for the physical differences that we see between individuals and between groups of organisms. Genetic variation is responsible for the diversity of organisms that are on this planet, from single-celled bacteria to the largest animal, the blue whale. This variation is a key factor in the ability of populations to evolve and ultimately adapt to their environments.

Mutations are the ultimate source of genetic variation

Anytime the DNA is replicated, even though it is a highly accurate process, mistakes can occasionally occur. Repair mechanisms are found in both prokaryotic and eukaryotic organisms and many of the mechanisms are **conserved**. Errors during DNA replication are not the only reason why mutations arise in DNA; they can also occur because of damage to DNA. Thus, mutations may be of two types: induced or spontaneous. Induced mutations are those that result from exposure to chemicals, UV rays, x-rays, or some other environmental agent. Spontaneous mutations occur without any exposure to any environmental agent; they are a result of natural reactions taking place within the body. Whether the damage to the DNA occurs as a result of environmental conditions or errors during DNA replication, cells have evolved a number of mechanisms to detect and repair the damage. It is only in rare cases that mistakes or DNA damage are not corrected, leading to mutations that can be potentially be inherited.

Small Scale Mutations

Small mutations may have a wide range of effects. Point mutations are those mutations that affect a single base pair (Fig. 2). The most common point mutations are substitutions, in which one base is replaced by another. These can be of two types, either transitions or transversions. Transition substitution refers to a purine or pyrimidine being replaced by a base of the same kind; for example, a purine such as adenine may be replaced by the purine guanine.

Transversion substitution refers to a purine being replaced by a pyrimidine, or vice versa; for example, cytosine, a pyrimidine, is replaced by adenine, a purine. If the substitution does not alter the amino acid sequence of the resulting protein, then the mutation is considered to be silent. If, however, the substitution results in a different amino acid becoming part of the protein then it is considered to be a missense mutation and is likely to alter the protein's structure and function. Substitutions can also result in the alteration of the sequence to include a stop codon where one did not exist before (nonsense). This often results in a truncated or unexpressed protein.

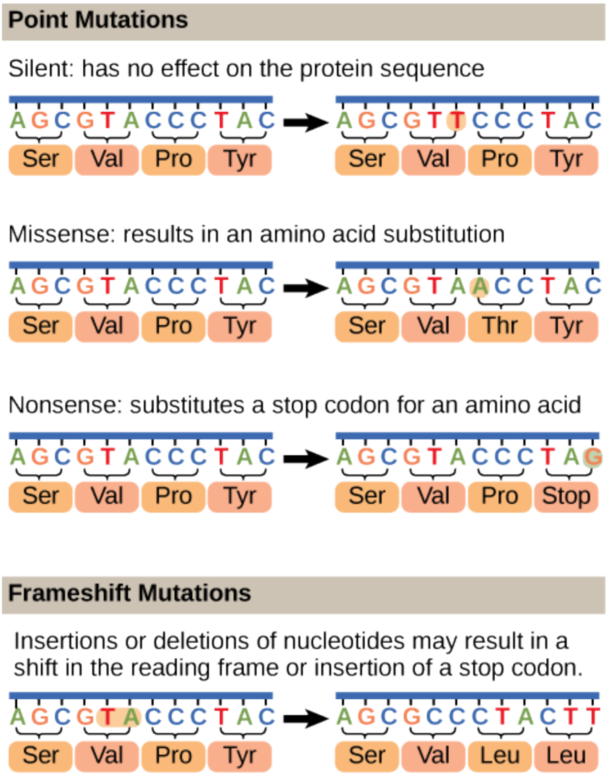


Figure 2. Mutations can lead to changes in the protein sequence encoded by the DNA.

Mutations can affect either somatic cells or germ cells. If a mutation occurs in a somatic cell then the mutation will be present in any cells that arise from that cell when it divides, but not in other parts of the body. Therefore, a somatic cell mutation is not inheritable by offspring during sexual reproduction. However if a mutation occurs in a germ cell (cells that produce gametes), then the mutation can be passed on to the next generation, therefore it is inheritable. Thus, mutations in germ cells can have an impact on the genetic diversity of the population in which the organism lives.

Mutations can also be the result of the addition of a base, known as an **insertion**, or the removal of a base, also known as **deletion**. These types of mutations can alter the reading frame (3 nucleotides code for 1 amino acid) of the amino acids, and thus the sequence of amino acids that are incorporated into the protein. The number of nucleotides that are inserted or deleted will determine how much of a change, and thereby how damaging the mutation is. If fewer than 3 insertions or deletions occur in a row, then a **frameshift mutation** can occur. This alters the reading of the triplet codons during translation of mRNA to proteins and most often results in a non-functional protein. Finally, sometimes a piece of DNA from one chromosome may get translocated to another chromosome or to another region of the same chromosome; this is also known as **translocation**.

Review Question:

A _____________ occurs when one purine is substituted for different purine.
A _____________ occurs when a purine is substituted for a pyrimidine.
A _____________ mutation occurs when a substitution results in a different amino acid becoming part of the protein being expressed.

A ____________ mutation occurs when a stop codon is the result of a substitution.

Chromosomal Mutations

Most mutations only involve one or a few nucleotides within the DNA sequence. However, some can affect much larger portions of the genome, extending over thousands or millions of nucleotides. Chromosomal mutations are ones that occur when double-stranded breaks in the DNA are incorrectly repaired or errors in DNA replication result in large segments being duplicate or deleted. Changes on this level, either duplications or deletions, result in changes in the copy numbers of genes and ultimately the amount of the products of these genes in a cell. In addition, chromosomal mutations may also include an alteration in the linear order of genes along a chromosome, or interchange of genes between non-homologous chromosomes. These latter types of mutations, while they do not change the number of copies of a gene, can impact chromosome pairing and segregation during meiosis.

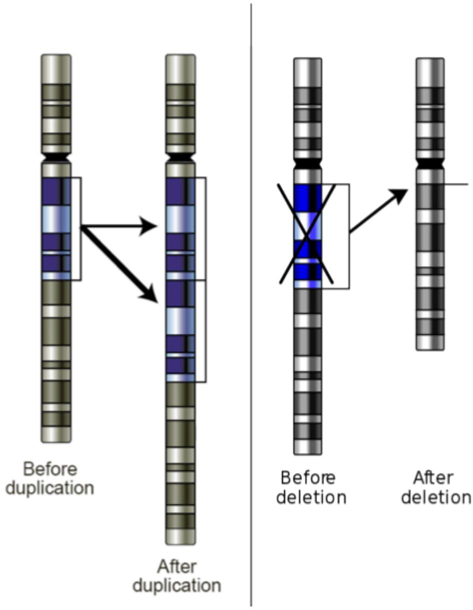


Figure 2. Duplications and deletions can alter the number of copies of genes and thus gene dosages.

The most common type of chromosomal abnormalities are the ones in which there are either two copies of a segment of DNA or a segment of DNA is missing completely (Fig. 2). A chromosome in which two copies of a segment occur is said to contain a **duplication**. When the duplicated segment is large it is also usually harmful and quickly eliminated from the population as individuals with these duplications are often non-functional (the mutation is lethal).

Smaller-scale duplications that include only one or a few genes can be maintained over many generations depending on the genes that are involved. **Deletions** can occur as a result of an error in replication or from the joining of breaks in a chromosome that eliminates a section. In some cases, deletions can persist in a population because chromosomes occur in homologous pairs in diploid organisms. This means that a copy of the deleted region is still present in one of the homologs and one copy may be enough for survival and reproduction. Some deletions, on the other hand, decrease the chance of survival and/or reproduction even when the homologous chromosome is normal.

Chromosomal Inversions and Translocations

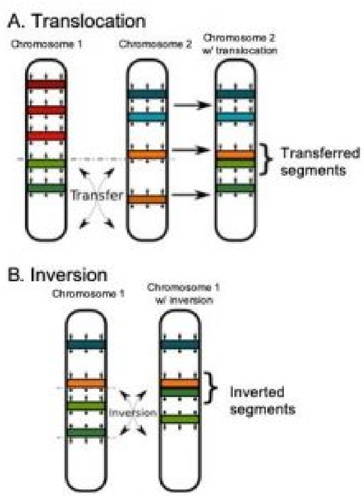


Figure 4. (A) Translocations occur when non-homologous chromosomes swap segments. (B) Inversions occur when segments of a chromosome are excised and then reinserted in the opposite orientation.

In addition to duplications and deletions, the order of genes within a chromosome can also be altered through **inversions** and reciprocal translocations. An inversion occurs when a block of genes within a chromosome is reversed, typically when a segment between two breaks and the segment is flipped in orientation. In larger genomes, these breaks are most likely to occur in noncoding regions rather than within a gene. Small inversions are common in many populations and because they do not delete or duplicate genes and so are less likely to cause problems. The accumulation of inversions over time long periods of time can explain, at least in part, why the order of genes can differ among closely related organisms.

Reciprocal translocations involve the exchange of segments of genes between two nonhomologous chromosomes. This occurs when there are breaks in both chromosomes and the terminal segments are exchanged before the breaks are repaired. As with inversions, reciprocal translocations change only the arrangement of genes and not their number. Thus, most of these types of mutations do not impact the survival of the organism. However, problems can arise during meiosis as the two chromosomes involved may not pair correctly with their homologs and thus not move properly into the daughter cells. This can result in inequality in gene dosages in the resulting cells, with some cells have duplicates and other missing genes.

Review Question:

What types of mutations can result in a change in the order of genes in chromosomes? (multiple answers)
A) point mutations
B) deletions
C) inversions
D) reciprocal translocations

Mutation Rates

There are multiple factors that can impact the rate at which mutations occur within an organism and within a population. In the absence of environmental conditions that can cause DNA damage (X-rays, ultraviolet radiation, exposure to mutagenic chemicals), most mutations are spontaneous and thus they occur randomly. It makes no difference whether a mutation would be beneficial or harmful to an organism, whether a mutation occurs is purely a matter of chance.

The most common type of mutation is the substitution of one nucleotide for another but even these types of mutations are relatively rare. The rate of mutations varies among different organisms as well as among different individuals within a population. Multiple factors can influence the rate of mutation and thus mutations rates can also vary over a large range. For example, RNA viruses and retroviruses store their genetic information in RNA rather than DNA. RNA is a less stable molecule than DNA and thus more susceptible to mutations. This means that mutation rates in these viruses are often higher than in viruses that utilize DNA as their genetic material.

Another factor that influences mutations is the proofreading mechanisms found within different groups of organisms. The efficiency with which errors are detected as well as the types of DNA repair mechanisms impact the rate of heritable mutations, mutations that are not corrected, and pass on to subsequent cells/offspring. Thus organisms that have highly efficient and complex detection and repair mechanisms tend to demonstrate lower rates of mutational changes in their genomes.

Since errors do occur, even if infrequently, during the replication of DNA, the mutation rate can vary between individuals within a population. For example, in male mammals, germ line cells undergo meiosis at a much higher rate than in females. This means that the DNA is replicated during each meiotic division and thus since replication occurs more often, the possibility of mutations also increases. The same holds true for different bacteria. Those that are in favorable environments will divide more often than those in less favorable conditions, meaning that their DNA will be replicated more often and thus there is a higher potential for mutations to occur.

Summary

Most errors in DNA replication that occur are corrected by built-in proofreading and repair mechanisms. However, if the errors are not repaired, they may result in a mutation, a permanent change in the

DNA sequence. Single base pair (point) mutations are the most common type and can involve insertion, deletion, or mismatches. Typically, these are detected by the cell and repaired. Mutations can also occur on a large scale in chromosomes. Inversions and reciprocal translocation can alter the sequence of genes within chromosomes while duplications and deletions can impact the gene dosage. Depending on the gene/s that is/are being impacted and the size of mutation, these alterations can be lethal, damaging, neutral, or in rare cases positive. If the mutation occurs in a cell that is a reproductive cell then the mutations can be inherited by the offspring. These mutations can have an impact on the genetic diversity of populations and thus play a role in the evolution of organisms.

End of Section Review Questions:

Types of Mutations: Match the mutation with its consequence

1) **Match the mutation with its consequence.**

1) silent	A) change in one amino acid
2) missense	B) an insertion/deletion alters the sequence
3) nonsense	C) a stop code is created
4) frameshift	D) no change in the resulting protein

Mutation Characteristics

2) **Most mutations are? (Multiple Answers)**

A) the result of environmental changes

B) random

C) spontaneous

D) favorable

Mutation Rates

3) **Which of the following has an impact on the rate at which mutations occur in cells? (Multiple Answers)**

A) the type of environmental change

B) the number of times DNA is replicated

C) the efficiency of DNA proofreading and repair mechanisms

D) the type of molecule used to store genetic information

Review: Think about this

4) Why would a mutation that involves a centromere have a greater impact than a mutation that occurs elsewhere on a chromosome?

References

Adapted from Morris et al. How Life Works 2nd edition (2017) Chapter 14 Mutation and DNA Repair.

Image AttributionFigure 1. Image (UV mutation of DNA) courtesy of derivative work: Mouagip (talk) DNA_UV_mutation.gif: NASA/David Herring. This W3C-unspecified vector image was created with Adobe Illustrator [Public domain]

Figure 2. Image (Point mutations) courtesy of CNX OpenStax[CC BY 4.0]

Figure 3. Left image courtesy of National Human Genome Research Institute [Public domain], via Wikimedia Commons. Right image (chromosomal deletion) was originally uploaded by Mirmillon at French Wikipedia. [Public domain], via Wikimedia Commons

Figure 4. Image courtesy of Guy Leonard / CC BY-SA 3.0 modified by D. Jennings 8/2020

4.

Learning Goals

By the end of this reading you should be able to:

- Describe the different types of variation in a population
- Explain why only heritable variation can be acted upon by natural selection
- Describe genetic drift and the bottleneck effect
- Explain how each evolutionary force can influence the allele frequencies of a population

Introduction

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

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**.

Evolutionary Forces

Changes in allele frequencies that are identified in a population can shed light on how it is evolving. 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 sizes 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, wasc the only one acting on the population. In other examples, better camouflage or a stronger resistance to drought might pose a selection pressure. In addition to natural selection, there are other evolutionary forces that could be in play: genetic drift, gene flow, mutation, nonrandom mating, and environmental variances.

Genetic Drift

Another way a population's allele and genotype frequencies can change is genetic drift 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).

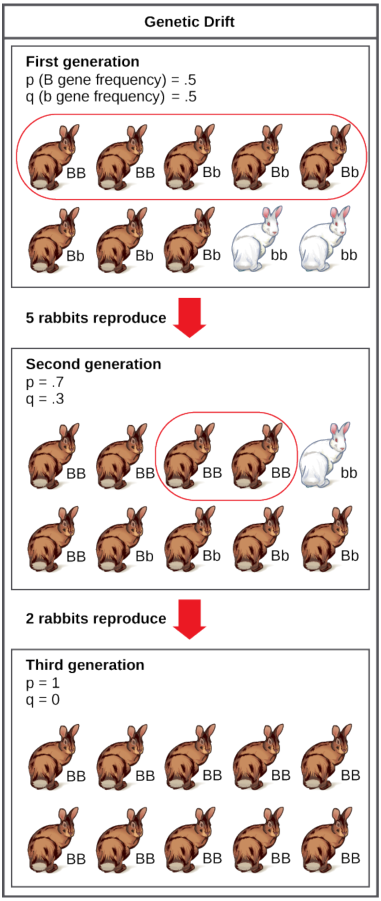


Figure 1. Illustration of genetic drift, or random change to gene frequencies over time.

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 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 (Fig. 1).

Use this link to watch an animation of random sampling and genetic drift in action.

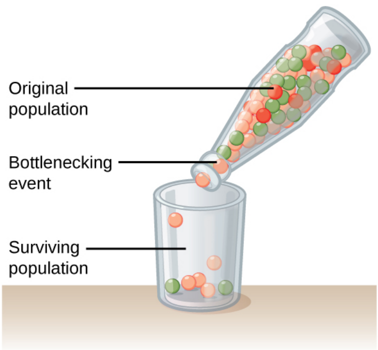
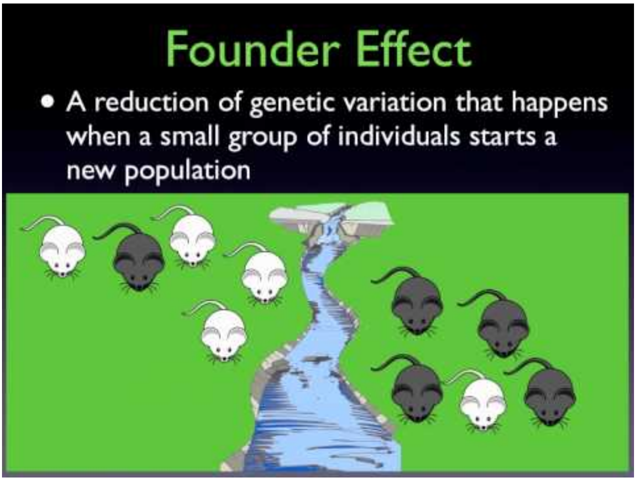


Figure 2. Bottleneck Effect

Natural events, like a natural disaster that kills—at random—a large portion of the population can magnify genetic drift. This event can result in a **bottleneck effect** (Fig. 2). In one fell swoop, the genetic structure of the survivors becomes the genetic structure of the entire population, which may be very different from the initial population.

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. This 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 since 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. [2]



A YouTube element has been excluded from this version of the text. You can view it online here: https://viva.pressbooks.pub/introbio2/?p=27

Thinking Question:

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

Gene Flow

Another important evolutionary force is **gene flow**: the flow of alleles in and out of a population due to the migration of individuals or gametes (Fig. 3). While some populations are fairly stable, others experience more flux. Many plants, for example, send their pollen far and wide, by wind or by bird, to pollinate other populations of the same species some distance away. Even a population that may initially appear to be stable, such as a pride of lions, can experience its fair share of immigration and emigration as developing males leave their mothers to seek out a new pride with genetically unrelated females. This variable flow of individuals in and out of the group not only changes the gene structure of the population but can also introduce new genetic variation to populations in different geological locations and habitats.

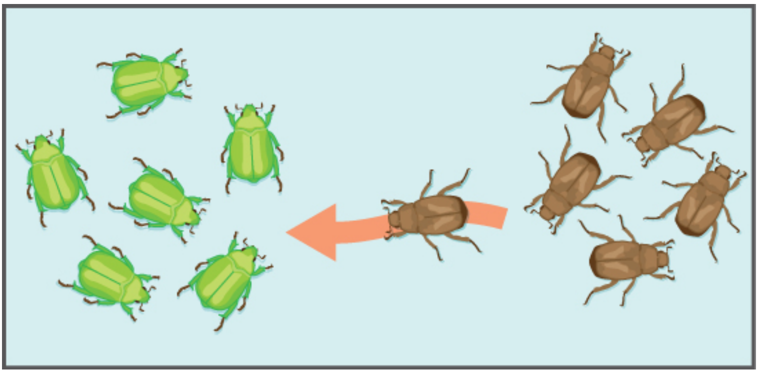


Figure 3. Gene flow can occur when an individual travels from one geographic location to another.

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 (Sexual Selection)

If individuals non-randomly 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, some female birds may prefer males with bigger, brighter tails. Traits that lead to more mating for an individual become selected for by natural selection. A 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.

Review Question:

What is assortative mating?
A) when individuals mate with those who are dissimilar to themselves
B) when individuals mate with those who are similar to themselves
C) when individuals mate with those who are the most fit in the population
D) when individuals mate with those who are least fit in the population

Environmental Variance

Genes are not the only players involved in determining population variation. Phenotypes are also influenced by other factors, such as the environment. 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 gender, are determined by the environment for some species. For example, some turtles and other reptiles have temperature-dependent sex determination (TSD). TSD means that individuals develop into males if their eggs are incubated within a certain temperature range, or females at a d different temperature range (Fig. 4).

Figure 4. Environmental factors like temperature can influence population variation. 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.

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.

Summary

Both genetic and environmental factors can cause phenotypic variation in a population. Different alleles can confer different phenotypes, and different environments can also cause individuals to look or act differently. Only those differences encoded in an individual's genes, however, can be passed to its offspring and, thus, be a target of natural selection. Natural selection works by selecting for alleles that confer beneficial traits or behaviors while selecting against those for deleterious qualities. Genetic drift stems from the chance occurrence that some individuals in the germ line have more offspring than others. When individuals leave or join the population, allele frequencies can change because of gene flow. Mutations to an individual's DNA may introduce new variation into a population. Allele frequencies can also be altered when individuals do not randomly mate with others in the group.

End of Section Review Questions:

Review: Mechanisms and Effects

1) One of the original Amish colonies rose from a ship of colonists that came from Europe. The ship's captain, who had polydactyly, a rare dominant trait, was one of the original colonists. Today, we see a much higher frequency of polydactyly in the Amish population. **What is this an example of?** (Multiple Answers)

A) natural selection
B) genetic drift
C) founder effect

Review: Mechanisms of Evolution

2) When male lions reach sexual maturity, they leave their group in search of a new pride. **This can alter the allele frequencies of the population through which of the following mechanisms?**

A) natural selection
B) genetic drift
C) gene flow
D) random mating

Review: Genetic Variation

3) **Which of the following evolutionary forces can introduce new genetic variation into a population?**

A) natural selection and genetic drift
B) mutation and gene flow
C) natural selection and nonrandom mating
D) mutation and genetic drift

Review: Mating Impacts

4) When closely related individuals mate with each other or inbreed, the offspring are often not as fit as the offspring of two unrelated individuals. **Why?**

A) Close relatives are genetically incompatible.
B) The DNA of close relatives reacts negatively in the offspring.
C) Inbreeding can bring together rare, deleterious mutations that

lead to harmful phenotypes.
D) Inbreeding causes normally silent alleles to be expressed.

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Figure 1. Genetic Drift courtesy of OpenStax, Rice University / CC BY (https://creativecommons.org/licenses/by/4.0)

Figure 2. Gene Flow courtesy of Tsaneda / CC BY (https://creativecommons.org/licenses/by/3.0)

Figure 3. Temperature-dependent sex determination. Left image courtesy of Planetseeker / CC BY-SA (https://creativecommons.org/licenses/by-sa/4.0). Right image courtesy of: Steve Hillebrand, USFWS Public Domain.

5.

Learning Goals

By the end of this reading you should be able to:

- Relate population genetics to the processes of evolution
- Explain how the Hardy-Weinberg principle is used in the biological sciences.
- Given an allele frequency calculate the frequency of different genotypes in a population.
- Use the Hardy-Weinberg principle to determine if a population is evolving.

While we currently have a complex understanding of the mechanisms of inheritance, or genetics, when Charles Darwin and Alfred Russel Wallace were developing their idea of natural selection this knowledge was unavailable. Not understanding how traits were inherited created 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 by Austrian monk Gregor Mendel, which was published in 1866, not long after the 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 in gene frequencies 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.

Review Question:

What is the difference between micro-and macroevolution?
A) Microevolution describes the evolution of small organisms, such as insects, while macroevolution describes the evolution of large organisms, like people and elephants.
B) Microevolution describes the evolution of microscopic entities, such as molecules and proteins, while macroevolution describes the evolution of whole organisms.
C) Microevolution describes the evolution of organisms in populations, while macroevolution describes the evolution of species over long periods of time.
D) Microevolution describes the evolution of organisms over their lifetimes, while macroevolution describes the evolution of organisms over multiple generations.

Population Genetics

Recall that a gene for a particular character may have several alleles, or variants, that code for different traits associated with that character. For example, in the ABO blood type system in humans, three alleles in the population 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. 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. This can also be thought of as the allele's percentage in the population relative to the other alleles of that gene in the 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 (i.e. microevolution). 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 the I^A allele to be 26.1 percent. The I^B and i alleles made up 13.4 percent and 60.5 percent of the alleles respectively, and all the frequencies added up to 100 percent (Figure 1). A change in this frequency over time would constitute evolution in the population.

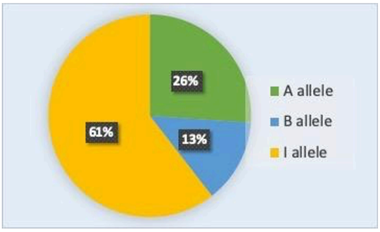

Figure 1. Frequencies of A, B *and* I *blood types alleles of the human population in Jordan* 1998-2003

The allele frequency within a given population can change under the following conditions: natural selection, sexual selection, genetic drift, gene flow, and mutations. The conditions are collectively called the mechanisms of evolution, specifically microevolution. If any of these mechanisms are in effect, then the population under investigation can undergo changes to its allele frequencies. For example, certain alleles may become more widespread than others through the process of natural selection. If a given allele confers a phenotype that allows an individual to better survive and/or have more offspring in a given habitat or environment. Because many of these offspring will also carry the beneficial allele, and often the corresponding phenotype, they will likely have more offspring of their own that also carry the allele, thus, perpetuating the cycle under those natural conditions. Over time, the allele will proliferate (spread) throughout the population, assuming those natural conditions remain the same (or similar). Some alleles will quickly become fixed in this way, meaning that every individual of the population will carry the allele, while deleterious (detrimental) alleles could potentially be swiftly eliminated from the gene pool, the sum of all the alleles in a population.

Review Question:

Population genetics is the study of:
A) how selective forces change the allele frequencies in a population over time
B) the genetic basis of population-wide traits
C) whether traits have a genetic basis
D) the degree of inbreeding in a population

Hardy-Weinberg Principle of Equilibrium

If you have ever endeavored to improve your performance in anything, then you probably were advised to take a baseline measurement and record your current performance. You might get your blood drawn, time laps in a pool, record weights you are lifting, record a video of a voice, instrument, or acting performance, or weigh yourself first. After some time practicing and improving, you'd record the same thing again. Without that baseline on record it is difficult to objectively measure your improvement. The same idea can be used to measure evolution. Constantly changing environments logically imply that gene frequencies are also constantly changing. The question becomes is this microevolution or just natural "noise"? To answer this, we must have a baseline, or a population that is not evolving, to which we can compare any changes.

In the early twentieth century, English mathematician Godfrey Hardy and German physician Wilhelm Weinberg formulated a mathematical principle of equilibrium that could be used to describe the genetic makeup of a population. The theorem, which later became known as the Hardy-Weinberg principle of equilibrium, states that a population's allele and genotype frequencies are inherently stable— unless, evolutionary forces are acting upon the population, neither the allele nor the genotypic frequencies should change. If a population is in this equilibrium, then it is not evolving and therefore can be thought of as the baseline measurement. Then we can compare all changes in allele frequencies to this baseline and statistically determine if the population is evolving. 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. Notice these conditions negate the mechanisms of evolution previously listed and therefore we should not expect allele frequencies to change.

Review Question:

Which of the following are criteria for maintaining Hardy-Weinberg equilibrium involving two alleles for a gene? (Multiple Answer)

A) Populations must be large
B) The frequency of all genotypes must be equal
C) No mutations occur
D) No emigration or immigration

Population geneticists represent different alleles as different variables in this mathematical model. The variable **p**, for example, often represents the frequency of a particular allele, say the dominant Y for the trait of yellow in peas, then the variable **q** would represent the frequency of the recessive y alleles that confer the color green. If these are the only two possible alleles for a given locus in the population, **p + q = 1** (or 100%). In other words, all the p alleles and all the q alleles make up all the alleles for that locus that are found in the population.

What ultimately interests most biologists is not the frequencies of different alleles, but the frequencies of the resulting genotypes, the population's genetic structure allows scientists to determine the distribution of phenotypes. When it is a phenotype that can be observed, only the genotype of the homozygous recessive alleles can be known; as individuals with the dominant phenotype can be either homozygous or heterozygous for the trait. However, the use of the Hardy-Weinberg equilibrium equation can be used to calculations an estimate of the remaining genotypes. Since each individual in this model carries two alleles per gene if the allele frequencies (p and q) are known, predicting the frequencies of these genotypes is simple.

One can easily calculate the probability of getting specific allele combinations (i.e. homozygous dominant, heterozygous, and homozygous recessive) if two alleles are drawn at random from the gene pool. So, in the above scenario, an individual pea plant could be homozygous dominant (YY, yellow peas), heterozygous (Yy, yellow peas), or homozygous recessive (yy, green peas) (Fig. 2). If the frequency of the allele Y = p, then the probability of randomly drawing two Y's from the gene pool is the product of each allele's individual probabilities, or p x p = $\mathbf{p^2}$. This is the frequency of the homozygous dominant genotype in the population. Likewise, the frequency of y is q, and thus drawing two y's at random is q x q = $\mathbf{q^2}$. This is the frequency of the homozygous recessive genotype in the population.

Figure 2. Genotypes and corresponding phenotypes for pea seeds.

The heterozygous genotype can be achieved in two ways: drawing a Y and then a y, or drawing a y and then a Y. As these are two separate events, we must add each combination's probability. First, Y then y equals p x q = pq. Second, y then Y equals q x p = qp. Combining the events: pq + qp = **2pq**. This is the frequency of the heterozygous genotype in the population. In this instance, Y and y are the only two alleles in the population, therefore **p2 + 2pq + q2 = 1** (or 100%) (Fig. 3).

Hardy-Weinberg Equilibrium Equations

Allele Frequencies: $p + q = 1$

Genotype Frequencies: $p^2 + 2pq + q^2 = 1$

Figure 3. Hardy-Weinberg Equilibrium Equations

So, how do population geneticists use these principles to study if the frequency of alleles for a gene in the population is changing? Let's start with a population of peas, where we can visually count the number of yellow seeds and the number of green seeds. We discover that out of a population of 1000 individuals, 910 individuals produce yellow seeds and 90 individuals produce green seeds. How can we determine the allele frequencies for the Y and y alleles from this information? Well, we know that the green seed individuals must be homozygous recessive (yy) and that the yellow seed individuals can be either homozygous dominant (YY) OR heterozygous (Yy).

As before, we will designate the frequency of the dominant Y allele to be p and the frequency of the recessive y allele to be q. Using the known number of green seed producers we can calculate q. Why? Because we know that all of the green seed producers have the homozygous recessive genotype.

So, frequency of yy equals q^2 and thus q^2 =90/1000 total or 0.09

The frequency of y = $\sqrt{q}$, in this case $\sqrt{.09}$ which is 0.3

Once we have q, we can calculate p; 1 − q = p

p = 1 − 0.3 = 0.7

Finally, the frequency of YY is p^2, in this case, 0.49 (0.72) and the frequency of Yy is 2pq (2*0.3*0.7) which is 0.42. Using these frequencies we can determine that of the 910 yellow seed producers 420 are heterozygotes (Yy) and 490 are homozygous dominant.

Review Question:

If the frequency of the dominant allele for a trait in the population is 0.57, what is the frequency of the recessive allele in the population assuming there are only two alleles for the trait?

In theory, if a population is at equilibrium—that is, there are no evolutionary mechanisms acting upon it— generation after generation would have the same gene pool and genetic structure, and these equations would all hold true all the time. Of course, both Hardy and Weinberg recognized that no natural population is immune to evolution. Populations in nature are constantly changing in genetic makeup due to genetic drift, mutation, possibly migration, and selection pressures. As a result, the only way to determine the exact distribution of phenotypes in a population is to go out and count them. What the Hardy-Weinberg principle gives scientists is a mathematical baseline of a non-evolving population to which they can compare natural populations and thereby infer if 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 must be evolving.

Review Question:

Which of the following populations is NOT in Hardy-Weinberg equilibrium?
A) a population with 12 homozygous recessive individuals (yy), 8 homozygous dominant individuals (YY), and 4 heterozygous individuals (Yy)
B) a population in which the allele frequencies do not change over time
C) $p^2 + 2pq + q^2 = 1$
D) a population undergoing natural selection

Summary

Modern synthesis of evolutionary theory grew out of the cohesion of Darwin's, Wallace's, and Mendel's thoughts on evolution and heredity, along with the more modern study of population genetics. It describes the evolution of populations and species, from small-scale changes among individuals (microevolution) to large-scale changes (macroevolution) over paleontological time periods. By tracking changes in populations' allele frequencies over time scientists can determine if evolutionary mechanisms are acting upon the population. The use of the Hardy-Weinberg equilibrium model can help scientists compare the natural population with a baseline. If the population's allele frequencies differ from those predicted by the model, scientists can conclude that the population is not in Hardy-Weinberg equilibrium, and is thus evolving.

End of Section Review Questions:

Review: Microevolution vs. Macroevolution

1) Changes in __________ frequencies in a __________ over time is part of the process of microevolution. Macroevolution focuses on changes __________ in over time.

Word Bank: mutation, species, allele, population, individual

Review: Using Hardy-Weinberg

2) In plants, violet flower color (V) is dominant over white (v). If p = 0.8 and q = 0.2 in a population of 500 plants, **how many individuals would you expect to be homozygous dominant (VV)**?
How many individuals would you expect to be heterozygous (Vv)?
How many individuals would you expect to be homozygous recessive (vv)?
How many plants would you expect to have violet flowers?
How many would have white flowers?

Review: Frequencies of Genotypes

3) In a Hardy-Weinberg population with two alleles, A and a, that are in equilibrium, the frequency of the recessive allele a is .7. **What is the percentage of the population that is homozygous for this allele**? (answer in %, not decimals)

Attribution

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

AttributionsText adapted from OpenStax Biology 2nd Edition, Biology 2e. OpenStax CNX. Nov 26, 2018 http://cnx.org/contents/8d50a0af- 948b-4204-a71d-4826cba765b8@15.1.

Figure 1. Courtesy of D. Jennings CC By 4.0

Figure 2. Courtesy of D. Jennings CC By 4.0

Evolution Connection:

Evolution and Flu Vaccines

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

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

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

6.

Learning Goals

By the end of this reading you should be able to;

- Describe how natural selection can result in adaptive evolution
- Differentiate between stabilizing, directional and diversifying selection.
- Describe how these different forces can lead to different outcomes in terms of the population variation
- Explain how frequency-dependent selection can impact the genetic structure of a population
- Describe the roles of sexual selection in the evolution of traits in populations

Introduction

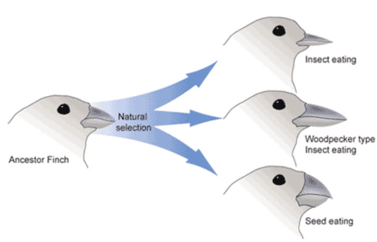

Figure 1. Natural selection can lead to adaptive evolution.

Natural selection only acts on the population's heritable traits: selecting for beneficial alleles and thus increasing their frequency in the population, while selecting against deleterious alleles and thereby decreasing their frequency—a process known as **adaptive evolution** (Fig. 1). Natural selection acts on entire organisms though and not on individual alleles. Natural selection acts at the level of the individual; and involves differences in individual contributions to the gene pool of the next generation, known as an organism's **evolutionary (Darwinian) fitness**. 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.

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 a differential number of offspring to the next generation, and thus, how the population might evolve. As natural selection influences the allele frequencies in a population, individuals can either become more or less genetically similar and as a result, the phenotypes displayed can also become less variable (more similar) or more variable (less similar).

Stabilizing Selection

If natural selection favors an average phenotype, selecting against extreme variation, the population will undergo **stabilizing selection** (Fig. 2). 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.

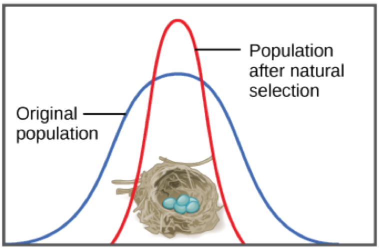

Figure 2. Robins typically lay four eggs. Larger clutches may result in malnourished chicks, while smaller clutches may result in no viable offspring. Thus selecting for the "middle", most successful number.

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.

Directional Selection

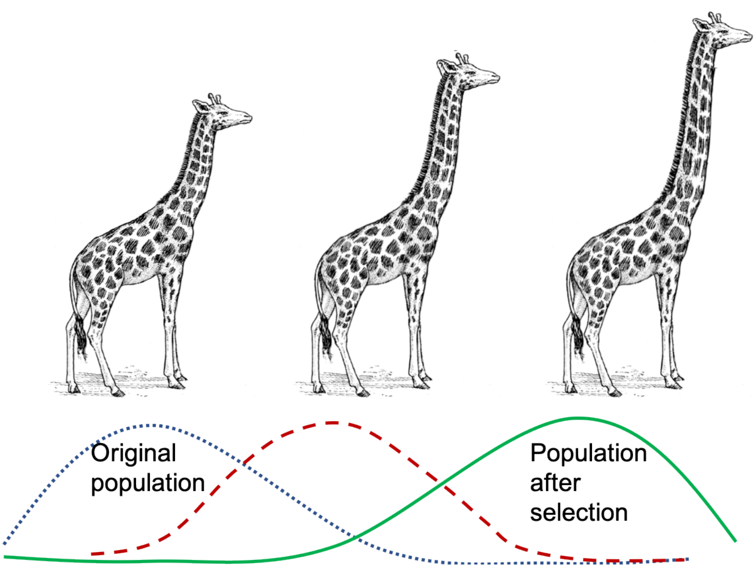

Figure 3. Directional selection leads to selection for one extreme of

a trait, and against the other extreme.
When the environment changes, populations will often undergo **directional selection** (Fig. 3), 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 (darker) 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 in the previous example 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.

Review Question:

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?

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, 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 sneaker 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.

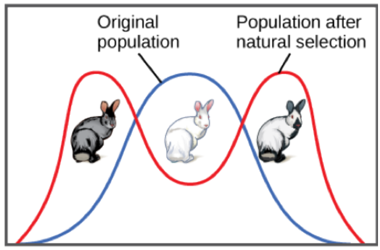

Figure 4. In a hypothetical population, gray and Himalayan (gray and white) rabbits are better able to blend with a rocky environment, resulting in diversify selection.

Diversifying selection can also occur when environmental changes favor individuals on either end of the phenotypic spectrum (Fig. 4). 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.

Review Question:

A scientist measures the circumference of acorns in a population of oak trees and discovers that the most common circumference is

2 cm. What would you expect the most common circumference(s) to be after 10 generations of diversifying selection?

A) still 2 cm
B) greater than 2 cm
C) less than 2 cm
D) both greater than 2 cm and less than 2 cm
E) either greater than 2 cm or less than 2 cm

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. Each of these forms has a different reproductive strategy: orange males are the strongest and can fight other males for access to their females; blue males are medium-sized and form strong pair bonds with their mates; and yellow males are the smallest, and look a bit like females, which allows them to sneak copulations (Fig. 5). Like a game of rock-paper-scissors, orange beats blue, blue beats yellow, and yellow beats orange in the competition for females. That is, the big, strong orange males can fight off the blue males to mate with the blue's pair-bonded females, the blue males are successful at guarding their mates against yellow sneaker males, and the yellow males can sneak copulations from the potential mates of the large, polygynous orange males.

Figure 5. Male blue and orange side-blotch lizards.

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. 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

Figure 6. The antlers (and horns) found on male deer are an example of a phenotypic trait that is linked to reproductive success. Deer with larger antlers are more likely to mate with females than deer with smaller antlers.

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**, 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 mating, while others receive none.

This can occur because the males are better at fighting other males, or because females will choose to mate with the bigger or more decorated males (Fig. 6). In either case, this variation in reproductive success generates a strong selection pressure among males to successfully mate, resulting in the evolution of bigger body size and elaborate ornaments to get the females' attention. Females, on the other hand, tend to mate less frequently; therefore, they are more likely to select more desirable males each time.

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 (Fig. 7).


(a) (b) (c)

Figure 7. 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 mating 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 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 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 intermediate morphs that are 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 that through selection the gradual change to dark coloration would be favored. However, remember that the intermediate phenotype, a medium-colored coat, is not favorable 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 gradual change to a dark coloration would not occur because those individuals that began displaying an intermediate phenotype would be less fit than those individuals who retained the light coloration.

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 reading and how they influence the genetic and phenotypic variance of a population.

Summary

Because natural selection acts to increase the frequency of beneficial alleles and traits in a given environment while decreasing the frequency of deleterious qualities, it is adaptive evolution. Natural selection acts at the level of the individual, selecting for those that have a higher overall fitness compared to the rest of the population and resulting in differential reproductive success. If the fit phenotypes are those that are similar, natural selection will result in stabilizing selection, and an overall decrease in the population's variation in those phenotypes will occur. Directional selection works to shift a population's variance toward a new, fit phenotype, as environmental conditions change. In contrast, diversifying selection results in increased genetic variance by selecting for two or more distinct phenotypes.

Other types of selection include frequency-dependent selection, in which individuals with either common (positive frequency-dependent selection) or rare (negative frequency-dependent selection) are selected for. Finally, sexual selection results from the fact that one sex has more variance in the reproductive success than the other. As a result, males and females experience different selective pressures, which can often lead to the evolution of phenotypic differences, or sexual dimorphisms, between the two.

End of Section Review Questions:

Review: Types of Selection

1) **Which type of selection results in greater genetic variance in a population?**

A) stabilizing selection
B) directional selection
C) diversifying selection
D) positive frequency-dependent selection

Review: Sexual Selection 1

2) **When males and females of a population look or act differently, it is referred to as?**

A) sexual dimorphism
B) sexual selection
C) diversifying selection
D) a cline

Review: Sexual Selection 2

3) **The good genes hypothesis is a theory that explains what?**

A) why more fit individuals are more likely to have more offspring

B) why alleles that confer beneficial traits or behaviors are selected for by natural selection
C) why some deleterious mutations are maintained in the population
D) why individuals of one sex develop impressive ornamental traits

CRITICAL THINKING QUESTION

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

Attributions

Footnotes

1. [1]Sahar S. Hanania, Dhia S. Hassawi, and Nidal M. Irshaid, ftAllele Frequency and Molecular Genotypes of ABO Blood Group System in a Jordanian Population,ft Journal of Medical Sciences 7 (2007): 51-58, doi:10.3923/jms.2007.51.58.
2. [2]A. J. Tipping et al., ftMolecular and Genealogical Evidence for a Founder Efect in Fanconi Anemia Families of the Afrikaner Population of South Africa,ft PNAS98, no. 10 (2001): 5734-5739, doi: 10.1073/pnas.091402398.

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Figure 1. Image courtesy of National Human Genome Research Institute's Talking Glossary [Public domain], via Wikimedia Commons

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Figure 3. Modified by D. Jennings from image created by Pearson Scott Foresman [Public domain], via Wikimedia Commons

Figure 4. Image modified from OpenStax Biology 2nd Edition, Biology 2e. OpenStax CNX. Nov 26, 2018 http://cnx.org/contents/8d50a0af-948b-4204-a71d-4826cba765b8@15.1

Figure 5. Blue male image and orange male images from the public domain. Combined by D. Jennings

Figure 6. Male deer CC By 0, public domain

Figure 7. Spider: modification of work by ftSanba38ft/Wikimedia Commons; Duck: modification of work by Kevin Cole

7.

Learning Goals

By the end of this reading you should be able to:

- Explain how species are defined
- Describe genetic variables that lead to speciation
- Identify prezygotic and postzygotic reproductive barriers
- Compare and contrast allopatric and sympatric speciation

Introduction

Populations are considered to be the key evolutionary unit but what are populations composed of? Populations consist of are of individuals that are of the same species that live in a distinct area or environment and reproduce with each other. To understand the role of populations in the evolution of species we need to understand how we define species. You will find that in some cases it is obvious that organisms are of different species, but in others, it is not as simple.

Species and the Ability to Reproduce

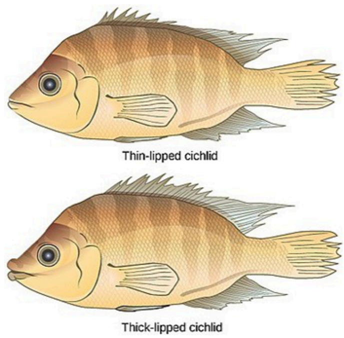

Figure 1. Speciation in cichlid fishes has resulted in species with unique phenotypes, thin-lipped versus thick-lipped

The biological definition of species, which works for sexually reproducing organisms, is a group of actual or potential interbreeding individuals. According to this definition, one species is distinguished from another when, in nature, it is not possible for mating between individuals from each species to produce fertile offspring. Members of the same species share both external and internal characteristics, which develop from their DNA (Fig. 1). The closer relationship two organisms share, the more DNA they have in common, just like people and their families. People's DNA is likely to be more like their father or mother's DNA than their cousin 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.

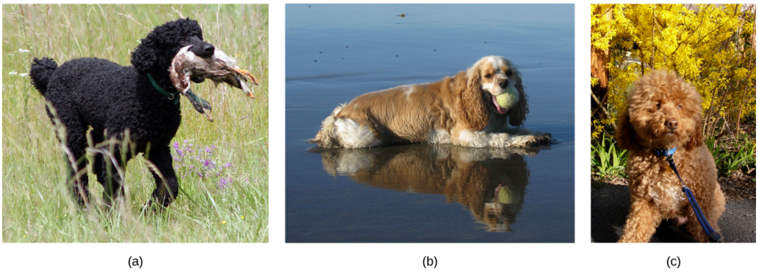

Figure 2. The (a) poodle and (b) cocker spaniel can reproduce to produce a breed known as (c) the cockapoo. (credit a: modification of work by Sally Eller, Tom Reese; credit b: modification of work by Jeremy McWilliams; credit c: modification of work by Kathleen Conklin)

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 (Fig. 3). If humans were to artificially intervene and fertilize a bald eagle's egg with an African fish eagle's sperm 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.

Figure 3. 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)

There are exceptions to this rule. Many species are similar enough that hybrid offspring are possible and may often occur in nature, but for the majority of species this rule generally holds. The presence in nature of hybrids between similar species suggests that they may have descended from a single interbreeding species, and the speciation process may not yet be completed.

While the inability to reproduce or produce viable offspring is the key to the definition of species that is most commonly used there are other ways in which species are defined. These can include separations based on the ecological area where the organism lives, the resources that the organism uses (particularly in bacteria and archaea), the behavioral patterns of the populations, and in some cases the specific sequences of genes in their DNA. It’s important to remember that it is humans who separate organisms into species and not a way that organisms identify themselves.

Review Question:

While the ability to produce fertile offspring is one means of defining species, what other characters can be used? (Multiple Answers)
A) the morphology of the organisms (what they look like)
B) the habitat in which the organisms live
C) behaviors within populations
D) the resources that the organisms use

Speciation

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 in On the Origin of Species (Fig. 4). Compare this illustration to the diagram of elephant evolution, which shows that as one species changes over time, it branches to form more than one new species, repeatedly, as long as the population survives or until the organism becomes extinct.

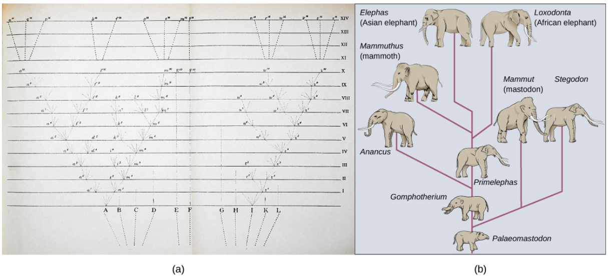

Figure 4. The only illustration in Darwin's On the Origin of Species is (a) a diagram showing speciation events leading to biological diversity. The diagram shows similarities to phylogenetic charts that today illustrate the relationships of species. (b) Modern elephants evolved from the Palaeomastodon, a species that lived in Egypt 35–50 million years ago.

For speciation to occur, two new populations must form 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. However, there is no reason why more than two species might not form at one time except that it is less likely and multiple events are most likely single splits occurring close in time.

Allopatric Speciation

A geographically continuous population has a gene pool that is relatively homogeneous. This is in part because gene flow, the movement of alleles across a species’ range, is relatively free, individuals can move and then mate with individuals in their new location. Thus, an allele’s frequency at one end of a distribution will be similar to the allele’s frequency at the other end. When populations become geographically discontinuous, it prevents alleles’ free-flow. When that separation lasts for a period of time, the two populations have the potential to evolve along different trajectories. Thus, their allele frequencies at numerous genetic loci can gradually become increasingly different as new alleles independently arise by mutation in each population. Typically, environmental conditions, such as climate, resources, predators, and competitors for the two populations will differ causing natural selection to favor divergent adaptations in each group.

Isolation of populations leading to allopatric speciation can occur in a variety of ways: a river forming a new branch, erosion creating a new valley, a group of organisms traveling to a new location without the ability to return, or seeds floating over the ocean to an island. The nature of the geographic separation necessary to isolate populations depends entirely on the organism’s biology and its potential for dispersal. If two flying insect populations took up residence in separate nearby valleys, chances are, individuals from each population would fly back and forth continuing gene flow.

However, if a new lake divided two rodent populations continued gene flow would be unlikely; therefore, speciation would be more likely.

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.

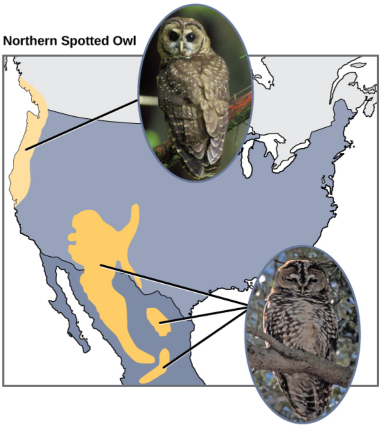

Figure 5. The northern spotted owl and the Mexican spotted owl inhabit geographically separate locations with different climates and ecosystems. The owl is an example of allopatric speciation. (credit "northern spotted owl": modification of work by John and Karen Hollingsworth; credit "Mexican spotted owl": modification of work by Bill Radke)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 spotted owl subspecies exist (Fig. 5). The northern spotted owl has genetic and phenotypic differences from its close relative: the Mexican spotted owl, which lives in the south. 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

Review Question:

Allopatric speciation may occur because __________ prevent __________
Word bank: gene flow, post-zygotic barriers, geographic barriers, mutations, genetic drift

Sympatric Speciation

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.

Can divergence occur if no physical barriers are in place to separate individuals who continue to live and reproduce in the same habitat? The answer is yes. We call the process of speciation within the same space sympatric. The prefix "sym" means same, so "sympatric" means "same homeland" in contrast to "allopatric" meaning "other homeland." Scientists have proposed and studied many mechanisms that could lead to **sympatric speciation**, the formation of separate species in the same area.

One mechanism is the occurrence of a major chromosomal error during cell division. In a normal cell, during division chromosomes replicate, pair up, and then separate so that each new cell has the same number of chromosomes. However, sometimes the pairs can fail to separate properly and the resulting cell product has too many or too few individual chromosomes, a condition that is called **aneuploidy** (Fig. 6).

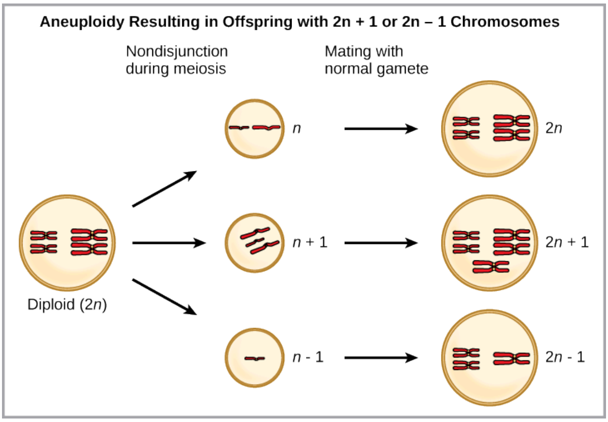

Figure 6. Aneuploidy results when the gametes have too many or too few chromosomes due to nondisjunction during meiosis. In this example, the resulting offspring will have 2n+1 or 2n-1 chromosomes.

Review Question:

Which is most likely to survive, offspring with 2n+1 chromosomes or offspring with 2n-1 chromosomes? Explain your reasoning.

Polyploidy is a condition in which a cell or organism has an extra set, or sets, of chromosomes. This is the result of an error in meiosis in which all of the chromosomes move into one cell instead of separating into two cells. Scientists have identified two main types of polyploidy that can lead to reproductive isolation (the inability to interbreed) of an individual in the polyploidy state. In **autopolyploidy** will have two or more complete sets of chromosomes from its own species.

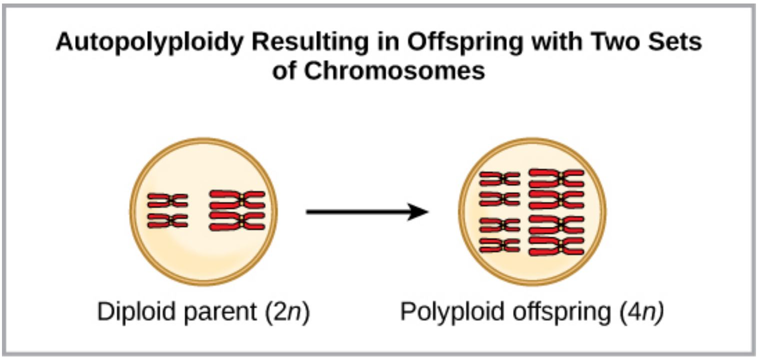

Figure 7. Autopolyploidy results when mitosis is not followed by cytokinesis.

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 (Fig. 7). These new gametes will be incompatible with the normal gametes that this plant species produces. However, they could either self-pollinate or reproduce with other autopolyploid plants with gametes having the same diploid number. In this way, sympatric speciation can occur quickly by forming offspring with 4n that we call a tetraploid. These individuals would only be able to reproduce with other individuals of this new kind and not those of the ancestral species, thus reproductively isolating them from the ancestral population.

The other form of polyploidy occurs when individuals of two different species reproduce to form a viable offspring that we call an **allopolyploid**. Figure 8 illustrates one possible way an allopolyploid (or alloploid) can form. Notice how it takes two generations, or two reproductive acts, before the viable fertile hybrid results.

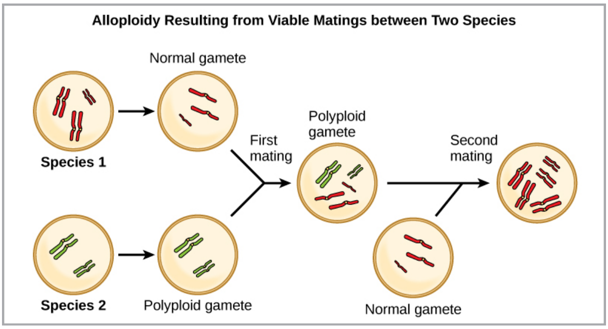

Figure 8. Alloploidy results when two species mate to produce viable offspring. In this example, a normal gamete from one species fuses with a polyploidy gamete from another. Two matings are necessary to produce viable offspring.

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

Review Question:

Which of these statements accurately describes the difference between an allopolyploid and an autopolyploid?
A) autopolyploids have chromosomes from two species, allopolyploids only have chromosomes from one species

B) allopolyploids have chromosomes from two species, autopolyploids only have chromosomes from one species
C) autopolyploids are always tetraploid, allopolyploids can be tetraploid or have more than four genome copies
D) allopolyploids are always tetraploid, autopolyploids can be tetraploid or have more than four genome copies

Summary

One of the key factors in defining species and in the process of speciation is the ability of populations of organisms to reproduce with each other. When there are populations that are isolated geographically this can prevent the actual movement of individuals between the populations, hence preventing gene flow. Over time if the environments in which the two populations inhabit are different or the populations are subjected to different selection pressures the two populations can become genetically different enough to prevent reproduction between them and allopatric speciation would have occurred. It is not always necessary for a population or populations to be geographically isolated for them to speciate.

End of Section Review Questions:

Review: Defining Species. (Multiple Answer)
1) **While the ability to produce fertile offspring is one means of defining species, what other characters can be used? (Multiple Answer)**
A) the habitat in which the organisms live
B) the morphology of the organisms (what they look like)
C) behaviors within populations
D) the resources that the organisms use
Review: Speciation Patterns

2) ___________ speciation involves geographic separation of a population while ___________ speciation occurs in a population in the same location.

Review: Allopatric and Sympatric Speciation

3) **A major difference between allopatric and sympatric speciation is whether…?**

A) resulting species are reproductively isolated or not
B) gene flow continues to occur or not
C) two or three species results
D) geographic isolation is required or not

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Figure 1. Speciation in cichlid Fishes: courtesy of CNX OpenStax /CC BY 4.0

Figure 2. Dog Breeding; courtesy of CNX OpenStax / CC BY 4.0 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

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Figure 4. Elephant Evolution: courtesy of CNX OpenStax / CC BY 4.0

Figure 5. Owl Speciation: courtesy of CNX OpenStax / CC BY 4.0 credit "northern spotted owl": modification of work by John and Karen Hollingsworth; credit "Mexican spotted owl": modification of work by Bill Radk.

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Figure 7. Autopolyploidy: courtesy of CNX OpenStax / CC BY 4.0

Figure 8. Allopolyploidy: courtesy of CNX OpenStax / CC BY 4.0

8.

Learning Goals

By the end of this reading you should be able to:

- Identify prezygotic and postzygotic reproductive barriers
- Discuss the role of habitat in the process of speciation
- Describe the process of adaptive radiation

Introduction

For speciation to occur, two new populations must form 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 think of speciation events as the splitting of one ancestral species into two descendant species. However, there is no reason why more than two species might not form at one time except that it is less likely and multiple events are most likely single splits occurring close in time.

Reproductive Isolation

Given enough time, the genetic and phenotypic divergence between populations will affect characters that influence reproduction: if individuals of the two populations were brought together, mating would be less likely, but if mating occurred, offspring would be nonviable or infertile. Many types of diverging characters may affect the reproductive isolation, the ability to interbreed, of the two populations. Scientists organize the means of reproductive isolation into two groups: prezygotic barriers and postzygotic barriers. Recall that a zygote is a fertilized egg: the first cell of a sexually reproducing organism's development. Therefore, a prezygotic barrier is a mechanism that blocks reproduction from taking place, thus no zygote is formed. A postzygotic barrier occurs after zygote formation. This includes organisms that don't survive the embryonic stage and those that are born sterile.

Prezygotic Barriers

Figure 1. These two frog species exhibit temporal reproductive isolation. (a) Rana aurora breeds earlier in the year than (b) Rana boylii

Some types of prezygotic barriers prevent reproduction entirely. Many organisms only reproduce at certain times of the year, often just annually. Differences in breeding schedules, which we call temporal isolation, can act as a form of reproductive isolation. For example, two frog species inhabit the same area, but one reproduces from January to March; whereas, the other reproduces from March to May (Fig. 1).

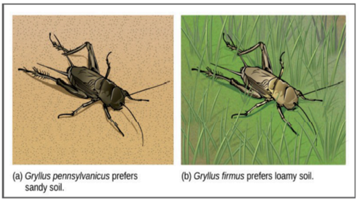

Figure 2. The cricket (a) Gryllus pennsylvanicus prefers sandy soils, and the cricket (b) Gryllus firmus prefers loamy soil. The two species can live in close proximity, but because of their different soil preferences, they became genetically isolated

In some cases, sub-populations of a species move or are moved to a new habitat and that no longer overlaps with the same species' original population. Reproduction with the parent species ceases, and a new group exists that is now reproductively and genetically independent. We call this situation habitat isolation. For example, a cricket population that was divided after a flood could no longer interact with each other (Fig. 2). Over time, natural selection forces, mutation, and genetic drift will likely result in the two groups diverging. The habitats need not be far apart for reproduction isolation to occur.

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

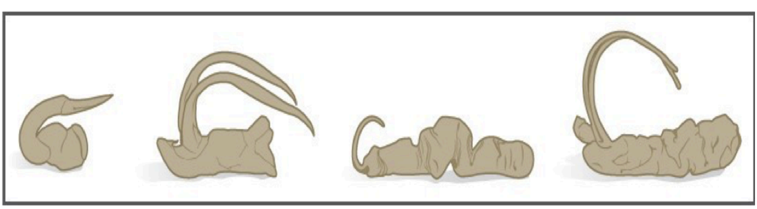

Figure 3. The shape of the male reproductive organ varies among male damselfly species and is only compatible with the female of that species. Reproductive organ incompatibility keeps the species reproductively isolated

Other prezygotic barriers work when differences in their gamete cells (eggs and sperm) prevent fertilization from taking place. This is gametic isolation and occurs after mating but before the formation of a zygote. In some cases, closely related organisms try to mate, but their reproductive structures simply do not fit together. This is mechanical isolation that prevents reproduction. 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 (Fig. 3).

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 cross-pollinating with a different species.

Postzygotic Barriers

When fertilization takes place and a zygote forms, postzygotic barriers can prevent reproduction in the resulting organisms. Hybrid individuals in many cases cannot form normally in the womb and simply do not survive past the embryonic stages. We call this hybrid inviability because the hybrid organisms simply are not viable. In another postzygotic situation, reproduction leads to hybrid birth and growth that is sterile. Such is the case in plants where autopoylploidy and allopolyploidy can impact the ability of individuals to produce viable offspring. When the organisms are unable to reproduce offspring of their own it is referred to as hybrid sterility.

Review Question:

Two species of wild lettuce grow in the same area; however, one species flowers in early spring and the other flowers during the summer. **What is this an example of?**

A) Hybrid sterility
B) Temporal isolation
C) Habitat isolation
D) Hybrid inviability
E) Gametic isolation

Habitat Influence on Speciation

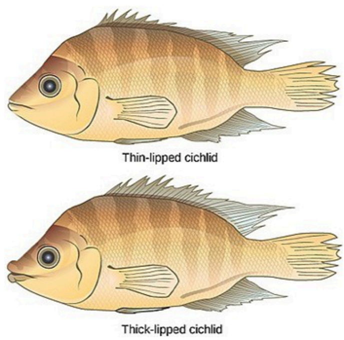

Figure 4. Speciation in cichlid fishes has resulted in species with unique phenotypes, thin-lipped versus thick-lipped

Sympatric speciation may also take place in response to the environment in which the population lives. For example, consider a fish species that lives in a lake. As the population grows, competition for food increases. Under pressure to find food, suppose that a group of these fish had the genetic flexibility to discover and feed off another resource that other fish did not use. What if this new food source was located at a different depth of the lake? Over time, those feeding on the second food source would interact more with each other than the original population of fish; therefore, they would be most likely to breed within their group rather than with the original population. Offspring of this subpopulation of 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.

An example of this scenario in nature occurred in Cichlid fish from Lake Apoyeque, Nicaragua. Lake Apoyeque is a crater lake that is 1800 years old where genetic evidence indicates that a single population of cichlid fish populated the lake only 100 years ago. In this lake, 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 (Fig. 4). Presently only the two populations with distinct morphologies and diets now exist in the lake, but scientists believe these populations may be in an early stage of additional speciation events.

Adaptive Radiation

In some cases, a population of one species disperses throughout an area, and each finds a distinct niche or isolated habitat. Over time, the varied demands of their new lifestyles lead to multiple speciation events originating from a single species. We call this adaptive radiation because many adaptations evolve from a single point of origin; thus, causing the species to radiate into several new ones. Island archipelagos like the Hawaiian Islands provide an ideal context for adaptive radiation events because water surrounds each island which leads to geographical isolation for many organisms. The Hawaiian honeycreeper illustrates one example of adaptive radiation. From a single species, the founder species, numerous species have evolved. Notice the differences in the species' beaks in Figure 5. Responses to natural selection based on specific food sources available in each new habitat led to

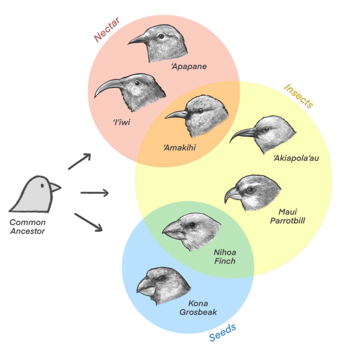

Figure 5. Example of adaptive rasdiation of honeycreepers.

evolution of different beaks suited to the specific food sources. 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.

When they are in the same geographic area speciation can be the result of habitat differences, behavioral differences, and/or differential ability to use resources. Changes in the populations can result in the evolution of traits that create reproductive barriers. If the trait results in lack of the ability to form an embryo, such as gametic isolation or temporal isolation, they are referred to a prezygotic mechanism. If the result is an infertile or inviable offspring then it is a post-zygotic isolation. These reproductive isolating mechanisms can eventually lead to the formation of new species.

Summary

It is not always necessary for a population or populations to be geographically isolated for them to speciate. When they are in the same geographic area speciation can be the result of habitat differences, behavioral differences, and/or differential ability to use resources. Changes in the populations can result in the evolution of traits that create reproductive barriers. If the trait results in a lack of the ability to form an embryo, such as gametic isolation or temporal isolation, they are referred to as a prezygotic mechanism. If the result is an infertile or inviable offspring then it is postzygotic isolation. These reproductive isolating mechanisms can eventually lead to the formation of new species.

End of Section Review Questions:

Review: Mechanisms of Speciation

1) Speciation can occur through a variety of mechanisms. **Match the correct term to the appropriate description.**

Term	Description
1) Prezygotic isolation	A. the isolation of two or more populations because of t
2) Vicariance	B. a population of one species disperses throughout an
3) Adaptive Radiation	C. that prevent reproduction prior to embryo formatio
4) Dispersal	D. mechanisms that prevent offspring from reproducin
5) Postzygotic isolation	E. some individuals from the main population colonize

Review: Adaptive Radiation

2) **What are some of the key aspects of adaptive radiation?**

A) Specialization of groups of individuals to specific habitats/niches

B) the presence of multiple ancestral species

C) multiple speciation events occurring

D) a single speciation event that occurs rapidly

Attribution

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Figure 1. Temporal Isolation in frogs: courtesy of CNX OpenStax / CC BY 4.0credit a: modification of work by Mark R. Jennings, USFWS; credit b: modification of work by Alessandro Catenazzi

9.

Learning Goals

By the end of this reading you should be able to:

- Describe how hybrid fitness can influence speciation in a hybrid zone
- Differentiate between gradual and punctuated equilibrium
- Explain how population size and environmental variables can impact speciation rates

Introduction

In some cases, after being geographically separated and undergoing adaptive evolution two populations can reconnect. What happens next depends on many factors, including the types of adaptations that have occurred as well as underlying genetic changes. Sympatric speciation, in which there is no geographic separation also occurs over a span of evolutionary time, so when a new species arises, there is a transition period during which the closely related species continue to interact. What happens when these populations reconnect?

Reconnection

In some cases, after two populations have been separated and evolved in different ways possibly even becoming different species, the two populations may come into contact again. It is possible that if they are still similar enough that they may recombine or just interact and remain separate indefinitely. In some instances, individual organisms within a population can and will mate with any nearby individual with whom they are capable of breeding. The area where two closely related species continue to interact and reproduce, forming hybrids is referred to as a hybrid zone. Over time, the hybrid zone may change depending on the fitness of the hybrids and the presence/absence of any reproductive barriers.

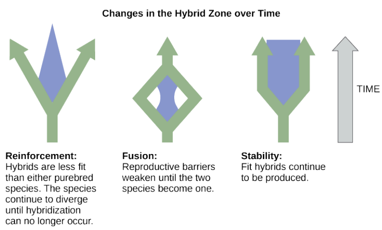

Figure 1. In hybrid zones, reinforcement, fusion, or stability may result, depending on reproductive barriers and the relative fitness of the hybrids.

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 we call reinforcement. The hybrids' reduced fitness and thus lower reproductive success reinforce the original speciation and overtime the species will continue to diverge until they can no longer hybridize. If the hybrids are as fit or more fit than the parents with which they will be competing then the two species may fuse back into one species. The weakening of reproductive barriers between the two species will reinforce this reconnection. Scientists have also observed that sometimes two species will remain separate but also continue to interact to produce some hybrid individuals. Scientists classify this as stability because no real net change is taking place. For a hybrid zone to be stable, the offspring produced by the hybrids have to be less fit than members of the parent species. (Fig. 1)

A final possibility that has been observed is the eventual development of the hybrids as a species of their own. In this case, the hybrids are fit but only in relation to other hybrids, meaning that they will be most likely to reproduce with other hybrids. Over time this can result in reproductive barriers between the hybrids and the original parental species and lead to the formation of a separate species. The ability to analyze DNA has shown that hybrid speciation is a fairly common phenomenon, particularly in plants.

Review Question:

When the hybrids are ________ than the parental species, reinforcement of speciation in hybrid zones can occur.

Varying Rates of Speciation

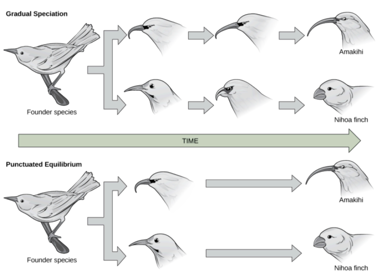

Figure 2. In gradual speciation (top), species diverge at a slow, steady pace as traits change incrementally. In punctuated equilibrium (bottom), species diverge quickly and then remain unchanged for long periods of time.

Scientists around the world study speciation, documenting observations of living organisms, and ancestral organisms 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 speciation rates. In terms of how quickly speciation occurs, we can observe two current patterns: the gradual speciation model and the punctuated equilibrium model.

In the gradual speciation model, species diverge gradually over time in small steps. In this model, a species evolves by accumulating small variations over a long period of time. In the punctuated equilibrium model, a new species forms when a small group undergoes changes quickly from the parent species and then remains largely unchanged for long periods of time afterward. We call this early change model 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 (Fig. 2).

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. Thus they are morphologically stable and 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 that differ from those in the larger population. Because its gene pool quickly became so small, any variation that surfaces and that aids in surviving the new conditions becomes the predominant form.

Review Question:

Which of the following statements is false?

dA) 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.

According to this idea, the changes leading to a new species don't usually occur from a slow incremental change in the mainstream population of a species but occur in those populations living in the periphery, or in small geographically isolated populations where their gene pools vary more widely due to the slightly different environmental conditions where they dwell. When the environment changes, these peripheral or geographic isolates possess variation in morphology which might enable them to have an adaptive advantage, leading to greater reproductive success. These new successful morphotypes spread through the geographic range of the ancestral species.[2]

Punctuated equilibrium does not:

- Suggest that Darwin's theory of evolution by natural selection is wrong.
- Mean that the central conclusion of evolutionary theory, that life is old and organisms share a common ancestor, no longer holds.
- Negate previous work on how evolution by natural selection works.
- Imply that evolution only happens in rapid bursts.

Punctuated equilibrium predicts that a lot of evolutionary change takes place in short periods of time tied to speciation events.[2]

Summary

In some instances speciation isn't always a precise division. Hybrid zones, areas in which closely related species both occur can form. In these zones some organisms may reproduce with other similar organisms of the other species. The fitness of the resulting hybrid offspring can affect the two species' evolutionary path, reinforcement, fusion or stability. 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 can occur and over time the two species may become one. If the hybrids are equally fit and thus reproductive: stability may occur and hybridization may continue.

Speciation rates can be influenced by many factors but one of the key ones is environmental changes. While natural selection patterns are consistent, there are two models for the rate of speciation. In the gradual changes are slow over a long period of time and in the punctated there is a rapid change followed by a long period without change. The fossil record can be used to study the changes but not all changes are reflected in the record.

End of Section Review Questions:

1) **How could hybrid reproduction cause two species to fuse into one?**

2) **Which term is used to describe the continued divergence of species based on the low fitness of hybrid offspring?**
A) fusion
B) reinforcement
C) stability

3) **Which components of speciation would be LEAST likely to be a part of punctuated equilibrium?**
A) a division in the population results in large and small subpopulations
B) a rapid change in environmental conditions
C) continuing gene flow among all parts of the population
D) a large number of simultaneous mutations

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Figure 1.Hybrid Zones courtesy of CNX OpenStax / CC BY 4.0

Figure 2. Gradual and punctuated equilibrium courtesy of CNX OpenStax / CC BY 4.0

Footnotes

1. Punctuated Equilibrium (http://www.pbs.org/wgbh/evolution/library/03/5/l_035_01.html)

2. Understanding evolution: more on punctated equilibrium. https://evolution.berkeley.edu/evolibrary/article/side_0_0/punctuated_01

10.

Learning Goals

By the end of this reading you should be able to:

- Discuss the need for a comprehensive classification system
- List the different levels of the taxonomic classification system
- Describe how systematics and taxonomy relate to phylogeny
- Discuss the components and purpose of a phylogenetic tree

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

Introduction

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

Phylogenetic Trees

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. 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.

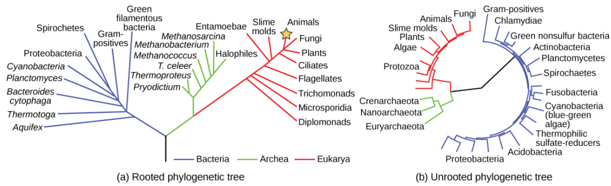


Figure 2. Both of these phylogenetic trees show the relationship of the three domains of life—Bacteria, Archaea, and Eukarya—but the (a) rooted tree attempts to identify when various species diverged from a common ancestor while the (b) unrooted tree does not. (credit a: modification of work by Eric Gaba)

Scientists call such trees rooted (Fig. 2), which means there is a single ancestral lineage (typically drawn from the bottom or left) to which all organisms represented in the diagram relate. Unrooted trees, on the other hand, don't show a common ancestor but do show relationships among species. Notice in the rooted phylogenetic tree that the three domains — Bacteria, Archaea, and Eukarya — diverge from a single point and branch off. In a rooted tree, the branching indicates evolutionary relationships.

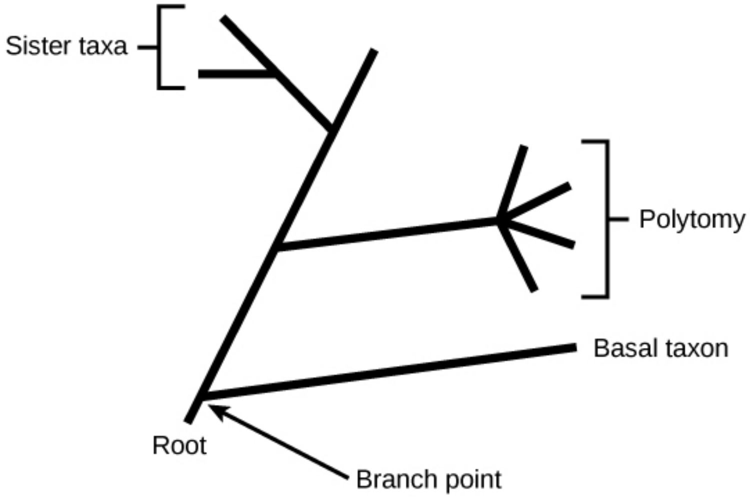


Figure 3. The root of a phylogenetic tree indicates that an ancestral lineage gave rise to all organisms on the tree. A branch point indicates where two lineages diverged. A lineage that evolved early and remains unbranched is a basal taxon. When two lineages stem from the same branch point, they are sister taxa. A branch with more than two lineages is a polytomy.

The point where a split occurs called a **branch point** represents where a single lineage evolved into a distinctly new one (Fig. 3). A lineage that evolved early from the root and remains unbranched is called a **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.

Diagrams can serve to show a pathway and aid our understanding of evolutionary history. The pathway can be traced from the origin of life to any individual species by navigating through the evolutionary branches between the two points. Also, by starting with a single species and tracing 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.

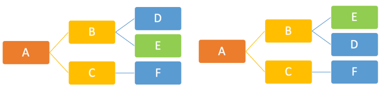


Figure 4. The rotation of the branch point that connects B, D & E does not alter their evolutionary connections

Another point to mention on the 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 (Fig. 4).

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.

Review Question:

Match the term with the appropriate definition.

1) polytomy	A) groups of organisms that are more closely related to each other than to any other groups
2) rooted	B) a diagram in which all of the included organisms are thought to have arisen from a common ancestor
3) basal taxon	C) branch on a phylogenetic tree that has not diverged significantly from the root ancestor
4) branch point	D) a point in the phylogenetic tree that indicates the last common ancestor of different groups
5) sister taxa	E) multiple lineages that arise from a common branch point

Limitations of Phylogenetic Trees

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.

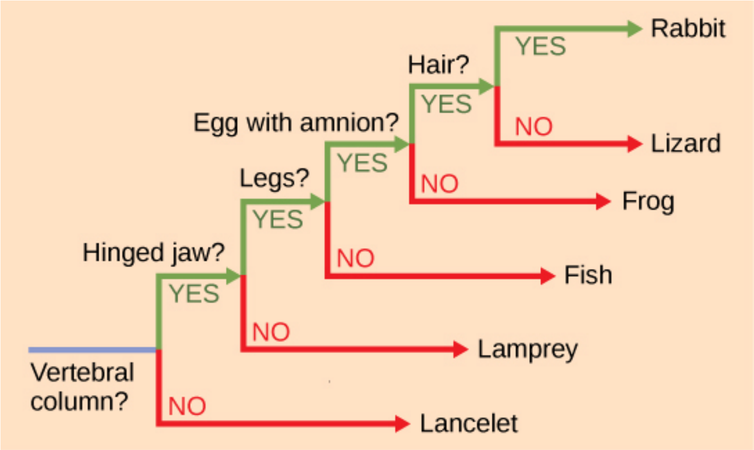


Figure 5. This ladder-like phylogenetic tree of vertebrates is rooted in an organism that lacked a vertebral column. At each branch point, organisms with different characters are placed in different groups based on the characteristics they share.

For example, the phylogenetic tree to the right (Fig. 5) shows that lizards and rabbits both have amniotic eggs, whereas frogs do not; yet lizards and frogs visually appear more similar to us than lizards and rabbits.

Another aspect of phylogenetic trees is that, unless otherwise indicated, the branches do not account for the 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. Figure 5 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. This particular 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 this tree, 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.

Review Question:

What are somethings that you cannot determine from looking at a phylogenetic tree

A) the actual evolutionary ages of the species in the tree
B) patterns of phenotypic similarities
C) patterns of evolutionary descent
D) whether sister taxa evolved from each other

The Levels of Classification

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**.

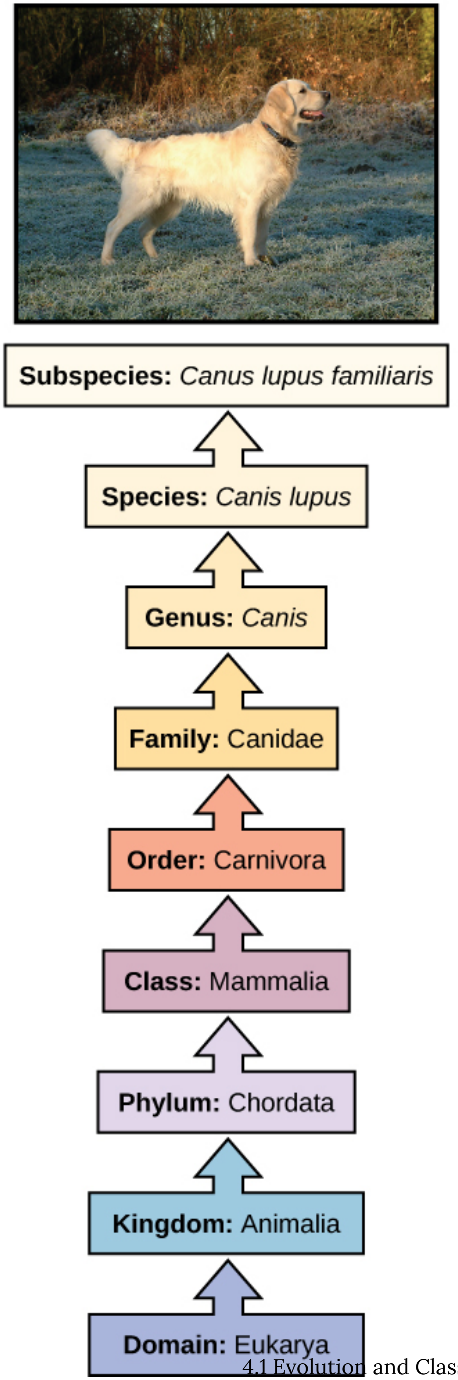

Subspecies: *Canus lupus familiaris*
Species: *Canis lupus*
Genus: *Canis*
Family: Canidae
Order: Carnivora
Class: Mammalia
Phylum: Chordata
Kingdom: Animalia
Domain: Eukarya

Figure 6. 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 are shown to the right. The full scientific name of an organism technically has eight terms. For the dog, it is Eukarya, Animalia, Chordata, Mammalia, Carnivora, Canidae, Canis, and *Canis lupus*. Notice that each name is capitalized except for the second term in the species name (called the specific epithet), and the genus and species names are italicized. Scientists generally refer to an organism only by its species, which is its two-word scientific name, in what is called binomial nomenclature. Therefore, the scientific name (or species) of the dog is Canis lupus. The name at each level is also called a taxon. In the case of dogs 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.

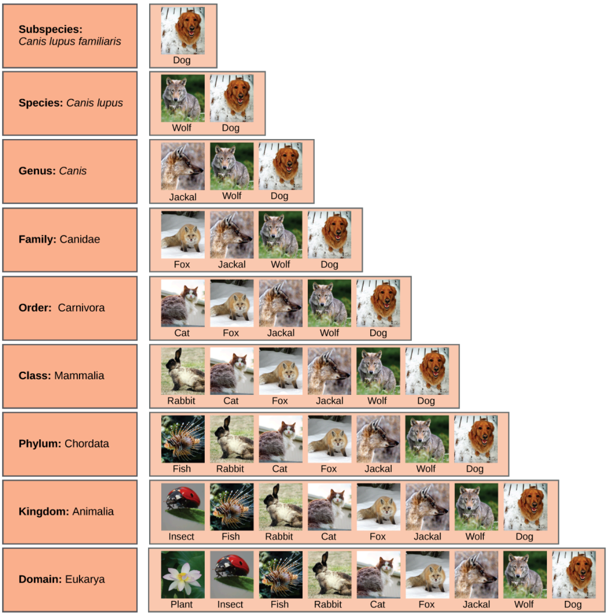


Figure 7. At each sublevel in the taxonomic classification system, organisms become more similar. (credit "plant": modification of work by "berduchwal" /Flickr; credit "insect": modification of work by Jon Sullivan; credit "fish": modification of work by Christian Mehlführer; credit "rabbit": modification 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)

Figure 7 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.

Review Question:

At what taxonomic level are cats and dogs first found in the same group?

Recall that phylogenetic trees are hypotheses and are modified as data become available. 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. 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.

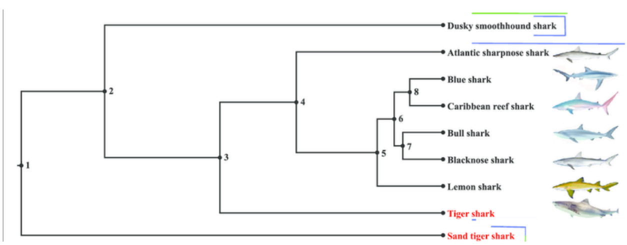
Link to Learning: Visit this Nova website (Classifying Life) to try your hand at classifying three organisms—bear, orchid, and sea cucumber—from kingdom to species. To launch the game, under Classifying Life, click the picture of the bear or the Launch Interactive button.

Summary

Scientists continually gain new information that helps us understand the evolutionary history of life on Earth. Each group of organisms went through its own evolutionary journey, called its phylogeny. Each organism shares relatedness with others, and based on morphologic and genetic evidence, scientists attempt to map the evolutionary pathways of all life on Earth. Historically, organisms were organized into a taxonomic classification system. However, today many scientists build phylogenetic trees to illustrate evolutionary relationships.

End of Section Review Questions:

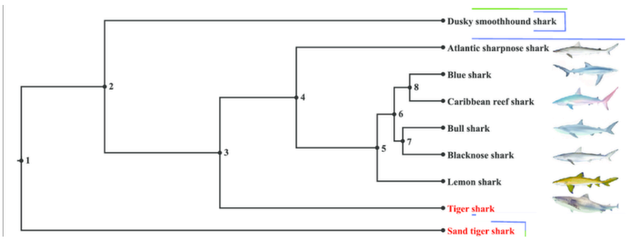
1)



Which of these are sister taxa?
A) Sand Tiger shark and Tiger Shark
B) Lemon Shark and Bull shark
C) Blue Shark and Caribbean reef Shark
D) Bull Shark and Blacknose shark

2) **Place the following in order from the most inclusive to the least inclusive taxonomic levels.**
A) Species
B) Class

C) Family
D) Kingdom
E) Order
3)



Which branch point indicates the most recent common ancestor of the Tiger Shark and the Atlantic Sharpnose Shark?

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Figure 1. credit: modification of work by John Beetham

Figure 7. (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":

11.

Learning Goals

By the end of this reading you should be able to:

- Distinguish between analogous and homologous traits
- Discuss the purpose of cladistics
- Explain ancestral and derived characters
- Describe maximum parsimony

Introduction

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 (Fig. 1).

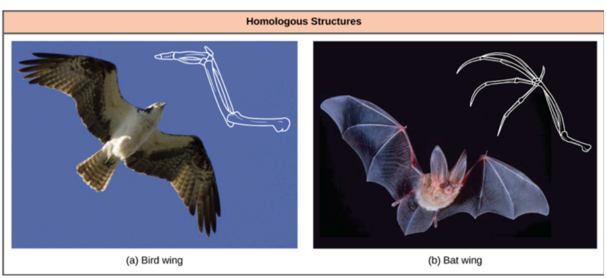


Figure 1. The wings of birds and bats are homologous structures due to a common evolutionary past

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 the 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 appear very much alike. This can happen when both organisms were in common environmental conditions which lead to the development of similar adaptations. When characteristics bearing similar functions occur because of environmental constraints, it is called an analogy. For example, insects use wings to fly like bats and birds, but the wing structure and embryonic origin is completely different (Fig. 2). Moreover, if the characteristics simply resemble each other, those structures are called a homoplasy.

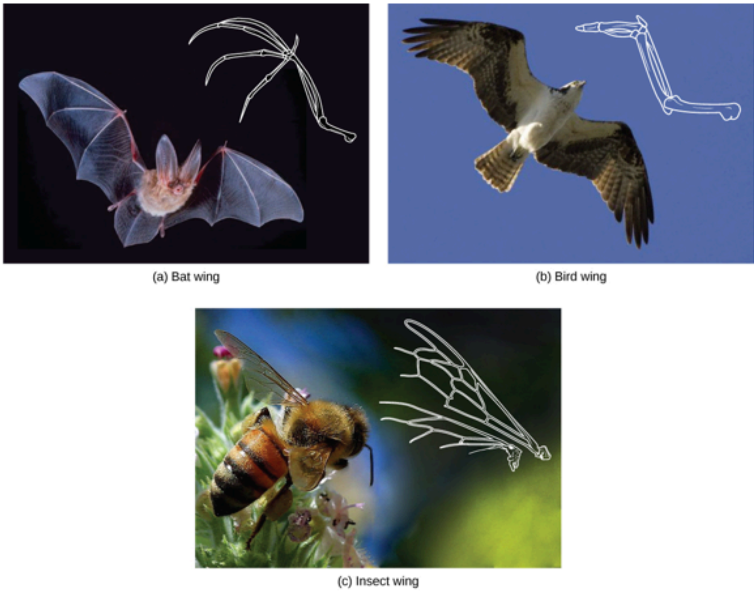


Figure 2. Insect wings are analogous to bird and bat wings.

Some structures are both analogous and homologous such as the wings of a bird and the wings of a bat (Fig. 2). Bats and birds share a common evolutionary pathway in their bone structure of the wings. However, the actual mechanics of the wing are different. Bat wings are composed of tissues stretched between the bones. Bird wings contain feathers that create the flight surfaces. Scientists must determine which type of similarity a feature exhibits to decipher the phylogeny of the organisms being studied. It should be noted that structures between two individuals may be any combination of homologous, analogous, and homoplastic, to include all three.

Review Question:

Characters that are similar because of descent from a common ancestor are _______; characters that are similar due to convergent evolution are _______.

Molecular Comparisons

DNA evolves by mutations being incorporated in the DNA and fixed in populations. This can lead to a divergence of DNA sequences in different species. With the advancement of DNA technology, the area of molecular systematics which describes the use of molecular information including DNA analysis has blossomed. New computer programs can be used to confirm the relationships of earlier classified organisms and to uncover new relationships between organisms. 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 (a frameshift). 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.

Building Phylogenetic Trees

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.

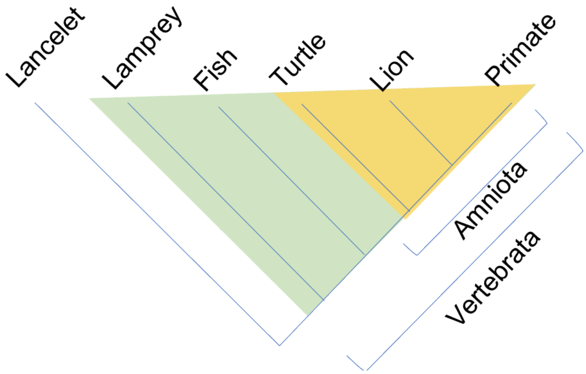


Figure 3. Part of the phylogenetic tree of amniotes

For example, all of the organisms in the yellow region in Figure 3 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.

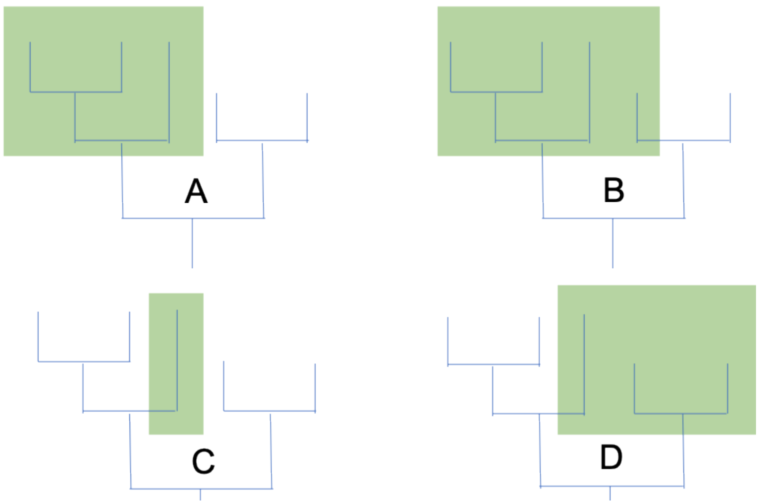
Review Question:

Which organisms belong to the clade "Amniota"?

A) turtles
B) fish
C) lampreys
D) lancelets
E) lions
F) primates

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. Monophyletic breaks down into “mono,” meaning one, and “phyletic,” meaning evolutionary relationship. Thus each clade comes from a single point, whereas the non-clade groups show branches that do not share a single point.

Review Question:



The green boxes in image _______ and image _______ show clades.

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 that enhances fitness and as a result becomes more prevalent in the group.

2. Many organisms descend from this point and have this trait.

3. New variations may arise after that branch point: 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 will
likely have that trait
.

In the phylogeny shown in Figure 3, the possession of vertebrae is a shared ancestral character. Now consider the amniotic egg characteristic in the same phylogeny. Only some of the organisms have this trait, and in those that do, it is 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 of 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 the phylogeny shown, 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 (lions and primates but not turtles). Shared ancestral and shared derived characteristics help scientists distinguish between clades in the building of phylogenetic trees.

Review Question:

Which evolved first, hair, or the amniotic egg?

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. With the advancement of DNA technology, new sequence data is being produced, analyzed, and changing our understanding of phylogenies.

To aid in the tremendous task of describing phylogenies accurately, scientists often use a concept called **maximum parsimony**. This concept predicts that the pathway with the least number of events that could have occurred is the most likely one. 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.

Review Question:

Why do scientists apply the concept of maximum parsimony?
A) to aid in figuring out the most likely evolutionary relationships
B) to eliminate analogous traits in phylogenies
C) to determine how long ago different taxa separated from each other

D) to find the maximum number of changes needed to alter a trait

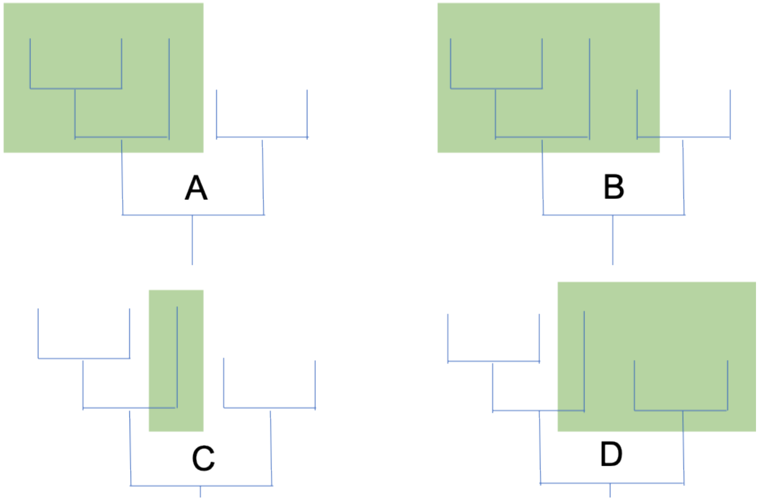
Summary

Using phylogenetic tools and concepts scientists can begin to tackle the task of revealing the evolutionary history of life on Earth. Similar traits can be either homologous or analogous. Homologous structures share a similar embryonic origin; analogous organs have a similar function. Within phylogenetic trees, organisms can be clustered into clades that show common ancestry. 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.

End of Section Review Questions:

1) If a characteristic is found in an ancestral group it is considered a shared _______ character, while if only some of the organisms within a tree share a characteristic it is considered a shared _______ character.

2)



The green boxes in image ________ and image ________ show groupings that are NOT clades.

Evolution Connection: Why Does Phylogeny Matter?

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 cancer, scientists might want to examine all of the relatives of that plant for other useful drugs.

A research team in China identified a segment of DNA thought to be common to some medicinal plants in the family Fabaceae (the legume family) and worked to identify which species had this segment. After testing plant species in this family, the team found a DNA marker (a known location on a chromosome that enabled them to identify the species) present. Then, using the DNA to uncover phylogenetic relationships, the team could identify whether a newly discovered plant was in this family and assess its potential medicinal properties.

Figure 4. Dalbergia

Attributions

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Figure 3. Image created and provided by D. Jennings

Figure 4. Image in Public Domain.

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12.

Learning Goals

By the end of this reading you should be able to:

- Describe the similarities and differences in bacterial and archaeal structures
- Explain differences between the plasma membranes of archaea and bacteria
- Differentiate between gram-positive and gram-negative bacteria
- Describe the types of cell walls and cell wall components that exist in *Archaea*
- Identify the additional structures that are found in some Bacteria and Archaea

Introduction

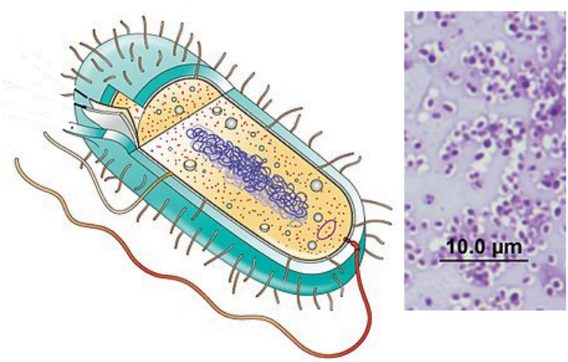

Figure 1. Prokaryotic cell diagram and electron micrograph

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 cells that could withstand these relatively harsh conditions.

These first cells and all the cells that evolved from them share four common components: 1) a plasma membrane, an outer covering that separates the cell's interior from its surrounding environment; 2) cytoplasm, consisting of a jelly-like cytosol within the cell in which other cellular components are found; 3) DNA, the genetic material of the cell; and 4) ribosomes, which synthesize proteins. Additional structures are the result of evolutionary processes.

Basic Prokaryotic Structure

Prokaryotes are unicellular (single-celled) organisms that lack any internal membrane-bound structures, thus they lack a nucleus. In general that have a single circular chromosome located in an area of the cell referred to as the **nucleoid or nucleoid region**, which also contains some proteins and RNA that are associated with replication, transcription, translation, and DNA packaging. Most prokaryotes have a cell wall external to the plasma membrane. The components of this wall are different in the Archaea and Bacteria, which is one way in which these groups differ. This cell wall acts as an extra layer of protection, helps the cell maintain its shape, and prevents cell lysis.

Plasma membranes

The plasma or cell membrane is the boundary that defines the cell and controls the interactions that the cell has with its environment. Membranes exclude some molecules, allow some molecules to pass freely into or out of the cell, and can be involved in transmitting signals from outside to inside the cell. Because the membrane is the main way the cell interacts with the environment it must be both flexible and responsive to changes.

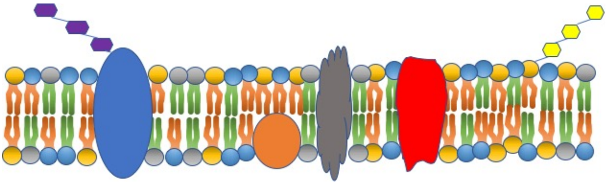

Figure 2. Model of the plasma membrane.

The integral proteins and lipids exist in the membrane as separate but loosely attached molecules. These resemble the separate, multicolored tiles of a mosaic picture, and they float, moving somewhat with respect to one another. The membrane is not like a balloon, however, that can expand and contract; rather, it is fairly rigid and can burst if penetrated or if a cell takes in too much water. However, because of its mosaic nature, a very fine needle can easily penetrate a plasma membrane without causing it to burst, and the membrane will flow and self-seal when the needle is extracted. In addition to the mosaic of proteins, lipids, and in some cases sterols and carbohydrates, the structure of the fatty acid chains of each phospholipid can also contribute to membrane properties. Saturated fatty acids help to provide structure while unsaturated tails can provide fluidity.

Review Question:

Increasing the proportions of which type of molecules will increase the stability of the membrane?
A) unsaturated fats
B) saturated fats
C) sterols

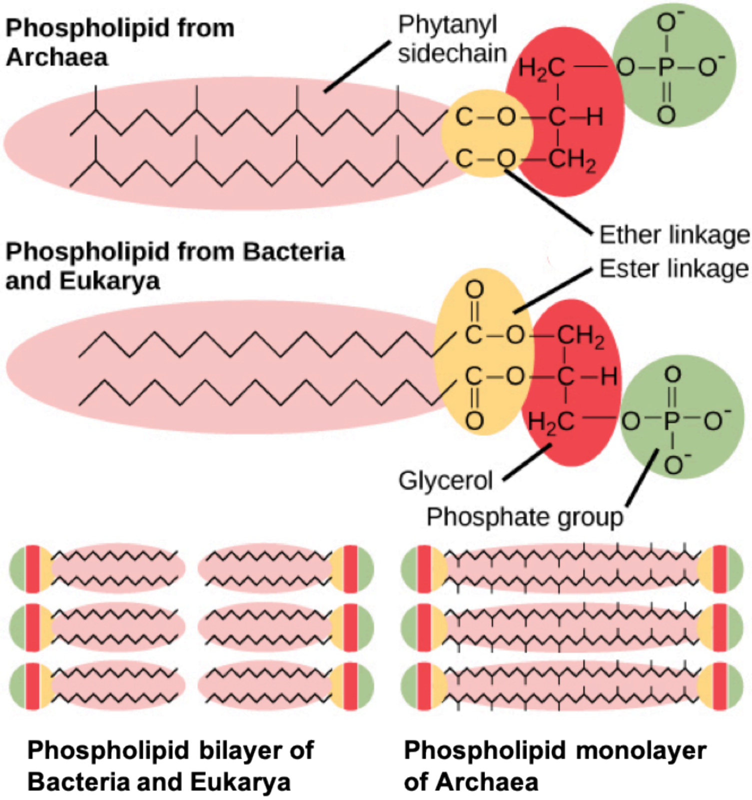

Figure 3. Bacterial and Eukaryotic phospholipids differ from those found in the Archaea.

The membranes of Archaea contain unique molecules that are not found in the membranes of either bacterial or eukaryotic cells. Rather than the fatty acid chains linked to glycerol that are the key components of bacterial and eukaryotic cells, the archaeal membranes are composed of isoprene (phytanyl) chains linked to glycerol. These molecules allow some archaeal membranes to form lipid monolayers instead of bilayers. This formation provides additional structure to the membrane and can be beneficial in some of the extreme environments in which Archaea are found to live.

Thinking Question:

How might the structure of the Archaeal membrane relate to the ability of this group to adapt to extreme environmental conditions (heat, cold, etc)? Be sure to explain your reasoning.

The Cell Wall

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. Most prokaryotic cells live in a liquid environment that is often hypotonic to the cell. In addition, the cytoplasm of prokaryotic cells often has a high concentration of dissolved solutes making it hypertonic to the surrounding environment. Therefore, the osmotic pressure within the cell is relatively high, making a cell wall an essential component for survival. In addition, the cell wall is important in keeping out certain molecules, such as toxins, and in certain bacteria, the cell wall can contribute to the pathogenicity or disease–causing ability of the cell.

Review Question:

Under what environmental conditions can a cell wall provide protection?
A) when the cell is in an isotonic environment
B) when the cell is hypertonic relative to the external environment
C) when the cell is hypotonic relative to the external environment
D) when the cell is in a hypotonic environment
E) when the cell is in a hypertonic environment

Bacterial cell walls contain peptidoglycan, a compound that is not found anywhere else, and additional ingredient molecules, making the bacterial cell wall a complex structure overall. Peptidoglycans are composed of alternating long polysaccharide chains of two glucose derivatives, N-acetylglucosamine (NAG) and N-acetylmuramic acid (NAM). A crosslink between the chains is formed by a tetrapeptide that extends off the NAM sugar unit and contains 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.

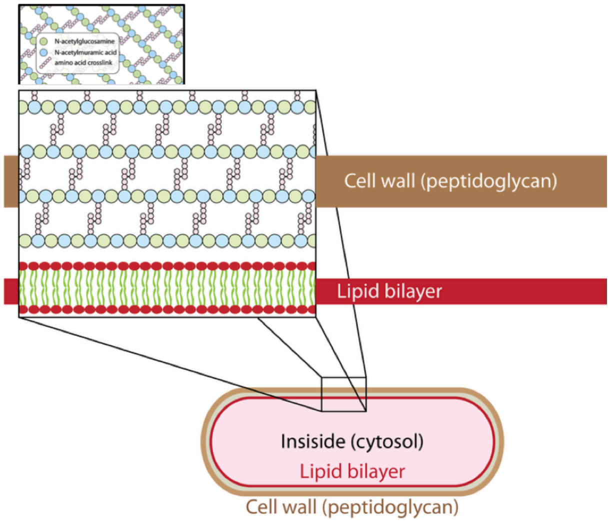

Figure 4. Structure of the bacterial peptidoglycan cell wall

90% of bacteria that do have a cell wall typically have one of two types: Gram-positive or Gram-negative. They can be differentiated in the lab using a staining method 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. 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.

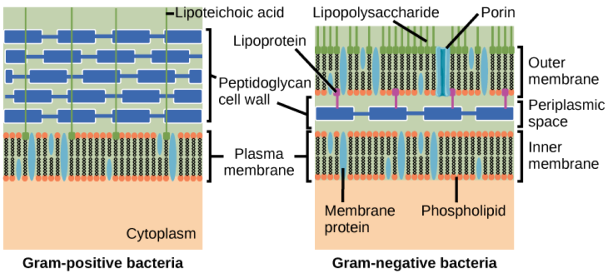

Figure 5. Comparison of the components and structures of gram-positive and gram-negative bacteria

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. Porin proteins in this cell membrane allow substances to pass through the outer membrane of Gram-negative bacteria. This outer envelope is sometimes referred to as a second lipid bilayer and it is made up of three different components. The outermost part is composed of **O-antigen or O-polysaccharide**, beneath this is the **core polysaccharide**, and finally **lipid A** anchors the whole structure to the outer membrane of the cell.

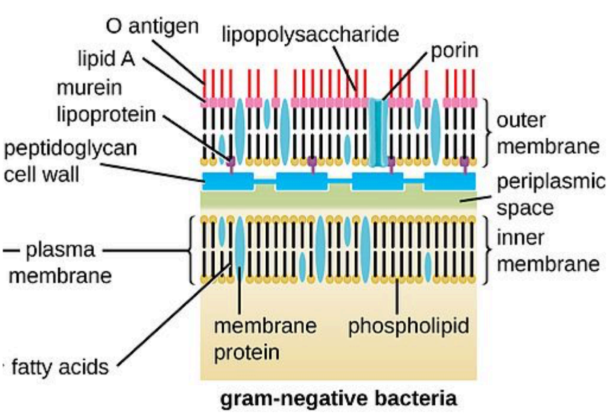

Figure 6. Components of the LPS layer in gram-negative bacteria

The LPS contributes to the net negative charge for the cell, helps to stabilize the outer membrane, and can provide protection from certain chemical substances by physically blocking access to parts of the cell wall. During infection of a host organism, the O-antigen in the LPS can trigger an immune response in an infected host, causing the generation of antibodies specific to that part of LPS. In addition, Lipid A can act as a toxin, specifically an

endotoxin

, causing general symptoms of illness such as fever and diarrhea. A large amount of lipid A released into the bloodstream can trigger endotoxic shock, a body-wide inflammatory response that can be life-threatening.

Review Question:

Which of the following statements is true?
A) Gram-negative bacteria have a cell wall made of peptidoglycan, whereas Gram-positive bacteria have a cell wall made of lipoteichoic acid.
B) Porins allow the entry of substances into both Gram-positive and Gram-negative bacteria.
C) The cell wall of Gram-positive bacteria is thicker than that of Gram-negative and contains teichoic acids
D) The cell wall of Gram-negative bacteria is thick, and the cell wall of Gram-positive bacteria is thin.

The cell walls of Archaea, unlike those of bacteria, do not contain peptidoglycan. In fact, archaea display a wide variety of cell wall types, each of which is adapted for the environment in which they are found. There are some archaea that lack a cell wall altogether.

A large number of Archaea have a proteinaceous **S-layer** made of either protein or glycoprotein, often anchored into the plasma membrane of the cell. This S-layer is considered to be part of the cell wall itself, unlike in Bacteria, where an S-layer is a structure in addition to the cell wall. For some Archaea, the S-layer is the only cell wall component, while in others it is joined by additional ingredients.

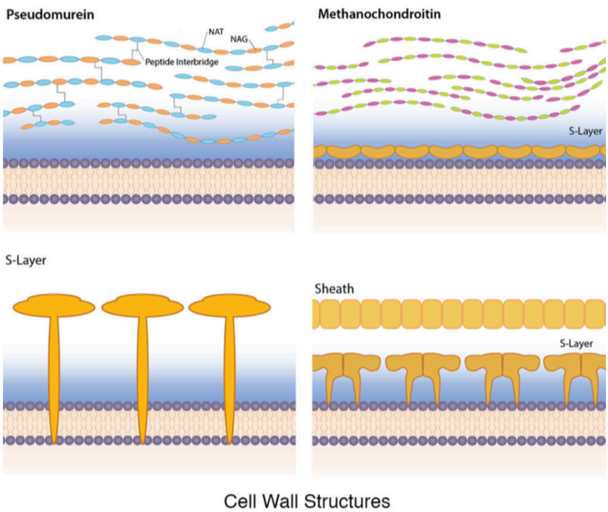

Figure 7. Archaeal cell walls can vary structurally but they do not contain peptidoglycan like bacterial cell walls.

Some archaea contain a substance with a similar chemical structure to peptidoglycan, known as **pseudomurein**. Instead of N-acetylmuramic acid (NAM), it contains **N-acetylalosaminuronic acid (NAT)** linked to N-acetylglucosamine (NAG), with peptide interbridges to increase strength. Other archaeal cell walls contain the polymer **methanochondroitin** which is similar in composition to the connective tissue component chondroitin, found in vertebrates. Finally, there are archaea that have a **protein sheath** composed of a lattice structure similar to an S-layer. These cells are often found in filamentous chains, however, and the protein sheath encloses the entire chain, as opposed to individual cells.

Ribosomes

While archaea have ribosomes that are 70S in size, the same as bacteria, it was the rRNA nucleotide differences that provided scientists with the conclusive evidence to argue that archaea deserved a domain separate from the bacteria. In addition, archaeal ribosomes have a different shape than bacterial ribosomes, with proteins that are unique to archaea. This provides them with resistance to antibiotics that inhibit ribosomal function in bacteria.

Additional Structures

Many of the structures found in bacteria have been discovered in archaea as well, although sometimes it is obvious that each structure was evolved independently based on differences in substance and construction.

Cannulae: a structure unique to some marine Archaeal strains. These hollow tube-like structures appear to connect cells after division, eventually leading to a dense network composed of numerous cells and tubes. This could serve as a means of anchoring a community of cells to a surface.

Hamus: another structure unique to Archaea. This structure is a long helical tube with three hooks at the far end. Hami appears to allow cells to attach both to one another and to surfaces, encouraging the formation of a community.

Pilus (pl. pili): found in both Bacteria and Archaeal species. In Archaea, pili are composed of proteins most likely modified from the bacterial pilin. These tube-like structures have been shown to be used for attachment to surfaces.

Flagellum: Found in some species of Bacteria as well as some species of Archaea. The archaeal flagellum, while used for motility, differs so markedly from the bacterial flagellum that it has been proposed to call it an “archaellum,” to differentiate it from its bacterial counterpart. In both groups, the flagellum is used for movement, where the cell is propelled by the rotation of a rigid filament extending from the cell. After that the similarities end;

1. The rotation of an archaeal flagellum is powered by ATP, as opposed to the
   proton motive force
   used in bacteria
2. The proteins making up the archaeal flagellum are similar to the proteins found in bacterial pili, rather than the bacterial flagellum
3. The archaeal flagellum filament is not hollow so growth occurs when flagellin proteins are inserted into the base of the filament, rather than being added to the end
4. The filament is made up of several different types of flagellin, while just one type is used for the bacterial flagellum filament.
5. Clockwise rotation pushes archaeal cells forward, while counterclockwise rotation pulls an archaeal cell backward. An alternation of runs and tumbles such as is seen in bacteria is not observed in archaea.

Summary

Prokaryotic cells and eukaryotic cells all have cell membranes, ribosomes, genetic material, and a cytosol. The main differentiation between them is the presence or absence of internal membrane-bound structures. Even within the prokaryotes, there are key differences in the structures of Archaeal and Bacterial cells. The membrane components vary, which results in membranes that have different properties and can be related to the environments in which these organisms live. In addition, there are key differences in the components and structures of the cell walls both within bacterial and archaeal groups as well as between the Bacteria and Archaea. Each component and structure can be related to the evolution of these organisms in different environments.

End of Section Review Questions:

1) Which component of the LPS can trigger the formation of antibodies in a host organism?
A) Lipid A
B) O-polysaccharide
C) Endotoxins
D) Core polysaccharide

2) Which of these structures is found in some archaea?
A) cell wall of peptidoglycan
B) cell wall with pseudomurein
C) pili
D) flagella powered by PMF
E) cannulae

3) What structures of Archaeal cells can help them to build a community of cells?
A) pili
B) cannulae
C) LPS
D) hami

4) How might the different structures found in Archaea and Bacteria have evolved? You should think about the mechanisms and patterns of evolution.

Extra: Review of Membrane Properties

The mosaic characteristics of the membrane explain some but not all of its fluidity. There are two other factors that help maintain this fluid characteristic. One factor is the nature of the phospholipids themselves, in particular the structure of the fatty acids that make up the tails.

In their saturated form, the fatty acids in phospholipid tails are saturated with bound hydrogen atoms. There are no double bonds between adjacent carbon atoms. This results in tails that are relatively straight. In contrast, unsaturated fatty acids do not contain a maximal number of hydrogen atoms, but they do contain some double bonds between adjacent carbon atoms; a double bond results in a bend in the string of carbons of approximately 30 degrees.

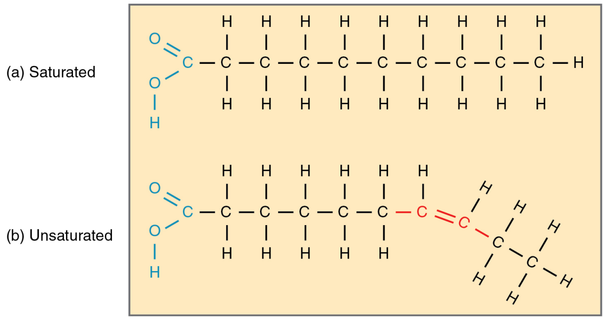

Figure 8. Structural elements of saturated and unsaturated fats

Thus, if saturated fatty acids, with their straight tails, are compressed by decreasing temperatures, they press in on each other, making a dense and fairly rigid membrane. If unsaturated fatty acids are compressed, the “kinks” in their tails elbow adjacent phospholipid molecules away, maintaining some space between the phospholipid molecules. This “elbow room” helps to maintain fluidity in the membrane at temperatures at which membranes with saturated fatty acid tails in their phospholipids would "freeze" or solidify. The relative fluidity of the membrane is particularly important in a cold environment. A cold environment tends to compress membranes composed largely of saturated fatty acids, making them less fluid and more susceptible to rupturing. Many organisms (fish are one example) are capable of adapting to cold environments by changing the proportion of unsaturated fatty acids in their membranes in response to the lowering of the temperature.

The other molecule that can play a role in membrane fluidity is steroids. In human cell membranes, the sterol that is most common is cholesterol. Like phospholipids, cholesterol is an amphipathic molecule. While the nonpolar portion of cholesterol tucks into the fatty acid part of the membrane, cholesterol's hydroxyl (OH) group is hydrophilic and thus associates with the phosphate heads of the phospholipids. Part of the steroid rings of cholesterol is closely attracted to the phospholipid tails and help to immobilize the outer surface of the membrane, keeping it more rigid. However, when found in high concentrations, like the 20-50% proportion found in human cells, it can also help prevent the saturated fatty acid tails from condensing too much and thus aid in maintaining the fluidity of the cell.

References

OpenStax, Biology. OpenStax CNX. Nov 7, 2018 http://cnx.org/contents/185cbf87-c72e-48f5-b51e-f14f21b5eabd@11.6. 22.2 Structure of Prokaryotes

Microbiology. Linda Bruslind http://library.open.oregonstate.edu/microbiology/

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13.

Learning Goals

By the end of this reading you should be able to:

- Describe the process of binary fission in bacteria
- Define the nutritional types of microbes in terms of their sources of carbon, electrons, and energy
- Explain horizontal gene transfer and the three mechanisms by which it occurs in bacteria
- Describe how antibiotics function and explain how some bacteria manage to disarm them

Introduction

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. When conditions are favorable prokaryotic populations can grow rapidly because they are asexual. They can also maintain genetic diversity through both mutation and the process of horizontal gene transfer. As a result, prokaryotes are one of the most diverse groups of organisms on Earth.

Microbial Growth

Provided with the right conditions (food, correct temperature, etc) microbes can grow very quickly. Depending on the situation, this could be a good thing for humans (yeast growing in the wort to make beer) or a bad thing (bacteria growing in your throat causing strep throat). It's important to have knowledge of their growth, so we can predict or control their growth under particular conditions. While growth for multicellular organisms is typically measured in terms of the increase in the size of a single organism, microbial growth is measured by the increase in population, either by measuring the increase in cell number or the increase in overall mass.

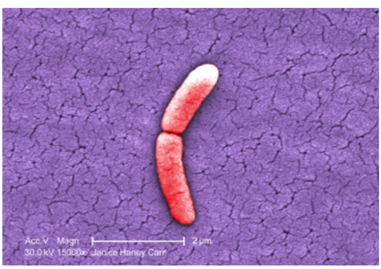

Figure 1. Colorized scanning electron micrograph (SEM) revealed a single Gram-negative Salmonella typhimurium bacterium, undergoing the process of cell division, resulting in the formation of two separate organisms.

Bacteria and Archaea reproduce asexually only, while eukaryotic microbes either sexually or asexually reproduce. Bacteria and archaea most commonly engage in a process known as binary fission, where a single cell splits into two equally sized cells. Other, less common processes can include multiple fission, budding, and the production of spores.

Binary fission begins with cell elongation, which requires careful enlargement of the cell membrane and the cell wall, in addition to an increase in cell volume. Once the cell reaches a certain size it will start to replicate its DNA, in preparation for having two copies of its chromosome, one for each newly formed cell.

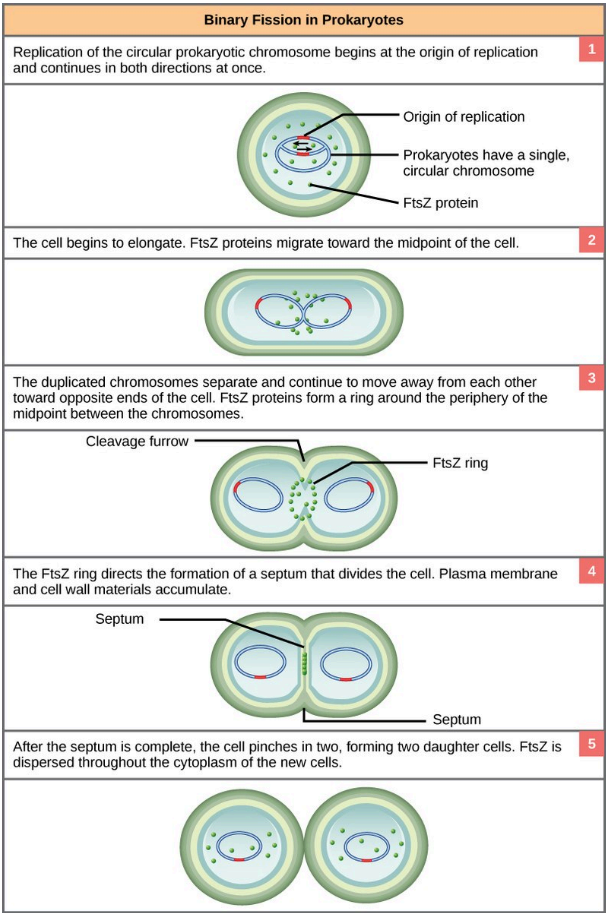

Figure 2. Binary fission in bacteria involves bidirectional replication of the DNA coupled with cell expansion.

The starting point (origin) of replication, is close to the binding site of the chromosome to the plasma membrane. Replication of the DNA is *bidirectional*, moving away from the origin on both strands of the loop simultaneously (Step 1 in Fig. 2). As the new double strands are formed, each origin point moves away from the cell wall attachment toward the opposite ends of the cell. As the cell elongates, the growing membrane aids in the transport of the chromosomes (Step 2 in Fig. 2). After the chromosomes have cleared the midpoint of the elongated cell, cytoplasmic separation begins. The formation of a ring composed of repeating units of a protein called FtsZ directs the partition between the nucleoids (Step 3 in Fig. 2). The formation of the FtsZ ring triggers the accumulation of other proteins that work together to recruit new membrane and cell wall materials to the site. A septum (wall) is formed between the nucleoids, extending gradually from the periphery toward the center of the cell (Step 4 in Fig. 2). When the new cell walls are in place, the daughter cells separate (Step 5 in Fig. 2). The protein FtsZ is essential for the formation of a septum, which initially manifests as a ring in the middle of the elongated cell. After the nucleoids are segregated to each end of the elongated cell, septum formation is completed, dividing the elongated cell into two equally sized daughter cells. The entire process (the cell cycle) can take as little as 20 minutes for an active culture of *E. coli* bacteria that is not resource-limited.

Review Question:

FtsZ proteins direct the formation of a _______ that will eventually form the new cell walls of the daughter cells.

Gathering Energy

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. Some microbes can synthesize certain organic molecules that they need from scratch, as long as they are provided with carbon source and inorganic salts. Other microbes require that certain organic compounds exist within their environment. These organic molecules essential for growth are called growth factors and fall into three categories: 1) amino acids (building blocks of protein), 2) purines and pyrimidines (building blocks of nucleic acid), and 3) vitamins (enzyme cofactors).

All microbes have a need for three things: carbon, energy, and electrons. There are specific terms associated with the source of each of these items, to help define organisms. Let us focus on carbon first. All organisms are carbon-based with macromolecules – proteins, carbohydrates, lipids, nucleic acid – having a fundamental core of carbon. On one hand, organisms can use reduced, preformed organic substances as a carbon source. These are the **heterotrophs** or "other eaters." Alternatively, they can rely on carbon dioxide (CO_2) as a carbon source, reducing or "fixing" this inorganic form of carbon into an organic molecule. These are the **autotrophs** or "self-feeders."

<table>
<tr><th>Energy Source</th><th>Electron Source</th><th>Carbon Source</th></tr>
<tr><td rowspan="4">Light
Photo</td><td rowspan="2">Organic
-organo-</td><td>Organic
-heterotroph</td></tr>
<tr><td>Carbon dioxide
-autotroph</td></tr>
<tr><td rowspan="2">Inorganic
-litho-</td><td>Organic
-heterotroph</td></tr>
<tr><td>Carbon dioxide
-autotroph</td></tr>
<tr><td rowspan="4">Chemical
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Chemo</td><td rowspan="2">Organic
-organo-</td><td>Organic
-heterotroph</td></tr>
<tr><td>Carbon dioxide
-autotroph</td></tr>
<tr><td rowspan="2">Inorganic
-litho-</td><td>Organic
-heterotroph</td></tr>
<tr><td>Carbon dioxide
-autotroph</td></tr>
</table>

Figure 3. Organisms can be classified based on their sources of energy, electrons, and carbon

For energy, there are two possibilities as well: light energy or chemical energy. Light energy comes from the sun, while chemical energy can come from either organic or inorganic chemicals. Those organisms that use light energy are called **phototrophs** ("light eaters"), while those that use chemical energy are called **chemotrophs** ("chemical eaters"). Chemical energy can come from inorganic sources or organic sources. An organism that uses inorganic sources is known as a **lithotroph** ("rock eater"), while an organism that uses organic sources is called an **organotroph** ("organic eater"). These terms can all be combined, to derive a single term that gives you an idea of what an organism is using to meet its basic needs for energy, electrons, and carbon.

Review Question:

What do chemoheterotrophs use for an energy source?
A) light
B) carbon dioxide
C) organic molecules
D) inorganic compounds

HGT, evolution, and antibiotic resistance

Let's talk about sex. Bacterial sex. That is going to be difficult since bacteria do not have sex. Which presents a real problem for bacteria (and archaea, too) – how do they get the genetic variability that they need? They might need a new gene to break down an unusual nutrient source or degrade an antibiotic threatening to destroy them – acquiring the gene could mean the difference between life and death. But where would these genes come from? How would the bacteria get a hold of them? We are going to explore the processes that bacteria use to acquire new genes, the mechanisms known as Horizontal Gene Transfer (HGT).

Horizontal gene transfer (HGT) is the introduction of genetic material from one species to another species by mechanisms other than the vertical transmission from the parent(s) to offspring. These transfers allow even distantly related species to share genes, influencing their phenotypes. Classically, this type of transfer has been thought to occur by three different mechanisms:

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

More recently, a fourth mechanism of gene transfer between prokaryotes has been discovered. Small, virus-like particles called gene transfer agents (GTAs) transfer random genomic segments from one species of prokaryote to another. GTAs have been shown to be responsible for genetic changes, sometimes at a very high frequency compared to other evolutionary processes. These GTAs, which are thought to be bacteriophages that lost the ability to reproduce on their own, carry random pieces of DNA from one organism to another. All of these types of gene transfers may occur between any two species that share an intimate relationship. 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.

The link between HGT and antibiotic resistance is an active area of interest for many scientists. This video brings the mechanism of HGT in bacteria together with the methods that some bacteria use to defend themselves against antibiotics.

Rise of the Superbug – Antibiotic-Resistant Bacteria: Dr. Karl Klose at TEDxSanAntonio

A YouTube element has been excluded from this version of the text. You can view it online here: https://viva.pressbooks.pub/introbio2/?p=54

Review Questions:

According to the scientist in "The Rise of the Superbugs", what features make bacteria so successful?
A) they multiply fast in favorable environments
B) they are small in size
C) they can kill other bacteria by passing bad genes to them
D) they can pick up genes from the environment

According to the scientist in the video, how do antibiotics work to kill bacteria?
A) they boost the hosts immune systems
B) they recognize and disable unique features of the bacteria
C) they allow immune cells to recognize the bacteria
D) they interfere with the ability of bacteria to infect cells

The mechanism of HGT has been shown to be quite common in the prokaryotic domains of Bacteria and Archaea, significantly changing the way their evolution is viewed. The majority of evolutionary models, such as in the
Endosymbiont Theory
, propose that eukaryotes descended from multiple prokaryotes, which makes HGT all the more important to understanding the phylogenetic relationships of all extant and extinct species.

Summary

Prokaryotic organisms are intimately connected with every aspect of their environments. Their small size and rapid reproduction by binary fission (or other asexual means) allow them to take quick advantage of changing resources in the environment. It is in the prokaryotes that we can begin to separate organisms based on where they get their energy (light or chemicals), where they obtained their electrons (organic or inorganic sources), and where they obtain the carbon building blocks for growth (organic molecules or carbon dioxide). When the ability to take up genes from the environment and exchange genetic material between different bacteria is added to the mix the potential for diversity within the prokaryotic domains is expansive.

End of Section Review Questions:

1) **Why characteristics of prokaryotes contribute to the potential for the rapid evolution of some species?**
A) Ability to reproduce rapidly in favorable conditions
B) Ability to mutate in response to environmental conditions
C) Ability to exchange DNA by transduction or transformation or conjugation

2) **Reproduction in prokaryotes is _______ and usually takes place by _________.**
3) The overprescription of antibiotics has been proposed to have lead to an increase in antibiotic resistance in bacteria. How might this increased resistance have evolved?

References

OpenStax, Biology. OpenStax CNX. Nov 7, 2018 http://cnx.org/contents/185cbf87-c72e-48f5-b51e-f14f21b5eabd@11.6. 22.3 Prokaryotic Metabolism

Microbiology. Linda Bruslind http://library.open.oregonstate.edu/microbiology/

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14.

Learning Goals

By the end of this reading you should be able to:

- Discuss how some prokaryotes could become adapted to extreme environments
- Give examples of symbiotic relationships that involve prokaryotes
- Describe the nature of the human microbiome and how it benefits humans
- Explain the formation of a biofilm and how it benefits the organisms involved
- Outline how quorum sensing works and how it is thought to have evolved

Introduction

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.

Microbes Are Adaptable: Life in Moderate and Extreme Environments

Some organisms have developed strategies that allow them to survive harsh conditions. Prokaryotes thrive in a vast array of environments: Some grow in conditions that would seem very normal to us, whereas others are able to thrive and grow under conditions that would kill a plant or animal. Almost all prokaryotes have a cell wall, a protective structure that allows them to survive in both hyper- and hypo-osmotic conditions. Some soil bacteria 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 (Figure 1), 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.

Extremophile Type	Optimal Growth Conditions
Acidophiles	pH 3 or below
Alkaliphiles	pH 9 or above
Thermophiles	Temp 60-80°C (140-176°F)
Hyperthermophiles	Temp 80-120°C (176-250°F)
Psychrophiles	Temp -15-10°C (5-50°F)
Halophiles	[Salt] > 0.2M
Osmophiles	High sugar concentration

Figure 1. Extremophiles and their environments

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. Other extremophiles, do not prefer an extreme environment but have adapted to survive in one.

Review Question:

What is likely to be true of a prokaryote that is adapted to higher temperatures?
A) It may proteins that are more heat resistant
B) It may have more saturated fats within its membrane phospholipids
C) It may have more unsaturated fats within its membrane phospholipids

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 (Fe2+, Ca2+, and Mg2+), 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.

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.

Thinking Questions:

What types of adaptations might you predict to find in these prokaryotes that can survive in the Dead Sea?

Microbial Symbioses

Symbiosis, strictly defined, refers to an intimate relationship between two organisms. Although many people use the term to describe a relationship beneficial to both participants, the term itself is not that specific. The relationship could be good, bad, or neutral for either partner. A **mutualistic** relationship is one in which both partners benefit, while a **commensalistic** relationship benefits one partner but not the other. In a **pathogenic relationship**, one partner benefits at the expense of the other.

Microbiomes

The human microbiome describes the genes associated with all the microbes that live in and on a human. All 10^{14} of them! The microbes are mostly bacteria but can include archaea, fungi, and eukaryotic microbes. These microbes can be found in locations such as the skin, upper respiratory tract, stomach, intestines, and urogenital tracts. Where do we get these colonizers? Colonization occurs soon after birth, as infants acquire microbes from people, surfaces, and objects that they come in contact with. It might help you to understand our biome better if you watch the following video:
Exploring the Human MicroBiome

A YouTube element has been excluded from this version of the text. You can view it online here: https://viva.pressbooks.pub/introbio2/?p=56

Review Questions:

What are some of the things that scientists think your microbiome does for you?
A) Helps our immune system recognize good and bad microbes
B) Revs and dampens our immune responses
C) Regulates our metabolism and fat storage

We are not the only organisms that have a microbiome and it's not just animals. These communities of microbes are found everywhere. Each has its own unique participants and each has its own ecology. We are only just beginning to explore microbiomes and how they impact the organisms and environments in which they are found.

Biofilms and Microbial Mats

Biofilms: Until a couple of decades ago, microbiologists used to think of prokaryotes as isolated entities living apart. This model, however, does not reflect the true ecology of prokaryotes, most of which prefer to live in communities where they can interact. Biofilms grow attached to surfaces. Some of the best-studied biofilms are composed of prokaryotes, although fungal biofilms have also been described as well as some composed of a mixture of fungi and bacteria.

The basic steps for biofilm formation can be broken down into four steps:

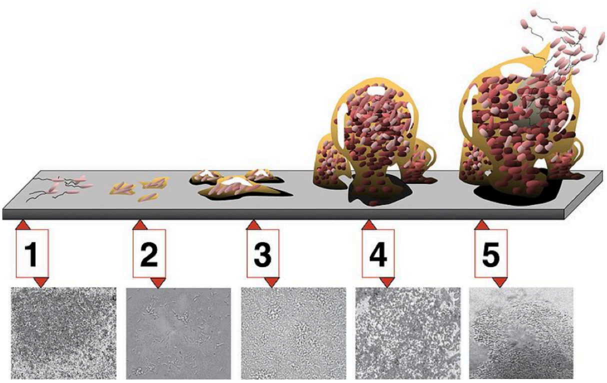

Figure 3. 5 stages of biofilm development. Stage 1, initial attachment; stage 2, irreversible attachment; stage 3, maturation I; stage 4, maturation II; stage 5, dispersion.

One: Cell disposition and attachment – in order for biofilm development to occur, free-floating (planktonic) cells must collide with a suitable surface. Typically the surface has been preconditioned with the deposits of environmental proteins and other molecules.

Two: Colonization – cell-to-cell signaling occurs, leading to the expression of biofilm specific genes. These genes are associated with the communal production of

extracellular polymeric

DNA released by some cells that can be taken up by others, stimulating the expression of new genes.

Three: Maturation – the EPS (exopolysaccharidic) matrix, composed of polysaccharides and proteins, fully incases all the cells. The biofilm continues to thicken and grow, forming a complex, dynamic community. Water channels form throughout the structure.

Four: Detachment and sloughing – individual cells or pieces of the biofilm are released to the environment, as a form of active dispersal. This release can be triggered by environmental factors, such as the concentration of nutrients or oxygen.

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

Biofilms are present almost everywhere and have huge impacts throughout many different types of industries. Medical implants ranging from catheters to artificial joints are particularly susceptible to biofilm formation, leading to huge problems for the medical industry. A type of biofilm that affects almost everyone is the formation of dental plaque, which can lead to cavity formation. In recent, large-scale outbreaks of bacterial contamination of food, biofilms have played a major role. They also colonize household surfaces, such as kitchen counters, cutting boards, sinks, and toilets, as well as places on the human body, such as the surfaces of our teeth.

Review Questions:

What are key ingredients in the EPS matrix that forms in biofilms?
A) Nucleic acids
B) Carbohydrates
C) Proteins
D) Lipids

Microbial mats: These are large biofilms and may represent the earliest forms of life on Earth; there is fossil evidence of their presence starting about 3.5 billion years ago. A microbial mat is a multi-layered sheet of prokaryotes that includes mostly bacteria, but also archaea. Microbial mats are a few centimeters thick, and they typically grow where different types of materials interface, mostly on moist surfaces.

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.

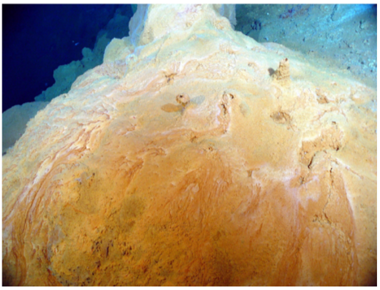

Figure 4. Yellow and orange microbial mats forming "bioreactor" mound with a thin crust and small chimneys on top. The crusty outer coating acts as a thermal blanket to elevate internal temperature from diffuse venting and help retain reduced microbial nutrients. The various types of prokaryotes that 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 the extracellular matrix.

Creating a quorum

The word quorum refers to having a minimum number of members needed for an organization to conduct business, such as hold a vote. **Quorum sensing** refers to the ability of some bacteria to communicate in a density-dependent fashion, allowing them to delay the activation of specific genes until it is the most advantageous for the population.

Quorum sensing involves cell-to-cell communication, using small diffusible substances known as autoinducers. An **autoinducer** is produced by a cell, diffusing across the plasma membrane to be released into the environment. As the cell population increases in the environment the concentration of autoinducer increases as well, causing the molecule to diffuse back into individual cells where it triggers the activation of specific genes. Essential what is happening is that the bacteria are actually using chemical signals to talk to each other. Sounds crazy right? This video is from a scientist who is not only studying the mechanisms of quorum sensing, she is working out how this system of communication might have evolved.

A YouTube element has been excluded from this version of the text. You can view it online here: https://viva.pressbooks.pub/introbio2/?p=56

1) **What type of symbiotic relationship exists between the bacteria *Vibrio fischerii* and the Hawaiian Bobtail Squid?**

2) **What type of molecule did they discover was the general communication molecule in all bacteria?**
A) a small five-carbon molecule (a carbohydrate)
B) a nucleic acid sequence
C) a small 5 amino acid protein
D) a lipopolysaccharide

End of Section Review Questions:

1) What can negatively impact our microbiome and lead to health

issues?
A) The use of antibiotics to treat infections
B) The foods that we eat
C) Taking pre or probiotics

2) In what order do these events in biofilm formation occur?
A) extra polymeric DNA is released and leads to new gene expression
B) active dispersal of the cell occurs in response to environmental stimuli
C) the community is fully encased on the EMS
D) planktonic cells attach to a surface

3) All of the examples in this reading demonstrate how diverse prokaryotes can be. They are only single-celled organisms but they display an amazing ability to adapted to many different conditions. Choose one example or come up with your own AND explain how it might have evolved? (Think about the mechanisms and processes of evolution)

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OpenStax, Biology. OpenStax CNX. Nov 7, 2018 http://cnx.org/contents/185cbf87-c72e-48f5-b51e-f14f21b5eabd@11.6. 22.1 Prokaryotic Diversity

Microbiology. Linda Bruslind http://library.open.oregonstate.edu/microbiology/

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15.

Learning Goals

By the end of this reading you should be able to:

- List and describe the key characteristics of Eukaryotes
- Correlate energy production in prokaryotes to the changing conditions on early Earth
- Explain the evidence that supports the theory of endosymbiosis
- Describe the evidence to support the second endosymbiosis of plastids

Introduction

Figure 1. Tree of Life showing the three domains

Living things fall into three large groups: Archaea, Bacteria, and Eukarya. The first two have prokaryotic cells, and the third contains all eukaryotes. A relatively sparse fossil record is available to help discern what the first members of each of these lineages looked like, so it is possible that all the events that led to the last common ancestor of extant eukaryotes will remain unknown. However, comparative biology of extant organisms and the limited fossil record provide some insight into the history of Eukarya. Data from these fossils have led comparative biologists to the conclusion that living eukaryotes are all descendants of a single common ancestor.

Characteristics of Eukaryotes

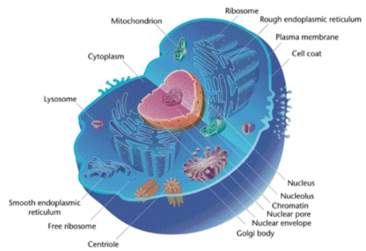

Figure 2. Model of eukaryotic animal cell

Mapping the characteristics found in all major groups of eukaryotes reveals that the following characteristics must have been present in the last common ancestor because these characteristics are present in at least some of the members of each major lineage. Some characteristics have been lost in some lineages over time.

1. Cells with nuclei surrounded by a nuclear envelope with nuclear pores.
2. Mitochondria. Some extant eukaryotes have very reduced remnants of mitochondria in their cells, whereas other members of their lineages have "typical" mitochondria.
3. A cytoskeleton containing the structural and motility components called actin microfilaments and microtubules.
4. Flagella and cilia, organelles associated with cell motility. Some extant eukaryotes lack flagella and/or cilia, but they are descended from ancestors that possessed them.
5. Chromosomes, each consisting of a linear DNA molecule coiled around basic (alkaline) proteins called histones. The few eukaryotes with chromosomes lacking histones clearly evolved from ancestors that had them.
6. Mitosis, a process of nuclear division wherein replicated chromosomes are divided and separated using elements of the

cytoskeleton. Mitosis is universally present in eukaryotes.

7. Sex, a process of genetic recombination unique to eukaryotes in which diploid nuclei at one stage of the life cycle undergo meiosis to yield haploid nuclei and a subsequent stage where two haploid nuclei fuse together to create a diploid zygote nucleus.

The Endosymbiotic Theory

Eukaryotic cells are differentiated from prokaryotic cells by a variety of features, one of which is the presence of internal membrane-bound structures (ex: nucleus, mitochondria, chloroplasts). How did these internal structures evolve? Before we can delve into that we need to talk about energy because it is one of the driving forces of life and there are some key points related to energy metabolism in prokaryotes and eukaryotes that we need to understand.

Prokaryotic Metabolism

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

While today's atmosphere is about one-fifth of molecular oxygen (O_2), geological evidence shows that it originally lacked O_2. Without oxygen, aerobic respiration would not be expected, and living things would have relied on fermentation instead. About 3.5 billion years ago some prokaryotes began using energy from sunlight to power anabolic processes that reduce carbon dioxide to form organic compounds. That is, they evolved the ability to photosynthesize. Hydrogen, derived from various sources, was captured using light-powered reactions to reduce fixed carbon dioxide in the Calvin cycle. The group of Gram-negative bacteria that gave rise to cyanobacteria used water as the hydrogen source and released O_2 as a waste product.

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

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

Review Question:

Based on the evidence place these types of metabolism in order, from what is likely the first type present to the most recent one.
A) anaerobic metabolism
B) aerobic metabolism
C) photosynthesis
D) fermentation

Lynn Margulis and the Endosymbiotic Theory

In the late 1960s, Lynn Margulis studied the structure of cells. Mitochondria, for example, are bodies within the cell that generate the energy required for metabolism. To Margulis, they looked remarkably like bacteria. She knew that scientists had been struck by the similarity ever since the discovery of mitochondria at the end of the 1800s. Some even suggested that mitochondria began from bacteria that lived in a permanent symbiosis within the cells of animals and plants. There were parallel examples in all plant cells. Algae and plant cells have a second set of bodies (chloroplasts) that they use to carry out photosynthesis. These structures capture incoming sunlight energy and use the energy to drive biochemical reactions including the combination of water and carbon dioxide to make organic matter. Chloroplasts, like mitochondria, bear a striking resemblance to bacteria. Scientists, and Margulis in particular, became convinced that chloroplasts, like mitochondria, evolved from symbiotic bacteria — specifically, that they descended from cyanobacteria, the light-harnessing small organisms that abound in oceans and freshwater (Figure 3).

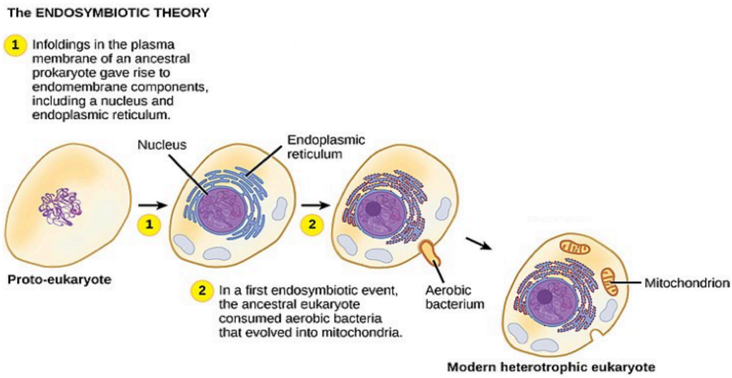

Figure 3. The Endosymbiotic Theory attempts to explain the unique characteristics of mitochondria as well as the presence of these organelles in all Eukaryotic lineages

This once-revolutionary hypothesis is now widely (but not completely) accepted, with work progressing on uncovering the steps involved in this evolutionary process and the key players involved. Much still remains to be discovered about the origins of the cells that now make up the cells in all living eukaryotes.[1] Broadly, it has become clear that many of our nuclear genes and the molecular machinery responsible for replication and expression appear closely related to those in Archaea. On the other hand, the metabolic organelles and genes responsible for many energy-harvesting processes had their origins in bacteria. Much remains to be clarified about how this relationship occurred; this continues to be an exciting field of discovery in biology. For instance, it is not known whether the endosymbiotic event that led to mitochondria occurred before or after the host cell had a nucleus. Such organisms would be among the extinct precursors of the last common ancestor of eukaryotes.

Review Question:

What characteristics do bacteria and mitochondria share?
A) a membrane composed predominately of phospholipids
B) genetic material (DNA)
C) the ability to self-replicate
D) ribosomes for protein synthesis
E) a double membrane (inner and outer)

Secondary Endosymbiosis

Endosymbiosis involves one cell engulfing another to produce, over time, a co-evolved relationship in which neither cell could survive alone. The chloroplasts of red and green algae, for instance, are derived from the engulfment of a photosynthetic cyanobacterium by an early prokaryote.

This leads to the question of the possibility of a cell containing an endosymbiont itself becoming engulfed, resulting in a secondary endosymbiosis. Molecular and morphological evidence suggest that the chlorarachniophyte protists are derived from a secondary endosymbiotic event. Chlorarachniophytes are rare algae indigenous to tropical seas and sand that can be classified into the rhizarian supergroup. Chlorarachniophytes extend thin cytoplasmic strands, interconnecting themselves with other chlorarachniophytes, in a cytoplasmic network. These protists are thought to have originated when a eukaryote engulfed a green alga, the latter of which had already established an endosymbiotic relationship with a photosynthetic cyanobacterium.

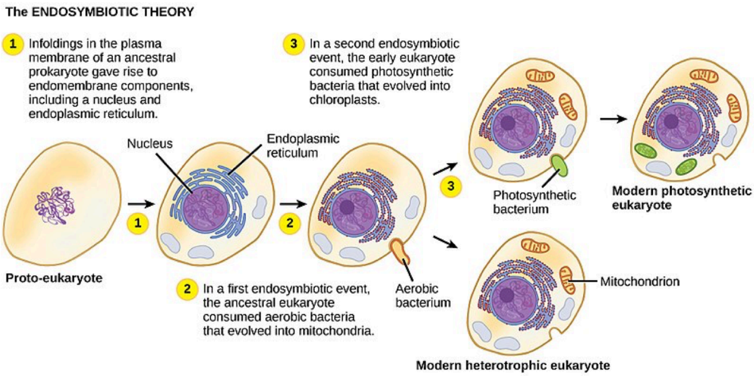

Figure 4. Secondary endosymbiosis in which a cell with an endosymbiont is engulfed by another cell.

Several lines of evidence support that chlorarachniophytes evolved from secondary endosymbiosis. The chloroplasts contained within the green algal endosymbionts still are capable of photosynthesis, making chlorarachniophytes photosynthetic. The green algal endosymbiont also exhibits a stunted vestigial nucleus. In fact, it appears that chlorarachniophytes are the products of an evolutionarily recent secondary endosymbiotic event. The plastids of chlorarachniophytes are surrounded by four membranes: The first two correspond to the inner and outer membranes of the photosynthetic cyanobacterium, the third corresponds to the green alga, and the fourth corresponds to the vacuole that surrounded the green alga when it was engulfed by the chlorarachniophyte ancestor. In other lineages that involved secondary endosymbiosis, only three membranes can be identified around plastids. This is currently rectified as a sequential loss of a membrane during the course of evolution.

The process of secondary endosymbiosis is not unique to chlorarachniophytes. In fact, secondary endosymbiosis of green algae also led to euglenid protists, whereas secondary endosymbiosis of red algae led to the evolution of dinoflagellates, apicomplexans, and stramenopiles.

Summary

The oldest fossil evidence of eukaryotes is about 2 billion years old. Fossils older than this all appear to be prokaryotes. It is probable that today's eukaryotes are descended from an ancestor that had a prokaryotic organization. The last common ancestor of today's Eukarya had several characteristics, including cells with nuclei that divided mitotically and contained linear chromosomes where the DNA was associated with histones, a cytoskeleton and endomembrane system, and the ability to make cilia/flagella during at least part of its life cycle. It was aerobic because it had mitochondria that were the result of an aerobic alpha-proteobacterium that lived inside a host cell. Whether this host had a nucleus at the time of the initial symbiosis remains unknown. The last common ancestor may have had a cell wall for at least part of its life cycle, but more data are needed to confirm this hypothesis. Today's eukaryotes are very diverse in their shapes, organization, life cycles, and the number of cells per individual.

End of Section Review Questions:

1) How are prokaryotic cells different from Eukaryotic cells?
A) They are unable to get energy from aerobic respiration
B) They lack internal membrane-bound structures
C) They have DNA but no chromosomes
D) They are unable to produce proteins

2) What evidence supports the theory that chlorarachniophytes evolved from secondary endosymbiosis?

A) endosymbiont chloroplasts are still photosynthetic
B) endosymbiont still has a vestigial nucleus
C) the plastids are surrounded by four membranes
D) the endosymbiont can survive outside of the algal cells

3) What features do all eukaryotes share that are not found in prokaryotes?
A) The production of gametes by meiosis
B) A cytoskeleton of actin microfilaments and microtubules
C) Mitochondria or at least evidence of having had mitochondria
D) linear DNA molecule(s) coiled around histone proteins (or evidence of this at one time)

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[1] "Endosymbiosis: Lynn Margulis" Understanding Evolution. University of California Museum of Paleontology. 22 August 2008 https://evolution.berkeley.edu/evolibrary/article/history_24

OpenStax, Biology. OpenStax CNX. Nov 7, 2018 http://cnx.org/contents/185cbf87-c72e-48f5-b51e-f14f21b5eabd@11.6. 23.1 Eukaryotic Origins

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16.

Learning Goals

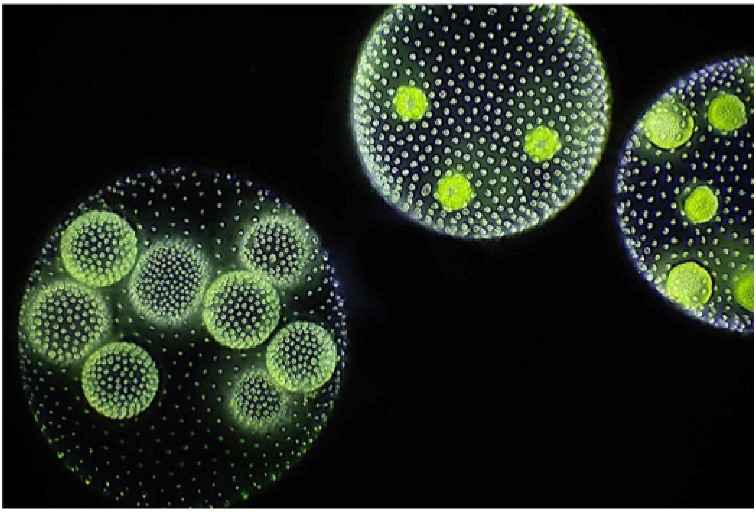

Figure 1. Volvox: a simple colonial green algae

By the end of this reading you should be able to:

- Explain the advantages of simple multicellularity
- Describe the evidence that supports the evolution of simple multicellularity in some protists
- Discuss the needed adaptations for simple multicellularity

Introduction

Among the Bacteria and Archaea, each cell usually functions as an individual, growing and reproducing, moving from one place to another, taking in nutrients, and both sensing and transmitting molecular signals. In contrast, multicellular organisms contain millions (or more) cells that work in close coordination. In your own body, for example, different cells are specialized for specific functions, so that while your body as a whole can perform the broad range of tasks accomplished by microorganisms, individual cells, for the most part, cannot. Cells lining the intestine absorb food molecules, but nutrients must then be transported to other parts of the body. Lungs take up oxygen from inhaled air, but this, too, must be distributed to other tissues and organs. And while cells at the body's surface sense signals from the environment, the signals affecting interior cells come mostly from surrounding cells. While the biological gulf between microbes and multicellular organisms is enormous, multicellularity has evolved a half dozen times in different groups.

The phylogeny of multicellularity

Most prokaryotic organisms are composed of a single cell, although some form simple filaments or live in colonies. A few types of bacterium, notably some cyanobacteria, differentiate to form several distinct cell types. No bacteria, however, develop macroscopic bodies with functionally differentiated tissues. Only eukaryotes have evolved those. Simple multicellular organisms, composed of multiple similar cells, occur widely within the eukaryotic tree of life, and a few of these evolved into more complex multicellular organisms characterized by differentiated tissues and organs. How are these different types of organization distribute on the eukaryotic tree of life?

A recent survey of eukaryotic organisms recognized 119 major groups within the supergroups. Of these, 83 contain only single-celled organisms, predominantly cells that engulf other microorganisms or ingest small organic particles, photosynthetic cells that live suspended in the water column, or parasitic cells that live within other organisms. Each of the 36 remaining branches exhibits some cases of simple multicellularity, mostly in the form of filaments, hollow balls, or sheets of little-differentiated cells. More complex multicellularity has evolved only in six eukaryotic groups: animals, fungi, brown algae, red algae, green algae, and land plants.

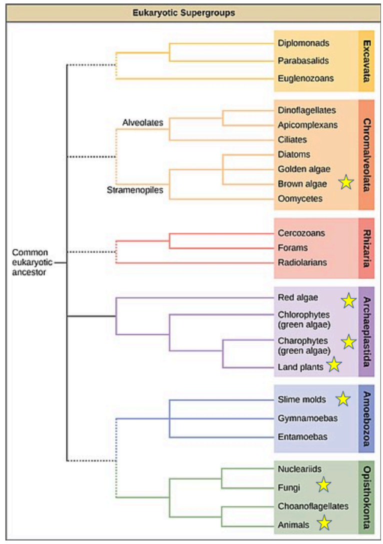

Figure 2. Stars indicate groups in which multicellularity has evolved at least one, if not more times.

Thinking Question:

Multicellularity is found in groups that are not directly related, and in some of the groups not all the organisms are multicellular. From an evolutionary standpoint, how might you explain this pattern?

Advantages of simple multicellularity

What selection did pressures favor the evolution of simple multicellular organisms from single-celled ancestors? One selective advantage is that multicellularity helps organisms avoid getting eaten. A number of experiments using single-celled green algae and exposure to a single cell predator have demonstrated the selection pressure for multicellularity. In the presence of the predators, within 10 to 20 generations, most of the algae were living in eight-cell colonies that were essentially invulnerable to predator attacks due to their larger size.[1,2]

Another advantage is that multicellular organisms may be able to maintain their position on a surface or in the water column better than their single-celled relatives. Seaweeds, for example, live anchored to the seafloor in places where light and nutrients support growth. Scientists have studied these phenomena using both single-celled algae and yeast cultures.[3,4] When exposed to consistent shaking in culture, the number of cells that formed aggregates (clumps) increases over a number of generations. By clumping together the cell groups settled on the bottom of the cultures and thus were exposed to less vigorous conditions.

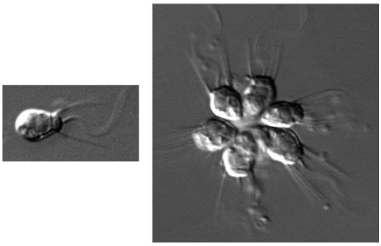

Figure 3. Left: lone choanoflagellate, Right: choanoflagellate rosette formed in presence of prey bacteria

Feeding provides a third potential advantage: In colonial heterotrophs such as the stalked ciliate Epistylis, the coordinated beating of flagella assists feeding by directing currents of food-laden water toward the cells. Studies using the choanoflagellate *Salpingoeca rosetta*, demonstrated a link between the presence of the prey species and the development of multicellular colonies (formation of a rosette). These colonies, unlike the ones in the yeast and algae mentioned earlier, appear to the result of cell division rather than cell aggregation.[5]

Adaptations need for multicellularity

The genome of the choanoflagellate *Monosiga brevicollis* provides a fascinating insight into the evolution of cell adhesion molecules. Choanoflagellates, the closest protistan relatives of animals, are unicellular microorganisms. Therefore, it came as a surprise that the genes of *M. brevicollis* code for many of the same protein families that promote cell adhesion in animals. This includes the genes for both cadherin and integrin proteins which in animals are involved in supporting epithelia. Clearly, these proteins are not supporting epithelia in *M. brevicollis*, so what are they doing?

One approach to an answer came from the observation that cells stick not only to one another but also to rock or sediment surfaces. Proteins that originally evolved to promote adhesion of individual cells to sand grains or a rock surface may have been modified during evolution for cell-cell adhesion. It is also possible that adhesion molecules were originally used in the capture of bacterial cells, to make prey adhere to the predator.

To date, cadherins have been found only in choanoflagellates and animals, but proteins of the integrin complex extend even deeper into eukaryotic phylogeny-they are found in single celled protists that branch near the base of the opisthokont superkingdom. Such a phylogenetic distribution provides strong support for the general hypothesis that cell adhesion in animals resulted from the redeployment of protein families that evolved to perform other functions before animals diverged from their closest protistan relatives.

Thinking Question:

Can you think of any other advantages to being a simple multicellular organism, other than the ones mentioned above?

Adhesion but no differentiation

In many protists, cell adhesion molecules cause adjacent cells to stick together, but there are few specialized cell types and relatively little communication or transfer of resources between cells. Most or all of the cells in simple multicellular organisms retain a full range of functions, including reproduction. As a result the organism/colony usually pays only a small penalty for individual cell death. Importantly, in simple multicellular organisms, nearly every cell is in direct contact with the external environment, at least during phases of the life cycle when the cells must acquire nutrients, which means that each can take up nutrients and excrete wastes directly.

Simple multicellularity occurs most prominently among algae, although stalk-like colonies of particle feeders have evolved in at least three groups of heterotrophic protists. In addition, simple filamentous fungi exist that can absorb organic molecules as sources of carbon and energy. Four eukaryotic groups have achieved temporary simple multicellularity by a different route, aggregating during just one stage of the life cycle. Slime molds are the best-known example.

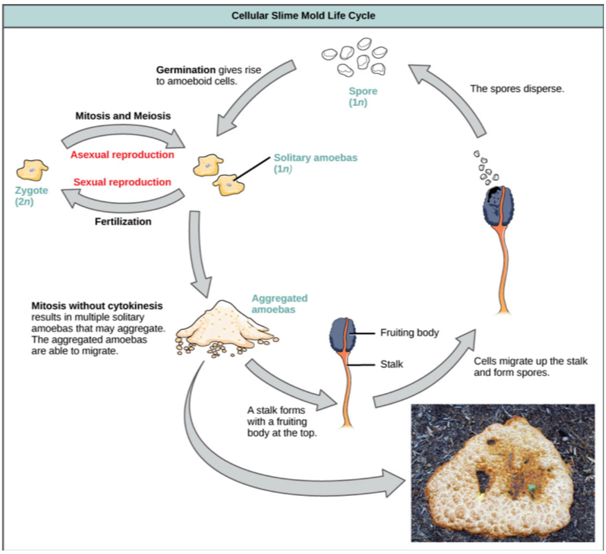

Figure 4. Cellular Slime can alternate between single cells (amoeboid) and a simple multicellular form. This occurs in response to environmental conditions.

Six groups (two algal, three protozoan, and one fungal) include species characterized by **coenocytic** organization. In coenocytic organisms, the nucleus divides multiple times, but the cell does not, so the nuclei are not partitioned into individual cells. The result is a large cell-sometimes even visible to the naked eye with many nuclei. The green algae *Codium* and *Caulerpa*, found along the shorelines of temperate and tropical seas, respectively, are common examples of coenocytic organisms. In addition, acellular slime molds are also coenocytic and can be so large that they look like fungi to us whereas they are only one really really large cell. There is no evidence that any coenocytic organisms evolved from truly multicellular ancestors, nor have any given rise to complex multicellular descendants.

Review Question:

In coenocytic organisms the _________ divides multiple times but the _________ does not.
word bank: mitochondria, cell, nucleus, nucleosomes, DNA

Summary

Given the benefits associated with being multicellular, it is no surprise that multiple lineages independently evolved multicellularity over time. This likely took advantage of traits that were already present in the organisms to help those ancestral cells adhere to a substrate. The first multicellular organisms were likely simple and the cells merely stuck together but did not differentiate and have different functions for the whole. Other lineages evolved processes in which the nucleus divides multiple times in the same cell, forming a coenocytic cell, but there is no evidence that multicellularity evolved from coenocytic cells.

End of Section Review Questions:

1) What are some advantages of being multicellular?
A) it can provide protection against predation
B) it can provide stability and help anchor the organism
C) it can increase the ability to acquire food/nutrients
D) it makes it so only some of the cells need to reproduce

2) What do features would you expect SIMPLE multicellular organisms have in common?
A) a means by which to hold cells together
B) simple patterns of cell differentiation
C) each cell retains a full range of functions
D) nearly every cell is in contact with the external solution

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17.

Learning Goals

By the end of this reading you should be able to:

- Describe the shared features of complex multicellular organisms
- Compare and contrast simple vs. complex multicellular organisms
- Explain the limitations to diffusion and the role of bulk flow in complex multicellular organisms
- Discuss the means by which cell adhesion, cell communication, and cell differentiation are accomplished in complex multicellular organisms
- Predict the order of acquisition of multicellular traits and the evolutionary consequences of complex multicellularity

Introduction

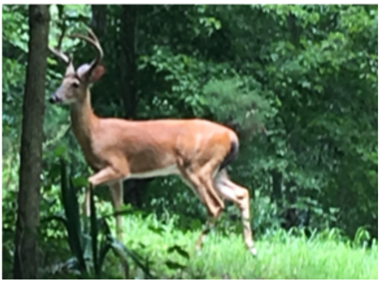

Figure 1. Animals are multicellular and most are complex multicellular organisms.

There are costs associated with multicellularity, particularly for complex multicellular organisms with differentiated reproductive tissues. In these organisms, most cells do not reproduce, instead of supporting the few that do. This requires cooperation among cells, but it creates opportunities for cells to "cheat"- to use nutrients for their own proliferation rather than the growth and reproduction of the organism as a whole. Complex multicellularity evolved at least six separate times in different eukaryotic groups; once in animal lineages, once in the green algal lineage that gave rise to land plants, twice in the fungi, once in the red algae, and once in the brown algae, producing the giant kelps that form forests in the sea.

Shared Features

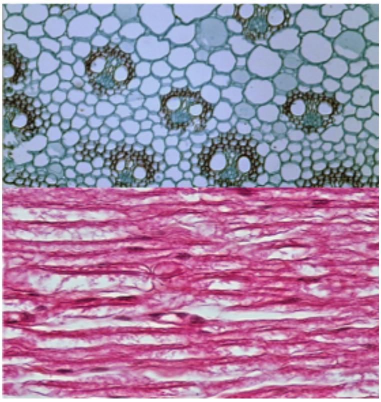

Figure 2. Top image: plant vascular tissue. Bottom image: animal nerve tissue

Complex multicellular organisms differ from one another in many ways, but they share three general features. (1) They have highly developed molecular mechanisms for adhesion between cells. (2) They display specialized structures that allow cells to communicate with one another. (3) They display complex patterns of cellular and tissue differentiation, guided by networks of regulatory genes. Without these features, complex multicellularity would be impossible.

For example, plants and animals both have differentiated cells and tissues with specialized functions. In plants, only some tissues photosynthesize or absorb organic molecules; other tissues transport food and oxygen through the body, and still, others generate the molecular signals that govern development. In both plants and animals, only a small subset of all cells contributes to reproduction. Because of this functional differentiation, cell or tissue loss can be lethal for the entire organism.

There is one more feature of complex multicellular organisms that is key to understanding their biology: They have a three dimensional organization, so only some cells are in direct contact with the environment. Cells that are buried within tissues, relatively far from the exterior of the organism, do not have direct access to nutrients or oxygen. Therefore, interior cells cannot grow as fast as surface cells unless there is a way to transfer resources from one part of the body to another. Similarly, interior cells do not receive signals directly from the environment, even though all cells must be able to respond to environmental signals if the organism is to grow, reproduce, and survive. Complex multicellular organisms, therefore, require mechanisms for transferring environmental signals received by cells at the body's surface to interior cells, where genes will be activated or repressed in response. Thus growth and development in complex multicellular organisms can be defined as increasing or decreasing gene expression in response to molecular signals from surrounding cells.

Review Question:

What are the characteristics that are found in both simple colonies of cells and complex multicellular organisms?
A) the ability of cells to communicate
B) the ability of each cell to reproduce
C) the ability of cells to adhere to each other
D) a wide variety of cell differentiation

Diffusion and Bulk Flow

A key functional challenge of complex multicellularity is transporting food, oxygen, and molecular signals rapidly across large distances within the body. How does oxygen get from the air in your lungs into your bloodstream? How does atmospheric carbon dioxide get into leaves? How does ammonia get from seawater into the cells of seaweeds? The answer to all three questions is the same: by diffusion. But oxygen absorbed by your lungs doesn't reach your toes by diffusion alone-it is transported actively, and in bulk, by blood pumped through your circulatory system. Water does not get from the roots to the leaves of plants by diffusion either, there are mechanisms at work to move it actively as well. For complex multicellular organisms to function, bulk flow of oxygen, nutrients, and signaling molecules, at rates and across distances far larger than can be achieved by diffusion alone is needed.

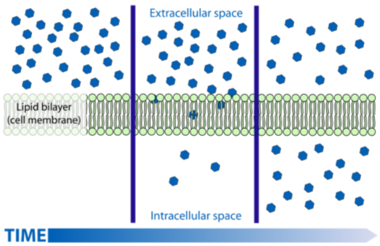

Figure 3. The concentration of molecules across a semi-permeable membrane influences the rate of diffusion of the molecules

So why is diffusion effective only over short distances? Diffusion is the random motion of molecules, with net movement from areas of higher to lower concentration. The distance and speed at which molecules can diffuse depends on several factors: (1) how great the concentration difference is, large larger the differences the faster the diffusion (2) distance between concentration differences, the closer the two concentrations the faster the rate of diffusion (3) the size of the molecule, smaller molecules tend to diffuse faster than larger ones, and (4) the nature of the medium the molecule is diffusing in; molecules diffuse faster if the medium is less thick (think air vs. water). Because diffusion supplies key molecules for metabolism, it exerts a strong constraint on the size, shape, and function of cells and ultimately how eukaryotic organisms function.

Let's use oxygen as an example. Most eukaryotes require oxygen for respiration. If the cells within a tissue must rely on diffusion for their individual oxygen supply, the thickness of the tissue is limited by the concentration difference in oxygen between the cells in the tissue and the surrounding environment. The concentration difference between the two areas depends on the amount of oxygen in the environment and the rate at which oxygen is used for respiration inside the organism. The distance between the environment and the cell that is using oxygen also plays a role.

Review Question:

Which of these would increase the rate of diffusion of a molecule?
A) a high concentration gradient between two areas involved
B) a medium that is fairly viscous in nature
C) a small distance between the two areas involved

Organisms can achieve larger sizes by circumventing limits imposed by diffusion.

Sponges can reach overall dimensions of a meter or more, but they actually consist of only a few types of cells that line a dense network of pores and canals and so remain in close contact with circulating seawater. The large size of a sponge is therefore achieved without placing metabolically active cells at any great distance from their environment. Similarly, in jellyfish, active metabolism is confined to thin tissues that line the inner and outer surfaces of the body. Essentially, a large flat surface is folded up to produce a three-dimensional structure. An increase in the surface area of a cell and or structure increases the area that is capable of interacting with the environment and ultimately the number of needed molecules to which a cell or structure has access.

Structures specialized for bulk flow

Bulk flow is any means by which molecules move through organisms at rates beyond those possible by diffusion across a concentration gradient. In humans and other vertebrate animals, the active pumping of blood through blood vessels supplies oxygen to tissues that may be more than a meter distance from the lungs. Our lungs gather the oxygen we need for respiration, but the lung is a prime example of diffusion in action, not a means of avoiding it. Because lung tissues have a very high ratio of surface area to volume, oxygen can diffuse efficiently from the air you breathe into lung tissue. A great deal of oxygen can be taken in this way, but how does it get from the lungs to our brains or toes? The distances are far too large for diffusion to be effective.

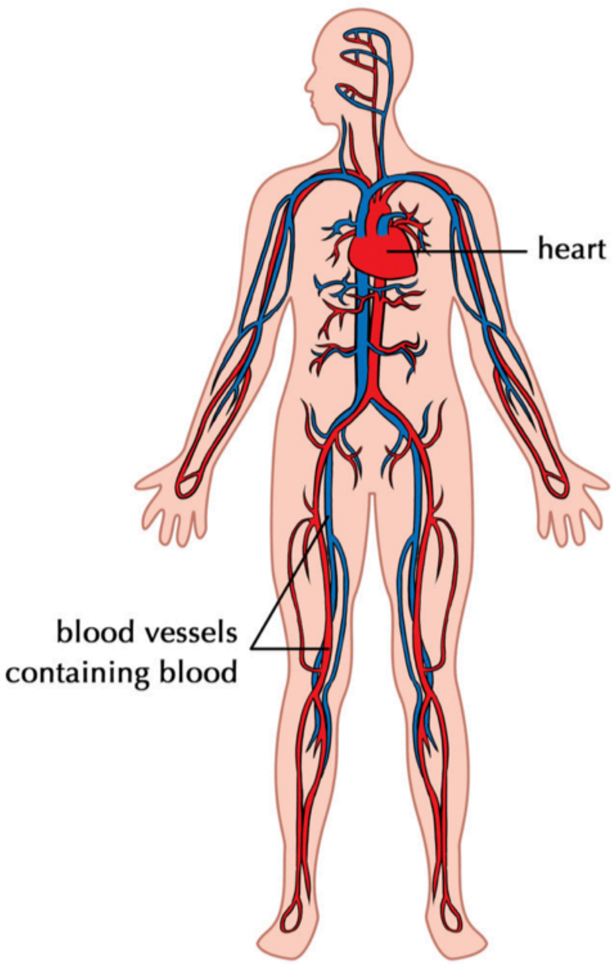

Figure 4. In humans and other animals the circulatory transports oxygen, nutrients, and carbon dioxide throughout the body by bulk flow

The answer is that oxygen binds to molecules of hemoglobin in red blood cells and then is carried through the bloodstream to distant sites of respiration. We circumvent diffusion by actively pumping oxygen-rich blood through our bodies. Most invertebrate animals lack well-defined blood vessels instead they have other mechanisms that circulate fluids freely throughout the body cavity. Indeed, without a mechanism like bulk flow, animals could not have achieved the range of size, shape, and function familiar to us.

Complex organisms other than animals also rely on bulk flow. A redwood tree must transport water upward from its roots to leaves that may be 100 m above the soil. If plants relied on diffusion to transport water, they would be only a few millimeters tall. How, then, do they move water? Plants move water by bulk flow through a system of specialized tissues powered by the evaporation of water from leaf surfaces. Vascular plants also have specialized tissues for the transport of nutrients and signaling molecules upward and downward through roots, stems, and leaves.

Multicellular fungi transport nutrients through networks of filaments that may be meters long, relying on osmosis to pump materials from sites of absorption to sites of metabolism. The giant kelps have an internal network of tubular cells that transports molecules through a body that can be tens of meters long. In general, when some cells within an organism are buried within tissues, far from the external environment, bulk flow is required to supply those cells with molecules needed for metabolism.

Other requirements for complex multicellular life

In addition to a means to move needed molecules over long distances and in sufficient concentration, there are three other general requirements for complex multicellular life: (1)Cells must stick together; (2) they must communicate with one another, and (3) they must participate in a network of genetic interactions that regulates cell division and differentiation. Once these are in place, the stage is set for the evolution of specialized tissues and organs in complex multicellular organisms.

Adhesion between cells

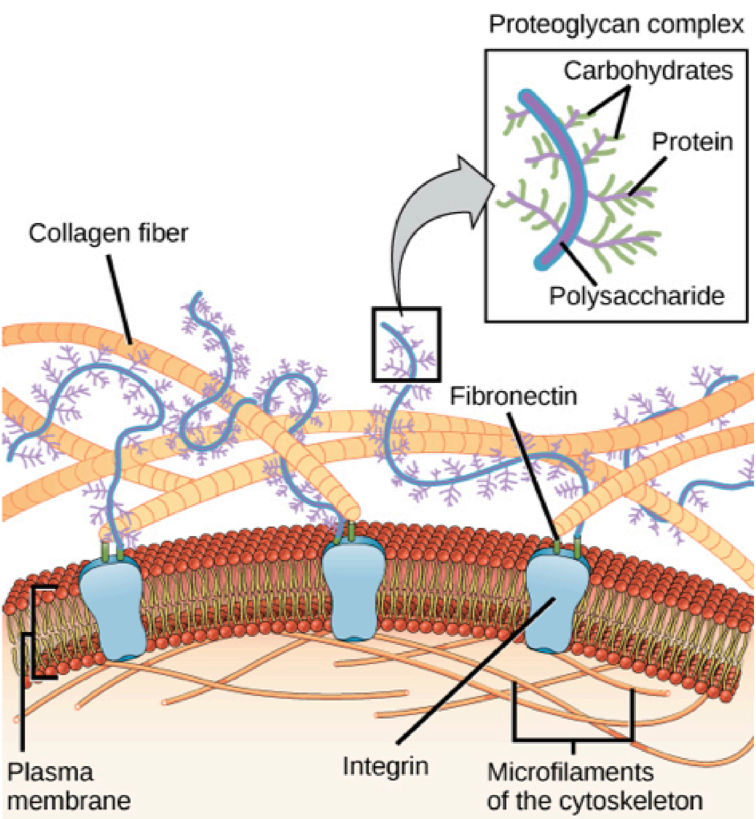

Figure 5. Model of the extracellular matrix in animal cells

If a fertilized egg is to develop into a complex multicellular organism, it must divide many times, and the cells produced from those divisions must stick together. In addition, they must retain a specific spatial relationship with one another in order for the developing organism to function. Most animal cells release materials into the extracellular space. The primary components of these materials are proteins, and the most abundant protein is *collagen*. Collagen fibers are interwoven with carbohydrate-containing protein molecules called *proteoglycans*. Some cells attach themselves to this matrix by means of other transmembrane proteins called integrins and transmembrane proteins, especially cadherins, can also be involved in the formation of molecular attachments between cells. The extracellular matrix also allows the cells within the tissue to communicate with each other.

In plants, the cell wall connects cells together into tissues. The plant cell wall is composed predominately of cellulose fibers which are embedded in a matrix of pectin and hemicellulose. These molecules allow plant cells to attach to each other to create the complex tissue structures that support the overall plant structure. Fungi also have cell walls, although they are composed of chitin rather than cellulose, that are involved in connecting the cells together into multicellular structures.

Communication between cells

In complex multicellular organisms, it is not sufficient for cells to adhere to one another. They must also be able to communicate. Communication is important during development, guiding the patterns of gene expression that differentiate cells, tissues, and organs. The functional integration of cells within tissues and tissues within organs also depends on the flow of information among cells. Cells communicate using signaling molecules (generally a protein) synthesized by one cell which binds with a receptor protein on the surface of a second cell. This interaction can essentially flip a molecular switch that activates or represses gene expression in the receptor cell's nucleus or stimulates another response from the receiving cells. Molecular evidence indicates that many of the signaling pathways used for communication between cells in complex multicellular organisms first evolved in single-celled eukaryotes.

Thinking Question:

What function might molecular signals and receptors have had in the ancestors of complex organisms?

All cells have transmembrane receptors that respond to signals from the environment. In some cases, the signal is a molecule released by a food organism (such as the bacteria that induce simple multicellularity in choanoflagellates), and in some cases the cells sense nutrients, temperature, or oxygen level. Single celled eukaryotes also communicate with other cells within the same species, for example, to ensure that two cells can find each other to fuse in sexual reproduction. Signaling between two cells within a complex multicellular organism (plant, animal, or fungal) can be seen as a variation on this more general theme of a cell responding to other cells and the physical environment.

While all eukaryotic cells have molecular mechanisms for communication between cells, complex multicellular organisms have distinct cellular pathways for the movement of molecules from one cell to another. For example, animals more complex than sponges have gap junctions, protein channels that allow ions and signaling molecules to move from one cell into another. Gap junctions not only help cells to communicate with their neighbors, they allow targeted communication between a cell and specific cells adjacent to it.

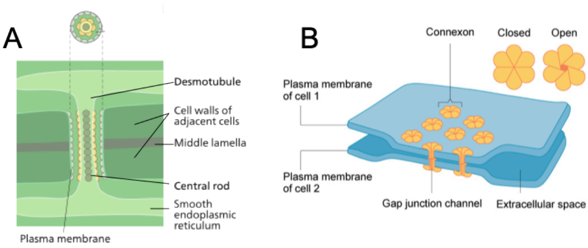

Figure 6. Cell to cell communication in plants can occur through plasmodesmata. This connection serves a similar function to the gap junctions found in animal cells.

Plants, in contrast, have intercellular channels are lined by extensions of the cell membrane. Tubules running through these channels connect the endomembrane systems of the two cells. Like gap junctions, plasmodesmata permit signaling molecules to pass between cells in such a way that they can be targeted to only one or a few adjacent cells. Complex red and brown algae also have plasmodesmata, and complex fungi have pores between cells that enable communication by means of cytoplasmic flow. As similar channels do not occur in most other eukaryotic organisms, they appear to represent an important step in the evolution of complex multicellularity.

Review Question:

Plasmodesmata in plant cells are MOST similar to which of the following structures of animal cells?

Genetic program for coordinated growth and cell

differentiation

In multicellular organisms, growth and development is the result of molecular communication between cells. Cells have different fates depending on which genes are switched off or on, and genes are switched off and on by the molecular signals that cells receive. A signal commonly alters the production of proteins-inducing the reorganization of the cytoskeleton, for example. As a result, a stem cell may become an epithelial cell, or a muscle cell, or a neuron. This observation leads to another question: What causes the same gene to be turned on in one cell and off in another? The ultimate answer is that two cells in the same developing organism can be exposed to very different environments.

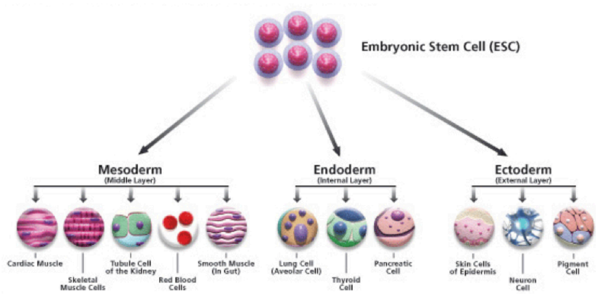

Figure 7. Stem cell differentiation results in one of three different categories of cells that sub-divide into specific cell types with specific roles

When we think about development as a process of programmed cell division and differentiation, the link to unicellular ancestors becomes clearer. Many biological innovations accompanied the evolution of complex multicellularity, but the differentiation of distinct cell types is not one of them. Many unicellular organisms have life cycles in which different cell types alternate in time, depending on environmental conditions. For example, if we experimentally starve dinoflagellate cells, two cells undergo sexual fusion to form morphologically and physiologically distinct resting cells protected by thick walls. That is, a nutrient shortage induces a change in gene expression that leads to the formation of resting cells. When food becomes available again, the cells undergo a meiotic cell division to form new feeding cells. Many other single-celled eukaryotes form resting cells in response to environmental cues, especially deprivation of nutrients or oxygen.

The innovation of complex multicellularity was to differentiate cells in space instead of time. In a three-dimensional multicellular organism, only surface cells are in direct contact with the outside environment. Interior cells are exposed to a different physical and chemical environment because nutrients, oxygen, and the light become less abundant with increasing depth within tissues. In effect, there is a gradient of environmental signals within multicellular organisms. We might, therefore, hypothesize that in the earliest organisms with three-dimensional multicellularity, a nutrient or oxygen gradient triggered oxygen- or nutrient-starved interior cells to differentiate, much as happens to trigger the formation of resting cells in their single-celled relatives. With increasing genetic control of cellular responses to signaling gradients, the seeds of complex development were sown.

Bulk flow, which transports nutrients, oxygen, and water within complex multicellular organisms, also carries developmental signals. Signals carried by bulk flow can travel far greater distances through the body than signals transmitted by diffusion alone. For example, in animals the endocrine system releases hormones directly into the bloodstream, enabling them to affect cells far from those within which they formed. Thus, the sex hormones estrogen and testosterone are synthesized in reproductive organs but regulate development throughout the body, contributing to the differences between males and females. In this way, signals carried by bulk flow can induce the formation of distinct cell types and tissues along the path of signal transport.

Review Question:

What is considered to be the greatest factor that leads to cell differentiation within complex multicellular organisms?
A) the lack of oxygen in internal spaces
B) the differing environments the cells are found in
C) the three-dimensional structure of the organism

Summary

The differences between an amoeba and a lobster seem vast, but research over the past decade increasingly shows how this apparent gap was bridged through a series of evolutionary innovations. Throughout this chapter, we have emphasized that complex multicellular organisms require mechanisms for cell adhesion, modes of communication between cells, and a genetic program to guide growth and development. These three requirements had to be acquired in a specific order. If the products of cell division don't stick together, there can be no complex multicellularity. Adhesion, however, is not sufficient. It must be followed by mechanisms for communication between cells. Moreover, cells must be able to send molecular messages to specific targets or regions, assisted in animals by gap junctions, and in plants by plasmodesmata.

With these requirements in place, natural selection would favor the increase and diversification of genes that regulate growth and development, making possible more complex morphology and anatomy. The biological stage was finally set for the functional key to complex multicellularity: the differentiation of tissues and organs that govern the bulk flow of fluids, nutrients, signaling molecules, and oxygen through increasingly large and complex bodies. This differentiation freed organisms from the tight constraints imposed by diffusion. When all these features are placed onto phylogenies, they show both the predicted order of acquisition and the tremendous evolutionary consequences of complex multicellularity

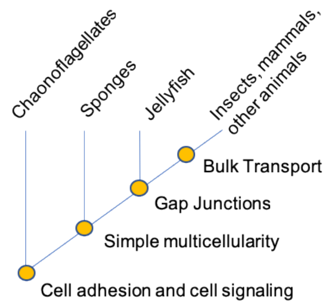

Figure 8. Phylogeny of the evolution of complex multicellularity in animals

End of Section Review Questions:

1) What types of molecules are used by complex multicellular organisms to attach cells to each other?
A) proteins like cadherin and adhesin
B) protein-carbohydrate complexes
C) pili and cannulae

2) In what order are the following thought to have evolved to have given rise to complex multicellularity?
A) Cell division
B) Diversification of regulatory genes
C) Cell communication
D) Cell adhesion

3) How does cell differentiation differ between unicellular and complex multicellular organisms?A) Unicellular organisms do not exhibit cell differentiation
B) Multicellular organisms have a spatial differentiation of cells
C) Unicellular organisms have a spatial differentiation of cells

References

Morris, J., Hartl, D. L., Knoll, A. H., & Lue, R. (2016). *Biology: How life works*. Chapter 28: Being Multicellular

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Extra: Review of Cellular Connections

Plant cell connections: In general, long stretches of the plasma membranes of neighboring plant cells cannot touch one another because they are separated by the cell wall that surrounds each cell. How then, can a plant transfer water and other soil nutrients from its roots, through its stems, and to its leaves? Such transport uses the vascular tissues (xylem and phloem) primarily. There are also structural modifications called plasmodesmata (singular = plasmodesma), numerous membrane channels that pass between cell walls of adjacent plant cells, connect their cytoplasm, and enable materials to be transported from cell to cell, and thus throughout the plant.

Animal cell connections: A tight junction is a watertight seal between two adjacent animal cells. The cells are held tightly against each other by proteins (predominantly two proteins called *claudins* and *occludins*). This tight adherence prevents materials from leaking between the cells; tight junctions are typically found in epithelial tissues that line internal organs and cavities and comprise most of the skin. Also found only in animal cells are desmosomes, which act like spot welds between adjacent epithelial cells. Short proteins called cadherins in the plasma membrane connect to intermediate filaments to create desmosomes. The cadherins join two adjacent cells together and maintain the cells in a sheet-like formation in organs and tissues that stretch, like the skin, heart, and muscles. Gap junctions in animal cells are like plasmodesmata in plant cells in that they are channels between adjacent cells that allow for the transport of ions, nutrients, and other substances that enable cells to communicate. Structurally, however, gap junctions and plasmodesmata differ. Gap junctions develop when a set of six proteins (called connexins) in the plasma membrane arrange themselves in an elongated donut-like configuration called a *connexon*. When the pores ("doughnut holes") of connexons in adjacent animal cells align, a channel between the two cells forms. Gap junctions are particularly important in cardiac muscle: The electrical signal for the muscle to contract is passed efficiently through gap junctions, allowing the heart muscle cells to contract in tandem.

18.

Learning Goals

By the end of this reading you should be able to:

- Identify the shared characteristics of fungi
- Describe the composition of the mycelium
- Describe the mode of nutrition of fungi
- Explain sexual and asexual reproduction in fungi

Introduction

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. While a typical fungal cell contains a true nucleus and many membrane-bound organelles, within the kingdom Fungi there is an enormous variety of living organisms collectively referred to as Eucomycota, or true Fungi. Scientists have identified about 100,000 species of fungi but 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.

Fungal Characteristics

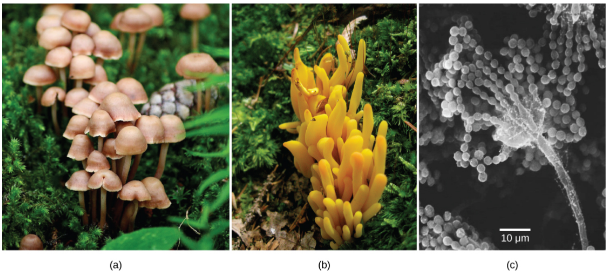


Figure 1. Many species of fungus produce the familiar mushroom (a) which is a reproductive structure. This (b) coral fungus displays brightly colored fruiting bodies. This electron micrograph shows (c) the spore-bearing structures of Aspergillus*, a type of toxic fungi found mostly in soil and plants. (credit "mushroom": modification of work by* Chris Wee*; credit "coral fungus": modification of work by* Cory Zanker*; credit "*Aspergillus*": modification of work by* Janice Haney Carr, Robert Simmons, CDC*; scale-bar data from* Matt Russell

Fungi, once considered plant-like organisms, are actually more closely related to animals than plants. Like animals, fungi are not capable of photosynthesis and therefore are heterotrophic.

Some fungal organisms multiply only asexually, whereas others undergo both asexual reproduction and sexual reproduction with a form of 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 into simple molecules (Fig. 1).

Fungi often interact with other organisms, forming beneficial associations. For example, most terrestrial plants form mutualistic relationships with fungi. The roots of the plant connect with the underground parts of the fungus forming **mycorrhizae**. Through mycorrhizae, the fungus and plant exchange nutrients and water, greatly aiding the survival of both species. Alternatively, lichens are an association between a fungus and its photosynthetic partner (usually an alga). Fungi also cause serious infections in plants and animals. For example, Dutch elm disease, which is caused by the fungus *Ophiostoma ulmi*, is a particularly devastating type of fungal infestation that destroys many native species of elm (*Ulmus* sp.) by infecting the tree's vascular system. The elm bark beetle acts as a vector, transmitting the disease from tree to tree. Accidentally introduced in the 1900s, the fungus decimated elm trees across the continent. Many European and Asiatic elms are less susceptible to Dutch elm disease than American elms.

Thinking Question:

If symbiotic fungi are absent from the soil, what impact do you think this would have on plant growth?

In humans, fungal infections are generally considered challenging to treat. Unlike bacteria, fungi do not respond to traditional antibiotic therapy, since they are eukaryotes. Fungal infections may prove deadly for individuals with compromised immune systems.

Fungi have many commercial applications. The food industry uses yeasts in baking, brewing, and cheese and wine production. Many industrial compounds are byproducts of fungal fermentation. Fungi are the source of many commercial enzymes and antibiotics.

Although humans have used yeasts and mushrooms since prehistoric times until recently the biology of fungi was poorly understood. Up until the mid-20th century, many scientists classified fungi as plants. Fungi, like plants, arose mostly sessile and 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.

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.

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 (Fig. 2). Pigments in fungi are associated with the cell wall and play a protective role against ultraviolet radiation. Some fungal pigments are toxic.

Figure 2. The poisonous Amanita muscaria is native to temperate and boreal regions of North America. (credit: Christine Majul)

Like plant cells, fungal cells have a thick cell wall. The rigid layers of fungal cell walls contain complex polysaccharides called chitin and glucans. Chitin, also found in the exoskeleton of insects, gives structural strength to the cell walls of fungi. The wall protects the cell from desiccation and predators. Fungi have plasma membranes 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, however, flagella are produced only by the gametes in the Phylum Chytridiomycota.

Review Question:

Which polysaccharide is usually found in the cell wall of fungi?

A) starch
B) glycogen
C) chitin
D) cellulose

Growth

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 (Fig. 3).

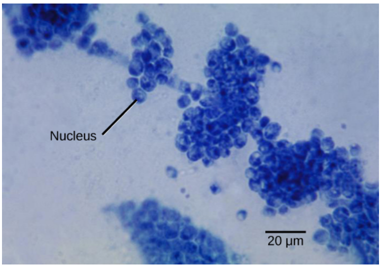


Figure 3. Candida albicans is a yeast cell and the agent of candidiasis and thrush. This organism has a similar morphology to coccus bacteria; however, yeast is a eukaryotic organism (note the nucleus). (credit: modification of work by Dr. Godon Roberstad, CDC; scale-bar data from Matt Russell)

Most fungi are multicellular organisms. They display two distinct morphological stages: vegetative and reproductive. The vegetative stage consists of a tangle of slender thread-like structures called **hyphae** (singular, **hypha**), whereas the reproductive stage can be more conspicuous. The mass of hyphae is a **mycelium** (Fig. 4). 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.

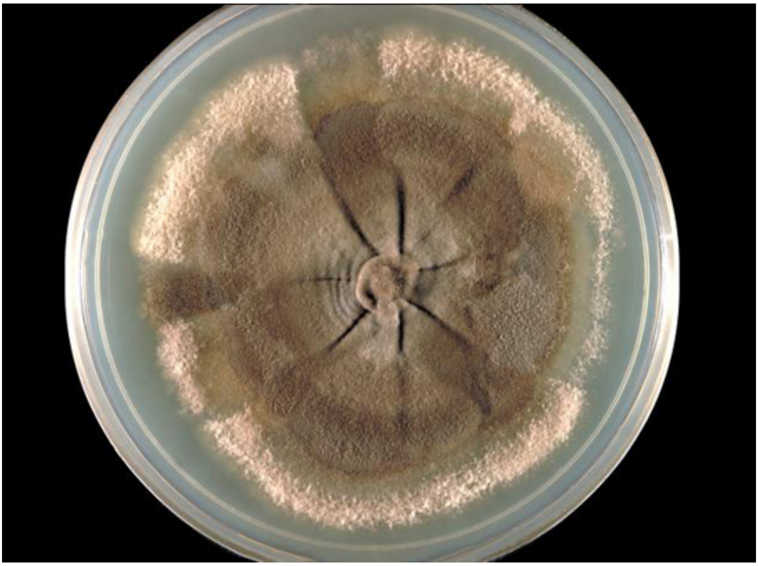


Figure 4. The mycelium of the fungus Neotestudina rosati can be pathogenic to humans. The fungus enters through a cut or scrape and develops a mycetoma, a chronic subcutaneous infection. (*credit*: CDC)

Most fungal hyphae are divided into separate cells by endwalls called **septa** (singular, **septum**) (Fig. 5a, 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** (SEE-no-SI-tic) **hyphae** (Fig. 5b).

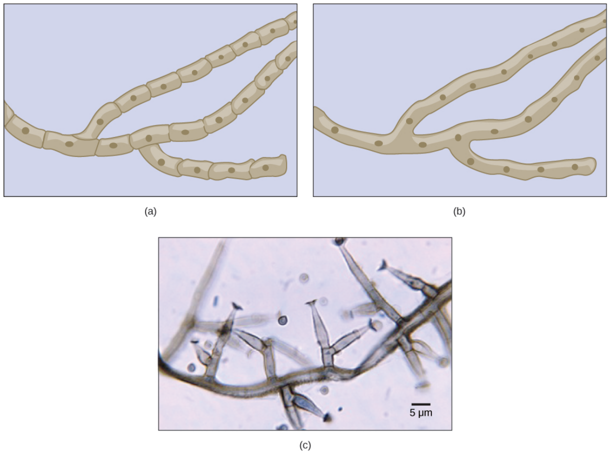


Figure 5. Fungal hyphae may be (a) septated or (b) coenocytic (coeno- = "common"; -cytic = "cell") with many nuclei present in a single hypha. A bright-field light micrograph of (c) Phialophora richardsiae shows septa that divide the hyphae. (credit c: modification of work by Dr. Lucille Georg, CDC; 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.

Review Question:

The wall dividing individual cells in a fungal filament is called a
A) thallus
B) hypha
C) mycelium
D) septum

Nutrition

Fungi are heterotrophs. In addition, fungi do not fix nitrogen from the atmosphere and so must obtain it from their diet, like animals. However, unlike most animals, 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** (saprophyte is an equivalent term): 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 (Fig. 6). 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.

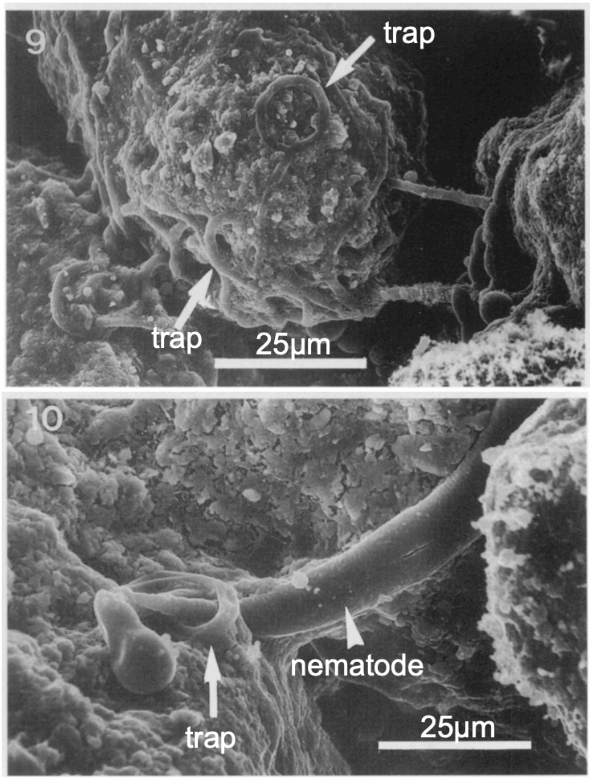


Figure 6. Predatory fungal hyphae modified to trap nematode worms (9). A nematode trapped in a fungal snare. Figures 9 and 10 taken from "Growth and Capture Activities of Nematophagous Fungi in Soil Visualized by Low Temperature Scanning Electron Microscopy" Jansson et al. 2000 Mycologia 92:10-15.

Review Question:

Regardless of the type of fungi the breakdown of food molecules is done by?

Reproduction

Fungi reproduce sexually and/or asexually. Perfect fungi reproduce both sexually and asexually, while the so-called imperfect fungi reproduce only asexually (by mitosis). In both sexual and asexual reproduction, fungi produce spores that disperse from the parent organism by either floating on the wind or hitching a ride on an animal. Fungal spores are smaller and lighter than plant seeds. The giant puffball mushroom bursts open and releases trillions of spores. The huge number of spores released increases the likelihood of landing in an environment that will support growth (Fig. 7).

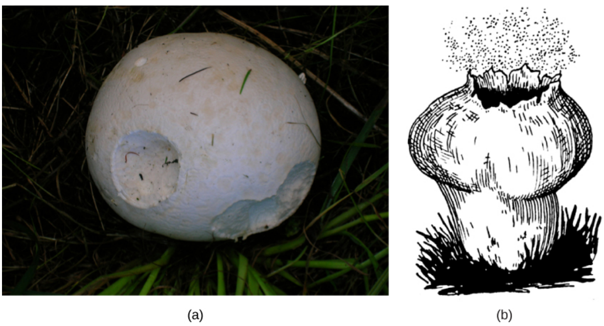


Figure 7. The (a) giant puffball mushroom releases (b) a cloud of spores when it reaches maturity. (credit a: modification of work by Roger Griffith; credit b: modification of work by Pearson Scott Foresman, donated to the Wikimedia Foundation)

Asexual Reproduction

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 (Fig. 8).

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 (Fig. 9). 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**.

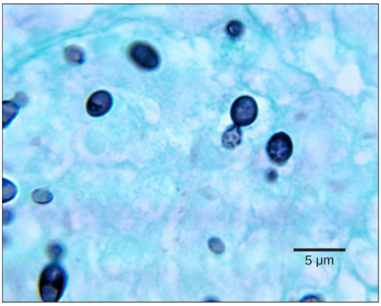


Figure 8. The dark cells in this bright field light micrograph are the pathogenic yeast Histoplasma capsulatum, seen against a backdrop of light blue tissue. Histoplasma primarily infects lungs but can spread to other tissues, causing histoplasmosis, a potentially fatal disease. (credit: modification of work by Dr. Libero Ajello, CDC; scale-bar data from Matt Russell)

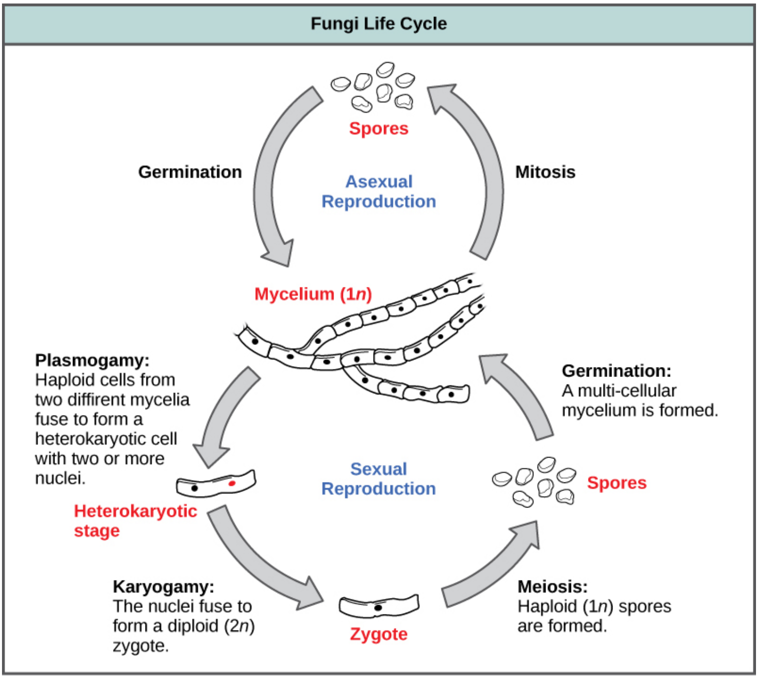


Figure 9. Fungi may have both asexual and sexual stages of reproduction.

There are many types of asexual spores. Conidiospores are unicellular or multicellular spores that are released directly from the tip or side of the hypha. Other asexual spores originate in the fragmentation of a hypha to form single cells that are released as spores; some of these have a thick wall surrounding the fragment. Yet others bud off the vegetative parent cell. Sporangiospores are produced in a sporangium (Fig. 10).

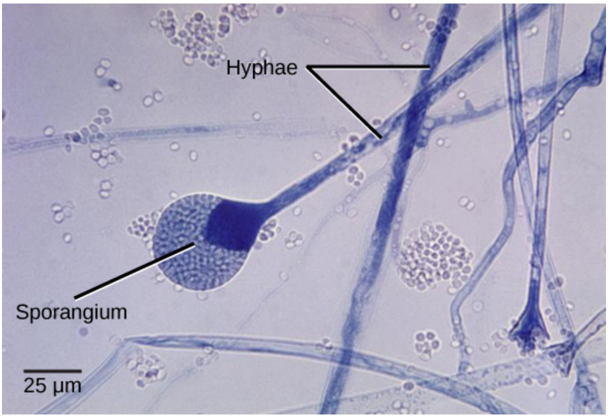


Figure 10 This bright field light micrograph shows the release of spores from a sporangium at the end of a hypha called a sporangiophore. The organism is a Mucor sp. fungus, a mold often found indoors. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Sexual Reproduction

Sexual reproduction introduces genetic variation into a population of fungi. In fungi, sexual reproduction often occurs in response to adverse environmental conditions. During sexual reproduction, two mating types are produced. When both mating types are present in the same mycelium, it is called **homothallic**, or self-fertile. **Heterothallic** mycelia require two different, but compatible, mycelia to reproduce sexually.

Although there are many variations in fungal sexual reproduction, all include the following three stages (**Figure 10**). 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.

Review the characteristics of fungi by visiting this **interactive site (http://openstaxcollege.org/l/fungi_kingdom)** from Wisconsin-online.

Review Question:

During sexual reproduction, a homothallic mycelium contains
A) all septated hyphae
B) all haploid nuclei
C) both mating types
D) none of the above

SUMMARY

Fungi are eukaryotic organisms that appeared on land more than 450 million years ago. They are heterotrophs and contain neither photosynthetic pigments such as chlorophyll nor organelles such as chloroplasts. Because fungi feed on decaying and dead matter, they are saprobes. Fungi are important decomposers that release essential elements into the environment. External enzymes digest nutrients that are absorbed by the body of the fungus, which is called a thallus. A thick cell wall made of chitin surrounds the cell. Fungi can be unicellular as yeasts or develop a network of filaments called a mycelium, which is often described as mold. Most species multiply by asexual and sexual reproductive cycles and display an alternation of generations. Another group of fungi does not have a sexual cycle. Sexual reproduction involves plasmogamy (the fusion of the cytoplasm), followed by karyogamy (the fusion of nuclei). Meiosis regenerates haploid individuals, resulting in haploid spores.

End of Section Review Questions:

Review: Organelles
1)Which of these organelles is not found in a fungal cell?
A) chloroplast
B) nucleus
C) mitochondrion
D) Golgi apparatus

Review: Reproduction
2) **How do fungi produce spores?**
A) meiosis
B) binary fission
C) mitosis

Review: Nutrition
3) **How do fungi obtain food?**
A) By absorbing it and then digesting it in the cytosol
B) By digesting it externally and absorbing the nutrients
C) By excreting lysosomes into the environment and then endocytosing them
D) By photosynthesis and cellular respiration

19.

Learning Goals

By the end of this reading you should be able to:

- Explain the roles fungi can play in ecosystems
- Describe mutualistic relationships of fungi with plant roots and photosynthetic organisms
- Describe the beneficial relationship between some fungi and insects

Introduction

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.

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, supplying other groups of organisms with some of the nutrients they need to live.

Decomposers and Recyclers

The food web would be incomplete without organisms that decompose organic matter. 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 (Fig. 1). Trace elements present in low amounts in many habitats are essential for growth and would remain tied up in rotting organic matter if fungi and bacteria did not return them to the environment via their metabolic activity.

Figure 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 ability of fungi to degrade many large and insoluble molecules is due to their mode of nutrition. In fungi, digestion precedes ingestion through the production of a variety of exoenzymes. These enzymes are either released into the substrate or remain bound to the outside of the fungal cell wall. Through the function of exoenzymes, large molecules are broken down into small molecules and then 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 (Fig. 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)

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 a mutualism. Fungi form mutualistic associations with many types of organisms, including cyanobacteria, algae, plants, and animals.

Review Question:

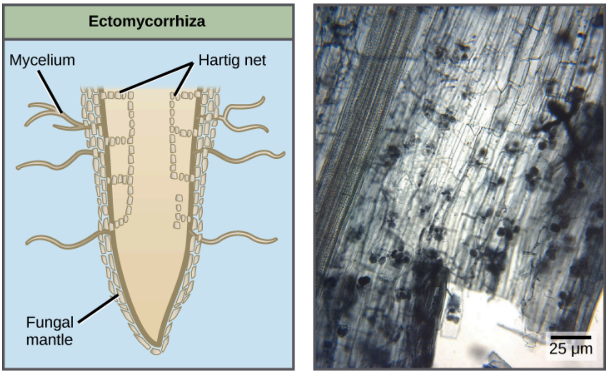
Why are fungi important decomposers?
A) They produce many spores.
B) They can grow in many different environments.

C) They produce mycelia and grow on the surface of the soil
D) They recycle carbon and inorganic minerals by the process of decomposition.

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 mycorrhizal. **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 (Fig. 3a). **Arbuscular mycorrhiza** sometimes called endomycorrhizae (Fig. 3b), form **arbuscules** that penetrate root cells and are the site of the metabolic exchanges between the fungus and the host plant (Fig 3 & 4). 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. 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 3. (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)

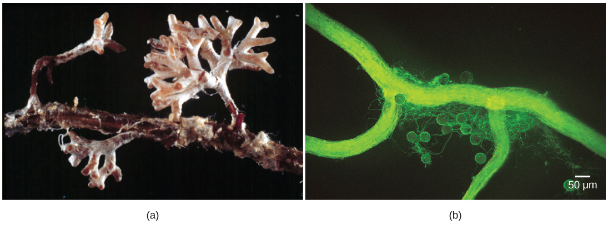


Figure 4. The (a) infection of Pinus radiata (Monterey pine) roots by the hyphae of Amanita muscaria (fly amanita) causes the pine tree to produce many small, branched rootlets. The Amanita hyphae cover these small roots with a white mantle. (b) Spores (round bodies) and hyphae (thread-like structures) 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)

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.

A well-accepted theory proposes that fungi were instrumental in the evolution of the root system in plants and contributed to the success of flowering plants. 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.

Review Question:

What term describes the close association of a fungus with the root of a tree?

A) a rhizoid
B) a lichen
C) a mycorrhiza
D) an endophyte

Lichens

Lichens display a range of colors and textures (Fig. 5) 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.

Explore the world of lichens using this **site(http://openstaxcollege.org/l/lichenland)** from Oregon State University.

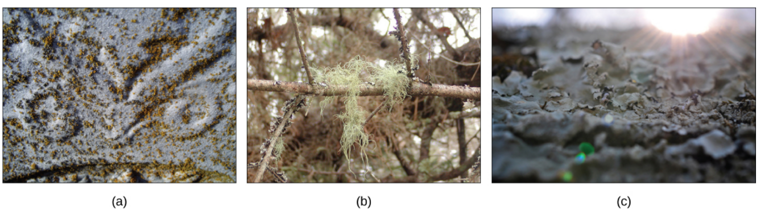


Figure 5. Lichens have many forms. They may be (a) crust-like, (b) hair-like, or (c) leaf-like. (credit a: modification of work by Jo Naylor; credit b: modification of work by "djpmapleferryman"/Flickr; credit c: modification of work by Cory Zanker)

Lichens are not a single organism, but rather an example of a mutualism, in which a fungus lives in close contact with a photosynthetic organism (a eukaryotic alga or a prokaryotic cyanobacterium). 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 from fungal hyphae wrapped around the photosynthetic partner (Fig. 6). 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.

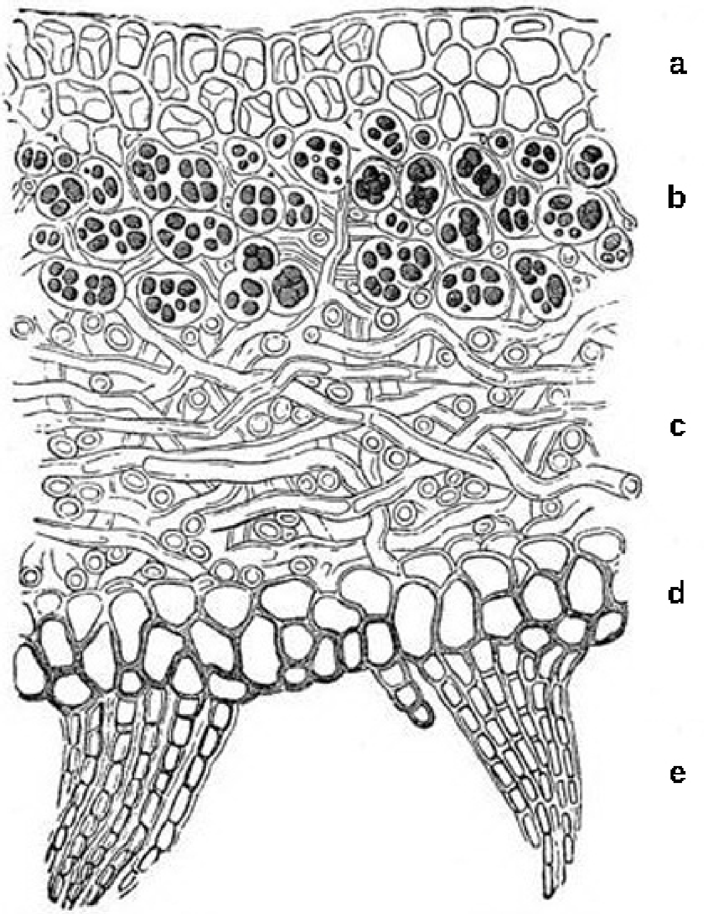


Figure 6. This cross-section of a lichen thallus shows the (a) upper cortex of fungal hyphae, which provides protection; the (b) algal zone where photosynthesis occurs, the (c) medulla of fungal hyphae, and the (d) lower cortex, which also provides protection and may have (e) rhizines to anchor the thallus to the substrate.

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, soredia, for reproduction. These structures are clusters of algal cells surrounded by mycelia and are dispersed by wind and water to 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 (http://openstaxcollege.org/l/lichen_monitrng)** from the United States Forest Service.

Fungus/Animal Mutualism

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 (Fig. 7). 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.

Figure 7. A leaf-cutting ant transports a leaf that will feed a farmed fungus. (credit: Scott Bauer, USDA-ARS)

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.

SUMMARY

Fungi have colonized nearly all environments on Earth, but are frequently found in cool, dark, moist places with a supply of decaying material. Fungi are saprobes that decompose organic matter. Many successful mutualistic relationships involve a fungus and another organism. Many fungi establish complex mycorrhizal associations with the roots of plants. Some ants farm fungi as a supply of food. Lichens are a symbiotic relationship between a fungus and a photosynthetic organism, usually an alga or cyanobacterium. The photosynthetic organism provides energy derived from light and carbohydrates, while the fungus supplies minerals and protection. Some animals that consume fungi help disseminate spores over long distances.

End of Section Review Questions:

Review: Mycorrhizae

1) **What characteristics do the fungi involved in mycorrhizal associations share with primitive fungi? (Multiple Answers)**

A) they produce simple spores

B) lack the ability to produce exoenzymes

C) do not have a sexual reproductive cycle

D) show little diversification

Review: Comparing partners

2) **How are the vascular plants that are involved in mycorrhizal associations and the photosynthetic cells involved in lichens alike?**

A) They both secrete acids that keep their fungal partners from growing too quickly

B) They both provide organic nutrients for their fungal partners

C) They are both intimate associations with Chytrid fungi

D) They are both digested by fungal exoenzymes while they are still living

Review: Lichen

3) **Which of the following best describes the physical relationship between the partners involved in lichens?**
A) Photosynthetic algal cells are surrounded by fungal hyphae
B) Fungi that grow on rocks and trees are covered by algae
C) Algal cells and fungal cells are randomly mixed together
D) Fungal cells are enclosed within photosynthetic algal cells

20.

Learning Goals

By the end of this reading you should be able to:

- Classify fungi into the five major phyla
- Describe each phylum in terms of major representative species and patterns of reproduction

Introduction

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. An older classification scheme grouped fungi that strictly use asexual reproduction into Deuteromycota, a group that is no longer in use.

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 (Fig 1). The evolutionary record shows that the first recognizable chytrids appeared more than 500 million years ago. Like all fungi, chytrids have chitin in their cell walls, and one group of chytrids has both cellulose and chitin in their cell wall. Most chytrids are unicellular, though a few form multicellular organisms. The hyphae of these multicellular chytrids have no septa between cells (they are coenocytic). Chytrids produce gametes and diploid zoospores that swim with the help of a single flagellum.

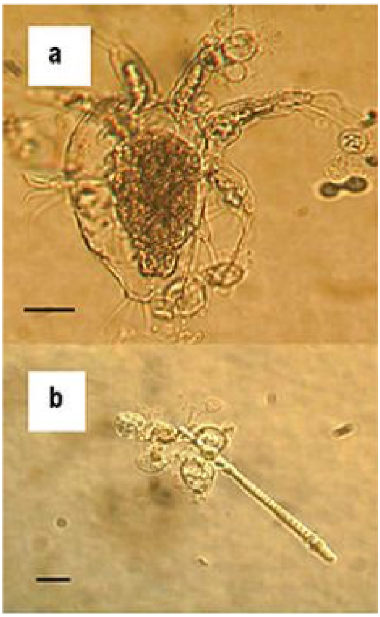


Figure 1. The chytrid Batrachochytrium dendrobatidis is seen in these light micrographs as transparent spheres growing on (a) a freshwater arthropod and (b) algae. This chytrid causes skin diseases in many species of amphibians, resulting in species decline and extinction. (credit: modification of work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

The ecological habitat and cell structure of chytrids have much in common with protists (single-celled eukaryotes that are not considered plants, animals or fungi). Chytrids usually live in aquatic environments, although some species live on land. Some species thrive as parasites on plants, insects, or amphibians, 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.

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 bread, 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.

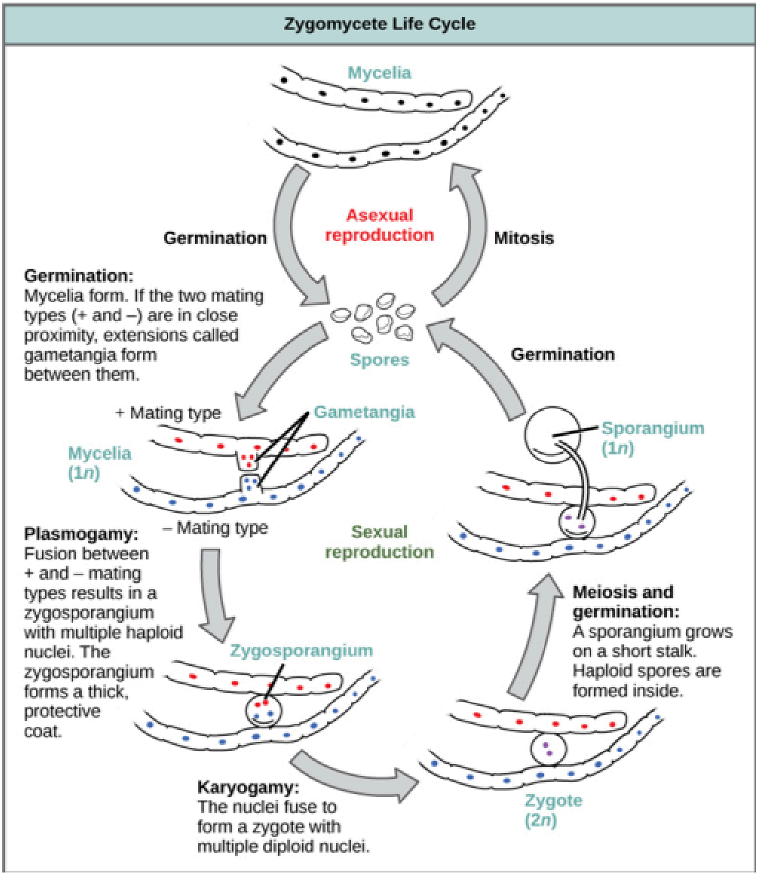


Figure 2. Zygomycete life cycle. Zygomycetes have asexual and sexual phases in their life cycles. In the asexual phase, spores are produced from haploid sporangia by mitosis (not shown).

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 (Fig. 2). The black tips of bread mold are the swollen sporangia packed with black spores (Fig. 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".

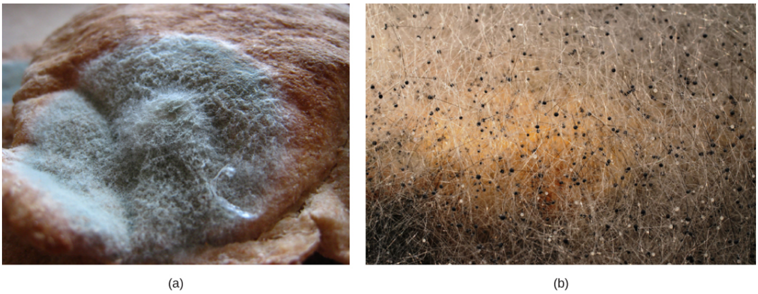


Figure 3. Sporangia grow at the end of stalks, which appear as (a) white fuzz seen on this bread mold, Rhizopus stolonifer. The (b) tips of bread mold are the spore-containing sporangia. (credit b: modification of work by "polandeze"/Flickr)

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 (Fig. 4), 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 but also produce poisonous secondary metabolites that make crops unfit for consumption. Filamentous ascomycetes produce hyphae divided by perforated septa, allowing the 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.

A YouTube element has been excluded from this version of the text. You can view it online here: https://viva.pressbooks.pub/introbio2/?p=68

Figure 4. Planet Earth series with David Attenborough. The

Cordyceps fungus at work.

Asexual reproduction is frequent and involves the production of conidiophores that release haploid conidiospores (Fig. 5). Sexual reproduction starts with the development of special hyphae from either one of two types of mating strains (Fig. 5). 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.

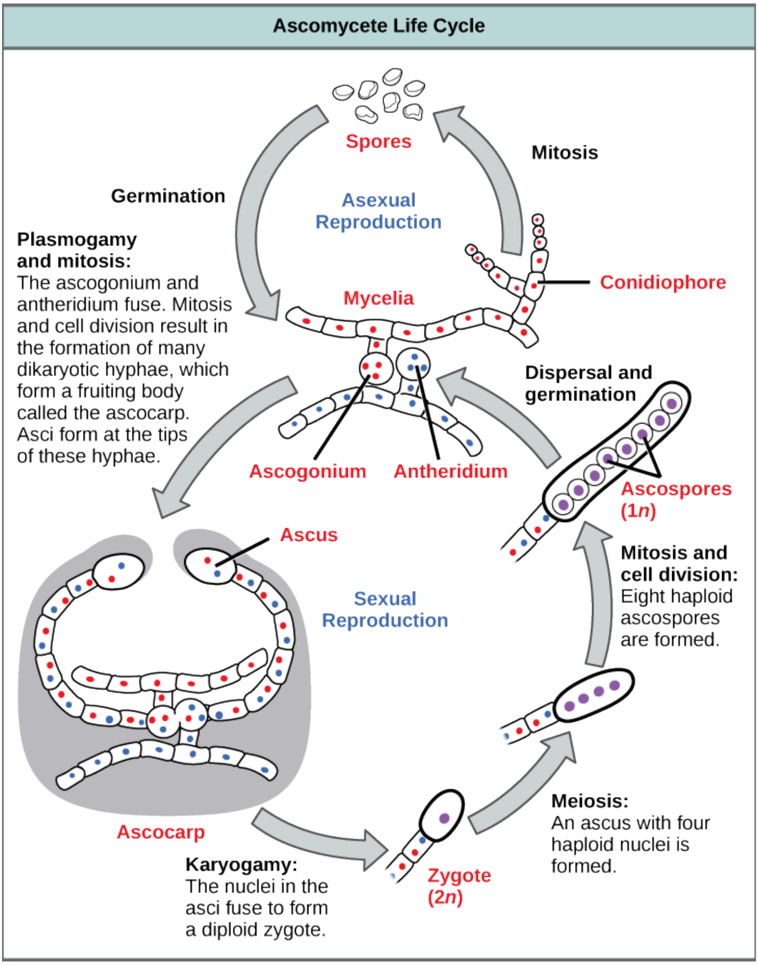


Figure 5. The lifecycle of an ascomycete is characterized by the production of asci during the sexual phase. The haploid phase is the predominant phase of the life cycle.

Review 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.

Basidiomycota: The Club Fungi

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 (Fig. 6). These mushroom-producing basidiomycetes 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 clings to the bark of trees like small shelves. In addition, the Basidiomycota includes smuts and rusts, which are important plant pathogens; toadstools, and shelf fungi stacked on tree trunks. Most edible fungi belong to the Phylum Basidiomycota; however, some basidiomycetes produce deadly toxins. For example, *Cryptococcus neoformans* causes severe respiratory illness.

Figure 6. The fruiting bodies of a basidiomycete form a ring in a meadow, commonly called "fairy ring." 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. (Credit: "Cropcircles"/Wikipedia Commons)]

The lifecycle of basidiomycetes includes alternation of generations (Fig. 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 basidiomycetes life cycle 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.

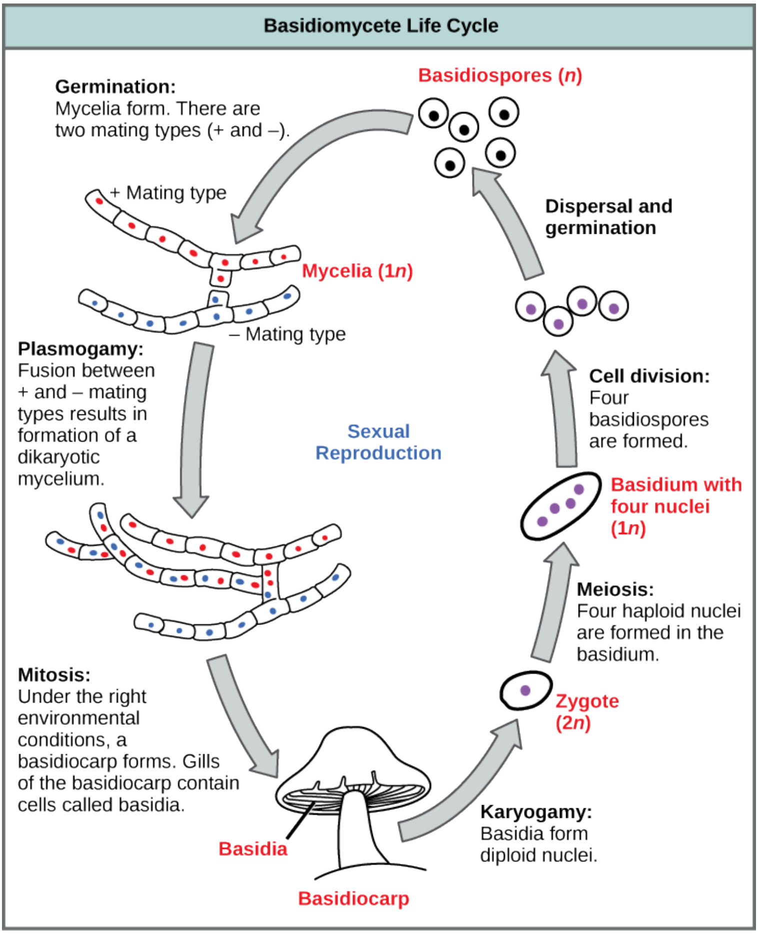


Figure 7. The lifecycle of a basidiomycete alternates generation with a prolonged stage in which two nuclei (dikaryon) are present in the hyphae.

Review 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.

Thinking Question:

What is the advantage of a basidiomycete to produce a showy and fleshy fruiting body?

Asexual Ascomycota and Basidiomycota

Imperfect fungi—those that do not display a sexual phase—use to be classified in the form phylum **Deuteromycota**, a classification group no longer used in the present, ever-developing classification of organisms. While Deuteromycota used to be a classification group, recent molecular analysis has shown that the members classified in this group belong to the Ascomycota or the Basidiomycota classifications. Since they do not possess the sexual structures that are used to classify other fungi, they are less well described in comparison to other members. Most members live on land, with a few aquatic exceptions. They form visible mycelia with a fuzzy appearance and are commonly known as **mold**.

The reproduction of the fungi in this group is strictly asexual and occurs mostly by the production of asexual conidiospores (Fig. 8). Some hyphae may recombine and form heterokaryotic hyphae.

Genetic recombination is known to take place between the different nuclei.

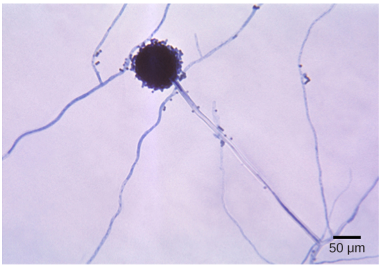


Figure 8. Aspergillus niger is an asexually reproducing fungus (phylum Ascomycota) commonly found as a food contaminant. The spherical structure in this light micrograph is a conidiophore. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

The fungi in this group 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 results 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. Other fungi in this group 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*.

Glomeromycota

The **Glomeromycota** is a newly established phylum that 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.

Summary

Chytridiomycota (chytrids) are considered the most primitive group of fungi. They are mostly aquatic, and their gametes are the only fungal cells known to have flagella. They reproduce both sexually and asexually; the asexual spores are called zoospores. Zygomycota (conjugated fungi) produce non-septated hyphae with many nuclei. Their hyphae fuse during sexual reproduction to produce a zygospore in a zygosporangium. Ascomycota (sac fungi) form spores in sacs called asci during sexual reproduction. Asexual reproduction is their most common form of reproduction. Basidiomycota (club fungi) produce showy fruiting bodies that contain basidia in the form of clubs. Spores are stored in the basidia. Most familiar mushrooms belong to this division. Fungi that have no known sexual cycle were classified in the form phylum Deuteromycota, which the present classification puts in the phyla Ascomycota and Basidiomycota. Glomeromycota forms tight associations (called mycorrhizae) with the roots of plants.

End of Section Review Questions:

Review: Primitive Fungi
1) The most primitive phylum of fungi is the _________.
A) Chytridiomycota
B) Zygomycota
C) Glomeromycota
D) Ascomycota

Review: Reproductive Structure
2) Members of which phylum produce a club-shaped structure that contains spores?
A) Chytridiomycota
B) Basidiomycota
C) Glomeromycota
D) Ascomycota

Review: No Sex
3) The fungi that do not reproduce sexually use to be classified as ________.
A) Ascomycota
B) Deuteromycota
C) Basidiomycota
D) Glomeromycota

Review: Symbiosis
4) What term describes the close association of a fungus with the root of a tree?
A) a rhizoid
B) a lichen
C) a mycorrhiza
D) an endophyte

Review: Decomposition
5) Why are fungi important decomposers?
A) They produce many spores.
B) They can grow in many different environments.
C) They produce mycelia.
D) They recycle carbon and inorganic minerals by the process of decomposition.

Review: Symbiosis
6) A fungus that climbs up a tree reaching higher elevation to release its spores in the wind and does not receive any nutrients from the tree or contribute to the tree's welfare is described as a

________.
A) commensal
B) mutualist
C) parasite
D) pathogen

Review: Compare
7) For each of the four groups of perfect fungi (Chytridiomycota, Zygomycota, Ascomycota, and Basidiomycota), compare the body structure and features, and provide an example.

21.

Learning Goals

- Describe fungal parasites and pathogens of plants
- Describe the different types of fungal infections in humans
- Explain why antifungal therapy is hampered by the similarity between fungal and animal cells

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 disease, whereas the parasite usually does not. **Commensalism** occurs when one member benefits without affecting the other.

Plant Parasites and Pathogens

The production of sufficient good-quality crops is essential to human existence. Plant diseases have ruined crops, bringing widespread famine. Many plant pathogens are fungi that cause tissue decay and eventual death of the host (Fig. 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, hallucinations, 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 a massive recall of produce. This sometimes ruins producers and causes food shortages in developing countries.

Animal and Human Parasites and Pathogens

Fungi can affect animals, including humans, in several ways. A **mycosis** is a fungal disease that results from infection and direct damage. Fungi attack animals directly by colonizing and destroying tissues. **Mycotoxicosis** is the poisoning of humans (and other animals) by foods contaminated by fungal toxins (mycotoxins). **Mycetismus** describes the ingestion of preformed toxins in poisonous mushrooms. In addition, individuals who display hypersensitivity to molds and spores develop strong and dangerous allergic reactions. Fungal infections are generally very difficult to treat because, unlike bacteria, fungi are eukaryotes. Antibiotics only target prokaryotic cells, whereas compounds that kill fungi also harm the eukaryotic animal host.

Many fungal infections are superficial; that is, they occur on the animal's skin. Termed cutaneous ("skin") mycoses, can have devastating effects. For example, the decline of the world's frog population in recent years may be caused by the chytrid fungus *Batrachochytrium dendrobatidis*, which infects the skin of frogs and presumably interferes with gaseous exchange. Similarly, more than a million bats in the United States have been killed by white-nose syndrome, which appears as a white ring around the mouth of the bat. It is caused by the cold-loving fungus *Geomyces destructans*, which disseminates its deadly spores in caves where bats hibernate. Mycologists are researching the transmission, mechanism, and control of *G. destructans* to stop its spread.

Fungi that cause the superficial mycoses of the epidermis, hair, and nails rarely spread to the underlying tissue (Fig. 2). 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.

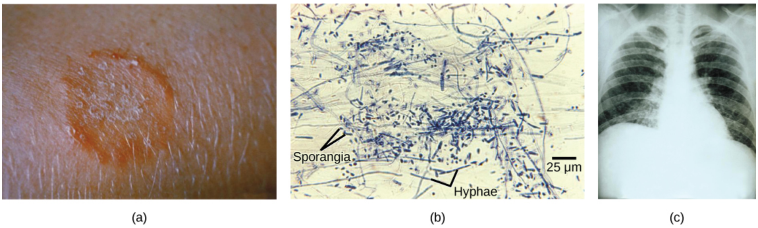


Figure 2 (a) Ringworm presents as a red ring on skin; (b) Trichophyton violaceum, shown in this bright field light micrograph, causes superficial mycoses on the scalp; (c) Histoplasma capsulatum is an ascomycete that infects airways and causes symptoms similar to influenza. (credit a: modification of 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 is altered.

Mycetismus can occur when poisonous mushrooms are eaten. It causes a number of human fatalities during the 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.

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. Accidentally 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.

Explain how you would go about testing your hypothesis for this theoretical Dutch Elm experiment. Include independent and dependent variables, your controls, what you will measure, and how you will analyze your data.

SUMMARY

Fungi establish parasitic relationships with plants and animals. Fungal diseases can decimate crops and spoil food during storage. Compounds produced by fungi can be toxic to humans and other animals. Mycoses are infections caused by fungi. Superficial mycoses affect the skin, whereas systemic mycoses spread through the body. Fungal infections are difficult to cure.

End of Section Review Questions:

Review: Infections
A fungal infection that affects nails and skin is classified as ________.
A) systemic mycosis
B) mycetismus
C) superficial mycosis
D) mycotoxicosis

Review: Human diseasesWhy can superficial mycoses in humans lead to bacterial infections?

22.

Learning Goals

- Describe the importance of fungi to the balance of the environment
- Summarize the role of fungi in food and beverage preparation
- Describe the importance of fungi in the chemical and pharmaceutical industries
- Discuss the role of fungi as model organisms

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 (Fig. 1).

Figure 1. 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)

The mycorrhizal relationship between fungi and plant roots is essential for the productivity of farmland. 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.

We also eat some types of fungi. Mushrooms figure prominently in the human diet. Morels, shiitake mushrooms, chanterelles, and truffles are considered delicacies (Fig. 2). The humble meadow mushroom, *Agaricus campestris*, appears in many dishes. Molds of the genus *Penicillium* ripen many kinds of cheese. 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.

Figure 2. The morel mushroom is an ascomycete much appreciated for its delicate taste. (credit: Jason Hollinger)

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 an 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.

SUMMARY

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.

Review: Wine and Beer!

1) **Yeast is a facultative anaerobe. This means that alcohol fermentation takes place only if**:

A) the temperature is close to 37°C

B) the atmosphere does not contain oxygen

C) sugar is provided to the cells

D) light is provided to the cells

Review: Biotechnology

2) **The advantage of yeast cells over bacterial cells to express human proteins is that:**

A) yeast cells grow faster

B) yeast cells are easier to manipulate genetically

C) yeast cells are eukaryotic and modify proteins similarly to human cells

D) yeast cells are easily lysed to purify the proteins

Review: mmmmmm… bread…

3) Historically, artisanal breads were produced by capturing wild yeasts from the air. Prior to the development of modern yeast strains, the production of artisanal breads was long and laborious because many batches of dough ended up being discarded. Can you explain this fact?

23.

Learning Goals

By the end of this reading you should be able to:

- Identify the two supergroups of Eukarya that contain plants, animals, and fungi
- Explain why the presence of photosynthesis is not used as a defining characteristic of Eukaryotic supergroups
- Compare the traits shared by green algae and land plants
- Explain the reasons why Charales are considered the closest relative to land plants

Introduction

The oldest fossils appear to all be prokaryotes, while the evidence of eukaryotes is about 2 billion years old (they appear later in the fossil record). Based on this it is probable that today's eukaryotes are descended from an ancestor that had a prokaryotic organization. The last common ancestor of today's Eukarya had several characteristics, including cells with nuclei that divided mitotically and contained linear chromosomes where the DNA was associated with histones, a cytoskeleton and endomembrane system, and the ability to make cilia/flagella during at least part of its life cycle. This ancestor was aerobic because it had mitochondria that were the result of endosymbiosis of an aerobic alpha-proteobacterium. Whether this ancestral cell had a nucleus at the time of the initial symbiosis remains unknown. Modern Eukarya are an amazingly diverse group of organisms, from single cells to complex multicellular organisms and with multiple means of acquiring both energy and the carbon need for building blocks.

Supergroups within the Eukarya

The emerging classification scheme groups the entire domain Eukaryota into six “supergroups” that evolved from a common ancestor and contains all of the protists as well as animals, plants, and fungi (Fig. 1).

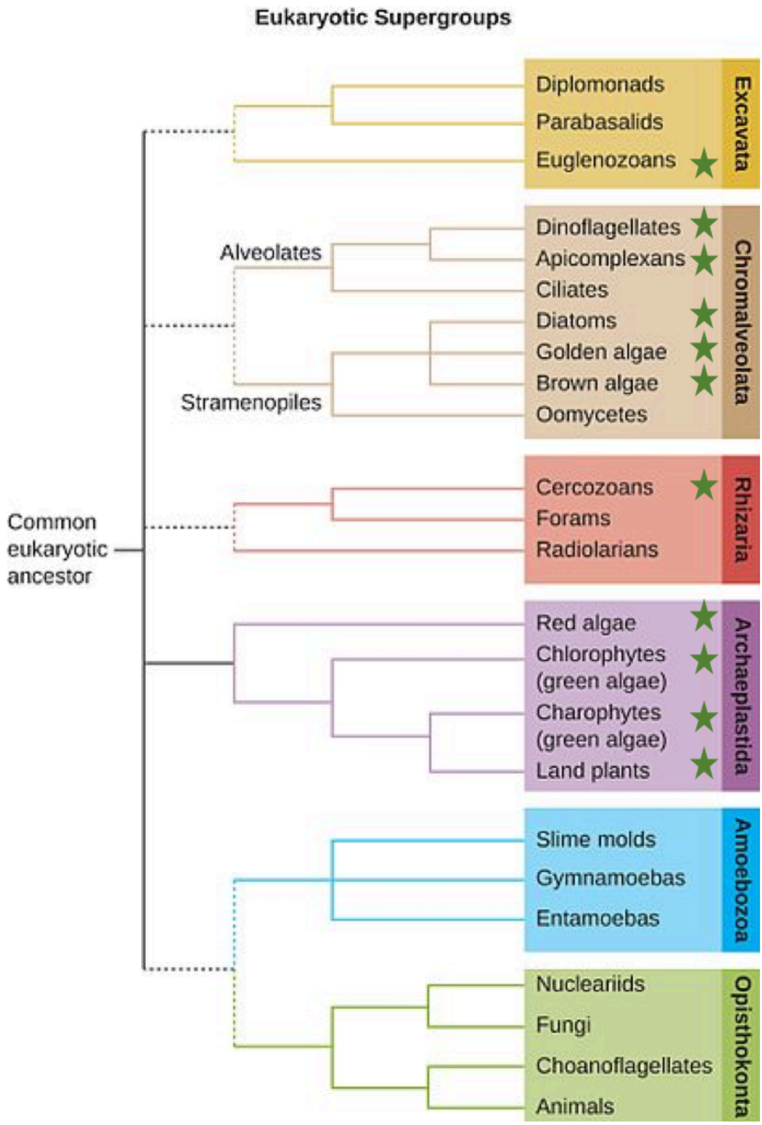


Figure 1. The Eukarya are separated into six supergroups. Green stars indicate groups that contain photosynthetic members.

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.

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.

Archaeplastida

The supergroup Archaeplastida is separated into three phylogenetic groups: the Glaucocytophyes, the Red Algae, and the Viridioplantae. With only a few exceptions all of the organisms within the supergroup are photosynthetic. Photosynthesis, however, is found in other groups that are not within the Archaeplastida, including the brown and golden algae, diatoms, dinoflagellates, some apicomplexans, some excavata (Euglenids), and some Rhizarians (see Fig. 2). Red algae and green algae, however, are included in the supergroup Archaeplastida. Molecular evidence supports that all Archaeplastida are descendants of an endosymbiotic relationship between a heterotrophic protist and a cyanobacterium.

Thinking Question:

What is a possible explanation for the pattern of distribution of photosynthetic eukaryotes (they are widely distributed but discontinuously among the different groups)? Be sure to provide support for your reasoning.

Glaucophytes:

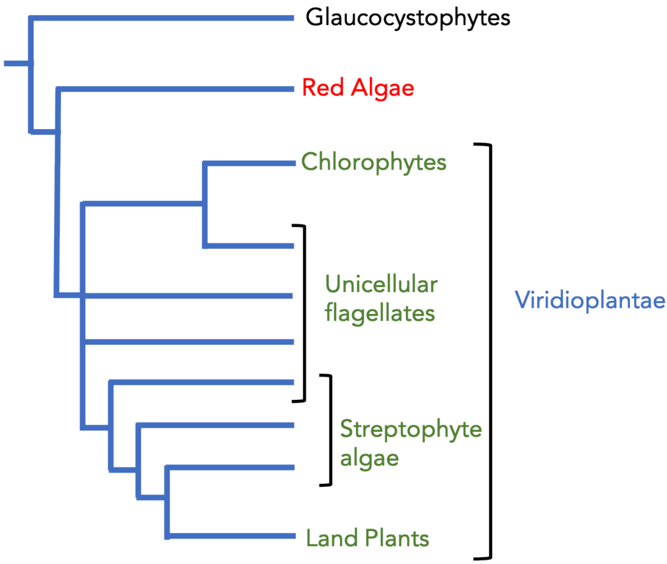


Figure 2. Phylogenetic tree of the Archaeplastida.

This is a small group of organisms that reside in freshwater ponds and lakes. They are unique in that their chloroplasts have walls of peptidoglycan, a feature retained from the ancestral cyanobacterial endosymbiont. In addition, their photosynthetic pigments include biliprotein which is also found in cyanobacteria.

Red Algae

Red algae, or rhodophytes, are primarily multicellular, most lack flagella, and range in size from microscopic, unicellular protists to large, multicellular forms that have differentiated tissues and in some cases complex morphology. Red algae, like land plants, have cell walls composed of cellulose and display a life cycle with an alternation of generations. There are many species of red algae that are seaweeds that are found in the shallow seafloor, however, and some species have unique pigment photosynthetic accessory pigments. These phycoerythrin pigments are red in color which allows the algae to utilize short (blue) wavelengths of light. These wavelengths are found at greater depths than the red wavelengths commonly used by other photosynthetic organisms and thus allow these algae to live at greater depths and outcompete other algae. Coralline red algae are found at the edges of coral reefs and they have the ability to secrete calcium carbonate ($CaCO_3$) to form an external skeleton-like structure that protects them from the motion of the waves. These tiny red algae are key to the establishment of the coral reefs as they provide a needed buffer for the newly attached corals.

Viridioplantae: Green Algae

Green algae are the most abundant group of algae and exhibit similar features to the land plants. The 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 land plants. In addition, 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 like starch. These similarities provide evidence that, even though green algae are classified as protists, they shared a relatively recent common ancestor with land plants.

There is wide diversity within the green algae, and while some groups are unicellular and flagellate, the Chlorophytes and the Charophytes contain members that are complex and multicellular.

The Chlorophytes include more than 7000 different species that live in fresh or brackish water, in seawater, or in snow patches. A few 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. *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. These chlorophyte species exhibit haploid gametes and spores, which are also found in other more complex species.

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. *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.

True multicellular organisms, such as the sea lettuce, *Ulva*, are also represented among the chlorophytes. Other chlorophytes exist as large, multinucleate, single cells. Within the genus *Caulerpa* some species undergo nuclear division, but their cells do not complete cytokinesis, remaining instead as massive and elaborate single cells.

While Chlorophytes share some features with land plants, the Charophytes are the closest living relatives to land plants and resemble them in both morphology and reproductive strategies. Within the charophytes, the order Charales, and the coleochaetes (microscopic green algae that enclose their spores in sporopollenin) are considered the closest living relatives of land plants. Charales have been discovered in the fossil record as far back as 420 million years ago. The organisms within this group live in a range of freshwater habitats and vary in size from a few millimeters to a meter in length.

Figure 3. Chara sp. with branches composed of smaller cells at the nodes. This picture shows the male antheridia (red) and female archegonia (brown) that are found at the nodes.

A representative species is *Chara* (Fig 3), which has large cells that form a thallus: the main stem of the alga. At the nodes, smaller cells can form branches and male and female reproductive structures are established. This group also produces flagellated sperm.

Unlike land plants, green algae within the Charales do not undergo alternation of generations in their lifecycle. However, Charales do exhibit a number of traits that are significant to the adaptation to land life. They produce the compound lignin, which provides support against gravity, and sporopollenin, which helps protect spores from drying out. In addition, they form plasmodesmata that connect the cytoplasm of adjacent cells which allows for greater ease in moving molecules including water between adjacent cells. Finally, the egg, and later, the zygote, form in a protected chamber on the parent plant, again this protects against drying out.

The separation of green algae from what are considered to be plants is one that is not always clear cut. While all algae are photosynthetic—that is, they contain some form of a chloroplast—they didn't all become photosynthetic via the same path. In contrast, the evolutionary pathways of photosynthesis in land plants can be traced back to a common ancestor. The presence of cellulose in cell walls, chlorophyll a and later chlorophyll b as well as structural features of chloroplasts that provide the clearest connections between modern land plants and their algal ancestors.

Review Question:

Which of these DOES NOT provide evidence that green algae are the most likely ancestor of land plants?
A) the presence of chloroplasts
B) the presence of both chlorophyll a and chlorophyll b
C) the ability to photosynthesize
D) the storage of photosynthetic sugars as starch

Summary

The Eukarya are a widely diverse group that is separated into six supergroups based on morphology and DNA evidence. Photosynthesis is found within four of those six groups, but only in the Archaeplastida are all members photosynthetic. In addition, many of the groups contain unicellular, simple multicellular and in some cases complex multicellular organisms. Land plants are considered to have evolved from green algal ancestors with the Charophytes due to a number of shared features including photosynthetic pigments, cellular structures, and reproductive strategies.

End of Section Review Questions:

Review: Glaucocystophytes

1) **What features do the Glaucocystophytes share with cyanobacteria? (Multiple Answers)**

A) some cell walls (chloroplast) that are composed of peptidoglycan
B) the photosynthetic pigment phycoerythrin
C) the ability to use biliprotein in photosynthesis

Review: Viridioplantae

2) **The Viridioplantae includes which groups of photosynthetic organisms? (Multiple Answers)**

A) brown algae
B) chlorophytes
C) red algae
D) charophytes
E) glaucocystophytes

Thinking Question

The chlorophyte (green algae) genera Ulva and Caulerpa both have macroscopic leaf-like and stem-like structures, but only Ulva species are considered truly multicellular. Explain why using your knowledge of multicellular features.

24.

Learning Goals

By the end of this reading you should be able to

- Discuss the challenges to plant life on land
- Describe common characteristics of all land plants
- Relate specific adaptive features to the unique challenges of life on land

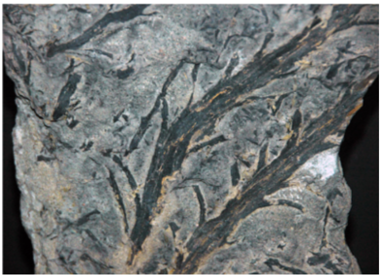


Figure 1. Chaleuria cirrosa fossil. Chaleuria is the oldest known plant that has heterospory

Introduction

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. At some point in the evolutionary history of plants, there was a transition from an aquatic environment to the terrestrial one. This transition from water to land imposed severe constraints on plants. Plants had to develop strategies to avoid drying out, to disperse reproductive cells in air, to provide structural support, to exchange gases without water, and as they grew larger to move molecules by bulk flow. While some groups of plants developed adaptations that allowed them to populate even the aridest habitats on Earth, full independence from the water did not happen in all plants. As a group, most seedless plants still require a moist environment for at least some of their physiological functions. Land plants can be separated by the degree of development of their structures, both vascular as well as reproductive, and the variation in their alternation of generations lifecycle.

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 the 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 that deterred predation: from spines and thorns to toxic chemicals.

Figure 2. The waxy cuticle and small size of Bryophytes (seedless non-vascular plants) help prevent them from drying out.

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 (Fig. 1), a gametangium that produces haploid cells, and apical meristem tissue involved in growth. The evolution of a waxy cuticle (Fig. 2) and a cell wall with lignin also contributed to the success of land plants, although not all land plants have lignin. These adaptations are noticeably lacking in the closely related green algae, further differentiating these two lineages.

Review Question:

What were some of the advantages of moving onto land? (Multiple Answers)
A) increased light radiation
B) increased levels of oxygen
C) faster diffusion of carbon dioxide
D) reduced predation initially

Alternation of Generations

Alternation of generations describes a life cycle in which an organism has both haploid and diploid multicellular stages (Fig 3).

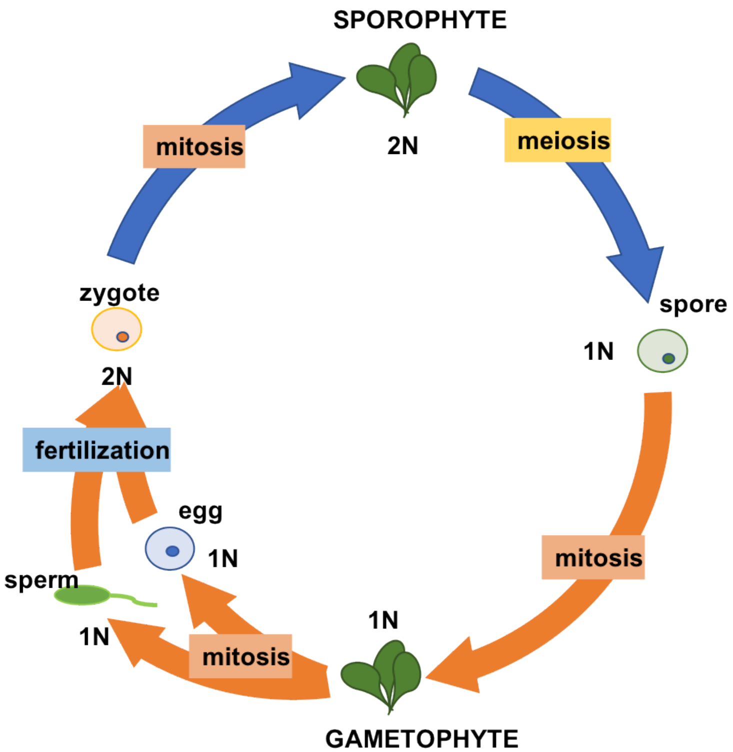


Figure 3. Alternation of generation in plants includes a multicellular diploid sporophyte and a multicellular haploid gametophyte.

Haplontic refers to a lifecycle in which there is a dominant haploid stage (like most fungi), and diplontic refers to a lifecycle in which the diploid is the dominant life stage (like animals). 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, like moss, or massively huge, like diplontic sequoia and pine trees. The sporophyte stage produces spores by meiosis and each spore is capable of giving rise to a multicellular gametophyte.

Regardless of the size of the gametophyte and/or sporophyte stage, the protection of the embryo is a major requirement for land plants. The vulnerable embryo must be sheltered from desiccation and other environmental hazards. In all land plants, the female gametophyte provides protection and nutrients to the embryo as it develops into the new generation of the sporophyte. This distinguishing feature of land plants, which is not present in green algae, makes all land plants embryophytes.

Review Question:

_____________ occurs when sporophytes produce spores
_____________ occurs when gametophytes produce gametes
The zygote undergoes _____________ to become the multicellular _____________
Word Bank: fertilization, mitosis, meiosis, gametophyte, sporophyte, spore

Sporangia in Seedless Plants

The sporophyte of seedless plants is diploid and results from syngamy (fusion) of two gametes. The sporophyte bears the **sporangia** (singular, sporangium) (Fig. 4): 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.

Inside the multicellular sporangia, the diploid **sporocytes**, or mother cells, produce haploid spores by **meiosis**. The spores are later released by the sporangia and disperse in the environment. 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 (Fig. 1). 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.

Figure 4. Sporangia are structures designed to both produce and disperse spores.

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. 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, germline 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.

Other adaptive features

- 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 the intake of carbon dioxide needed for the synthesis of carbohydrates through photosynthesis. To overcome this, stomata or pores that open and close to regulate the 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. 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.

Thinking Question:

Which trait(s) are likely to have evolved first as the ancestors of land plants adapted to more terrestrial environments? Defend your answer.

Summary

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, the 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.

End of Section Review Questions:

Review: Reproductive terminology
1) **Match the term with the best description**

1) Homosporous	A) undergo meiosis to produce haploid spores
2) Microspore	B) producing two different types of spores
3) Sporopollenin	C) polymer found in spore cell walls
4) Sporocytes	D) produce only one type of spore (seedless non-vascular plants)
5) Heterosporous	E) where precursor cells give rise to gametes by mitosis
6) Gametangia	F) develops into the male gametophyte

Review: Challenges on Land

2) **Which of the following was NOT a challenge to the first land plants?**

A) sufficient light for photosynthesis

B) drying out

C) increased UV radiation

D) water for reproduction

Review: Alternation of Generations

3) **Which is true about alternation of generations in land plants? (Multiple Answers)**

A) Meiosis only occurs in sporophyte tissues often the sporangia

B) Gametes are produced by meiosis in gametangia

C) The gametophyte and sporophyte differ in chromosome number

D) The zygote gives rise to the sporophyte through mitosis

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25.

Learning Goals

By the end of this reading you should be able to:

- Identify the main characteristics of bryophytes
- Describe the distinguishing traits of liverworts, hornworts, and mosses
- Chart the development of land adaptations in the bryophytes
- Describe the events in the bryophyte lifecycle

Introduction

Seedless non-vascular plants all fall into the group Bryophyta, a group of plants that are the closest extant relative of early terrestrial plants. The first bryophytes (liverworts) most likely appeared 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.

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 non-vascular 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 (embryophytes).

The bryophytes are divided into three phyla: the liverworts (Hepaticophyta), the hornworts (Anthocerotophyta), and the mosses (true Bryophyta).

Liverworts:

Liverworts 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. The most obvious structure of the liverworts is the lobate flat thallus, this is the gametophyte. Since there is no cuticle the plant takes up water over its entire surface but lacks protection from desiccation. Openings that allow the movement of gases may be observed in liverworts but these are not stomata, because they do not actively open and close.

The liverwort life 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. Like all sporophytes in non-vascular plants, the sporophyte will remain dependent on the gametophyte for nutrients throughout its life. The sporophyte will give rise, by meiosis, to the next generation of spores.

Figure 1. Gemma cups are small cup-shaped structures on the thallus that contain undifferentiated cells (gemmae). Water disperses these cells which grow into a new gametophyte

Liverwort plants can also reproduce asexually, by the breaking of branches or the spreading of a single cell, or a mass of cells, called **gemmae**. This type of asexual reproduction is sometimes referred to as fragmentation. On the thallus, the gemmae are produced in a cup and are splashed out of the cup by raindrops. The gemmae then land nearby and develop into new gametophytes. This allows the organisms to spread when conditions (presence of water) are favorable.

Hornworts

The hornworts (*Anthocerotophyta*) have colonized a variety of habitats on land, although they are never far from a source of moisture. Like liverworts, the gametophyte is the dominant phase of the lifecycle. The blue-green hornwort gametophytes grow as flat thalli on the soil with embedded gametangia. In each of the photosynthetic cells of the thallus, there is a single chloroplast. At the base of the plant, there is a meristem, where cells continuously divide and add to the height.

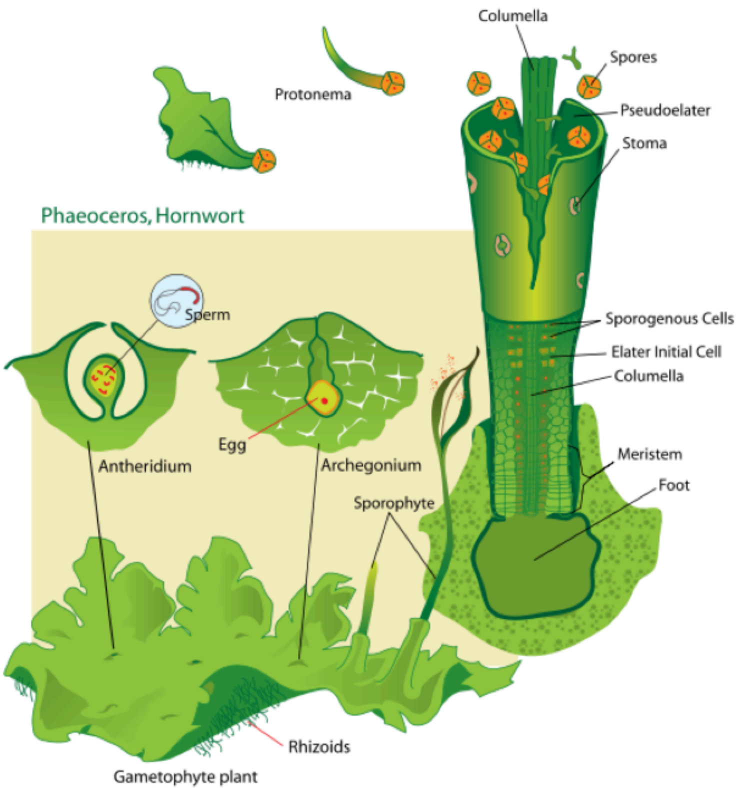

Figure 2. The sporophyte of hornworts is dependent on the gametophyte. It has specially adapted cells, pseudoelaters that are involved in spore dispersal.

The archegonia and antheridia on the gametophyte undergo mitosis to produce gametes and then the flagellated sperm swim to the archegonia and fertilize eggs. After fertilization, the zygote develops into a long narrow, pipe-like sporophyte, a defining characteristic of this group. Once spore formation begins, the tip of the sporophyte splits open, releasing spores. Thin cells called pseudoelaters surround the spores and help propel them further in the environment. Once they reach a favorable environment the haploid spores germinate and give rise to the next generation of gametophytes. Stomata appear in the hornworts and are abundant on the sporophyte. Because they are often found in nutrient-poor environments, many hornworts establish symbiotic relationships with cyanobacteria that fix nitrogen from the environment.

Review Question:

What features of hornworts are not present in liverworts? (Multiple Answers)
A) a sporophyte that is dependent on the gametophyte
B) psuedoelator cells that aid in spore dispersal
C) stomates
D) a flat haploid thallus

Mosses

The habitats of the 10,000+ moss species 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 that originate from the base of the gametophyte. These structures are not roots, as they are not involved in the uptake of water or nutrients. , 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.

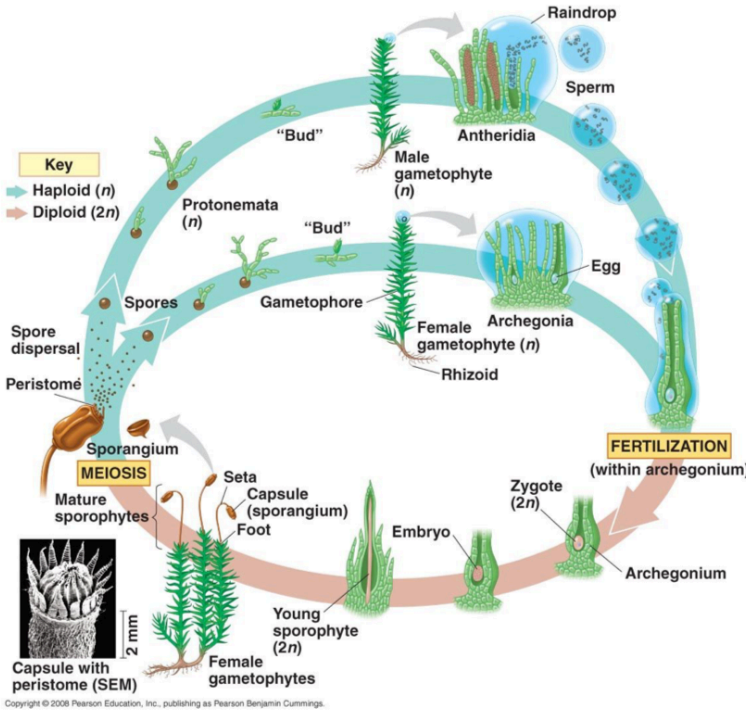

Figure 3. Moss lifecycles are similar to those of liverworts and hornworts. The key differences are in the specific structures involved.

In the moss lifecycle, the haploid gametophyte germinates from a haploid spore and forms first a **protonema**—usually, a tangle of single-celled filaments that hug the ground. Cells that function like 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 cells, 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.

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.

Review Question:

You may have noticed that some of these groups produce archegonia and antheridia on separate gametophytes. What are some of the advantages AND some of the disadvantages of this adaptation?

Summary

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 the release of spores away from the parent plant.

End of Section Review Questions:

Review: Shared features

1) **What is a common feature that the liverworts, hornworts and mosses share? (Multiple Answers)**

A) lack of true roots and leaves
B) sporophyte that is independent of the gametophyte
C) flagellated sperm

Review: Liverworts

2) **What are gemmae? (Multiple Answers)**

A) a means of sexual reproduction in liverworts
B) a cell or group of undifferentiated cells
C) a means of asexual reproduction

Review: Structures of Bryophytes

3) **Match the structure to the type of Bryophyte in which it is found**

1) protonema	A) Liverworts
2) rhizoids	B) Mosses
3) gemmae	C) Hornworts and Mosses
4) pseudoelators	D) Hornworts

Review: Adaptations to Land

4) **For each group indicate what adaptations they have that are related to terrestrial environments**

1) pores for gas exchange	A) Liverworts
2) stomata and pseudoelators	B) Hornworts
3) rhizoids and peristome	C) Mosses

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26.

Learning Goals

By the end of this reading you should be able to:

- Identify the adaptations to life on land that appear in seedless vascular plants
- Describe the classes of seedless tracheophytes
- Compare the lifecycle of seedless nonvascular and seedless vascular plants
- Explain the role of seedless plants in the ecosystem

Introduction

The vascular plants (also called tracheophytes) are the dominant and most conspicuous group of land plants. The 260,000+ species of tracheophytes compose greater 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. In this group, photosynthetic organs evolved to become leaves, and pipe-like cells evolved into vascular tissues that transport water, minerals, and fixed carbon throughout the organism.

One group of tracheophytes is the seedless vascular plants, in which the diploid sporophyte is the dominant phase of the lifecycle. The gametophyte in this group is an inconspicuous, but still independent, organism. Throughout plant evolution, there is a shift of roles in the dominant phase of the lifecycle; gametophytes in the non-vascular plants to sporophytes in the vascular plants. Like nonvascular plants, the seedless vascular plants still depend on water during fertilization, as the sperm must swim on a layer of moisture to reach the egg. This characteristic limits both of the groups to mainly moist environments.

Adaptations for Life on Land

Xylem

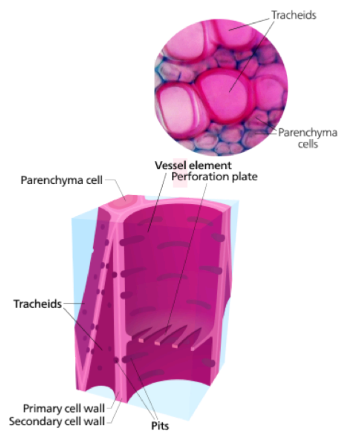

Figure 1. Xylem tissues are specially adapted to bulk flow of water. In addition, the cell walls are impregnated with lignin which provides needed support against gravity on land.

Xylem (Fig. 1) 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. When xylem cells are mature they are dead, meaning that the internal membrane and structures are lost, leaving just an empty tube. Xylem conductive cells incorporate the compound lignin into their walls and are thus described as lignified. Lignin is a complex polymer that is impermeable to water which “seals' the dead xylem cells and confers mechanical strength to vascular tissue. With their rigid cell walls, xylem cells provide support to the plant and allow the plant to grow upwards against the pull of gravity. Taller plants often 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 er plants cast their shadow on shorter plants and limit competition for light, water, and precious nutrients in the soil.

Phloem

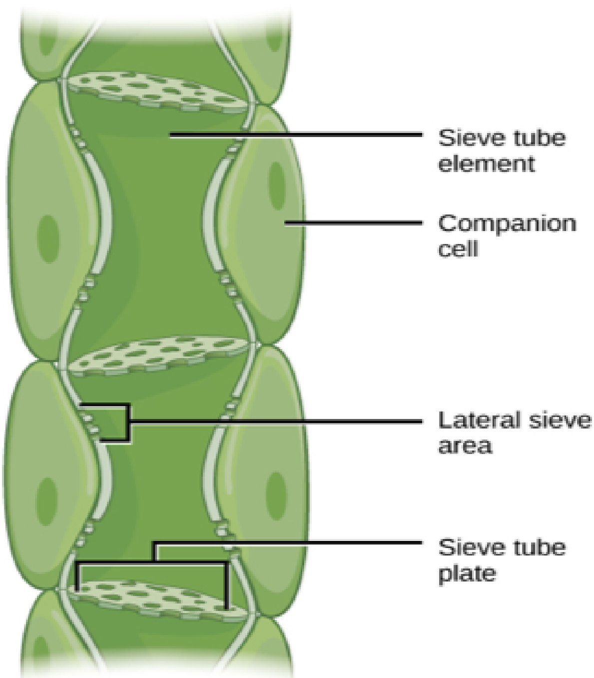

Figure 2. Phloem cells are specifically adapted to bulk flow of sugars and other nutrients.

Phloem (Fig. 2) 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 (companion cells). Unlike xylem, phloem consists of living cells that are connected by highly developed pores. In order to aid in the transport of materials, mature conducting cells often lack a nucleus and other internal organelles and must rely on nearby cells for needed proteins. Without the internal organelles, the flow of materials is unimpeded and therefore more efficient.

Roots

Roots (Fig. 3) 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 mosses (nonvascular plants) 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 taller plants by acting as a ballast or anchor.

Figure 3. Roots provide both an anchor as well as increased surface area for absorption of water and nutrients.

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.

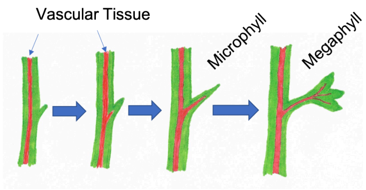

Figure 4. Leaves evolved as a result of changes in vascular tissue morphology. The increased vasculature allowed increased surface areas for photosynthesis

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. 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 (Fig. 4). 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 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.

Review Question:

What are considered to be evolutionary adaptations of vascular plants to life on land?
A) xylem and phloem
B) roots
C) leaves
D) spore production
How did the evolution of a vascular system allow an increase in plant size? Be sure to provide information that supports your assertion.

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 is the dominant phase of the lifecycle. Water is still required for the 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, quillworts and spike mosses

Figure 5. Club moss with strobili.

The Lycophytes, which are not true mosses, are the earliest group of seedless vascular plants. They dominated the landscape of the Carboniferous, growing as tall as trees and forming large swamp forests. Today's club mosses. however, are small, evergreen plants consisting of a stem (which may be branched) and microphylls. The phylum Lycopodiophyta consists of close to 1,200 species, including the quillworts (*Isoetales*), the club mosses (*Lycopodiales*) (Fig. 5), and spike mosses (*Selaginellales*) (Fig. 6).

Figure 6. Left image: Quillwort-Isoetes bolanderi (Bolander's quillwort) Right Image: Spike Moss-Selaginella kraussiana (Krauss' spike moss).

Lycophytes display an alternation of generations in which the sporophyte is the major stage of the lifecycle. In addition, the gametophytes grow separately and thus do not depend on the sporophyte for nutrients. There are some species of Lycophyte in which the gametophytes develop underground and form mycorrhizal associations with fungi. Lycophyte species can be homosporous, producing only one type of spore or heterosporous, producing two different types of spores. In club mosses, the sporophyte gives rise to sporophylls arranged in strobili, cone-like structures that give the class its name.

Phylum Monilophyta: Class Equistopsida (Horsetails)

Figure 7. Horsetails have modified leaves, this is the fringe around the stem in this image. The stem is characterized by obvious joints (nodes).

Horsetails (Fig. 7), whisk ferns and ferns belong to the phylum Monilophyta, with horsetails placed in the Class Equisetopsida. There is only a single genus *Equisetum* that is the survivor of a large group of plants, known as Arthrophyta. During the Carboniferous period this group, like the Lycophytes, produced large plants and entire swamp forests. Today's *Equisetum*(Horsetail) plants are usually found in damp environments and marshes and have a unique morphology. The stem of a horsetail is characterized by the presence of joints or nodes, hence the name Arthrophyta (arthro- = "joint"; -phyta = "plant"). Modified 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. Another unique feature is that silica collects in the epidermal cells of these plants, contributing to the stiffness of horsetail plants. Underground stems are known as rhizomes anchor the plants to the ground. Modern-day horsetails are homosporous, producing bisexual gametophytes.

Phylum Monilophyta: Class Psilotopsida (Whisk Ferns)

Figure 8. Whiskfern (Psilotum nudum)

While most ferns form large leaves and branching roots, the whisk ferns (Fig. 8), Class Psilotopsida, lack both roots and leaves. Photosynthesis takes place in their green stems, while water and mineral absorption occur in the horizontal underground rootlike stems (rhizomes)that have mycorrhizal associations with fungi. Small yellow knobs form at the tip of the branch stem and contain the sporangia. There are two phases in the life cycle of a whisk fern. The large asexual plants (sporophytes) produce spores that develop into very small colorless gametophytes, which are similar to rhizomes in overall appearance. Eggs and sperm are produced in special structures on the gametophyte. The union of these gametes initiates the sporophyte phase. Whisk ferns were considered an early pterophyte. However, recent comparative DNA analysis suggests that this group may have lost both leaves and roots through evolution, and are most closely related to ferns.

Phylum Monilophyta: Class Psilotopsida (Ferns)

With their large fronds, ferns (Fig. 9) are the most readily recognizable seedless vascular plants. They are considered the most complex seedless vascular plants and display characteristics commonly observed in seed plants. 20,000+ species of ferns live in environments ranging from tropics to temperate forests. Although some species survive in dry environments, most ferns are restricted to moist, shaded places. Ferns made their appearance in the fossil record during the Devonian period and expanded during the Carboniferous.

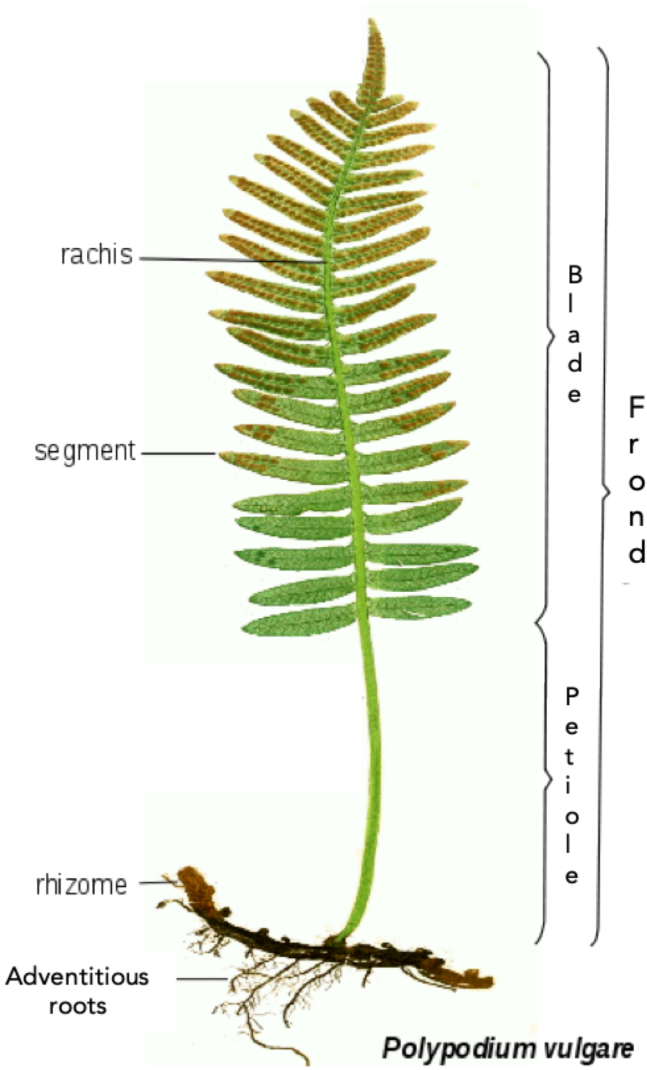

Figure 9. The megaphylls (fronds) of ferns increased the surface area for both photosynthesis and spore production.

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. Adventitious organs are those that grow in unusual places, such as roots growing from the side of a stem.

In some fern species, the tip of a developing fern frond is rolled into a crozier or fiddlehead. Fiddleheads unroll as the frond develops. 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 (Fig. 10). Inside the sori, spores are produced by meiosis and released into the air.

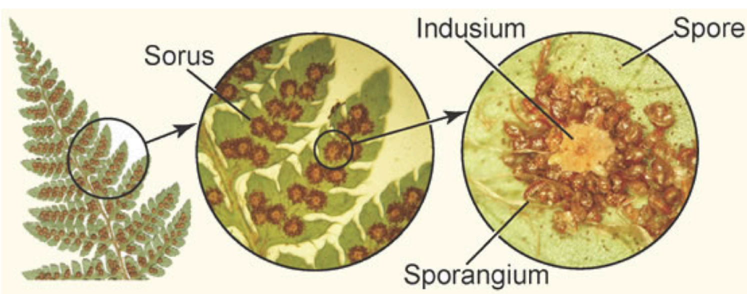

Figure 10. Sori (plural of sorus) contain large numbers of sporangium that produce spores.

Those that land on a suitable substrate germinate and form a heart-shaped gametophyte, which is attached to the ground by thin filamentous rhizoids. 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. Each gametophyte only produces one sporophyte but each sporophyte produces millions of spores.

Summary

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.

The seedless plants (nonvascular and vascular) 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 succession to occur. They contribute to the enrichment of the soil and provide shelter and nutrients for animals in hostile environments.

End of Section Review Questions:

Review: Adaptations to life on land
Which of the following traits of land plants allows them to grow

in height?
A) alternation of generations
B) production of leaves
C) lignin in tracheid cell walls
D) sporopollenin in spore cell walls
Review: Evolution of leaves
Microphylls are characteristic of which types of plants?
A) mosses
B) liverworts
C) club mosses
D) ferns
Review: Fern Life Cycles
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.
Review: Fern Structures
The following structures are found on the underside of fern fronds and are involved in spore production?
A) adventitious tissues
B) rhizomes
C) sori
D) archegonia
Review: Seedless Vascular Plant Life Cycles
The dominant phase of the seedless vascular plants is?
A) antheridia
B) spore
C) gametophyte
D) sporophyte

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Figure 3. Image courtesy of RoRo [CC0]

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27.

Learning Goals

By the end of this reading you should be able to:

- Identify the adaptations to life on land that appear in seedless vascular plants
- Describe the classes of seedless tracheophytes
- Compare the lifecycle of seedless nonvascular and seedless vascular plants
- Explain the role of seedless plants in the ecosystem

Introduction

The vascular plants (also called tracheophytes) are the dominant and most conspicuous group of land plants. The 260,000+ species of tracheophytes compose greater 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. In this group, photosynthetic organs evolved to become leaves, and pipe-like cells evolved into vascular tissues that transport water, minerals, and fixed carbon throughout the organism.

One group of tracheophytes is the seedless vascular plants, in which the diploid sporophyte is the dominant phase of the lifecycle. The gametophyte is this group is an inconspicuous, but still independent, organism. Throughout plant evolution, there is a shift of roles in the dominant phase of the lifecycle; gametophytes in the non-vascular plants to sporophytes in the vascular plants. Like nonvascular plants, the seedless vascular plants still depend on water during fertilization, as the sperm must swim on a layer of moisture to reach the egg. This characteristic limits both of the groups to mainly moist environments.

Adaptations for Life on Land

Xylem

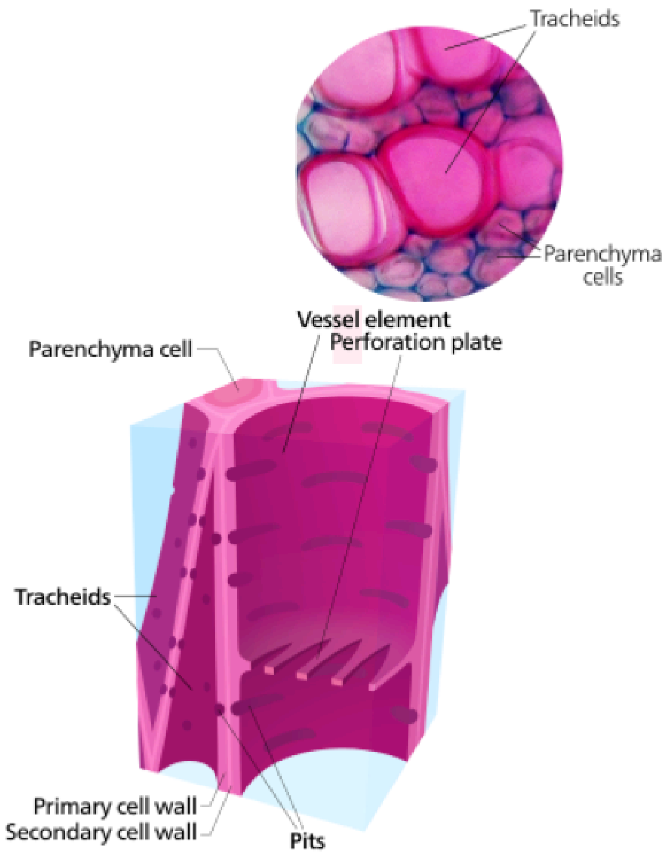

Figure 1. Xylem tissues are specially adapted to the bulk flow of water. In addition, the cell walls are impregnated with lignin which provides needed support against gravity on land.

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 (Fig. 1). When xylem cells are mature they are dead, meaning that the internal membrane and structures are lost, leaving just an empty tube. Xylem conductive cells incorporate the compound lignin into their walls and are thus described as lignified. Lignin is a complex polymer that is impermeable to water which "seals' the dead xylem cells and confers mechanical strength to vascular tissue. With their rigid cell walls, xylem cells provide support to the plant and allow the plant to grow upwards against the pull of gravity. Taller plants often 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 er plants cast their shadow on shorter plants and limit competition for light, water, and precious nutrients in the soil.

Phloem

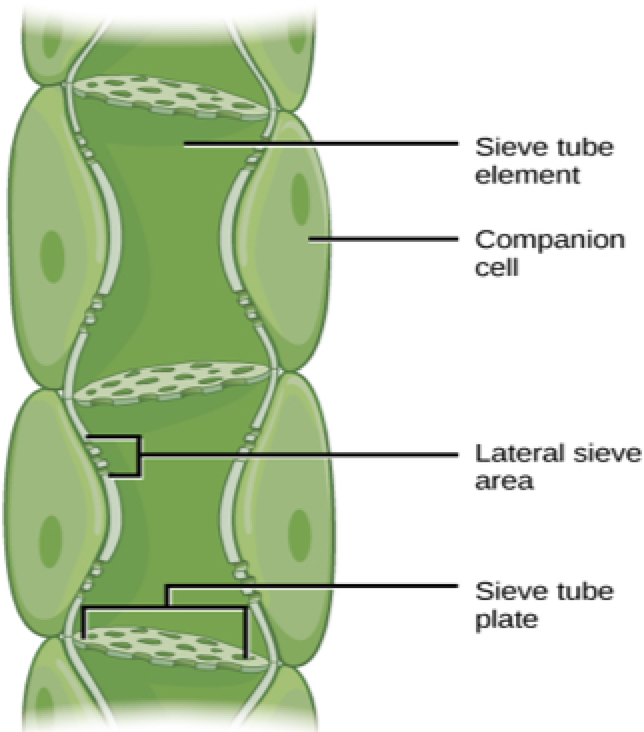

Figure 2. Phloem cells are specifically adapted to the bulk flow of sugars and other nutrients.

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 (companion cells) (Fig. 2). Unlike xylem, phloem consists of living cells that are connected by highly developed pores. In order to aid in the transport of materials, mature conducting cells often lack a nucleus and other internal organelles and must rely on nearby cells for needed proteins. Without the internal organelles, the flow of materials is unimpeded and therefore more efficient.

Roots

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 mosses (nonvascular plants) 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.

Figure 3. Roots provide both an anchor as well as increased surface area for the absorption 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 taller plants by acting as a ballast or anchor (Fig. 3).

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.

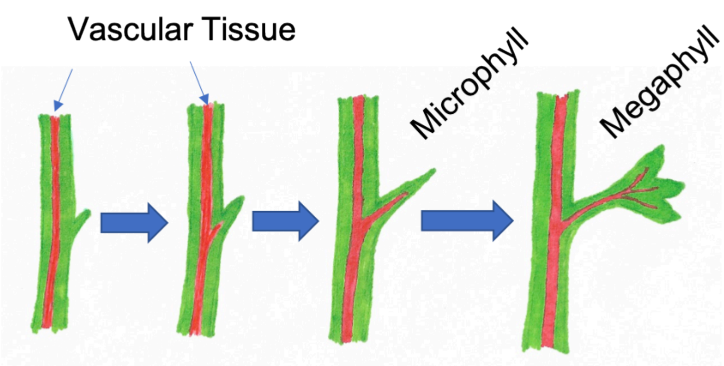

Figure 4. Leaves evolved as a result of changes in vascular tissue morphology. The increased vasculature allowed increased surface areas for photosynthesis

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. A microphyll is small and has a simple vascular system (Fig. 4). 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.

Review Question:

What are considered to be evolutionary adaptations of vascular plants to life on land? (Multiple Answers)

A) xylem and phloem
B) roots
C) leaves
D) spore production

Thinking Question:

How did the evolution of a vascular system allow an increase in plant size? Be sure to provide information that supports your assertion.

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 is the dominant phase of the lifecycle. Water is still required for the 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, quillworts, and spike mosses

Figure 5. Club moss with strobili

The Lycophytes, which are not true mosses, are the earliest group of seedless vascular plants. They dominated the landscape of the Carboniferous, growing as tall as trees and forming large swamp forests. Today's club mosses. however, are small, evergreen plants consisting of a stem (which may be branched) and microphylls. The phylum Lycopodiophyta consists of close to 1,200 species, including the quillworts (*Isoetales*), the club mosses (*Lycopodiales*), and spike mosses (*Selaginellales*).

Figure 6. Left image: Quillwort – Isoetes bolanderi (Bolander's quillwort) Right Image: Spike Moss – Selaginella kraussiana (Krauss' spike moss)

Lycophytes display an alternation of generations in which the sporophyte is the major stage of the lifecycle. In addition, the gametophytes grow separately and thus do not depend on the sporophyte for nutrients. There are some species of Lycophyte in which the gametophytes develop underground and form mycorrhizal associations with fungi. Lycophyte species can be homosporous, producing only one type of spore or heterosporous, producing two different types of spores. In club mosses, the sporophyte gives rise to sporophylls arranged in strobili, cone-like structures that give the class its name.

Review Question:

Lycophytes are the only modern group of plants with __________.
The ___________ is the dominant phase of their lifecycle.
Some species are ___________ producing only one type of spore while others are ___________.
Word Bank: gametophyte, sporophyte, spore, megaphyll, microphyll, diasporous, homosporous, heterosporous

Phylum Monilophyta: Class Equistopsida (Horsetails)

Figure 7. Horsetails have modified leaves, this is the fringe around the stem in this image. The stem is characterized by obvious joints (nodes).

Horsetails, whisk ferns and ferns belong to the phylum Monilophyta, with horsetails placed in the Class Equisetopsida. There is only a single genus *Equisetum* that is the survivor of a large group of plants, known as Arthrophyta. During the Carboniferous period this group, like the Lycophytes, produced large plants and entire swamp forests. Today's *Equisetum*(Horsetail) plants are usually found in damp environments and marshes and have a unique morphology. The stem of a horsetail is characterized by the presence of joints or nodes, hence the name Arthrophyta (arthro- = "joint"; -phyta = "plant"). Modified 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. Another unique feature is that silica collects in the epidermal cells of these plants, contributing to the stiffness of horsetail plants. Underground stems are known as rhizomes anchor the plants to the ground. Modern-day horsetails are homosporous, producing bisexual gametophytes.

Phylum Monilophyta: Class Psilotopsida (Whisk Ferns)

Figure 8. Whiskfern (Psilotum nudum)

While most ferns form large leaves and branching roots, the whisk ferns, Class Psilotopsida, lack both roots and leaves. Photosynthesis takes place in their green stems, while water and mineral absorption occur in the horizontal underground rootlike stems (rhizomes)that have mycorrhizal associations with fungi. Small yellow knobs form at the tip of the branch stem and contain the sporangia. There are two phases in the life cycle of a whisk fern. The large asexual plants (sporophytes) produce spores that develop into very small colorless gametophytes, which are similar to rhizomes in overall appearance. Eggs and sperm are produced in special structures on the gametophyte. The union of these gametes initiates the sporophyte phase. Whisk ferns were considered early pterophytes. However, recent comparative DNA analysis suggests that this group may have lost both leaves and roots through evolution, and are most 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 complex seedless vascular plants and display characteristics commonly observed in seed plants. 20,000+ species of ferns live in environments ranging from tropics to temperate forests. Although some species survive in dry environments, most ferns are restricted to moist, shaded places. Ferns made their appearance in the fossil record during the Devonian period and expanded during the Carboniferous.

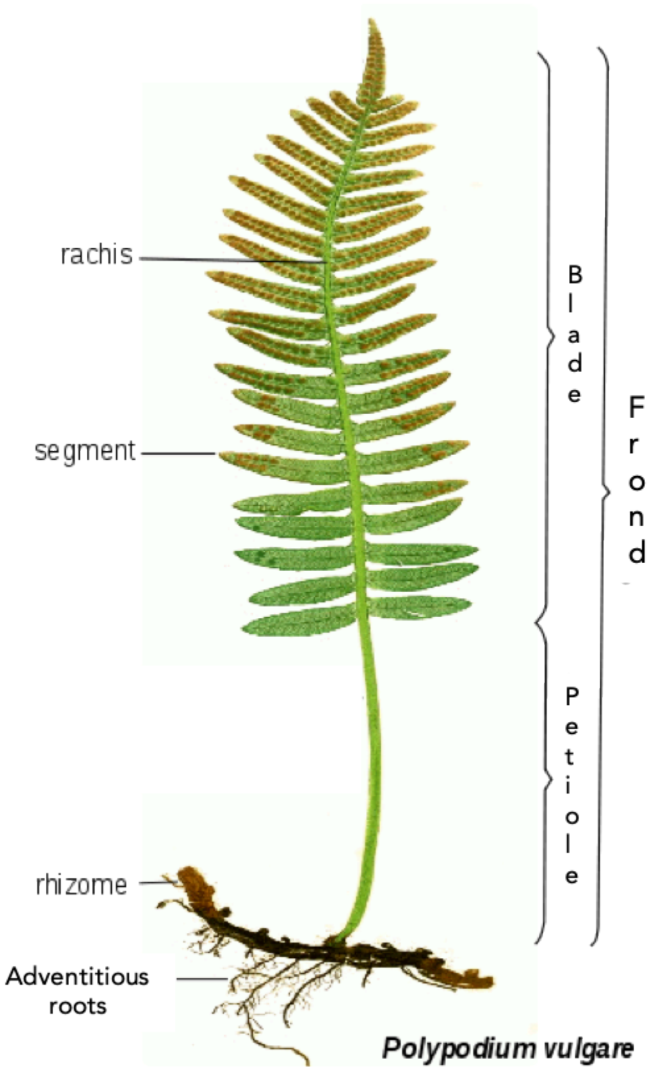

Figure 9. The megaphylls (fronds) of ferns increased the surface area for both photosynthesis and spore production

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. Adventitious organs are those that grow in unusual places, such as roots growing from the side of a stem.

In some fern species, the tip of a developing fern frond is rolled into a crozier or fiddlehead. Fiddleheads unroll as the frond develops. 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. Inside the sori, spores are produced by meiosis and released into the air.

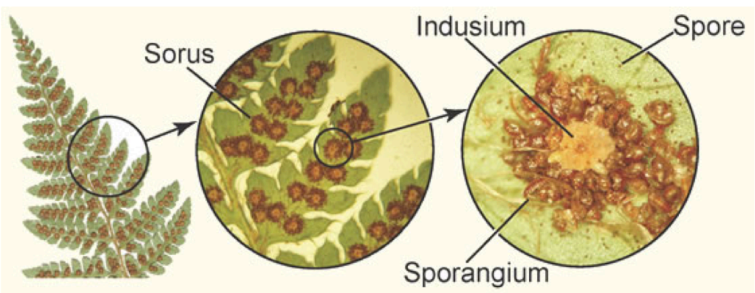

Figure 10. Sori (plural of sorus) contain large numbers of sporangium that produce spores.

Those that land on a suitable substrate germinate and form a heart-shaped gametophyte, which is attached to the ground by thin filamentous rhizoids. 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. Each gametophyte only produces one sporophyte but each sporophyte produces millions of spores.

Review Question:

The sporophyll(s) of a fern are? (Multiple Answers)
A) photosynthetic organs
B) reproductive organs
C) composed of haploid tissue
D) dependent on the gametophyte
E) the dominant phase of the fern life cycle

Summary

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.

The seedless plants (nonvascular and vascular) 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 succession to occur. They contribute to the enrichment of the soil and provide shelter and nutrients for animals in hostile environments.

End of Section Review Questions:

Review: Adaptations to life on land

1) **Which of the following traits of land plants allows them to grow in height?**

A) alternation of generations
B) production of leaves
C) lignin in tracheid cell walls
D) sporopollenin in spore cell walls

Review: Evolution of leaves

2) **Microphylls are characteristic of which types of plants?**

A) mosses
B) liverworts
C) club mosses
D) ferns

Review: Fern LifeCycles

3) **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.

Review: Fern Structures

4) **The following structures are found on the underside of fern fronds and are involved in spore production?**

A) adventitious tissues
B) rhizomes
C) sori

D) archegonia

Review: Seedless Vascular Plant Life Cycles
5) **The dominant phase of the seedless vascular plants is?**
A) anteridia
B) spore
C) gametophyte
D) sporophyte

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28.

Learning Goals

By the end of this reading you should be able to:

- Explain when seed plants first appeared and when gymnosperms became the dominant plant group
- Describe the two major innovations that allowed seed plants to reproduce in the absence of water
- Discuss the purpose of pollen grains and seeds
- Discuss the type of seeds produced by gymnosperms, as well as other characteristics of gymnosperms

Introduction

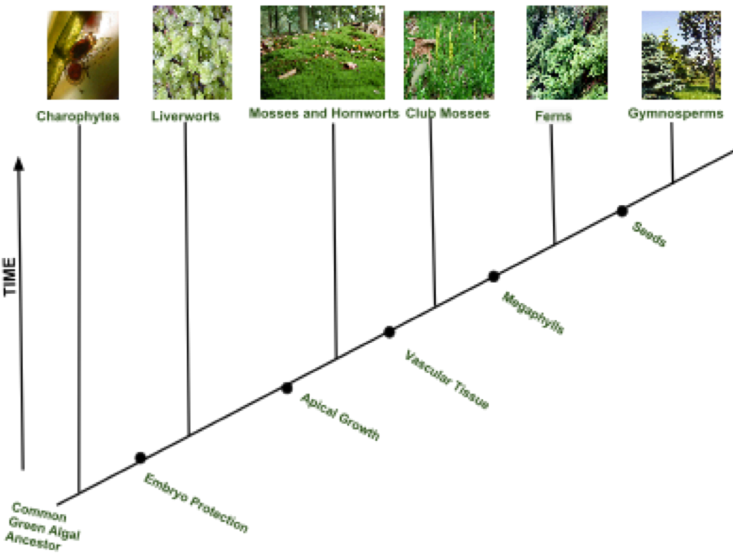

Figure 1. Evolution of Gymnosperms from Green Algae

In seed plants (Fig. 1), 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.

The first naked seed plants (progmnosperms), arose about 380 million years ago and 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, the progymnosperms still reproduced like ferns, releasing spores into the environment.

Two critical adaptations to dry land

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.

Pollen: The **pollen grains** are male gametophytes that contain the sperm (gametes) of the plant and are carried by the wind, water, or a pollinator. 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 and can reach the female organs without dependence on water. Male gametes reach the female gametophyte and the egg cell gamete through a pollen tube: an extension of a cell within the pollen grain. The sperm of ost modern gymnosperms lack flagella, except in cycads and the *Gingko*, where the sperm still possess flagella that allow them to swim down the **pollen tube** to the female gamete.

Seeds: Unlike bryophyte and fern spores (which are single haploid cells dependent on moisture for the rapid development of gametophytes), **seeds** contain a multicellular diploid embryo that will germinate into a sporophyte (Fig. 2). 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.

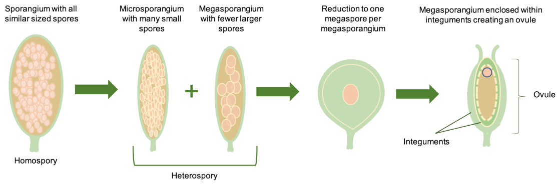

Figure 2. Evolution of the seed from a megasporangium reduced to contain only one megaspore to the enclosing of the megasporangium within integuments to form the ovule.v

The seed coat provides several layers of hardened tissue around the embryo that prevents desiccation and frees 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. Within the seed and surrounding the embryo are storage tissues that provide the embryo with needed nutrients when it begins to germinate and before it becomes photosynthetically active.

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. Seeds, therefore, allow plants to disperse the next generation through both space and time. With such evolutionary advantages, seed plants(Gymnosperms and Angiosperms) have become the most successful and familiar group of plants, in part because of their size and their vast diversity and distribution.

Review Question:

What are some of the advantages of seeds over spores? (Multiple Answers)A) they have mechanisms to prevent desiccation and spores do not
B) they are multicellular while spores are single cells
C) they contain nutrient stores which spores do not have
D) they are composed of haploid cells and spores are diploid

Key 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. The shared characteristics of this group include naked seeds, separate female and male gametes, pollination by wind, and tracheids (which transport water and solutes in the vascular system).

Most Gymnosperms are adapted to live where freshwater 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. Many evergreen conifers are capable of low levels of photosynthesis during the cold months, and because of this, they can take advantage of the first sunny days of spring. However, evergreen conifers can be more susceptible than deciduous trees to infestations because these conifers do not lose their leaves all at once. They cannot, therefore, shed parasites and restart with a fresh supply of leaves in spring.

Gymnosperm seeds are not enclosed in an ovary like seeds of Angiosperms; rather, they are exposed on cones or modified leaves. These cones are composed of specialized sporophylls tightly arranged around a central stalk.

Life Cycle of a Conifer

The life cycle of a conifer can be seen in Figure 3. 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 staminate cones, the microsporocytes give rise to pollen grains (microspores) by meiosis. These cones release large amounts of yellow pollen that is readily carried by the wind. Some of the pollen grains, containing the male gametophytes will land on a female cone. When the initiation of a pollen tube begins then pollination has occurred. The pollen tube develops slowly, and a specialized 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 to create the diploid zygote.

Female ovulate cones, or, contain two ovules per scale. One megaspore mother cell, the megasporocyte, undergoes meiosis in each ovule producing four spore cells. Three of the four cells break down and the single surviving cell develops into a female multicellular gametophyte which encloses the

archegonium

. Upon fertilization, the diploid zygote will give rise to the embryo 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.

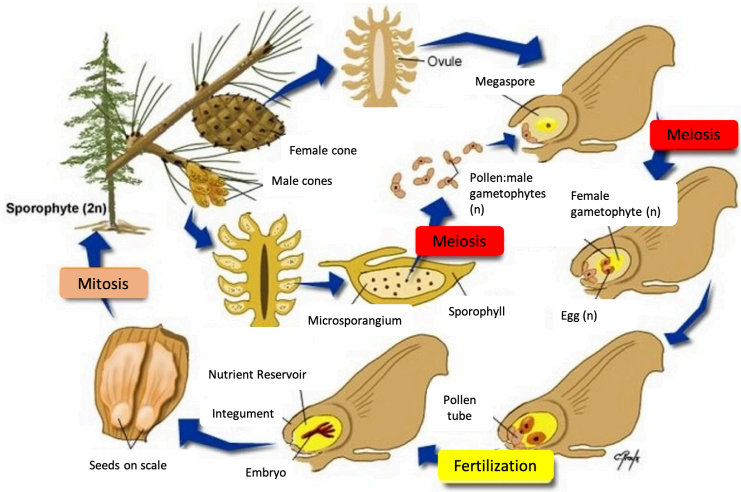

Figure 3. The representative life cycle of a pine tree.

Review 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

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 is considered the closest group to angiosperms because they produce true xylem tissue.

Conifers (Coniferophyta)

Figure 4. 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) coastal redwood or sequoia Sequoia sempervirens, and (d) the tamarack Larix larcinia. Notice the deciduous 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 Micky Zlimen)

Conifers are the dominant phylum of gymnosperms, with the most variety of species (Fig. 4). 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 the 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 the fall. The European larch and the tamarack are examples of deciduous conifers. 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 "softwood."

Cycads

Figure 5. Cones of a female Modjadji cycad in Manie van der Schijff Botanical Garden at the University of PretoriaImage courtesy of JMK [CC BY-SA 3.0 (https://creativecommons.org/licenses/by-sa/3.0)]

Cycads thrive in mild climates and are often mistaken for palms because of the shape of their large, compound leaves (Fig. 5). Cycads bear large cones and may be pollinated by beetles rather than wind: unusual for a gymnosperm. They dominated the landscape during the age of dinosaurs in the Mesozoic, but only a hundred or so species persisted to modern times. They face possible extinction, and several species are protected through international conventions. Because of their attractive shape, they are often used as ornamental plants in gardens in the tropics and subtropics.

Gingkophytes

Figure 6. Gingko trees are unique Gymnosperms that are deciduous with fan-shaped leaves.

The single surviving species of the **gingkophytes** group is the *Gingko biloba* (Fig. 6). 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.

Gnetophytes

Figure 7. A female specimen of Welwitschia mirabilis

Gnetophytes are the closest relative to modern angiosperms and include three dissimilar genera of plants: *Ephedra*, *Gnetum*, and *Welwitschia* (Fig. 7). 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.

Summary

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.

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 altitudes and latitudes. Cycads (phylum Cycadophyta) resemble palm trees and grow in tropical climates. *Gingko Biloba* is the only representative of the phylum Gingkophyta. The last phylum, Gnetophyta, is a diverse group of shrubs that produce vessel elements in their wood.

Review Questions

Review: Seed Plant Characteristics

1) **Seed plants are?**

A) all homosporous.

B) mostly homosporous with some heterosporous.

C) mostly heterosporous with some homosporous.

D) all heterosporous.

Review: Gymnosperm Characteristics

2) **Which of the following traits characterizes gymnosperms?**

A) The plants carry exposed seeds on modified leaves.

B) Reproductive structures are located in a flower.

C) After fertilization, the ovary thickens and forms a fruit.

D) The gametophyte is the longest phase of the life cycle.

Review: Life Cycle Features

3) **Megasporocytes will eventually produce which of the following?**

A) pollen grain

B) sporophytes

C) male gametophytes

D) female gametophytes

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29.

Learning Goals

By the end of this reading you should be able to:

- Explain why angiosperms are the dominant form of plant life in most terrestrial ecosystems
- Describe the main parts of a flower and their purposes
- Detail the life cycle of an angiosperm
- Discuss the two main groups of flowering plants

Introduction

Undisputed fossil records place the massive appearance and diversification of angiosperms in the middle to the late Mesozoic era. Angiosperms ("seed in a vessel") produce a flower containing male and/or female reproductive structures. Fossil evidence indicates that flowering plants first appeared in the Lower Cretaceous, about 125 million years ago, and were rapidly diversifying by the Middle Cretaceous, about 100 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 (Fig. 1).

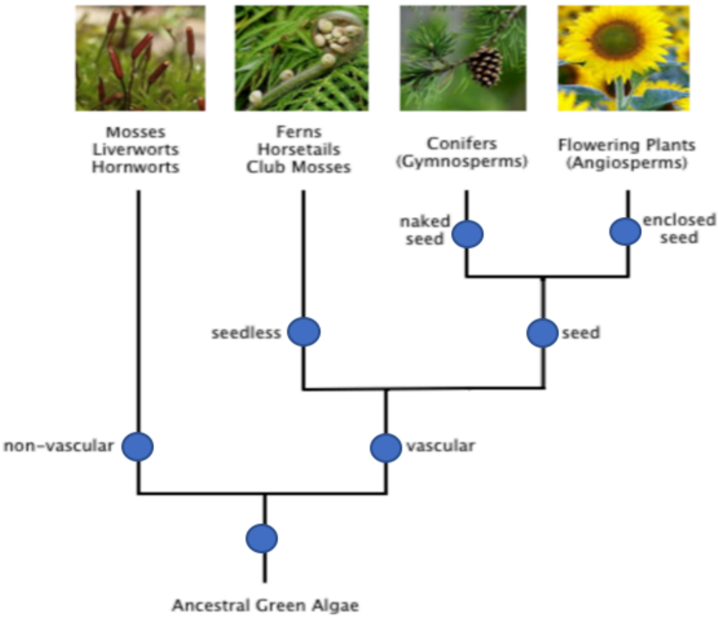

Figure 1. Phylogenetic tree of land plants indicating key evolutionary adaptations to life on land

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 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 descendants) that developed in parallel with the gymnosperms.

From their humble and still obscure beginning during the early Jurassic period, the angiosperms—or flowering plants—have evolved to dominate most terrestrial ecosystems. With more than 250,000 species, the angiosperm phylum (Anthophyta) is second only to insects in terms of diversification. The success of angiosperms is due to two novel reproductive structures: flowers and fruit. 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.

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

Flowers: Angiosperms produce their gametes in separate organs, which are usually housed in a flower (Fig. 2). 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.

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.

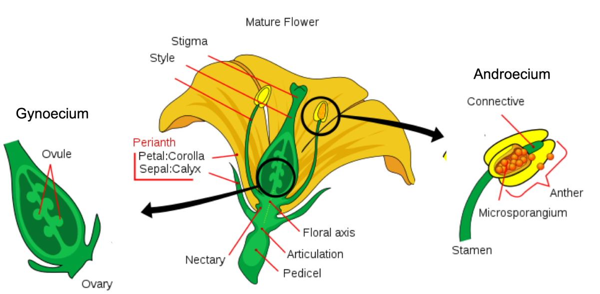

Figure 2. Diagram of a typical flower containing both male and female reproductive tissues.

Styles, stigmas, and ovules constitute the female organ: the gynoecium or carpel. The 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.

Review Question:

Which of the following structures in a flower is not directly involved in reproduction?
A) the style
B) the stamen
C) the sepal
D) the anther

Fruit: Following fertilization of the egg, the ovule grows into a seed (Fig. 3). 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.

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 a 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.

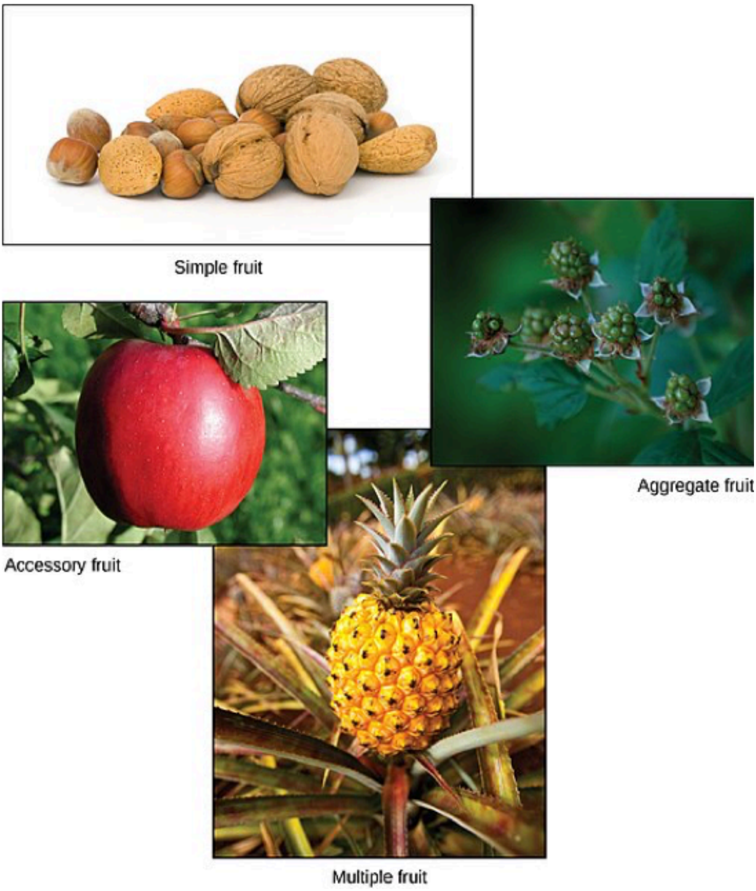

Figure 3. Fruits develop from the ovary which surrounds the seed. Some fruits also encase the pericarp and receptacle of the floral structure.

Mature fruit can be fleshy or dry. Fleshy fruit includes 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. The 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 (Fig. 4). Like gymnosperms, angiosperms are heterosporous. Therefore, they generate microspores, which will generate pollen grains as the male gametophytes, and megaspores, which will form an ovule that contains female gametophytes. Inside the anthers' microsporangia, male gametophytes divide by meiosis to generate haploid microspores, which, in turn, undergo mitosis and give rise to pollen grains. Each pollen grain contains two cells: one generative cell that will divide into two sperm and a second cell that will become the pollen tube cell.

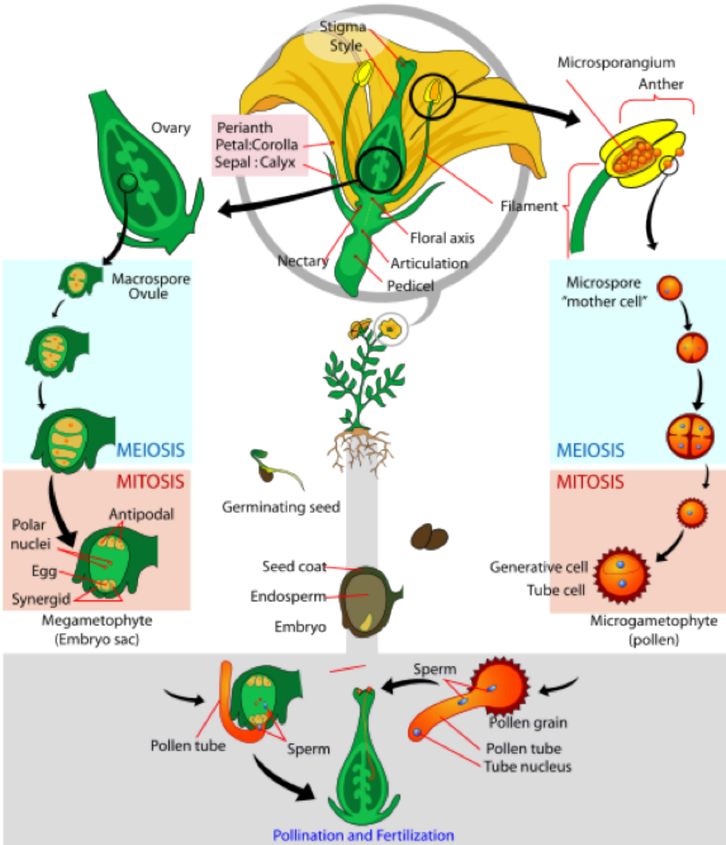

Figure 4. The life cycle of a typical Angiosperm

If a flower lacked a megasporangium, what type of gamete would not form? If the flower lacked a microsporangium, what type of gamete would not form? 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 2n 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 2n polar nuclei, forming a triploid cell that will develop into the endosperm, which is the 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. 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.

Review Question:

Which of the following do monoecious flowers contain?
A) both male and female parts
B) only male parts
C) only female parts

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 (Fig. 5). 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.

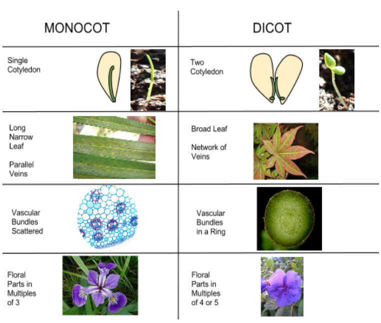

Figure 5. Key characteristics that separate monocots and dicots

Basal Angiosperms

The Magnoliidae are represented by the magnolias: tall trees bearing large, fragrant flowers that have many parts and are considered archaic. 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, spicebush, and avocado tree. The *Nymphaeales* are comprised of the water lilies, lotus, 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 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* are the familiar black peppercorns that are used to flavor many dishes.

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 modern monocots. The vascular tissue of the stem is not arranged in any particular pattern. The root system is mostly adventitious and unusually positioned, with no major taproot. 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

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, the 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. 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.

Review Question:

Which of these is a trait that is found in monocots and not dicots?
A) floral parts in 4s or 5s or whorls
B) a single cotyledon
C) Network of fibrous roots
D) ring pattern in vascular tissue

Summary

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.

End of Section Review Questions:

Review: Adaptations to land

1) **Besides the seed, what other major structure diminishes a plant's reliance on water for reproduction?**

A) flower
B) fruit
C) pollen

D) spore

Review: Floral Structures

2) **Pollen grains develop in which structure?**

A) the anther
B) the stigma
C) the filament
D) the carpel

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30.

Learning Goals

By the end of this reading you should be able to:

- Describe the modular nature of plant structure
- Explain the role of the apical meristem in plant growth patterns
- Describe how gene expression controls plant growth patterns

Introduction

In tropical forests, vines weave their way upward through the branches of trees. Many of these vines have long, thin stems with widely spaced leaves (Fig 1. a). In contrast, a barrel cactus, living in the desert, has thick stems and leaves modified to form sharp spines (Fig. 1. b). Although they look nothing alike, these two plants are constructed in the same way. Plant shoots are modular, meaning that they are formed of repeating units. Each unit consists of a node, the point where one or more leaves are attached, and an internode, the segment between two nodes (Fig. 1. c).

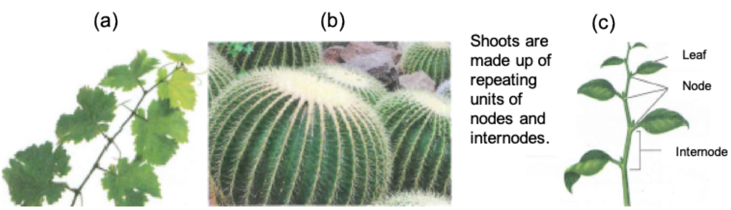


Figure 1. Shoot organization. A grape vine (a) and barrel cacti (b) look very different, but their shoot systems are built from the same repeating units of nodes and internodes (c).

In vines the internodes are long and the leaves large, whereas in cacti the internodes are short and the leaves thin and sharp. The modular nature of plants helps us understand how the capacity for continued growth gives rise to the tremendous variation in plant form that we see around us.

Shoots grow by adding new cells at their tips.

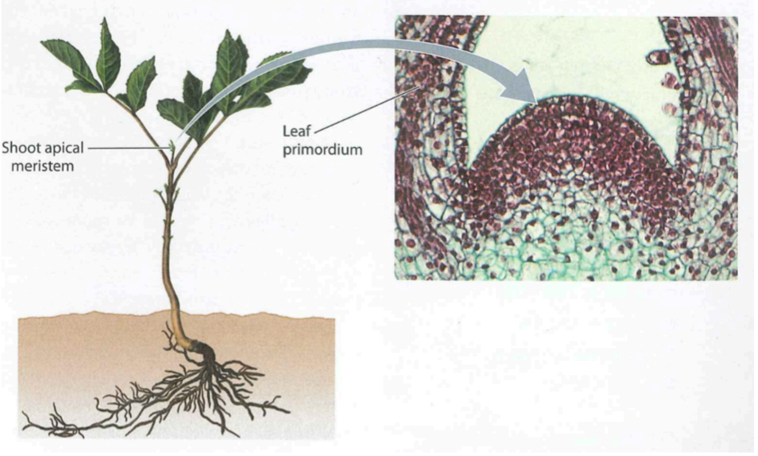


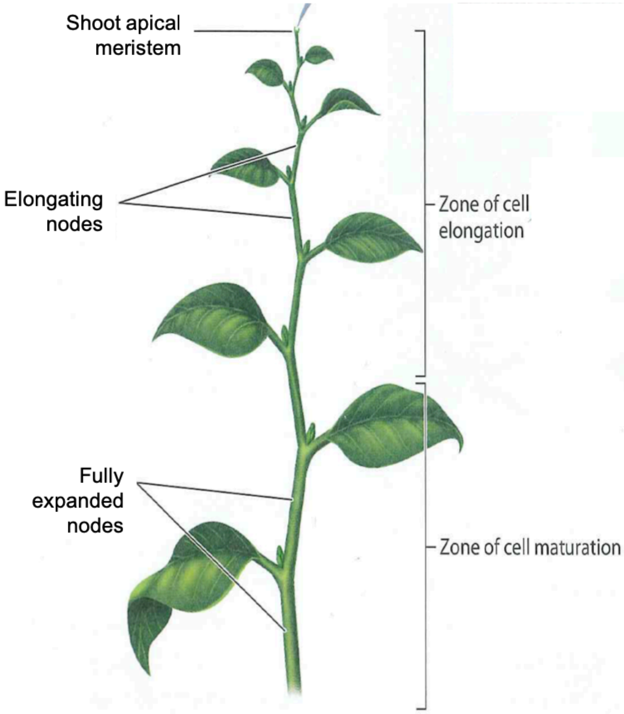
Figure 2. At the tip of the shoot is an apical meristem that gives rise to new plant tissues.

At the very tip of each branch, commonly hidden beneath an array of young leaves called leaf primordia (singular, primordium), lies a tiny dome of cells called the shoot apical meristem (Fig. 2). The shoot apical meristem is a group of totipotent cells that, like embryonic stem cells in animals, gives rise to new tissues. Plants have meristems in several parts of their bodies, but upward growth occurs exclusively in and just below the shoot apical meristem. This is where cell division occurs, generating all the new cells that serve to elongate stems. The shoot apical meristem also initiates leaves and produces new meristems, which allow plants to branch. Some plants have more than one apical meristem, as there is one at the tip of each growing shoot.

An important characteristic of the shoot-meristem is that it maintains a constant size even though it is a region of active cell division. As new cells are added near the shoot tip, cells that are farther from the shoot tip cease to divide. This means that some of the cells of the meristem are constantly being lost as they are pushed outward during division while others in the primordium are retained. The cells that are within the meristem maintain their totipotency by the expression of meristem identity genes, genes that contribute to meristem stability and function. The expression of these meristem identity genes is controlled by a network of chemical signals produced by cells at the very tip of the stem. Because these signals can be diffuse only over a limited distance, only the cells close to the shoot tip express meristem identity genes. Thus only these cells retain their totipotency and continue to give rise to new cells.

Stem elongation occurs primarily in a zone just below the apical meristem

In animals, cell division and cell enlargement typically go hand in hand. In plants, most of the increase in cell size occurs after mitotic cell division is complete. Cells that are too far from the shoot tip to receive the needed chemical signals do not express meristem identity genes and thus cease to divide. However, they do continue to grow in size. This results in a zone of cell elongation located just beneath the shoot apical meristem(the zone of cell division). It is here that most of the elongation of stems occurs. Without cell elongation all the cells in the stem of a redwood tree would remain the size they were when they left the zone of cell division and the tree would be less than 5 m tall.



In the zone of cell elongation, each cell grows many times more in length than in width. The reason is that the strong cellulose microfibrils wrapped around the cell make it difficult for the cell to expand in girth. However, the cellulose is looser along the length of the cell, allowing the cell to expand in length. The large central vacuole that characterizes mature plant cells forms when the cell is in the zone of cell elongation. In fact, most of the increase in cell volume is due to the uptake of water and solutes that fill the vacuole. This explains in part why plant growth is markedly reduced during periods of drought.

Farther from the shoot tip, cells reach their final size and complete their differentiation into the mature cell types in leaves and stems.

This organization into successive zones of cell division, cell elongation, and cell maturation allows stems to grow without any predetermined limit to their length. It also means that the time course of development can be determined by moving along the stem from the tip toward the base(the tip is the youngest tissue and the base is the oldest).

Once cells have matured, they no longer expand. Thus, during the upward growth of the shoot, it is the production and elongation of cells at the shoot tip that lifts the meristem ever higher into the air. Imagine that, as a 10-year-old, you carved your initials into a tree. Twenty years later, your initials will be exactly the same distance from the ground as they were on the day you inscribed them.
Quick Review: Plant Growth

Show Correct Answer

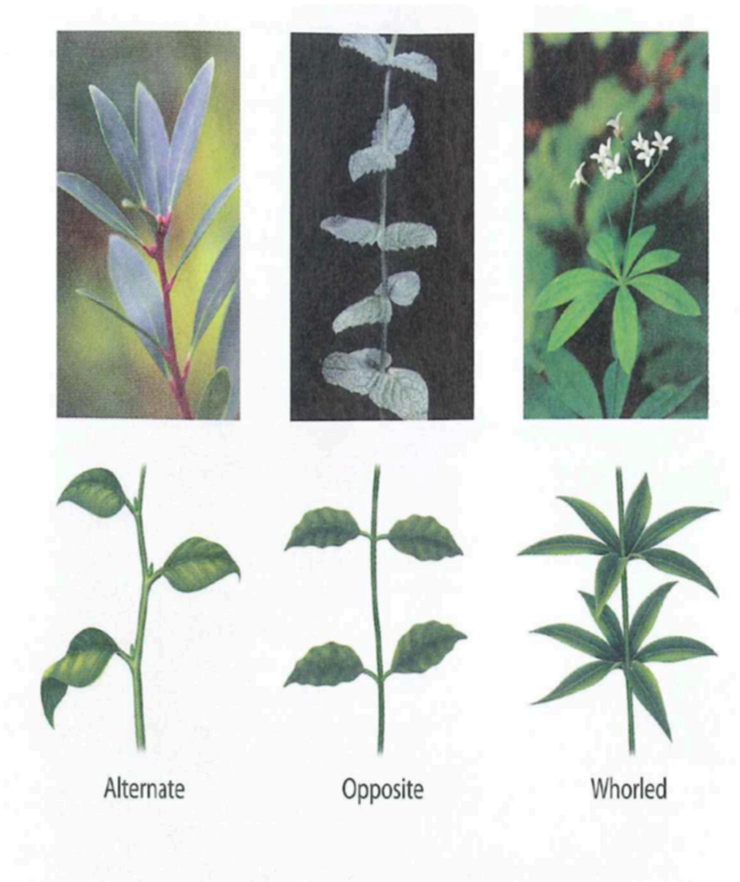
Show Responses

Multiple answers:Multiple answers are accepted for this question
How plant shoots grow?
A
through cell division in the internodes
B
through cell elongation in immature cells in the stem
C
through cell division in the apical meristem
D
through cell elongation in the differentiated mature cells

The shoot apical meristem controls the production and arrangement of leaves.

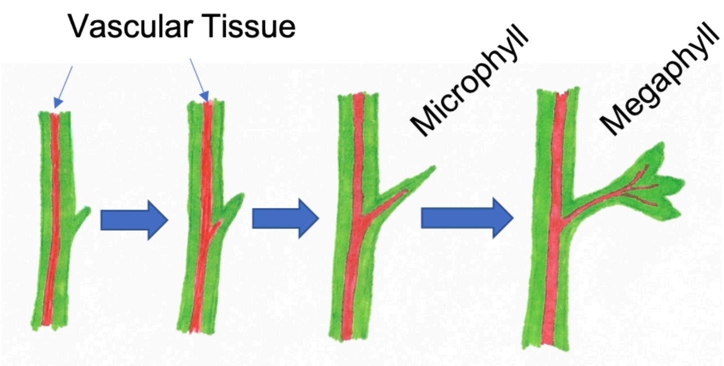
In most plants, leaves are the principal sites of photosynthesis.

Because light is needed for photosynthesis, the arrangement of the leaves along a stem has a major impact on their function. Each species has a characteristic number of leaves attached at each node along the stem. Some species have only a single leaf at each node, whereas others have two or more. How the leaves are positioned around the stem varies in a predictable fashion. The regular placement of leaves reduces the shading of one leaf by another and thus enhances the ability of plants to obtain sunlight.



Leaves begin as small bumps, the leaf primordia, which form on the sides of the shoot apical meristem. The regular arrangement of leaves around the stem is controlled by the fact that each successive leaf primordium is located as far away as possible from all previously formed primordia. One hypothesis proposed to explain this developmental pattern is that the diffusion of chemical signals from developing leaf primordia creates regions where the growth of new primordia is inhibited. The result is an arrangement that prevents leaves from being produced one on top of another.

As noted previously, the earliest vascular plants were simple branching stems, and photosynthesis took place along the length of the shoot. As evolution proceeded, however, some branch systems became flattened, their axes growing in a plane that facilitated the capture of light. These planar branches lost the capacity for continued growth. By about 380 million years ago, the planar branches became modified into structures recognizable as leaves.

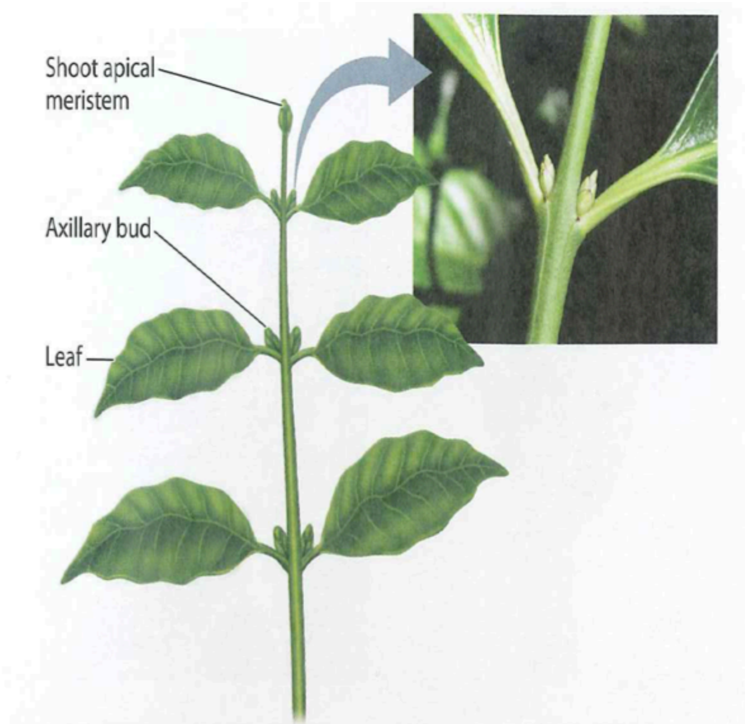


The evolution of leaves required three developmental changes. First, the genetic program to produce a three dimensional stem became modified to form flattened organs. Second, apical meristem identity genes were down regulated and leaf identity genes up-regulated, resulting in a specialized organ incapable of continuing growth. And third, new meristems evolved, enabling leaves to expand into flattened photosynthetic structures that capture sunlight. In fern leaves, these meristems are located along the leaf margin. In pine needles, they occur at the base of each needle. In flowering plants, meristematic cells can be distributed throughout the developing leaf, making possible a diversity of leaf shape. In contrast to cells in the shoot apical meristems which can divide continuously throughout the lifetime of a plant, leaf meristematic cells divide only for a relatively short period of time. This explains why leaves grow to a final size.

When we think of leaves, it is the green photosynthetic ones that first come to mind. However, many plants produce leaves that are specialized for functions other than photosynthesis, including climbing, trapping insects, and attracting pollinators. Plants that overwinter produce bud scales that protect shoot apical meristems from desiccation and damage due to cold. Bud scales may not look like leaves, but they form from leaf primordia and are arranged in the same way around the stem as the green leaves produced in spring.

The development of new apical meristems allows stems to branch.

Vascular plants evolved the ability to branch even before they evolved either roots or leaves. Branching was important to these first plants because it allowed them to produce more sporangia. Branching allows present-day plants to support greater numbers of both reproductive structures and leaves.



In lycophytes and in ferns and horsetails, branching occurs when the shoot apical meristem divides in two, giving rise to two stems. In seed plants, branches grow out from axillary buds (also called lateral buds), which are meristems that form at the base of each leaf. Axillary buds have the same structure and developmental potential as the apical meristem and express the same meristem identity genes. However, the axillary buds remain dormant until triggered to grow, remaining attached to the stem even after leaves are shed. Thus, axillary buds provide seed plants with many points along their stem where new branches can form.

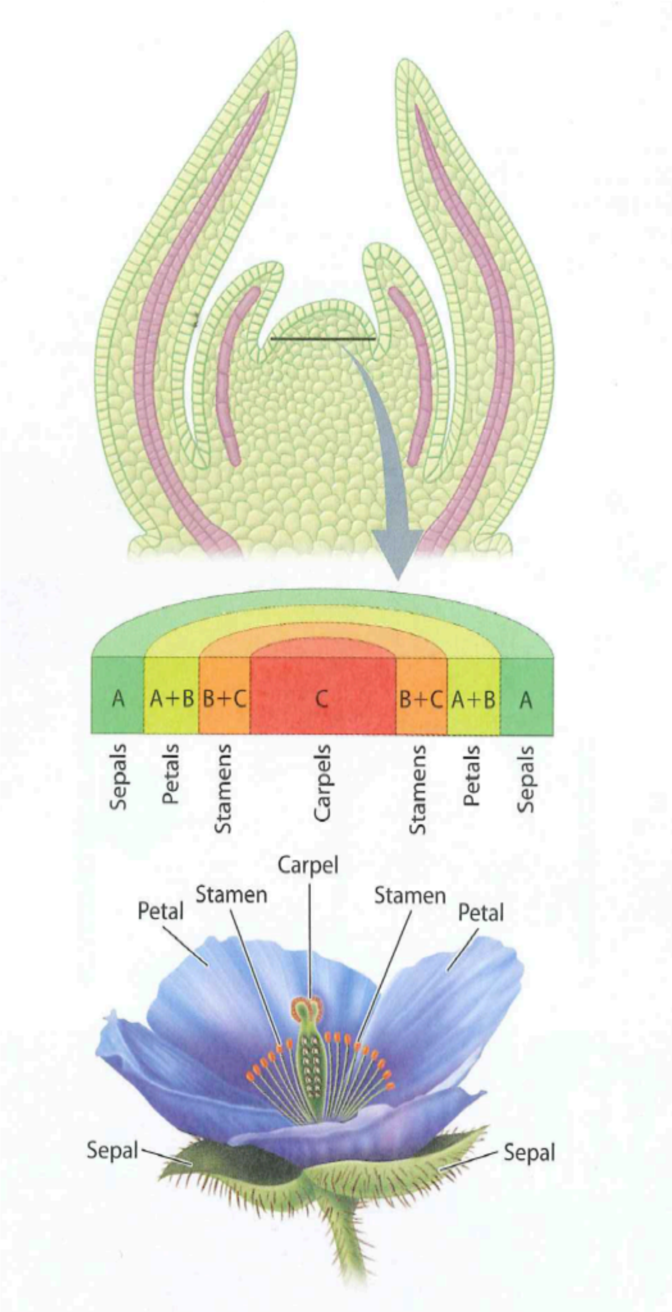
Quick Review: Stems

Show Correct Answer

Show Responses

Where on the stem would you find the axillary buds?
A
between the leaf petiole and the leaf blade
B
between the internodes
C
at the nodes
D
at the apical meristem

Flowers grow from and consume shoot meristems. Just as leaves and branches grow from meristems, so, too, do flowers. Flowers can be produced at the tip of a plant or shoot as a result of the conversion of the apical meristem into a floral meristem, or at the base of leaves as the products of axillary buds. As with leaves, floral meristems lose their capacity for continued growth. All the cells differentiate entirely during flower development.


A
A+B
B+C
C
B+C
A+B
A
Sepals
Petals
Stamens
Carpels
Stamens
Petals
Sepals
Carpel
Stamen
Stamen
Petal
Petal
Sepal
Sepal

Each zone in the flower is controlled by different combinations of genes. Some whorls, like petals and stamens, share some of the same genes.

Flowering is triggered by florigen, a protein produced in leaves and transported through the phloem to apical meristems and axillary buds. Florigen triggers the transition to floral meristems by initiating the downregulation of meristem identity genes and the up-regulation of genes that govern floral identity. The arrangement of primordia is altered to produce four whorls that give rise to the sepals, petals, stamens, and carpels. Once the meristem is launched along the trajectory for flower development, the identity of each whorl is controlled by the expression of homeotic genes. Three classes of genes referred to as A, B, and C, are expressed in overlapping rings around the meristem and serve as master controllers for the development of specific floral organs.
Quick Review: Floral Identity Genes

Show Correct Answer

Show Responses

Match the classes of floral genes with the flower structures they control the development of.
Premise
Response
1
“A” class genes only

A
Pistils
2
“A” and “B” class genes together

B
Carpels

3
“B” and “C” class genes together

C
Petals
4
“C” class genes only

D
Sepals

Summary

Plant structures are very modular in nature, this means that plants are often composed of repeating units. This does not mean that across all plant species the structures are exactly identical. The regulation of specific genes in different areas of the plant can result in significant changes in the overall morphology of the plant. Plants are unique in that the primary areas for new growth are located at the tips of the shoots and the roots. This means that plants grow towards or away from the environmental stimuli (light, water). Gene regulation plays a key role in the positioning of leaves and in Angiosperms the shapes of flowers. These impact the growth and reproduction of plants and are related to the environments in which each species grows.

Review Questions:

REVIEW: Stem structure

Show Correct Answer

Show Responses

Plant shoots are , as they are formed from repeating units of where leaves attach and the segments between leaves.
Word Bank:apical, modular, nodes, axillary buds, internodes, leaves
REVIEW: Apical Meristem

Show Correct Answer

Show Responses

Multiple answers:Multiple answers are accepted for this question
What is the apical meristem involved in?
A
the production of new cells that elongate the stem
B
the control of leaf formation and placement on the stem
C
the increase in girth (diameter) of the stem
D
the formation of axillary buds
REVIEW: Controlling totipotency

Show Correct Answer

Show Responses

What is involved in maintaining the totipotency of the cells at the shoot tip?
A
apoptosis
B
shoot meristem genes
C
florigen
REVIEW: Shoot dynamics

Show Correct Answer

Show Responses

What happens in each of the following areas of the plant shoot?
Premise
Response
1
apical meristem

A
cells behind/below the shoot tip expand by taking up fluids
2
zone of elongation

B
cells reach their final size and complete their differentiation
3
zone of maturation

C
new cells are added to the tip of the shoot

31.

Learning Goals

By the end of this reading you should be able to:

- Describe the structure of xylem and differentiate between tracheids and vessel elements
- Explain how water is moved from roots to leaves of plants
- Relate the movement of water in xylem to the properties of water
- Explain how xylem structure helps to prevent collapse and cavitation

Introduction

On a summer day, a tree can transport many hundreds of liters of water from the soil to its leaves. This is an impressive feat given that it is accomplished without any moving parts. Even more remarkable, trees and other plants transport water without any direct expenditure of energy. The upward transport of water is possible because the structure of vascular plants allows them to use the evaporation of water from leaves to pull water from the soil.

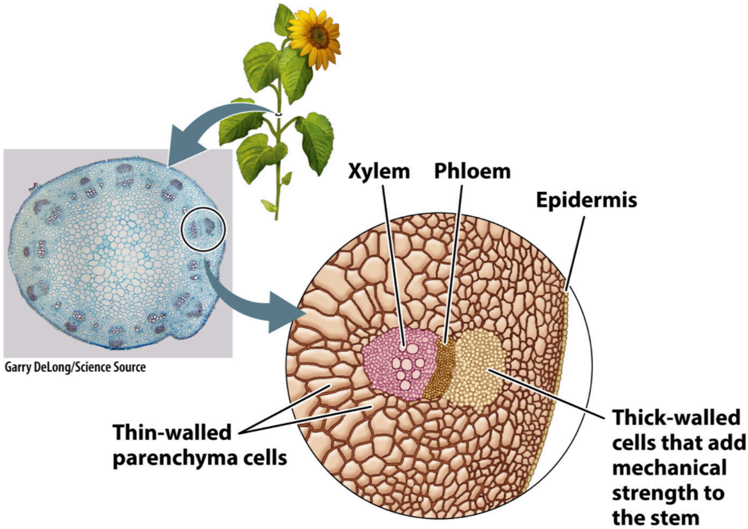


Figure 1. Cross-section of a sunflower (dicot) stem

This figure shows the cross-section of a sunflower stem. Like a leaf, it has a surface layer of epidermal cells. This layer encloses thin-walled parenchyma cells in the interior. Notice that the stem also contains differentiated tissues that lie in a ring near the outside of the stem. These are the vascular tissues, which form a continuous pathway that extends from near the tips of the roots, through the stem, and into the network of veins within leaves. The outer tissue, called phloem, transports carbohydrates from leaves to the rest of the plant body. The inner tissue, called xylem, transports water and nutrients from the roots to the leaves.

Quick Review: Xylem Functions

Show Correct Answer

Show Responses

Multiple answers:Multiple answers are accepted for this question

What are some of the key functions of xylem?

A

movement of water
B
structural support of the plant body
C
movement of sugars
D
movement of minerals and ions

Xylem Structure: A Low Resistant Pathway for Water

Water travels with relative ease through xylem because of the structure of the water-transporting cells within this tissue. As they develop, these cells become greatly elongated. When they complete their growth, they secrete an additional wall layer that is very thick and which contains lignin, a chemical compound that increases mechanical strength. Most remarkable is the final stage of development when the nucleus and cytoplasm are lost, leaving behind only the cell walls.

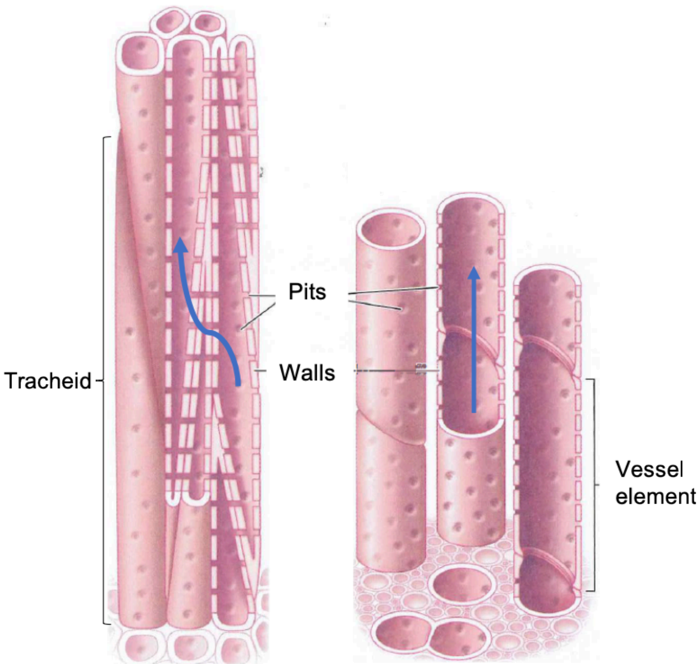


Figure 2. Xylem can be composed of tracheids, vessel elements or a combination of the two depending on the plant species.

These thick walls form a hollow conduit through which water can flow. Water enters and exits xylem conduits through pits, circular or ovoid regions in the walls where the lignified cell wall layer is not produced. Instead, pits contain only the thin, waterpermeable cell wall that surrounded each cell as it grew. As we will see, pits play an important role in xylem because they allow the passage of water, but not air, from one conduit to another.

Xylem conduits can be formed from a single cell or multiple cells stacked to form a hollow tube. Unicellular conduits are called tracheids, and multicellular conduits are called vessels. Because tracheids are the product of a single cell, they are typically 4 to 40 μ,m in diameter and no more than 2 to 3 cm long. Vessels, which are made up of individual cells called vessel elements, can be much wider and longer. Vessel diameters range from 5 to 500 µm, and lengths can be up to several meters.

Water enters a tracheid through pits, travels upward through the conduit interior, and then flows outward through other pits into an adjacent, partially overlapping tracheid. Water also enters and exits a vessel through pits. In contrast to tracheids, however, once the water is inside the vessel, little or nothing blocks the flow of water from one cell to the next. That is because during the development of a xylem vessel, the end walls of the vessel elements are digested away, allowing water to flow along the entire length of the vessel without having to cross any pits. At the end of a vessel, however, the water must flow through pits if it is to enter an adjacent vessel and thereby continue its journey from the soil to the leaves.

The rate at which water moves through xylem is a function of both the number of conduits and their size. Conduit length determines how often water must flow across pits, which exert a significant resistance to flow. Conduit width also has a strong effect on the rate of water transport. Like the flow through pipes, water flow through xylem conduits is greater when the conduits are wider. The flow is proportional to the radius of the conduit raised to the fourth power, so doubling the radius increases flow sixteenfold. Because vessels are both longer and wider than tracheids, plants with vessels achieve greater rates of water transport than is possible through tracheids alone. Tracheids are the most common conduits in lycophytes, ferns and horsetails, and gymnosperms, whereas vessels are the principal conduit in angiosperms.

Moving water without energy

Water is pulled through xylem by an evaporative pump. If you cut a plant's roots off underwater, the leaves continue to transpire for some time. The persistence of transpiration when roots are absent demonstrates that the driving force for water transport is not generated in the roots, but instead comes from the leaves. In essence, water is pulled through the xylem from above rather than being pushed from below.

The forces pulling water upward through the plant are large. Not only must these forces be able to lift water against gravity, but they must also be able to pull water from the soil, which becomes increasingly difficult as the soil dries. In addition, they must be able to overcome the physical resistance associated with moving water through the plant itself. To replace water lost by transpiration with water pulled from the soil, the leaves must exert forces that are many times greater than the suctions that we can generate with a vacuum pump. How do leaves exert this force?

When stomata are open, water evaporates from the walls of cells lining the intercellular air spaces of leaves. The partial dehydration of the cell walls creates a force that pulls water towards the sites of evaporation. One hypothesis for how this force is generated is that water is pulled by capillary action into spaces between the cellulose microfibrils in the cell wall, the same reason that water is drawn into a sponge. A second hypothesis is that the pectin gel in which the cellulose microfibrils are embedded causes water to flow into the partially dehydrated cell walls by osmosis. Osmotic forces can be generated in cell walls because the negatively charged pectin network restricts the diffusion of positively charged ions, much as the plasma membrane maintains a high concentration of solutes in the cytoplasm.

Once generated by the evaporation of water from leaves, this force is transmitted through the xylem, beginning in the leaf veins, then down through the stem, and out through the roots to the soil

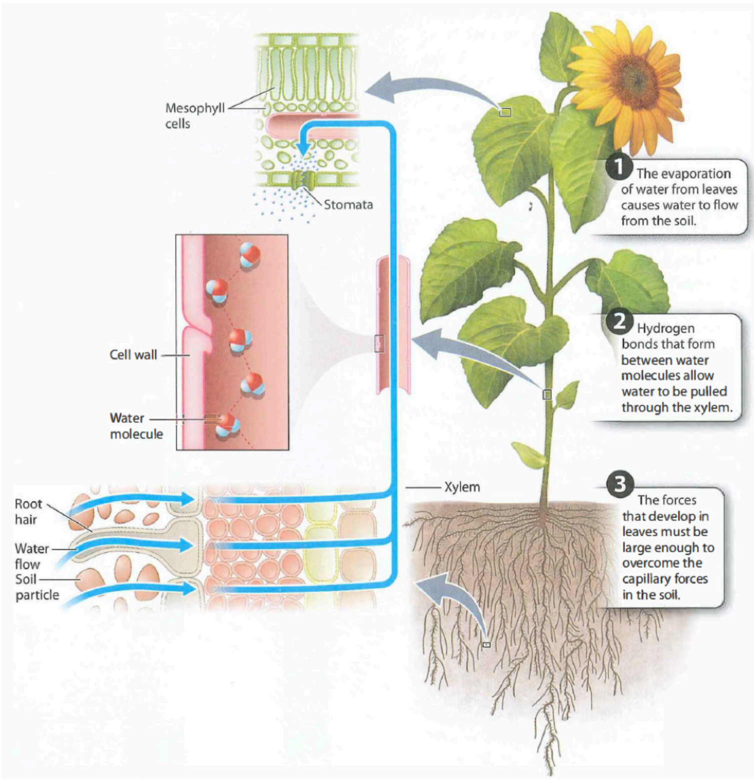
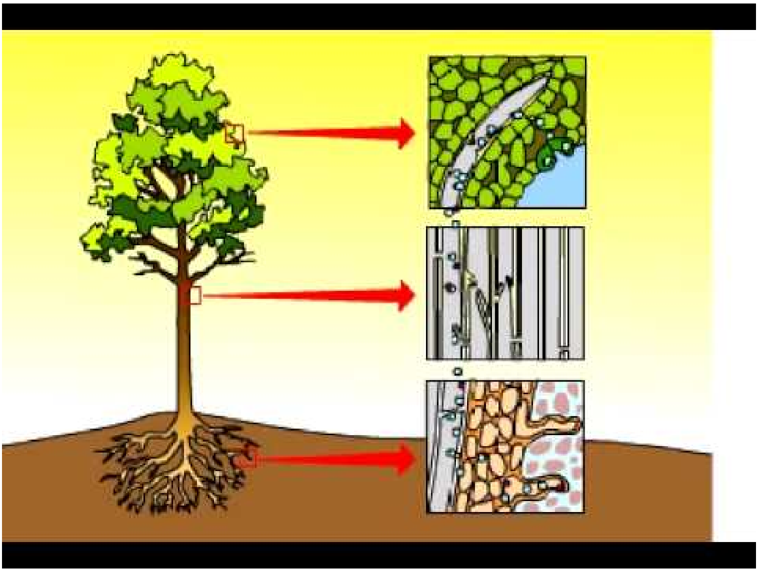


Figure 3. Water is pulled from roots to leaves through evaporation. The cohesion and adhesive properties of water and the structure of the xylem cells play key roles in this process.

Water can be pulled through xylem because of the strong hydrogen bonds that form between water molecules(cohesion). The xylem structure also enhances the ability of water molecules to bind to other surfaces (adhesion). These mechanisms of water transport only work, however, if there is a continuous column of water in the xylem that extends from the roots to the leaves. This video will help you to visualize the process of transpiration.



Quick Review: Moving Water

Show Correct Answer

Show Responses

What is the main force that drives most of the water movement within xylem vessels toward the top of a plant?

A

active transport of ions into the roots

B

passive transport of water out of the leaves

C

diffusion of water along a concentration gradient

D

a build up of pressure in the root tissues

The structure of xylem conduits reduces the risks

of collapse and cavitation.

The fact that water is pulled from the soil means that xylem conduits must be structured in such a way as to minimize two distinct risks. The first is the danger of collapse. If you suck too hard on a drinking straw, it will collapse inward, blocking flow. Much the same thing can happen in the xylem. Although in metabolic terms, lignin is more costly to produce than cellulose, lignin makes conduit walls rigid, reducing the risk of collapse.

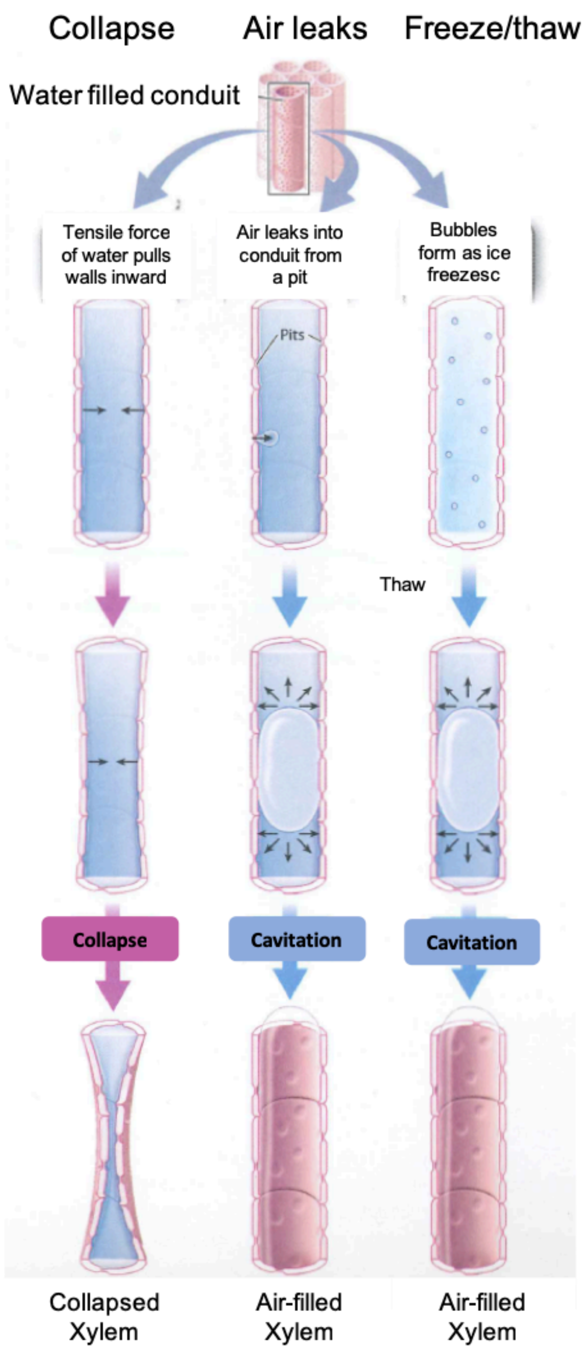

Collapse
Air leaks
Freeze/thaw
Water filled conduit
Tensile force of water pulls walls inward
Air leaks into conduit from a pit
Bubbles form as ice freezesc
Pits
Thaw
Collapse
Cavitation
Cavitation
Collapsed Xylem
Air-filled Xylem
Air-filled Xylem

Figure 4. Pressure from high levels of transpiration can result in xylem collapse. Air entering the xylem or freezing-thawing can create air bubbles. Both interfere with the movement of water in plants.

The second danger associated with pulling water through the xylem is cavitation, which occurs when the water in a conduit is abruptly replaced by water vapor. Because cavitation disrupts the continuity of the water column, cavitated conduits can no longer transport water from the soil. Cavitation in xylem results from the presence of microscopic gas bubbles in the water that are sufficiently large that they expand under the tensile, or pulling, the force exerted by the leaves. The microscopic bubbles that cause cavitation can be formed in either of two ways. The first is if an air bubble is pulled through a pit because of lower pressure in the water compared to the air. The larger the tensile forces exerted by leaves, the more likely it is that air will be pulled across a pit. Thus, higher rates of transpiration increase the risk of cavitation.

The second way that gas bubbles can form within xylem is if gases come out of solution during freezing. Gases are much less soluble in ice than in water, so as a conduit freezes, dissolved gas molecules aggregate into tiny bubbles that can cause cavitation when the conduit thaws. Wide vessels are especially vulnerable to cavitation at freezing temperatures. The susceptibility of wide vessels to cavitation partly explains why boreal (that is, subarctic) forests contain few angiosperms, which commonly have large vessel diameters.

Once cavitation has occurred, the liquid phase will not re-form as long as tension persists within the xylem. Thus, xylem is organized in ways that minimize the likelihood and impact of cavitation. For example, xylem consists of many conduits in parallel, so the loss of any one conduit to cavitation does not result in a major loss of transport capacity. Similarly, as water flows from the soil to the leaves, it passes from one conduit to another, each one of finite length. The likelihood that cavitation will spread is thereby reduced because air can be pulled through pits only when the tensile forces in the xylem are large.

Thinking about it: Water Movement and Energy

How is the statement that water is transported through the xylem without requiring any input in energy by the plant both correct and Incorrect?

Responses

Reply

Ordered by

Newest Responses

Summary

The structure of xylem tracheids and vessel elements in a key component to the movement of water from plant roots to leaves. In addition, the properties of water, adhesion and cohesion, allow the formation of a continuous column of water in the xylem. As the water is pulled up by transpiration cohesion keeps water molecules together, and adhesion of water to the xylem walls helps to keep it from reversing direction. When excessive pressure or the introduction of air bubbles occurs this can impair the capacity of xylem to move water. Xylem tissue, however, is composed of large numbers of cells and thus a large number of pathways within the cells for water movement, thus collapse or cavitation of individual cells has a smaller impact as water moves around these in surrounding cells.

Review Questions

REVIEW: Transpiration Process

Show Correct Answer

Show Responses

Transpiration in plants requires all of the following except?

A

cohesion between water molecules

B

active transport of water between cells

C

transport through tracheids and/or vessel elements

D

adhesion of water molecules to cellulose

E

evaporation of water molecules

REVIEW: Driving Forces

Show Correct Answer

Show Responses

In plants water moves from areas of high water potential to areas of low water potential by osmosis and diffusion. In the xylem water stream, where is the lowest water potential?

A

In the xylem tissue of the roots

B

In the xylem tissues in the stems

C

Outside the stomata of leaves

D

In the soil outside of the roots

REVIEW: Comparing structures

Show Correct Answer

Show Responses

Compared to tracheids, vessel elements are?
A
capable of greater water flow
B
contain fewer connections to other cells
C
have greater diameters
D
only capable of moving water through pits on their sides

32.

Learning Goals

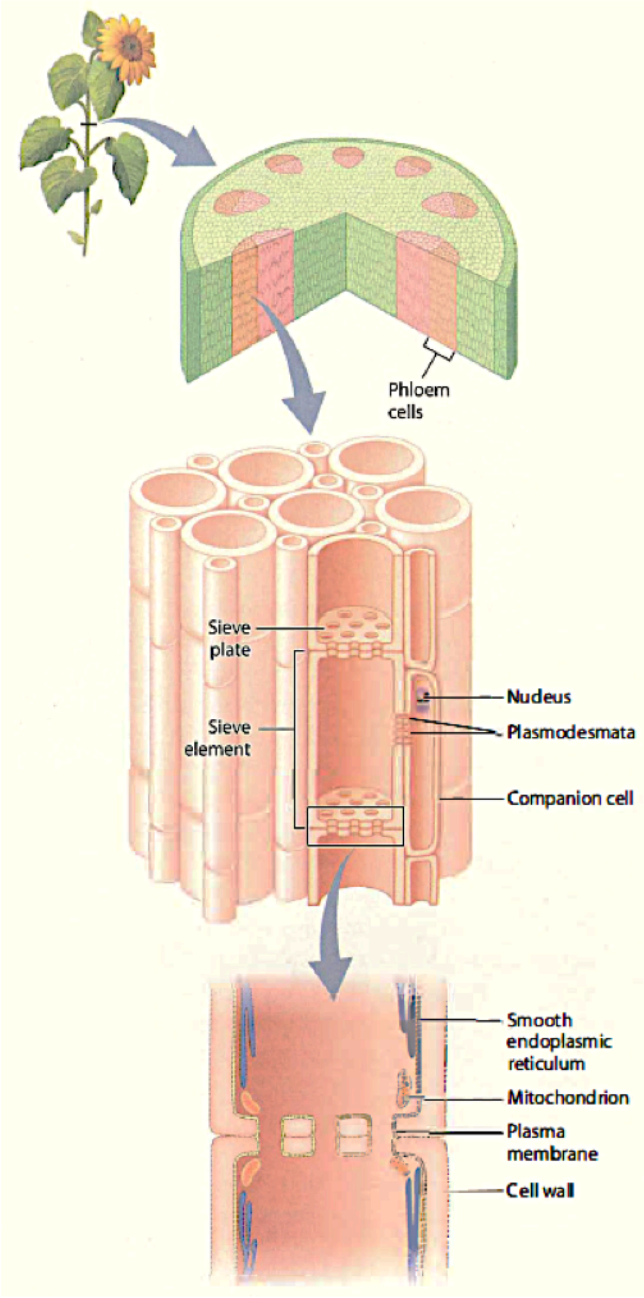
By the end of this reading you should be able to:

- Describe the structure of phloem
- Differentiate between source and sink tissues in plants
- Explain the pressure-flow mechanism of sugar transport in phloem
- Compare and contrast xylem and phloem structures and functions
- Describe the link between phloem sugars and the rhizosphere

Introduction

Much of the body of a vascular plant is devoted to the uptake and transport of the water required by leaves rather than to photosynthesis. In contrast, all cells of the algal ancestors of plants would have been capable of photosynthesis. Roots and stems contribute indirectly to photosynthesis but produce little or no carbohydrate themselves. Thus, although vascular plants are photosynthetic, a large part of their body must be supplied internally with food.

Phloem Structure


Phloem
cells
Sieve
plate
Sieve
element
Nudeus
Plasmodesmata
Companion cell
Smooth
endoplasmic
reticulum
Mitochondrion
Plasma
membrane
Cell wall

Phloem transport takes place through multicellular sieve tubes, which are composed of highly modified cells called sieve elements that are connected end to end. During development, sieve elements lose much of their intracellular structure, including the nucleus and the vacuole. At maturity, sieve elements retain an intact plasma membrane that encloses a modified cytoplasm containing only smooth endoplasmic reticulum and a small number of organelles, including mitochondria. Cellular functions such as protein synthesis are carried out by an adjacent companion cell, to which the sieve element is connected by numerous plasmodesmata. Sieve elements are linked by sieve plates, which are modified end walls with large (1 to 1.5 µ,m diameter) pores. The plasma membrane of adjacent sieve elements is continuous through each of these pores, so each multicellular sieve tube can be considered a single cytoplasm-filled compartment. Phloem sap is the sugar-rich solution that flows through both the lumen of the sieve tubes and the sieve plate pores.
Quick Review: Sieve Elements

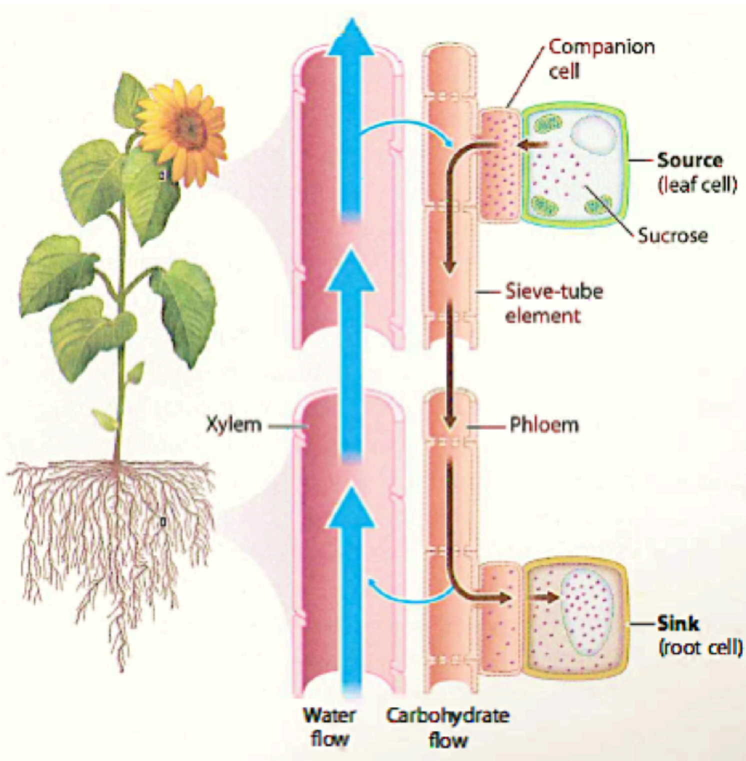
Show Correct Answer

Show Responses

Multiple answers:Multiple answers are accepted for this question
At maturity what would you expect to find in sieve elements
A
large numbers of plasmodesmata with companion cells
B
a nucleus and internal organelles
C
mitochondria
D
cytoplasmic connections with other sieve elements

Sources and Sinks

Phloem transports carbohydrates as sucrose (glucose plus fructose) or larger sugars, assembled from monosaccharides in the cytoplasm. Phloem also transports amino acids, inorganic forms of nitrogen, and ions including K+, which are present in much lower concentrations. Finally, phloem transports informational molecules such as hormones, protein signals, and even RNA. Thus, phloem forms a multicellular highway for the movement of raw materials and signaling molecules across the entire length of the plant.



Phloem transports its molecular cargo from source to sink. In plants, sources are the regions that produce or store carbohydrates. For example, leaves are sources because they produce carbohydrates by photosynthesis, and potato tubers after they have been formed are sources because they can supply stored carbohydrates to the rest of the plant body. Sinks are any portion of the plant that needs carbohydrates to fuel growth and respiration-examples are roots, young leaves, and developing fruits. Whereas the direction of xylem transport is always up toward the leaves, the direction of phloem transport can be either up or down, depending on where the source and sink are relative to each other.

Quick Review: Sources and Sinks

Show Correct Answer

Show Responses

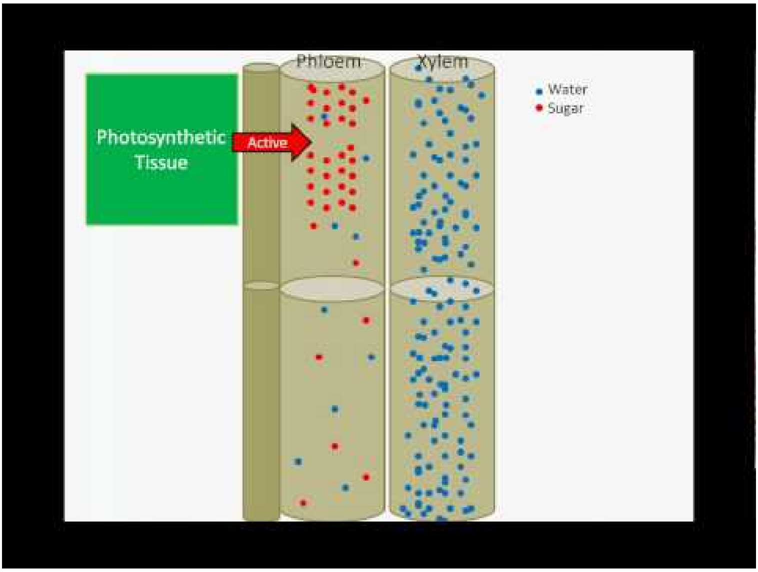
are plant tissues that are capable of providing to tissues which require them for growth.

Pressure-Flow in Phloem Transport

How does phloem transport sugars from source to sink? In some plants, active transporters powered by ATP move sucrose into the phloem. The buildup of sugar concentration causes water to be drawn into the phloem by osmosis. Because the cell walls of the sieve tube resist being stretched outward to accommodate the influx of water, they press back (inward) against the cytoplasm. Their resistance to stretching increases the

turgor pressure

at the source end of a sieve tube. At sinks, sugars are transported out of the phloem into surrounding cells. This withdrawal of sugars causes water to leave the sieve tube, again by osmosis, reducing turgor pressure at the sink end. It is the difference in turgor pressure that drives the movement of phloem sap from source to sink. This video demonstrates how pressure-flow results in the movement of sugars and how this transport is linked to the movement of water.



The water that exits the phloem can be used locally to support the enlargement of sink cells or it can be carried back to the leaves in the xylem. Thus, some of the water in the phloem sap is recirculated in the xylem. The volume of water that moves through the phloem, however, is tiny compared to the amount that must be transported through the xylem to replace water lost by transpiration. Therefore, the number and size of xylem conduits greatly exceed the number and size of sieve tubes.

Phloem transport is sometimes referred to as “translocation,” a term that pairs well with “transpiration.” Yet in almost every way, phloem and xylem are a study in contrasts. In phloem, the plant generates the gradient that drives transport, whereas water moving through xylem is driven by the difference in hydration between soil and air. Furthermore, water is pulled upward through xylem conduits, while transport through phloem is more of a push.

These fundamental differences in function explain the cytological differences between xylem and phloem: Phloem conduits retain an intact plasma membrane and modified cytoplasm, whereas xylem conduits retain only their cell walls. What xylem and phloem have in common is that both are essential in enabling vascular plants to carry out photosynthesis on land. Moreover, like xylem, phloem is subject to risks that arise from the way flow through sieve tubes is generated. Damaged sieve tubes are at risk of having their contents leak out, pushed out by high turgor pressures in the phloem. Damage is an ever-present danger because the sugar content of phloem makes it an attractive target for insects. Cell damage activates sealing mechanisms that repair breaks in sieve tubes. In some respects, these mechanisms are comparable to the formation of blood clots in humans, except that phloem can seal itself much more rapidly, typically in less than a second.

Thinking About It: Sugar movement in two directions

How is phloem able to transport carbohydrates from the shoot to the roots, as well as from the roots to the shoot (although not at the same time)?

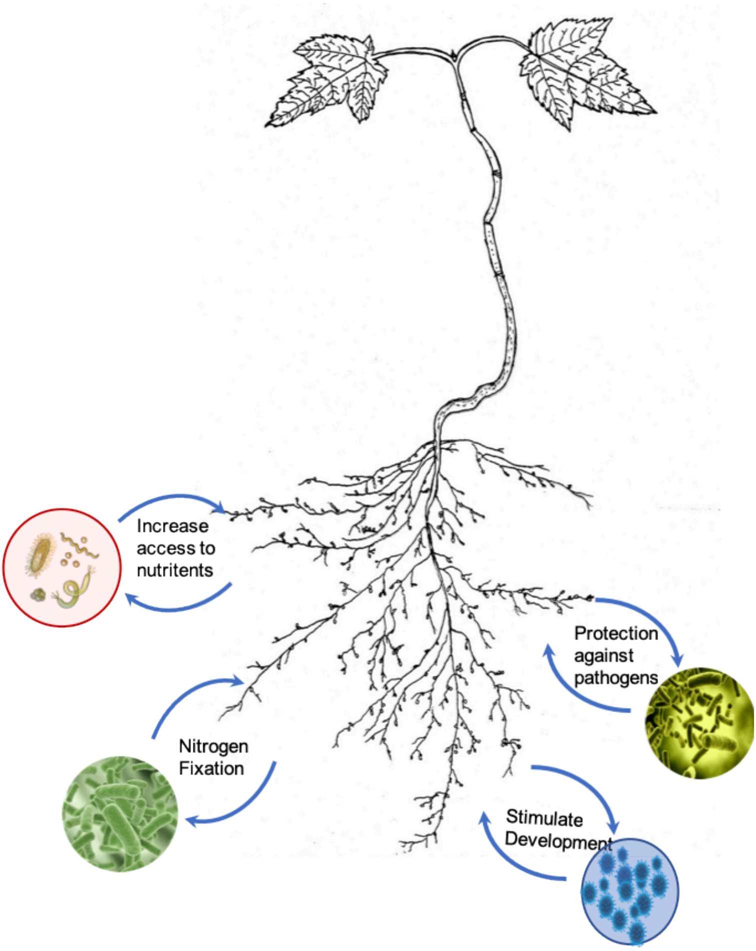
Responses

Reply

Ordered by

Newest Responses

Phloem and the Rhizosphere



Phloem also supplies carbohydrates to organisms outside the plant. A fraction of the carbohydrates transported to the roots spills out into the rhizosphere, the soil layer that surrounds actively growing roots. This supply of carbohydrates stimulates the growth of soil microbes. As a result, the densities of microbial organisms near roots are much greater than in the rest of the soil. The interactions between soil microbes and plants can vary greatly. Those soil bacteria that are decomposers of soil organic matter, can make nutrients such as nitrogen and phosphorus more accessible to the plant. Other soil microbes can release hormones that stimulate plant growth, aid in atmospheric nitrogen fixation, and some even provide protection against soil plant pathogens. Thus, the release of carbohydrates by roots into the soil is beneficial to the overall growth and survival of the plants.

Summary

All the cells in a plant's body contain mitochondria since all cells need a constant supply of ATP. Typically, about 50% of the carbohydrates produced by photosynthesis in one day are converted back to CO_2 by respiration within 24 hours. Carbohydrates that are not immediately consumed in respiration can be used as raw materials for growth, or they can be stored for later use. Carbohydrates stored within roots and stems, or in tubers (specialized storage organs such as potatoes), can support new growth in the spring or following a period of drought. Stored reserves can also be used to repair mechanical damage or replace leaves consumed by insects or grazing mammals. Like their green algal ancestors, vascular plants store carbohydrates primarily as starch, a large molecule that is not soluble and so does not affect the osmotic balance of cells.

What determines how carbohydrates become distributed within the plant? Where phloem sap ends up is determined by the sinks. Phloem transport to reproductive organs appears to have priority over the movement to stems and leaves, and these have priority over movement to roots. Hormones play a key role in controlling the growth and development of plants and these hormones may influence the ability of different sinks to compete successfully for resources delivered by the phloem.

Review Questions

REVIEW: Xylem vs. Phloem

Show Correct Answer

Show Responses

Indicate where these are characteristics of xylem, phloem or both.
Cells are dead at maturity
Generation of a pressure gradient
Mature cells do not have nuclei
Molecules move due to hydration differences
Are linked to companion cells

REVIEW: Sink Tissues

Show Correct Answer

Show Responses

Multiple answers:Multiple answers are accepted for this question
Examples of sink tissues in plants include?

A
young leaves
B
mature storage organs (like tubers)
C
developing fruit
D
root tissues

REVIEW: Starch

Show Correct Answer

Show Responses

Starch, which is formed from glucose, is not soluble and thus is not transported by the phloem.
A
True
B
False
REVIEW: Roots and sugars

Show Correct Answer

Show Responses

Multiple answers:Multiple answers are accepted for this question
What advantage does release of sugars from roots provide plants?
A
attraction of microbes that can protect against pathogen
B
attraction of microbes that can fix nitrogen
C
attraction of microbes that enhance access to nutrients
D
enhances uptake of water from the soil environment

33.

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)

Learning Goals

By the end of this reading you should be able to:

- List the features that distinguish the kingdom Animalia from other kingdoms
- Explain the processes of animal reproduction and embryonic development
- Describe the roles that Hox genes play in development

Introduction

Animal evolution began in the ocean over 600 million years ago with tiny creatures that probably do not resemble any living organism today. Since then, animals have evolved into a highly diverse kingdom. Although over one million extant (currently living) species of animals have been identified, scientists are continually discovering more species as they explore ecosystems around the world. The number of extant species is estimated to be between 3 and 30 million.

But what is an animal? While we can easily identify dogs, birds, fish, spiders, and worms as animals, other organisms, such as corals and sponges, are not as easy to classify. Animals vary in complexity—from sea sponges to crickets to chimpanzees—and scientists are faced with the difficult task of classifying them within a unified system. They must identify traits that are common to all animals as well as traits that can be used to distinguish among related groups of animals. The animal classification system characterizes animals based on their anatomy, morphology, evolutionary history, features of embryological development, and genetic makeup. This classification scheme is constantly developing as new information about species arises. Understanding and classifying the great variety of living species help us better understand how to conserve the diversity of life on earth.

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 (Fig. 2ab). 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.

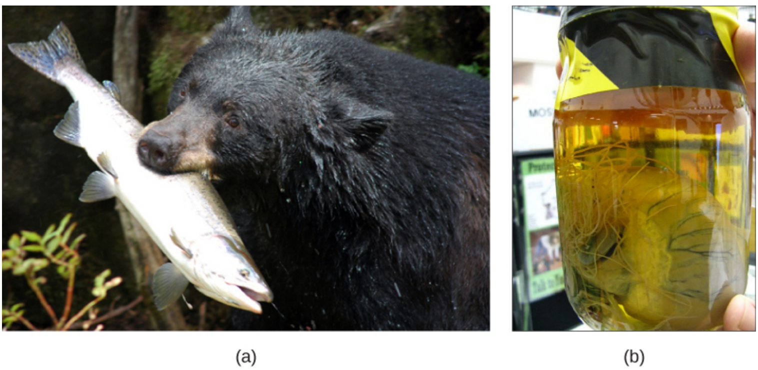


Figure 2. All animals are heterotrophs that derive energy from food. The (a) black bear is an omnivore, eating both plants and animals. The (b) heartworm Dirofilaria immitis is a parasite that derives energy from its hosts. It spends its larval stage in mosquitoes and its adult stage infesting the heart of dogs and other mammals, as shown here. (credit a: modification of work by USDA Forest Service; credit b: modification of work by Clyde Robinson)

Complex Tissue Structure

As multicellular organisms, animals differ from plants and fungi because their cells don't have cell walls, their cells may be embedded in an extracellular matrix (such as bone, skin, or connective tissue), and their cells have unique structures for intercellular communication (such as gap junctions). In addition, animals possess unique tissues, absent in fungi and plants, which allow coordination (**nerve tissue**) of motility (**muscle tissue**). Animals are also characterized by specialized connective tissues that provide structural support for cells and organs. This connective tissue constitutes the extracellular surroundings of cells and is made up of organic and inorganic materials. In vertebrates, bone tissue is a type of **connective tissue** that supports the entire body structure. The complex bodies and activities of vertebrates demand such supportive tissues. **Epithelial tissues** cover, line, protect, and secrete. Epithelial tissues include the epidermis of the integument, the lining of the digestive tract and trachea, and make up the ducts of the liver and glands of advanced animals.

The animal kingdom is divided into **Parazoa** (sponges) and **Eumetazoa** (all other animals). As very simple animals, the organisms in group Parazoa ("beside animal") do not contain true specialized tissues; although they do possess specialized cells that perform different functions, those cells are not organized into tissues. These organisms are considered animals since they lack the ability to make their own food. Animals with true tissues are in the group Eumetazoa ("true animals"). When we think of animals, we usually think of Eumetazoans, since most animals fall into this category.

The different types of tissues in true animals are responsible for carrying out specific functions for the organism. This differentiation and specialization of tissues is part of what allows for such incredible animal diversity. For example, the evolution of nerve tissues and muscle tissues has resulted in animals' unique ability to rapidly sense and respond to changes in their environment. This allows animals to survive in environments where they must compete with other species to meet their nutritional demands.

Review Question:

How do the Parazoa (sponges) differ from other animals?

A) they do not have cells organized into tissues like other animals
B) they are mostly unicellular and other animals are multicellular
C) they do not display any cell differentiation
D) they are autotrophs and all other animals are heterotrophs

Animal Reproduction and Development

Most animals are diploid organisms, meaning that their body (somatic) cells are diploid and haploid reproductive (gamete) cells are produced through meiosis. Some exceptions exist: For example, in bees, wasps, and ants, the male is haploid because it develops from unfertilized eggs. Most animals undergo sexual reproduction: This fact distinguishes animals from fungi, protists, and bacteria, where asexual reproduction is common or exclusive. However, a few groups, such as cnidarians, flatworms, and roundworms, undergo asexual reproduction, although nearly all of those animals also have a sexual phase to their life cycle.

Processes of Animal Reproduction and Embryonic Development

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

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

After fertilization, a series of developmental stages occur during which primary germ layers are established and reorganize to form an **embryo**. During this process, animal **tissues** begin to specialize and organize into **organs** and **organ systems**, determining their future morphology and physiology. Some animals, such as grasshoppers, undergo **incomplete metamorphosis**, in which the young resemble the adult. Other animals, such as some insects, undergo **complete metamorphosis** where individuals enter one or more larval stages that may in differ in structure and function from the adult (Fig. 3). For the latter, the young and the adult may have different diets, limiting competition for food between them. Regardless of whether a species undergoes complete or incomplete metamorphosis, the series of developmental stages of the embryo remains largely the same for most members of the animal kingdom.

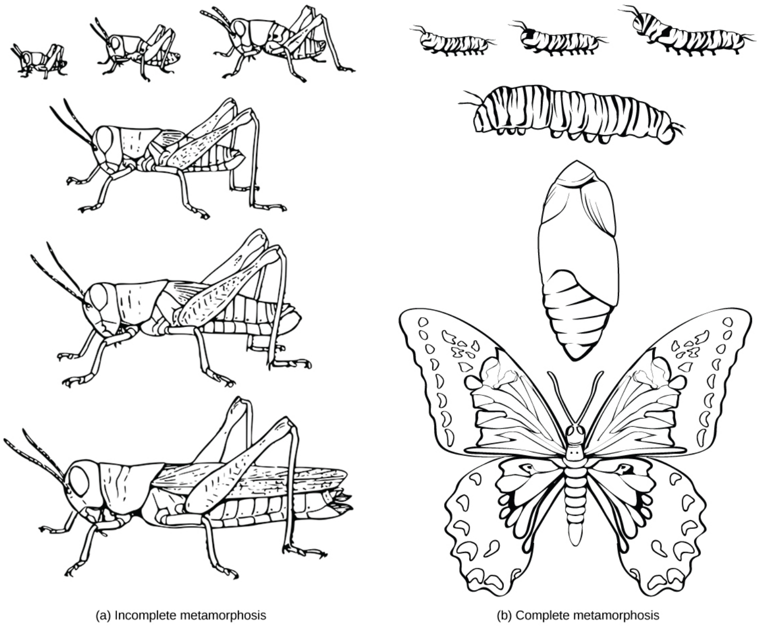


Figure 3. (a) The grasshopper undergoes incomplete metamorphosis. (b) The butterfly undergoes complete metamorphosis. (credit: S.E. Snodgrass, USDA)

Review Question:

In what ways does asexual reproduction occur in some animals?
A) budding
B) fragmentation
C) parthenogenesis
D) binary fission

The process of animal development begins with the **cleavage**, or series of mitotic cell divisions, of the zygote (Fig. 4). 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**.

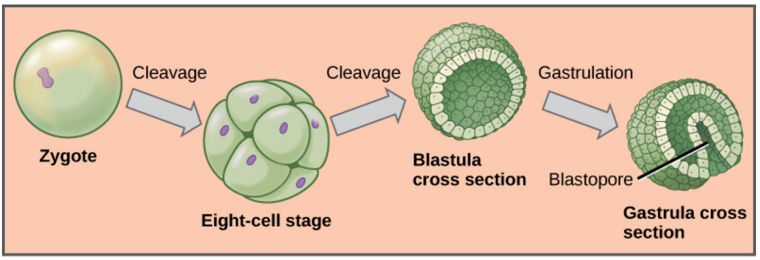


Figure 4. During embryonic development, the zygote undergoes a series of mitotic cell divisions, or cleavages, to form an eight-cell stage, then a hollow blastula. During a process called gastrulation, the blastula folds inward to form a cavity in the gastrula.

Watch the following to see how human embryonic development (after the blastula and gastrula stages of development) reflects evolution. https://youtu.be/uAZmLYWEPGk

Review Question:

During embryonic development, unique cell layers develop and distinguish during a stage called ________.

A) the blastula stage
B) the germ layer stage
C) the gastrula stage
D) the organogenesis stage

The Role of Homeobox (Hox) Genes in Animal Development

Since the early 19^{th} century, scientists have observed that many animals, from the very simple to the complex, shared similar embryonic morphology and development. Surprisingly, a human embryo and a frog embryo, at a certain stage of embryonic development, look remarkably alike. For a long time, scientists did not understand why so many animal species looked similar during embryonic development but were very different from adults. They wondered what dictated the developmental direction that a fly, mouse, frog, or human embryo would take. Near the end of the 20^{th} century, a particular class of genes was discovered that had this very job. These genes that determine animal structure are called "**homeotic genes**," and they contain DNA sequences called **homeoboxes**. The animal genes containing homeobox sequences are specifically referred to as ***Hox* genes**. This family of genes is responsible for determining the general body plan, such as the number of body segments of an animal, the number and placement of appendages, and animal head-tail directionality. The first *Hox* genes to be sequenced were those from the fruit fly (*Drosophila melanogaster*). A single *Hox* mutation in the fruit fly can result in an extra pair of wings or even appendages growing from the "wrong" body part.

While there are a great many genes that play roles in the morphological development of an animal, what makes *Hox* genes so powerful is that they serve as master control genes that can turn on or off large numbers of other genes. *Hox* genes do this by coding transcription factors that control the expression of numerous other genes. *Hox* genes are homologous in the animal kingdom, that is, the genetic sequences of *Hox* genes and their positions on chromosomes are remarkably similar across most animals because of their presence in a common ancestor, from worms to flies, mice, and humans (**Figure 5**). One of the contributions to increased animal body complexity is that *Hox* genes have undergone at least two duplication events during animal evolution, with the additional genes allowing for more complex body types to evolve.

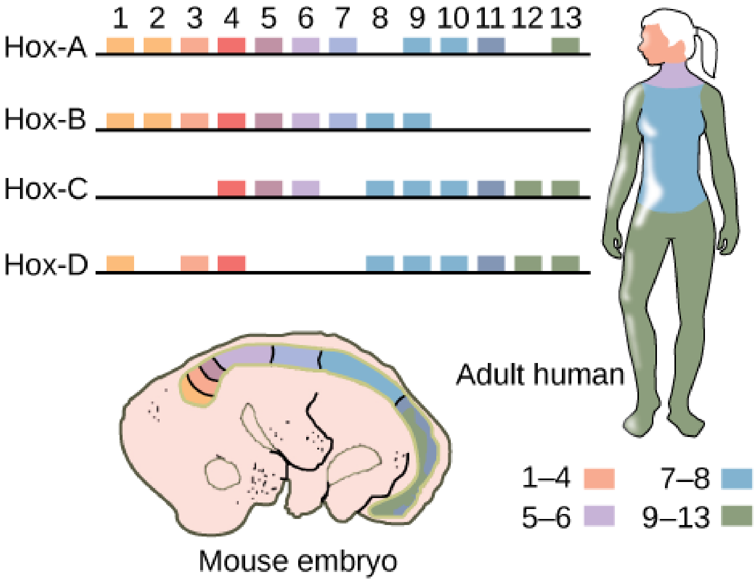


Figure 5. Hox genes are highly conserved genes encoding transcription factors that determine the course of embryonic development in animals. In vertebrates, the genes have been duplicated into four clusters: Hox-A, Hox-B, Hox-C, and Hox-D. Genes within these clusters are expressed in certain body segments at certain stages of development. Shown here is the homology between Hox genes in mice and humans. Note how Hox gene expression, as indicated with orange, pink, blue and green shading, occurs in the same body segments in both the mouse and the human.

Review Question:

If a *Hox* 13 gene in a mouse was replaced with a *Hox* 1 gene, how might this alter animal development?

Which of the following phenotypes would most likely be the

result of a *Hox* gene mutation?
A) abnormal body length or height
B) two different eye colors
C) the contraction of a genetic illness
D) two fewer appendages than normal

SUMMARY

Animals constitute an incredibly diverse kingdom of organisms. Although animals range in complexity from simple sea sponges to human beings, most members of the animal kingdom share certain features. Animals are eukaryotic, multicellular, heterotrophic organisms that ingest their food and usually develop into motile creatures with a fixed body plan. A major characteristic unique to the animal kingdom is the presence of differentiated tissues, such as nerve, muscle, and connective tissues, which are specialized to perform specific functions. Most animals undergo sexual reproduction, leading to a series of developmental embryonic stages that are relatively similar across the animal kingdom. A class of transcriptional control genes called *Hox* genes directs the organization of the major animal body plans, and these genes are strongly homologous across the animal kingdom.

End of Section Review Questions:

Review: General Animal Characteristics
Which of the following is NOT a feature common to *most* animals?
A) development into a fixed body plan
B) asexual reproduction
C) specialized tissues
D) heterotrophic nutrient sourcing

Extra: E.O. Wilson on the importance of diversity

https://youtu.be/e-txR1WSPBs

34.

Learning Goals

By the end of this reading you should be able to:

- Explain the differences in animal body plans that support basic animal classification
- Compare and contrast the embryonic development of protostomes and deuterostomes

Introduction

Scientists have developed a classification scheme that categorizes all members of the animal kingdom, although there are exceptions to most "rules" governing animal classification (Fig. 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.

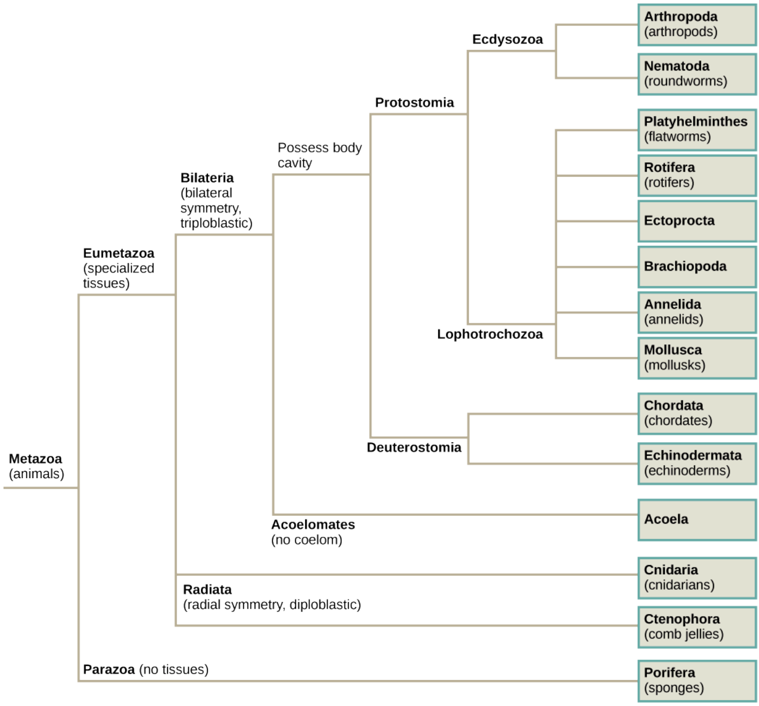


Figure 1. The phylogenetic tree of animals is based on morphological, fossil, and genetic evidence.

Animal Characterization Based on Body Symmetry

At a very basic level of classification, true animals can be largely divided into three groups based on the type of symmetry of their body plan: radially symmetrical, bilaterally symmetrical, and asymmetrical. Asymmetry is a unique feature of Parazoa (Fig. 2a). Only a few animal groups display radial symmetry. All types of symmetry are well suited to meet the unique demands of a particular animal's lifestyle.

Radial symmetry is the arrangement of body parts around a central axis, as is seen in a pie. It results in animals having top and bottom surfaces but no left and right sides, or front or back. The two halves of a radially symmetrical animal may be described as the side with a mouth or "oral side," and the side without a mouth (the "aboral side"). This form of symmetry marks the body plans of animals in the phyla Ctenophora and Cnidaria, including jellyfish and adult sea anemones (**Figure 2bc**). Radial symmetry equips these sea creatures (which may be sedentary or only capable of slow movement or floating) to experience the environment equally from all directions.

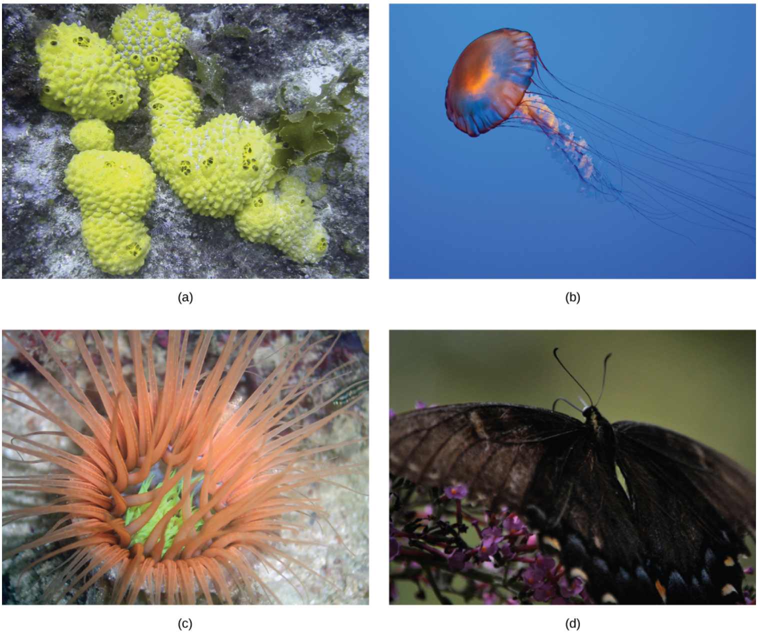


Figure 2. The (a) sponge is asymmetrical. The (b) jellyfish and (c) anemone are radially symmetrical, and the (d) butterfly is bilaterally symmetrical. (credit a: modification of work by Andrew Turner; credit b: modification of work by Robert Freiburger; credit c: modification of work by Samuel Chow; credit d: modification of work by Cory Zanker)

Bilateral symmetry involves the division of the animal through a sagittal plane, resulting in two mirror images, right and left halves, such as those of a butterfly (Fig. 2d), crab, or human body. Animals with bilateral symmetry have a "head" and "tail" (cranial vs. caudal), front and back (dorsal vs. ventral), and right and left sides (Fig. 3). All true animals except those with radial symmetry are bilaterally symmetrical. The evolution of bilateral symmetry that allowed for the formation of cranial and caudal (head and tail) ends promoted a phenomenon called cephalization, which refers to the collection of an organized nervous system at the animal's cranial end. In contrast to radial symmetry, which is best suited for stationary or limited-motion lifestyles, bilateral symmetry allows for streamlined and directional motion. In evolutionary terms, this simple form of symmetry promoted active mobility and increased sophistication of resource-seeking and predator-prey relationships.

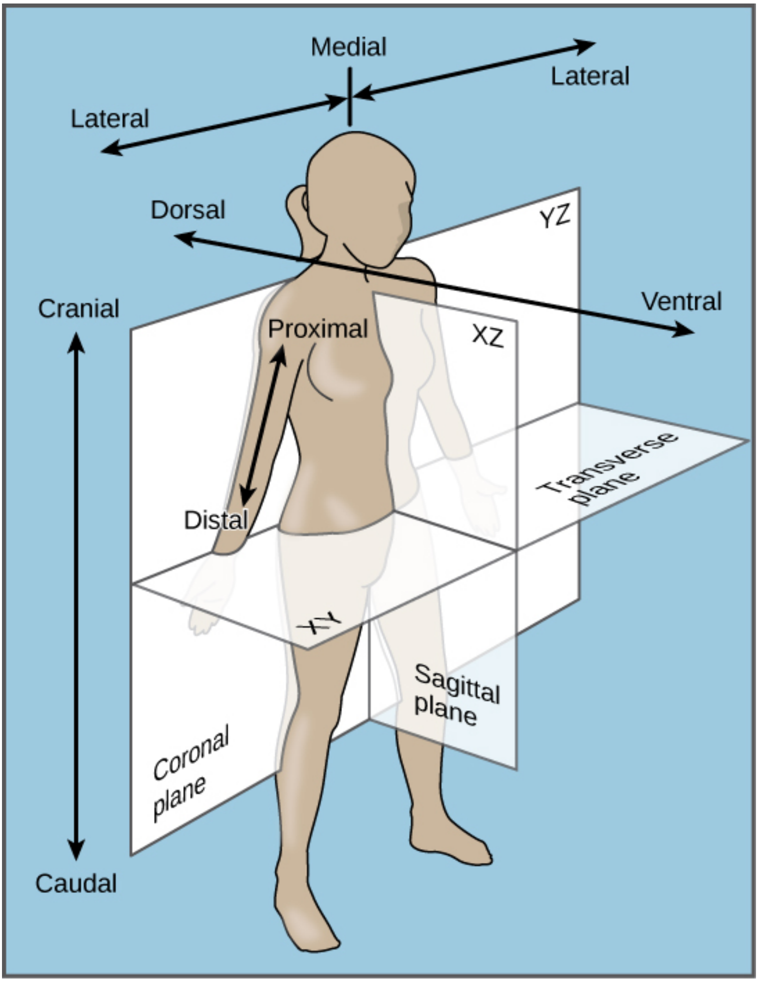


Figure 3. The bilaterally symmetrical human body can be divided into planes.

Animals in the phylum Echinodermata (such as sea stars, sand dollars, and sea urchins) display radial symmetry as adults, but their larval stages exhibit bilateral symmetry. This is termed secondary radial symmetry. They are believed to have evolved from bilaterally symmetrical animals; thus, they are classified as bilaterally symmetrical.

Watch this **video (http://openstaxcollege.org/l/symmetry)** to see a quick sketch of the different types of body symmetry.

Animal Characterization Based on Features of Embryological Development

Most animal species undergo a separation of tissues into germ layers during embryonic development. Recall that these germ layers are formed during gastrulation, and that they are predetermined to develop into the animal's specialized tissues and organs. Animals develop either two or three embryonic germs layers (Fig. 4). The animals that display radial symmetry develop two germ layers, an inner layer (**endoderm**) and an outer layer (**ectoderm**). These animals are called **diploblasts**. Diploblasts have a non-living layer between the endoderm and ectoderm. More complex animals (those with bilateral symmetry) develop three tissue layers: an inner layer (endoderm), an outer layer (ectoderm), and a middle layer (mesoderm). Animals with three tissue layers are called **triploblasts**.

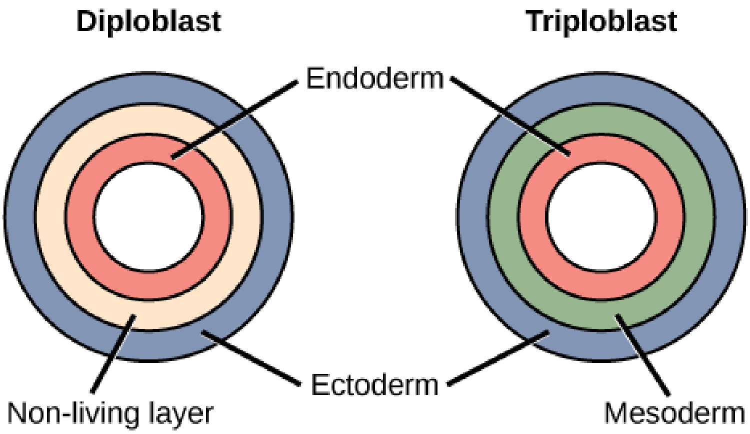


Figure 4. During embryogenesis, diploblasts develop two embryonic germ layers: an ectoderm and an endoderm. Triploblasts develop a third layer—the mesoderm—between the endoderm and ectoderm.

Review Question:

Diploblast vs Triploblast
Which of the following statements about diploblasts and triploblasts is false?
A) Animals that display radial symmetry are diploblasts.
B) Animals that display bilateral symmetry are triploblasts.
C) The endoderm gives rise to the lining of the digestive tract and the respiratory tract.
D) The mesoderm gives rise to the central nervous system.

Each of the three germ layers is programmed to give rise to particular body tissues and organs. In tetrapod vertebrates, 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** (sē'-lûm), 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) (Fig. 5). A true coelom arises entirely within the mesoderm germ layer and is lined by an epithelial membrane. This membrane also lines the organs within the coelom, connecting and holding them in position while allowing them some free motion. Annelids, mollusks, arthropods, echinoderms, and chordates are all eucoelomates. The third group of triploblasts has a slightly different coelom derived partly from mesoderm and partly from endoderm, which is found between the two layers. Although still functional, these are considered false coeloms, and those animals are called **pseudocoelomates**. The phylum Nematoda (roundworms) is an example of a pseudocoelomate. True coelomates can be further characterized based on certain features of their early embryological development.

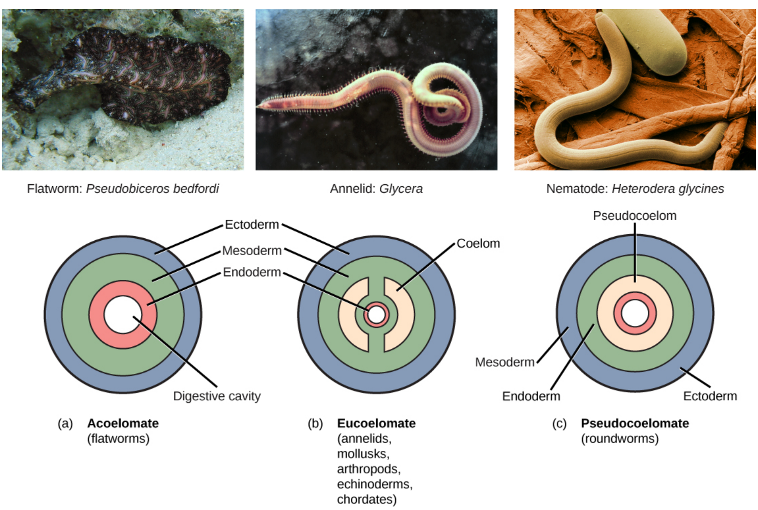


Figure 5. Triploblasts may be (a) acoelomates, (b) eucoelomates, or (c) pseudocoelomates. Acoelomates have no body cavity. Eucoelomates have a body cavity within the mesoderm, called a coelom, which is lined with mesoderm. Pseudocoelomates also have a body cavity, but it is sandwiched between the endoderm and mesoderm. (credit a: modification of work by Jan Derk; credit b: modification of work by NOAA; credit c: modification of work by USDA, ARS)

Embryonic Development of the Mouth

Bilaterally symmetrical, triploblastic 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 6**). The **blastopore** is the indentation formed during the initial stages of gastrulation. In later stages, a second opening forms, and these two openings will eventually give rise to the mouth and anus (**Figure 6**). It has long been believed that the blastopore develops into the mouth of protostomes, with the second opening developing into the anus; the opposite is true for deuterostomes. Recent evidence has challenged this view of the development of the blastopore of protostomes, however, and the theory remains under debate.

Another distinction between protostomes and deuterostomes is the method of coelom formation, beginning from the gastrula stage. The coelom of most protostomes is formed through a process called **schizocoely**, meaning that during development, a solid mass of the mesoderm splits apart near the blastopore 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 lining the **archenteron**, or primitive digestive tube. These pouches eventually fuse to form the mesoderm, which then gives rise to the coelom.

The earliest distinction between protostomes and deuterostomes is the type of cleavage undergone by the zygote. Protostomes undergo **spiral cleavage**, meaning that the cells of one pole of the embryo are rotated, and thus misaligned, with respect to the cells of the opposite pole. This is due to the oblique angle of the cleavage. Deuterostomes undergo **radial cleavage**, where the cleavage axes are either parallel or perpendicular to the polar axis, resulting in the alignment of the cells between the two poles.

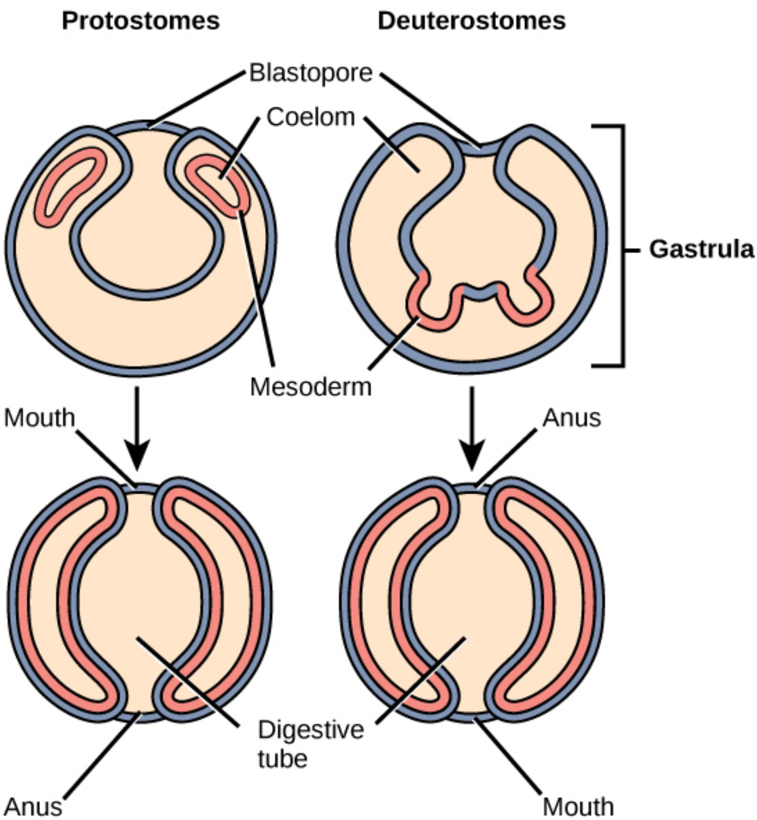


Figure 6. Eucoelomates can be divided into two groups based on their early embryonic development. In protostomes, part of the mesoderm separates to form the coelom in a process called schizocoely. In deuterostomes, the mesoderm pinches off to form the coelom in a process called enterocoely. It was long believed that the blastopore developed into the mouth in protostomes and into the anus in deuterostomes, but recent evidence challenges this belief.

There is a second distinction between the types of cleavage in protostomes and deuterostomes. In addition to spiral cleavage, protostomes also undergo **determinate cleavage**. This means that even at this early stage, the developmental fate of each embryonic cell is already determined. A cell does not have the ability to develop into any cell type. In contrast, deuterostomes undergo **indeterminate cleavage**, in which cells are not yet pre-determined at this early stage to develop into specific cell types. These cells are referred to as undifferentiated cells. This characteristic of deuterostomes is reflected in the existence of familiar embryonic stem cells, which have the ability to develop into any cell type until their fate is programmed at a later developmental stage as well as the capability of producing identical twins.

Summary

Organisms in the animal kingdom are classified based on their body morphology and development. True animals are divided into those with radial versus bilateral symmetry. Generally, the simpler and often non-motile animals display radial symmetry. Animals with radial symmetry are also generally characterized by the development of two embryological germ layers, the endoderm and ectoderm, whereas animals with bilateral symmetry are generally characterized by the development of a third embryological germ layer, the mesoderm. Animals with three germ layers, called triploblasts, are further characterized by the presence or absence of an internal body cavity called a coelom. The presence of a coelom affords many advantages, and animals with a coelom may be termed true coelomates or pseudocoelomates, depending on which tissue gives rise to the coelom. Coelomates are further divided into one of two groups called protostomes and deuterostomes, based on a number of developmental characteristics, including differences in zygote cleavage and method of coelom formation.

End of Section Review Questions:

Review: Diploblast
1) Which of the following organism is most likely to be a diploblast?
A) sea star
B) shrimp
C) jellyfish
D) insect

Review: Organization
2) Which of the following is not possible?
A) radially symmetrical diploblast
B) diploblastic eucoelomate
C) protostomic coelomate
D) bilaterally symmetrical deuterostome

Review: Organization 2
3) An animal whose development is marked by radial cleavage and enterocoely is ________.
A) a deuterostome
B) an annelid or mollusk
C) either an acoelomate or eucoelomate
D) none of the above

Review: Tissue evolution
4) Why might the evolution of specialized tissues be important for animal function and complexity?

Review: Humans
5) Describe and give examples of how humans display all of the features common to the animal kingdom.
Review: Humans 2
6) Using the following terms, explain what classifications and groups humans fall into, from the most general to the most specific: symmetry, germ layers, coelom, cleavage, embryological development.

Review: Bilateral Symmetry and Coelom
7) Explain some of the advantages brought about through the evolution of bilateral symmetry and coelom formation.

35.

Learning Goals

By the end of this reading you should be able to:

- Describe the organizational features of the simplest multicellular animals
- Explain the various body forms and bodily functions of sponges
- Compare structural and organizational characteristics of Porifera and Cnidaria
- Describe the progressive development of tissues and their relevance to animal complexity

Introduction

Biologists strive to understand the evolutionary history and relationships of members of the animal kingdom, and all of life, for that matter. Currently, most biologists divide the animal kingdom into 35 to 40 phyla. 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 (choan – Greek for "funnel"). These protist cells strongly resemble the sponge choanocyte cells today (Fig. 1).

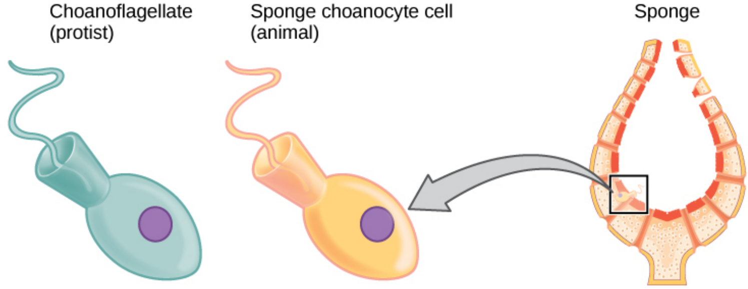


Figure 1. Cells of the protist choanoflagellate resemble sponge choanocyte cells. The beating of choanocyte flagella draws water through the sponge so that nutrients can be extracted and the waste removed.

Eumetazoa is subdivided into radially symmetrical animals and bilaterally symmetrical animals, and are thus classified into the clades Bilateria or Radiata, respectively. 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). Ecdysozoa includes nematodes and arthropods (Fig. 2); they are so named for a commonly found characteristic among the group: exoskeletal molting (termed ecdysis). Lophotrochozoa is named for two structural features, each common to certain phyla within the clade. Some lophotrochozoan phyla are characterized by a larval stage called trochophore larvae, and other phyla are characterized by the presence of a feeding structure called a lophophore.

(a) (b)

Figure 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)

Phylum Porifera

The invertebrates (Invertebrata) are animals that do not contain bony structures, such as a cranium and vertebrae. The simplest of all invertebrate animals are the Parazoans, which include only the phylum Porifera: the sponges. Parazoans do not display tissue-level organization, although they do have specialized cells that perform specific functions. While the larvae of sponges are able to swim the adults are non-motile (sessile) and spend their life attached to a solid surface. 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.

Morphology of Sponges

Figure 3. Sponges are members of the Phylum Porifera, which contains the simplest invertebrates. (credit: Andrew Turner)

The morphology of the simplest sponges (Fig. 3) takes the shape of a cylinder with a large central cavity, the spongocoel, occupying the inside of the cylinder (Fig. 4). Water can enter into the spongocoel from numerous pores in the body wall. Water entering the spongocoel is expelled through 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. N*ote 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. https://youtu.be/pTZ211cIjX8

The second crucial cells in sponges are called amoebocytes, 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.

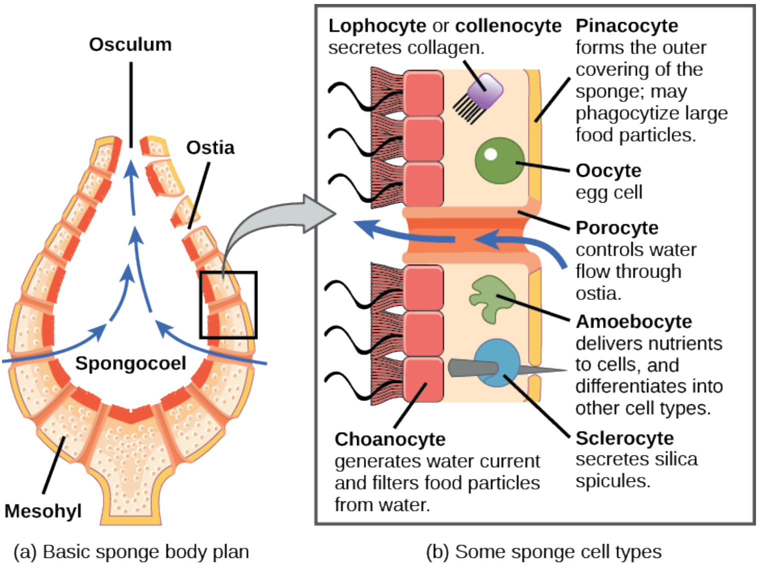


Figure 4. The sponge's (a) basic body plan and (b) some of the specialized cell types found in sponges are shown.

Review Question:

Sponges

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.

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.

Physiological Processes in Sponges

Sponges, despite being simple organisms, regulate their different physiological processes through a variety of mechanisms. These processes regulate their metabolism, reproduction, and locomotion.

Digestion: Sponges lack complex digestive, respiratory, circulatory, reproductive, and nervous systems. Their food is trapped when water passes through the ostia and out through the osculum. Bacteria smaller than 0.5 microns in size are trapped by choanocytes, which are the principal cells engaged in nutrition, and are ingested by phagocytosis. Particles that are larger than the ostia may be phagocytized by pinacocytes. In some sponges, amoebocytes transport food from cells that have ingested food particles to those that do not. For this type of digestion, in which food particles are digested within individual cells, the sponge draws water through diffusion. The limit of this type of digestion is that food particles must be smaller than individual cells. All other major body functions in the sponge (gas exchange, circulation, excretion) are performed by diffusion between the cells that line the openings within the sponge and the water that is passing through those openings. All cell types within the sponge obtain oxygen from water through diffusion. Likewise, carbon dioxide is released into seawater by diffusion. In addition, nitrogenous waste produced as a byproduct of protein metabolism is excreted via diffusion by individual cells into the water as it passes through the sponge.

Reproduction: Sponges reproduce by sexual as well as asexual methods. The typical means of asexual reproduction is either fragmentation (where a piece of the sponge breaks off, settles on a new substrate, and develops into a new individual) or budding (a genetically identical outgrowth grows from the parent and eventually detaches or remains attached to form a colony). An atypical type of asexual reproduction is found only in freshwater sponges and occurs through the formation of gemmules. Gemmules are environmentally resistant structures produced by adult sponges wherein the typical sponge morphology is inverted. In gemmules, an inner layer of amoebocytes is surrounded by a layer of collagen (spongin) that may be reinforced by spicules. The collagen that is normally found in the mesohyl becomes the outer protective layer. In freshwater sponges, gemmules may survive hostile environmental conditions like changes in temperature and serve to recolonize the habitat once environmental conditions stabilize. Gemmules are capable of attaching to a substratum and generating a new sponge. Since gemmules can withstand harsh environments, are resistant to desiccation, and remain dormant for long periods, they are an excellent means of colonization for a sessile organism.

Sexual reproduction in sponges occurs when gametes are generated. Sponges are monoecious (hermaphroditic), which means that one individual can produce both gametes (eggs and sperm) simultaneously. In some sponges, the 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 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.

Phylum Cnidaria

The 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.

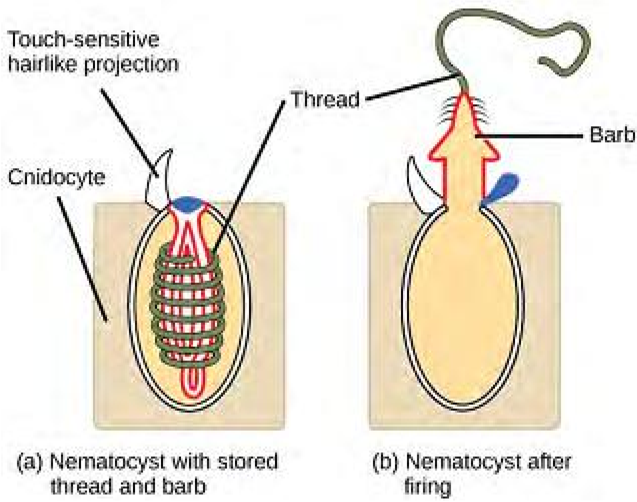


Figure 5. Animals from the phylum Cnidaria have stinging cells called cnidocytes. Cnidocytes contain large organelles called (a) nematocysts that store a coiled thread and barb. When hairlike projections on the cell surface are touched, (b) the thread, barb, and a toxin are fired from the organelle.

Cnidarians contain specialized cells known as cnidocytes ("stinging cells") with organelles called nematocysts that contain coiled threads that may bear barb (stingers) (Fig. 5). These cells are present around the mouth and tentacles. The outer wall of the cell has hairlike projections, 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 or ensnare it. These coiled threads release toxins into the target and can often immobilize prey or scare away predators.

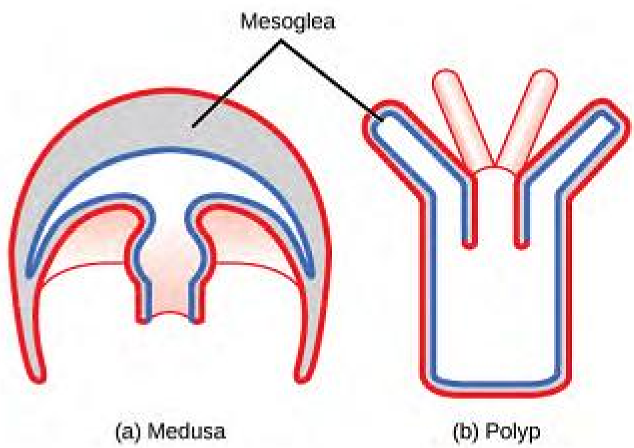


Figure 6. Cnidarians have two distinct body plans, the medusa (a) and the polyp (b). All cnidarians have two membrane layers, with a jelly-like mesoglea between them.

Cnidarians display two distinct morphological body plans: polyp or "stalk" and medusa or "bell" (Fig. 6). 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.

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.

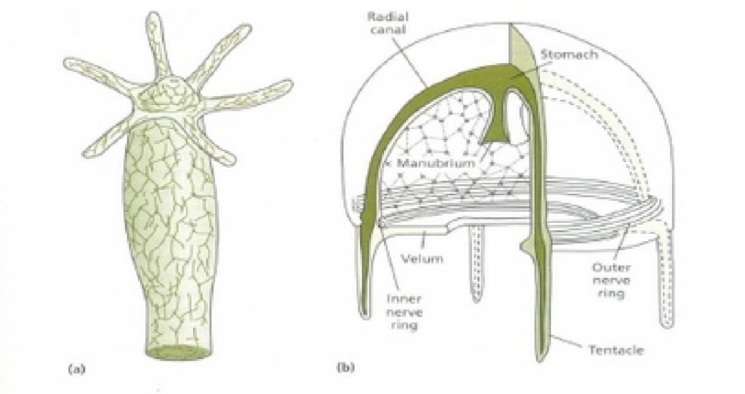


Figure 7. Nerve cells are scattered throughout the body of the (a) polyp and (b) medusa. This creates a nerve net that allows for both motion and sensing.

The nerve cells show mixed characteristics of motor as well as sensory neurons (Fig. 7). The predominant signaling molecules in these primitive nervous systems are chemical peptides, which perform both excitatory and inhibitory functions. Despite the simplicity of the nervous system, it coordinates the movement of tentacles, the drawing of captured prey to the mouth, the digestion of food, and the expulsion of waste.

The cnidarians perform extracellular digestion in which the food is taken into the gastrovascular cavity, enzymes are secreted into the cavity, and the cells lining the cavity absorb nutrients. The gastrovascular cavity has only one opening that serves as both a mouth and an anus, which is termed an incomplete digestive system.

Cnidarian cells exchange oxygen and carbon dioxide by diffusion between cells in the epidermis with water in the environment, and between cells in the gastrodermis with water in the gastrovascular cavity. The lack of a circulatory system to move dissolved gases limits the thickness of the body wall and necessitates a non-living mesoglea between the layers. There is no excretory system or organs, and nitrogenous wastes simply diffuse from the cells into the water outside the animal or in the gastrovascular cavity. There is also no circulatory system, so nutrients must move from the cells that absorb them in the lining of the gastrovascular cavity through the mesoglea to other cells.

Summary

Animals included in phylum Porifera are parazoans because they do not show the formation of true embryonically derived tissues, although they have a number of specific cell types and "functional" tissues such as pinacoderm. These organisms show very simple organization, with a rudimentary endoskeleton of spicules and spongin fibers. Glass sponge cells are connected together in a multinucleated syncytium. Although sponges are very simple in organization, they perform most of the physiological functions typical of more complex animals.

Cnidarians represent a more complex level of organization than Porifera. They possess outer and inner tissue layers that sandwich a noncellular mesoglea between them. Cnidarians possess a well-formed digestive system and carry out extracellular digestion in a digestive cavity that extends through much of the animal. The mouth is surrounded by tentacles that contain large numbers of cnidocytes—specialized cells bearing nematocysts used for stinging and capturing prey as well as discouraging predators. Cnidarians have separate sexes and many have a lifecycle that involves two distinct morphological forms—medusoid and polypoid—at various stages in their life cycles. In species with both forms, the medusa is the sexual, gamete-producing stage and the polyp is the asexual stage. Cnidarian species include individual or colonial polypoid forms, floating colonies, or large individual medusa forms (sea jellies).

End of Section Review Questions:

Review: Key Characteristics

1) Match each group with the appropriate characteristic

1) Parazoa	A) no true tissues
2) Cnidarians	B) bilateral symmetry
3) Ecdysozoa	C) radial symmetry

Review: Sponges

2) Amongst the different species of sponges how do body forms vary?

A) differences in the size of the spongocoel
B) differences in the types of tissues that are found in mesophyl
C) differences in the number of osculi
D) alterations in where the cells that filter food from the water are located

Review: Sponge amoebocytes

3) What are some of the functions of amoebocytes in sponges?

A) delivering nutrients from choanocytes to other cells within the sponge
B) giving rise to eggs for sexual reproduction
C) delivering phagocytized sperm from choanocytes to eggs
D) moving water through the mesohyl

Review: Porifera vs Cnidaria

4) What features do Cnidarians have that Poriferans do not?

A) Cnidarians have simple tissues

B) Cnidarians have differentiated cells

C) Cnidarians have intercellular connections

D) Cnidarians utilize diffusion for gas exchange

36.

Learning Goals

- List and describe the functions of the structural components of a neuron
- List and describe the four main types of neurons
- Compare the functions of different types of glial cells

Introduction

When you're reading this, your nervous system is performing several functions simultaneously. The visual system is processing what is seen on the page; the motor system controls the turn of the pages (or click of the mouse); the prefrontal cortex maintains attention. Even fundamental functions, like breathing and regulation of body temperature, are controlled by the nervous system. A nervous system is an organism's control center: it processes sensory information from outside (and inside) the body and controls all behaviors—from eating to sleeping to finding a mate.

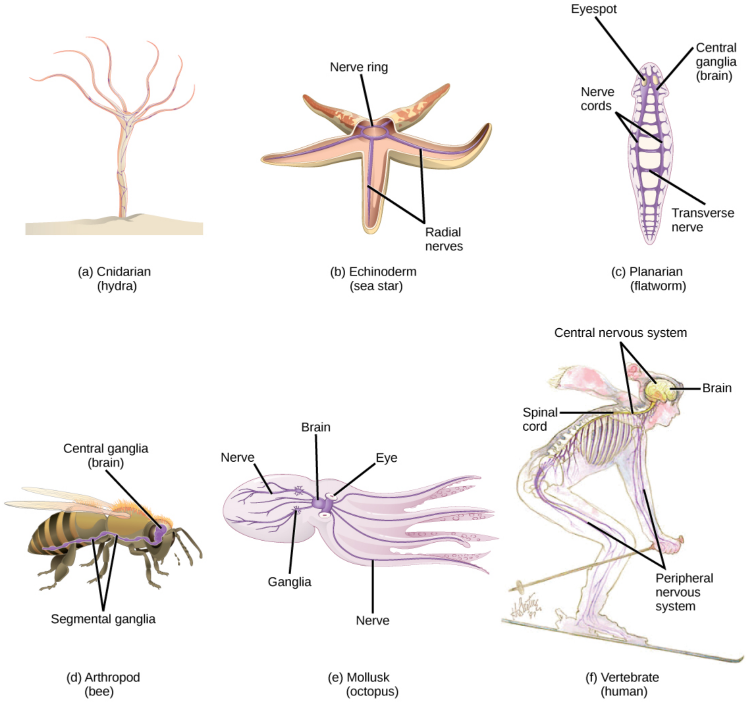


Figure 1. Nervous systems vary in structure and complexity. (credit e: modification of work by Michael Vecchione, Clyde F.E. Roper, and Michael J. Sweeney, NOAA; credit f: modification of work by NIH)

Nervous systems throughout the animal kingdom vary in structure and complexity, as illustrated by the variety of animals shown in Figure 1. Some organisms, like sea sponges, lack a true nervous system. Others, like jellyfish, lack a true brain and instead have a system of separate but connected nerve cells (neurons) called a "nerve net." Regardless of the animal, the nervous system is made up of neurons, specialized cells that can receive and transmit chemical or electrical signals, and glia, cells that provide support functions for the neurons by playing an information processing role that is complementary to neurons. A neuron can be compared to an electrical wire—it transmits a signal from one place to another.

Glia can be compared to the workers at the electric company who make sure wires go to the right places, maintain the wires, and take down wires that are broken. Although glia have been compared to workers, recent evidence suggests that also usurp some of the signaling functions of neurons. There is great diversity in the types of neurons and glia that are present in different parts of the nervous system.

Neurons

The nervous system of the common laboratory fly, *Drosophila melanogaster*, contains around 100,000 neurons, the same number as a lobster. This number compares to 75 million in the mouse and 300 million in the octopus. A human brain contains around 86 billion neurons. Despite these very different numbers, the nervous systems of these animals control many of the same behaviors—from basic reflexes to more complicated behaviors like finding food and courting mates. The ability of neurons to communicate with each other as well as with other types of cells underlies all of these behaviors. Most neurons share the same cellular components. But neurons are also highly specialized—different types of neurons have different sizes and shapes that relate to their functional roles.

Parts of a Neuron

Like other cells, each neuron has a cell body (or soma) that contains a nucleus, smooth and rough endoplasmic reticulum, Golgi apparatus, mitochondria, and other cellular components. Neurons also contain unique structures, for receiving and sending the electrical signals that make neuronal communication possible. Dendrites are tree-like structures that extend away from the cell body to receive messages from other neurons at specialized junctions called synapses. Although some neurons do not have any dendrites, some types of neurons have multiple dendrites. Dendrites can have small protrusions called dendritic spines, which further increase surface area for possible synaptic connections.

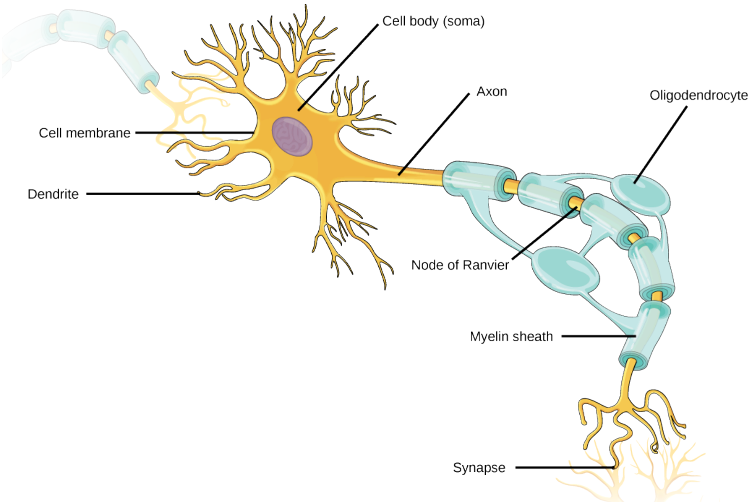


Figure 2. Neurons contain organelles common to many other cells, as well as more specialized structures that are related to how they function.

Once a signal is received by the dendrite, it then travels passively to the cell body. The cell body contains a specialized structure, the axon hillock that integrates signals from multiple synapses and serves as a junction between the cell body and an axon. An axon is a tube-like structure that propagates the integrated signal to specialized endings called axon terminals. These terminals in turn synapse on other neurons, muscles, or target organs. Chemicals released at axon terminals allow signals to be communicated to these other cells. Neurons usually have one or two axons, but some neurons, like amacrine cells in the retina, do not contain any axons. Some axons are covered with myelin, which acts as an insulator to minimize the dissipation of the electrical signal as it travels down the axon, greatly increasing the speed of conduction. This insulation is important as the axon from a human motor neuron can be as long as a meter—from the base of the spine to the toes. The myelin sheath is not actually part of the neuron. Myelin is produced by glial cells. Along the axon, there are periodic gaps in the myelin sheath. These gaps are sites where the signal is "recharged" as it travels along the axon.

It is important to note that a single neuron does not act alone—neuronal communication depends on the connections that neurons make with one another (as well as with other cells, like muscle cells). Dendrites from a single neuron may receive synaptic contact from many other neurons. For example, dendrites from a Purkinje cell in the cerebellum are thought to receive contact from as many as 200,000 other neurons.

Review Question:

Quick Review: Neurons

Which of the following is not an accurate statement about neurons?

A) The soma is the cell body of a nerve cell.
B) Myelin sheath provides an insulating layer to the dendrites.
C) Axons carry the signal from the soma to the target.
D) Dendrites carry the signal to the soma.

Types of Neurons

There are four different types of neurons, and the functional role of a given neuron is intimately dependent on its structure. There is an amazing diversity of neuron shapes and sizes found in different parts of the nervous system (and across species).

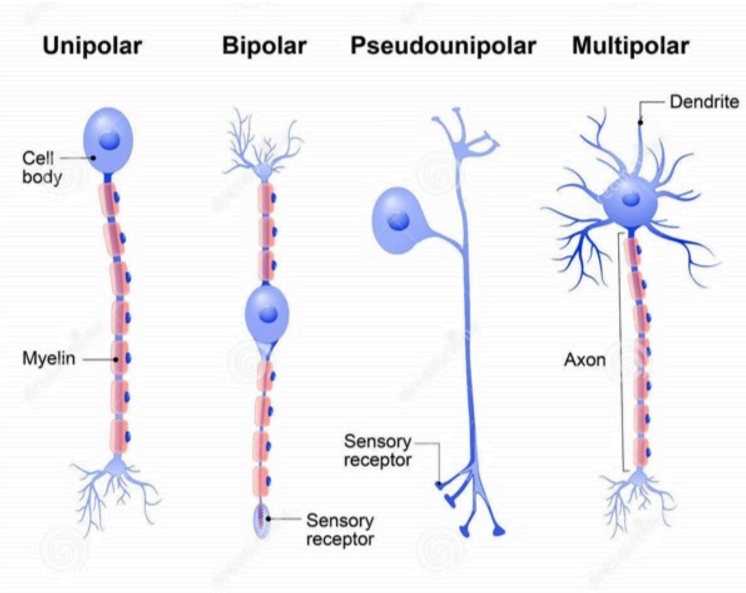


Figure 3. Representative structures of the four different types of neurons.

While there are many defined neuron cell subtypes, neurons are broadly divided into four basic types: unipolar, bipolar, multipolar, and pseudounipolar. Unipolar neurons have only one structure that extends away from the soma. These neurons are not found in vertebrates but are found in insects where they stimulate muscles or glands. A bipolar neuron has one axon and one dendrite extending from the soma. An example of a bipolar neuron is a retinal bipolar cell, which receives signals from photoreceptor cells that are sensitive to light and transmits these signals to ganglion cells that carry the signal to the brain. Multipolar neurons are the most common type of neuron. Each multipolar neuron contains one axon and multiple dendrites. Multipolar neurons can be found in the central nervous system (brain and spinal cord). An example of a multipolar neuron is a Purkinje cell in the cerebellum, which has many branching dendrites but only one axon. Pseudounipolar cells share characteristics with both unipolar and bipolar cells. A pseudounipolar cell has a single process that extends from the soma, like a unipolar cell, but this process later branches into two distinct structures, like a bipolar cell. Most sensory neurons are pseudounipolar and have an axon that branches into two extensions: one connected to dendrites that receive sensory information and another that transmits this information to the spinal cord.

Neurogenesis: At one time, scientists believed that people were born with all the neurons they would ever have. Research performed during the last few decades indicates that neurogenesis, the birth of new neurons, continues into adulthood. Neurogenesis was first discovered in songbirds that produce new neurons while learning songs. For mammals, new neurons also play an important role in learning: about 1000 new neurons develop in the hippocampus (a brain structure involved in learning and memory) each day. While most of the new neurons will die, researchers found that an increase in the number of surviving new neurons in the hippocampus correlated with how well rats learned a new task. Interestingly, both exercise and some antidepressant medications also promote neurogenesis in the hippocampus. Stress has the opposite effect. While neurogenesis is quite limited compared to regeneration in other tissues, research in this area may lead to new treatments for disorders such as Alzheimer's, stroke, and epilepsy

Glia

While glia are often thought of as the supporting cast of the nervous system, the number of glial cells in the brain actually outnumbers the number of neurons by a factor of ten. Neurons would be unable to function without the vital roles that are fulfilled by these glial cells. Glia guide developing neurons to their destinations, buffer ions and chemicals that would otherwise harm neurons and provide myelin sheaths around axons. Scientists have recently discovered that they also play a role in responding to nerve activity and modulating communication between nerve cells. When glia do not function properly, the result can be disastrous—most brain tumors are caused by mutations in glia.

Types of Glia

Each type of glial cell has different functions and thus different interactions with the nervous system:

- *Astrocytes* make contact with both capillaries and neurons in the CNS. They provide nutrients and other substances to neurons, regulate the concentrations of ions and chemicals in the extracellular fluid, and provide structural support for synapses. Astrocytes also form the blood-brain barrier—a structure that blocks entrance of toxic substances into the brain. Astrocytes become active in response to nerve activity, transmit calcium waves between neurons, and modulate the activity of surrounding synapses.
- Satellite glia provide nutrients and structural support for neurons in the peripheral nervous system (PNS).
- Microglia scavenge and degrade dead cells and protect the brain from invading microorganisms.
- Oligodendrocytes form myelin sheaths around axons in the central nervous system (CNS). One axon can be myelinated by several oligodendrocytes, and one oligodendrocyte can provide myelin for multiple neurons.
- Schwan cells form myelin sheaths around axons in the PNS where a single Schwann cell provides myelin for only one axon

as the entire Schwann cell surrounds the axon.

- Radial glia give rise to new neurons (neurogenesis) and serve as scaffolds for developing neurons as they migrate to their end destinations.
- Ependymal cells line fluid-filled ventricles of the brain and the central canal of the spinal cord. They are involved in the production of cerebrospinal fluid, which serves as a cushion for the brain, moves the fluid between the spinal cord and the brain, and is a component for the choroid plexus.

This quick two-minute video reviews the functions of the different types of glial cells. https://youtu.be/AwES6R1_9PM

Quick Review: Glial cell functions
What glial cell types are involved in forming the myelin sheathing of neurons?
A) Microglia
B) Oligodendrocytes
C) Radial glia
D) Schwan cells

Summary

The nervous system is made up of neurons and glia. Neurons are specialized cells that are capable of sending electrical as well as chemical signals. Most neurons contain dendrites, which receive these signals, and axons that send signals to other neurons or tissues. There are four main types of neurons: unipolar, bipolar, multipolar, and pseudounipolar neurons. Glia are non-neuronal cells in the nervous system that support neuronal development and signaling. There are several types of glia that serve different functions.

End of Section Review Questions:

Review: Neuron Structure

1) Neurons contain _______, which can receive signals from other neurons.

A) axons

B) mitochondria

C) dendrites

D) Golgi bodies

Review: Neuron types

2) A(n) __________ neuron has one axon and one dendrite extending directly from the cell body.

A) unipolar

B) bipolar

C) multipolar

D) pseudounipolar

Review: Glial cell functions

3) What type of glial cell is involved in the immune defense of the CNS

A) Schwann cells

B) oligodendrocytes

C) microglia

D) astrocytes

4) How are neurons similar to other cells? How are they unique?

37.

Learning Goals

By the end of this reading you should be able to:

- Differentiate between different types of skeletons and give examples of organisms with each type
- Describe the advantages and disadvantages of each type of skeleton

Introduction

Figure 1. Jellyfish are simple animals with hydrostatic skeletons

The earliest forms of life evolved in the oceans. The fact that this is an aquatic environment is key. Water is about 1,000 times denser than air. The high density of water allows organisms to float, due to a physical, upward force inherent in liquids known as buoyancy. Buoyancy allowed organisms to grow and reach large sizes because the buoyancy force supported the bodyweight of these animals. However, the density of water also provides resistance to movement, and animals had to adapt to ensure that they were able to move efficiently through the water.

An early adaptation by organisms was the ability to change the hydrostatic pressure within different chambers of their bodies to enable quick movement. This resulted in the development of **hydrostatic skeletons**. Animals with this type of skeleton include jellyfish, octopuses, and sea anemones. The changing shape of the animal reduces both friction and drag.

Over time, in order to refine movement and improve protection from predators, some organisms developed a hard chitinous **exoskeleton**. Exoskeletons first developed in the aquatic environment in ancient arthropods. Animals with this type of skeleton include crustaceans like crabs and lobsters.

Eventually, there were some animals that developed a skeletal structure internal to the body, which would become the vertebrate group of animals. These animals have an **endoskeleton**. Initially, all endoskeletons were made of cartilage, which is a dense rubbery type of tissue. Later, endoskeletons of bone evolved.

Hydrostatic Skeletons

A hydrostatic skeleton is a structure found in many cold-blooded and soft-bodied organisms. It consists of a fluid-filled cavity, which is surrounded by muscles. The cavity is called a **coelom** and in some animals, this cavity is filled with a blood-like substance called **haemocoel**. The fluid presses against the muscles, which in turn contract against the pressure of the fluid. The fluid is incompressible and thus maintains a constant volume against which the muscles can contract. The hydrostatic skeleton prevents the collapse of the body. The muscles in the body act against the fluid and in doing so bring about movement. If the body is segmented, the pressure of the fluid is localised in a few segments at a time. Hydrostatic skeletons occur in flatworms, roundworms, earthworms, starfish and slugs.

Figure 2. By moving water from the vascular system into the tiny feet, the sea star can make a foot move by expanding it.

Movement in a hydrostatic skeleton is provided by muscles that surround the coelom. The muscles in a hydrostatic skeleton contract to change the shape of the coelom; the pressure of the fluid in the coelom produces movement. For example, earthworms move by waves of muscular contractions of the skeletal muscle of the body wall hydrostatic skeleton, called peristalsis, which alternately shorten and lengthen the body. Lengthening the body extends the anterior end of the organism. Most organisms have a mechanism to fix themselves in the substrate. Shortening the muscles then draws the posterior portion of the body forward.

Although a hydrostatic skeleton is well-suited to invertebrate organisms such as earthworms and some aquatic organisms, it is not an efficient skeleton for terrestrial animals.

Advantages of a hydrostatic skeleton

- **Fluid shape:** This allows organisms with hydrostatic skeletons to fit through oddly shaped passages, which is useful for burrowing or swimming.
- **Strength:** Creatures with hydrostatic skeletons can squeeze between spaces and expand, making a 'prying open' movement which allows them to force their way into various regions of rock and soil surfaces.
- **Healing:** Healing takes place faster in organisms with hydrostatic skeletons than in organisms with bone structures. This is because the haemocoel contained within the hydrostatic skeleton is made up mostly of water, and thus, can be refilled quickly. This allows many organisms with hydrostatic skeletons such as earthworms to grow back their body mass after damage.
- **Lightweight:** The hydrostatic skeleton allows the animal to move in a more flexible manner as it requires very little muscle mass for movement.
- **Circulation:** The fluid cavity allows the circulation of nutrients and waste.
- **Protection:** The hydrostatic skeletons cushions the internal organs of the animal from shock.
- **Suited to the environment:** Hydrostatic skeletons are suited for life in moist or aquatic environments, depending on the animal's adaptations.

Disadvantages of a hydrostatic skeleton

- **Structure and surface for attachment:** The hydrostatic skeleton lacks a structure and does not have surfaces for the attachment of muscles or limbs.

- **Lack of protection:** There is very little protection for the internal organs.
- **Desiccation:** A moist or water habitat is essential for the survival of these animals in order to prevent desiccation (drying out).
- **Limited strength:** Terrestrial animals with hydrostatic skeletons cannot increase their body size as they would collapse under their own body weight.

Review Question:

Quick Review: Features of Hydrostatic Skeletons
Which of the following statements about hydrostatic skeletons is accurate?
A) The pressure of the fluid in the coelom produces movement
B) Hydrostatic skeletons are efficient skeletons for terrestrial animals.
C) Movement in a hydrostatic skeleton is provided by muscles that surround the coelom.
D) Lengthening the muscles draws the posterior portion of the body forward.

Exoskeletons

An exoskeleton is an external skeleton that supports and protects an animal's body. The skeleton is non-living and consists of a cuticle strengthened by chitin, a substance secreted by the epidermis (skin). Crustaceans such as crabs have their exoskeleton further strengthened by calcium carbonate. There are muscles attached to the inside of the exoskeleton which provides the resistance needed for muscle action.

This skeleton-type provides defence against predators, supports the body, and allows for movement through the contraction of attached muscles. As with vertebrates, muscles must cross a joint inside the exoskeleton. Shortening of the muscle changes the relationship of the two segments of the exoskeleton. Arthropods such as crabs and lobsters have exoskeletons that consist of 30–50 per cent chitin, a polysaccharide derivative of glucose that is a strong but flexible material. Chitin is secreted by the epidermal cells. The exoskeleton is further strengthened by the addition of calcium carbonate in organisms such as the lobster. Because the exoskeleton is acellular, arthropods must periodically shed their exoskeletons because the exoskeleton does not grow as the organism grows.

Figure 3. Exoskeletons come in different shapes and sizes. They can also be composed of different materials.

The exoskeleton is confined to animals such as insects, spiders, scorpions, crabs etc., all of which belong to the Phylum Arthropoda (jointed-legged and jointed-bodied animals). The exoskeleton acts as a hard outer covering and is made up of a series of plates or tubes. We often call large exoskeletons `shells'.

Advantages of the exoskeleton

- **Muscle attachment:** The exoskeleton forms the point of attachment of internal muscles needed for locomotion thereby providing better leverage for muscle action.
- **Protection:** The exoskeleton protects the soft internal tissues

and organs.

- **Support:** The exoskeleton provides structural support and shape.
- **Prevents Desiccation:** The exoskeleton prevents desiccation (drying out) on land.
- **Light-weight:** The exoskeleton of insects has a low density and is therefore lightweight, to allow for flight.
- **Diversity:** The mouth-parts can be modified for biting, sucking, piercing grasping thus providing for a diversified diet for organisms possessing an exoskeleton compared to those that do not.

Disadvantages of the exoskeleton

- **Size restriction:** The final body size is limited because as the body size increases, the surface area to volume ratio decreases. The larger the animal, the heavier the exoskeleton, making movement more difficult.
- **The non-living skeleton does not grow with animals:** The overall growth of the animal is restricted due to periodic moulting. Since the exoskeleton restricts growth, moulting is required to accommodate for increases in the size of the animal.
- **Vulnerability during moulting:** The animal is vulnerable when it is in the moulting process because the new skeleton is very soft until the new exoskeleton has dried and hardened.
- **Sites of structural weakness:** Exoskeletons are weaker at the joints.

Quick Review: Exoskeletons

What is the key limitation to exoskeletons?

A) they are composed of living tissues

B) they cannot grow with the organisms

C) they can be molted (shed) as the organism grows

Endoskeletons

An endoskeleton is a skeleton that consists of hard, mineralized structures located within the soft tissue of organisms. The bones of vertebrates are composed of tissues and can consist of bone (all vertebrates except sharks) or cartilage (sharks) and some endoskeletons consist of both. Endoskeletons provide support for the body, protect internal organs, and allow for movement through the contraction of muscles attached to the skeleton.

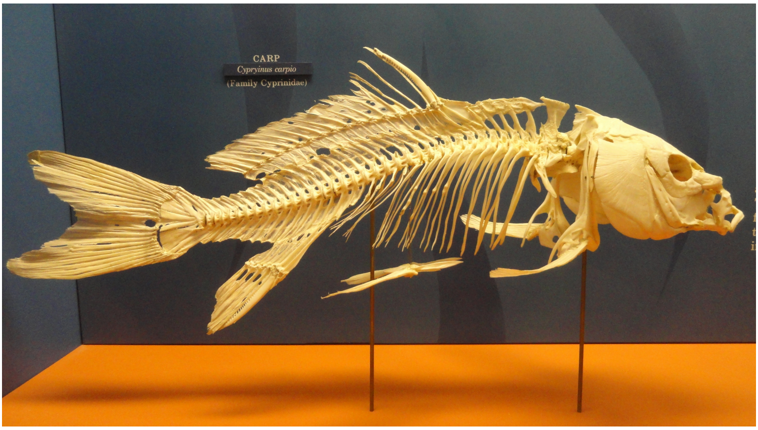


Figure 4. Fish skeleton

Advantages of the endoskeleton

- **Living:** Endoskeletons consist of living tissue, so it is able to grow steadily within the animal enabling some to reach a large size.
- **Structure and support:** The endoskeleton provides shape and structural support.
- **Structural diversity and adaptation:** The bones can vary in size and shape to support the animal's mass.
- **Flexible:** The endoskeleton is jointed which allows for flexible

movement and support.

- **Muscle attachment:** The muscles attach directly to the skeletal bones to allow for movement and support.
- **Protection:** The endoskeleton protects the vital organs such as the heart and lungs which are protected by the ribcage.
- **Diversified locomotion:** The development of an endoskeleton has allowed animals to become successfully adapted to locomotion in the environment in which they live. Vertebrates (organisms with a vertebral column and an endoskeleton) have become adapted to move in a number of different modes of locomotion, e.g. running, jumping, swimming, and flying.

Disadvantages of the endoskeleton

- **Vulnerable to the external environment:** The endoskeleton does not offer the animal any protection from the exterior, be it a physical attack or changes in environmental conditions. The animal is therefore very vulnerable.
- **Susceptible to disease:** The skeleton consists of living tissue so is susceptible to infections and disease.

Quick Review: Endoskeleton Benefits

Which of these is/are an advantage of endoskeletons?

A) they provide protection from the environment for organisms
B) they provide attachment sites for muscles
C) bone shapes and size vary providing a diversity of motion
D) can provide protection for internal organs

Summary

The three types of skeleton designs are hydrostatic skeletons, exoskeletons, and endoskeletons. A hydrostatic skeleton is formed by a fluid-filled compartment held under hydrostatic pressure;

movement is created by the muscles producing pressure on the fluid. An exoskeleton is a hard external skeleton that protects the outer surface of an organism and enables movement through muscles attached to the inside. An endoskeleton is an internal skeleton composed of hard, mineralized tissue that also enables movement by attachment to muscles.

REVIEW: Endo vs. Exoskeletons

1) How do endoskeletons vary from exoskeletons?

A) an endoskeleton lies internal to most of the body's soft tissues: exoskeletons lie outside these tissues

B) endoskeletons grow with an organism: exoskeletons must be shed and regrown

C) Exoskeletons can be repaired easily following damage: endoskeletons are more difficult to repair

D) Exoskeletons can provide protection for internal organs: endoskeletons cannot

REVIEW: Exoskeletons

2) The main component of the insect exoskeleton is __________ . Interestingly this molecule is also found in the _________ of what group of organisms? ___________

3) As animals evolved to live on land they didn't all adapt their skeletons in the same way. In a terrestrial environment what are the advantages of an exoskeleton? What about an endoskeleton?

References

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38.

Learning Goals

By the end of this reading you should be able to:

- Describe the different types of muscle tissue
- Draw the basic structure of a skeletal muscle fiber
- Explain the sliding filament model of muscle contraction
- Describe the factors that control muscle tension

Introduction

Muscle cells are specialized for contraction. Muscles allow for motions such as walking, and they also facilitate bodily processes such as respiration and digestion. The body contains three types of muscle tissue: skeletal muscle, cardiac muscle, and smooth muscle.

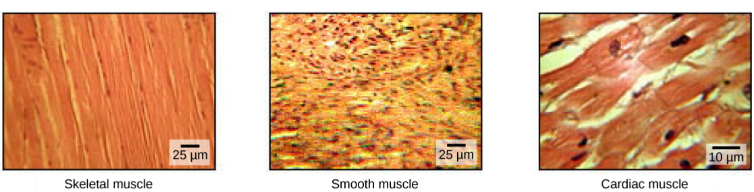

Figure 1. The body contains three types of muscle tissue: skeletal muscle, smooth muscle, and cardiac muscle, visualized here using light microscopy. Smooth muscle cells are short, tapered at each end, and have only one plump nucleus in each. Cardiac muscle cells are branched and striated, but short. The cytoplasm may branch, and they have one nucleus in the center of the cell. (credit: modification of work by NCI, NIH; scale-bar data from Matt Russell)

Skeletal muscle tissue forms skeletal muscles, which attach to bones or skin and control locomotion and any movement that can be consciously controlled. Because it can be controlled by thought, skeletal muscle is also called voluntary muscle. Skeletal muscles are long and cylindrical in appearance; when viewed under a microscope, skeletal muscle tissue has a striped or striated appearance. The striations are caused by the regular arrangement of contractile proteins (actin and myosin). Actin is a globular contractile protein that interacts with myosin for muscle contraction. Skeletal muscle also has multiple nuclei present in a single cell.

Smooth muscle tissue occurs in the walls of hollow organs such as the intestines, stomach, and urinary bladder, and around passages such as the respiratory tract and blood vessels. Smooth muscle has no striations, is not under voluntary control, has only one nucleus per cell, is tapered at both ends, and is called involuntary muscle.

Cardiac muscle tissue is only found in the heart, and cardiac contractions pump blood throughout the body and maintain blood pressure. Like skeletal muscle, cardiac muscle is striated, but unlike skeletal muscle, cardiac muscle cannot be consciously controlled and is called involuntary muscle. It has one nucleus per cell, is branched, and is distinguished by the presence of intercalated disks.

Review Question:

Quick Review: Differences in muscle tissues

Which type of muscle tissue has multinucleate cells?

A) smooth
B) skeletal
C) cardiac

Skeletal Muscle Fiber Structure

Each skeletal muscle fiber is a skeletal muscle cell. These cells are incredibly large, with diameters of up to 100 μm and lengths of up to 30 cm. The plasma membrane of a skeletal muscle fiber is called the sarcolemma. The sarcolemma is the site of action potential conduction, which triggers muscle contraction. Within each muscle fiber are myofibrils—long cylindrical structures that lie parallel to the muscle fiber. Myofibrils run the entire length of the muscle fiber, and because they are only approximately 1.2 μm in diameter, hundreds to thousands can be found inside one muscle fiber. They attach to the sarcolemma at their ends, so that as myofibrils shorten, the entire muscle cell contracts.

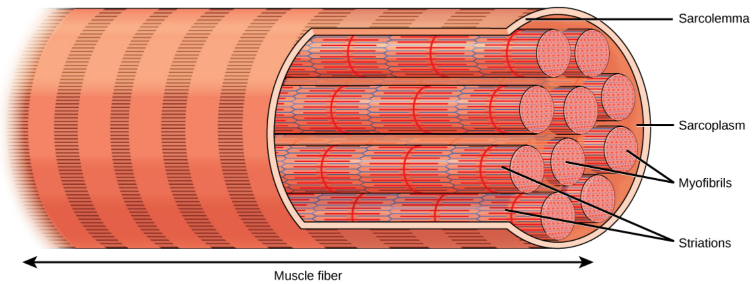

Figure 2. A skeletal muscle cell is surrounded by a plasma membrane called the sarcolemma with a cytoplasm called the sarcoplasm. A muscle fiber is composed of many fibrils, packaged into orderly units.

The striated appearance of skeletal muscle tissue is a result of repeating bands of the proteins actin and myosin that are present along the length of myofibrils. Dark A bands and light I bands repeat along myofibrils, and the alignment of myofibrils in the cell causes the entire cell to appear striated or banded.

Each I band has a dense line running vertically through the middle called a Z disc or Z line. The Z discs mark the border of units called sarcomeres, which are the functional units of skeletal muscle. One sarcomere is the space between two consecutive Z discs and contains one entire A band and two halves of an I band, one on either side of the A band. A myofibril is composed of many sarcomeres running along its length, and as the sarcomeres individually contract, the myofibrils and muscle cells shorten.

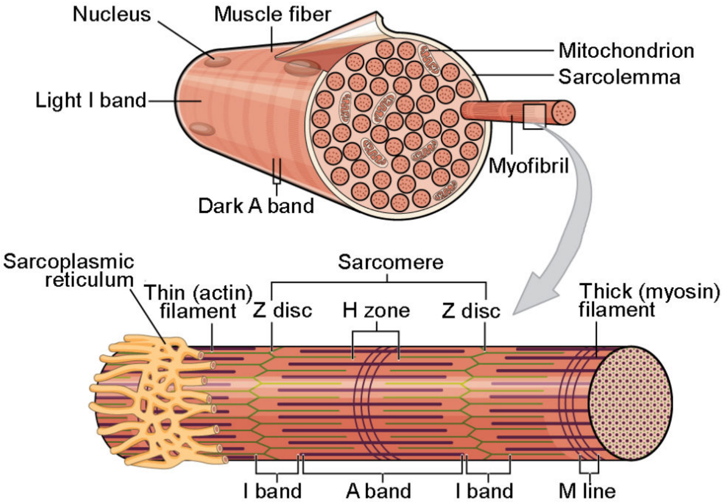

Figure 3. Anatomy of the muscle fiber and sarcomere.

Myofibrils are composed of smaller structures called myofilaments. There are two main types of filaments: thick filaments and thin filaments; each has different compositions and locations. Thick filaments are composed of the protein myosin and occur only in the A band of a myofibril. Thin filaments are comprised primarily of actin, attach to a protein in the Z disc and occur across the entire length of the I band and partway into the A band. Actin has binding sites for myosin but strands of tropomyosin filaments block the sites and prevent actin-myosin interactions when the muscles are at rest. The final component of the thin filaments in troponin, which is a globular protein with three subunits. One subunit binds to the topomyosin, one to the actin and the last to Ca^{2+} ions.

This video reviews some of the key components of skeletal muscles: https://youtu.be/XoP1diaXVCI

Review Question:

Quick Review: Filaments
Thick filaments are comprised mainly of ___________
Thin filaments are comprised mainly of ___________

Sliding Filament Model of Contraction

For a muscle cell to contract, the sarcomere must shorten. However, thick and thin filaments—the components of sarcomeres—do not shorten. Instead, they slide by one another, causing the sarcomere to shorten while the filaments remain the same length. The sliding filament theory of muscle contraction was developed to fit the differences observed in the named bands on the sarcomere at different degrees of muscle contraction and relaxation. The mechanism of contraction is the binding of myosin to actin, forming cross-bridges that generate filament movement.

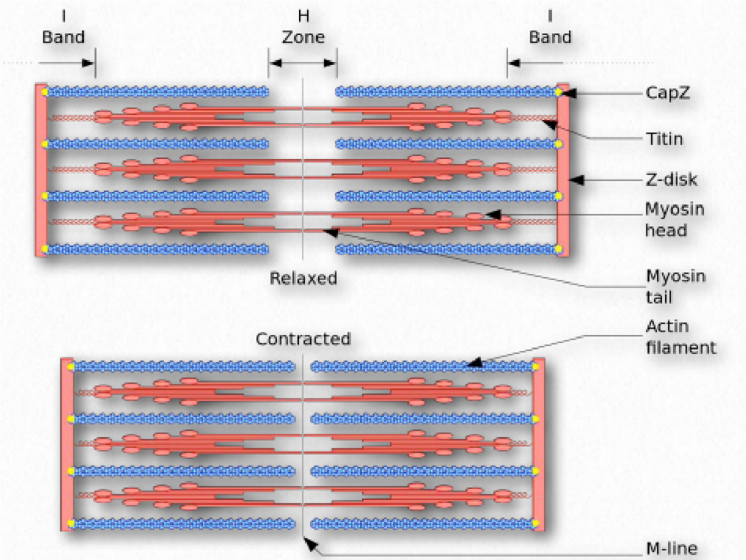

Figure 4. Sarcomere contraction

The sliding filament theory of muscle contraction can be broken down into four distinct stages;

1. Muscle activation: Each skeletal muscle fiber is controlled by a motor neuron, which conducts signals from the brain or spinal cord to the muscle. The area of the sarcolemma on the muscle fiber that interacts with the neuron is called the motor end plate. Electrical signals travel along the neuron's axon, which branches through the muscle and connects to individual muscle fibers at a neuromuscular junction. In response to a neural signal, acetylcholine (a neurotransmitter) is released from the axon terminal and binds to receptors on the sarcolemma. An action potential is generated that stimulates calcium ion release from the sarcoplasmic reticulum.

2. Muscle contraction: Calcium floods into the muscle cell where it binds to troponin, causing conformational changes in troponin that allow tropomyosin to move away from the myosin-binding sites

on actin. Once the tropomyosin is removed, a cross-bridge can form between actin and myosin. The myosin head at this point is "cocked," it contains energy and is in a high-energy configuration. Pi is then released, allowing myosin to expend the stored energy as a conformational change. The myosin head moves toward the M line, pulling the actin along with it. As the actin is pulled, the filaments move toward the M line. This movement is called the power stroke, as it is the step at which force is produced. As the actin is pulled toward the M line, the sarcomere shortens, and the muscle contracts. After the movement, ADP is released; however, the cross-bridge formed is still in place, and actin and myosin are bound together.

3. Recharging: ATP can then attach to myosin, ATP binding causes myosin to release actin, allowing actin and myosin to detach from each other. After this happens, the newly bound ATP is converted to ADP and inorganic phosphate, Pi by an enzyme at the binding site on myosin called ATPase. The energy released during ATP hydrolysis changes the angle of the myosin head into a "cocked" position. The myosin head is then in a position for further movement, possessing potential energy, but ADP and Pi are still attached. This conformation change in myosin allows the cross-bridge cycle to start again and further muscle contraction can occur triggering contraction.

4. Relaxation: Relaxation occurs when stimulation of the nerve stops. Calcium is then pumped back into the sarcoplasmic reticulum breaking the link between actin and myosin. Actin and myosin return to their unbound state causing the muscle to relax. Alternatively, relaxation (failure) will also occur when ATP is no longer available.

This video demonstrates how all the parts of the system work together to create muscle movement. https://youtu.be/BVcgO4p88AA

Review Question:

Quick Review: Muscle movement

In order for a skeletal muscle contraction to occur;

A) There must be a neural stimulus

B) There must be calcium in the muscle cells

C) ATP must be available for energy

D) Troponin levels must be low in the muscle cell

Control of Muscle Tension

Neural control initiates the formation of actin-myosin cross-bridges, leading to the sarcomere shortening involved in muscle contraction. These contractions extend from the muscle fiber through connective tissue to pull on bones, causing skeletal movement. The pull exerted by a muscle is called tension, and the amount of force created by this tension can vary. This enables the same muscles to move very light objects and very heavy objects. In individual muscle fibers, the amount of tension produced depends on the cross-sectional area of the muscle fiber and the frequency of neural stimulation.

The number of cross-bridges formed between actin and myosin determines the amount of tension that a muscle fiber can produce. Cross-bridges can only form where thick and thin filaments overlap, allowing myosin to bind to actin. If more cross-bridges are formed, more myosin will pull on actin, and more tension will be produced.

The ideal length of a sarcomere during the production of maximal tension occurs when thick and thin filaments overlap to the greatest degree. If a sarcomere at rest is stretched past an ideal resting length, thick and thin filaments do not overlap to the greatest degree, and fewer cross-bridges can form. This results in fewer myosin heads pulling on actin, and less tension is produced. As a sarcomere is shortened, the zone of overlap is reduced as the thin filaments reach the H zone, which is composed of myosin tails. Because it is myosin heads that form cross-bridges, actin will not bind to myosin in this zone, reducing the tension produced by this myofiber. If the sarcomere is shortened, even more, thin filaments begin to overlap with each other—reducing cross-bridge formation even further and producing even less tension. Conversely, if the sarcomere is stretched to the point at which thick and thin filaments do not overlap at all, no cross-bridges are formed and no tension is produced. This amount of stretching does not usually occur because accessory proteins, internal sensory nerves, and connective tissue oppose extreme stretching.

The primary variable determining force production is the number of myofibers within the muscle that receive an action potential from the neuron that controls that fiber. When using the biceps to pick up a pencil, the motor cortex of the brain only signals a few neurons of the biceps, and only a few myofibers respond. In vertebrates, each myofiber responds fully if stimulated. When picking up a piano, the motor cortex signals all of the neurons in the biceps, and every myofiber participates. This is close to the maximum force the muscle can produce. As mentioned above, increasing the frequency of action potentials (the number of signals per second) can increase the force a bit more, because the tropomyosin is flooded with calcium.

Summary

The body contains three types of muscle tissue: skeletal muscle, cardiac muscle, and smooth muscle. Skeleton muscle tissue is composed of sarcomeres, the functional units of muscle tissue. Muscle contraction occurs when sarcomeres shorten, as thick and thin filaments slide past each other, which is called the sliding filament model of muscle contraction. ATP provides the energy for cross-bridge formation and filament sliding. Regulatory proteins, such as troponin and tropomyosin, control cross-bridge formation. The number of muscle fibers contracting determines how much force the whole muscle produces.

End of Section Review Questions:

Review: Muscle Structure

1) In addition to action, what other proteins are associated with thin filaments?

A) sarcomeres
B) troponin
C) acetylcholine
D) tropomyosin

Review: Blocking binding

2) In relaxed muscle, the myosin-binding site on actin is blocked by what molecule?

Review: Muscle Structure

3) The cell membrane of a muscle fiber is called a?

Review: Driving muscle contraction

4) When does muscle contraction occur?

A) when ATP is hydrolyzed to ADP and phosphate.
B) when ADP and phosphate dissociate from the myosin head.
C) when ADP and phosphate dissociate from the actin active site
D) when Ca2+ binds to the calcium head of actin

References:

https://cnx.org/contents/GFy_h8cu@11.6:t8m3ArRs@6/Muscle-Contraction-and-Locomotion

https://www.ptdirect.com/training-design/anatomy-and-physiology/skeletal-muscle-the-physiology-of-contraction

39.

Learning Goals:

By the end of this reading, you should be able to:

- List the synapomorphic traits of the Superphylas Lophotrochozoa and Ecdysozoa
- Describe the key features of Platyhelminthes
- Discuss the shared characteristics of mollusks and the unique features of Bivalvia, Gastropoda, and Cephalopoda classes
- Describe the features of animals classified in phylum Annelida and discuss the advantages of body segmentation
- Compare the features of Nematodes and Annelids
- Describe the internal systems and appendage specializations of phylum Arthropoda
- Discuss the reasons for arthropod success and abundance

Introduction

Protostomes are animals whose blastopore (initiated by gastrulation) becomes the mouth of the future digestive system. 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. Based on molecular evidence, protostomes are divided into two major groups. Lophotrochozoans are characterized by either the presence at some point in the organism's development of a lophophore (ciliated, horse-shoe feeding shaped structure) or a trochophore larval stage (free-swimming planktonic marine larva with several bands of cilia). Ecdysozoans are characterized by ecdysis, a feature in which the organism molts its exoskeleton as it grows.

Superphylum Lophotrochozoa

As lophotrochozoans, the organisms in this superphylum possess either a lophophore or trochophore larvae. The lophophores are a set of ciliated tentacles surrounding the mouth. Trochophore larvae are characterized by two bands of cilia around the body.

The lophotrochozoans are triploblastic and thus possess an embryonic mesoderm sandwiched between the ectoderm and endoderm which is not 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 indicates 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.

Phyla of this superphylum include Platyhelminthes (*platy* = flat, *helminth* = worm; flatworms), Rotifera (rotifers), Nemertea (ribbon worms), Mollusca (mollusks), and Annelida (segmented worms). Ecdysozoans include the phyla Nematoda (roundworms) and Arthropoda, the largest animal phylum in the world that include the subphyla Hexapoda (insects), Myriapoda (centipedes and millipedes), Crustacea (crustaceans), and Chelicerata (spiders, ticks, scorpions, etc.). For the sake of this course, we will only focus on the groups and material for which you are responsible.

Phylum Platyhelminthes

The flatworms are acoelomate organisms that include many free-living and parasitic forms. 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). Their bodies are solid between the outer surface and the cavity of the digestive system. The free-living species of flatworms are predators or scavengers. Parasitic forms feed on the tissues of their hosts.

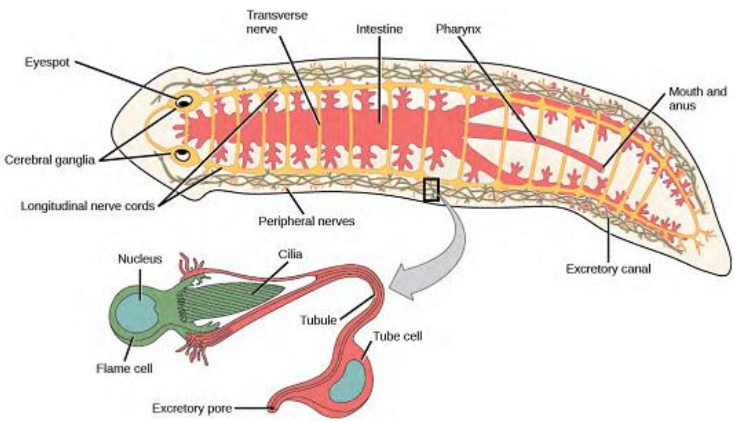

Figure 1. The planarian is a flatworm that has a gastrovascular cavity with one opening that serves as both mouth and anus. The excretory system is made up of tubules connected to excretory pores on both sides of the body. The nervous system is composed of two interconnected nerve cords running the length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

Most flatworms 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. Digestion is extracellular, with digested materials taken into the cells of the gut lining by phagocytosis. The nervous system consists of a pair of nerve cords running the length of the body with connections between them and a large ganglion or concentration of nerves at the anterior end of the worm, where there may also be a concentration of photosensory and chemosensory cells.

There is neither a circulatory nor respiratory system, with gas and nutrient exchange dependent on diffusion and cell-cell junctions. This necessarily limits the thickness of the body in these organisms, constraining them to be “flat” worms. Most flatworm species are monoecious, and fertilization is typically internal. Asexual reproduction is common in some groups.

Review Question:

Quick Review: Platyhelminthes
What are common characteristics of the Platyhelminthes?
A) they are triploblastic
B) they are pseudocoelomate
C) they have an incomplete digestive system
D) they are acoelomate

Phylum Mollusca

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.

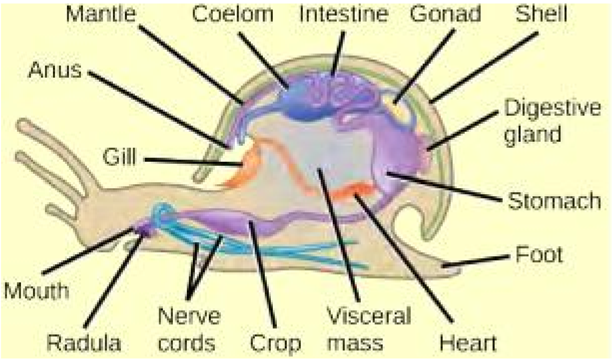

Figure 2. There are many species and variations of mollusks; this illustration shows the anatomy of an aquatic gastropod.

The muscular foot is used for locomotion and anchorage, and varies in shape and function, depending on the type of mollusk. 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.

The visceral mass is present above the foot, in the visceral hump. This includes the 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 is the dorsal epidermis in mollusks; shelled mollusks are specialized to secrete a chitinous and hard calcareous shell. 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.

Classification of Phylum Mollusca

Phylum Mollusca is a very diverse (85,000 species) group with a dramatic variety of forms, ranging from large predatory squids and octopuses, some of which show a high degree of intelligence, to grazing forms with elaborately sculpted and colored shells. While this phylum can be segregated into seven classes: Aplacophora, Monoplacophora, Polyplacophora, Bivalvia, Gastropoda, Cephalopoda, and Scaphopoda. this section will only focus on the classes Bivalvia, Gastropoda, and Cephalopoda.

Class Bivalvia

Bivalves ("two shells") include clams, oysters, mussels, scallops, and geoducks that 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. The overall morphology is laterally flattened, and the head region is poorly developed. Eyespots and statocysts may be absent in some species. Since these animals are suspension feeders, a radula is absent in this class of mollusks. Respiration is facilitated by a pair of ctenidia, whereas excretion and osmoregulation are brought about by a pair of nephridia. Bivalves often possess a large mantle cavity. In some species, the posterior edges of the mantle may fuse to form two siphons that serve to take in and exude water.

Animation of Clams Feeding

Figure 3. These mussels, found in the intertidal zone in Cornwall, England, are bivalves. (credit: Mark A. Wilson)

One of the functions of the mantle is to secrete the shell. Some bivalves like oysters and mussels possess the unique ability to secrete and deposit a calcareous nacre or “mother of pearl” around foreign particles that may enter the mantle cavity. This property has been commercially exploited to produce pearls.

Class Gastropoda

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)

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. 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.

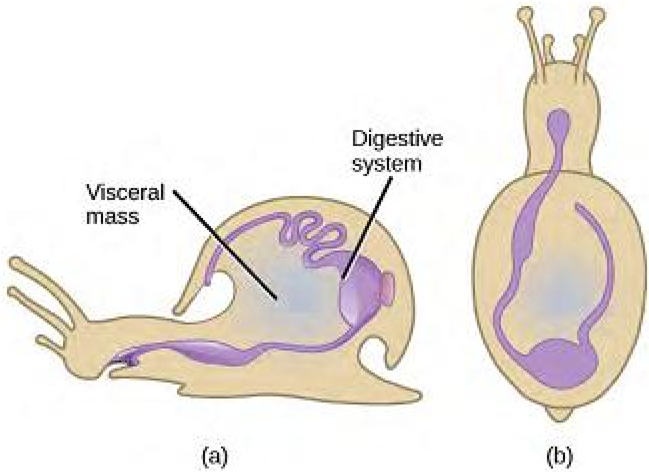

Figure 5. During embryonic development of gastropods, the visceral mass undergoes torsion, or counterclockwise rotation of anatomical features. As a result, the anus of the adult animal is located over the head. Torsion is an independent process from coiling of the shell.

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. 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.

Class Cephalopoda

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 the exchange of water.

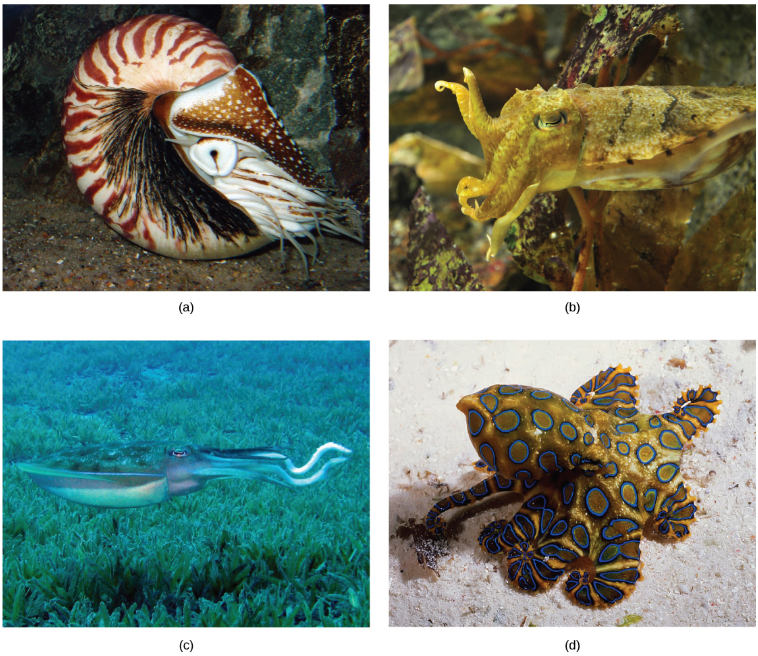

Figure 6. The (a) nautilus, (b) giant cuttlefish, (c) reef squid, and (d) blue-ring octopus are all members of the class Cephalopoda. (credit a: modification of work by J. Baecker; credit b: modification of work by Adrian Mohedano; credit c: modification of work by Silke Baron; credit d: modification of work by Angell Williams)

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.

Review Question:

Mollusk Anatomy

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.

Phylum Annelida

Annelids include segmented worms which comprise the class Polychaeta (the polychaetes) and the class Oligochaeta (the earthworms, leeches, and their relatives). These animals are found in marine, terrestrial, and freshwater habitats, but the 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. Approximately 16,500 species have been described in phylum Annelida, some of which show parasitic and commensal symbioses with other species in their habitat. 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.

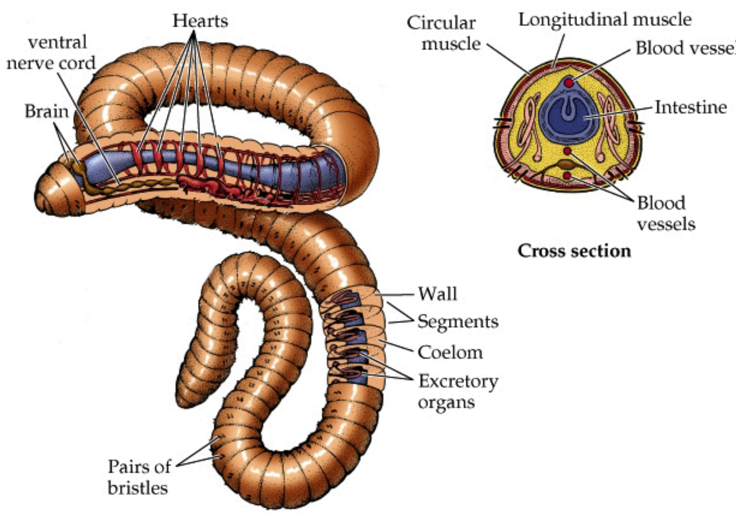

Figure 7. Segmented worm anatomy showing the complete digestive system, nervous system, and circulatory systems.

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. 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. 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. Each segment is limited by a membranous septum that divides the coelomic cavity into a series of compartments.

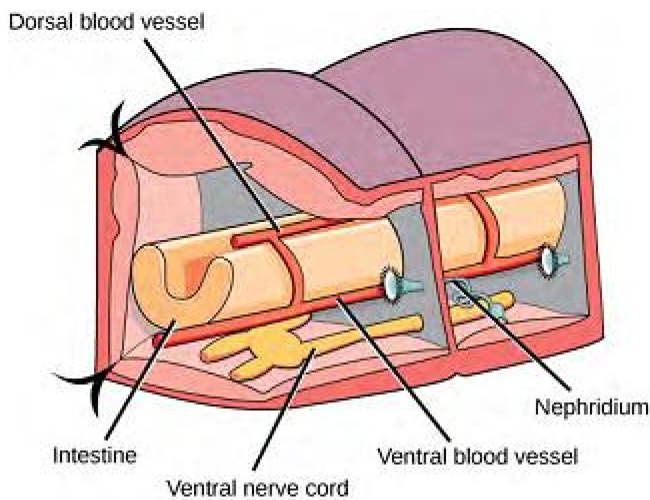

Figure 8. This schematic drawing shows the basic anatomy of annelids in a cross-sectional view.

Annelids possess a closed circulatory system (fluid of the circulatory system always remains in vessels and never bathes the tissues directly, as in an open 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.

Review Question:

Quick Review: annelids
What are key features of the annelids?
A) They have coelem
B) They are segmented
C) They have an open circulatory system
D) They have a cuticle that is acellular

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 prominent distinguishing 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.

Phylum Nematoda

The Nematoda, like most other animal phyla, are triploblastic and possess an embryonic mesoderm and are bilaterally symmetrical. Furthermore, the nematodes, or roundworms, possess a pseudocoelom and consist of both free-living and parasitic forms. This phylum 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.

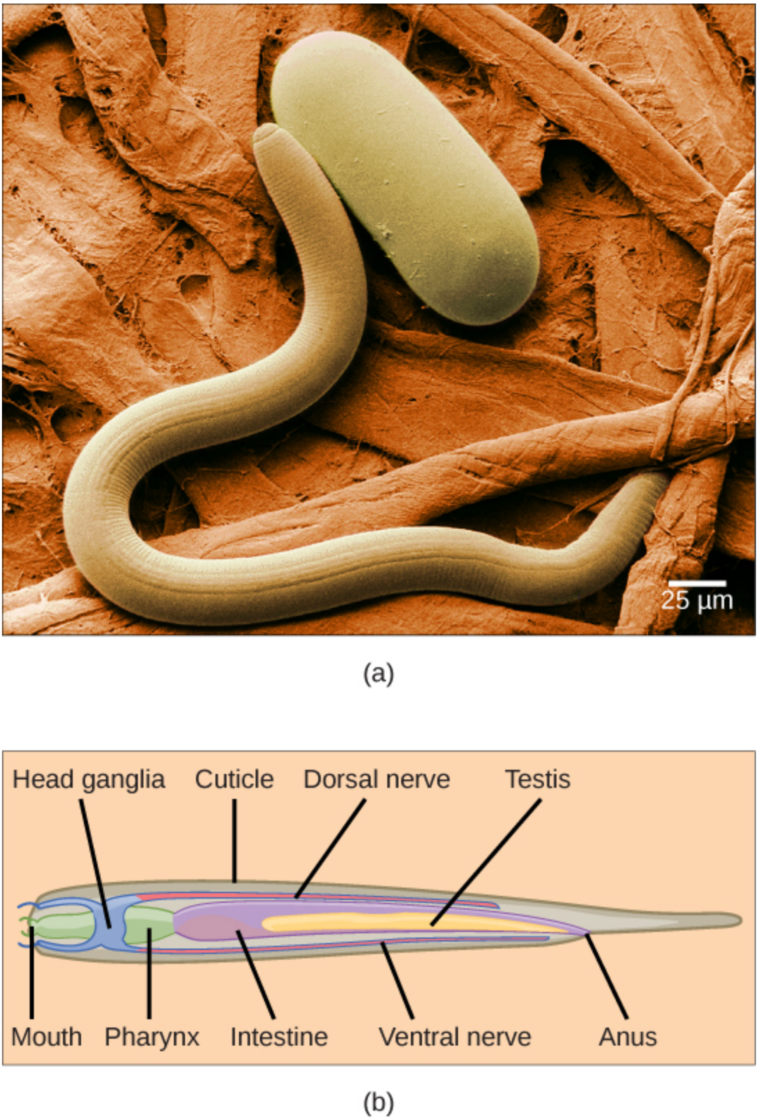

Figure 9. Scanning electron micrograph shows (a) the soybean cyst nematode (Heterodera glycines) and a nematode egg. (b) A schematic representation shows the anatomy of a typical nematode. (credit a: modification of work by USDA ARS; scale-bar data from Matt Russell)

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. 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. 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.

Phylum Arthropoda

The name "Arthropoda" means "jointed legs" (in Greek, "arthros" means "joint" and "podos" means "leg"); it aptly describes the enormous number of invertebrates included in this phylum. Arthropoda dominates 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 the presence of jointed appendages. Arthropods also show the presence of an exoskeleton made principally of chitin, which is a waterproof, tough polysaccharide. Phylum Arthropoda is the largest phylum in the animal world, and insects form the single largest class within this phylum. Arthropods are eucoelomate, protostomic organisms.

Phylum Arthropoda includes animals that have been successful in colonizing terrestrial, aquatic, and aerial habitats. This phylum is further classified into five subphyla: Trilobitomorpha (trilobites, all extinct), Hexapoda (insects and relatives), Myriapoda (millipedes, centipedes, and relatives), Crustaceans (crabs, lobsters, crayfish, isopods, barnacles, and some zooplankton), and Chelicerata (horseshoe crabs, arachnids, scorpions, and daddy longlegs).

Figure 10. Trilobites, like the one in this fossil, are an extinct group of arthropods. (credit: Kevin Walsh)

A unique feature of animals in the arthropod phylum is the presence of a segmented body and the 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.

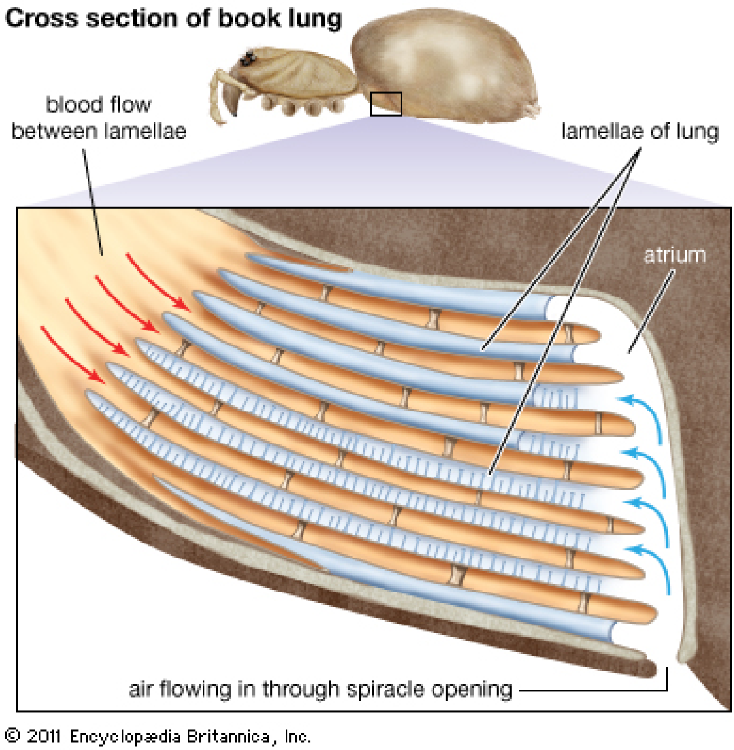

Figure 11. Arachnid book lungs.

The book lungs of arachnids (scorpions, spiders, ticks, and mites) contain a vertical stack of hemocoel wall tissue that somewhat resembles the pages of a book. Between each of the "pages" of tissue is an air space. This allows both sides of the tissue to be in contact with the air at all times, greatly increasing the efficiency of gas exchange. The gills of crustaceans are filamentous structures that exchange gases with the surrounding water. Groups of arthropods also differ in the organs used for excretion, with crustaceans possessing green glands and insects using Malpighian tubules, which work in conjunction with the hindgut to reabsorb water while ridding the body of nitrogenous waste.

The cuticle is the covering of an arthropod. It is made up of two layers: the epicuticle, which is a thin, waxy water-resistant outer layer containing no chitin, and the layer beneath it, the chitinous procuticle. Chitin is a tough, flexible polysaccharide. In order to grow, the arthropod must shed the exoskeleton during a process called ecdysis ("to strip off"); this is a cumbersome method of growth, and during this time, the animal is vulnerable to predation. The characteristic morphology of representative animals from each subphylum is described below.

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.

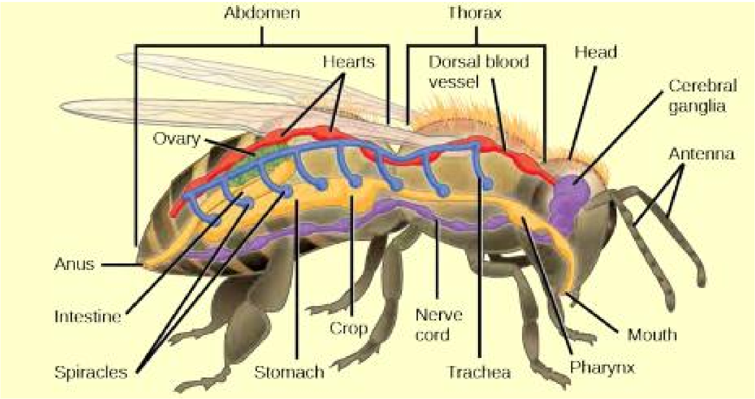

Figure 12. In this basic anatomy of a hexapod insect, note that insects have a developed digestive system (yellow), a respiratory system (blue), a circulatory system (red), and a nervous system (red).

Amongst the hexapods, the insects 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).

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.

Figure 13. (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)

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*) 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 the 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

Subphylum Crustacea

Figure 14. 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 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. Terrestrial species like the woodlice (*Armadillidium* spp.) (also called pill bugs, rolly pollies, potato bugs, or isopods) are also crustaceans, although the number of non-aquatic species in this subphylum is relatively low.

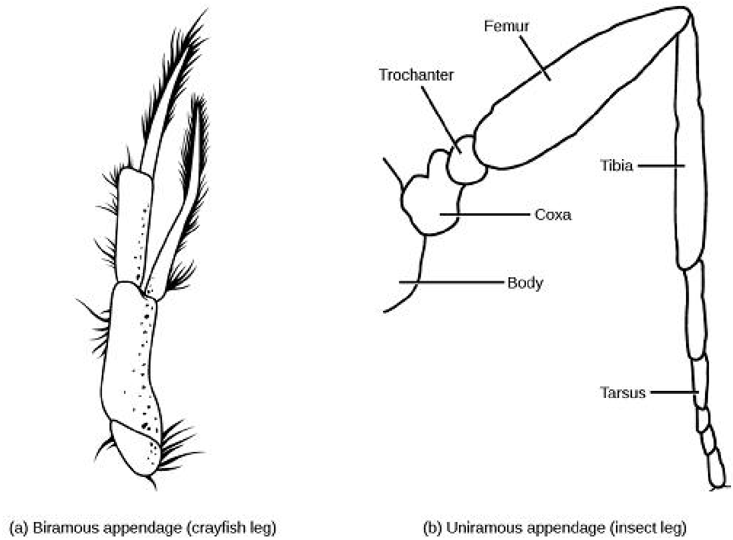

Figure 15. Arthropods may have (a) biramous (two-branched) appendages or (b) uniramous (one-branched) appendages. (credit b: modification of work by Nicholas W. Beeson)

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.

Unlike that of the Hexapoda, the head and thorax of most crustaceans are fused to form a cephalothorax, which is covered by a plate called the carapace, thus producing a body structure of two tagmata. 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.

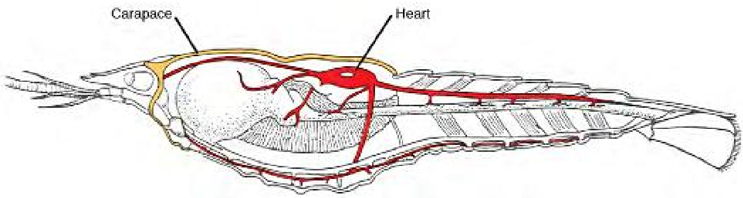

Figure 16. The crayfish is an example of a crustacean. It has a carapace around the cephalothorax and the heart in the dorsal thorax area. (credit: Jane Whitney)

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.

Figure 17. 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)

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. 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.

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 the 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 the 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, 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 18. The chelicerae (first set of appendages) are well developed in the scorpion. (credit: Kevin Walsh)

Chelicerae are mostly used for feeding, but in spiders, these are often modified into fangs that inject venom into their prey before feeding. Members of this subphylum have an open circulatory system with a heart that pumps blood into the hemocoel. Aquatic species have gills, whereas terrestrial species have either trachea or book lungs for gaseous exchange.

Figure 19. The trapdoor spider, like all spiders, is a member of the subphylum Chelicerata. (credit: Marshal Hedin)

Most chelicerates ingest food using a preoral cavity formed by the chelicerae and pedipalps. Some chelicerates may secrete digestive enzymes to pre-digest food before ingesting it. Parasitic chelicerates like ticks and mites have evolved blood-sucking apparatuses.

The nervous system in chelicerates consists of a brain and two ventral nerve cords. These animals use external fertilization as well as internal fertilization strategies for reproduction, depending upon the species and its habitat. Parental care for the young ranges from absolutely none to relatively prolonged care.

Visit https://evolution.berkeley.edu/evolibrary/article/arthropodstory to click through a lesson on arthropods, including interactive habitat maps, and more.

Summary

Phylum Annelida includes vermiform, segmented animals. Segmentation is seen in internal anatomy as well, which is called metamerism. Annelids are protostomes. These animals have well-developed neuronal and digestive systems. Some species bear a specialized band of segments known as a clitellum.

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. Cestodes, or tapeworms, infect the digestive systems of primary vertebrate hosts.

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.

Nematodes are pseudocoelomate animals akin to flatworms, yet display more advanced neuronal development, a complete digestive system, and a body cavity. A peculiar feature of nematodes is the secretion of a collagenous/chitinous cuticle outside the body.

Arthropods represent the most successful phylum of animals 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, a 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.

End of Section Review Questions:

REVIEW: Annelids

1) Annelids have a:

A) pseudocoelom
B) a true coelom
C) no coelom
D) none of the above

REVIEW: Arthropods

2) Which of these not a shared feature of arthropods?

A) a tracheal system

B) an exoskeleton
C) jointed appendages
D) functional segmentation

REVIEW: Nematodes
3) Which of these is a unique feature of nematodes?
A) they have a mesoderm
B) they have cuticle that lines internal systems
C) they need to molt as they grow larger
D) they have a complete digestive system

Footnotes

1. [1] Stoll, N. R., "This wormy world. 1947," Journal of Parasitology 8=m /lkmaD

40.

Learning Goals Chapter Outline

- Describe the distinguishing characteristics of echinoderms
- Describe the distinguishing characteristics of chordates
- Identify the derived character of craniates that sets them apart from other chordates
- Describe the developmental fate of the notochord in vertebrates

The phyla Echinodermata and Chordata (the phylum in which humans are placed) both belong to the **superphylum** Deuterostomia. Recall that protostome and deuterostomes differ in certain aspects of their embryonic development, and they are named based on which opening of the digestive cavity develops first. The word deuterostome comes from the Greek word meaning "mouth second," indicating that the anus is the first to develop. There are a series of other developmental characteristics that differ between protostomes and deuterostomes, including the mode of formation of the coelom and the early cell division of the embryo. In deuterostomes, internal pockets of the endodermal lining called the **archenteron** fuse to form the coelom. The endodermal lining of the archenteron (or the primitive gut) forms membrane protrusions that bud off and become the mesodermal layer. These buds, known as coelomic pouches, fuse to form the coelomic cavity, as they eventually separate from the endodermal layer. The resultant coelom is termed an **enterocoelom.** The archenteron develops into the alimentary canal, and a mouth opening is formed by invagination of ectoderm at the pole opposite the blastopore of the gastrula. The blastopore forms the anus of the alimentary system in the juvenile and adult forms. The fates of embryonic cells in deuterostomes can be altered if they are experimentally moved to a different location in the embryo due to indeterminate cleavage in early embryogenesis.

Phylum Echinodermata

Echinodermata are so named owing to their spiny skin (from the Greek "echinos" meaning "spiny" and "dermos" meaning "skin"), and this phylum is a collection of about 7,000 described living species. **Echinodermata** are exclusively marine organisms. Sea stars (Fig. 1), sea cucumbers, sea urchins, sand dollars, and brittle stars are all examples of echinoderms. To date, no freshwater or terrestrial echinoderms are known.

Morphology and Anatomy

Adult echinoderms exhibit pentaradial symmetry and have a calcareous endoskeleton made of ossicles, although the early larval stages of all echinoderms have bilateral symmetry. The endoskeleton is developed by epidermal cells and may possess pigment cells, giving vivid colors to these animals, as well as cells laden with toxins. Gonads are present in each arm. In echinoderms like sea stars, every arm bears two rows of tube feet on the oral side. These tube feet help in attachment to the substratum. These animals possess a true coelom that is modified into a unique circulatory system called a **water vascular system**. An interesting feature of these animals is their power to regenerate, even when over 75 percent of their body mass is lost.

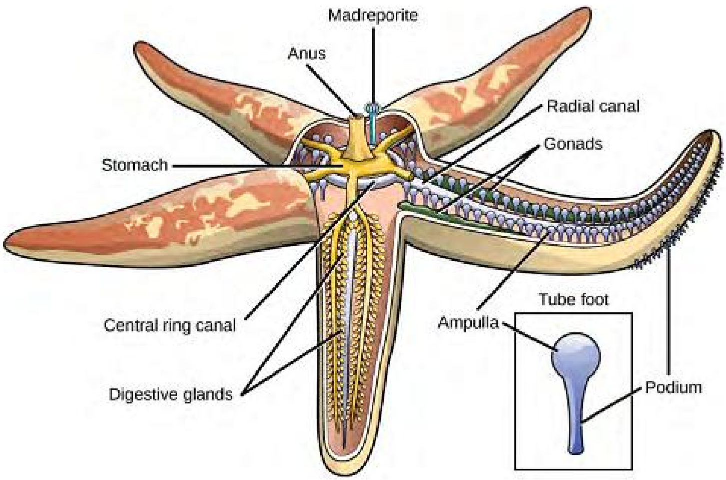

Figure 1. This diagram shows the anatomy of a sea star.

Water Vascular System

Echinoderms possess a unique ambulacral or water vascular system, consisting of a central ring canal and radial canals that extend along each arm. Water circulates through these structures and facilitates gaseous exchange as well as nutrition, predation, and locomotion. The water vascular system also projects from holes in the skeleton in the form of tube feet. These tube feet can expand or contract based on the volume of water present in the system of that arm. By using hydrostatic pressure, the animal can either protrude or retract the tube feet. Water enters the madreporite on the aboral side of the echinoderm. From there, it passes into the stone canal, which moves water into the ring canal. The ring canal connects the radial canals (there are five in a pentaradial animal), and the radial canals move water into the ampullae, which have tube feet through which the water moves. By moving water through the unique water vascular system, the echinoderm can move and force open mollusk shells during feeding.

Nervous System

The nervous system in these animals is a relatively simple structure with a nerve ring at the center and five radial nerves extending outward along the arms. Structures analogous to a brain or derived from fusion of ganglia are not present in these animals.

Excretory System

Podocytes, cells specialized for ultrafiltration of bodily fluids, are present near the center of echinoderms. These podocytes are connected by an internal system of canals to an opening called the **madreporite**.

Reproduction

Echinoderms are sexually dimorphic and release their eggs and sperm cells into the 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) (Fig. 2).

The most well-known echinoderms are members of class Asteroidea, or sea stars. They come in a large variety of shapes, colors, and sizes, with more than 1,800 species known so far. The key characteristic of sea stars that distinguishes them from other echinoderm classes includes thick arms (ambulacra) that extend from a central disk where organs penetrate into the arms. Sea stars use their tube feet not only for gripping surfaces but also for grasping prey. Sea stars have two stomachs, one of which can protrude through their mouths and secrete digestive juices into or onto prey, even before ingestion. This process can essentially liquefy the prey and make digestion easier. Explore the **sea star's body plan (http://openstaxcollege.org/l/sea_star)** up close, watch one move across the seafloor, 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.

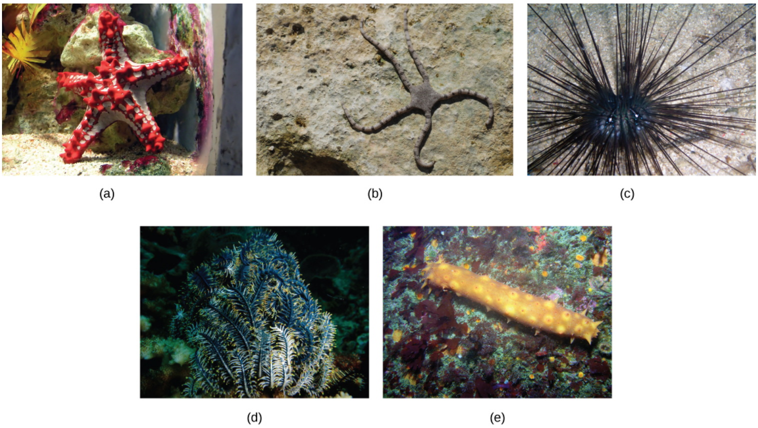

Figure 2. Different members of Echinodermata include the (a) sea star of class Asteroidea, (b) the brittle star of class Ophiuroidea, (c) the sea urchins of class Echinoidea, (d) the sea lilies belonging to class Crinoidea, and (e) sea cucumbers, representing class Holothuroidea. (credit a: modification of work by Adrian Pingstone; credit b: modification of work by Joshua Ganderson; credit c: modification of work by Samuel Chow; credit d: modification of work by Sarah Depper; credit e: modification of work by Ed Bierman)

Review Question:

Echinoderm Review

Echinoderms have _____.

A) triangular symmetry

B) radial symmetry

C) hexagonal symmetry

D) pentaradial symmetry

Echinoderm Review 2

The circulatory fluid in echinoderms is _____.

A) blood

B) mesohyl

C) water

D) saline

Phylum Chordata

Animals in the phylum **Chordata** (Fig. 3) share five key features that appear at some stage of their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, a post-anal tail, and an endostyle. 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.

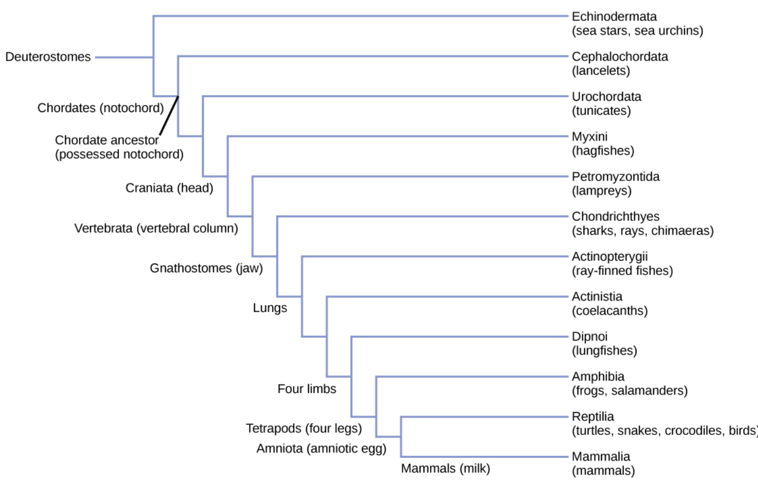

Figure 3. All chordates are deuterostomes possessing a notochord.

Characteristics of Chordata

Animals in the phylum **Chordata** share five key features that appear at some stage during their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, post-anal tail, and an endostyle (Fig. 4). 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).

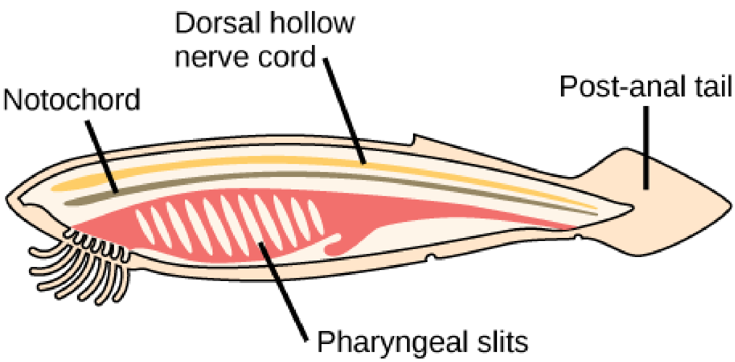

Figure 4. In chordates, five common features appear at some point during development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, a post-anal tail, and an endostyle (not labeled; in the floor of the pharynx).

Review Question:

Chordates

Which of the following statements about common features of

chordates is true?
A) The dorsal hollow nerve cord is part of the chordate central nervous system.
B) In vertebrate fishes, the pharyngeal slits become the gills.
C) Humans are not chordates because humans do not have a tail.
D) Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.

The **dorsal hollow nerve cord** derives from ectoderm that rolls into a hollow tube during development. In chordates, it is located dorsal to the notochord. In contrast, other animal phyla are characterized by solid nerve cords that are located either ventrally or laterally. The nerve cord found in most chordate embryos develops into the brain and spinal cord, which compose the central nervous system.

Pharyngeal slits are openings in the pharynx (the region just posterior to the mouth; in you, it's your throat/neck region) 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.

The **endostyle** is a structure that develops on the floor of the pharynx. In more primitive chordates, it helps to capture food as they are filter feeders. In more recently evolved chordates the endostyle becomes the thyroid gland, an organ that secretes hormones that primarily influence the metabolic rate and protein synthesis.

Click for a **video (http://openstaxcollege.org/l/chordate_evol)** discussing the evolution of chordates and five characteristics that they share.

Chordates and the Evolution of Vertebrates

Chordata also contains two clades of invertebrates: Urochordata and Cephalochordata. Members of these groups also possess the four distinctive features of chordates at some point during their development.

Urochordata

Members of **Urochordata** are also known as **tunicates** (**Figure 5**). The name tunicate derives from the cellulose-like carbohydrate material, called the tunic, which covers the outer body of tunicates. Although adult tunicates are classified as chordates, they do not have a notochord, a dorsal hollow nerve cord, or a post-anal tail, although they do have pharyngeal slits. The larval form, however, possesses all four structures. Most tunicates are hermaphrodites. Tunicate larvae hatch from eggs inside the adult tunicate's body. After hatching, a tunicate larva swims for a few days until it finds a suitable surface on which it can attach, usually in a dark or shaded location. It then attaches via the head to the surface and undergoes metamorphosis into the adult form, at which point the notochord, nerve cord, and tail disappear.

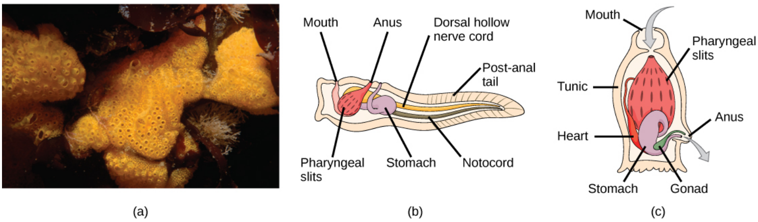

Figure 5 (a) This photograph shows a colony of the tunicate Botrylloides violaceus. (b) The larval stage of the tunicate possesses all of the features characteristic of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. (c) In the adult stage, the notochord, nerve 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 6**). 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.

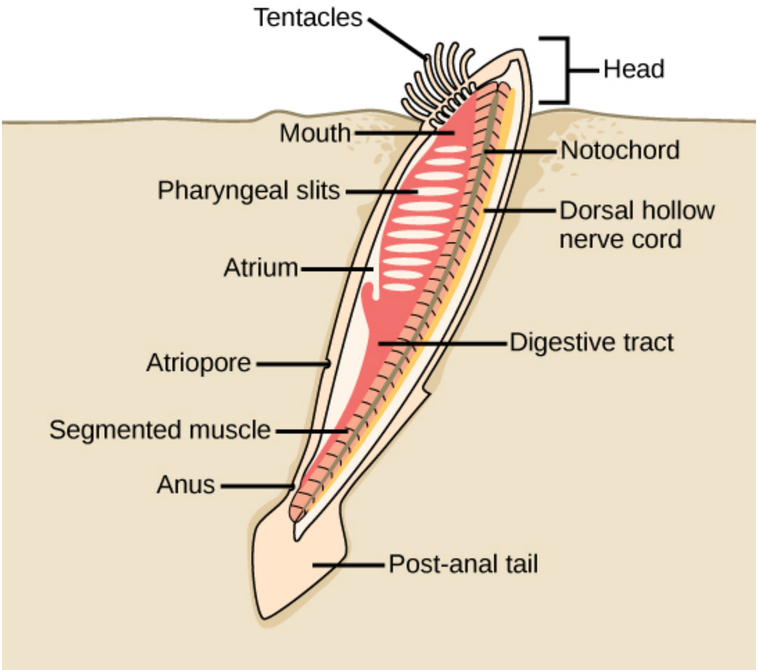

Figure 6. The lancelet, like all cephalochordates, has a head. Adult lancelets retain the four key features of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Water from the mouth enters the pharyngeal slits, which filter out food particles. The filtered water then collects in the atrium and exits through the atriopore.

Craniata and Vertebrata

A **cranium** is a bony, cartilaginous, or fibrous structure surrounding the brain, jaw, and facial bones (**Figure 7**). 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 (AKA invertebrate, and all of the organisms called "vertebrates."

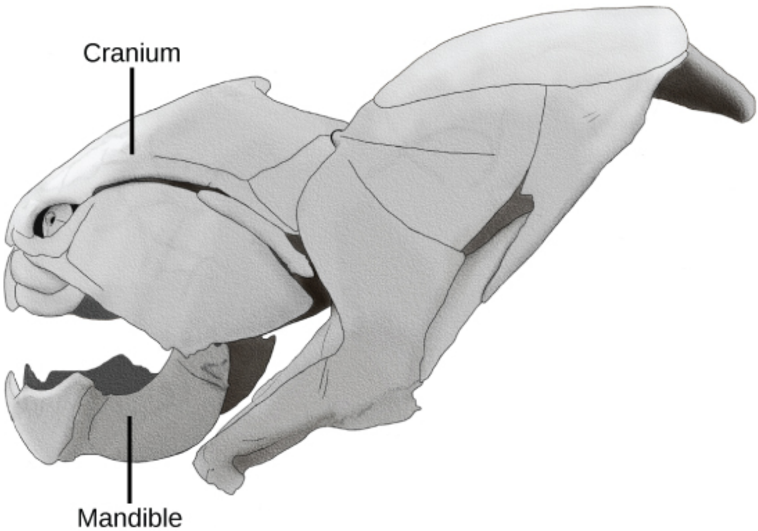

Figure 7. Craniata, including this fish (Dunkleosteus sp.), are characterized by the presence of a cranium, mandible, and other facial bones. (credit: "Steveoc 86"/Wikimedia Commons)

Vertebrates are members of the clade **Vertebrata**. Vertebrates display the five 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 (Fig. 8). In adult vertebrates, the vertebral column replaces the notochord, which is only seen in the embryonic stage.

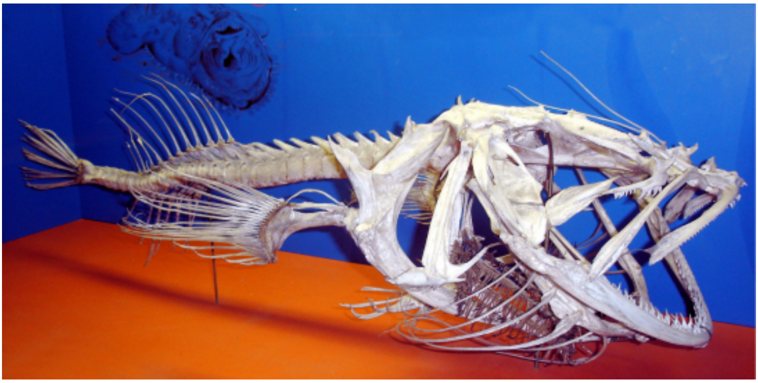

Figure 8. Vertebrata are characterized by the presence of a backbone, such as the one that runs through the middle of this fish. All vertebrates are in the Craniata clade and have a cranium. (credit: Ernest V. More; taken at Smithsonian Museum of Natural History, Washington, D.C.)

Based on molecular analysis, vertebrates appear to be more closely related to lancelets (cephalochordates) than to tunicates (urochordates) among the invertebrate chordates. This evidence suggests that the cephalochordates diverged from Urochordata and the vertebrates subsequently diverged from the cephalochordates. This hypothesis is further supported by the discovery of a fossil in China from the genus *Haikouella*. This organism seems to be an intermediate form between cephalochordates and vertebrates. The *Haikouella* fossils are about 530 million years old and appear similar to modern lancelets. These organisms had a brain and eyes, as do vertebrates, but lack the skull found in craniates.[1] This evidence suggests that vertebrates arose during the Cambrian explosion. Recall that the "Cambrian explosion" is the name given to a relatively brief span of time during the Cambrian period during which many animal groups appeared and rapidly diversified. Most modern animal phyla originated during the Cambrian explosion.

Vertebrates are the largest group of chordates, with more than 62,000 living species. Vertebrates are grouped based on anatomical and physiological traits. More than one classification and naming scheme is used for these animals. Here we will consider the traditional groups Agnatha, Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves, and Mammalia, which constitute classes in the subphylum Vertebrata. Many modern authors classify birds within Reptilia, which correctly reflects their evolutionary heritage. We consider them separately only for convenience. Further, we will consider hagfishes and lampreys together as jawless fishes, the agnathans, although emerging classification schemes separate them into chordate jawless fishes (the hagfishes) and vertebrate jawless fishes (the lampreys).

Animals that possess jaws are known as **gnathostomes**, which means "jawed mouth." Gnathostomes include fishes and tetrapods—amphibians, reptiles, birds, and mammals. Tetrapods can be further divided into two groups: amphibians and amniotes. Amniotes are animals whose eggs are adapted for terrestrial living, and this group includes mammals, reptiles, and birds. Amniotic embryos, developing in either an externally shed egg or an egg carried by the female, are provided with a water-retaining environment and are protected by amniotic membranes.

Review Question:

Review: Chordate Groups

Which of the following is not contained in phylum Chordata?

A) Cephalochordata
B) Echinodermata
C) Urochordata
D) Vertebrata

Review: Invertebrates and Vertebrates

Which group of invertebrates is most closely related to vertebrates?

A) cephalochordate

B) echinoderms
C) arthropods
D) urochordates

Summary

Echinoderms are deuterostomic marine organisms. This phylum of animals bears a calcareous endoskeleton composed of ossicles. These animals also have spiny skin. Echinoderms possess water-based circulatory systems. A pore termed the madreporite is the point of entry and exit for water into the water vascular system. Osmoregulation is carried out by specialized cells known as podocytes. The characteristic features of Chordata are a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets), together with the vertebrates in Vertebrata. Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms. Vertebrata is named for the vertebral column, which is a feature of almost all members of this clade.

End of Section Review Questions:

Review: Cranium Evolution
1) What can be inferred about the evolution of the cranium and vertebral column from examining hagfishes and lampreys?

Review: Evolution of the jaw
2) Why did gnathostomes replace most agnathans?

References

1. [1] Chen, J. Y., Huang, D. Y., and Li, C. W., "An early Cambrian craniate-like chordate," Nature 402 (1999): 518–522, doi:10.1038/990080.

2. [2] Daeschler, E. B., Shubin, N. H., and Jenkins, F. J. "A Devonian tetrapod-like fish and the evolution of the tetrapod body plan," Nature 440 (2006): 757–763, doi:10.1038/nature04639, http://www.nature.com/nature/journal/v440/n7085/abs/nature04639.html.

41.

Learning Goals

By the end of this reading you should be able to:

- Describe the difference between jawless and jawed fishes
- Discuss the distinguishing features of sharks and rays compared to other modern fishes
- Differentiate between the two groups of bony fishes
- Explain the evolution of bone in the fishes

Modern fishes include an estimated 31,000 species. Fishes were the earliest vertebrates, with jawless species being the earliest and jawed species evolving later. They are active feeders, rather than sessile, suspension feeders. Jawless fishes—the hagfishes and lampreys—have a distinct cranium and complex sense organs including eyes, distinguishing them from the invertebrate chordates.

Jawless Fish

Jawless fishes are craniates that represent an ancient vertebrate lineage that arose over one-half-billion years ago. In the past, the hagfishes and lampreys were classified together as agnathans. Today, hagfishes and lampreys are recognized as separate clades, primarily because lampreys are true vertebrates, whereas hagfishes are not. A defining feature is the lack of paired lateral appendages (fins). Some of the earliest jawless fishes were the ostracoderms (which translates to “shell-skin”). Ostracoderms were vertebrate fishes encased in bony armor, unlike present-day jawless fishes, which lack bone in their scales.

Myxini: Hagfishes

The clade Myxini includes at least 20 species of hagfishes. Hagfishes are eel-like scavengers that live on the ocean floor and feed on dead invertebrates, other fishes, and marine mammals. Hagfishes (Fig. 1) are entirely marine and are found in oceans around the world, except for the polar regions.

Figure 1. Jawless fish include lamprey (left) and hagfish (right).

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

The clade Petromyzontidae includes approximately 35–40 or more species of lampreys (Fig 2.). 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. Lateral view of a lamprey's head showing gill slits.

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 freshwater. 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.

Review Question:

Review: Shared traits

What traits do lampreys and hagfish share with their most common ancestors?

A) jaws
B) vertebrae
C) craniums

Gnathostomes: Jawed Fishes

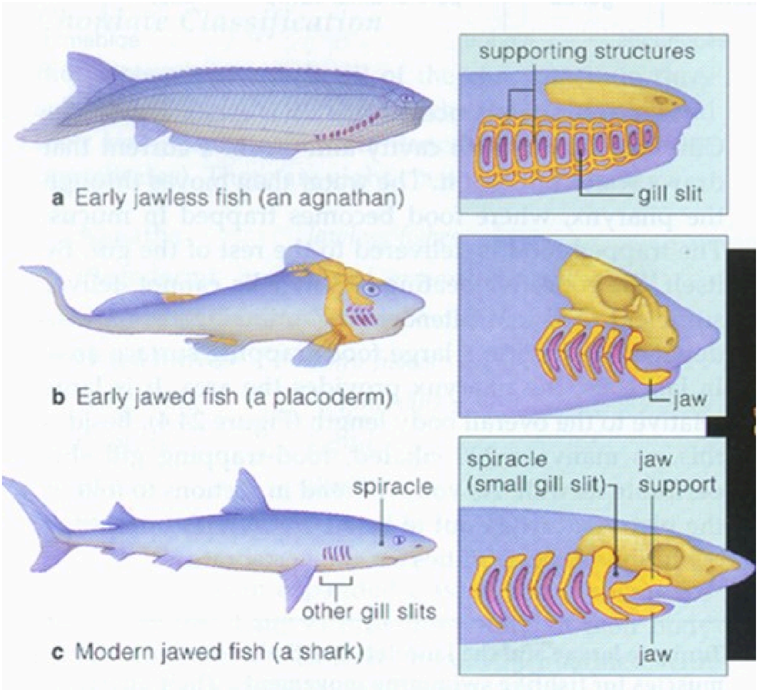

Figure 3. Evolution of jaws in fish

Gnathostomes or "jaw-mouths" are vertebrates that possess jaws (Fig. 3). 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.

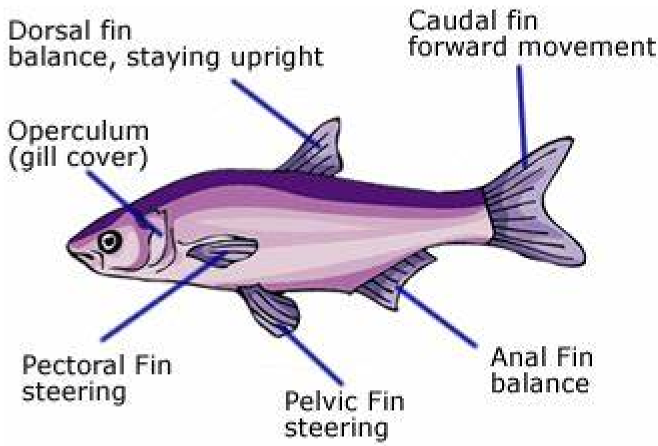

Figure 4. Modern actinopterygian, an example of a gnathostome.

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. The 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, which arose in the late Silurian period and are now extinct. Most modern fishes are gnathostomes that belong to the clades Chondrichthyes and Osteichthyes (Fig. 4).

Review Question:

Quick Review: Jaws and Paired fins
What is likely to have been the selection pressure that led to the evolution of jaws and paired fins?

A) enhanced swimming capacity (speed and maneuvering)
B) reduction in energy expenditure
C) Increased reproductive traits
D) increased ability to capture needed resources (food)

Chondrichthyes: Cartilaginous Fishes

The clade Chondrichthyes is diverse, consisting of sharks, 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 (Fig. 5).

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.

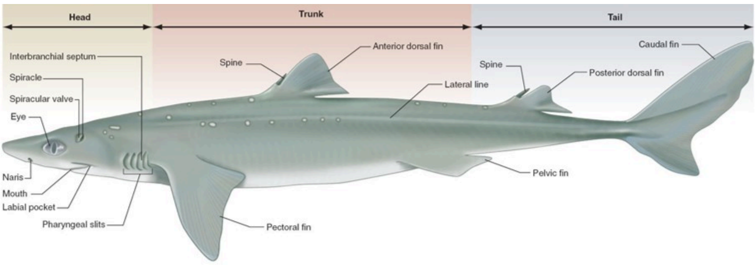

Figure 5. External anatomy of a shark.

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" 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.

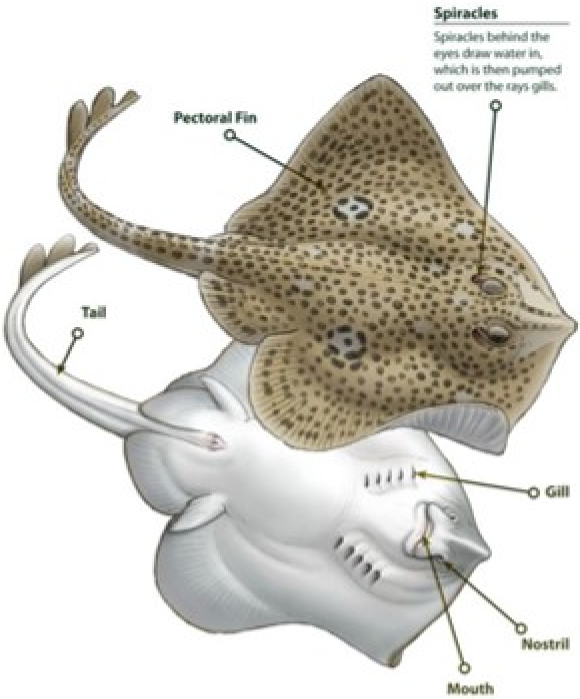

Figure 6. Skate anatomy

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. Like sharks, rays and skates have a cartilaginous skeleton. Most species are marine and live on the sea floor, with nearly a worldwide distribution.

Review Question:

Quick Review: Chondricthyes

What traits do the Chondrichthyes share?
A) they are all jawed fish
B) they have paired fins
C) they have ossified skeletons
D) they have swim bladders
E) they have cartilagenous skeletons

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 the 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.

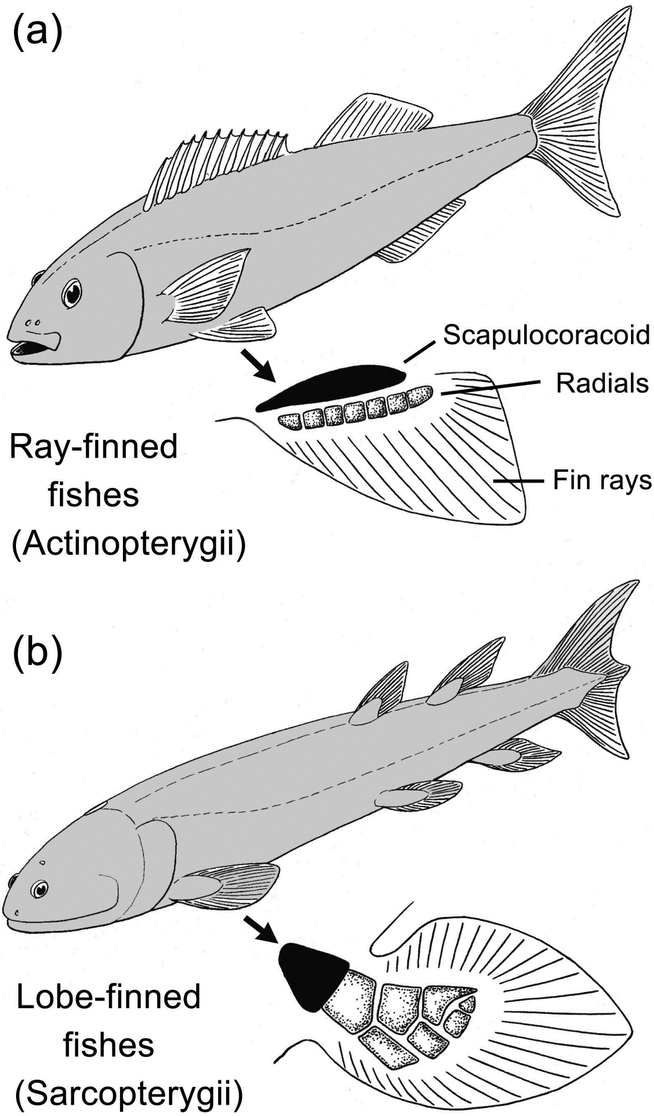

Figure 7. Comparison of fin anatomy in Actinopterygians and Sarcopterygians.

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, 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 . Living members of this clade include the less-familiar lungfishes and coelacanths.

Review Question:

Quick Review: Osteichthyes
What traits do all of the bony fish share?
A) swim bladders
B) gills for respiration
C) fins with bony spines
D) jaws and paired fins

The Evolution of Bones in Fishes

The evolution of bone begins in fish, as they were the first vertebrates. The first bone to evolve in the early fish is different from the bone found in later vertebrates. Bone or osseous tissue is a connective tissue that constitutes the skeleton, internal or external, of vertebrates. Components of bone are the mineralized portion, hydroxylapetite (a mineral formed from calcium phosphate), collagen fibres that support the formation of mineralized bone, and some vascular tissue that supplies blood to the living cell component of bone. Calcification is the process of deposition of mineral salts on the collagen fiber matrix that crystallizes and hardens the tissue. The process of calcification only occurs in the presence of collagen fibers.

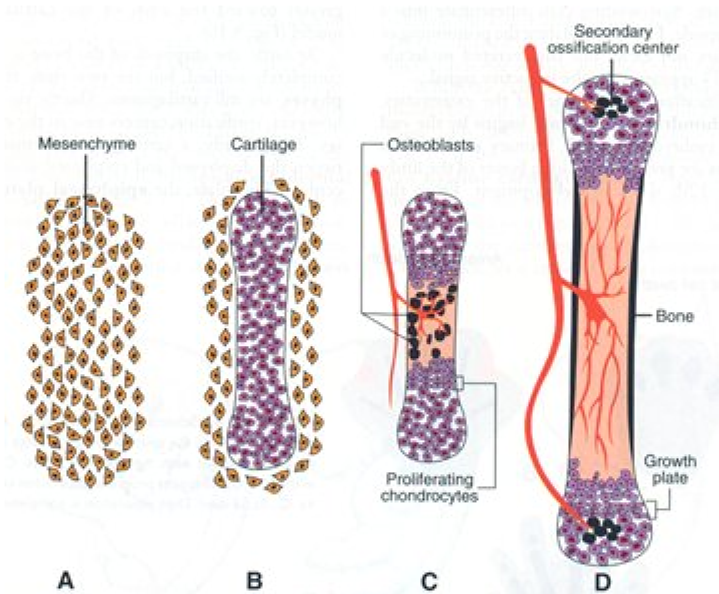

Figure 8. Development of bone.

The bone of early vertebrates is of 2 main types, cellular and acellular. The structure of these bone types consists of the same basic components, the only difference is that there are spaces in cellular bone for the osteocytes, the bone-forming cells that occur throughout the bone. The earliest forms of acellular bone have a tendency to be laminated, forming in successive layers that were deposited by the dermis. Some early agnathans have an acellular bone that is called aspidin. Acellular bone is also found in the layered bones of more advanced fish. In placoderms, a group of gnathostomes most closely related to sharks, an acellular bone is found had in bony plates around the edge of their mouths that acted as teeth (this was not the origin of teeth, however).

In the earliest fish most of the skeleton is formed of bone produced by the dermis, hence its name dermal bone. Dermal bone composed all the externally visible bones of the head and trunk and the scales and biting surfaces inside the mouth. There were other types of specialized bone that developed in various early osteichthyans. These bone types are characterized by the complexity, nature, and composition of the external layers of the dermal bones, as well as their growth processes and whether or not resorption was involved in their development.

Among other bone types found in early vertebrates are perichondral bone (a thinly laminated acellular bone) and endochondral bone. Perichondral bone is often found surrounding soft tissue that passes through cartilage, as can be found in the placoderms with cartilage braincases where the nerves and arteries passing through the braincase wall can have perichondral bone surrounding them. The endogirdles that support the pelvic and pectoral fins also have perichondral bone surrounding them.

Endochondral bone forms around a cartilage precursor. These bones make up much of the internal skeleton in reptiles and mammals and form the arm and leg bones of the appendicular skeleton. Endochondral bone first evolved as a specialized feature in some groups of gnathostomes (osteichthyans and acanthodians).

As well as these basic tissue types, there are many types of bone involved in dental tissues that evolved in fish and continued on to the higher land animals. Chondrichthyans have a mostly cartilaginous skeleton, but in the dorsal fin spines, they have a type of dentine with a thin enameloid layer. Nearly all the fossil parts of sharks are a similar type of dental tissue, including the placoid scales covering the body that are similar to small teeth. In many early agnathans, there are layers of dentine covering the dermal bone.

Review Question:

Quick Review: Components of bone

What are the three components of bone?

A) vascular tissue
B) collagen fibers
C) desomal cells
D) hydroxylapetite

Summary

The earliest vertebrates that diverged from the invertebrate chordates were the jawless fishes. Fishes with jaws (gnathostomes) evolved later. Jaws allowed early gnathostomes to exploit new food sources. Agnathans include the hagfishes and lampreys. Hagfishes are eel-like scavengers that feed on dead invertebrates and other fishes. Lampreys are characterized by a toothed, funnel-like sucking mouth, and most species are parasitic on other fishes. Gnathostomes include the cartilaginous fishes and the bony fishes, as well as all other tetrapods. Cartilaginous fishes include sharks, rays, skates, and ghost sharks. Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for part or all of their lives. The vast majority of present-day fishes belong to the clade Osteichthyes, which consists of approximately 30,000 species. Bony fishes can be divided into two clades: Actinopterygii (ray-finned fishes, virtually all extant species) and Sarcopterygii (lobe-finned fishes, comprising fewer than 10 extant species but which are the ancestors of tetrapods).

End of Section Review Questions:

REVIEW: Agnathans
The agnathans (jawless fish) include?
A) sharks
B) lampreys
C) placoderms

D) hagfish

REVIEW: Chondrichthyes
Members of Chondrichthyes are thought to be descended from fishes that had what feature?
A) a cartilagenous skeleton
B) mucus glands
C) bony skeletal features
D) slime glands

Thinking about it
What were the key adaptations that occurred in the evolution of fishes and what advantage did each provide?

References:

https://austhrutime.com/bone.htm

42.

Learning Goals:

By the end of this reading you should be able to:

- Describe the different means by which animals exchange gases
- Explain the role that diffusion plays in different systems of gas exchange
- Describe the process of countercurrent gas exchange
- Compare and contrast the tracheal system of insects with the mammalian respiratory system

Introduction

The primary function of the respiratory system is to deliver oxygen to the cells of the body's tissues and remove carbon dioxide, a cell waste product. All aerobic organisms require oxygen to carry out their metabolic functions. Along the evolutionary tree, different organisms have devised different means of obtaining oxygen from the surrounding atmosphere. As with other organisms, the environment in which the animal lives greatly determines how an animal respires. In addition, the complexity of the respiratory system usually correlates with the size of the organism. As animal size increases, diffusion distances increase and the ratio of surface area to volume drops. In unicellular organisms, diffusion across the cell membrane is sufficient for supplying oxygen to the cell. However, diffusion is a slow, passive transport process. In order for diffusion to be a feasible means of providing oxygen to the cell, the rate of oxygen uptake must match the rate of diffusion across the membrane. In other words, if the cell were very large or thick, diffusion would not be able to provide oxygen quickly enough to the inside of the cell. Therefore, dependence on diffusion as a means of obtaining oxygen and removing carbon dioxide remains feasible only for small organisms or those with highly-flattened bodies, such as many flatworms (Platyhelminthes). Larger organisms had to evolve specialized respiratory tissues, such as gills, lungs, and respiratory passages accompanied by complex circulatory systems, to transport oxygen throughout their entire body.

Direct Diffusion

Figure 1: Aquatic flatworm – example of an organism with no need of a complete respiratory system given the large surface area to volume ratio achieve by its flat body.

For many small multicellular organisms (less than 1mm in diameter), diffusion across the outer membrane is sufficient to meet their oxygen needs. In simple organisms, such as cnidarians and flatworms (Fig 1), every cell in the body is close to the external environment. Thus the cells are kept moist and gases can diffuse quickly via direct diffusion. Flatworms are small, literally flatworms, which 'breathe' through diffusion across the outer membrane. The flat shape of these organisms increases the surface area for diffusion, ensuring that each cell within the body is close to the outer membrane surface and has access to oxygen. If the flatworm had a cylindrical body, then the cells in the center would not be able to get oxygen.

Skin and Gills

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

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

Figure 2: Exposed gill lamellae in a bony fish.

Gills are thin tissue filaments that are highly branched and folded (Fig. 2). When water passes over the gills, the dissolved oxygen in water rapidly diffuses across the gills into the bloodstream. The circulatory system can then carry the oxygenated blood to the other parts of the body. In animals that contain coelomic fluid instead of blood, oxygen diffuses across the gill surfaces into the coelomic fluid. Gills are found in mollusks, annelids, and crustaceans.

The folded surfaces of the gills provide a large surface area to ensure that the fish gets sufficient oxygen. Diffusion is a process in which material travels from regions of high concentration to low concentration until equilibrium is reached. In this case, blood with a low concentration of oxygen molecules circulates through the gills.

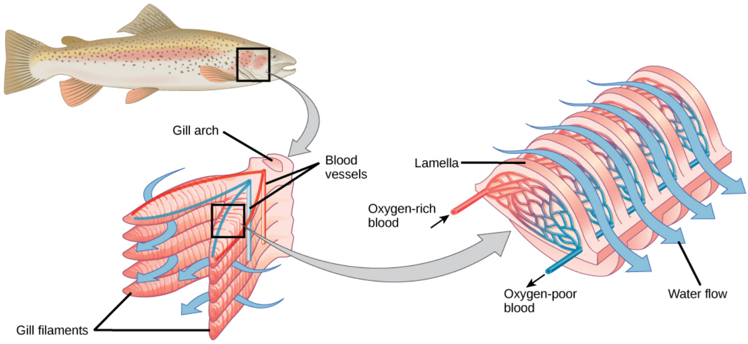

Figure 3. Countercurrent gas exchange occurs across the gills of fish. Highly oxygenated water enters and passes across the gills where diffusion occurs.

The concentration of oxygen molecules in water is higher than the concentration of oxygen molecules in gills. As a result, oxygen molecules diffuse from water (high concentration) to blood (low concentration), as shown in. Similarly, carbon dioxide molecules in the blood diffuse from the blood (high concentration) to water (low concentration). It will probably help to watch this video that shows how this countercurrent gas exchange works.

Watch this video to see how countercurrent gas exchange is achieved in fish gills: https://youtu.be/cVFqME-NW9s

Quick Review: Countercurrent gas exchange

The concentration of oxygen molecules in water is ______ than the concentration of oxygen molecules in gills. As a result, oxygen molecules ______ water to blood. Similarly, carbon dioxide molecules in the blood ______ the blood where the concentration is ______ to water where the concentration is ______.

Word bank: lower, higher, diffuse from, diffuse to, osmose

Tracheal Systems

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

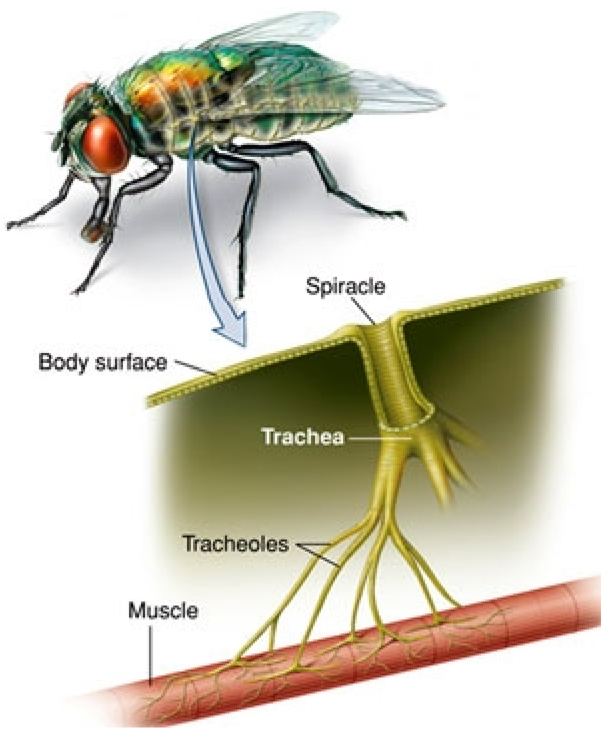

Figure 4. Diagram of the tracheal system found in insects.

Insect bodies have openings, called spiracles, along the thorax and abdomen. These openings connect to the tubular network, allowing oxygen to pass into the body and regulating the diffusion of CO_2 and water vapor. Air enters and leaves the tracheal system through the spiracles. Some insects can ventilate the tracheal system with body movements.

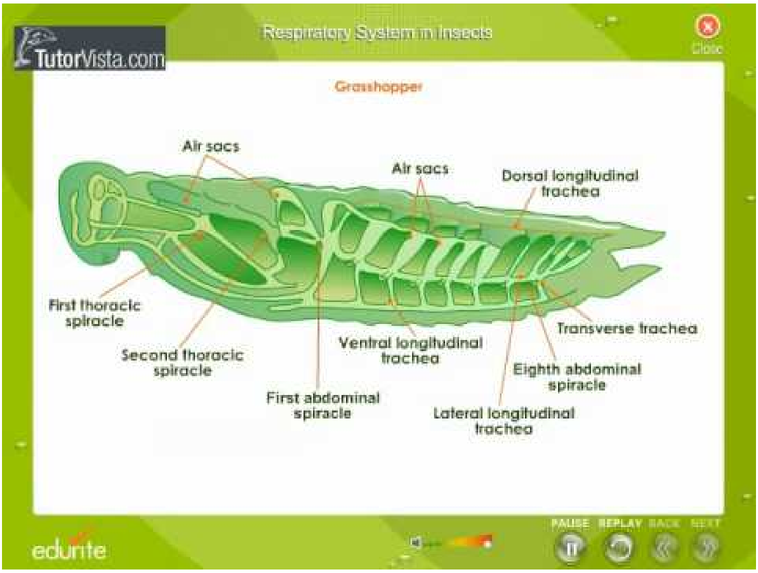

Figure 5. Detailed diagram of the trachael system of grasshoppers.

Review Question:

Quick Review: Tracheal Systems

In tracheal systems oxygen transport is ______ of the movement of ______.

Word bank: muscles, dependent, blood, independent

Mammalian Systems

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

From the nasal cavity, air passes through the pharynx (throat) and the larynx (voice box), as it makes its way to the trachea. The main function of the trachea is to funnel the inhaled air to the lungs and the exhaled air back out of the body. The human trachea is a cylinder about 10 to 12 cm long and 2 cm in diameter that sits in front of the esophagus and extends from the larynx into the chest cavity where it divides into the two primary bronchi at the midthorax. It is made of incomplete rings of hyaline cartilage and smooth muscle). The trachea is lined with mucus-producing goblet cells and ciliated epithelia. The cilia propel foreign particles trapped in the mucus toward the pharynx. The cartilage provides strength and support to the trachea to keep the passage open. The smooth muscle can contract, decreasing the trachea's diameter, which causes expired air to rush upwards from the lungs at a great force. The forced exhalation helps expel mucus when we cough. Smooth muscle can contract or relax, depending on stimuli from the external environment or the body's nervous system.

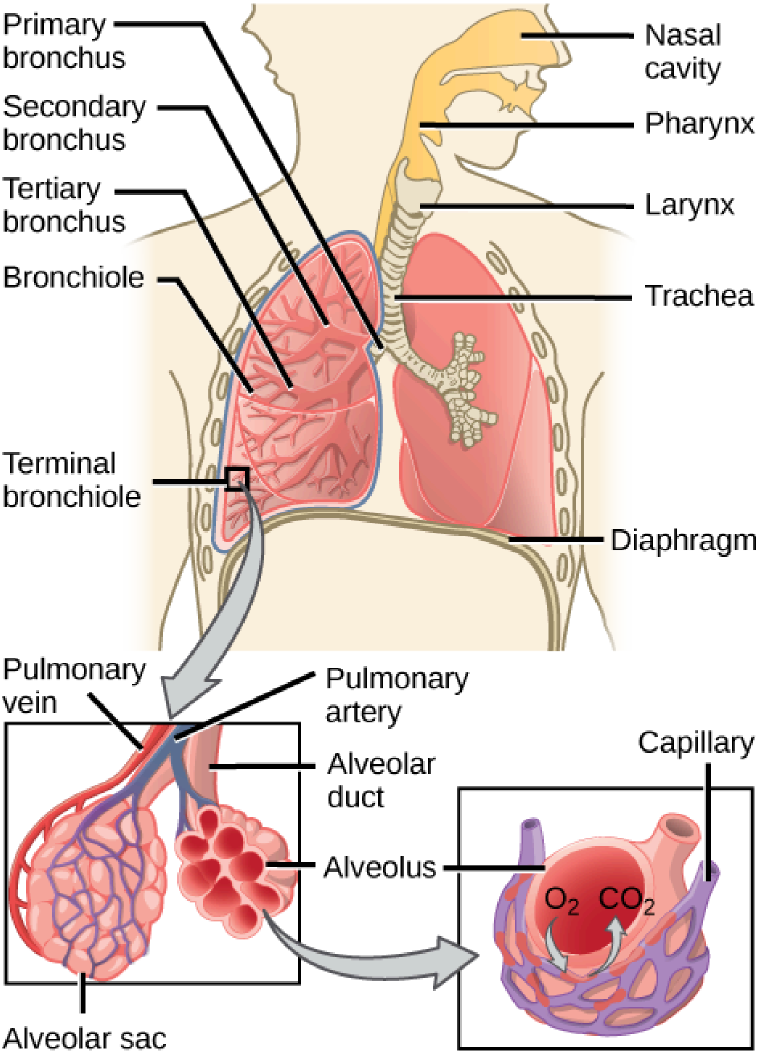

Figure 6. Representative diagram of mammalian lungs. Air enters the respiratory system through the nasal cavity and pharynx and then passes through the trachea and into the bronchi, which bring air into the lungs. (credit: modification of work by NCI)

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

The terminal bronchioles subdivide into microscopic branches called respiratory bronchioles. The respiratory bronchioles subdivide into several alveolar ducts. Numerous alveoli and alveolar sacs surround the alveolar ducts. The alveolar sacs resemble bunches of grapes tethered to the end of the bronchioles. In the acinar region, the alveolar ducts are attached to the end of each bronchiole. At the end of each duct are approximately 100 alveolar sacs, each containing 20 to 30 alveoli that are 200 to 300 microns in diameter.

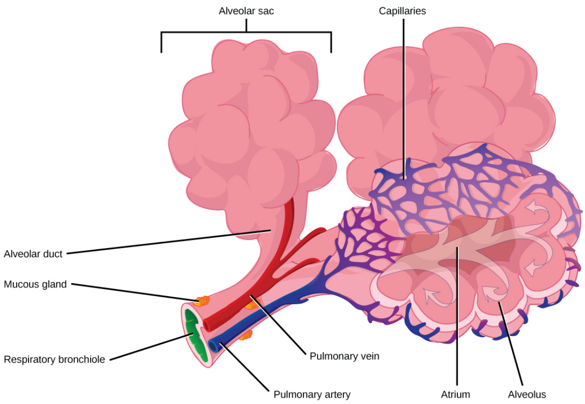

Figure 7. Terminal bronchioles are connected by respiratory bronchioles to alveolar ducts and alveolar sacs. Each alveolar sac contains 20 to 30 spherical alveoli and has the appearance of a bunch of grapes. Air flows into the atrium of the alveolar sac, then circulates into alveoli where gas exchange occurs with the capillaries. Mucous glands secrete mucous into the airways, keeping them moist and flexible. (credit: modification of work by Mariana Ruiz Villareal)

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

Click here to see the respiratory system in humans in action: https://youtu.be/bfxfydYFlhg

Quick Review: Airflow

What is the order of gas exchange starting outside the body and moving inward?

A) alveoli
B) nasal cavity
C) bronchioles
D) larynx
E) bronchi
F) trachea

Protective Mechanisms

The air that organisms breathe contains particulate matter such as dust, dirt, viral particles, and bacteria that can damage the lungs or trigger allergic immune responses. The respiratory system contains several protective mechanisms to avoid problems or tissue damage. In the nasal cavity, hairs and mucus trap small particles, viruses, bacteria, dust, and dirt to prevent their entry.

If particulates do make it beyond the nose, or enter through the mouth, the bronchi and bronchioles of the lungs also contain several protective devices. The lungs produce mucus—a sticky substance made of mucin, a complex glycoprotein, as well as salts and water—that traps particulates. The bronchi and bronchioles contain cilia, small hair-like projections that line the walls of the bronchi and bronchioles. These cilia beat in unison and move mucus and particles out of the bronchi and bronchioles back up to the throat where it is swallowed and eliminated via the esophagus.

In humans, for example, tar and other substances in cigarette smoke destroy or paralyze the cilia, making the removal of particles more difficult. In addition, smoking causes the lungs to produce more mucus, which the damaged cilia are not able to move. This causes a persistent cough, as the lungs try to rid themselves of particulate matter, and makes smokers more susceptible to respiratory ailments.

Summary

Animal respiratory systems are designed to facilitate gas exchange. In mammals, air is warmed and humidified in the nasal cavity. Air then travels down the pharynx, through the trachea, and into the lungs. In the lungs, air passes through the branching bronchi, reaching the respiratory bronchioles, which house the first site of gas exchange. The respiratory bronchioles open into the alveolar ducts, alveolar sacs, and alveoli. Because there are so many alveoli and alveolar sacs in the lung, the surface area for gas exchange is very large. Several protective mechanisms are in place to prevent damage or infection. These include the hair and mucus in the nasal cavity that trap dust, dirt, and other particulate matter before they can enter the system. In the lungs, particles are trapped in a mucus layer and transported via cilia up to the esophageal opening at the top of the trachea to be swallowed.

Review Questions

REVIEW: Simple animals

1) What features of some simple animals allow them to use only diffusion for gases exchange?

A) a thin structure
B) large surface to volume ratios
C) increase membrane transport molecules
D) a smaller surface area

REVIEW: Surface area to volume

2) What part of the mammalian respiratory system is likely to have the largest surface to volume ratio?

A) bronchi
B) alveoli
C) bronchioles
D) larynx

REVIEW: Gas exchange limitations

3) Why is gas exchange more difficult for aquatic animals with gills than for terrestrial animals with lungs?

A) gills allow only unidirectional transport
B) water contains much less O2 than air per unit volume
C) gills have less surface area than lungs
D) water is less dense than air and thus slows the rate of diffusion

43.

Learning Goals

By the end of this reading, you should be able to

- Order the events that lead to the current adaptations of terrestrial tetrapods
- Describe key adaptations that allow for support in terrestrial environments
- Explain how changes in vertebral structure lead to the current mobility of terrestrial tetrapods
- Delineate between ancestral and derived traits of tetrapods

Introduction

The word "tetrapod" means "four feet" and includes all species alive today that have four feet — but this group also includes many animals that don't have four feet. That's because the group includes all the organisms (living and extinct) that descended from the last common ancestor of amphibians, reptiles, birds, and mammals. So, for example, the ichthyosaur, an extinct swimming reptile, is a tetrapod even though it did not use its limbs to walk on land. Snakes are also tetrapods even though they do not have limbs. Birds and humans are tetrapods even though they only walk on two legs. All these animals are tetrapods because they descend from the tetrapod ancestor.

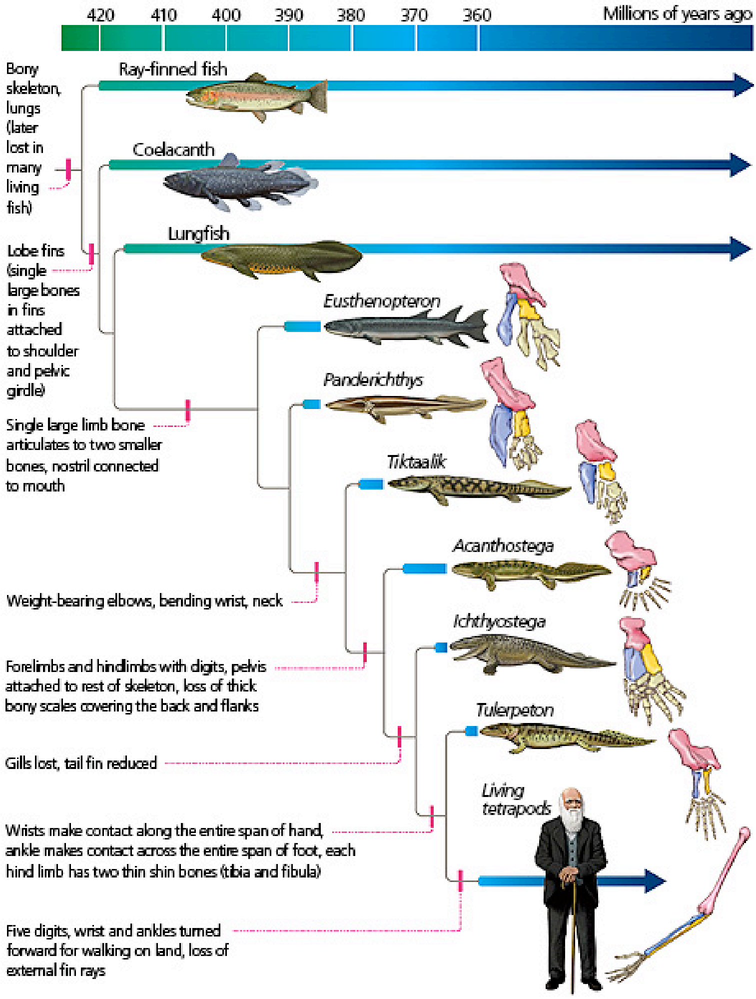

Figure 1. Evolution of tetrapods from a common ancestor

Characteristics of fish ancestors

Most 25,000 living species of animals that we call fishes are ray-finned fishes. There in fact far more of these types of fishes than all the other vertebrates combined. The fins of these fish have a unique structure— that is, they have a system of often branching bony rays (called lepidotrichia) that emanate from the base of the fin. In contrast, the other animals in the phylogenetic tree — coelacanths, lungfishes, all the other extinct animals, plus tetrapods (represented by Charles Darwin) — have what we call "fleshy fins" or "lobe fins." That is, their limbs are covered by muscle and skin. Some, such as coelacanths, retain lepidotrichia at the ends of these fleshy limbs, but in most fleshy-finned animals these have been lost.

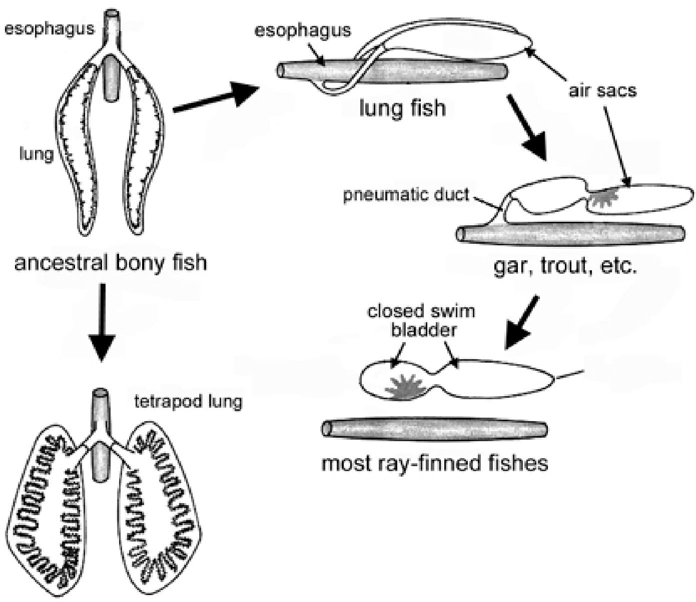

Figure 2. Proposed evolutionary pathways of tetrapod lungs and ray-finned swim bladders

The common ancestor of all those different organisms (ray-fins, coelacanths, lungfishes, tetrapods, etc.) was neither a lobe-fin nor a ray-fin. This ancient vertebrate lineage had fins (with lepidotrichia), scales, gills, and lived in the water. Yet they also had air bladders (air-filled sacs) connected to the back of their throats that could be used for breathing air (i.e., as lungs) or for buoyancy control. The air bladders of many current ray-finned fish no longer connect to their throats, and so they are not able to breathe air. In these ray-fins, the air bladder is used mainly for buoyancy control and is known as a swim bladder. By contrast, tetrapods have taken an alternative route: they have lost the buoyancy control function of their air bladders, and instead, this organ has been altered to form the lungs that we all rely on to provide gases on land.

When we get past coelacanths and lungfishes on the phylogenetic tree, we find a series of fossil forms that lived between about 390 and 360 million years ago during the Devonian Period. During this interval, this lineage of fleshy-finned organisms evolved adaptations that allowed them to leave the water and begin to live on land. Many of these adaptations involved parts of the skeleton that were altered to both structural support and locomotion in a terrestrial environment.

Review Question:

Quick Review: Tetrapod Ancestors

What does our current evidence suggest about tetrapods?

A) Tetrapods include some fish; amphibians; reptiles; birds and mammals

B) Tetrapod lungs are likely to have evolved from the air bladder of fish ancestors

C) Tetrapods are thought to have evolved from a common rayed-finned ancestor

Changes to the skeletons

The ancestors of the tetrapods lived fully in the water and had skulls that were tall and narrow, with eyes facing sideways and forwards. This allowed them to look around in their watery environments for predators and prey. However, as ancestors of the first tetrapods began to live in shallower waters, their skulls evolved to be flatter, with eyes on the tops of their heads. This probably allowed them to look up to spot food. Then, as tetrapods finally moved fully onto land and away from the water, many lineages once again evolved skulls that were tall and narrow, with eyes facing sideways and forwards, allowing them to look around their terrestrial environments for predators and prey.

Figure 3. Individuals fish vertebrae are similar down the length of the body which limits the range of motion.

As lineages moved into shallower water and onto land, the vertebral column gradually evolved as well. You may have noticed that fishes have no necks. Their heads are simply connected to their shoulders, and their individual vertebrae look quite similar to one another, all the way down the body. In shallow water dwellers and land dwellers, the first neck vertebra evolved different shapes. This adaptation allowed greater movement of the vertebrae and thus made it possible for these animals to move their heads up and down. Eventually, a second modification of the neck vertebra occurred that made it possible for a group of these animals to move their heads left and right. Mobile necks allow land animals to look down to see the things on the ground that they might want to eat and to watch for predators. Later tetrapods evolved necks with seven or more vertebrae, some long and some short, permitting even more mobility.

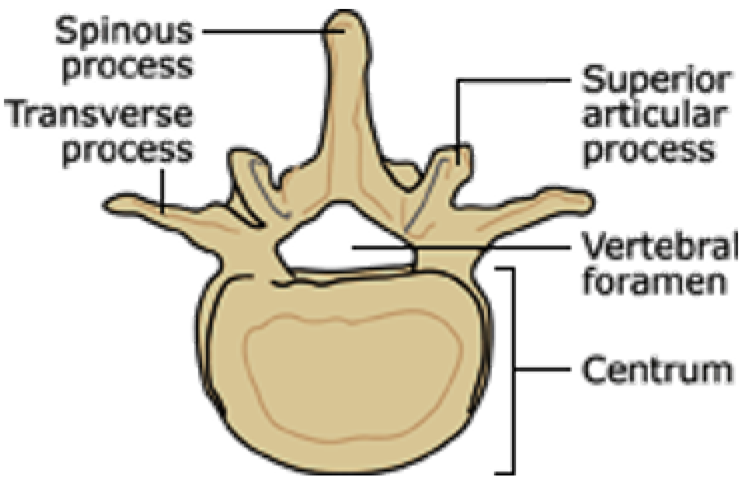

Figure 4. Mammalian vertebrae showing centrum and processes where muscle attachment occurs.

The vertebrae you are probably most familiar with (like our own!) consist of a spool-like centrum, which connects in front and back with other centra. On top of the centra are vertebral spines and arches to which muscle segments attach, and lateral to the centra are the ribs; these anchor muscles that flex as the animals move. Fishes swim with simple lateral motions, so their arches are relatively straight and needle-like, and so are their ribs. When you eat fish and pick out the bones, these are mostly what you're finding. Because fishes live in the water, gravity is not a big problem for them. But on land, a quadruped with a backbone between forelimbs and hindlimbs faces the same problems as a bridge designer: sag. As the fleshy-finned organisms began to venture onto land, they evolved a series of interlocking articulations on each vertebra, which helped them overcome sag and hold the backbone straight with minimal muscular effort.

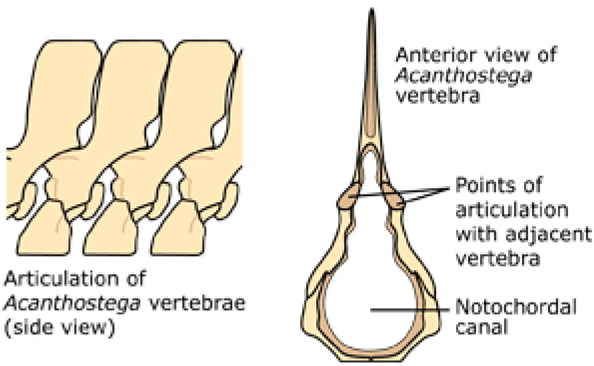

Figure 5. Articulation of vertebrae allowed them to interlock closely and provided support against gravity

The connection between the pelvis and hindlimbs in early tetrapods is a prime example of exaptation. We call this fused connection the sacrum. It is extremely useful for terrestrial organisms because it allows them to use their hindlimbs efficiently for locomotion on land. Since the aquatic ancestors of fishes and tetrapods had no such connection, one might guess that this feature first evolved serving the function of enabling terrestrial locomotion. However, the earliest form of this connection (as seen in Acanthostega) evolved while these tetrapod precursors were still living in the water. Based on current evidence, Acanthostega appears to have been fully aquatic, so this connection likely evolved to function in something other than terrestrial locomotion. Only later, as tetrapod ancestors moved onto land, was this trait co-opted for terrestrial support — and as it was, additional vertebrae were fused in the same way, providing further support.

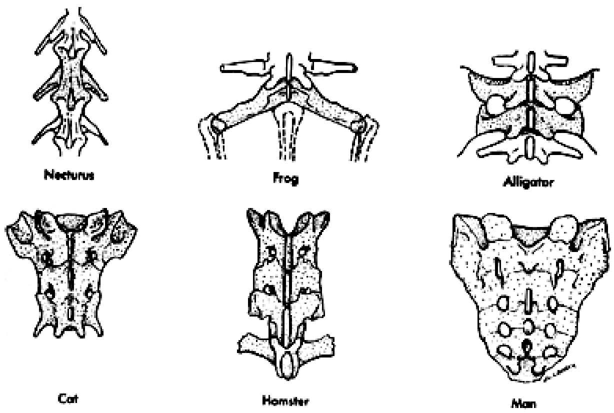

Figure 6. In order for hind limbs to facilitate locomotion, adaptations had to occur in sacral bones. This alters the angle and mode of attachment of the hind limbs.

As the limbs and their connections to the rest of the skeleton evolved, limb bones took on distinct roles and many bones were lost. The humerus and the femur were already connected to two outer bones (the radius and ulna in the forelimb, the tibia and fibula in the hindlimb). This is something that evolved about 30 million years before vertebrates came onto land. However, muscular connections between these bones began to change on the road to land and allowed the limbs to be used for terrestrial locomotion. The ankle was originally composed of many small bones arranged in two rows, but gradually many of these small bones were lost. The first animals to get close to walking on land had eight digits on each limb. Over time, some of these digits were lost, leading to animals with seven digits, then six, and then five, which is the common condition now seen in living tetrapods.

Review Question:

Quick Review: Articulation

What advantage did the development of articulation provide early terrestrial tetrapods?

A) the ability to move their heads up and down
B) the ability to move their head from side to side
C) the prevention of sagging of the backbone

Other adaptations to land

As these animals evolved to live on land, other changes in the rest of their bodies evolved. Many would eventually lose their gills, which only work well for getting oxygen when wet, and their tail fins got smaller. Similarly, they lost the lateral line system, a network of vibration-sensitive canals along the skull and jaw, which doesn't work out of water.

The environments of the animals also changed through time. In fact, if you were to venture back to Arizona at the beginning of the "Age of Dinosaurs" in the Triassic Period, some 225 million years ago, you would find ray-fins, coelacanths, and lungfishes living in the marshes, streams, and temporary ponds of that day, along with freshwater sharks. So the habitats that these animals occupy today are not necessarily the ones in which they have always lived, or in which they originally evolved. It is still unclear exactly where the transition from water to land took place ecologically. Paleontologists have discovered fossils involved in this transition preserved from freshwater, brackish, and marine habitats. Regardless of where the transition occurred, eventually, early ancestors of the first tetrapods came up onto land — although not all stayed. Some, like the whales, made the transition back into the water.

Click here to learn more about the origin of the four-legged vertebrates: https://youtu.be/zK8XGEDcTfo

Summary

All modern-day tetrapods share a common ancestry that begins with the fish. It is likely that some ancestral fishes evolved the capacity to breathe air and to move out of the water. The terrestrial environment required changes in the structures of the bones that provided support as well as those involved in the mobility of the organism. Additional adaptations that altered bone morphology and physiological processes occurred as new environments on land were entered.

End of Section Review Questions:

REVIEW: Vertebral adaptations
1) Place the following vertebral adaptations of tetrapods in the order in which they occurred.
A) change in vertebrae shape that allowed up and down head movement
B) change in vertebral shape that allowed side to side movement
C) addition of additional vertebrae to the neck region

Thinking About It: Changes in bone shapes
2) Explain why modifications to the sacrum needed to take place before tetrapods evolved to live on land.

Thinking about it: Changes to bone numbers
3) The earliest terrestrial tetrapods appear to have had eight digits but modern ones have five and in some cases fewer digits. Why might this loss of digits have occurred?

References:

https://evolution.berkeley.edu/evolibrary/article/evograms_04

44.

Learning Goals

By the end of this reading you should be able to:

- Compare and contrast open and closed circulatory systems
- Explain why some animals do not have circulatory systems
- Compare and contrast the organization and evolution of the different vertebrate circulatory systems.

Introduction

The circulatory system is effectively a network of cylindrical vessels: the arteries, veins, and capillaries that emanate from a pump, the heart. In all vertebrate organisms, as well as some invertebrates, this is a closed-loop system, in which the blood is not free in a cavity. In a closed circulatory system, blood is contained inside blood vessels and circulates unidirectionally from the heart around the systemic circulatory route, then returns to the heart again. As opposed to a closed system, arthropods—including insects, crustaceans, and most mollusks—have an open circulatory system. In an open circulatory system, the blood is not enclosed in the blood vessels but is pumped into a cavity called a hemocoel and is called hemolymph because the blood mixes with the interstitial fluid. As the heartbeats and the animal moves, the hemolymph circulates around the organs within the body cavity and then reenters the hearts through openings called ostia. This movement allows for gas and nutrient exchange. An open circulatory system does not use as much energy as a closed system to operate or to maintain; however, there is a trade-off with the amount of blood that can be moved to metabolically active organs and tissues that require high levels of oxygen. In fact, one reason that insects with wingspans of up to two feet wide (70 cm) are not around today is probably because they were outcompeted by the arrival of birds 150 million years ago. Birds, having a closed circulatory system, are thought to have moved more agilely, allowing them to get food faster and possibly to prey on the insects.

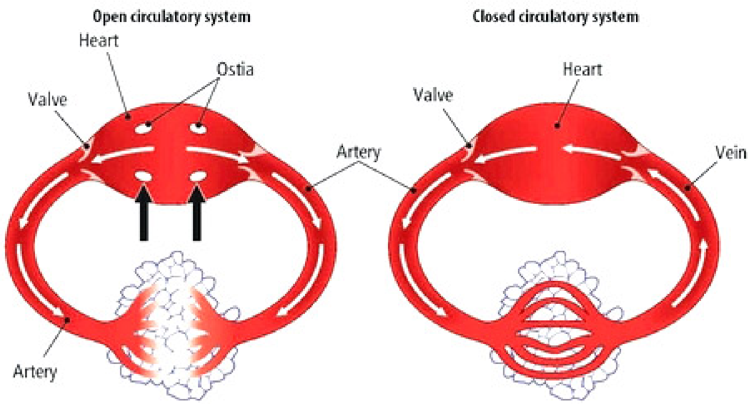

Figure 1. Open vs closed circulatory system.

Circulatory System Variation in Animals

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

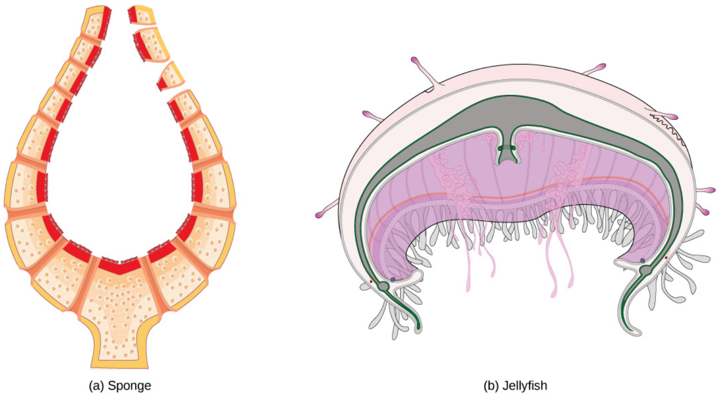

Figure 2. In simple animals like sponges and cnidarians, the cells are in close contact with the environment. Coupled with a large surface-to-volume ratio this allows gas and other molecules to move by diffusion.

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

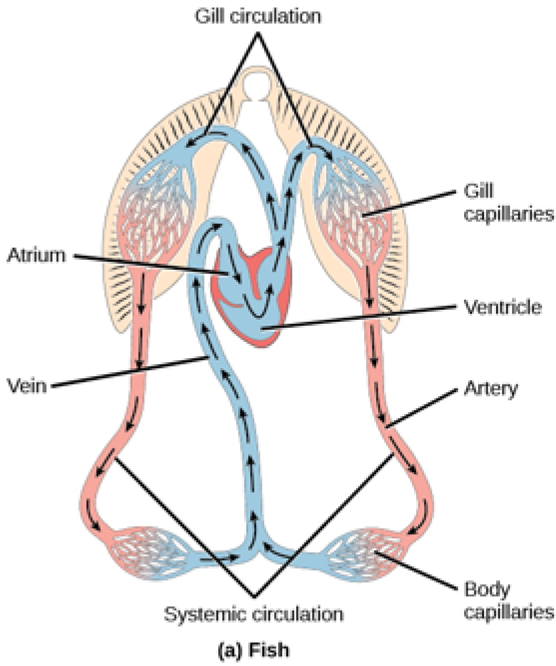

Figure 3. Diagram of the general fish circulatory system.

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

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

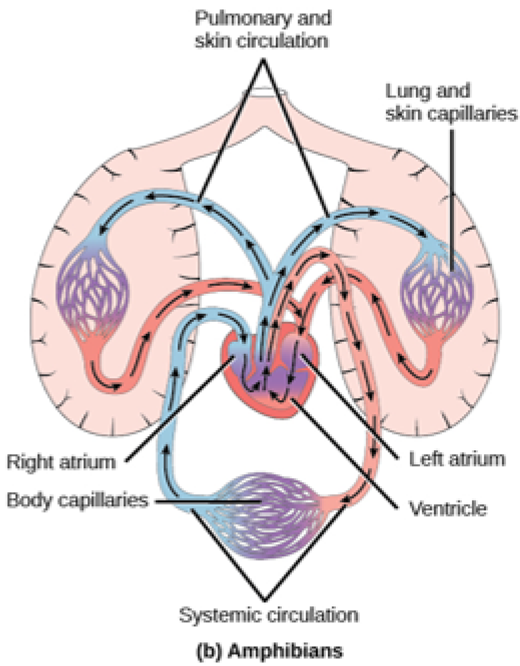

Figure 4. Diagram of the general amphibian circulatory system.

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

Most reptiles also have a three-chambered heart similar to the amphibian heart that directs blood to the pulmonary and systemic circuits. The ventricle is divided more effectively by a partial septum, which results in less mixing of oxygenated and deoxygenated blood.

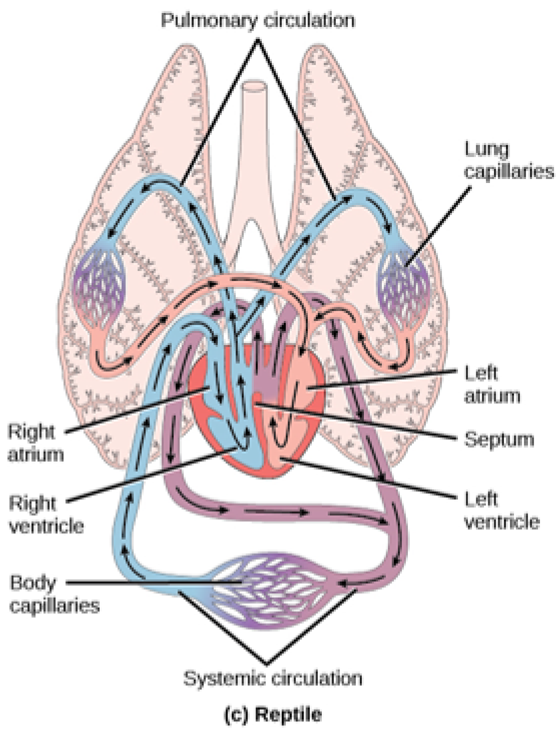

Figure 5. Diagram of the general reptilian circulatory system.

Some reptiles (alligators and crocodiles) are the most primitive animals to exhibit a four-chambered heart. Crocodilians have a unique circulatory mechanism where the heart shunts blood from the lungs toward the stomach and other organs during long periods of submergence, for instance, while the animal waits for prey or stays underwater waiting for prey to rot. One adaptation includes two main arteries that leave the same part of the heart: one takes blood to the lungs and the other provides an alternate route to the stomach and other parts of the body. Two other adaptations include a hole in the heart between the two ventricles, called the foramen of Panizza, which allows blood to move from one side of the heart to the other, and specialized connective tissue that slows the blood flow to the lungs. Together these adaptations have made crocodiles and alligators one of the most evolutionarily successful animal groups on earth.

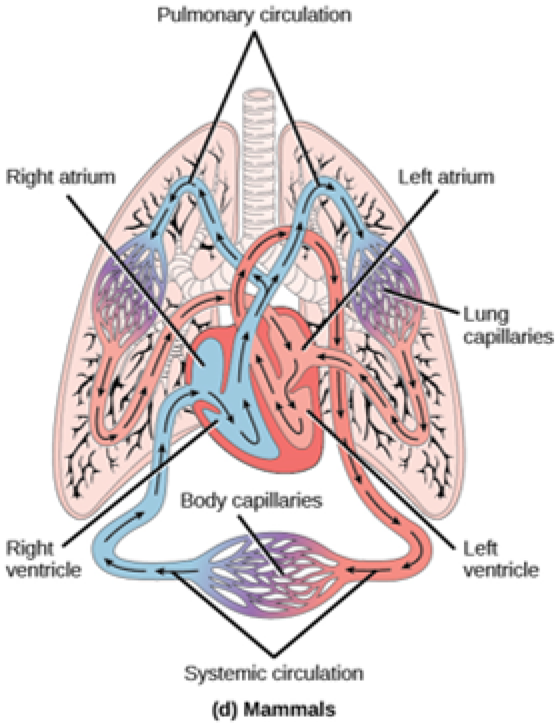

Figure 6. Diagram of the general mammalian circulatory system.

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

Review Question:

Thinking about it: Convergent evolution
Why might a four-chambered heart have evolved independently in birds and mammals?

Summary

In most animals, the circulatory system is used to transport blood through the body. Some primitive animals use diffusion for the exchange of water, nutrients, and gases. However, complex organisms use the circulatory system to carry gases, nutrients, and waste through the body. Circulatory systems may be open (mixed with the interstitial fluid) or closed (separated from the interstitial fluid). Closed circulatory systems are a characteristic of vertebrates; however, there are significant differences in the structure of the heart and the circulation of blood between the different vertebrate groups due to adaptions during evolution and associated differences in anatomy. Fish have a two-chambered heart with unidirectional circulation. Amphibians have a three-chambered heart, which has some mixing of the blood, and they have double circulation. Most non-avian reptiles have a three-chambered heart, but have little mixing of the blood; they have double circulation. Mammals and birds have a four-chambered heart with no mixing of blood and double circulation.

End of Section Review Questions:

REVIEW: Circulation
In what type of blood flow is the blood directed through the lungs and back to the heart?

A) unidirectional circulation
B) gill circulation
C) pulmonary circulation
D) pulmocutaneous circulation

REVIEW: Open circulation
Why are open circulatory systems advantageous to some animals?
A) They use less metabolic energy.
B) They help the animal move faster.
C) They do not need a heart.
D) They help large insects develop.

REVIEW: Diffusion
What animals rely on diffusion instead of a circulatory system?
A) jellyfish
B) arthropods
C) mollusks
D) sponges

REVIEW: Unique adaptations
What are unique adaptations of the circulatory systems of crocodiles?
A) two main arteries that leave the heart but go to different parts of the body
B) a hole in the heart between the two ventricles allowing blood flow between them
C) a pulmoncutaneous circuit of blood flow
D) specialized tissues that slow blood flow to the lungs

45.

Learning Goals

By the end of this reading you should be able to:

- Compare and contrast the advantages of internal and external fertilization
- Describe adaptations of animals related to fertilization
- Discuss the differences between oviparity, ovoviviparity, and viviparity

The Evolution of Reproduction

Once multicellular organisms evolved and developed specialized cells, some also developed tissues and organs with specialized functions. An early development in reproduction occurred in the Annelids. These organisms produce sperm and eggs from undifferentiated cells in their coelom and store them in that cavity. When the coelom becomes filled, the cells are released through an excretory opening or by the body splitting open.

Reproductive organs evolved with the development of gonads that produce sperm and/or eggs. These organs contained cells that went through meiosis, an adaption of mitosis, which reduced the number of chromosomes in each reproductive cell by half while increasing the number of cells through cell division. The process of meiosis also contributed to the genetic diversity between gametes, through crossing over and independent assortment of chromosomes.

Complete reproductive systems developed in insects, where separate sexes are present. Sperm are made in testes and then travel through coiled tubes to the epididymis for storage. Eggs mature in the ovary. When they are released from the ovary, they travel to the uterine tubes for fertilization. Some insects have a specialized sac, called a spermatheca, which stores sperm for later use, sometimes up to a year. This allows fertilization to be timed with environmental or food conditions that are optimal for offspring survival.

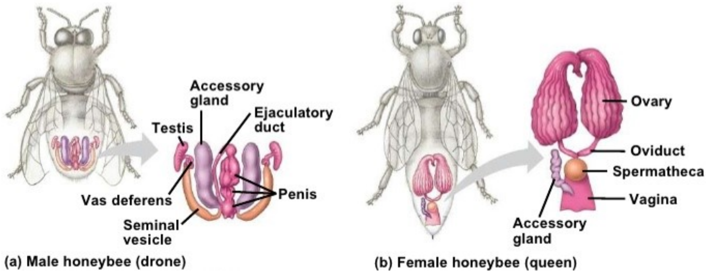

Figure 1. Honeybee reproductive systems

Vertebrates also have complete reproductive systems and separate sexes. Within the vertebrates, there are different adaptations within groups related to reproductive structures. Non-mammals, such as birds and reptiles, have a common body opening, called a cloaca, for the digestive, excretory, and reproductive systems. Coupling in these groups usually involves positioning the cloaca openings opposite each other for the transfer of sperm. Mammals, on the other hand, have separate openings for the systems in the female, In addition, female mammals also have a uterus that supports developing offspring. The uterus has two chambers in species that produce large numbers of offspring at a time, while species that produce one offspring, such as primates, have a single uterus.

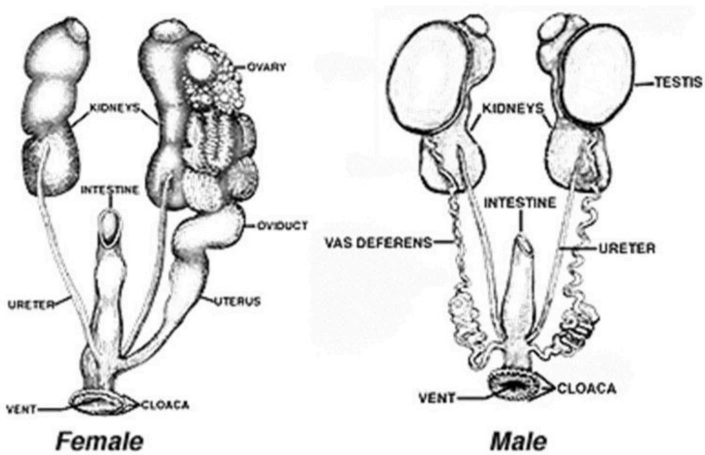

Figure 2. Bird reproductive systems

Sexual reproduction starts with the combination of a sperm and an egg in a process called fertilization. Sperm transfer from the male to the female during reproduction ranges from releasing the sperm into the watery environment for external fertilization to the joining of the cloaca in birds or the development of a penis for direct delivery into the female's vagina in mammals for internal fertilization.

External Fertilization

External fertilization usually occurs in aquatic environments where both eggs and sperm are released into the water. After the sperm reaches the egg, fertilization takes place. Most external fertilization happens during the process of spawning where one or several females release their eggs and the male(s) release sperm in the same area, at the same time. The release of the reproductive material may be triggered by water temperature or the length of daylight. Nearly all fish spawn, as do crustaceans (such as crabs and shrimp), mollusks (such as oysters), squid, and echinoderms (such as sea urchins and sea cucumbers). Broadcast spawning can result in a greater mixture of the genes within a group, leading to higher genetic diversity and a greater chance of species survival in a hostile environment. For sessile aquatic organisms like sponges, broadcast spawning is the only mechanism for fertilization and colonization of new environments.

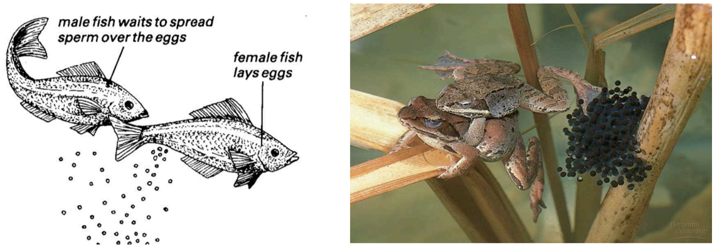

Figure 3. Paired spawning results in increased possibility of successful fertilization.

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

External fertilization in an aquatic environment protects the eggs from drying out. However, the presence of the fertilized eggs and developing young in the water provides opportunities for predation resulting in a loss of offspring. Therefore, millions of eggs must be produced by individuals, and the offspring produced through this method must mature rapidly, in order to ensure that at least some of the offspring survival. In general, the survival rate of eggs produced through broadcast spawning is low.

Review Question:

Quick Review: External Fertilization
Compare to broadcast spawning, pair spawning?
A) increases the likelihood of more genetic variability
B) enhances the likelihood of fertilization
C) increases the likelihood of offspring survival
D) enable the female to choose a specific mate

Internal Fertilization

Internal fertilization occurs most often in land-based animals, although some aquatic animals also use this method. Internal fertilization has the advantage of protecting the fertilized egg from dehydration on land. The embryo is isolated within the female, which limits predation on the young. Internal fertilization enhances the fertilization of eggs by a specific male. Fewer offspring are produced through this method, but their survival rate is higher than that for external fertilization.

There are three ways that offspring are produced following internal fertilization:

Oviparity: The fertilized eggs that result from internal fertilization are laid outside the female's body and develop there, receiving nourishment from the yolk that is a part of the egg. This occurs in most bony fish, many reptiles, some cartilaginous fish, most amphibians, two mammals (duck-billed platypi, echidnas), and all birds. Reptiles and insects produce leathery eggs, while birds and turtles produce eggs with high concentrations of calcium carbonate in the shell, making them hard.

Figure 4. Some sharks are ovoviviparous, retaining the egg inside the female and then giving birth to "hatched" offspring

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

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

For each of the ways that offspring are produced, there is a trade-off in offspring survival and energy expended by the parents. Oviparous organisms often produce a much larger number of fertilized eggs because the survival of the offspring is lower. Viviparous organisms in contrast produce fewer offspring and expend larger amounts of energy in protecting and nourishing the offspring prior to live birth.

Review Question:

Quick Review: Offspring development

Match the type of offspring development with the proper terminology

1) Viviparity A) offspring in an egg outside the female
2) Oviparity B) young develop inside the female
3) Ovoviviparity C) young remain in egg inside the female

Summary

Sexual reproduction starts with the combination of a sperm and an egg in a process called fertilization. This can occur either outside the bodies or inside the female. Both methods have advantages and disadvantages. Once fertilized, the eggs can develop inside the female or outside. If the egg develops outside the body, it usually has a protective covering over it. Animal anatomy evolved various ways to fertilize, hold, or expel the egg. The method of fertilization varies among animals. Some species release the egg and sperm into the environment, some species retain the egg and receive the sperm into the female body and then expel the developing embryo covered with shell, while still other species retain the developing offspring through the gestation period.

Review Questions

REVIEW: External Fertilization

1) External fertilization occurs in which type of environment?
A) aquatic
B) forested
C) savanna
D) steppe

REVIEW: Offspring of internal fertilization
2) Which term applies to egg development within the female with nourishment derived from a yolk?
A) oviparity
B) viviparity
C) ovoviparity
D) ovovoparity

REVIEW: Offspring of Internal Fertilization
3) Which term applies to egg development outside the female with nourishment derived from a yolk?
A) oviparity
B) viviparity
C) ovoviparity
D) ovovoparity

Thinking About It
4) What are the relative advantages and disadvantages of each of the types of parity that follow internal fertilization?

Attributions:

Materials based on :https://cnx.org/contents/GFy_h8cu@10.99:m2mqXRb6@4/Fertilization

46.

Learning Goals

By the end of this reading you should be able to:

- Describe the factors affecting homeostasis
- Discuss positive and negative feedback mechanisms used in homeostasis
- Describe thermoregulation of endothermic and ectothermic animals
- Give examples of how different animals regulate their body temperature

Introduction

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 the blood or in external temperatures. Homeostasis means maintaining dynamic equilibrium in the body. It is dynamic because it is constantly adjusting to the changes that the body’s systems encounter. It is an equilibrium because body functions are kept within specific ranges. Even an animal that is apparently inactive is maintaining this homeostatic equilibrium.

The goal of homeostasis is the maintenance of equilibrium around a point or value called a set point. While there are normal fluctuations from the setpoint, 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 deviation parameter toward the set point. For instance, if the body becomes too warm, adjustments are made to cool the animal. If the blood glucose rises after a meal, adjustments are made to lower the blood glucose level by getting the nutrient into tissues that need it or storing it for later use.

Control of Homeostasis

When a change occurs in an animal's environment, an adjustment must be made. The receptor senses the change in the environment, then sends a signal to the control center (in most cases, the brain) which in turn generates a response that is signaled to an effector. The effector is a muscle (that contracts or relaxes) or a gland that secretes. Homeostasis 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. In mammals, homeostasis is controlled by the nervous and endocrine systems.

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. 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."

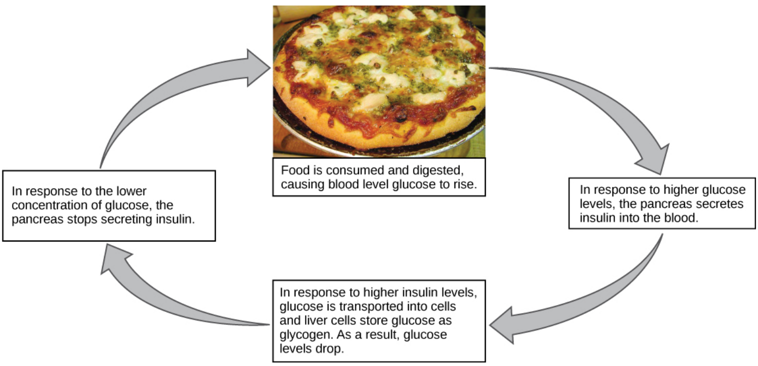

Figure 1. Blood sugar levels are controlled by a negative feedback loop. (credit: modification of work by Jon Sullivan)

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 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.

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.

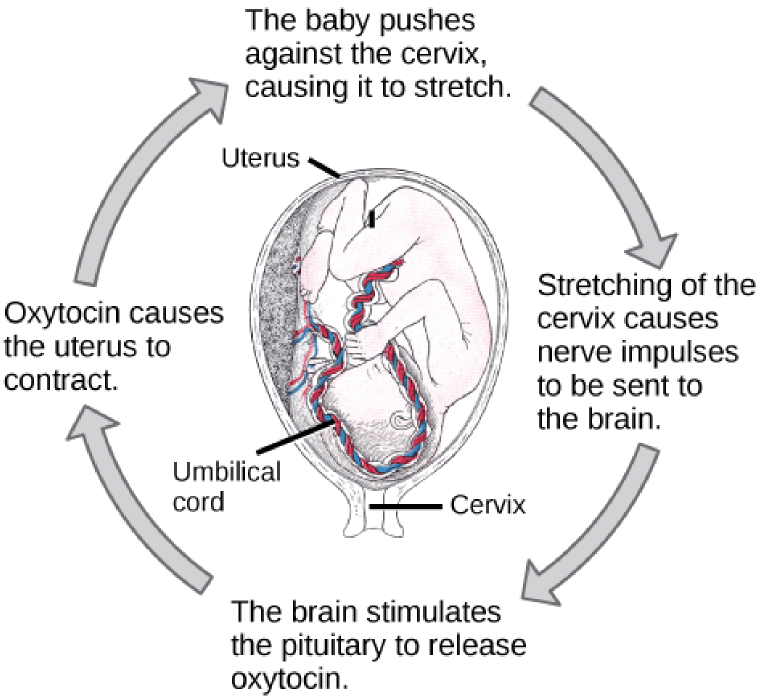

Figure 2. Contractions are an example a positive feedback loop.

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.

Review Question:

Quick Review: Feedback

State whether each of the following processes is regulated by a positive feedback loop or a negative feedback loop. A person feels satiated after eating a large meal. _ _ _ _ _ _ feedback
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. _ _ _ _ _ _ feedback

VIEW ME: This video provides an overview of feedback and how it works. It may help you to visualize how these processes work. https://youtu.be/_QbD92p_EVs

SetPoint

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.

Figure 3. Mountain climbers often pause for hours and even days to allow their bodies to acclimatize to the changes in available oxygen at different elevations.

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.

Homeostasis: Thermoregulation

Body temperature affects body activities. Generally, as body temperature rises, enzyme activity rises as well. For every ten-degree centigrade rise in temperature, enzyme activity doubles, up to a point. Body proteins, including enzymes, begin to denature and lose their function with high heat (around 50oC 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.

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. 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. In contrast to ectotherms, which rely on external temperatures to set their body temperatures, poikilotherms are animals with constantly varying internal temperatures. An animal that maintains a constant body temperature in the face of environmental changes is called a homeotherm. 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 the cooler temperatures, which an ectotherm cannot due to differing enzyme levels of activity.

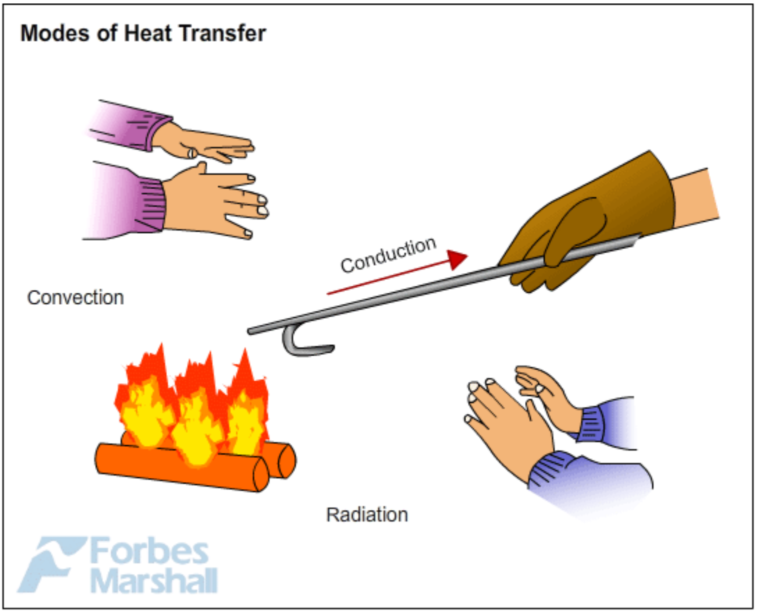

Figure 4. Three of the four methods of heat exchange. The fourth is evaporation.

Heat can be exchanged between an animal and its environment through four mechanisms: radiation, evaporation, convection, and conduction (Fig. 4). 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.

Quick Review: Energy Exchange

Which method of heat exchange occurs during direct contact between the source and animal?

A) radiation

B) evaporation

C) convection

D) conduction

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.

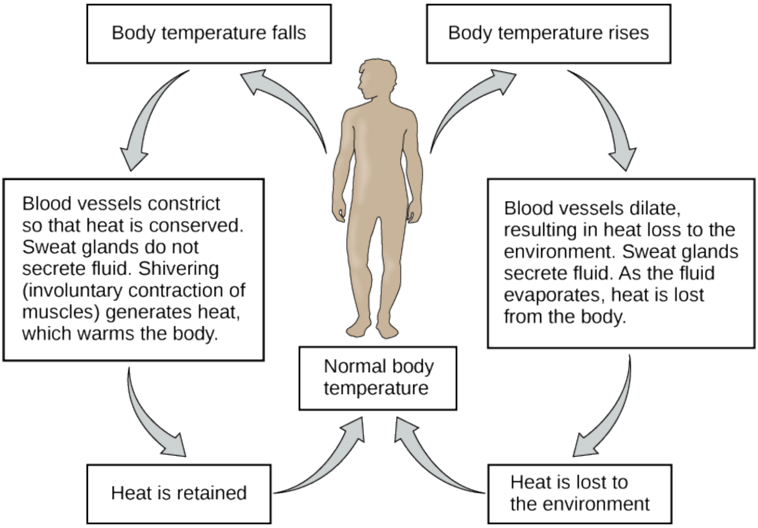

Figure 5. Regulation of internal temperature in endotherms involves both the nervous and circulatory systems.

Endotherms use their circulatory systems to help maintain body temperature. Vasodilation brings more blood and heat to the body's 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 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 activities 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.

VIEW ME: This video discusses some of the ways in which different animals regulate their body temperatures. https://youtu.be/NJEBfl_LKno

Summary

Homeostasis is a dynamic equilibrium that is maintained in body tissues and organs. It is dynamic because it is constantly adjusting to the changes that the systems encounter. It is in equilibrium because body functions are kept within a normal range, with some fluctuations around a set point for the processes.

End of Section Review Questions:

REVIEW: Types of maintenance

1) Which type of animal maintains a constant internal body temperature?

A) endotherm

B) ectotherm
C) coelomate
D) mesoderm

REVIEW: Feedback
2) Which is an example of negative feedback?
A) lowering of blood glucose after a meal
B) blood clotting after an injury
C) lactation during nursing
D) uterine contractions during labor

REVIEW: Endothermy
3) When faced with a sudden drop in environmental temperature, an endothermic animal will:
A) experience a drop in its body temperature
B) wait to see if it goes lower
C) increase muscle activity to generate heat
D) add fur or fat to increase insulation

REVIEW: Body Temperature Regulation
4) Different groups of animals maintain different body temperatures. Match each term with the most appropriate description
1) poikilothermic A) maintain a constant body temperature
2) endothermic B) does not regulate its body temperature
3) homeotherm C) rely on internal sources for body temperature
4) ectotherm D) constantly varying internal temperatures

Thinking About It
5) Explain why it is inaccurate to refer to ectotherms as "cold-blooded" and endotherms as "warm-blooded"

47.

Learning Goals

By the end of the reading you should be able to:

- Describe factors that can influence population densities and distributions
- Differentiate between different types of survivorship curves
- Explain how life history patterns are the result of natural selection

Introduction

Populations are dynamic entities. A population contains all of the individuals of a species living within a specific area, and populations fluctuate due to 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 in a specific area, 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. Below is a graph of data comparing Australian mammal sizes to their population densities. Take a moment to look at the data presented and then provide an answer to the question provided.

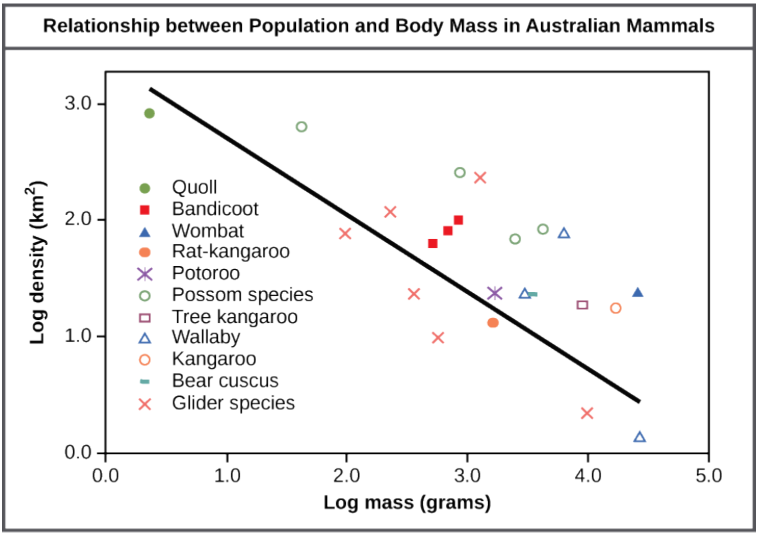

Figure 1. Relationship between population and body mass in Australian mammals

Thinking About It
According to the data on Australian mammals presented in the graph, the population density typically decreased with increasing body size. Why do you think this is the case?

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.

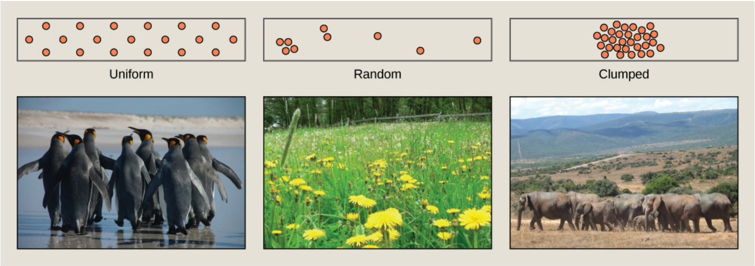

Figure 2. Territorial birds such as penguins tend to have a uniform distribution. Plants such as dandelions with wind-dispersed seeds tend to be randomly distributed. Animals such as elephants that travel in groups exhibit clumped distribution. (credit a: modification of work by Ben Tubby; credit b: modification of work by Rosendahl; credit c: modification of work by Rebecca Wood)

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.

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's characteristics; size, density, and distribution. 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.

Survivorship Curves

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. These curves allow us to compare the life histories of different populations.

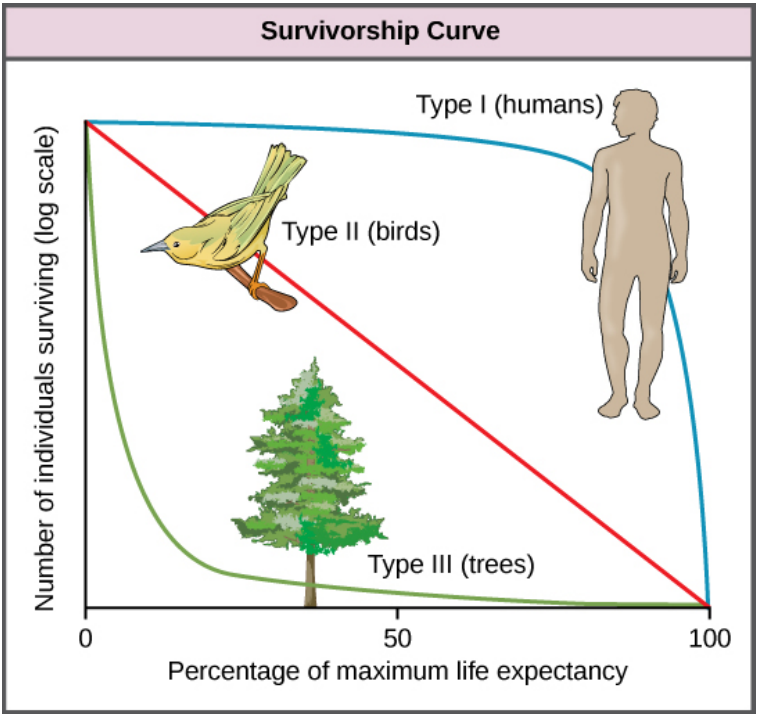

Figure 3. Survivorship curves show the distribution of individuals in a population according to age.

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.

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

Figure 4. Octopi produce large numbers of eggs but most do not provide any parental care for their offspring.

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 that maximizes 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.

Figure 5. Humpback whales only produce 1-2 offspring at a time and provide extensive parental care.

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 trade-off 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.

Review Question:

Quick Review: Parental Care
Which of the following is most likely to be associated with long-term parental care?
A) many large offspring
B) many smaller offspring
C) fewer offspring
D) smaller animals

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 fish. 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 and 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, reproducing early before they die. Other species delay reproducing and become stronger, more experienced individuals ensuring they are strong enough to provide parental care if necessary.

Single versus Multiple Reproductive Events

Some life history traits, such as fecundity, the 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, 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. 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.

Summary

Populations are individuals of a species that live in a particular habitat. Ecologists measure characteristics of populations: size, density, dispersion pattern, age structure, and sex ratio. Life tables are useful to calculate the life expectancies of individual population members. Survivorship curves show the number of individuals surviving at each age interval plotted versus time.

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.

End of Section Review Questions:

REVIEW: Density
1) In general, organisms tend to be more densely distributed than organisms.

REVIEW: Distributions
2) What type of distribution pattern would you expect to see in tigers which are highly territorial animals?

REVIEW: Survivorship Curves
3) What type of survivorship curb would you see for oak trees that produce thousands of acorns, but very few of the acorns grow into mature oak trees?

A) Type I
B) Type II
C) Type III

REVIEW: Reproductive Events
_______ occurs when a species reproduces only once and then dies
________occurs when a species can reproduce multiple times over its lifetime

48.

Learning Goals

By the end of this reading you should be able to:

- Describe the conditions in which exponential growth might occur
- Calculate the intrinsic and maximum growth rate of a population
- Explain the relationship between logistic growth and carrying capacity
- Describe how intraspecific competition can impact population growth
- Predict the effect of changing environmental conditions on population growth

Introduction

Life histories describe the way many characteristics of a population (such as their age structure) change over time in a general way. However, there are other factors, including environmental conditions that impact the rate that a population can grow. When resources are unlimited (or in many cases just readily available) populations can often grow at very fast rates and in an exponential manner. When resources becoming limiting the rate of growth usually begins to slow and in some cases the population may actually begin to decline. Scientists have developed some models that help to predict the growth of populations based on the life histories of organisms and the environmental conditions. However, these models are only predictors and newer more complex models are constantly being built to take into account new or changing factors.

Exponential Growth

Charles Darwin, in his theory of natural selection, was greatly influenced by the English clergyman Thomas Malthus. Malthus published a book in 1798 stating that populations with unlimited natural resources grow very rapidly, and then population growth decreases as resources become depleted. This accelerating pattern of increasing population size is called exponential growth.

The best example of exponential growth is seen in bacteria. Bacteria are prokaryotes that reproduce by binary fission. In some species of bacteria the time between bouts of binary fission can be as short as 60 minutes, and in some species even as quickly as 20 minutes. Consider this, if 1000 bacteria can divide every 60 minutes are placed in a large flask with an unlimited supply of nutrients (so the nutrients will not become depleted), after an hour, assuming each individual divides, there will be 2000 organisms—an increase of 1000. In another hour, each of the 2000 organisms will divide, producing 4000, an increase of 2000 organisms. After the third hour, there should be 8000 bacteria in the flask, an increase of 4000 organisms. The important concept of exponential growth is that the population growth rate—the number of organisms added in each reproductive generation—is accelerating; that is, it is increasing at a greater and greater rate. After 1 day and 24 of these cycles, the population would have increased from 1000 to more than 16 billion. When the population size, N, is plotted over time, a J-shaped growth curve is produced.

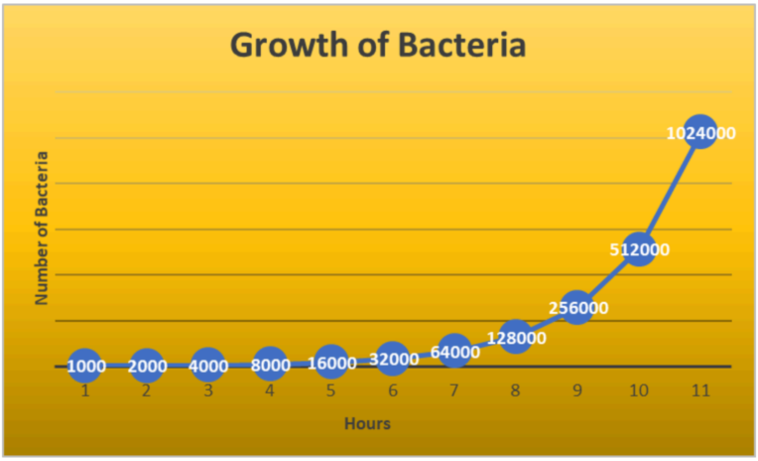

Figure 1. Exponential growth curve for a bacterial population with the capacity to divided every 60 minutes and unlimited resources.

The bacteria example is not representative of the real world where resources are limited. Furthermore, some bacteria will die during the experiment and thus not reproduce, lowering the growth rate. Therefore, when calculating the growth rate of a population, the death rate (*D*) (number of organisms that die during a particular time interval) is subtracted from the birth rate (*B*) (number of organisms that are born during that interval). This is shown in the following formula:

$$\Delta N \text{ (change in number)} \Delta T \text{ (change in time)} = B \text{ (birth rate)} - D \text{ (death rate)}$$

The birth rate is usually expressed on a per capita (for each individual) basis. Thus, B (birth rate) = *bN* (the per capita birth rate "*b*" multiplied by the number of individuals "N") and *D* (death rate) =*dN* (the per capita death rate "d" multiplied by the number of individuals "N"). Additionally, ecologists are interested in the population at a particular point in time, an infinitely small time interval. For this reason, the terminology of differential calculus is used to obtain the "instantaneous" growth rate, replacing the *change* in number and time with an instant-specific measurement of number and time.

$$dNdT = bN - dN = (b - d)N$$

Notice that the "*d*" associated with the first term refers to the derivative (as the term is used in calculus) and is different from the death rate, also called "*d*." The difference between birth and death rates is further simplified by substituting the term "*r*" (intrinsic rate of increase) for the relationship between birth and death rates:

$$dNdT = rN$$

The value "*r*" can be positive, meaning the population is increasing in size; or negative, meaning the population is decreasing in size; or zero, where the population's size is unchanging, a condition is known as zero population growth. A further refinement of the formula recognizes that different species have inherent differences in their intrinsic rate of increase (often thought of as the potential for reproduction), even under ideal conditions. Obviously, a bacterium can reproduce more rapidly and have a higher intrinsic rate of growth than a human. The maximal growth rate for a species is its biotic potential, or *rmax*, thus changing the equation to:

$$dNdT=rmaxN$$

Review Question:

Quick Review: Intrinsic Growth

For each of the values of r, indicate if the population is increasing, decreasing, or not changing

r=-345 _______

r=75 _______

r=0 _______

Logistic Growth

Exponential growth is possible only when infinite natural resources are available; this is not the case in the real world. Charles Darwin recognized this fact in his description of the "struggle for existence," which states that individuals will compete (with members of their own or other species) for limited resources. The successful ones will survive to pass on their own characteristics and traits (which we know now are transferred by genes) to the next generation at a greater rate (natural selection). To model the reality of limited resources, population ecologists developed the logistic growth model.

Carrying Capacity and the Logistic Model

In the real world, with its limited resources, exponential growth cannot continue indefinitely. Exponential growth may occur in environments where there are few individuals and plentiful resources, but when the number of individuals gets large enough, resources will be depleted, slowing the growth rate. Eventually, the growth rate will plateau or level off (Fig. 2a). This population size, which represents the maximum population size that a particular environment can support, is called the carrying capacity, or *K*.

The formula we use to calculate logistic growth adds the carrying capacity as a moderating force in the growth rate. The expression "*K* – N" is indicative of how many individuals may be added to a population at a given stage, and "*K* – N" divided by "*K*" is the fraction of the carrying capacity available for further growth. Thus, the exponential growth model is restricted by this factor to generate the logistic growth equation:

dNdT=*r*max*dNdT*=*r*maxN(*K* − N)*K*

Notice that when N is very small, (*K*-N)/*K* becomes close to *K*/

K or 1, and the right side of the equation reduces to *rmax*N, which means the population is growing exponentially and is not influenced by carrying capacity. On the other hand, when N is large, (*K*-N)/*K* *comes* close to zero, which means that population growth will be slowed greatly or even stopped. Thus, population growth is greatly slowed in large populations by the carrying capacity *K*. This model also allows for the population of negative population growth, or a population decline. This occurs when the number of individuals in the population exceeds the carrying capacity (because the value of (K-N)/K is negative).

A graph of this equation yields an S-shaped curve (Fig. 2b), and it is a more realistic model of population growth than exponential growth. There are three different sections to an S-shaped curve. Initially, growth is exponential because there are few individuals and ample resources available. Then, as resources begin to become limited, the growth rate decreases. Finally, growth levels off at the carrying capacity of the environment, with little change in population size over time.

Role of Intraspecific Competition

The logistic model assumes that every individual within a population will have equal access to resources and, thus, an equal chance for survival. For plants, the amount of water, sunlight, nutrients, and the space to grow are important resources, whereas in animals, important resources include food, water, shelter, nesting space, and mates.

In the real world, phenotypic variation among individuals within a population means that some individuals will be better adapted to their environment than others. The resulting competition between population members of the same species for resources is termed **intraspecific competition** (intra- = "within"; -specific = "species").

Intraspecific competition for resources may not affect populations that are well below their carrying capacity—resources are plentiful and all individuals can obtain what they need. However, as population size increases, this competition intensifies. In addition, the accumulation of waste products can reduce an environment's carrying capacity.

Examples of Logistic Growth

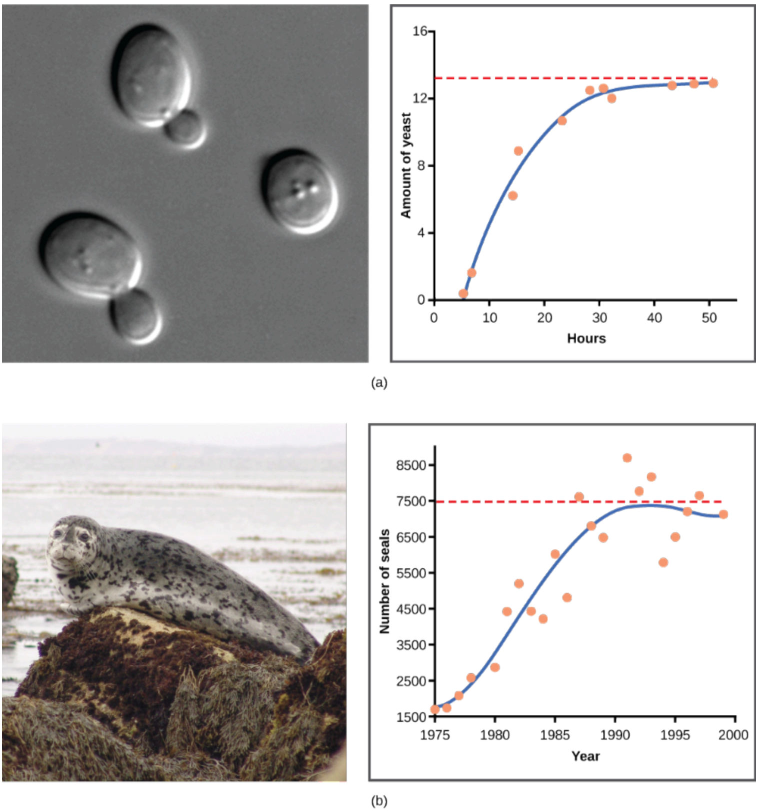

Figure 2. Yeast, a microscopic fungus used to make bread and alcoholic beverages, exhibits the classical S-shaped curve when grown in a test tube (a). Its growth levels off as the population depletes the nutrients that are necessary for its growth. In the real world, however, there are variations to this idealized curve. Examples in wild populations include sheep and harbor seals (b). In both examples, the population size exceeds the carrying capacity for short periods of time and then falls below the carrying capacity afterward. This fluctuation in population size continues to occur as the population oscillates around its carrying capacity. Still, even with this oscillation, the logistic model is confirmed.

Review Question:

Quick Review: Logistic Growth
If the major food source of the seals declines due to pollution or overfishing, which of the following would likely occur?
A) The carrying capacity of seals would decrease, as would the seal population.
B) The carrying capacity of seals would decrease, but the seal population would remain the same.
C) The number of seal deaths would increase but the number of births would also increase, so the population size would remain the same.
D) The carrying capacity of seals would remain the same, but the population of seals would decrease.

Summary

Populations with unlimited resources grow exponentially, with an accelerating growth rate. When resources become limiting, populations follow a logistic growth curve. The population of a species will level off at the carrying capacity of its environment.

End of Section Review Questions:

REVIEW: Growth Curves
1) Species with limited resources usually exhibit a(n) __________ growth curve.
A) logistic
B) logical
C) experimental
D) exponential

REVIEW: Rates of growth

2) The maximum growth rate of a species is called its __________.

A) limit

B) carrying capacity

C) biotic potential

D) exponential growth pattern

REVIEW: Limits to growth

3) The population size of a species capable of being supported by the environment is called its __________.

A) limit

B) carrying capacity

C) biotic potential

D) logistic growth pattern

49.

Learning Goals

By the end of this reading, you should be able to:

- Explain how the carrying capacity of a habitat may change
- Compare and contrast density-dependent growth regulation and density-independent growth regulation, giving examples
- Give examples of exponential and logistic growth in wild animal populations
- Describe how natural selection and environmental adaptation leads to the evolution of particular life history patterns

Introduction

The logistic model of population growth, while valid in many natural populations and a useful model, is a simplification of real-world population dynamics. Implicit in the model is that the carrying capacity of the environment does not change, which is not the case. The carrying capacity varies annually: for example, some summers are hot and dry whereas others are cold and wet. In many areas, the carrying capacity during the winter is much lower than it is during the summer. Also, natural events such as earthquakes, volcanoes, and fires can alter an environment and hence its carrying capacity. Additionally, populations do not usually exist in isolation. They engage in interspecific competition: that is, they share the environment with other species competing for the same resources. These factors are also important to understanding how a specific population will grow.

Nature regulates population growth in a variety of ways. These are grouped into density-dependent factors, in which the density of the population at a given time affects growth rate and mortality, and density-independent factors, which influence mortality in a population regardless of population density. Note that in the former, the effect of the factor on the population depends on the density of the population at the onset. Conservation biologists want to understand both types because this helps them manage populations and prevent extinction or overpopulation.

Density-Dependent Regulation

Most density-dependent factors are biological in nature (biotic), and include predation, inter-and intraspecific competition, accumulation of waste, and diseases such as those caused by parasites. Usually, the denser a population is, the greater its mortality rate. For example, during intra- and interspecific competition, the reproductive rates of the individuals will usually be lower, reducing their population's rate of growth. In addition, low prey density increases the mortality of its predator because it has more difficulty locating its food source.

An example of density-dependent regulation is shown in Fig. 1 with results from a study focusing on the giant intestinal roundworm (*Ascaris lumbricoides*), a parasite of humans and other mammals. Denser populations of the parasite exhibited lower fecundity: they contained fewer eggs. One possible explanation for this is that females would be smaller in more dense populations (due to limited resources) and that smaller females would have fewer eggs. This hypothesis was tested and disproved in a 2009 study that showed that female weight had no influence. The actual cause of the density-dependence of fecundity in this organism is still unclear and awaiting further investigation.

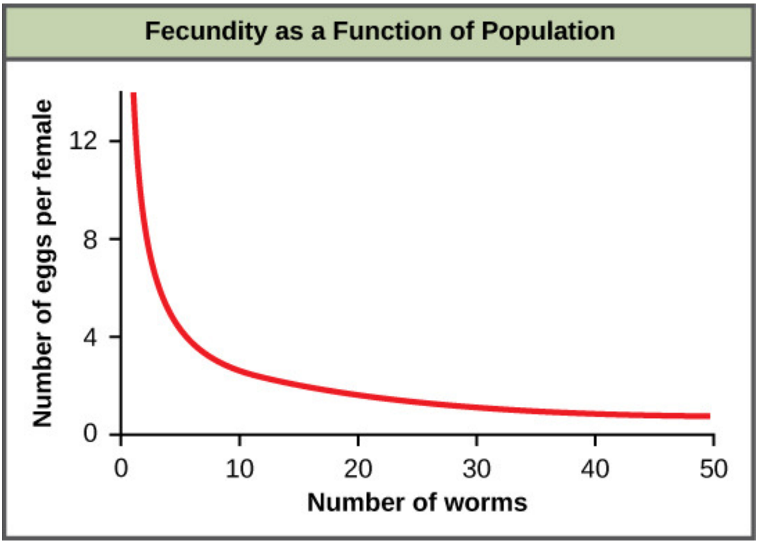

Figure 1. In this population of roundworms, fecundity (the number of eggs) decreases with population density.

Density-Independent Regulation and Interaction with Density-Dependent Factors

Many factors, typically physical or chemical in nature (abiotic), influence the mortality of a population regardless of its density, including weather, natural disasters, and pollution. An individual deer may be killed in a forest fire regardless of how many deer happen to be in that area. Its chances of survival are the same whether the population density is high or low. The same holds true for cold winter weather.

In real-life situations, population regulation is very complicated and density-dependent and independent factors can interact. A dense population that is reduced in a density-independent manner by some environmental factor(s) will be able to recover differently than a sparse population. For example, a population of deer affected by a harsh winter will recover faster if there are more deer remaining to reproduce.

Life Histories of *K*-selected and *r*-selected Species

While reproductive strategies play a key role in life histories, they do not account for important factors like limited resources and competition. The regulation of population growth by these factors can be used to introduce a classical concept in population biology, that of *K*-selected versus *r*-selected species.

The concept relates to a species' reproductive strategies, habitat, and behavior, especially in the way that they obtain resources and care for their young. It includes the length of life and survivorship factors as well. Population biologists have grouped species into the two large categories—*K*-selected and *r*-selected—although the categories are really two ends of a continuum.

K-selected species are species selected by stable, predictable environments. Populations of *K*-selected species tend to exist close to their carrying capacity (hence the term *K*-selected) where intraspecific competition is high. These species have few, large offspring, a long gestation period, and often give long-term care to their offspring. While larger in size when born, the offspring are relatively helpless and immature at birth. By the time they reach adulthood, they must develop skills to compete for natural resources. In plants, scientists think of parental care more broadly: how long fruit takes to develop or how long it remains on the plant are determining factors in the time to the next reproductive event. Examples of *K*-selected species are primates (including humans), elephants, and plants such as oak trees.

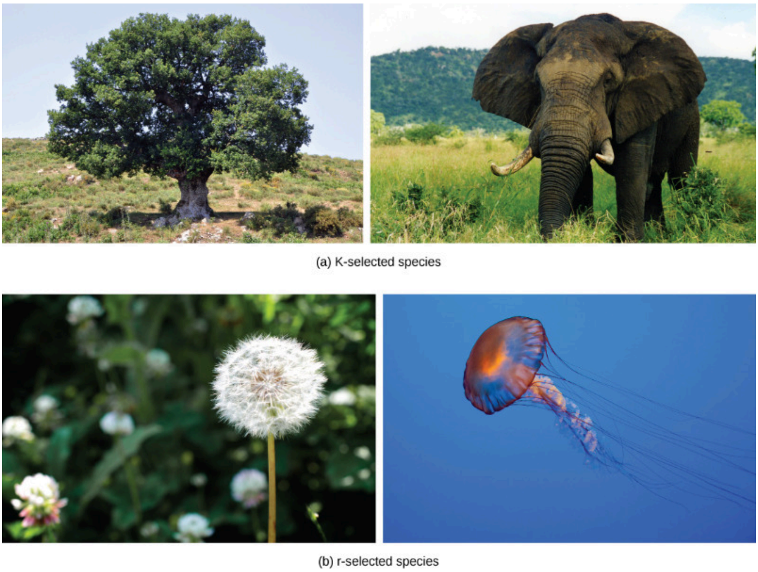

Figure 2. Examples of r- and K-selected species

Oak trees grow very slowly and take, on average, 20 years to produce their first seeds, known as acorns. As many as 50,000 acorns can be produced by an individual tree, but the germination rate is low as many of these rot or are eaten by animals such as squirrels. In some years, oaks may produce an exceptionally large number of acorns, and these years may be on a two- or three-year cycle depending on the species of oak (*r*-selection).

As oak trees grow to a large size and for many years before they begin to produce acorns, they devote a large percentage of their energy budget to growth and maintenance. The tree's height and size allow it to dominate other plants in the competition for sunlight, the oak's primary energy resource. Furthermore, when it does reproduce, the oak produces large, energy-rich seeds that use its energy reserve to become quickly established (*K*-selection).

In contrast, *r*-selected species have a large number of small offspring (hence their r designation). This strategy is often employed in unpredictable or changing environments. Animals that are r-selected do not give long-term parental care and the offspring are relatively mature and self-sufficient at birth. Examples of r-selected species are marine invertebrates, such as jellyfish, and plants, such as the dandelion. Dandelions have small seeds that are wind-dispersed long distances. Many seeds are produced simultaneously to ensure that at least some of them reach a hospitable environment. Seeds that land in inhospitable environments have little chance for survival since their seeds are low in energy content. Note that survival is not necessarily a function of energy stored in the seed itself.

R-selected species	K-selected species
Early maturation	Later maturation
Shorter lifespan	Longer lifespan
Less/no parental care	More parental care
Larger # offspring	Fewer offspring
Offspring smaller in size	Offspring larger in size

Table 1. Characteristics of r- and K-selected species.

Summary

By the second half of the twentieth century, the concept of K- and r-selected species was used extensively and successfully to study populations. The r– and K-selection theory, although accepted for decades and used for much groundbreaking research, has now been reconsidered, and many population biologists have abandoned or modified it. Over the years, several studies attempted to confirm the theory, but these attempts have largely failed. Many species were identified that did not follow the theory's predictions.

Furthermore, the theory ignored the age-specific mortality of the populations which scientists now know is very important. New demographic-based models of life history evolution have been developed which incorporate many ecological concepts included in r– and K-selection theory as well as population age structure and mortality factors.

End of Section Review Questions:

REVIEW: Selection strategies

1) Mice and rabbits produce a large number of offspring with each reproductive event. How would you classify these animals?

A) r-selected
B) K-selected
C) both r- and K-selected
D) not selected

REVIEW: Dependent vs. Independent regulation

2) Natural disturbances, like forest fires or hurricanes, would be examples of what type of population regulation?

A) density-dependent
B) density-independent
C) r-selected
D) K-selected

REVIEW: Selection strategies

3) What types of organisms are often K-selected species?

A) small annual plants
B) large mammals
C) insects
D) large flowering trees (oaks; chestnuts; walnuts)

Thinking about it

4) Describe the environments in which r and k selected species would like to be found and explain why this type of life history

would be beneficial in those environments.

50.

Learning Goals

By the end of this reading, you should be able to:

- Discuss the predator-prey cycle
- Give examples of defenses against predation and herbivory
- Describe the competitive exclusion principle
- Give examples of symbiotic relationships between species
- Explain how species interactions can play a role in the adaptation and evolution of species

Introduction

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.

Predation and Herbivory

Perhaps the classical example of species interaction is predation: the consumption of prey by its predator. While we usually think of animals hunting other animals, herbivory, in which plants are eaten by animals is also a form of predation. The predator-prey relationship is considered to be an antagonist one, where one species has a negative impact on the other species. Within a community the sizes of the populations of predators and prey are often not constant over time: in most cases, the respective populations' sizes will vary in cycles that appear to be related.

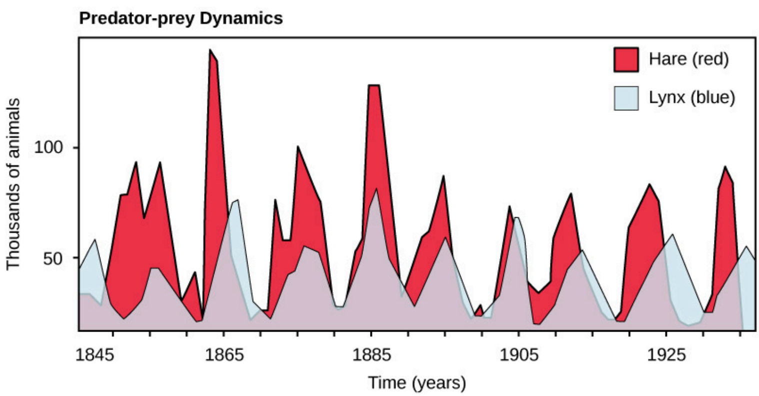

Figure 1. The cycling of lynx and snowshoe hare populations in Northern Ontario is an example of predator-prey dynamics.

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. 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 the hare population begins to decline, followed by a decline in the lynx population because of the 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.

Some researchers question the idea that predation models entirely control the population cycling of the two species. More recent studies have pointed to undefined density-dependent factors as being important in cycling, in addition to predation. One possibility is that 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.

Review Question:

Quick Review: Causes of Cycling
In addition to the negative impact of predation, what other factors might be causing cycling in a prey population?
A) changes in fecundity
B) alterations in environmental conditions
C) density-dependent increases in disease

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.

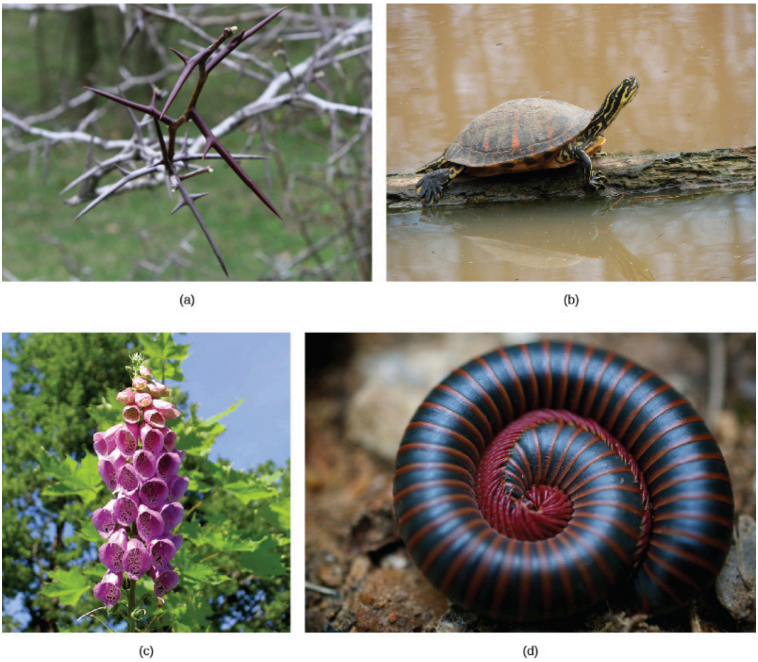

Figure 2. credit a: modification of work by Huw Williams; credit b: modification of work by "JamieS93"/Flickr; credit c: modification of work by Philip Jägenstedt; credit d: modification of work by Cory Zanker

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.

(a) (b)

Figure 3. credit a: modification of work by Linda Tanner; credit b: modification of work by Frank Vassen

Other 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 (**a**) which makes it very hard to see when stationary against a background of real twigs. In another example, the chameleon can change its color to match its surroundings (**b**). Both of these are examples of camouflage or avoiding detection by blending in with the background.

The use of specific coloration as a way of warning predators to avoid eating them can be found in some species of organisms. For example, the cinnabar moth caterpillar, the fire-bellied toad, and many species of beetle have bright colors that warn of a foul taste, the presence of toxic chemicals, and/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. credit a: modification of work by Jay Iwasaki; credit b: modification of work by Dan Dzurisin*

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

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

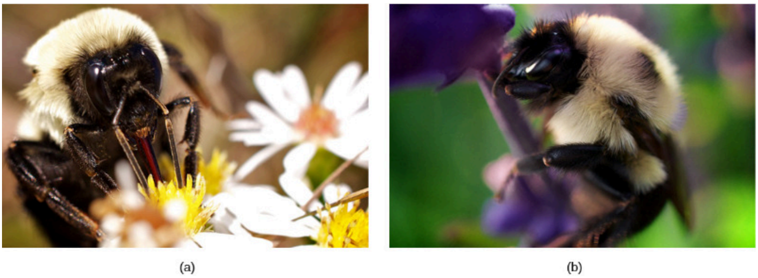

Figure 5. Batesian mimicry occurs when a harmless species mimics the coloration of a harmful species, as is seen with the (a) bumblebee and (b) bee-like robber fly. (credit a, b: modification of work by Cory Zanker)

In Müllerian mimicry, multiple species share the same warning coloration, but all of them actually have defenses. This means that they mimic each other in some way creating a larger grouping and thus can be more easily recognized by potential predators.

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

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

Review Question:

Quick Review: Mimcry
In mimicry, all of the species have some type of harmful toxin.
In mimicry, a toxic species mimics a non-toxic or less toxic species
In a non-toxic/not dangerous species mimics a more toxic/dangerous species

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 can be seen with two protozoan species, *Paramecium aurelia* and *Paramecium caudatum.*

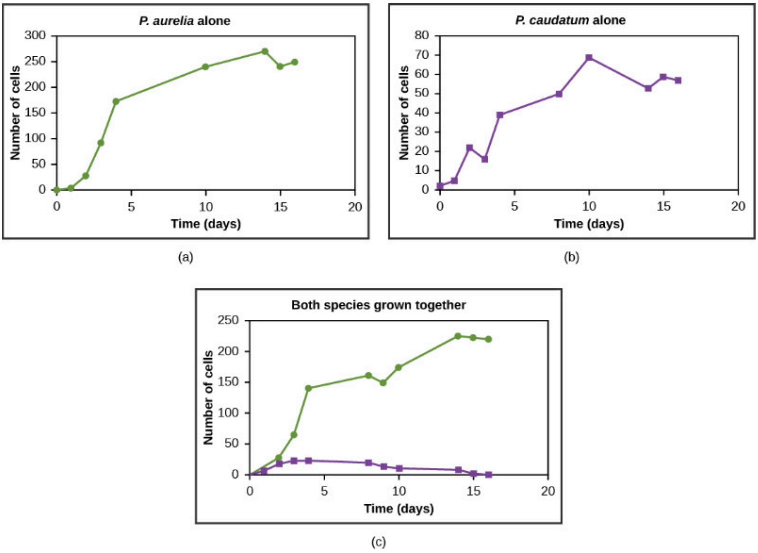

Figure 7. Paramecium aurelia and Paramecium caudatum grow well individually, but when they compete for the same resources, the P. aurelia outcompetes the P. caudatum.

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

Review Question:

Quick Review: Competitive Exclusion

When two species live in the same environment and use the same

resources what is likely to happen?

A) one species will outcompete the other

B) both species will be able to coexist but at lower population sizes

C) resource partitioning between the two species may evolve

D) one of the species may become locally extinct

Symbiosis

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

Commensalism

A commensal relationship occurs when one species benefits from the close, prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provides an example of a commensal relationship.

Figure 8.

Typically 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 clownfish and the sea anemone. The sea anemone is not harmed by the fish and the fish benefits from protection from predators who would be stung upon nearing the sea anemone.

Mutualism

The second type of symbiotic relationship is called mutualism, where two species benefit from their interaction. For example, termites have a mutualistic relationship with protozoa that live in the insect's gut (**a**). 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 (**b**). 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.

(a) (b)

Figure 9. 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 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 is consumed. d\The tapeworm can live inside the intestine of the host for several years, benefiting from the food the host is eating and may grow to be over 50 ft long by adding segments. The parasite moves from species to species in a cycle, making two hosts necessary to complete its life cycle.

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

Review Question:

Quick Review: Symbiotic Relationships
For each of the examples below indicate the type of symbiotic relationship that is occurring:
Cows have prokaryotic organisms (archaea) that live in their gut and aid in the digestion of grasses:_______
A dog tick (*Amblyomma americana*) attaches to and feed off the blood of dogs:_______
The remora (a fish) rides attached to sharks and other types of

fish for protection:_______

Summary

Communities include all the different species living in a given area. The variety of these species is called species richness. Many organisms have developed defenses against predation and herbivory, including mechanical defenses, warning coloration, and mimicry, as a result of evolution and the interaction with other members of the community. Two species cannot exist in the same habitat competing directly for the same resources. Species may form symbiotic relationships such as commensalism or mutualism.

End of Section Review Questions:

REVIEW: Mimicry
1) Which type of mimicry involves multiple species with similar warning coloration that are all toxic to predators?
A) Batesian mimicry
B) Müllerian mimicry
C) Emsleyan/Mertensian mimicry
D) Mertensian mimicry

REVIEW: Competition
2) Resource partitioning is most likely to occur when?
A) two species occupy the same area
B) two species utilize the same resource(s)
C) one species preys upon the other species
D) one species mimics the defensive coloration of the other

Thinking about it
3) Why might it take 1-2 reproductive cycles (or even years) before

a predator population size changes as a result of a downsizing of the prey population?

Thinking about it

4) Each of the types of interspecific interactions can result in changes in both populations. Explain the potential evolutionary impacts of interspecific interactions.

This is where you can add appendices or other back matter.