A PHOTOGRAPHIC ATLAS FOR BOTANY



Maria Morrow
College of the Redwoods



A Photographic Atlas for Botany

Written and assembled by Maria Morrow



Cover Image: Moss sporophytes in UV light. Image by Alan Rockefeller, (CC-BY-NC) https://www.inaturalist.org/observations/67338234.

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1: DIVERSITY OF LIFE

1.1: Diversity of Life Introduction

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1.1: Diversity of Life Introduction

The Domains of Life

As of the 1970's, life has been classified into three domains: Bacteria, Archaea, and Eukarya (shown in Figure 1.1.1 as Eukaryota). All known life on Earth is thought to have descended from a single common ancestor: LUCA (last universal common ancestor). The relationship between the three domains of life is depicted in the phylogenetic tree below. This diagram represents Archaea and Eukarya as sister taxa, more closely related than either group is to Domain Bacteria.

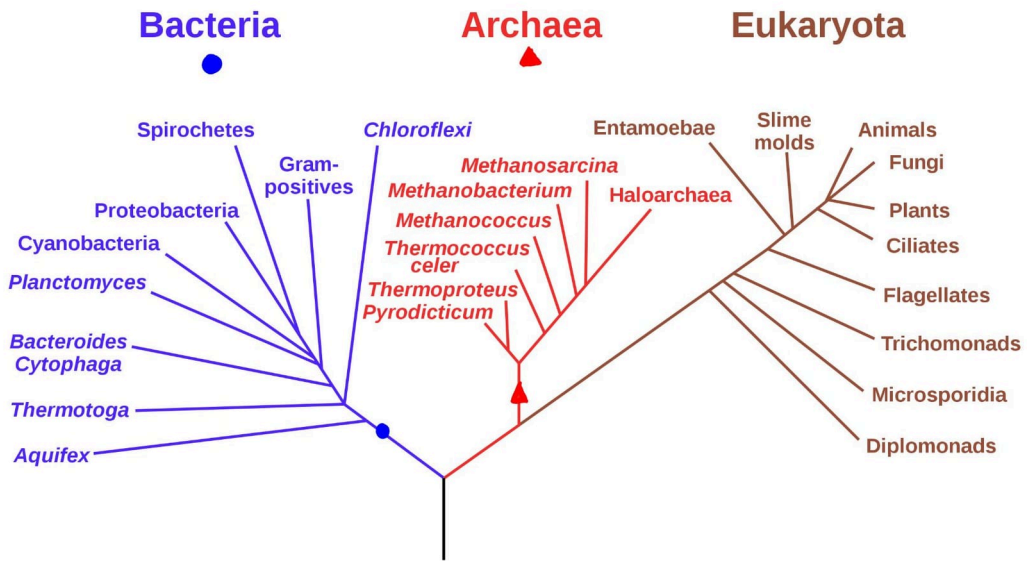
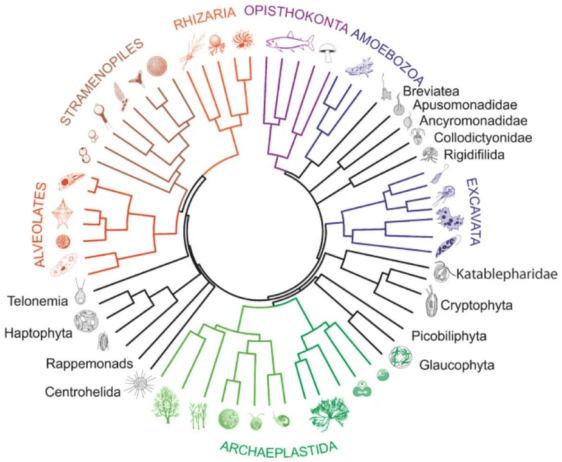


Figure 1.1.1: "A phylogenetic tree of living things, based on RNA data and proposed by Carl Woese, showing the separation of bacteria, archaea, and eukaryotes. Trees constructed with other genes are generally similar, although they may place some early-branching groups very differently, thanks to long branch attraction. The exact relationships of the three domains are still being debated, as is the position of the root of the tree. It has also been suggested that due to lateral gene transfer, a tree may not be the best representation of the genetic relationships of all organisms. For instance some genetic evidence suggests that eukaryotes evolved from the union of some bacteria and archaea (one becoming an organelle and the other the main cell)." This vector version produced in 2006: Eric Gaba (Sting, fr:Sting), Cherkash, Public domain, via Wikimedia Commons.

Relationships Within Eukarya

Figure 1



Deep phylogeny of eukaryotes showing the position of small eukaryotic lineages that branch outside the seven supergroups (modified after Burki *et al.* [12]; drawings S Chraiti).

Depicting Relationships

Branching tree diagrams (like the phylogenies shown above) are used to communicate a hypothesis for how organisms are related. In Figure 1.1.3 and Figure 1.1.4, some example trees are drawn to show how this works.

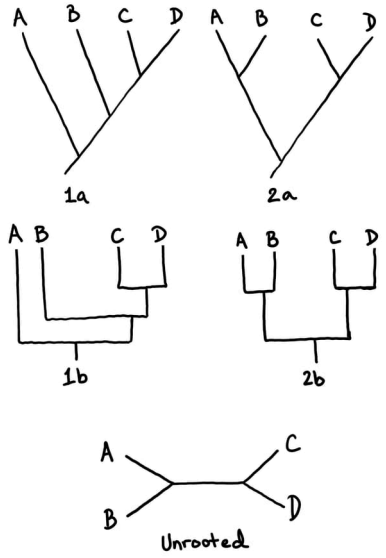


Figure 1.1.3: These diagrams (cladograms) show hypotheses for four different **taxa**: A, B, C, and D. These taxa could represent individuals, different species, or any other level of classification. Trees 1a and 1b are drawn differently but represent the same hypothesis: C and D are most closely related (sister taxa) and A is the most ancestral lineage. Trees 2a and 2b represent a slightly different hypothesis: C and D are sister taxa, but A and B are also sister taxa; neither lineage is depicted as "older" than the other. This last relationship is also represented in the "Unrooted" tree: there is no hypothesis in this tree for which group is most ancestral (no "root"). Images drawn by Maria Morrow, CC-BY.

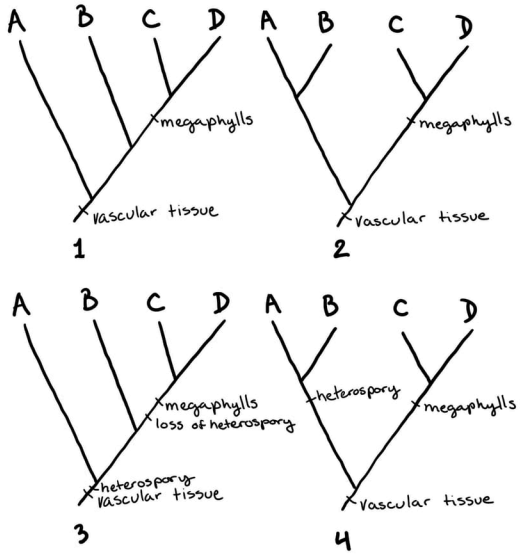


Figure 1.1.4: In these four trees, we are again looking at hypotheses for how A, B, C, and D are related. However, in these trees we have some information about why these determinations were made: traits have been included. In trees 1 and 2, vascular tissue and megaphylls have been added to the two different hypotheses presented in Figure 1.1.3. Vascular tissue appears on the root of the trees as an ancestral trait. This means that A, B, C, and D all have vascular tissue. Megaphylls appears in both trees as a shared derived characteristic (synapomorphy) of C and D. This means C and D have megaphylls, but A and B do not. Both tree 1 and tree 2 are equally parsimonious. In trees 3 and 4, a third trait has been added: heterospory. In addition to the information from trees 1 & 2, we now see that A and B are heterosporous, while C and D are not. In tree 3, heterospory appears as an ancestral trait which is lost in C and D. In tree 4, heterospory is a synapomorphy of A and B. Tree 3 has four changes, while tree 4 only has three. This means that tree 4 is more parsimonious and therefore more likely (though not necessarily correct!). Images drawn by Maria Morrow, CC-BY.

Genetic Information as Traits

```
VEGF-A HUMAN (P15692)   VVKFMDVYQRSYCHPIETLVDIFQEYPDEIEYIFKPSCVPLMRCGGCCNDEGLECVPTEESNITMQIMRIKPHQGQH--IGEMSFLQHNKCECRPKKD
VEGF-A MOUSE (Q00731)   VIKFMDVYQRSYCRPIETLVDIFQEYPDEIEYIFKPSCVPLMRCAGCCNDEALECVPTSESNITMQIMRIKPHQSQH--IGEMSFLQHSRCECRPKKD
PIGF HUMAN (P49763)     VVPFQEVWGRSYCRALERLVDVVSEYPSEVEHMFSPSCVSLLRCTGCCGDENLHCVPVETANVTMQLLKIRSGDRPS--YVELTFSQHVRCECRHSPG
PIGF MOUSE (P49764)     VVPFNEVWGRSYCRPMEKLVYILDEYPDEVSHIFSPSCVLLSRCSGCCGDEGLHCVPIKTANITMQILKIPPNRDPHF-YVEMTFSQDVLCECRPILE
VEGF-B HUMAN (P49765)   VVSWIDVYTRATCQPREVVVPLTVELMGTVAKQLVPSCVTVQRCGGCCPDDGLECVPTGQHQVRMQILMIRYPSSQ---LGEMSLEEHSQCECRPKKK
VEGF-B MOUSE (P49766)   VVPWIDVYARATCQPREVVVPLSMELMGNVVKQLVPSCVTVQRCGGCCPDDGLECVPTGQHQVRMQILMIQYPSSQ---LGEMSLEEHSQCECRPKKK
VEGF-C HUMAN (P49767)   LKSIDNEWRKTQCMPREVCIDVGKEFGVATNTFFKPPCVSVYRCGGCCNSEGLQCMNTSTSYLSKTLFEITVPLSQGPKPVTISFANHTSCRCMSKLD
VEGF-C MOUSE (P97953)   LKSIDNEWRKTQCMPREVCIDVGKEFGAATNTFFKPPCVSVYRCGGCCNSEGLQCMNTSTGYLSKTLFEITVPLSQGPKPVTISFANHTSCRCMSKLD
VEGF-D HUMAN (PO43915) LKVIDEEWQRTQCSPRETCVEVASELGKSTNTFFKPPCVNVFRCGGCCNEESLICMNTSTSYISKQLFEISVPLTSVPELVPVKVANHTGCKCLPTAP
VEGFD MOUSE (P97946)    LKVIDEEWQRTQCSPRETCVEVASELGKTTNTFFKPPCVNVFRCGGCCNEEGVMCMNTSTSYISKQLFEISVPLTSVPELVPVKIANHTGCKCLPTGP
VEGF-F BOTJA (Q90X23)   VMPFMEVYRHSVCQPRETLVSILEEYPGEISHIFRPSCVTALRCGGCCTDESLECTATGKRSVGREIMRLSPHKGTSE-KEVMQFTEHTDCECRPRSA
VEGF-E ORFV (Q772M8)    TKTWSEVFENSGCKPRPMVFRVHDEHPELTSQRFNPPCVTLMRCGGCCNDESLECVPTEEANVTMQLMGASVSGGNG--MQHLSFVEHKKCDCKPPLT
```

Figure 1.1.4: This image shows amino acid sequences for the same protein (VEGF) in humans and mice. The sequences have been aligned to find similarities and differences. The bars across the sequences show amino acids that are unchanged across the organisms tested. These positions are considered shared ancestral characteristics. At all other locations, there may be differences in the amino acids between organisms. We can use these as synapomorphies to build a tree, assuming that organisms who share more similar sequences are more closely related. This information has revolutionized the way phylogenies are built. "Alignment of the VEGF Homology Domain of representative VEGFs (all mammalian VEGFs from human and mouse plus one VEGF-E (viral) and one VEGF-F (snake venom)" Mjeltsch, CC BY-SA, via Wikimedia Commons.

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2: PROKARYOTES

The earliest cells on Earth were prokaryotic (pro- meaning before, karyo- referring to the nucleus). As is implied by the name, prokaryotic cells lack a nucleus, as well as any membrane bound organelles. Prokaryotes have been divided into two domains: Bacteria and Archaea. Alongside domain Eukarya, these three domains compose the tree of life, as we currently understand it.

Cell Structure

In their simplest form, these unicellular organisms possess a cell wall, cell membrane, cytosol, ribosomes, and DNA. As the vast diversity of life on Earth is prokaryotic, you can imagine that there is a great diversity of forms and many exceptions to these general guidelines.

The DNA in prokaryotic cells is a single chromosome in the form of a loop, often bundled into a condensed region called a nucleoid. There may be small loops of DNA present called plasmids. These small loops of DNA can be exchanged between prokaryotes and the environment and are frequently the location of antibiotic resistance genes.

On the exterior, prokaryotes have a cell wall. They may also have flagella (sing. flagellum) for movement and/or pili (sing. pilus) for interacting with other organisms.

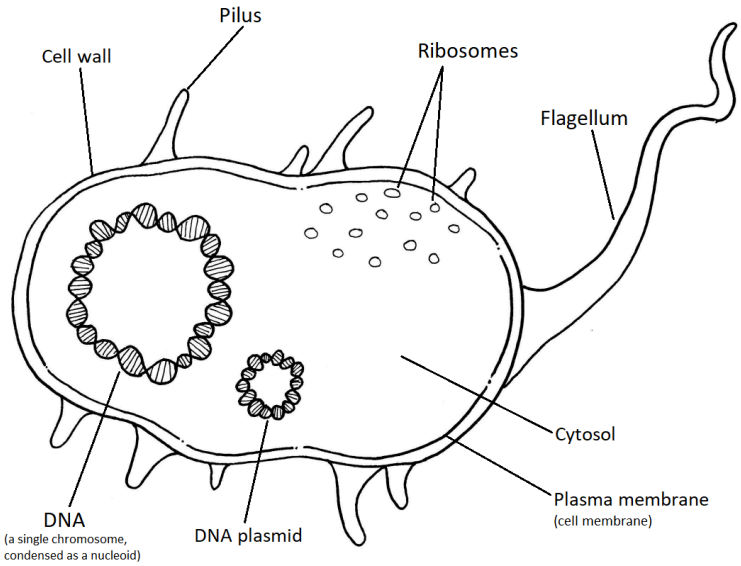


Figure 2.1: The diagram above shows the structures present in a prokaryotic cells. There is a single, double-stranded circle of DNA and a smaller circle of double-stranded DNA that represents a plasmid. There is a cluster of ribosomes floating in the cytosol (the jelly-like matrix that fills the cell), but there are no membrane-bound organelles. The cell is surrounded by a cell wall with the cell membrane just inside of the cell wall. There is a single, long flagellum, as well as many shorter pili. Artwork by Nikki Harris CC BY-NC with added labels by Maria Morrow.

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There is no nucleus in a prokaryotic cell, so they cannot undergo mitosis or meiosis. Instead, prokaryotes replicate by a process called binary fission (bi- meaning two, fission meaning to split apart).

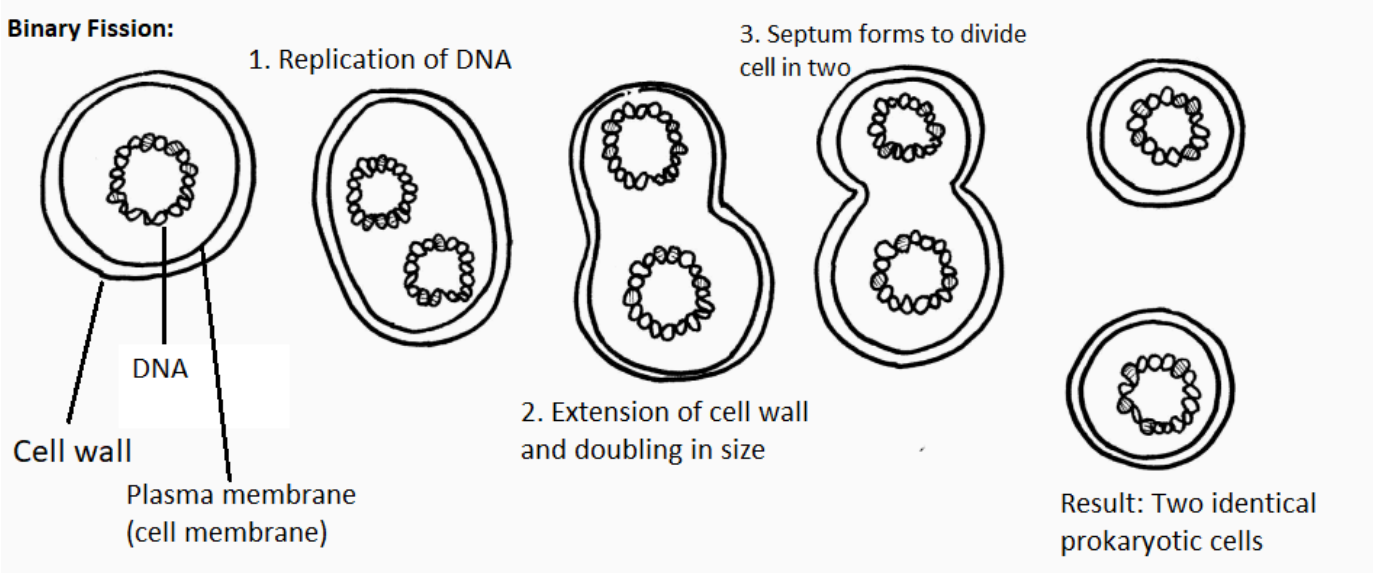


Figure 2.2: The diagram above shows how one prokaryotic cell divides into two identical cells via binary fission. In the first step, the DNA is replicated. In step two, a copy of the DNA is segregated to each different side of the cell as it elongates. In step 3, a septum (division) begins to form in the center of the elongated cell, forming a new cell wall and dividing the original cell in two. The result is two identical cells, each with an identical DNA chromosome. Artwork by Nikki Harris CC BY-NC with added labels by Maria Morrow.

Endosymbiosis

Endosymbiosis (endo- meaning inside, symbiosis meaning shared life) is a process by which several organelles were acquired by lineages of eukaryotic organisms, including mitochondria and plastids.

Primary Endosymbiosis

Both mitochondria and the chloroplasts in plants were acquired through a process called primary endosymbiosis. In the primary endosymbiosis that resulted in chloroplasts, a photosynthetic prokaryote similar to modern day cyanobacteria was engulfed by a heterotrophic eukaryote (a method of eating called phagocytosis). Something went wrong during this process and the prokaryotic cell was not digested. Instead, it was trapped within the eukaryotic cell. It continued to photosynthesize, producing sugars that resulted in increased fitness for its host. Over a long period of time, genes were eventually transferred between the prokaryote and the eukaryotic nucleus and an organelle was formed: the chloroplast.

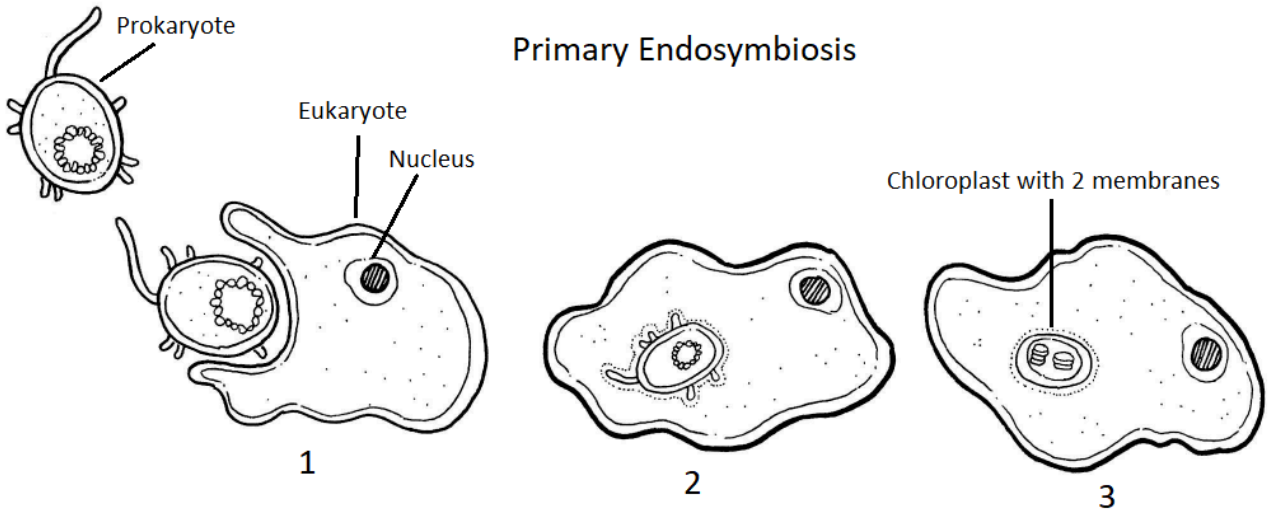


Figure 2.3: This diagram shows a prokaryotic cell on the far left. In step one, this cell is engulfed by a eukaryotic cell. In step two, we see the prokaryotic cell trapped within the eukaryotic cell, though it still looks the same as before it was engulfed. It is surrounded by a membrane of the eukaryote (dotted line). In step three, assumedly after a long period of evolution and intermediate stages, we see a fully formed chloroplast with two membranes. Artwork by Nikki Harris CC BY-NC with added labels by Maria Morrow.

Secondary Endosymbiosis

Many unrelated groups of photosynthetic organisms obtained the ability to photosynthesize by a process called secondary endosymbiosis. This is similar to primary endosymbiosis, except the organism that gets engulfed is a photosynthetic eukaryote (whose chloroplasts were the result of primary endosymbiosis somewhere in their evolutionary history). For example, brown algae and diatoms are both the result of a secondary endosymbiotic event in which a heterotrophic heterokont (see Chapter 5.2 Water Molds) engulfed a red alga.

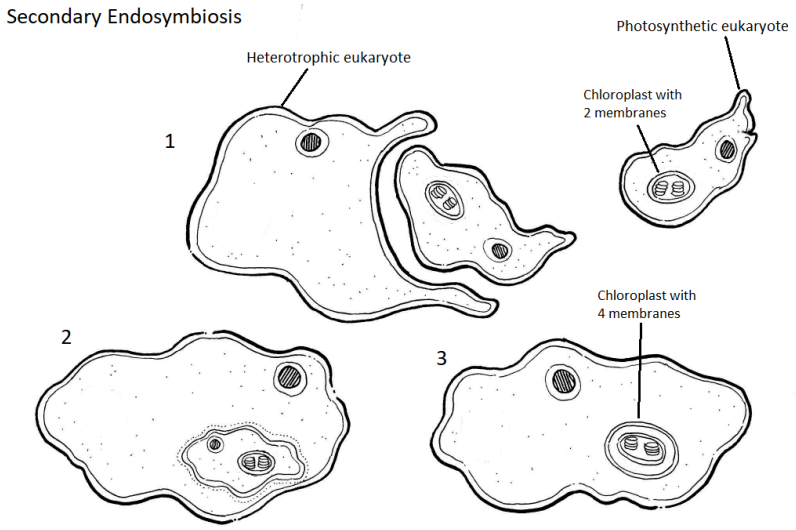


Figure 2.4: In the diagram above, we see a unicellular photosynthetic eukaryote with a 2-membrane chloroplast. In step one, this organism is engulfed by a heterotrophic eukaryote. In step two, we see the photosynthetic organism inside the heterotrophic organism. In step three, the original photosynthetic organism has been reduced to a chloroplast with 4 membranes. Artwork by Nikki Harris CC BY-NC with added labels by Maria Morrow.

2.1: Cyanobacteria

2.2: Root Nodules

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2.1: Cyanobacteria

Stromatolites

The earliest fossils are interpreted to be unicellular organisms similar to modern day cyanobacteria, sometimes referred to as blue green algae. The most widely accepted of these fossils dates back to 3.4 billion years ago from the Strelley Pool Formation in Western Australia. These particular fossils are called **stromatolites** and are composed of alternating layers of fossilized cells and calcium carbonate. We can use evidence from modern day stromatolite formation in Western Australia to infer that these fossilized cells were doing a process called photosynthesis, using dissolved CO_2 in the water to form sugar molecules. This causes calcium to precipitate out of the seawater, forming hardened layers of calcium carbonate on top of the colony of organisms. Because they need access to light to continue photosynthesizing, living cells begin forming a new layer on top of the calcium carbonate. This process continues, making a ringed pattern as the formation grows, much like we see in trees and corals.



Figure 2.1.1: The images above show stromatolites. The first image shows present day stromatolites formed on the coast of Western Australia. The second image shows a fossil stromatolite with the rings of growth formed by successive layers of Cyanobacteria. First photo by AndyGo, CC-BY-NC. Second image: Stromatolite Fossil from Wyoming by James St. John via Wikimedia Commons. CC-BY 2.0.

Modern Cyanobacteria

Free-Living

Cyanobacteria can be found in a vast diversity of places, from floating in the ocean to living in cryptobiotic crusts in the desert. *Nostoc* is a type of cyanobacteria that can often be found living in gelatinous colonies in wet, terrestrial environments. The colony secretes a **mucilaginous sheath** that provides a protective barrier and allows for the exchange of materials between cells in the colony.



Figure 2.1.2: Each of these glassy orbs contains a colony of *Nostoc pruniforme* surrounded by a mucilaginous sheath. The bacteria are not visible to the naked eye, so appear as a single organism. Photo by René Stalder, CC-BY-NC.

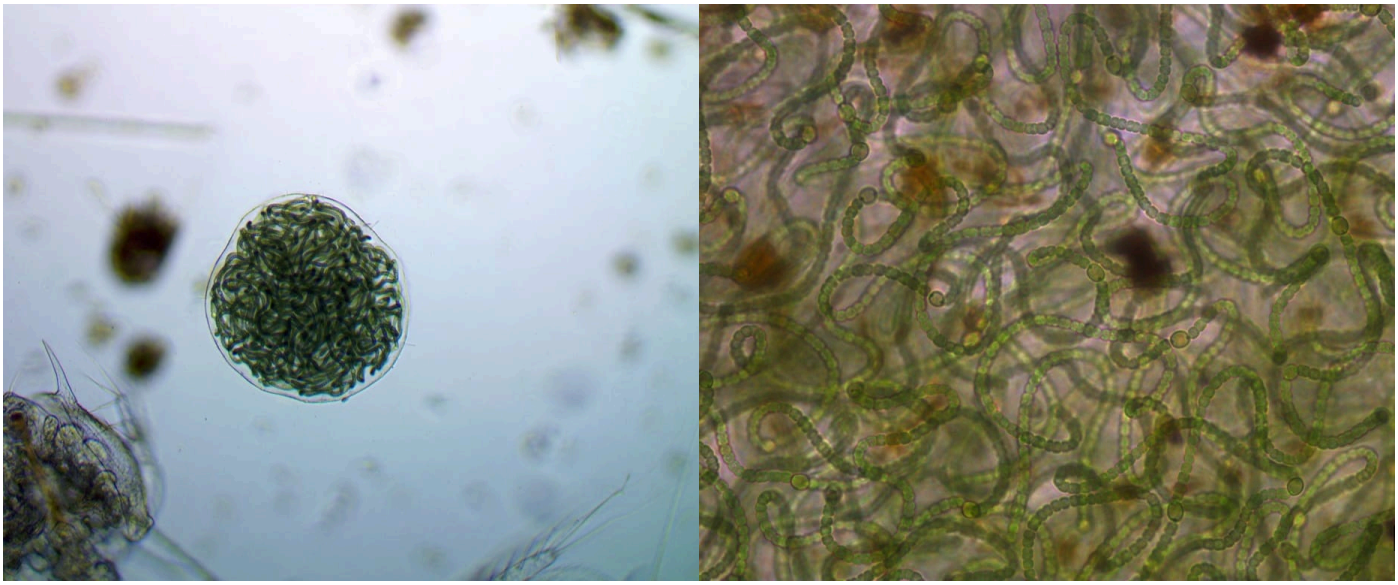


Figure 2.1.3: A view of a *Nostoc* colony through a microscope. The colony consists of chains of individuals, wrapped together into a ball. This ball is coated by a transparent mucilaginous sheath (visible in the first photo). The green color of the ball is due to the photosynthetic pigments in the Cyanobacteria. In the photo on the right, a colony is shown at a higher magnification. Individuals can be distinguished, including some larger, yellow cells. These latter individuals have converted into heterocysts. First photo by Ivan, CC-BY. Second photo by Mindy Morales, CC-BY-NC.

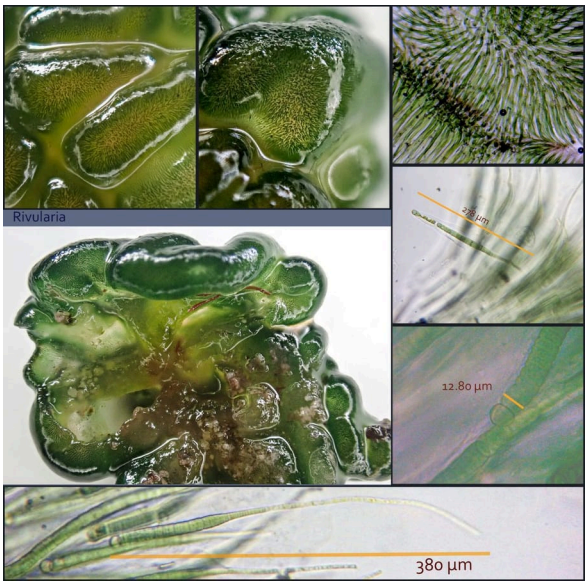


Figure 2.1.4: Multiple views of a gelatinous colony formed by Rivularia polyotis. The thick mucilaginous sheath is visible in the two images in the upper left corner, as well as the central image on the left. Chains of individuals can be distinguished, looking like hairy projections. At lower magnification, colonies are not easily distinguished, surrounded by a thick gelatinous layer. As images reach higher magnification, individual chains can be distinguished, composed of flat, disc-like cells. Photos by Luigi, CC-BY-NC.

Mutualists

Many cyanobacteria that you'll see in botany will be in mutualistic relationships. *Anabaena* is a genus of colonial cyanobacteria that can be found within the leaves of the water fern *Azolla*, fixing nitrogen in the fern's relatively nutrient-poor aquatic environment. *Nostoc* is another genus of colonial cyanobacteria capable of fixing nitrogen. It can be found free-living in gelatinous colonies shown above or, as you are likely to see it in your botany course, in compartments of a hornwort thallus. Cyanobacteria can also be found in a mutualistic relationship with fungi in **cyanolichens** (Figure 2.1.5).



Figure 2.1.5: Darkly colored lichens, such as this *Peltigera* (first) and *Nephroma* (second), often have a cyanobacterial partner. Photos by Maria Morrow CC-BY-NC.

Looking at Cyanobacteria in Water Ferns

If you were to chop up a sample of the water fern *Azolla* and look at it under the microscope, you'd see what looked like strings of

green beads. Each bead is an individual cyanobacterium of the genus *Anabaena*. However, even though each one is an individual, some cells will specialize to provide a service for the colony, as a whole.

- **Heterocysts** are thick-walled, chlorophyll-free cells that are fixing atmospheric nitrogen into bioavailable forms using the enzyme nitrogenase. Heterocysts cannot do photosynthesis, as that process produces oxygen and nitrogenase cannot function in the presence of oxygen.
- **Akinetes** are individuals that still perform photosynthesis, but also function as a sort of failsafe. Akinetes store large amounts of lipids and carbohydrates so that they have enough energy to begin a new colony if conditions become too cold or too dry for survival. Their formation is triggered by these conditions (dry or cold), so you may not see them from a fresh water fern leaf, as this is a relatively stable, comfortable environment.

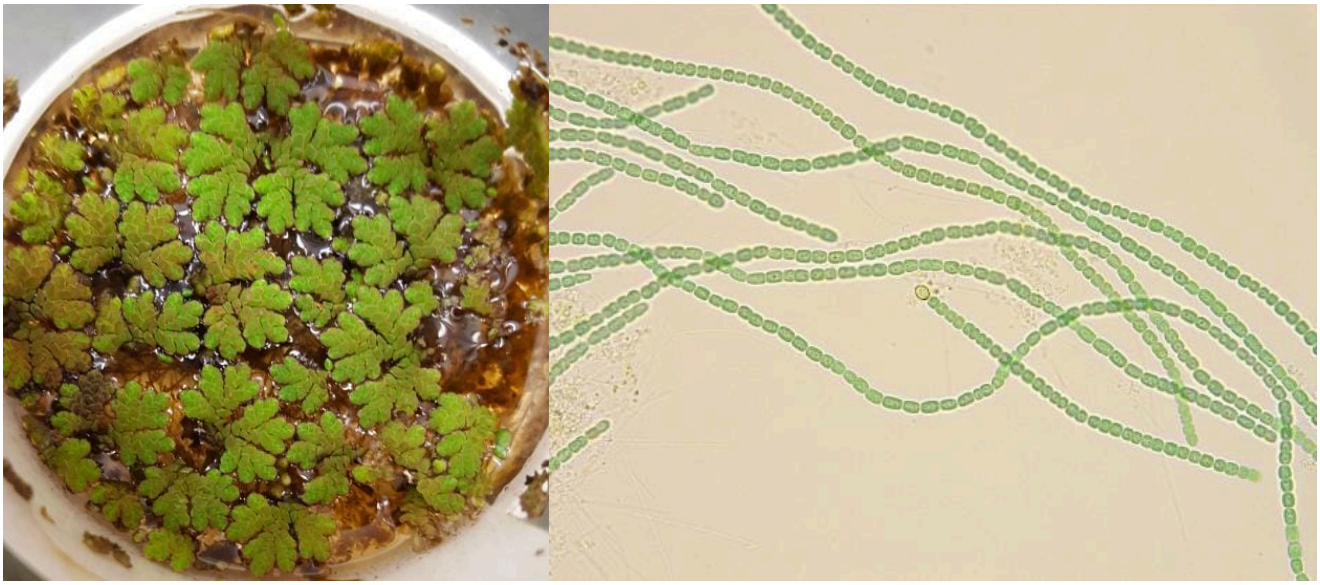


Figure 2.1.6 : In the first image, many *Azolla* plants can be seen floating in a dish of shallow water. Each fern is about the size of a dime (approx. 1 cm across). In the second image, individual *Anabaena* cells are strung together in colonies. These cells were once inside the leaves of the water fern. Photos by Melissa Ha, CC BY-NC.

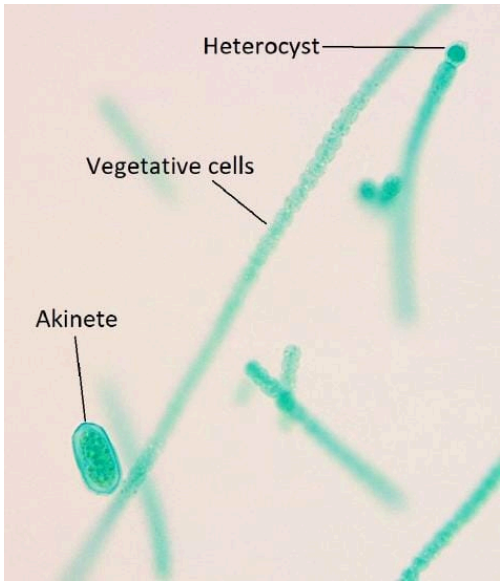


Figure 2.1.7: Three different cell types are visible in this Anabaena colony. There is one large, thick-walled akinete in the lower left. In the upper right, there is a smaller, round heterocyst that is about the size of two vegetative cells. The rest of the cells distinguishable in the image are "normal" vegetative cells. Photo credit: Melissa Ha, CC BY-NC.

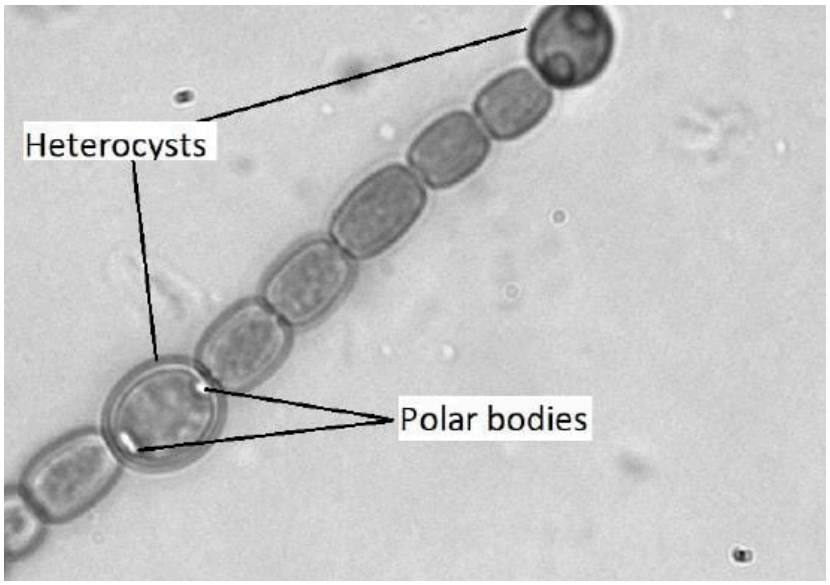


Figure 2.1.8: Heterocysts usually appear yellow and are more round than the vegetative cells. However, beginners often confuse the larger ones for akinetes (particularly when no akinetes are present. Something that makes heterocysts easier to distinguish from akinetes is the presence of polar bodies. Heterocysts have two distinct regions on either side called polar bodies. Akinetes don't have these and appear more granular. Photo by Maria Morrow.[1]

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2.2: Root Nodules

Several different groups of prokaryotes form mutualistic relationships with plant roots. Nitrogen is an essential nutrient for plants, yet it is difficult to obtain in many ecosystems. Though it is abundant in our atmosphere, this form a nitrogen (N_2) is triple-bonded to itself, a bond which most organisms cannot break. However, certain bacteria have an enzyme called nitrogenase that can break the triple bond and convert nitrogen into usable forms for plants, such as ammonia (NH_3). These bacteria can be found free-living in the environment or in mutualistic relationships with certain plants. A common relationship between plants and these nitrogen-fixing bacteria is the formation of root nodules--swellings in the plant roots that connect to the vascular tissue, allowing for the exchange of sugars and nutrients between the two different organisms.

Root Nodules in Legumes

Plants in the bean family (*Fabaceae*) form mutualistic relationships in the form of root nodules with nitrogen-fixing bacteria in the order *Rhizobiales*.



Figure 2.2.1: Nodules formed on the roots of Robinia provide a safe place and plenty of sugars for the nitrogen-fixing *Rhizobium* bacteria living inside. Photo by Thomas Koffel, CC-BY-NC.

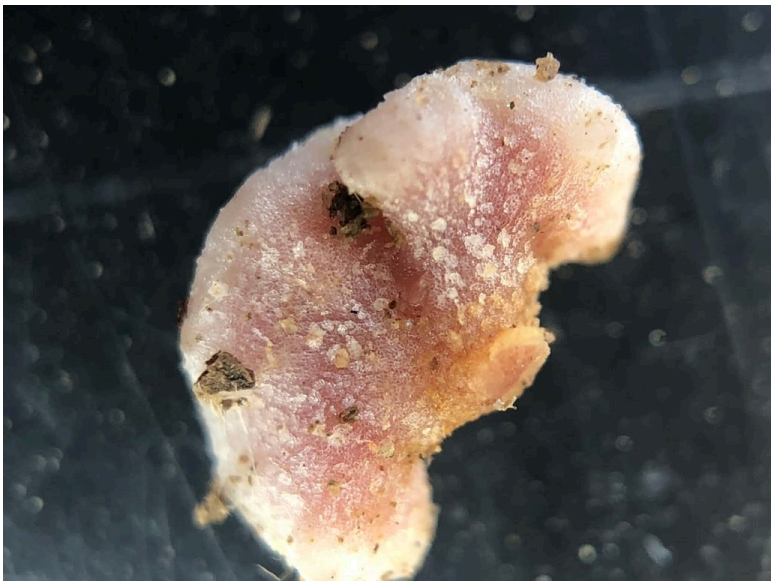


Figure 2.2.2: Root nodules from a leguminous plant. In the first image, several amorphous nodules can be seen emerging from the roots. In the second image, one of these nodules has been removed. The nodules appear pinkish due to the activity of leghemoglobin transporting oxygen away from the nodule, indicating that the enzyme nitrogenase is actively fixing nitrogen inside. Photos by Olive Long, CC-BY-NC.

Root Nodules in Alder

Frankia is a genus of bacteria that grows filamentously, called an actinomycete. Root nodules present on alder and few other groups of woody plants contain *Frankia*.



Figure 2.2.3: The image on the left shows excavated roots from a living alder tree (*Alnus rubra*). There are many yellow-orange nodules in clusters on the roots where *Frankia* is actively fixing nitrogen. In the image on the right, a dead alder tree is washed up on the beach in California. The arrow is indicating clusters of root nodules that were formed when the tree was alive and housed nitrogen-fixing *Frankia*. Photos by Maria Morrow CC BY-NC.

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3: FUNGI AND LICHENS

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3.1: Kingdom Fungi

The Mycelium

The growth form for most fungi is a network of thread-like cells called **hyphae** (sing. hypha). En masse, the network of hyphae is called a **mycelium**.



Figure 3.1.1: The mycelium of a fungus fans out across a woody substrate, branching successively. Photo by Dr Mary Gillham Archive Project, CC BY 2.0, via Wikimedia Commons.



Figure 3.1.2: In the image above, there are several long, transparent, thread-like structures (hyphae). In this particular fungus, the hyphae are divided into compartments by cross walls called septa (**septum**, singular). There are four arrows in the image, each one is pointing to a septum. Photo by Maria Morrow, CC-BY-NC.

Spores

Fungi reproduce by making haploid **spores**. Spores can be formed through asexual or sexual reproduction. The method by which

fungi produce spores via sexual reproduction is a useful characteristic for grouping them into different phyla. The shape, size, number, color, and texture of spores are all often useful characteristics in identifying fungi to a more specific level.



Figure 3.1.3: Spores produced by *Psilocybe cyanescens*, Basidiomycota (first) and *Tuber gibbosum,* Ascomycota (second). Photos by Alan Rockefeller, CC-BY-NC.

Molds

"Molds" are filamentous fungi producing spores (usually asexually). Many different groups of fungi produce molds, including many of the former Zygomycota, Ascomycota, and Basidiomycota.



Figure 3.1.4: The image above shows a petri plate with at least 10 mold colonies. Each colony has a central point that would have started with a single, haploid spore. This spore would germinate and grow outward, producing more spores asexually by mitosis. Photo by Maria Morrow, CC-BY-NC.

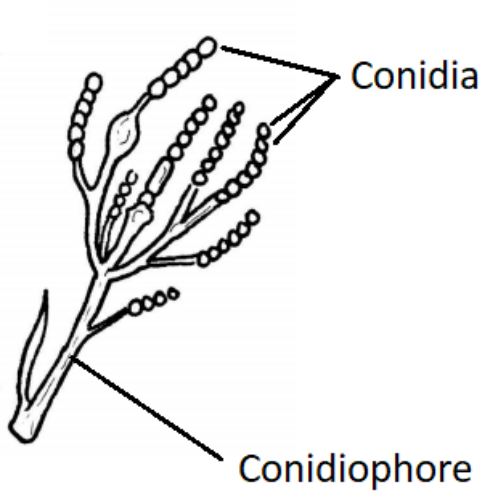


Figure 3.1.5: This diagram shows a forking structure called a conidiophore with many single cells being produced in rows at the ends of these forks. These cells are haploid conidia, spores produced by mitosis in Ascomycete and Basidiomycete molds. Artwork by Nikki Harris, CC-BY-NC.

YouTube Video

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View this YouTube Video online

Video 3.1.1: In this epic digital rendering (cue electric guitar on synthesizer), a fungus in the genus *Aspergillus* is producing tall, lollipop-like conidiophores. From these, chains of conidia are formed. As the conidiophores sway and bump into each other, the conidia are dispersed into the air.

Yeasts

Normally, fungi have a filamentous form. However, many groups within Kingdom Fungi produce **yeasts**. Yeasts are unicellular fungi. Though some yeasts can reproduce sexually, they are usually found reproducing asexually via a process called **budding**. In budding, the parent yeast cell replicates its nucleus by mitosis. A small protrusion forms in the cell wall and the new nucleus and cytoplasm are pushed into this protrusion or "bud". A wall forms between the bud and the parent cell, leaving a **bud scar** on the parent cell. The new yeast cell can then grow to a mature size.

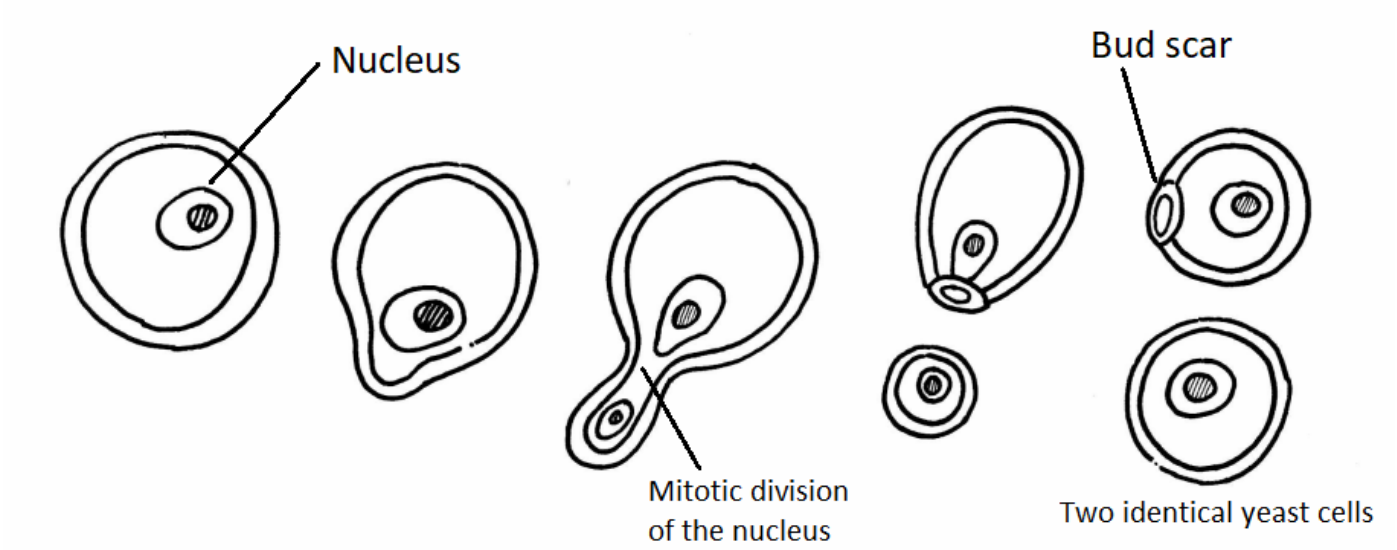


Figure 3.1.6: In the diagram above, a yeast cell reproduces by budding. On the far left, we see the parent yeast cell (the nucleus is labeled). Moving from left to right, the yeast cell forms a protrusion, then produces a copy of the nucleus by mitosis. In the next frame, a cell wall has formed between the protrustion (bud) and the parent cell and they have physically separated. In the final frame, the two yeast cells are equal in size and genetically identical, but the parent cell can be identified by the presence of a circular bud scar. Artwork by Nikki Harris, CC-BY-NC.

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3.2: Aquatic Fungi (Chytrids)

Like many of the earlier fungal lineages, this group has been divided into several distinct lineages. Once all classified as Chytridiomycota, these early, aquatic fungi are now grouped into Blastocladiomycota, Chytridiomycota, and Neocallimastigomycota. Though likely not directly related, these fungi share a few characteristics:

- Primarily aquatic, though some are parasites of terrestrial plants
- Swimming spores (zoospores) with a single whiplash flagellum

Saprotrophic Chytrids



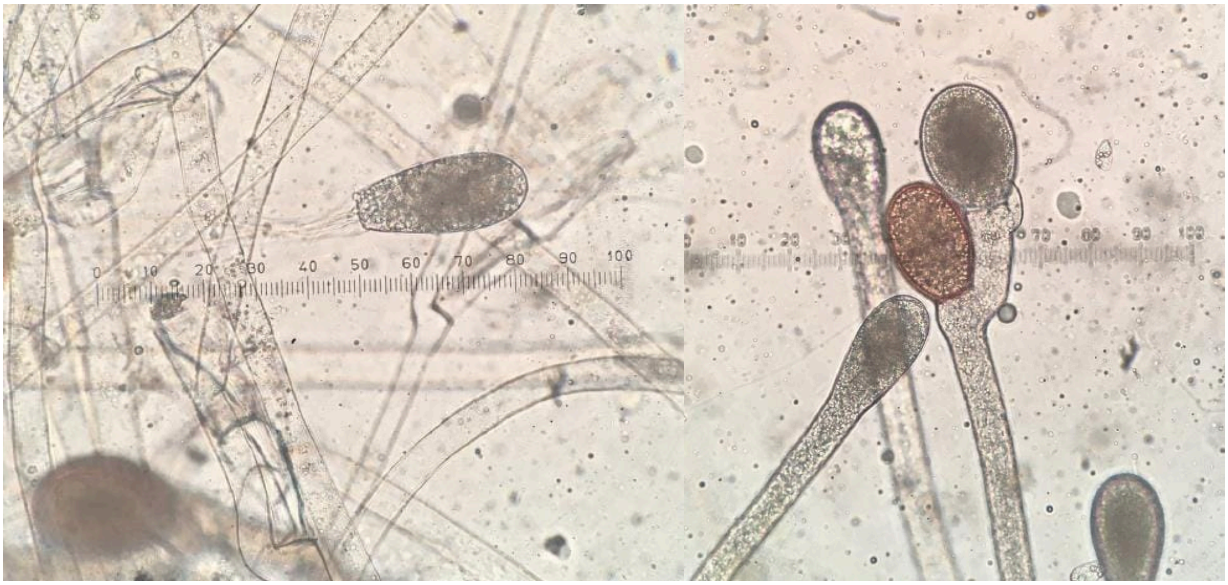


Figure 3.2.1: Chytrids in the genus *Allomyces* are aquatic decomposers. The top image shows sesame seeds floating in pond water with fungus growing off of them. The second image (bottom left) shows a microcopic image of a zoosporangium produced at the end of a hyphal filament (asexual reproduction). The final image (bottom right) shows two resting sporangia, the result of sexual reproduction. Photos by Tom Bruns, CC-BY-NC.

Parasitic Chytrids

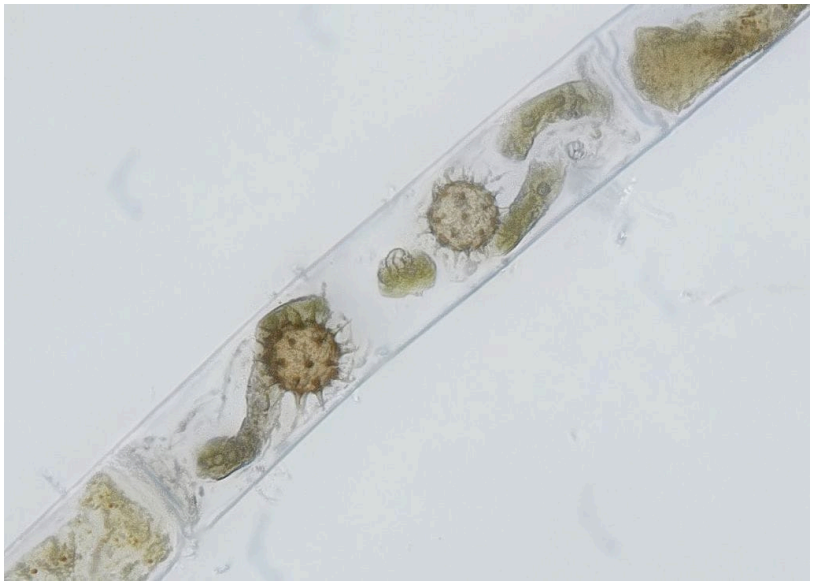


Figure 3.2.2: This image shows *Micromyces zygogonia* (Chytridiomycota), a parasite with spiky structures (prosori), inside the cells of the alga *Spirogyra*. Photo Credit Fahrenheit_66, CC-BY-NC.

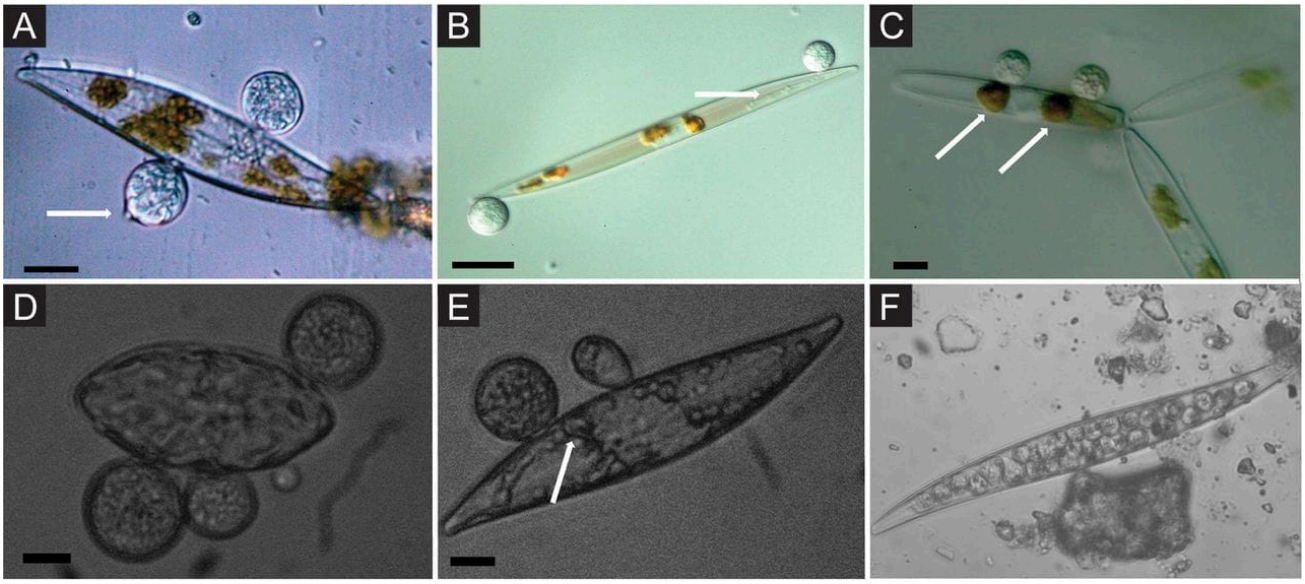


Figure 3.2.3: In these images, the part of the chytrids you can see is the large, globose struture attached to the outside of the diatom. This is the part of the thallus where spores are made. "Chytrid parasites of marine diatoms. (A) Chytrid sporangia on Pleurosigma sp. The white arrow indicates the operculate discharge pore. (B) Rhizoids (white arrow) extending into diatom host. (C) Chlorophyll aggregates localized to infection sites (white arrows). (D and E) Single hosts bearing multiple zoosporangia at different stages of development. The white arrow in panel E highlights branching rhizoids. (F) Endobiotic chytrid-like sporangia within diatom frustule. Bars = 10 µm. For more details see: Hassett BT, Gradinger R (2016) "Chytrids dominate arctic marine fungal communities". *Environ Microbiol*, **18**(6):2001–2009." Unknown author, CC BY 4.0, via Wikimedia Commons.



Figure 3.2.4: A parasite on Geranium, this *Synchytrium papillatum* (Chytridiomycota) is forming pink growths on the calyx and peduncle of these flowers. Photo Credit: James Bailey, CC BY-NC.



Figure 3.2.5: Likely the most infamous chytrid, *Batrachochytrium dendrobatidis* (Chytridiomycota) causes a lethal skin infection in many amphibians. This now widespread invasive pathogen is contributing to global amphibian declines and extinctions. Photo by Jonathan (JC) Carpenter, CC BY-NC.

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3.3: Zygospore-forming Fungi

These organisms were formerly classified in a group called the Zygomycota because they sexually reproduce by forming a structure called a zygospore. However, they have since been broken into several different lineages.

Mitosporangium (Asexual Reproduction) and Coenocytic Hyphae

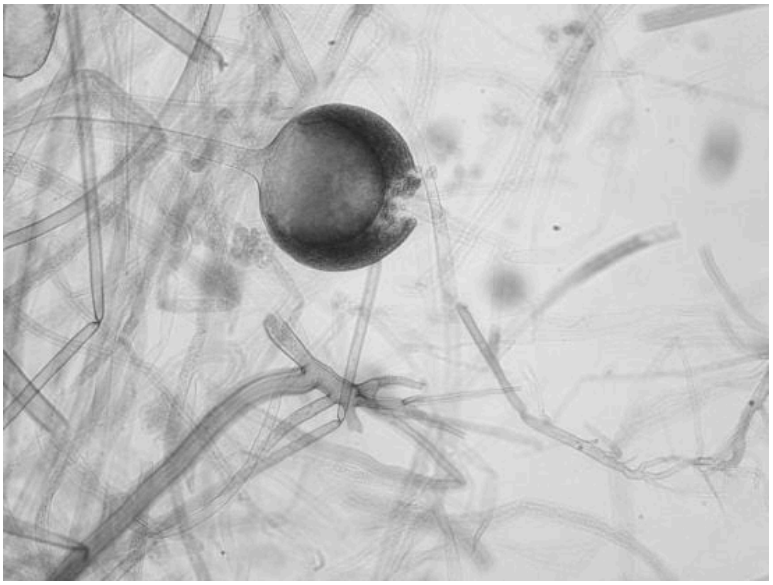


Figure 3.3.1: Rhizopus stolonifer asexually reproducing. The globose structure is a mitosporangium. The peridium (outer covering of the sporangium) has split and haploid spores are being released. At the center of the sporangium is a swollen structure called the columella. Photo by Maria Morrow, CC BY.

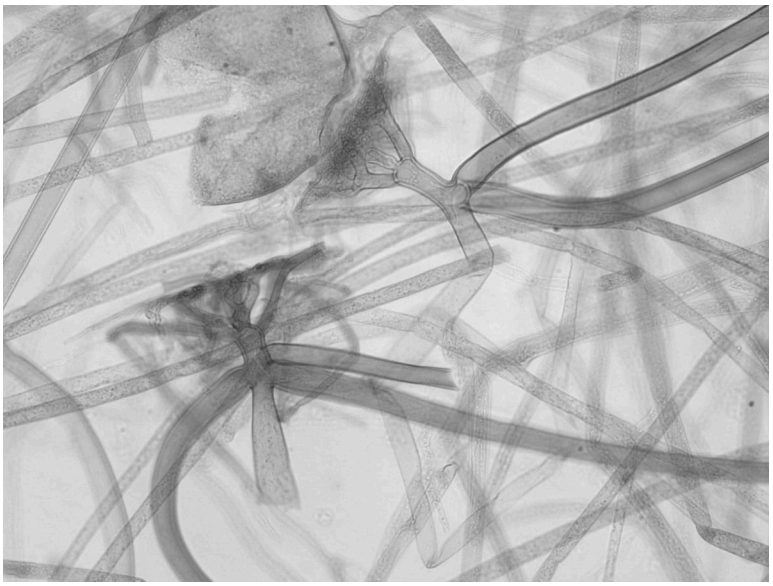


Figure 3.3.2: These branching structures called rhizoids are formed at the base of each mitosporangium. Photo by Maria Morrow, CC BY.

Zygospore Formation

When the mycelium of one fungus encounters another fungus of the same species and a complementary mating type, it can start to produce compounds to interact with the new fungus. Through a series of chemical exchanges, the two fungi each begin to extend toward each other. When they touch, they wall off an area of that extension by creating a septum. This area, filled with

haploid nuclei, is called a gametangium (see Figure 3.3.3). The walls between the gametangia of each fungus dissolve and the two fungi combine cytoplasm (plasmogamy) and then fuse the nuclei together (karyogamy) to form many diploid nuclei. As this happens, a thick, orange, ornamented wall forms around the nuclei. This is the zygosporangium.



Figure 3.3.3: Gametangia of *Phycomyces blakesleeanus*. Two complementary mycelia have formed gametangia (indicated by white arrows) by forming a cell wall to make a distinct compartment at the end of each hyphal filament. These structures are filled with haploid nuclei that will fuse together when the cell walls between the two gametangia dissolve. This new joined structure is the zygosporangium. User:Xerantheum, CC BY-SA, via Wikimedia Commons.

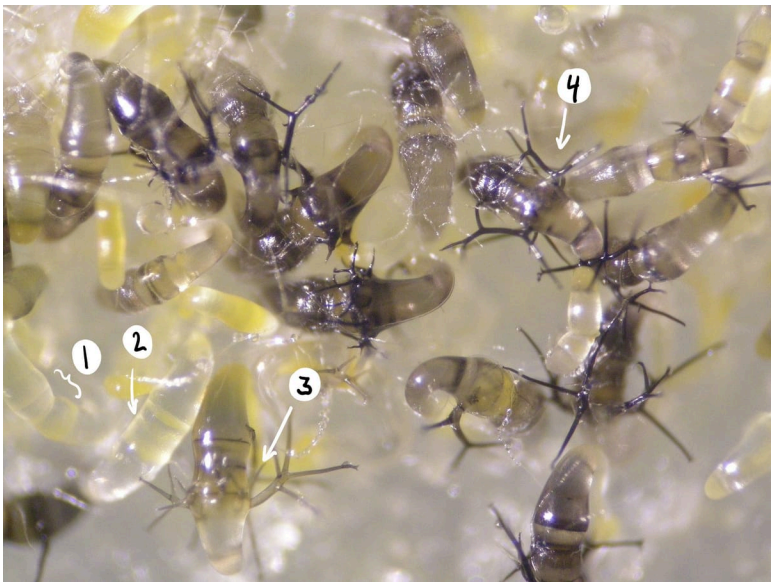


Figure 3.3.4: Phycomyces blakesleeanus forming zygosporangia. Many pairs of hyphae have begun conjugation. In (1), gametangia have formed, but plasmogamy has not yet occurred. In (2), plasmogamy has occurred as the walls separating the gametangia from each other have dissolved. In (3), the developing zygosporangium and suspensor hyphae begin to darken and ornamentations begin to form. In (4), the zygosporangium is nearing maturity with black branching ornamentations. Photo by Xerantheum, CC BY-SA, via Wikimedia Commons with labels added by Maria Morrow.

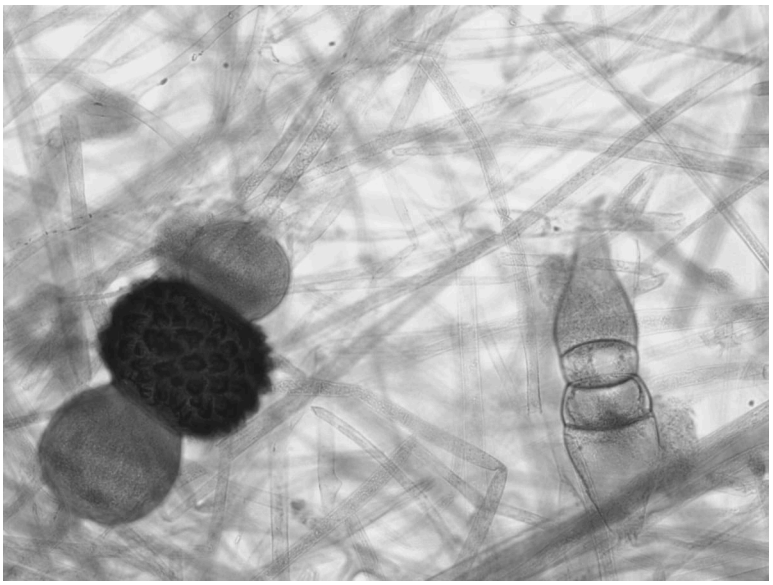


Figure 3.3.5: Rhizopus stolonifer sexually reproducing. The large, warty zygosporangium (left) is being held by two suspensors, one from each mycelial parent. On the right side of the image, suspensors hold gametangia that would soon fuse to form a zygosporangium. Photo by Maria Morrow, CC BY.

Rhizopus stolonifer Life Cycle

The life cycle below shows both sexual and asexual reproduction in *Rhizopus stolonifer*. Both sexual and asexual reproduction result in the production of haploid spores that can germinate and grow into a haploid mycelium. However, the spores produced by the mitosporangia will all be genetically identical, while the spores produced by the sporangia emerging from the zygosporangium will be genetically distinct.

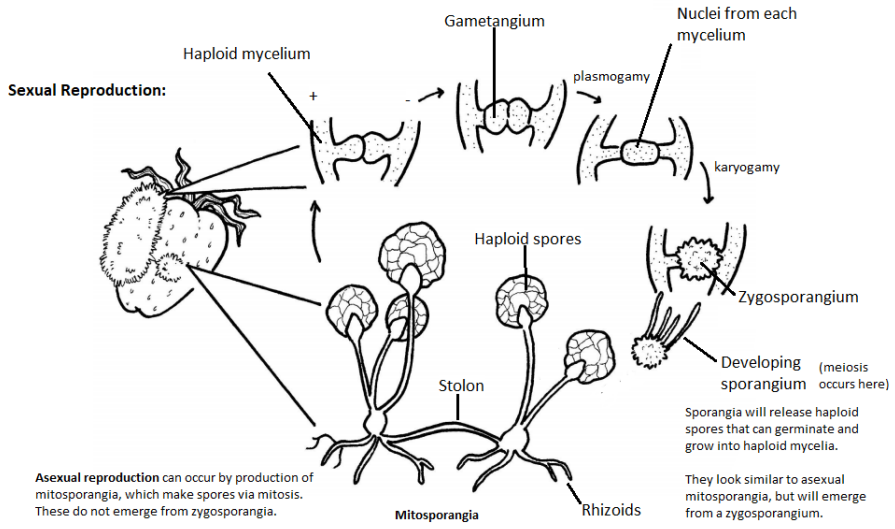


Figure 3.3.6: In sexual reproduction, two compatible haploid mycelia identify each other. Where the two mycelia meet, gametangia are formed, each containing haploid nuclei. The wall between the gametangia dissolves and plasmogamy occurs. The nuclei fuse to form diploid zygospores within the zygosporangium. A sporangium germinates from the zygosporanigum and produces haploid spores via meiosis. These haploid spores can germinate and grow into new mycelia. In asexual reproduction, mitosporangia produce haploid spores by mitosis. Mitosporangia do not emerge from a zygosporangium. Instead, they have a network of hyphae (rhizoids) that look like roots and lateral connections (stolons) to clusters of other mitosporangia. Artwork by Nikki Harris, CC BY with labels added by Maria Morrow.

Watch the video below to see the microscopic structures involved in the asexual portion of the life cycle of *Rhizopus stolonifer*.

- 0:50 The video starts, showing coenocytic hyphae growing
- 1:25 Mitosporangium formation (asexual reproduction)
- 2:00 Mitospores, haploid spores produced via mitosis, are shown
- 2:30 Video ends

YouTube Video

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View this YouTube Video online

Video 3.3.1: Asexual structures of *Rhizopus stolonifer*. Sourced from YouTube.

Examples of Zygospore-forming Fungal Lineages

These groups of fungi can be found in your daily life, if you know what to look for. Molds on fruits and bread are often (but certainly not always) from the Mucorales, as well as molds that form on dog poop (specifically, a genus called Phycomyces). You can also find a diverse assortment of former "Zygomycota" members parasitizing other fungi and insects.

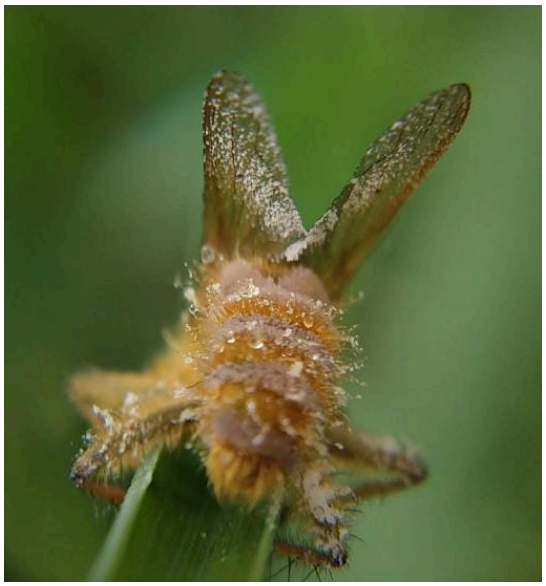


Figure 3.3.7: A fly killed by *Entomophthora*, a parasitic fungus whose name means "insect destroyer". The powdery white spores can be seen on the wings and forming in bands on the abdomen. Photo by Maria Morrow, CC BY.



Figure 3.3.8: Three Mycena at different stages of parasitization by the mycoparasitic fungus *Spinellus fusiger*. Photo by Maria Morrow, CC BY.



Figure 3.3.9: Fruiting bodies of *Pilobilus* fruiting on deer scat. The swollen region acts as a lens, focusing light to heat the liquid and create turgor pressure. This causes the black spore packet to rocket off onto an adjacent grass patch. Photos by Maria Morrow, CC BY.

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3.4: Glomeromycota (Endomycorrhizal Fungi)

Glomeromycota represent the endomycorrhizal fungi. These fungi form a mutualistic relationship with plant roots, forming hyphal structures within the plant cell walls. Thus, these images contain primarily plant roots. They are a mysterious bunch, though well-studied for their importance in crop production.

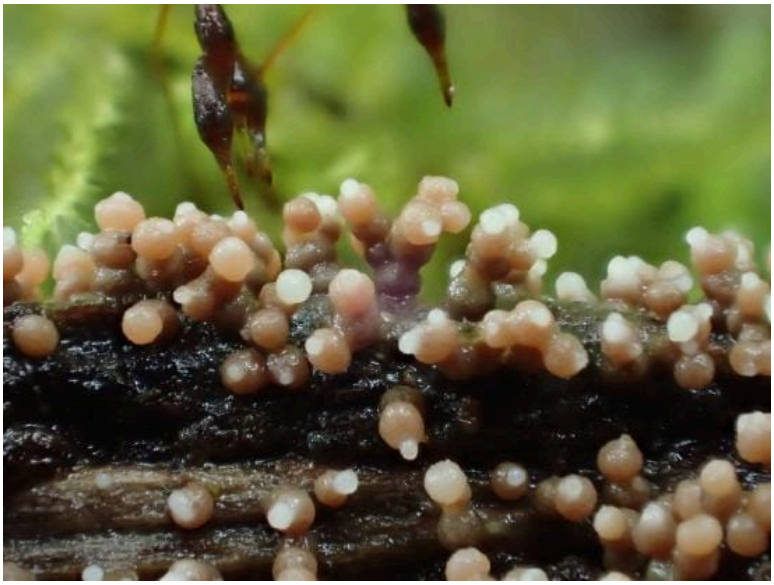


Figure 3.4.1: Glomus coremioides forming sporocarps, an unusual characteristic in this fungal phylum. The white to tan ones are still forming. Spores are produced within these structures. The ecology of this species is a bit mysterious. Photos by Damon Tighe, CC-BY-NC.

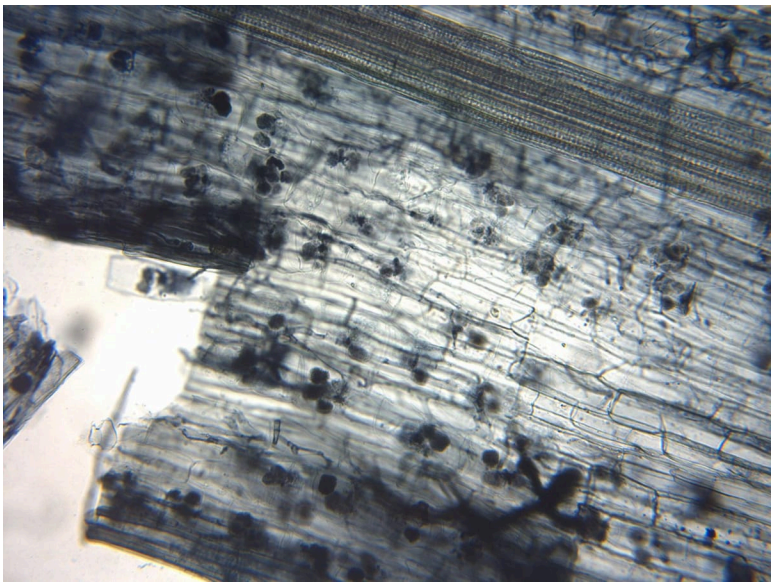


Figure 3.4.2: Endomycorrhizal fungi can form arbuscules (branching structures) and vesicles (globose structures). In this micrograph, a root has been stained and viewed at high magnification. The hyphal structures of the fungus can be seen within the root cells, particularly the vesicles, which stain darker. Msturmel, Public domain, via Wikimedia Commons.



Figure 3.4.3: A root of a mycoheterotrophic plant, *Corallorhiza*. Arbuscules can be seen in many cells of the cortex of the plant root. Three of these arbuscules have been indicated with a note that says "cells filled with branching fungal hyphae". Photo by Melissa Ha, CC-BY-NC.

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3.5: ASCOMYCOTA (SAC FUNGI)



Figure 3.5.1: A small sampling of the vast diversity of ascomycetes. Top left photo by SMWhite (*Morchella americana*), top right by Siburanlai (*Gibellula pulchra*), bottom left by Christian Schwarz (*Chlorociboria aeruginascens*), and bottom right by Riley Walsh (*Rhytisma americanum*). All photos licensed CC-BY-NC.

3.5.1: Characteristics

3.5.2: Types of Ascocarps

3.5.3: Life Cycle

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3.5.1: Characteristics

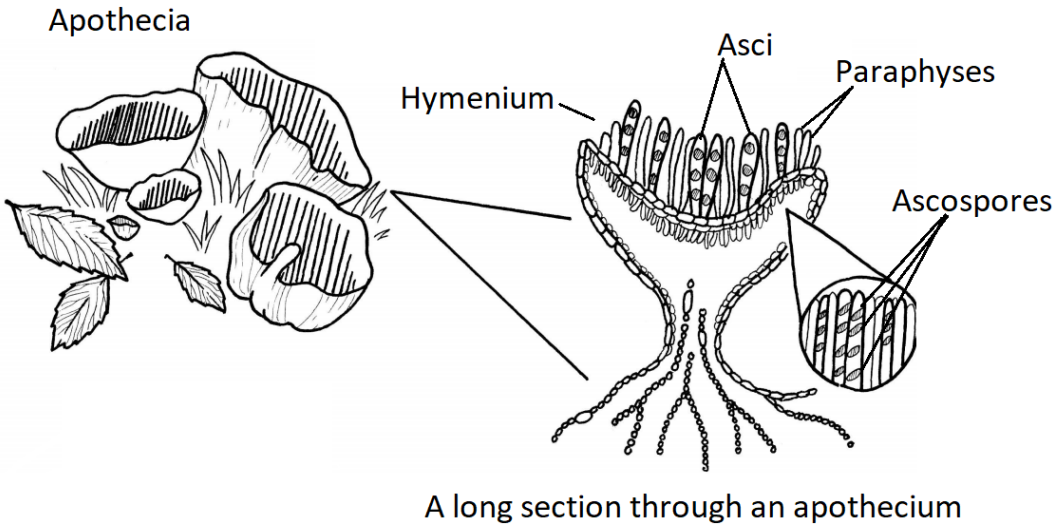


Figure 3.5.1.1: Ascomycetes are called the cup fungi after the cup-shaped fruiting body formed by many of the larger organisms in this group, the apothecium. A few apothecia are shown on the left side of the diagram. The right side shows a long section through an apothecium. Septate hyphae comprise most of the structure. On the interior surface of the cup is the hymenium, which is composed of asci and paraphyses. Ascospores are produced by meiosis within each ascus. Diagram by Nikki Harris, CC-BY-NC, with labels added by Maria Morrow.

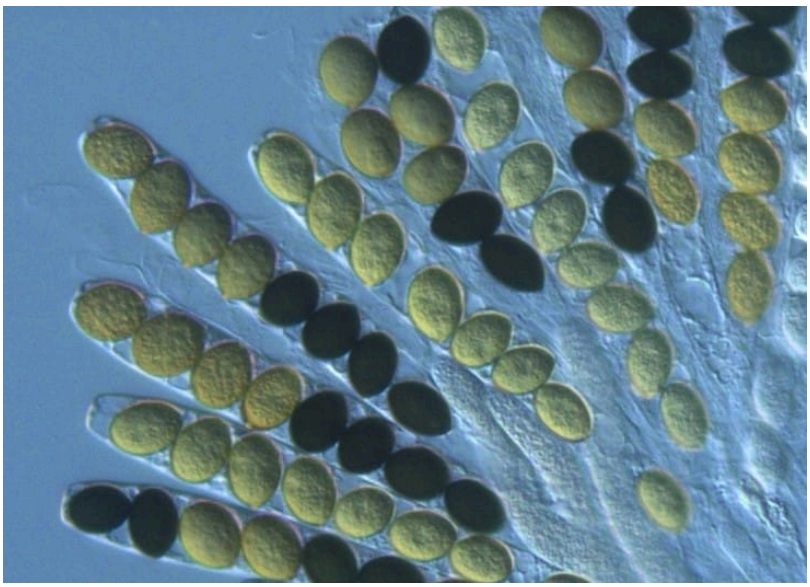


Figure 3.5.1.2: In this photo, light and dark colored ascospores are produced inside the asci of the fungus *Sordaria macrospora*. This demonstrates the linear division of the spores, as pairs of genetically identical light or dark spores are adjacent, produced after mitosis occurs within the ascus. Photo by Aurora Storlazzi, CC BY 4.0, via Wikimedia Commons.

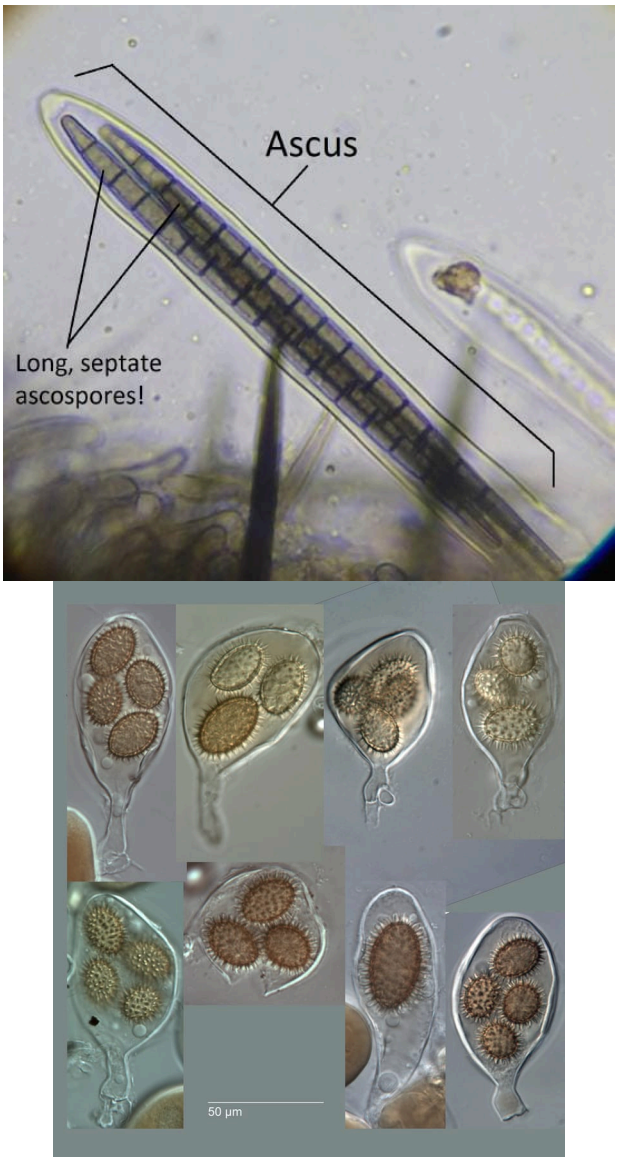


Figure 3.5.1.3: Ascospores and asci can have an incredible diversity of sizes, shapes, and structure. In the first photo (left), a single ascus surrounds several ascospores (approximately three can be distinguished, here). Each ascospore is as long as the ascus and looks striped. These stripes are septations and each spore has many septa. In the next photo (right), 3-4 enormous spiny spores of *Tuber rufum* are produced in wider, bag-like asci. First photo by Maria Morrow, CC-BY-NC. Second photo by Jerry Cooper, CC-BY.

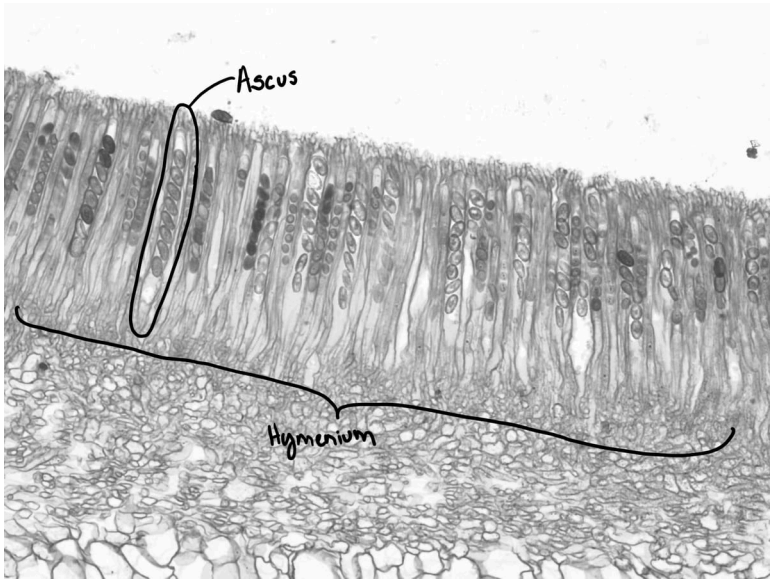


Figure 3.5.1.4: Asci, some filled with ascospores, lining the hymenium of a *Peziza* fruiting body. Photo by Maria Morrow, CC-BY-NC.

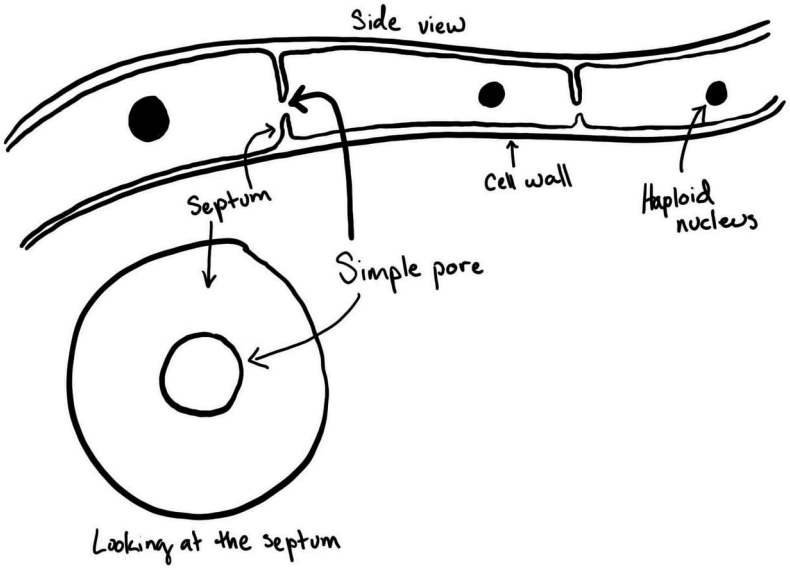


Figure 3.5.1.5: Ascomycetes have septate hyphae with a simple pore (hole) in the center. This separates hyphae into distinct cells yet still allows for the passage of materials between these compartments. This drawing shows a side view of a hypha with two septations drawn. Each septation has a gap in the center. Below, a septum is shown as if you were looking straight at it, showing that it is a ring of tissue with a hole in the center. Each compartment of the hypha has a single haploid nucleus. Drawing by Maria Morrow, CC-BY-NC.

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3.5.2: Types of Ascocarps

Apothecium

Apothecia are cup-shaped with the hymenium fully exposed (lining the interior of the cup), though this can be inverted and take on strange shapes (see Figure 3.5.2.3).



Figure 3.5.2.1: A diversity of apothecia. Upper left: The stalked apothecium of *Microstoma floccosum*, photo by Alan Rockefeller. Upper right: The more classic disc-shaped apothecium of *Pithya vulgaris*, photo by Tyson Ehlers. Lower left: Gelantinous apothecia of *Ascobolus furfuraceus*, photo by Salvatore Bacciu and Paola Mereu. Lower right: The apothecium of *Chlorioactis geaster* splits into a star shape, photo by Bob O'Kennon. All photos licensed CC-BY-NC.



Figure 3.5.2.2: Three apothecia of the delightfully squishy *Urnula padeniana*. This type of fruiting body has a cup shape. The interior of the cup is where the spores are produced. Photo by Maria Morrow, CC-BY-NC.



Figure 3.5.2.3: Two apothecia of *Helvella* in the first image. This ascomycete, much like a morel, has an apothecium at the end of a stalk. The apothecium at the top of the stalk is not cup-shaped because the cup has been inverted. The spores are produced on the surface of the apothecium that you can see in this image. The second image shows another ascoymcete, *Heyderia abietis*, with a similar strategy. The inverted cup shape makes a smooth tongue-like structure on the top of the stalk. These are only about 1 cm tall. Photos by Maria Morrow, CC-BY-NC.

Perithecium

A flask-shaped fruiting structures, often microscopic and/or embedded within either the substrate it is fruiting in or a fungal structure called a stroma.

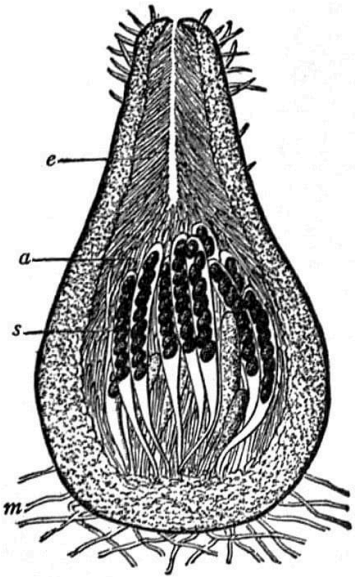


Figure 3.5.2.4: A flask-shaped perithecium, with asci emerging within the base of the flask. Labels in the diagram are as follows: m=the mycelium, s=asci with black ascospores inside, a=paraphyses (sterile cells surrounding the asci), e=the ostiole (opening). From Strasburger's Lehrbuch der Botanik. After v. Tavel., Public domain, via Wikimedia Commons.

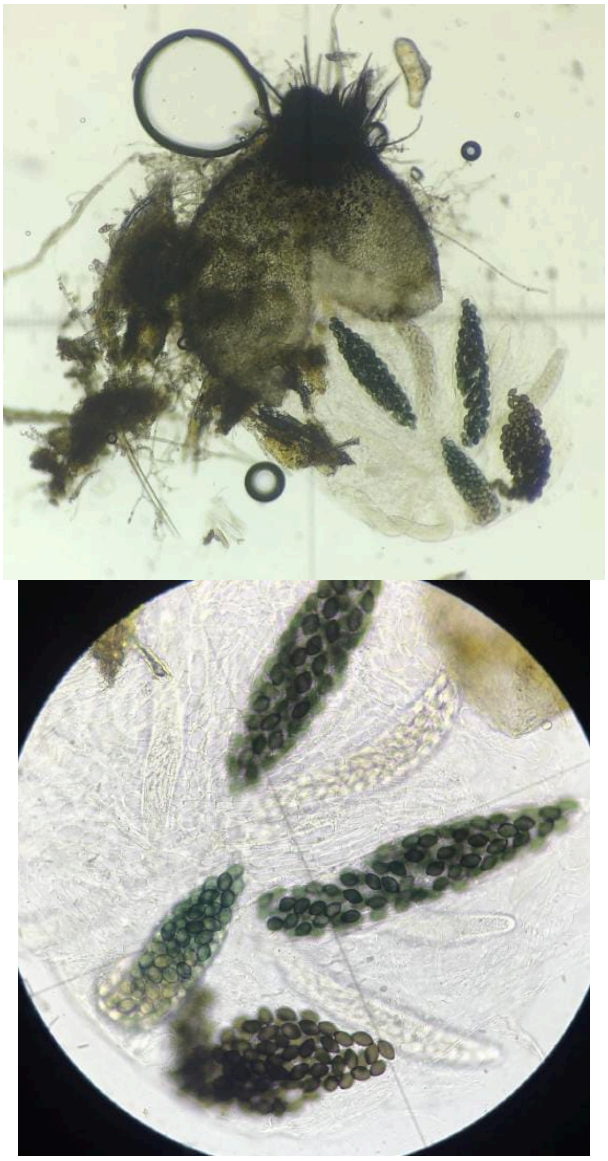


Figure 3.5.2.5: A *Podospora* perithecium viewed under the microscope. Short hairs surround the ostiole. It has been squished a bit and the asci have erupted out the base. Unlike many ascomycetes, many spores are produced inside the asci of this species. Photos by Sigrid Jakob, CC-BY-NC.

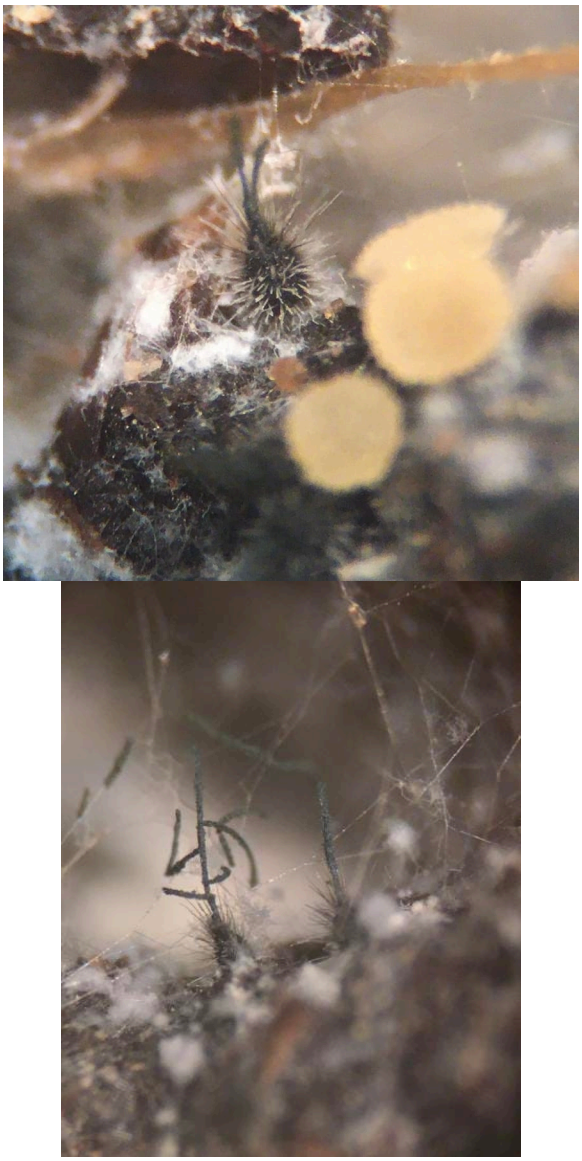


Figure 3.5.2.6: Some perithecial fungi, like the *Chaetomium* sp. pictured here, form their perithecia on the surface of whatever substrate they are growing on. Look for the small, hairy, black, pear-shaped fruiting bodies in the images above. Photos by Photos by Sigrid Jakob, CC-BY-NC.



Figure 3.5.2.7: Xylaria species produce perithecia embedded in sterile fungal tissue called a stroma. In *Xylaria tucumanensis*, the perithecia are large and are not surrounded by much stroma. In the first photo (left), each lumpy projection has a distinct dot in its center; this is the ostiole (opening) of the perithecium. The second photo (right) shows a long section through a fruiting structure. The white tissue is the stroma. The black, concave structures are the perithecia. An arrow points to an ostiole of one of the perithecia. Photos by Danny Newman, CC-BY-NC-SA.

Cleistothecium

A cleistothecium is a fully-enclosed fruiting structure. These typically have bag-like asci. Some split open to release their spores and are called chasmothecia.

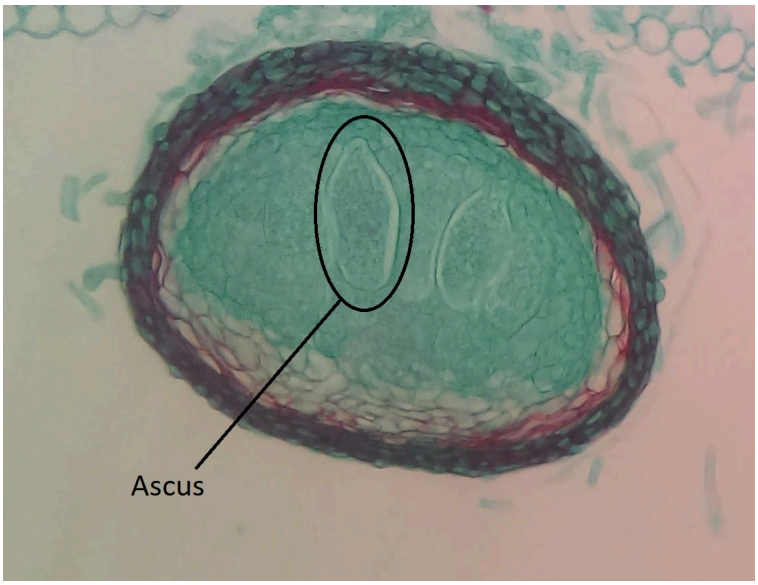


Figure 3.5.2.8: A section through a cleistothecium with an ascus circled. A cleistothecium is a fully enclosed fruiting body, generally microscopic, that encloses many bag-like asci. Photo by Melissa Ha, CC-BY-NC with labels added.

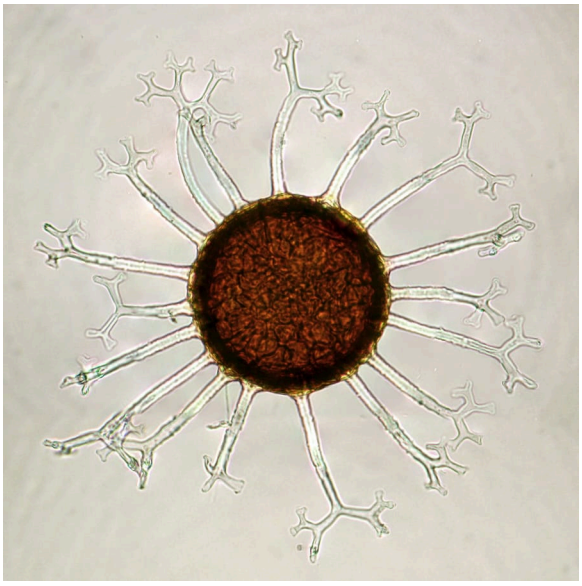


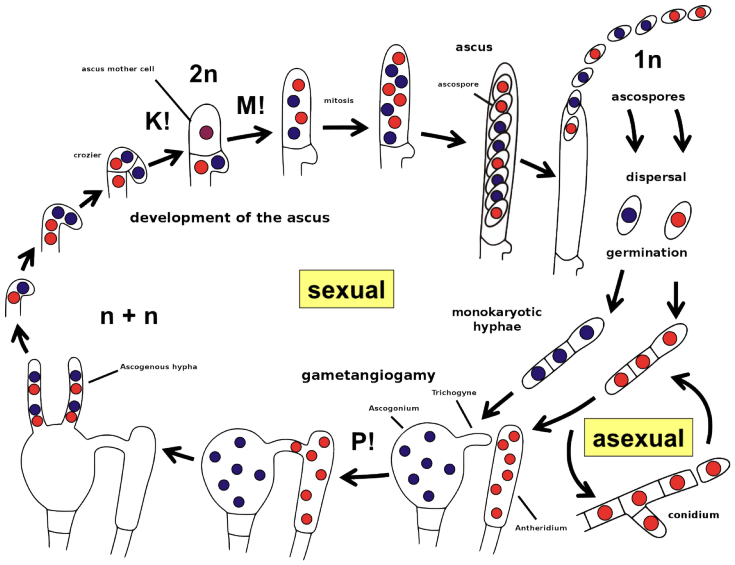
Figure 3.5.2.9: Some cleistothecia, such as those of the powdery mildews (in the order Erysiphales), are beautifully ornamented. Gubin Olexander, CC BY 4.0, via Wikimedia Commons.



Figure 3.5.2.10: Powdery mildews (Erysiphales) are plant parasites that form cleistothecia. They get their name from the powdery white look they give to the surface of plants they are parasitizing (first photo). Sometimes within this powdery white fluff (mycelium), cleistothecia can be seen with some magnification (second photo). Photos by ðejay (Orkney), CC-BY-NC.

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3.5.3: Life Cycle



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Figure 3.5.3.1: Ascomycota life cycle. On the right side of the diagram, there are haploid ascospores of two different mating types produced (dark blue and red). The life cycle follows one of each of these ascospores as they each germinate and grow by mitosis into a monokaryon (a haploid thallus). During this stage, asexual production might occur by producing haploid conidia by mitosis. If the two complementary monokaryons meet, a chemical exchange might occur to stimulate the production of sexual structures: either a globose ascogonium with a hairlike projection called a trichogyne or an elongate antheridium. Each of these structures are filled with haploid nuclei (gametes). When the antheridium fuses with the trichogyne, plasmogamy (P!) occurs and the new hyphae generated from the asogonium are dikaryotic, meaning there are two different, unfused nuclei. During this period, ascocarp formation would occur around these tissues. Ascogenous, dikaryotic hyphae would form the asci. This occurs by first forming a crozier--the two different nuclei undergo mitosis while the tip of the hypha hooks sideways and two new septa form, isolating one dark blue nucleus in the tip, one red nucleus and one dark blue nucleus together in the hooked over region, and another red nucleus below the hook. The two nuclei in the hooked over portion of the crozier (the ascus mother cell) fuse together (K!=karyogamy) to form a diploid nucleus. This diploid nucleus instantly divides by meiosis, forming 4 haploid nuclei (half red, half dark blue). Each of these nuclei then divides by mitosis and the ascus elongates. Cell walls for around each nucleus, forming the ascospores. The ascospores are released, completing the life cycle. Diagram from SiliconProphet, CC BY-SA 4.0, via Wikimedia Commons.

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3.6: BASIDIOMYCOTA (CLUB FUNGI)



Figure 3.6.1: A small sampling of the amazing morphological diversity within phylum Basidiomycota. These fungi are all from the Agaricomycotina, only one of three major subdivisions within Basidiomycota. Photos from top left to bottom right: The tiny, branching fruiting bodies of *Dendrocollybia racemosa* photographed by Christian Schwarz, CC-BY-NC; the vibrantly red star-shaped *Asteroe rubra* photographed by Noah Siegel, CC-BY-NC, UV fluorescence in *Cortinarius flavobasilis* photographed by Drew Parker, CC-BY-NC-SA, the enormous fruiting body of *Macrocybe titans* photographed by Danny Newman, CC-BY-NC-SA, and the cobalt blue velvety crust formed by *Terana coerulea* photographed by Korvidai, CC-BY-NC.

3.6.1: Characteristics

3.6.2: Types of Basidiocarps

3.6.3: Life Cycles of Basidiomycetes

3.6.4: Rusts and Smuts

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3.6.1: Characteristics

Fungi with the following structures can be placed in the Basidiomycota*:

*It is important to note that these features may look different or not be present at all in some groups of Basidiomycota, such as the rusts (Pucciniomycotina) and smuts (Ustilagomycotina). However, there are many physiological and genetic similarities that support grouping these organisms together in the Basidiomycota.

Basidia and Basidiospores

Both karyogamy and meiosis occur within a cell called the basidium. Haploid basidiospores from atop projections on the basidum called sterigmata (sing. sterigma). There are generally four spores, as shown in the image below, though the number of spores produced can vary by species. For example, the mushroom you are likely most familiar with, *Agaricus bisporus* (though you probably know it as a crimini or button mushroom at its immature stage and portobello at maturity), only produces two spores on each basidium (bi- meaning two).



Figure 3.6.1.1: A section through the gills of a mushroom. On the left, a basidium has four basidiospores sitting atop its four sterigmata. On the right, the spores have been released and the sterigmata are easier to distinguish. Photo by Maria Morrow, CC-BY-NC.

Clamp Connections

Basidiomycetes maintain their dikaryotic (n+n) state in each hyphal compartment by making structures called clamp connections. These are not always present, but provide a helpful identification feature when they are!

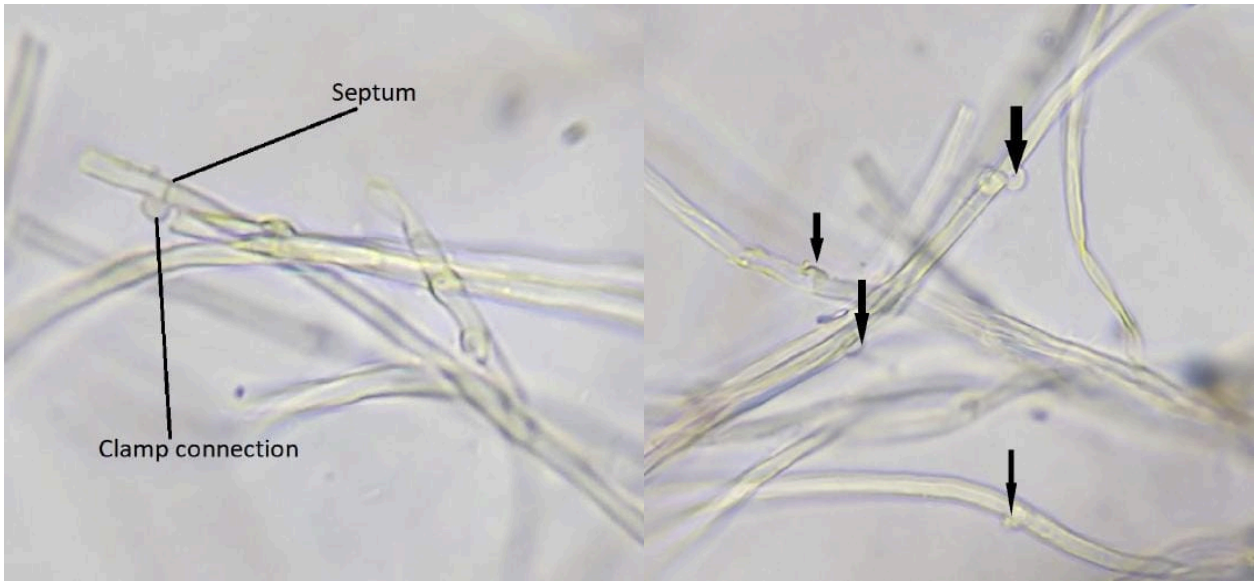


Figure 3.6.1.2: These two images show hyphae from a mushroom. In the image on the left, a clamp connection is visible at the septum. In the image on the right, four clamp connections are indicated by arrows. Photos by Maria Morrow, CC-BY-NC.

Complex Septations

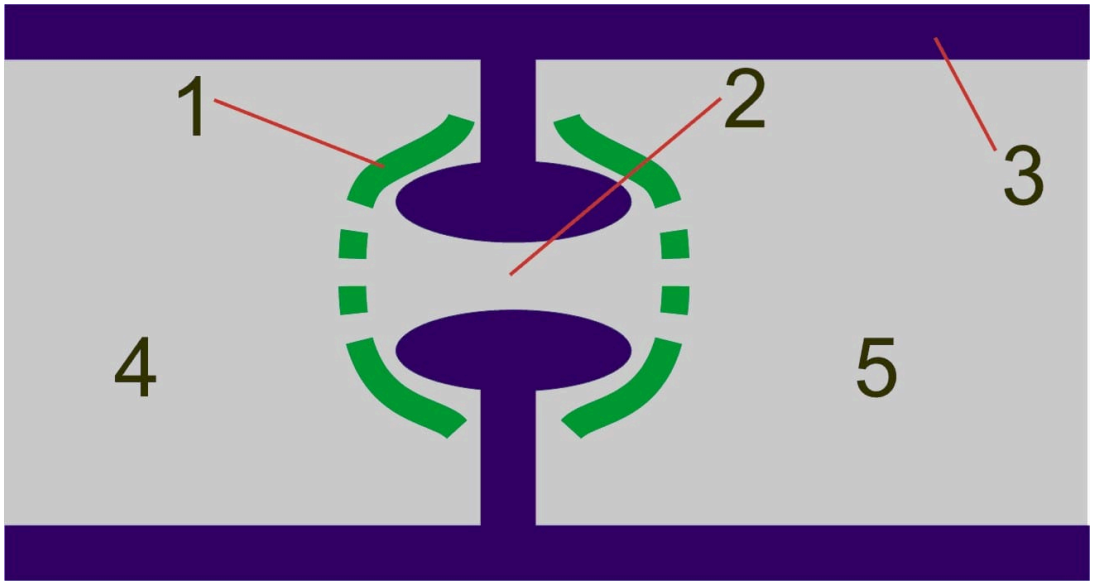


Figure 3.6.1.3: The complex dolipore septum found in basidiomycetes. This is not a feature that can be seen with the naked eye or in a standard microscope. "In hyphae of basidiomycete fungi, parenthesomes (1) "cap" a dolipore septum (2). The cell wall (3) swells around the septal pore to form a barrel-shaped ring. Perforations in the parenthesome allow cytoplasm to flow between (4) and (5)." Miguelferig, CC0, via Wikimedia Commons.

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3.6.2: Types of Basidiocarps

The fruiting body of a basidiomycete is called a basidiocarp. These structures produce haploid spores by meiosis and come in an incredible variety of shapes and sizes.

General Mushroom Anatomy

Though only a subset of basidiocarps look this way, they are the model for how we describe "mushrooms". In mycology, this type of basidiocarp is called "agaricoid" or "agaric" because it is the general form we see in the genus *Agaricus*. A more complex version of the agaric mushroom is seen in the genus *Amanita*, which is shown below.

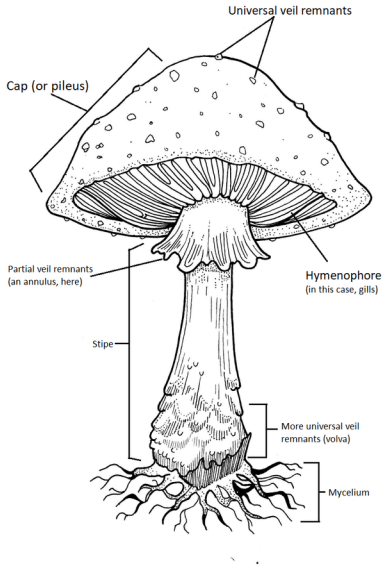


Figure 3.6.2.1: The anatomy of an *Amanita muscaria* basidiocarp. The cap (also called the pileus) protects the spore producing region, the hymenophore. The diagram shows a hymenophore composed of gills. However, you might see mushrooms with pores, teeth, or other types of spore-producing surfaces. The partial veil covers the hymenophore while the mushroom develops. When the cap extends as the mushroom grows, the partial veil is pulled and can either end up as an annulus or attached to the edges of the cap. Not all mushrooms have a partial veil and those that do often look quite different from this one! The universal veil (only present in a few mushrooms) covers the entire mushroom when it is young. As the mushroom expands, the universal veil is also pulled apart. Here, the cap has tiny fragments of the universal veil (warts) and the rest is at the base of the stipe (forming a volva). The stipe is the "stem" or "stalk" of the mushroom. Artwork by Nikki Harris CC-BY-NC.

Veils

Partial Veils



Figure 3.6.2.2: Veils can be difficult to conceptualize until you see them in person. The image above shows a few developmental stages of an Agaricus basidiocarp. In the fruiting body on the right (which has been cut in half), you can see the partial veil is still covering the gills. In the older fruiting body on the left, you can see the partial veil pulling away from the edges of the cap. This will end up as an annulus, as shown in the diagram of mushroom anatomy above. Photo by Maria Morrow, CC-BY-NC.



Figure 3.6.2.3: Partial veils can also take on a variety of forms. In the image on the left (*Cortinarius*), the partial veil is cobwebby instead of thick and sheet-like. In the image on the right (*Gomphidius*), the partial veil is made of slime! What you can also see in the image on the right are arthropods (likely springtails) on the gills. The partial veil protects the spores from predators like these, until it begins to open. Photos by Maria Morrow, CC-BY-NC.



Figure 3.6.2.4: Partial veils can also end up on the margin of the cap, instead of the stipe. In the image above, you can see the cottony partial veil (black arrow) of *Stropharia ambigua* dangling from the margin (edge) of the cap. Photo by Maria Morrow, CC-BY-NC.

Universal Veils



Figure 3.6.2.5: In the image on the left, you can see two Amanita buttons with a universal veil. As the veil dries out and the mushroom expands, it begins to crack into peaks. In the image on the right, an Amanita in a later stage of development shows similar peak-shaped universal veil remnants on the cap, but they are much farther apart. This is because the cap is expanding, much like a balloon, and the universal veil is staying the same size. Photos by Maria Morrow, CC-BY-NC.

Variety of Hymenophores

Gills (lamellate)



Figure 3.6.2.6: The underside of a gilled mushroom. The sheet-like membranes that travel between the cap and the stipe are called gills or lamellae. The spores are produced from basidia that cover the gills. Photo by Maria Morrow, CC-BY-NC.

Pores (poroid)



Figure 3.6.2.7: The underside of three mushrooms with pores. The pores of the *Suillus umbonatus* in the image on the far left are large and easily distinguished. The spores are produced on the internal surfaces of the pores, which are tube-like in structure. In the center, another *Suillus* species has smaller pores, but they can still be distinguished with the naked eye. In the *Picipes badius* on the right, the pores are so small that it almost looks smooth. Photos by Maria Morrow, CC-BY-NC.

Teeth (dentate)



Figure 3.6.2.8: The underside of two mushrooms with teeth. Teeth are like a pore that has been turned inside-out. Each stalactite-like tooth is covered by spore-producing basidia. The *Hydnellum* on the left has much smaller teeth than the *Hydnum* on the right. Photos by Maria Morrow, CC-BY-NC.

Smooth



Figure 3.6.2.8: This *Stereopsis humphreyi* has a hairy stipe and a saddle-shaped cap. On the underside of the cap, where you might expect to find gills or pores, the surface is completely smooth. However, spores are still formed here! Photo by Kilasiak, CC-BY-NC.

Other Basidiocarps

There are a vast diversity of basidiocarp forms out there. Below are a few examples of the more common ones you might run into.

Puffballs



Figure 3.6.2.9: Lycoperdon is a puffball-producing group. The spores are produced in a mass within the puffball. As it matures, it dries and a pore in the top opens. When the puffball is disturbed, such as by feet or raindrops, it puffs out spores, much like a bellows. Photo by Maria Morrow, CC-BY-NC.

Clubs & Corals

Figure 3.6.2.10: On the left are the club-shaped fruiting bodies of *Clavariadelphus occidentale*. On the right, is the branched, antler-like fruiting body. The branching-forms are generally referred to as corals. Spores can be produced on both clubs and corals on any exterior surface. Photos by Maria Morrow, CC-BY-NC.

Brackets and Shelves



Figure 3.6.2.11: Brackets formed by *Trametes versicolor*. These brackets have a hymenophore composed of tiny pores that cover the underside. The pileus (top) on these brackets has many concentric zones of brown stipes. Brackets tend to be relatively small and flimsy. Photos by Maria Morrow, CC-BY-NC.

Jellies



Figure 3.6.2.12: Two different types of jelly fungi. Jelly fungi can occur in a variety of forms. The gelatinous blobs on the left are produced by *Dacrymyces*. The vase-shaped jellies on the right are found in *Guepinia helvelloides*. Spores are produced on the exterior surface of jelly fruiting bodies. Photos by Maria Morrow, CC-BY-NC.

Crusts



Figure 3.6.2.13: Some fungi form fruiting bodies that spread flat across the surface of what they are eating, like this *Serpula himantioides* fruiting on a log. The spores are produced on the exposed surface. This type of fruiting body is referred to as a crust. Photo by Maria Morrow, CC-BY-NC.

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3.6.3: Life Cycles of Basidiomycetes

Agaricomycotina

The fungi covered so far in this chapter have all been in the subdivision Agaricomycotina. These fungi follow some version of the life cycle in Figure 3.6.3.1 below.

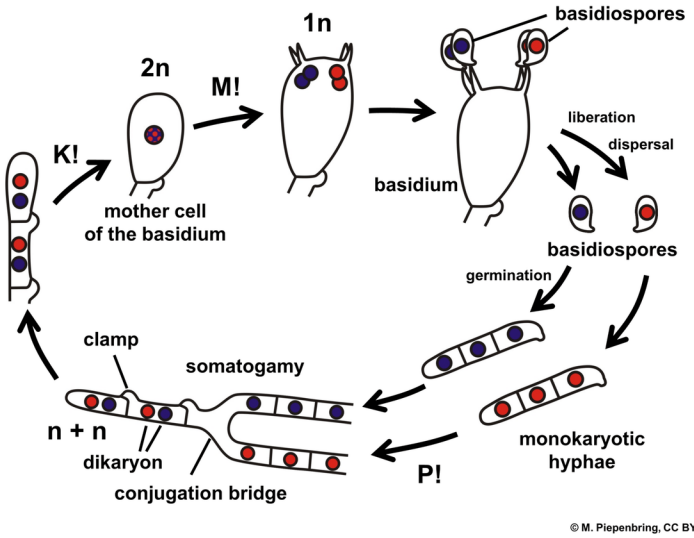


Figure 3.6.3.1: Generalized life cycle of the mushroom-forming basidiomycetes (Agaricomycotina). On the right side of the diagram, haploid basidiospores of two different mating types produced (dark blue and red). The life cycle follows one of each of these basidiospores as they each germinate and grow by mitosis into a monokaryon (a haploid thallus). Unlike ascomycetes, basidiomycetes do not spend long in the monokaryotic state. The two monokaryons fuse (P!=plasmogamy) via a conjugation bridge and a dikaryon is formed. This new dikaryotic (n+n) thallus has clamp connections due to the way nuclei divide and are kept in the dikaryotic state (one dark blue nucleus and one red nucleus between each septum). Sexual reproduction occurs with the formation of a basidium. Within the basidium, the two different nuclei fuse (K!=karyogamy), forming a diploid nucleus. This nucleus instantly divides by meiosis (M!), forming 4 haploid nuclei (two dark blue, two red). Small projections called sterigmata emerge from the basidium and each nucleus is moved through a sterigma, extending the cell wall around each to form basidiospores. M. Piepenbring, CC BY-SA 3.0, via Wikimedia Commons.

Pucciniomycotina

Rust fungi are in the Pucciniomycotina. These fungi have complex life cycles that can have a variety of different spore stages that require different plant hosts. A macrocyclic life cycle (containing all of the five spore stages) of *Puccinia gramminis* is represented in Figure 3.6.3.2.

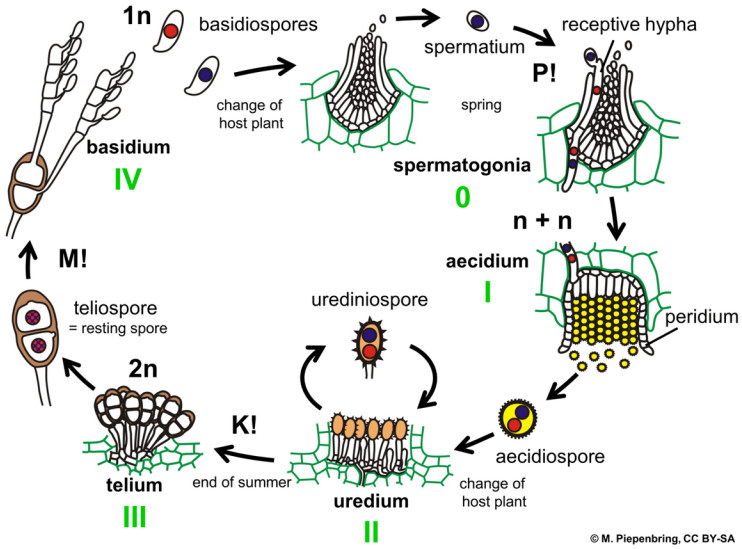


Figure 3.6.3.3: Generalized life cycle of the rusts (Pucciniomycotina). This life cycle is macrocyclic (contains all five stages) and heteroecious (involves two different host plants). In the upper left corner of the diagram, haploid basidiospores of two different mating types produced (dark blue and red). The life cycle follows one of these basidiospores (dark blue) as it lands on a new host plant that has a vase-like structure called a spermatogonium. The spermatogonium has receptive hyphae with red nuclei. The basidiospore fuses with the receptive hyphae, forming a dikaryon (n+n). The dikaryotic hyphae then grow to the underside of the leaf and form an aecidium where dikaryotic aecidiospores are produced. These aecidiospores are released and infect a second, different species of host plant where the fungus forms a pustule in the plant tissue called a uredinium. Within the uredinium, dikaryotic urediniospores are produced and can cause new infections in the same host plant species. Later in the season (end of summer, in this diagram), nuclei fuse (K!=karyogamy) and a telium is formed. Diploid teliospores (resting spores) are released. The teliospores germinate to produce basidia, meiosis (M!) occurs, and haploid basidiospores are formed. M. Piepenbring, CC BY-SA 3.0, via Wikimedia Commons.

Ustilaginomycotina

Smut fungi are in the Ustilaginomycotina. These fungi often have a saptrotrophic phase where they form yeasts and a biotrophic phase during which they act as parasites. The life cycle of the corn smut fungus *Ustilago maydis* is shown in Figure 3.6.3.3.

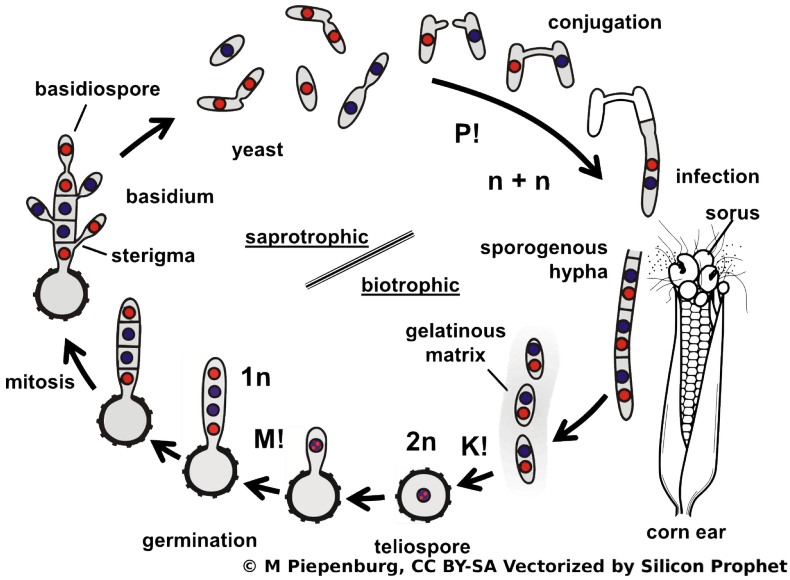


Figure 3.6.3.3: Generalized life cycle of the smuts (Ustilaginomycotina). In the upper left corner of the diagram, haploid basidiospores of two different mating types produced (dark blue and red). These basidiospores begin a saprotrophic yeast phase (sporidia), dividing by mitosis. When the fungi switch to a biotrophic (parasitic) feeding strategy, two different mating types of sporidia will begin to grow conjugation tubes, fusing cytoplasm (P!=plasmogamy) and growing together as a dikaryon. The fungus forms an infection sorus within its host, producing sporogenous hyphae. These fragment into dikaryotic cells within a gelatinous matrix. The two nuclei with each cell fuse (K!=karyogamy) forming a diploid nucleus inside the now teliospore. Teliospores are released from the host plant as a resting stage. The teliospores germinate to produce basidia, meiosis (M!) occurs, and haploid basidiospores are formed. M. Piepenbring, CC BY-SA 3.0, via Wikimedia Commons.

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3.6.4: Rusts and Smuts

Rusts (Pucciniomycotina)

Rusts are plant pathogens in the subphylum Pucciniomycotina that infect one or more host species. Rusts have amazing and complex life cycles (as you saw in chapter 3.6.3) potentially involving multiple hosts and as many as five different spore stages! Autoecious rusts continue to infect the same host species, while heteroecious rusts must use multiple species of plant hosts to complete their life cycle. Rusts that form all five different types of propagules during their life cycle are called macrocyclic, while rusts that lack one or more of these spore stages are called microcyclic.



Figure 3.6.4.1: *Puccinia lapsanae,* a rust fungus, forming small orange pustules in reddened regions on a *Lapsana communis* leaf. H. Krisp, CC BY 3.0, via Wikimedia Commons.

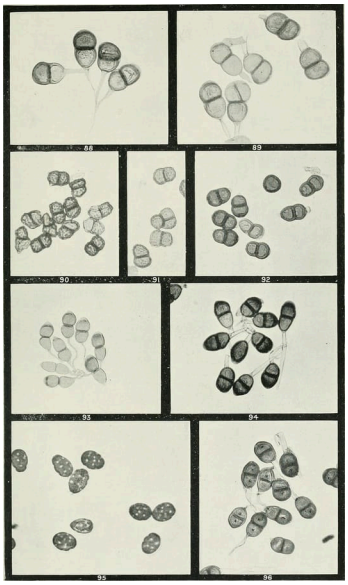


Figure 3.6.4.2: A variety of teliospores and urediniospores. These spore stages look incredibly similar and are generally easiest to distinguish based on seasonality (usually summer vs. fall formation). Image by McAlpine, Daniel, 1848-1932, No restrictions, via Wikimedia Commons.



Figure 3.6.4.3: Teliospores of *Puccina helianthi*. Photo by Vyzhdova V, CC BY 4.0, via Wikimedia Commons.



Figure 3.6.4.4: Heteroecious rusts alternate between different host plants. *Pucciniastrum goeppertianum*, fir-huckleberry rust, produces spermatogonia and aecia (yellowish columns on underside of needles, indicated by white arrows in first image) on firs. Aeciospores are then released and, if they are lucky, infect a huckleberry plant. On the huckleberry, infections manifest as swellings under the bark of younger branches (second image, the central branch is oddly enlarged and wrinkled), eventually bursting open to release spores. Urediniа and telia are produced on the huckleberry host. Urediniospores can reinfect the huckleberry plant or other huckleberries. Later in the season, teliospores are formed and can overwinter in the soil, germinating in the spring to release basidiospores that can then infect fir. Images by Maria Morrow, CC-BY 4.0.

Smuts (Ustilaginomycotina)

Smuts are the third subphylum within Basidiomycota. These fungi form saprotrophic yeasts and can have a variety of ecological roles, but are most famous for their plant pathogens and perhaps the smut fungus (*Malassezia*) that lives on the oils produced on human skin, sometimes causing the formation of dandruff on your scalp.



Figure 3.6.4.5: *Ustilago maydis*, Ustilaginaceae, Corn smut. The strange growths on these ears of corn are swollen kernels, infected by a smut fungus. In the image on the right, dark brown powdery teliospores are bursting from one of the kernels. Left: H. Krisp, CC BY 3.0, via Wikimedia Commons. Right: Ustilago_maydis_002.JPG: H. Zellderivative work: Ak ccm, CC BY 3.0, via Wikimedia Commons.

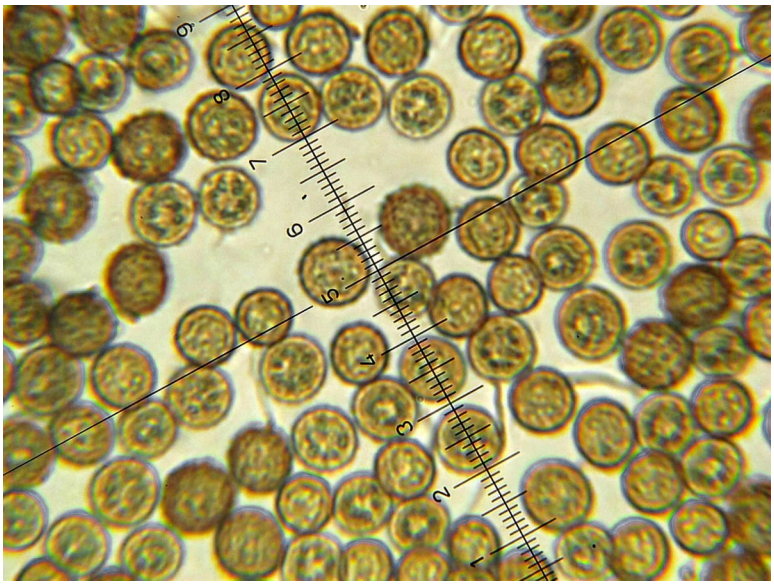


Figure 3.6.4.6: Teliospores of *Ustilago maydis*. Image credit: 2011-08-27_Ustilago_maydis_(DC.)_Corda_183839.jpg: This image was created by user Alan Rockefeller (Alan Rockefeller) at Mushroom Observer, a source for mycological images.You can contact this user here. +/−derivative work: Ak ccm, CC BY-SA 3.0, via Wikimedia Commons.

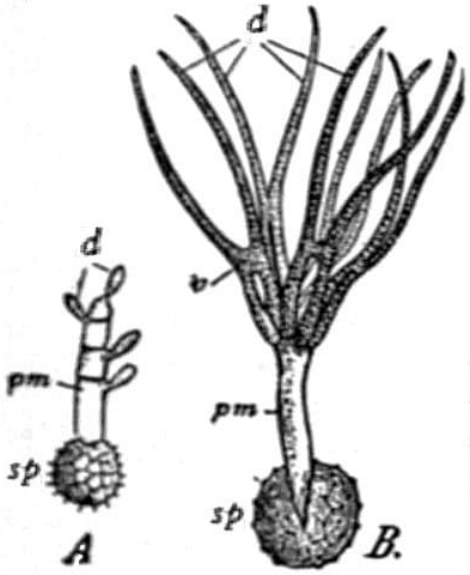


Figure 3.6.4.7: A diagram of germinating teliospores from A, *Ustilago receptaculorum*; *B*, of *Tilletia caries*. The drawings are labeled as follows: d=basidiospore (AKA sporidia), pm=basidium (AKA promycelium), sp=teliospore. Image from Vine's Students' Text Book of Botany, Public domain, via Wikimedia Commons.

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3.7: Lichens

Biology

Lichens are not individual organisms, but a single body formed from multiple symbiotic organisms. Lichens contain a fungal partner (the mycobiont) that forms the majority of the lichen body (called a thallus) and one or more photosynthetic partners (the photobiont) that are typically found in a thin layer or in isolated pockets. The mycobiont is typically an ascoymycete, but can very rarely be a basidiomycete (basidiolichen). The photobiont is usually green algae, but can also be cyanobacteria (cyanolichen) or both green algae and cyanobacteria (tripartite lichen). The mycobiont is responsible for maintenance of the lichen thallus, while the photobiont is responsible for producing food for both partners through photosynthesis. A cyanobacterial partner might also be fixing nitrogen for the lichen. As the study of lichens progresses, we are uncovering more partners with as yet unknown roles, such as basidiomycete yeasts and bacteria.

The Lichen Mutualism

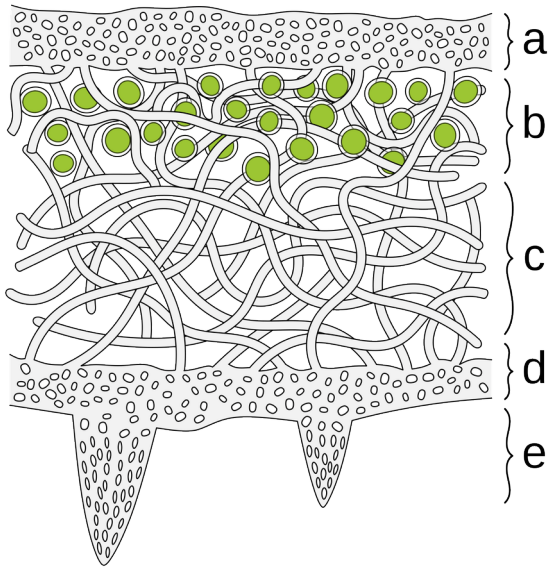


Figure 3.7.1: Cross-section through a lichen thallus, showing the general organization: a) upper cortex b) layer containing the photobiont, shown as green algal cells wrapped in fungal hyphae c) medulla d) lower cortex e) rhizines (root-like structures that protrude from the lower cortex and anchor the lichen to its substrate). Diagram by Nefronus, CC BY-SA 4.0, via Wikimedia Commons.



Figure 3.7.2: A log covered in foliose lichens and free-living green algae. The lichens shown in this picture are the result of a mutualistic relationship between fungi and green algae. The "green" alga in this image appears orange, due to the production of carotenoids. This algae, *Trentepohlia*, is likely the same algal species that is present within the lichens shown. Photo by Maria Morrow, CC-BY.

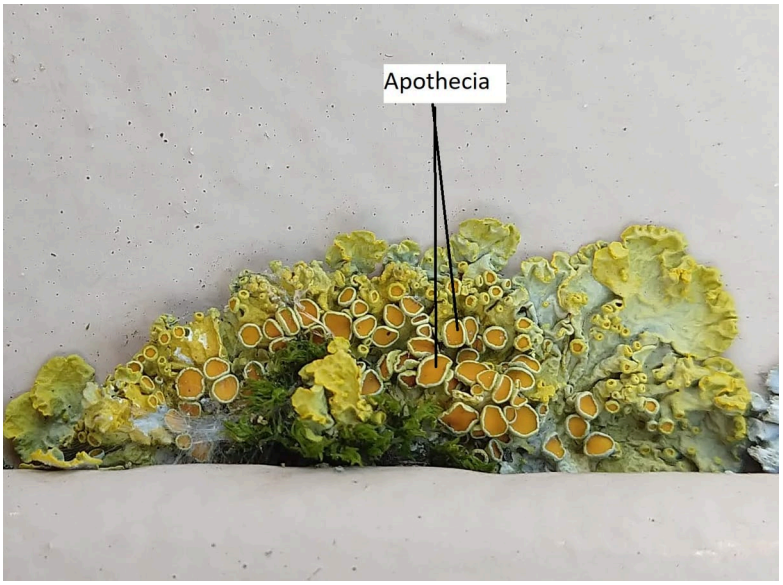


Figure 3.7.3: A lichen growing in a crack with a moss. This lichen is producing many round, orange apothecia. You may recognize these as belonging to the Ascomycota. Most lichens are formed with an ascomycete as the mycobiont. When apothecia are formed, the spores are reproducing only the mycobiont, not the photobiont. Photo by Maria Morrow, CC-BY.

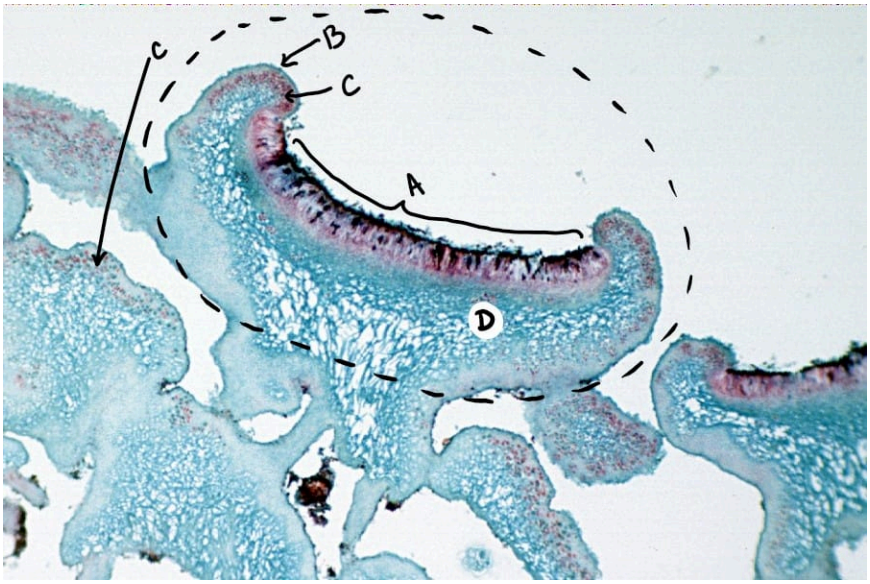


Figure 3.7.4: A cross section through an apothecium of the lichen *Physcia*. The apothecium is circled by a dotted line, A) hymenium composed of asci and paraphyses, B) upper cortex, C) photobiont layer (stained pink), D) medulla. Micrograph by Curtis Clark, CC BY-SA 3.0, via Wikimedia Commons with labels added by Maria Morrow.

Basidiolichens



Figure 3.7.5: In the image on the left, there is a green slime covering the log. That green slime is primarily composed of the algal partner (the photobiont) of the basidiolichen. There is a small brown mushroom protruding from the slime. That mushroom is the fruiting body of the basidiomycete that is the mycobiont in this lichen. The image on the right shows a (dried out) mushroom produced by the basidiolichen *Lichenomphalia*. Photo by Maria Morrow, CC-BY.

Cyanolichens



Figure 3.7.6: Peltigera membranacea is a cyanolichen. Cyanolichens often appear darker in color than lichens with an algal partner. This lichen is a dark, steely blue color when wet. This lichen is called the dog tooth lichen because the orange-brown apothecia are produced in rolls on the margins, looking like horns or teeth. Photo by Maria Morrow, CC-BY.



Figure 3.7.7: A dark brown, foliose lichen is growing intermixed with other lichens and moss. This *Nephroma* sp. is a cyanolichen. Here, the apothecia are also produced on the edges, but the fertile side is facing downward. Photo by Maria Morrow, CC-BY.



Figure 3.7.8: Cyanobacteria in the genus *Nostoc* are housed in structures called cephalodia (cephalodium sing.). This image shows a close up (scale bar = 1 mm) of cephalodia on the lichen *Nephroma arcticum,* which appear dark brown. This contrasts the surrounding green pigment produced by the algal photobiont in the medulla. Photo by Jason Hollinger, CC BY 2.0, via Wikimedia Commons.

Additional Features



Figure 3.7.8: The first image (left) shows a foliose lichen that is a minty green on the upper surface and black on the lower surface. If you look closely at the undersurface, you can see many short hair-like protrusions. These rhizines help anchor the lichen to its substrate. In the next photo (right) a dark blue-grey foliose lichen (*Peltigera*) has many long white rhizines protruding from the lower cortex. First photo by Maria Morrow (CC-BY). Second photo by Kyle Copas (CC-BY).

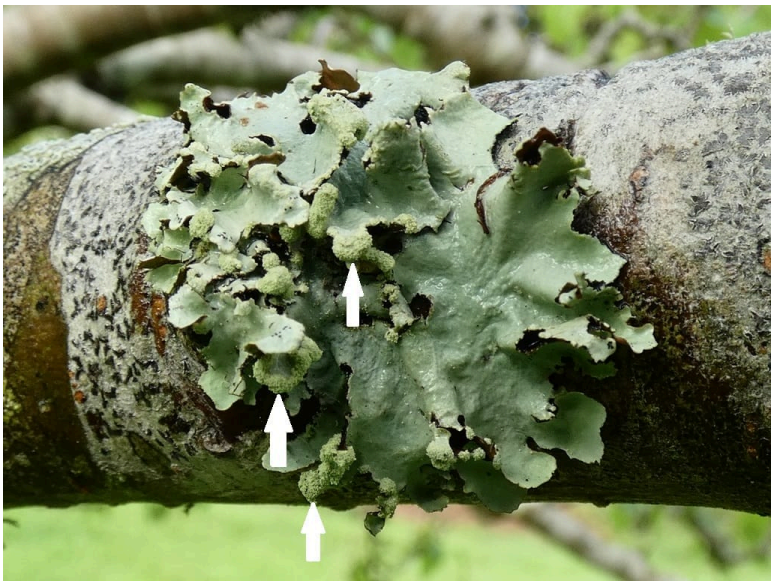


Figure 3.7.9: A foliose lichen with marginal **soralia**. The powdery regions on the edges of this lichen are called soralia. In these soralia, the lichen is producing many soredia--loose bundles of fungal hyphae and algal cells that allow the lichen to reproduce asexually. Three of these soralia have been indicated by white arrows. Photo by Maria Morrow, CC-BY.



Figure 3.7.9: Lichens with **isidia**. Much like soralia, these are asexual reproductive structures containing both fungal and algal cells. Unlike soralia, these structures appear shiny (not powdery) because they are covered in a thin layer of cortex. First photo of *Flavoparmelia baltimorensis* by Jason Hollinger, CC BY 2.0, via Wikimedia Commons. Second photo of *Letharia vulpina* by Walter Siegmund, CC BY-SA 3.0, via Wikimedia Commons, has been cropped and labeled by Maria Morrow.

Forms

Lichens can generally be classified into three general forms: crustose, foliose, and fruticose. However, there are some lichens that don't really fit into these categories as nicely, such as the "dustose" lichens that form powdery crusts.

Crustose

Figure 3.7.10: This image shows several different crustose lichens (and one foliose lichen) on the bark of a young pear tree. The crustose lichen closest to the camera is in the genus *Graphis*. It looks as though it has been painted onto the tree bark, but has small raised black lines running through it, giving it the common name "script lichen". These lines are the elongated apothecia. Photo by Maria Morrow, CC-BY.



Figure 3.7.11: This image shows a crustose lichen growing on a rock. The thallus is not as flat as the Graphis lichen shown above. However, it is still tightly apressed to the surface of the rock, as if it were painted on. Photo by Maria Morrow, CC-BY.



Figure 3.7.12: This image shows a single crustose lichen (*Lepra*) growing out radially from a central point. There are not other crustose lichens growing adjacent to it, so it does not have the distinct boundaries that we saw with the crustose lichens on the pear bark above. The dots forming concentric circles on the surface of the lichen are apothecia. Photo by Maria Morrow, CC-BY.

Foliose

Foliose lichens have a distinct upper and lower surface, much like a leaf. Sometimes these can grow appressed to a substrate, but unlike crustose lichens, they can usually be separated from it (with some effort).



Figure 3.7.13: A foliose lichen (*Lobaria pulmonaria*). The first image shows the upper cortex. The second image shows the lower cortex. These two surfaces make a distinct 'upper' and 'lower', unlike the fruticose lichens. Photos by Maria Morrow, CC-BY.

Fruticose



Figure 3.7.14: A fruticose lichen growing in the crevices of a tree's bark. Fruticose lichens do not have a distinct upper and lower surface. Instead, they appear more bushy in structure. This *Letharia* lichen is a vibrant neon yellow color due to its production of vulpinic acid, which is toxic to canines. Photo by Maria Morrow, CC-BY.



Figure 3.7.15: This *Pilophorus* is technically a fruticose lichen, due to the upright structures it makes (podetia). Each podetium has a black apothecium at the top, which has been inverted (much like in the *Helvella* mushrooms from the ascomycete section). However, the granular powder coating the surface of the rock is also part of the lichen thallus, making it seem a bit like a crustose or "dustose" lichen. Photo by Maria Morrow, CC-BY.

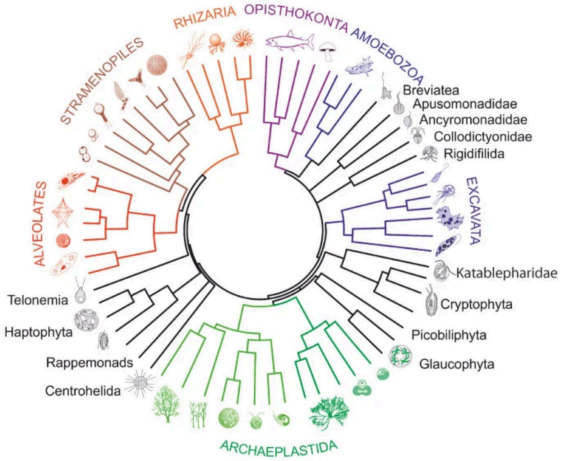
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4: "PROTISTS"

Protists are not a phylogenetically related group of organisms. In the very recent past--and still in many textbooks today--eukaryotic organisms were lumped into four groups: Animals, Plants, Fungi (only separated from plants since around the same time we figured out how to get to THE MOON), and Protists. Organisms were classified as belonging to Kingdom Protista by saying "Well, it isn't an animal, plant, or fungus," so it isn't surprising to find out that these organisms are not actually genetically related to each other. Protists encompass an incredibly diverse group of organisms that span many evolutionary lineages. Below are a few supergroups discussed in Pawlowski (2013) that include groups you'll find in the "Protists" chapter of this book:

- Stramenopiles: Includes the water molds, brown algae, and diatoms
- Archaeplastida: Includes the red and green algae (and plants!)
- Amoebozoa: Includes the slime molds

Figure 1



Deep phylogeny of eukaryotes showing the position of small eukaryotic lineages that branch outside the seven supergroups (modified after Burki *et al.* [12]; drawings S Chraiti).

Figure from Pawlowski (2013).

4.1: Slime Molds

4.2: Water Molds

4.3: Brown Algae

4.4: Diatoms

4.5: Red Algae

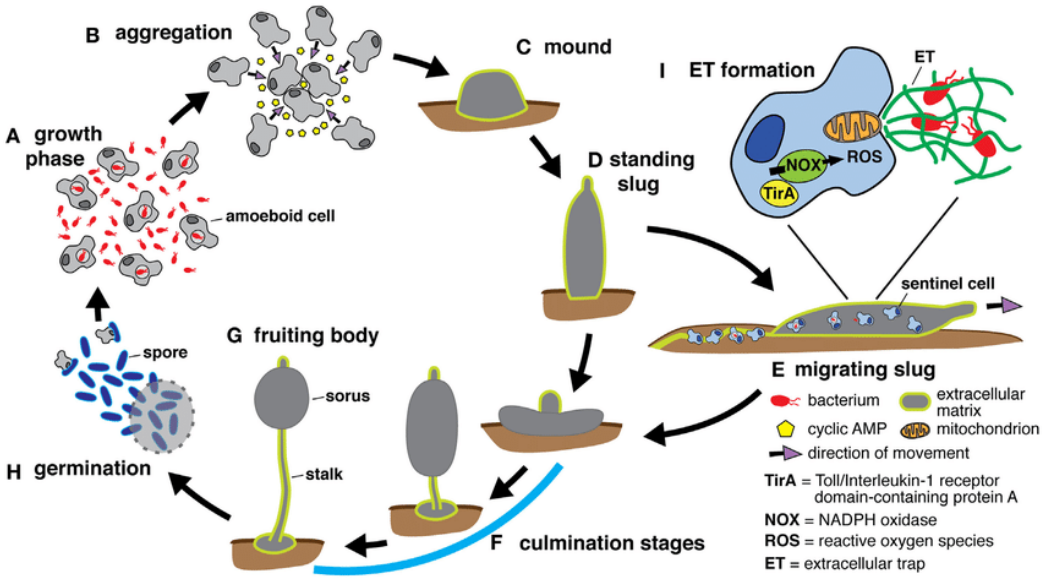
4.6: Green Algae

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4.1: Slime Molds

Slime molds encompass organisms from several lineages. Here, we look at three main groups. **Cellular slime molds** (dictyostelids) are groups of unicellular amoebae that collaborate to form fruiting structures to disperse spores. **Protostelids** make small fruiting bodies that have cellular stalks. **Plasmodial slime molds** (classified under Myxogastria or Myxomycetes) form a large, multinucleate amoeba with no cell wall that will eventually wall off individual nuclei to form spores.

Cellular Slime Molds



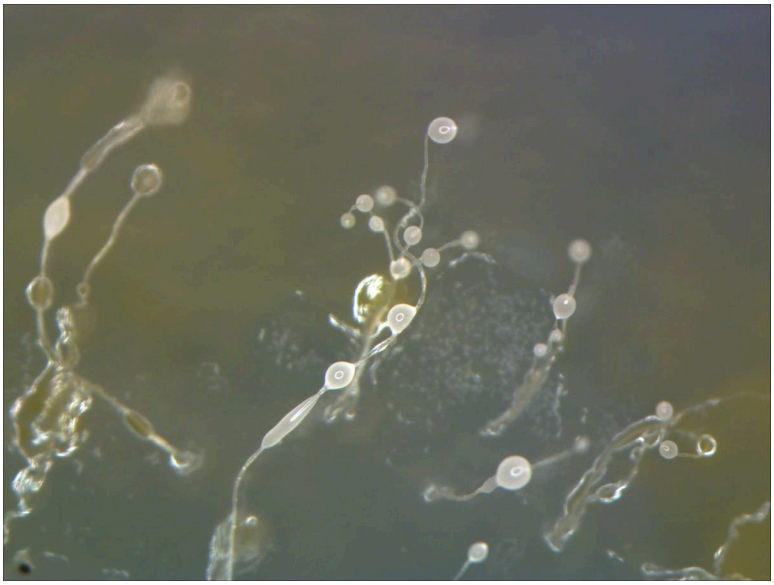


Figure 4.1.2: These images show a species of *Dictyostelium* developing fruiting bodies. In the image on the left, the culmination stages are visible. These appear as teardrop or worm-like shapes. On the right, several sporangia are in the process of forming, with individuals still migrating up the stalk to the apex. Only the individuals who end up in the sporangium will survive to "reproduce" as spores. Photos by Jerry Cooper CC BY 4.0.

YouTube Video

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

Video 4.1.1 : A video showing the cellular slime mold *Dictyostelium*, both as individual amoebae and collaborating to form fruiting structures. Link to the YouTube video.

Protostelids

The examples shown here are *Ceratiomyxa fruticulosa*. This organism may not actually be a protostelid, but the small, stalked fruiting bodies with a single sporangium produced on the external surfaces are similar to what would be seen in a protostelid.



Figure 4.1.3: This image shows the slime mold *Ceratiomyxa fruticulosa*, which looks a bit like an organism you'd find under the sea. This slime mold (likely) belongs to the protostelid group because it makes its spores externally. Each coral-like extension of this slime mold is covered with tiny spores. Photo by Maria Morrow, CC BY-NC.



Figure 4.1.4: A close-up of *Ceratiomyxa fruticulosa*, showing the fruiting structures covering the outside of the strange, coralloid projections. Photo by Damon Tighe, CC BY-NC. See another great example here.

Plasmodial Slime Molds

Plasmodial slime molds represent a vast diversity of morphologies. While still a plasmodium (see Figure 4.1.5), they can be difficult to distinguish. However, once they have formed into a fruiting structure, they can form distinct, varied, and amazing shapes (see Figure 4.1.6 – 9)!

The Plasmodium



Figure 4.1.5: This image shows *Physarum polycephalum* exploring some decaying wood. This is the feeding **plasmodium**. During this stage, the giant, multinucleate amoeba moves over the substrate engulfing bacteria. The veins allow for streaming of the cytoplasm and efficient connections between sources of food. Photo by Daniel Folds, CC BY-NC.

Sporocarp Diversity



Figure 4.1.6: Hemitrichia serpula forms an uncommon fruiting body called a **plasmodiocarp**. The feeding stage accumulates its protoplasm into the veins of the plasmodium, forming strange linear, intertwining shapes. Photo by Roman Providukhin, CC-BY-NC.



Figure 4.1.7: Fruiting bodies of the plasmodial slime mold *Lycogala epidendrum* form into cushion-like structures called **aethalia**. The plasmodium has formed into pink ball-like structures on the surface of a rotten log. One of these structures has been popped and is oozing a pink slime, full of immature spores. This pink slime gives *Lycogala* its name, wolf's milk. Photo by Maria Morrow, CC BY-NC.



Figure 4.1.8: Another option for a fruiting structure is the **pseudoaethalium,** where there are distinct sporangia but they still form together like a cushion. This is the type of fruiting structure formed by Tubifera ferruginosa, the red raspberry slime mold. Photo by Hiromi Karagiannis, CC BY-NC.



Figure 4.1.9: Fruiting bodies of *Diachea leucopodia* have a distinct stalk and **sporangium**. The stalk in this species is white, while the elongate sporangium displays an oil-sheen rainbow of colors. Photo by Sypster, CC BY-NC.

Other Features



Figure 4.1.10: This fruiting body of *Arcyria denudata* shows an interesting feature of slime mold anatomy. The sporangium is composed of a **peridium** (skin) that encloses the spores. The spores are often intermixed with a tangle of filaments called the **capillitium**, which helps disperse the spores. In this image, the pink capillitium (full of spores) can be seen bursting out of the sporangium. Photo by Alexander Shirokikh, CC BY-NC.

In addition to having interesting macroscopic morphologies, they also have interesting microscopic features! Ornamentation and size of the spores, as well as the appearance of the capillitial threads, can be necessary for identification.

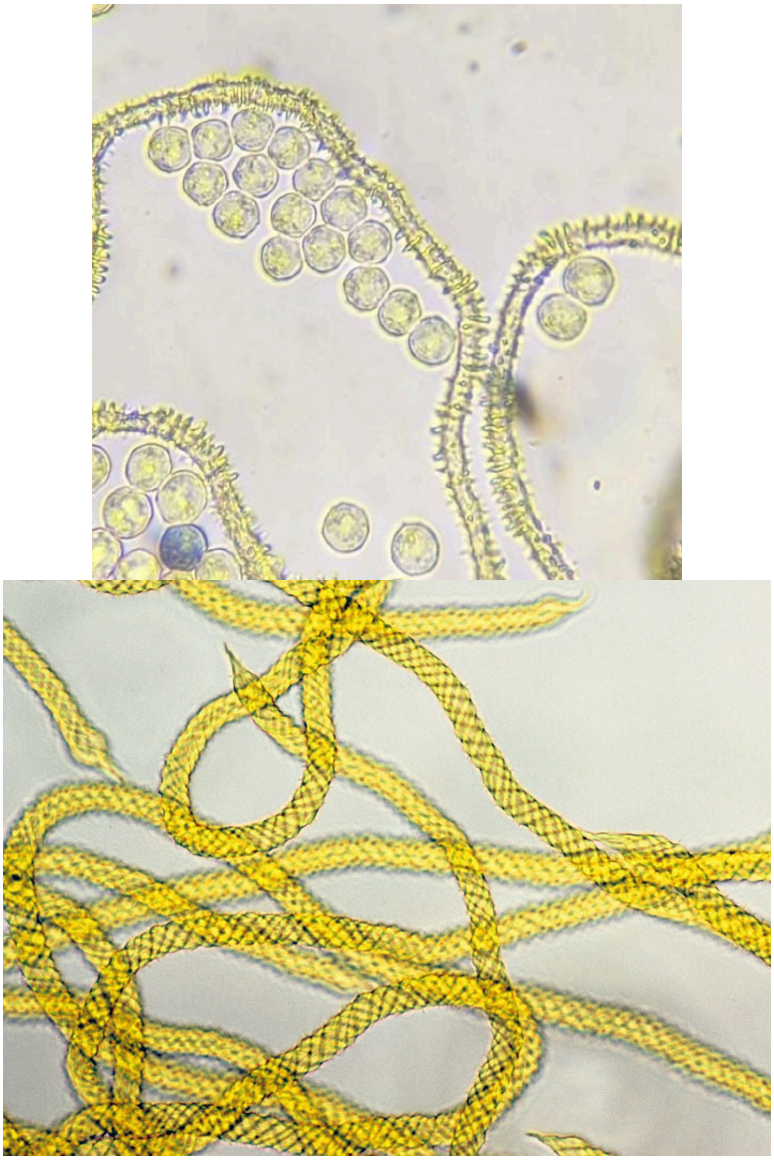


Figure 4.1.11: Ornamentation of the capillitial threads can be a helpful identification feature. On the left are the spiny ornamentations characteristic of *Arcyria obvelata*. On the right are the twisted threads of *Trichia botrytis*. Photo on the left by Maria Morrow CC BY-NC. Photo on the right by George Barron, for non commercial academic and research use only.

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4.2: Water Molds

Water molds belong to the phylum Oomycota in the Stramenopile supergroup. Oomycetes are also fungus-like organisms with cell walls made of cellulose. Similar to myxomycetes, they have motile spores with 2 flagella. However, one of these flagella is "normal"-looking (called a whiplash flagellum) and the other is ornamented. This strange characteristic puts organisms into a group called the heterokonts (meaning "different flagella").

Many oomycetes, such as *Saprolegnia*, are important decomposers in aquatic ecosystems, while others -- namely those in the genus *Phytophthora* -- have adapted to life on land and are some of the most destructive plant pathogens.

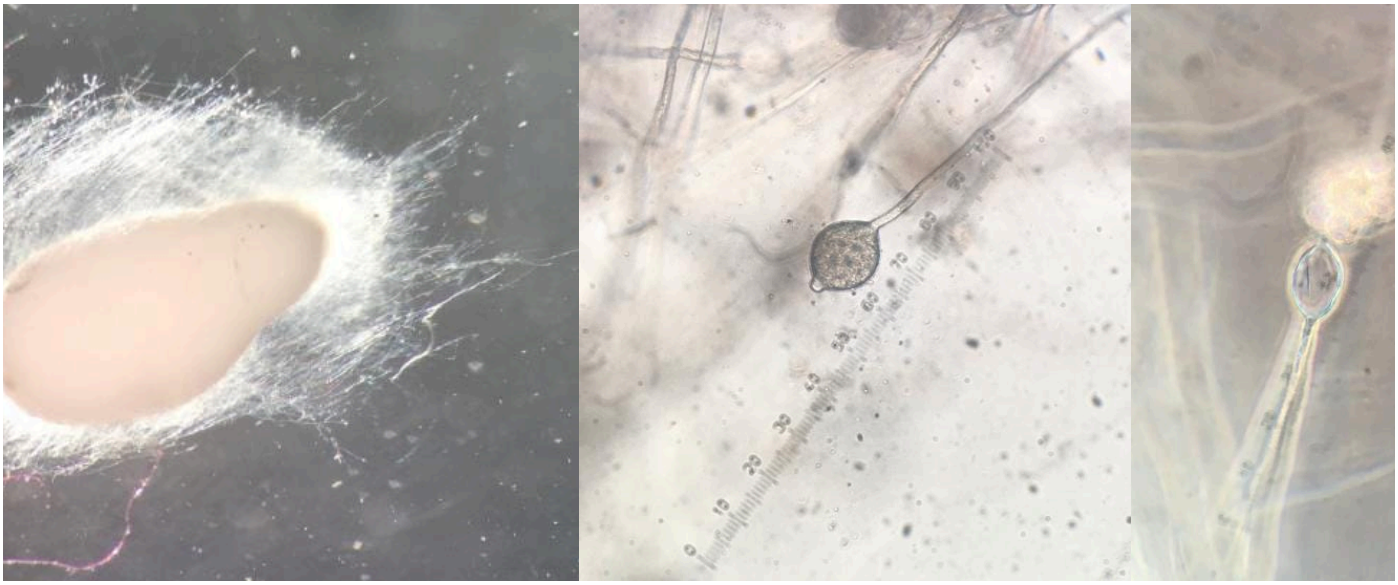


Figure 4.2.1: A water mold from the genus *Phytopythium* growing on a sesame seed (first image). The fine fuzz surrounding the seeds is the filamentous thallus. The other two images show a zoosporangium, with the zoospores released in a single mass (last image). All photos by Tom Bruns (pogon) CC-BY-NC.

Saprolegnia

This organism reproduces asexually by producing **zoospores** (zoospores are spores that swim, zoo- meaning ‘to live’) inside of an elongated sac called a **zoosporangium** (-angium meaning vessel, so a zoosporangium is what zoospores are produced inside of). These zoospores grow by mitosis into a diploid **thallus**, an undifferentiated body.

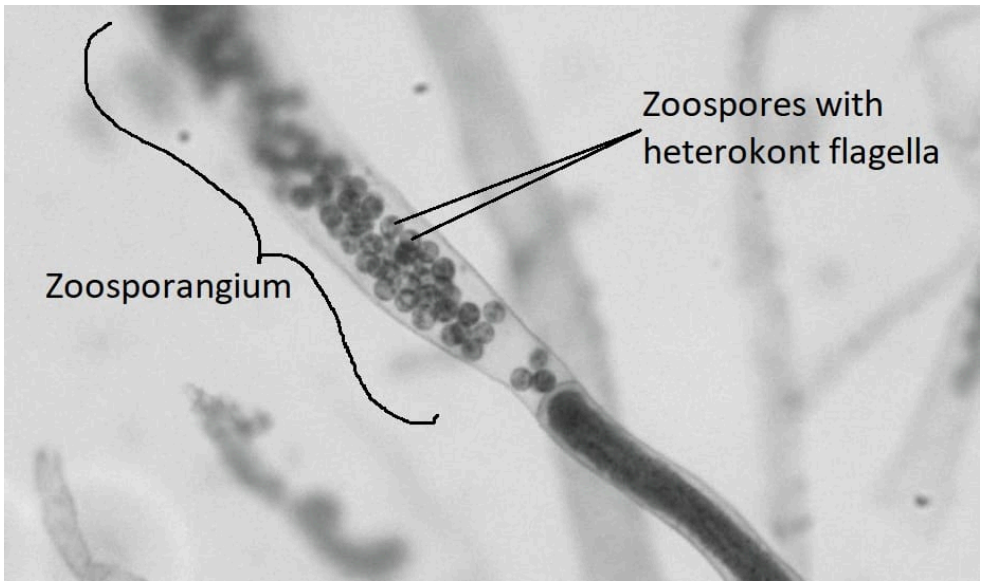


Figure 4.2.2: A zoosporangium of *Saprolegnia* with mature zoospores. The elongated, sac-like zoosporangium is partially visible in this image, located at the end of a filament of the thallus. Inside the zoosporangium are many small, round zoospores. Each of these would have two flagella: one whiplash and one tinsel. Photo by Maria Morrow, CC-BY-NC.

Saprolegnia's sexual reproducing structures include the globose **oogonium** and smaller, pad-like **antheridia** (singular, antheridium) that attach to the oogonium. Because these structures produce gametes--much like spores are produced in sporangia--the oogonia and antheridia are also referred to as **gametangia** (gametangium singular). The oogonium produces haploid **eggs** via meiosis. These eggs are fertilized by the haploid **male nuclei** produced by meiosis within the antheridium, creating a diploid, thick-walled zygote called an **oospore**.



Figure 4.2.3: Multiple antheridia can be seen appressed to the outside of the globose oogonium. Photo by Tom Bruns (pogon), CC-BY-NC.

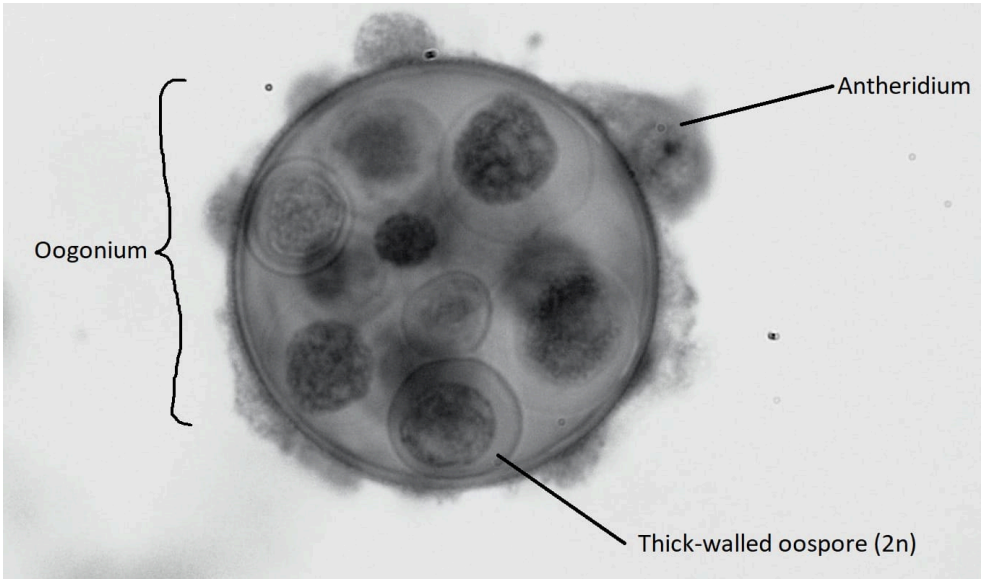


Figure 4.2.4: An oogonium of *Saprolegnia* with fertilized oospores. This large, globose oogonium would be located at the end of a filament on the thallus. Within the oogonium, there are many diploid oospores, which you can distinguish from unfertilized eggs by the thick wall that encloses them. On the outside of the oogonium, there are several antheridial pads apressed to the surface. The haploid nuclei within these antheridia have already been released into the oogonium. Photo by Maria Morrow, CC-BY-NC.

The oospore will be released and grow by mitosis to create a new multicellular **thallus**, completing the diplontic life cycle.

Phytophthora

Phytophthora is a genus of water molds that parasitize plants. They have specialized zoosporangia that detach, allowing zoospores to be transported terrestrially and await germination until moisture is present. Some notable Phytophthoras are *P. ramorum* (causal agent of sudden oak death, see Figure 4.2.5) and *P. infestans* (causal agent of late blight of potato and the Irish potato famine, see Figure 4.2.6).



Figure 4.2.5: Phytophthora ramorum can infect hundreds of different plant species, sometimes causing a leaf blight (as seen in the first photo), sometimes causing root disease. When it infects certain species of oak (*Quercus* spp.) and tanoak (*Notholithocarpus densiflorus*), it causes a lethal stem canker that oozes and stains a dark reddish color (second photo). First photo by Kerry Wininger, CC-BY-NC. Second photo by Chris Shuck, CC-BY-NC.



Figure 4.2.6: The image on the left shows two lemon-shaped sporangia, each at the end of a hyphal filament. These sporangia will release zoospores when conditions are favorable. The image on the right shows the leaf where these sporangia were produced, seen here as a discolored region with some white fuzz. Photos by 大肚魚 CC-BY-NC.

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4.3: Brown Algae

Secondary Endosymbiosis in Heterokonts

Brown algae are a photosynthetic lineage of heterokonts. They derived their golden brown chloroplasts from **secondary endosymbiosis**. In this event, an ancestral oomycete engulfed a red alga. As in primary endosymbiosis, instead of being digested, overtime the red alga degenerated into a chloroplast, this time with 4 membranes -- the engulfing membrane from the oomycete, the red alga's plasma membrane, and the two membranes of the original chloroplast within the red alga. In many groups derived from secondary endosymbiosis, the chloroplast has lost one of these membranes.

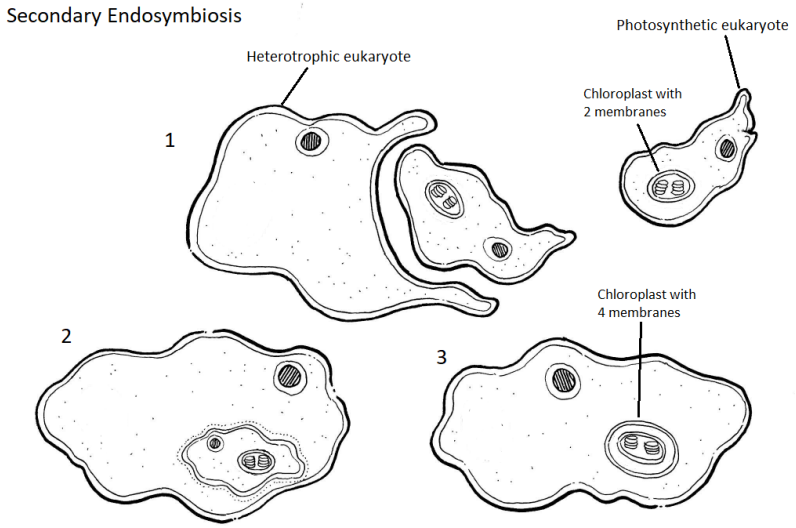


Figure 4.3.1: In the diagram above, we see a unicellular photosynthetic eukaryote with a 2-membrane chloroplast. In step one, this organism is engulfed by a heterotrophic eukaryote. In step two, we see the photosynthetic organism inside the heterotrophic organism. In step three, the original photosynthetic organism has been reduced to a chloroplast with 4 membranes. Artwork by Nikki Harris CC-BY-NC with added labels by Maria Morrow.

Brown Algae, Phylum Phaeophyta

Brown algae are brown due to the large amounts of carotenoids they produce, primarily one called **fucoxanthin**. These organisms are exclusively **multicellular** and can get so large that they require special conductive cells to transport photosynthates from their blades down to the rest of their tissues. These conductive cells are called **trumpet hyphae** and have sieve plates and resemble sieve tubes found in flowering plants.

Much like *Saprolegnia*, the body of an alga is termed a thallus because it is not differentiated into specialized tissues. The general morphology of a brown alga includes a **holdfast, stipe, gas bladder**(s)**,** and **blade**(s).

Kelp



Figure 4.3.2: In the diagram above, there are two kelp thalli. The one on the left side is labeled. At the bottom of the thallus is a network of root-like projections that make up the holdfast. The stem-like structure that travels up from the holdfast is the stipe, which terminates in an inflated gas bladder. There are several leaf-like structures attached to the gas bladder. These are blades. The thallus on the right has all of these components, but in a slightly different arrangement. Can you find them? Artwork by Nikki Harris CC-BY-NC with added labels by Maria Morrow.

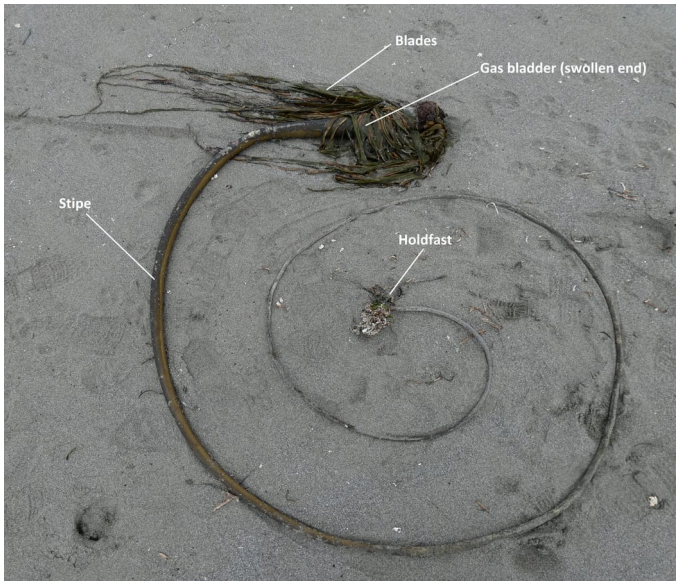


Figure 4.3.3: A bull kelp thallus that was washed up on the beach and arranged in a spiral so all parts would be visible in one image. At the center of the spiral is the holdfast. This would be attached to the sea floor. A long stipe connects the holdfast to a gas bladder that is obscured by many thin blades, which all attach to the top of the gas bladder. Photo by Maria Morrow, CC-BY-NC.

Figure 4.3.4: A piece of feather boa kelp with several small gas bladders. The four gas bladders shown all attach to the edge of the stipe. If the full thallus were visible, gas bladders would be attached down the entire length of both sides of the flattened stipe. Do you see any blades present? Photo by Maria Morrow, CC-BY-NC.



Figure 4.3.5: This kelp thallus was found in a tide pool. It has a prominent blade and stipe, but no gas bladder is visible. Where would the holdfast be? Photo by Maria Morrow, CC-BY-NC.

Fucus

A model organism for the Phaeophyta life cycle is *Fucus* (rockweed), which, like its relative *Saprolegnia,* has a diplontic life cycle.

The *Fucus* thallus has dichotomous branching (forking into two equal branches) and swollen, heart-shaped reproductive tips of the branches. These swollen branch tips are called **receptacles**.

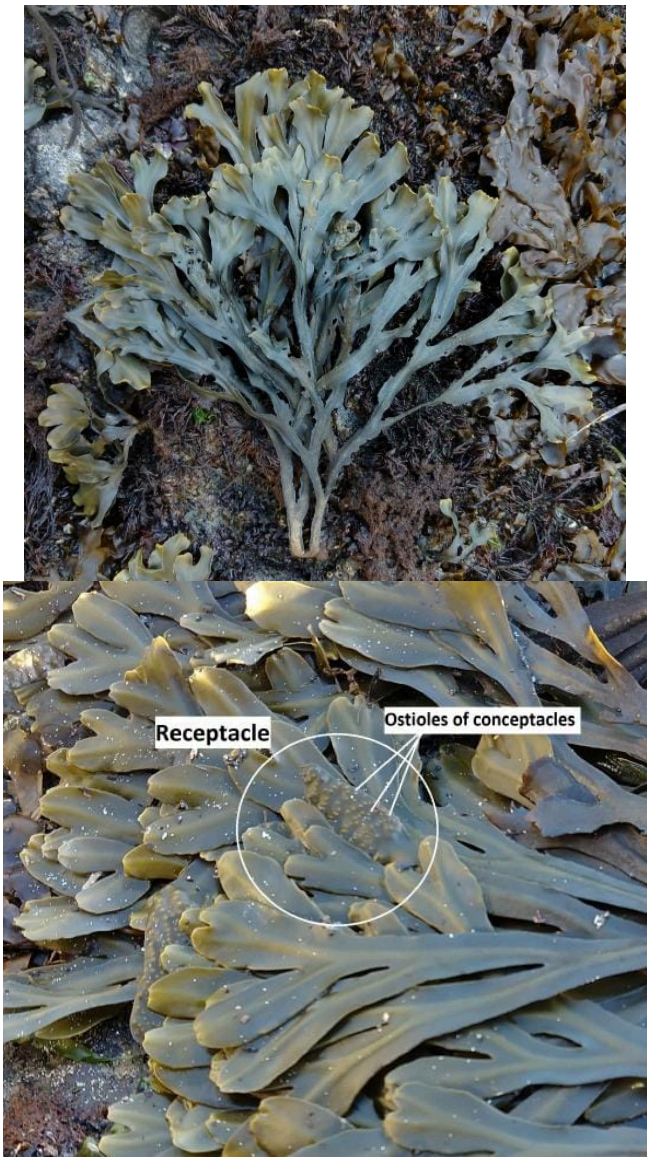


Figure 4.3.6: The image on the left shows a Fucus thallus (though a bit of the holdfast remained attached to the rock). The thallus branches dichotomously, making Y shapes each time it branches and forks into two equal pieces. The image on the right is a closer view of the ends of the branches. The swollen, heart-shaped ends are called receptacles. The bumps on these receptacles are the tops of the conceptacles--vase-like chambers embedded within the receptacle. Photos by Maria Morrow, CC-BY-NC.

The receptacles are covered in small bumps, each with a pore at the center of the bump called an **ostiole**. The bumps are **conceptacles**, chambers that house the male and female gametangia.

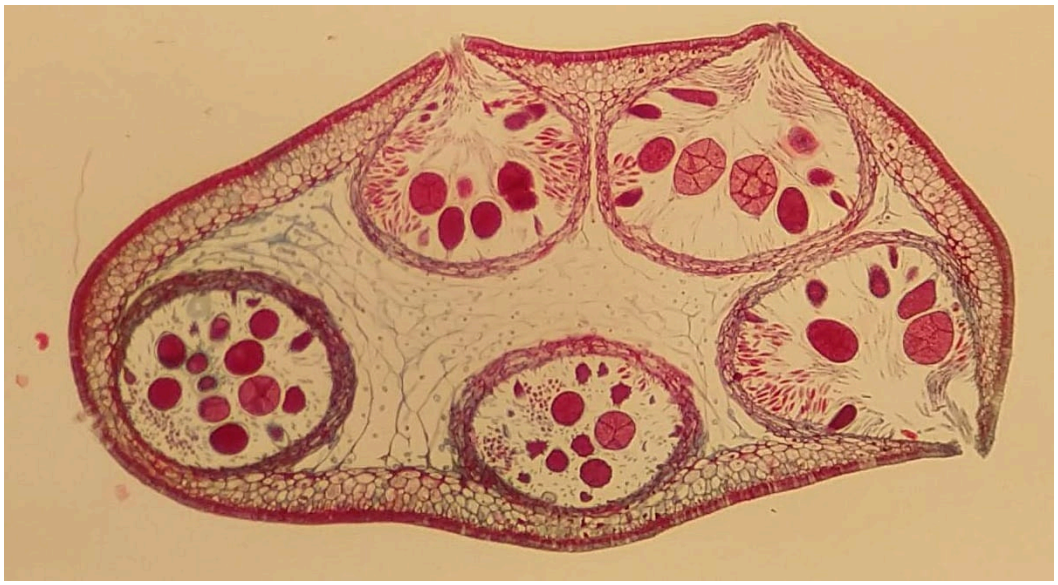


Figure 4.3.7: A microscope slide of a cross section through a *Fucus* receptacle. The cross section reveals the conceptacles, which appear as spherical chambers within the receptacle. In each conceptacle, there are globose structures (oogonia) and branching, tree-like structures (antheridia). Photo by Melissa Ha, CC-BY-NC.

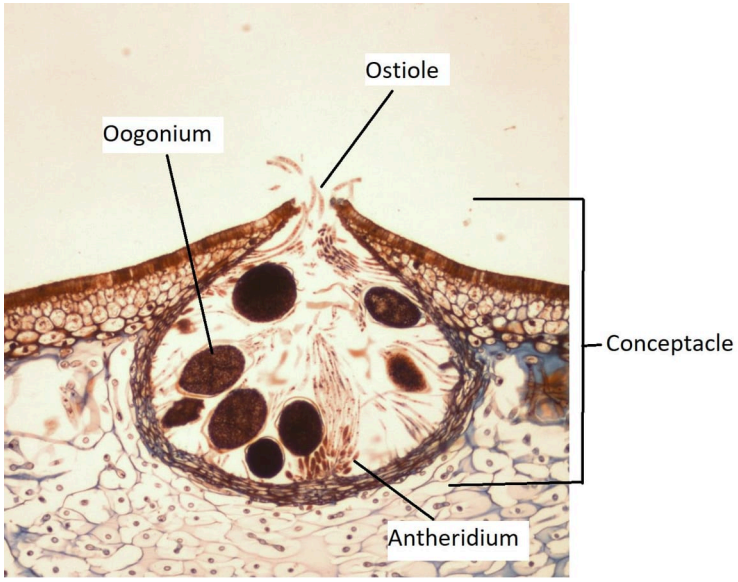


Figure 4.3.8: A cross section through a *Fucus* receptacle shows inside a conceptacle. The male and female gametangia are housed within the conceptacle chamber. The antheridia are branched structures that look like small trees. These produce sperm with heterokont flagella (not visible in this image). The oogonia are globose structures divided into sections as eggs are produced. The eggs will be fertilized by sperm that swim in through the ostiole, forming a diploid zygote that will be released in the marine water. This zygote will grow by mitosis into a multicellular, diploid thallus. Photo by Maria Morrow, CC-BY-NC.

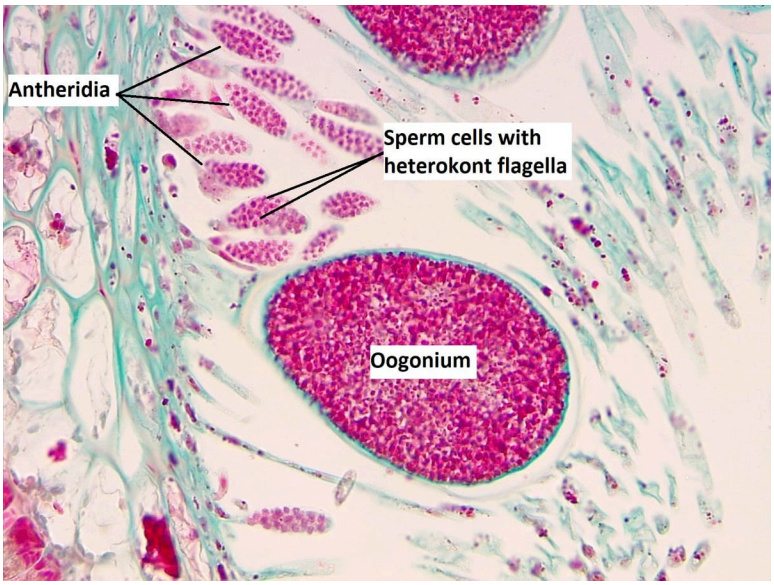


Figure 4.3.9: A closer view of the antherida and oogonium inside a *Fucus* conceptacle. There are no eggs distinguishable within the oogonium. However, individual sperm cells can be seen within the antheridia. These sperm cells would each have the typical heterokont flagella. Photo by Melissa Ha, CC-BY-NC.

Full Life Cycle Diagram

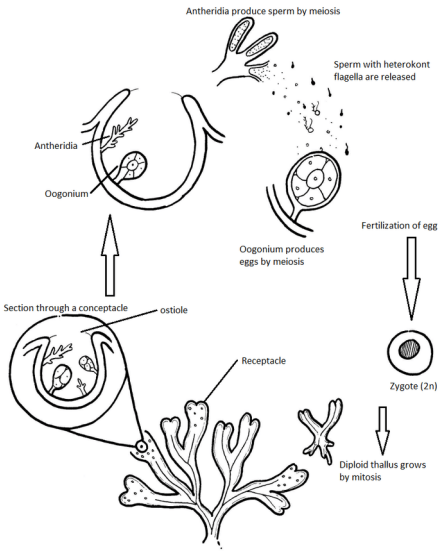


Figure 4.3.10: The diplontic life cycle of *Fucus*. If you start at the bottom of the diagram, there is a diploid thallus. The ends of the thallus branches are receptacles. A cross section through a receptacle shows us the inside of a conceptacle: the opening of the conceptacle is an ostiole. Within the conceptacle, there is a globose oogonium that has been divided into many compartments. These are egg cells and are the result of meiosis within the oogonium. The branched antheridia produce sperm by meiosis, all of which have heterokont flagella. The haploid sperm are released and swim to fertilize an egg, forming a diploid zygote. The zygote grows by mitosis into a diploid thallus, which brings us back to the beginning. Diagram by Nikki Harris, CC-BY-NC with labels added by Maria Morrow.

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4.4: Diatoms

Diatoms, Phylum Bacillariophyta

Diatoms are another photosynthetic lineage of heterokonts that was derived from the secondary endosymbiosis of the red alga. Diatoms are an incredibly diverse group of unicellular organisms containing anywhere from 20,000 to 2 million species. These organisms are unicellular and surrounded by a **frustule**, a silica shell made from two distinct valves that enclose the plasma membrane. Frustules are amazingly intricate, covered with small pores in an arrangement specially adapted for capturing sunlight (Figure 4.4.1). They have golden chloroplasts due to the carotenoid pigment **fucoxanthin** (Figure 4.4.2).

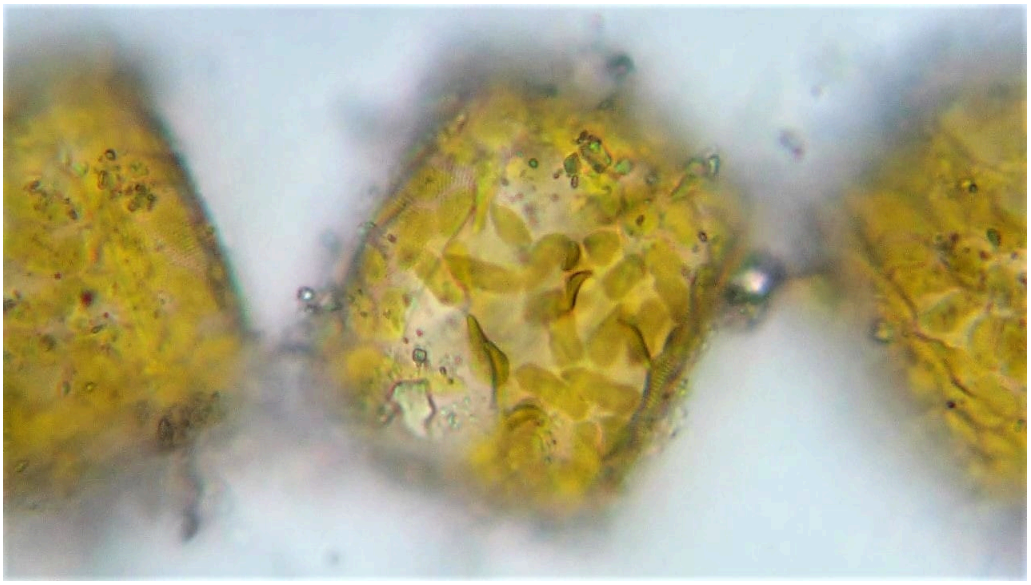


Figure 4.4.1: A diatom filled with golden organelles (chloroplasts). Photo by Vicente Franch Meneu, CC-BY-NC.

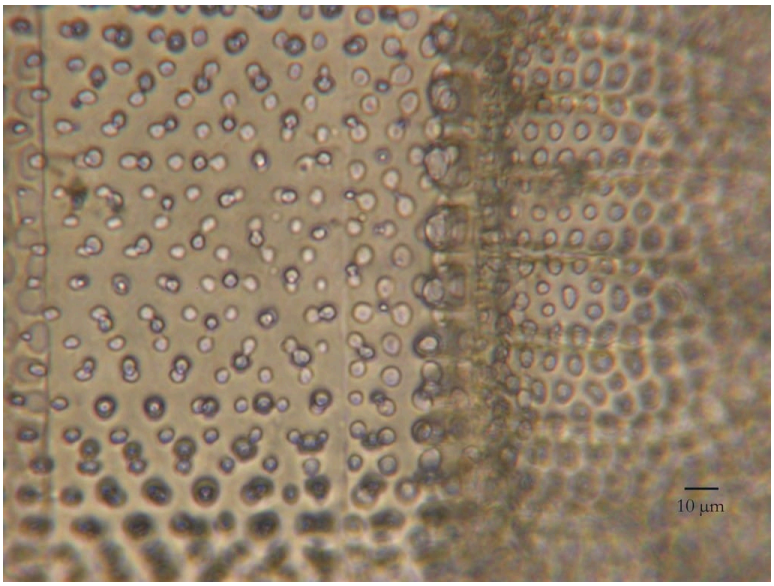


Figure 4.4.2: An *Isthmia nervosa* frustule showing the intricate pattern of pores. There appear to be multiple layers with a different pattern of pores to each. Photos by Lama Mark Webber, CC-BY-NC.

Morphology

We are still trying to figure out how to determine what a diatom "species" is and, so far, they have been classified based on the morphology of their frustules. Using this classification, historically there were two major groups of diatoms: **centric** (have radial symmetry) and **pennate** (have bilateral symmetry). These classifications have improved and increased in complexity, so here we will cover just the broad strokes. For a more in-depth look at current diatom morphological classification and fantastic images, check out this great website.

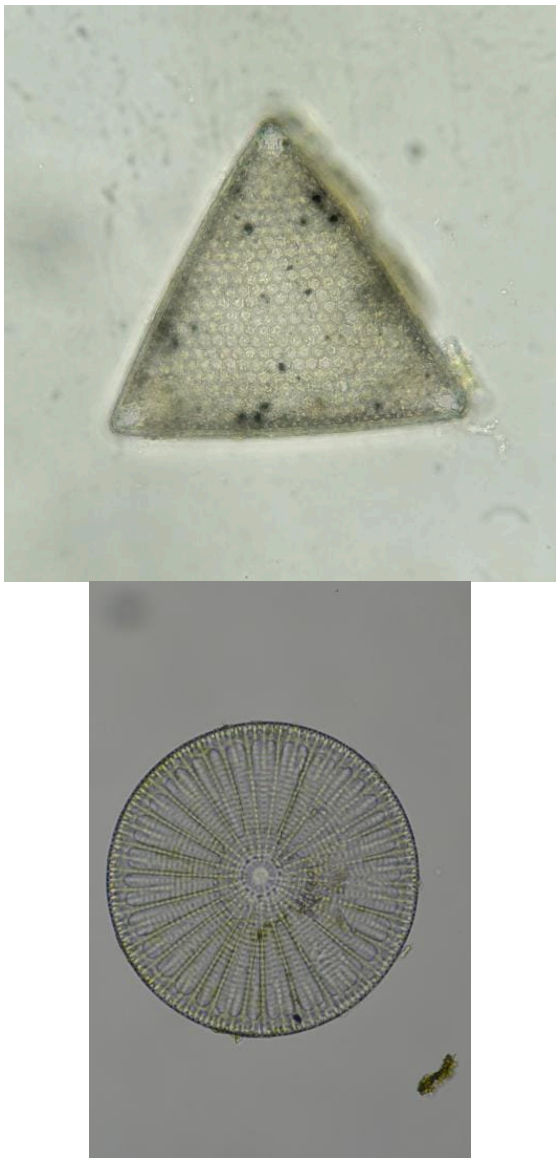


Figure 4.4.3: These images show centric diatoms. You can draw several lines of symmetry through each of these organisms. Centric is still a morphological description used for diatom genera. First: *Triceratium,* photo by Ryan Watson, CC-BY. Second: *Arachnoidiscus ehrenbergii* found on *Ulva,* photo by Randall, CC0.

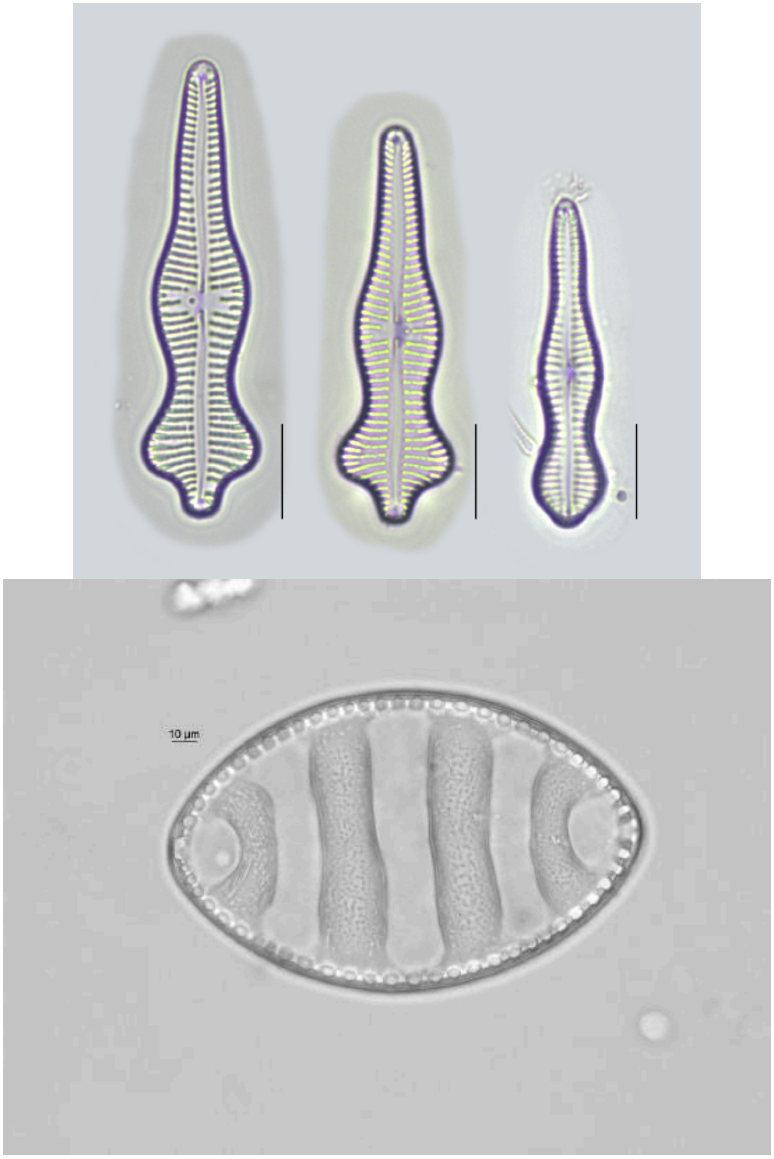


Figure 4.4.4: These images show "pennate" diatoms. This has historically classified many varieties of bilaterally symmetric diatoms which have since been further divided into better-described groups (some even asymmetrical). When considered three-dimensionally, only one line of symmetry can be drawn through this type of diatom. First: *Gomphonema acuminatum*, scale bar = 10 µm. Photo by Enviroethan, CC-BY-NC. Second: *Surirella undulata,* photo by Lila_137, CC-BY-NC.

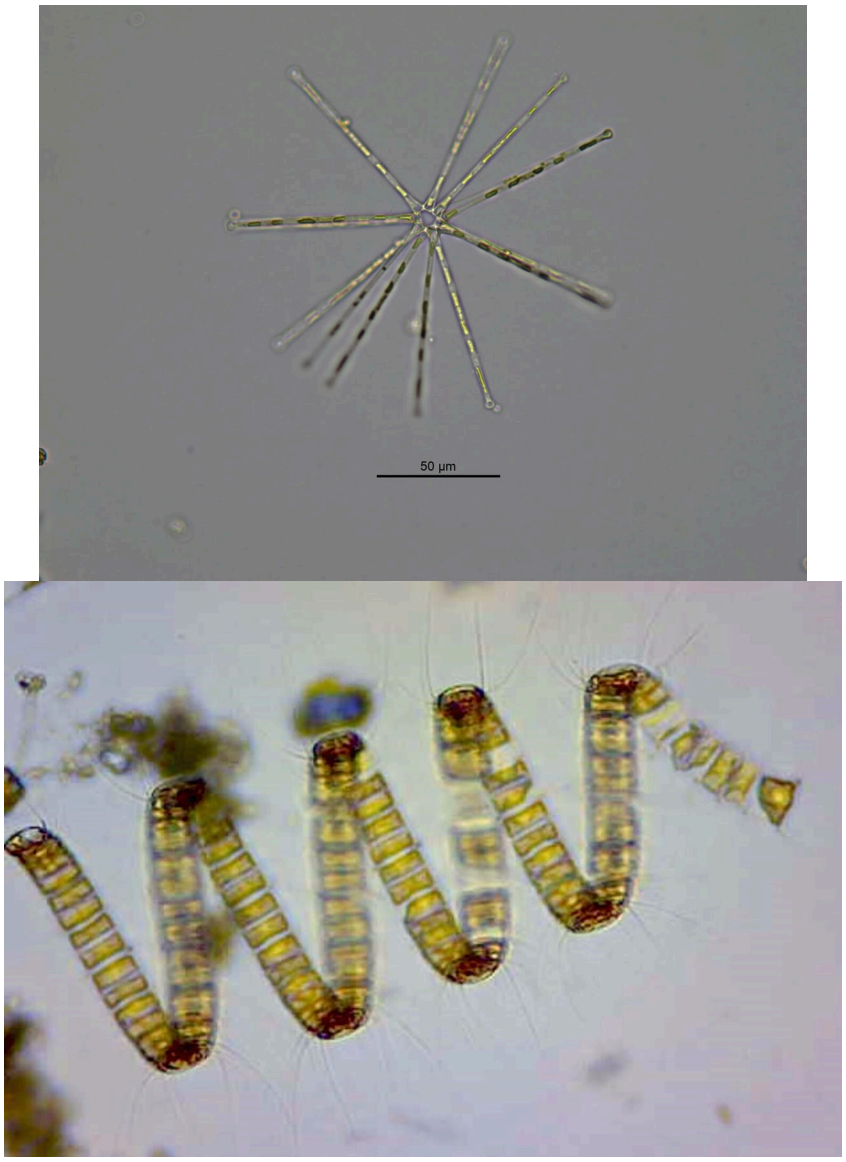


Figure 4.4.5: Many diatoms live in colonies, where unicellular diatoms adhere together to make a more complex structure. This may make it easier to float in the water column (raft-formation) or make it more difficult to be engulfed by predators The examples above show colonies of diatoms in a variety of shapes. Left: *Asterionella formosa*, a bilaterally symmetric diatom, forming a star-shaped colony. Photo by Mindy Morales, CC-BY-NC. Right: *Chaetoceros debilis*, a centric diatom forming a spiral-shaped colony. Photo by Sarka Martinez, CC-BY-NC.

Ecology

In addition to morphology, diatoms can also be classified by where they occur. Free-floating diatoms are **planktonic**. Diatoms attached to other organisms (like giant kelp) are **epiphytic**. **Benthic** diatoms tend to dwell toward the bottom of a body of water.

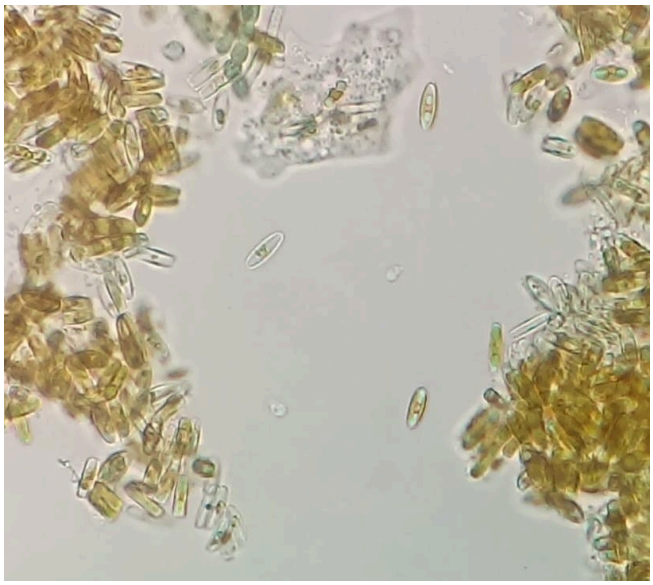


Figure 4.4.6: This image shows many diatoms, though they tend to be clumped on either side of the picture. When they are clumped together, they appear much more golden in color. This is due to their golden chloroplasts, which contain the carotenoid fucoxanthin. Photo by Melissa Ha, CC-BY-NC .

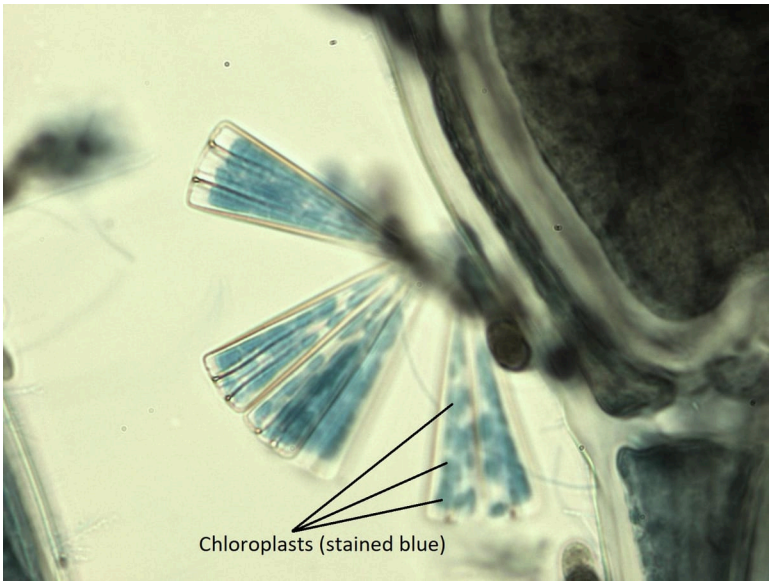


Figure 4.4.7: Epiphytic diatoms. These diatoms were photographed from a prepared slide of the red alga Polysiphonia. It is a fan-like colony of pennate diatoms that have attached to the surface of the red alga specimen used to make the slide. When the slide was made, it went through a staining bath. This turned the many golden chloroplasts within the diatoms blue. You can see the chloroplasts within the diatoms because the silica frustules are transparent, like glass. Photo by Maria Morrow, CC-BY-NC .

Reproduction

Diatoms primarily reproduce asexually by **binary fission**, similar to prokaryotes. During binary fission, the two valves of the frustule are separated and each new cell forms a new valve inside the old one. However, the new valve is always smaller. If diatoms only reproduce in this way, it results in a continual decrease in average size. When some minimal size is reached, this can trigger sexual reproduction. When diatoms sexually reproduce, they have a diplontic life cycle and produce a very large **auxospore**.



Figure 4.4.8: When diatoms sexually reproduce, they make a large structure called an auxospore. In this picture, the auxospore is a lightbulb-shaped cell located at the end of the colony of epiphytic diatoms. There are many golden chloroplasts visible each diatom. Photo by Maria Morrow, CC-BY-NC.

Diversity

YouTube Video

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

Video 4.4.1: This video shows some of the incredible diversity of diatom shapes and the amazing art Klaus Kemp makes with them. Sourced from YouTube.

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4.5: Red Algae

The red and green algae are descendents of the primary endosymbiosis event that resulted in the first chloroplast. Their plastids have two membranes, an inner membrane that was the cyanobacterial cell wall and an outer membrane from the organism that first engulfed it. The story of these algal groups is the evolutionary history of all plants.



Figure 4.5.1: The red algae are a fascinating group that have evolved a diversity of morphologies and strategies. This red alga, *Asterocolax gardneri*, is a parasite on other red algae. Note that it lacks the color characteristic of the *Rhodophyta*. Because it feeds off other algae, it does not need to make its own food via photosynthesis and so does not require photosynthetic pigments. Photo by Chloe and Trevor, CC-BY-NC.

Red Algae, Phylum Rhodophyta

Morphology

Red algae have a diverse range of morphologies. They can be unicellular or multicellular. Unicellular forms may live solitarily or as colonies. Multicellular forms can be filamentous, leafy, sheet-like, coralloid, or even crust-like (some examples in Figure 4.5.2 and Figure 4.5.3).



Figure 4.5.2: These images are all of multicellular red algae, which can range from filamentous (left) to "leafy" (center) to sheet-like (right). The red color is due to an abundance of the red pigment phycoerythrin, which gives this group red chloroplasts. Image on the left by Melissa Ha CC-BY-NC. Image on the right by Maria Morrow CC-BY-NC.



Figure 4.5.3: Above are examples of the strange coralline red algae. These have calcerous deposits in the cell walls that make the thallus hard, like a coral. These can take a variety of forms and are able to live at depths other algae cannot (over 500 feet deep for some!). The first image shows the thallus of a *Calliarthon tuberculosum* alga that has washed up on the beach. Having lost its characteristic pink color, the white, calcerous walls are more obvious. The second photo shows a crustose coralline red alga (species unknown to the author) forming pinkish blotches on a rock. There are a pair of forceps pointing at one of these blotches. First photo by Jennifer Rycenga, CC-BY-NC. Second photo by by Gsaunders, CC-BY-NC.

Cells of multicellular species are connected via incomplete cytokinesis, resulting in **pit connections**.

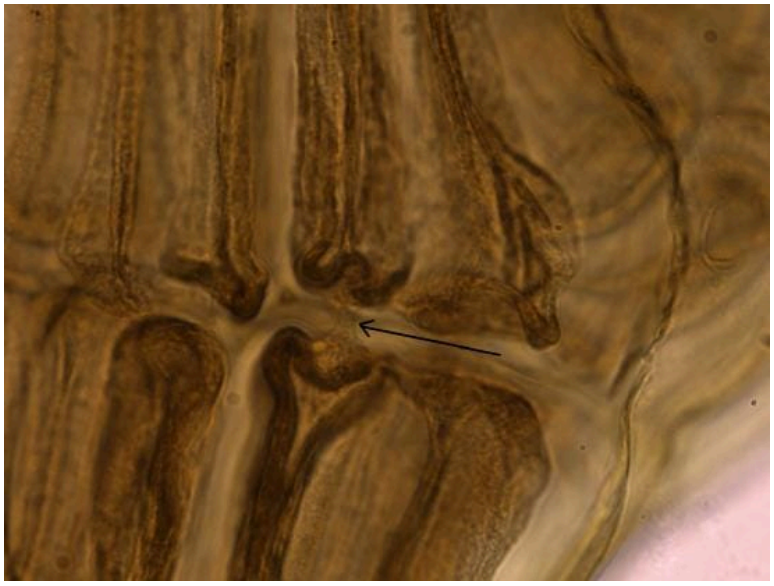


Figure 4.5.4: A pit connection between *Polysiphonia* cells. The images shows a channel connecting two adjacent cells, indicated by an arrow. This channel passes through the cell walls of both cells, as well as the middle lamellae. Photo by Maria Morrow CC-BY-NC.

Polysiphonia Life Cycle

Red algae have an alternation of generations life cycle that has an extra diploid stage: the carposporophyte. *Polysiphonia* is the model organism for Rhodophyta. The gametophytes of *Polysiphonia* are isomorphic (iso- meaning same, morph- meaning form), meaning they have the same basic morphology.



Figure 4.5.5: All stages of the *Polysiphonia* life cycle have the same basic morphology. If you were to see them without magnification, they would all look more or less like this: a small, red, finely branching thallus. The reproductive structures are used to differentiate the life stages: does it have spermatangia, cystocarps, or tetrasporangia? Any difference you see in coloration of the images in this section is due to staining. They would all appear this deep red color in an unstained slide. Photo by Gsaunders, CC-BY-NC.

Male Gametophyte

The male gametophyte has elongated structures that emerge from the tips of the thallus branches. These are **spermatangia**, where **spermatia** are produced by mitosis.

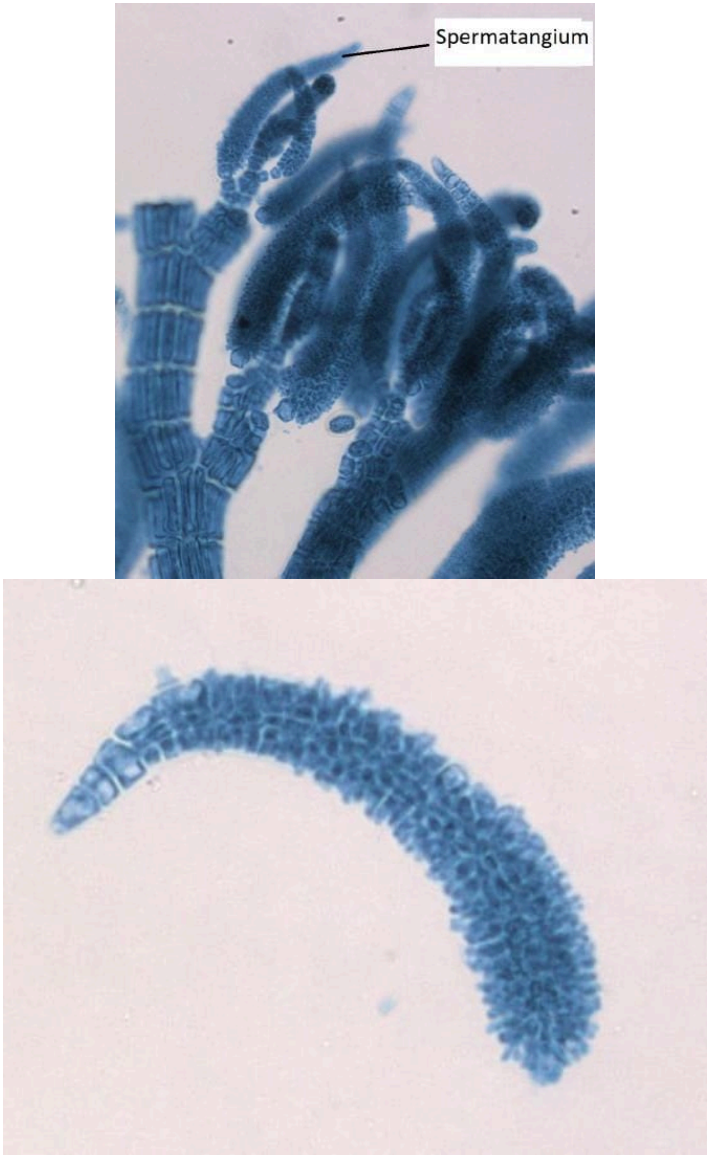


Figure 4.5.6: A *Polysiphonia* male gametophyte. In the image on the left, branches of the male gametophyte each terminate with several elongated structures that look almost like ears of corn. Each of these structures is a spermatangium. In the image on the right, a spermatangium is shown by itself, detached from the gametophyte. Cells in the spermatangum undergo mitosis to produce haploid, non-motile, unicellular gametes called spermatia. The image is not clear enough to distinguish individual spermatia. Photos by Maria Morrow, CC-BY-NC.

Female Gametophyte and Carposporophyte

The female gametophyte produces an egg that is contained within a structure called the **carpogonium**. This structure has a long, thin projection called a **trichogyne** (trich- meaning hair, -gyne meaning female). During fertilization, a spermatium fuses with the trichogyne and the nucleus of the spermatium travels down the tube to the **egg**. When the nucleus of the spermatium fuses with the egg, a **zygote** is produced. This zygote is retained and nourished by the female gametophyte as it grows.

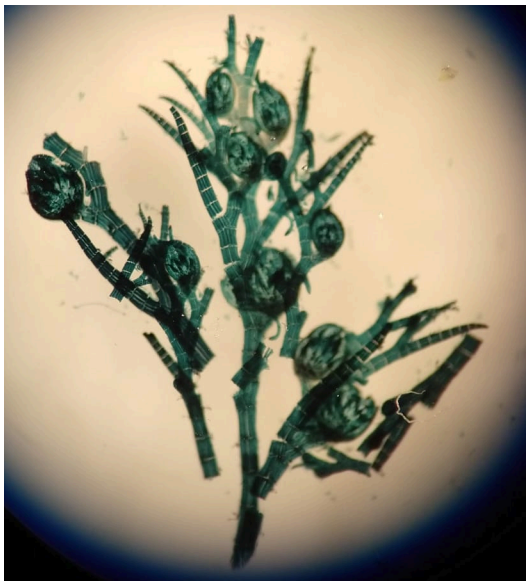


Figure 4.5.7: A female gametophyte from a prepared slide. During the slide-making process, the gametophyte broke into several pieces and was stained a deep blue-green. Normally, the thallus would appear red (see the tetrasporophyte thallus). There are many large, cup-like structures attached to the branches, indicating that the eggs in these regions were fertilized and a cystocarp developed. Photo by Maria Morrow, CC-BY-NC.

The globose structures you see growing from the female gametophyte thallus are called cystocarps. A **cystocarp** is composed of both female gametophyte tissue (n) and carposporophyte tissue (2n). The outer layer of the cystocarp, the **pericarp** (peri- meaning around) is derived from the female gametophyte and is haploid. The interior of the cystocarp consists of the **carposporophyte**, which is diploid, and produces structures called **carposporangia,** inside of which it produces **carpospores** by mitosis. All of these--carposporophyte, carposporangia, and carpospores--are diploid.

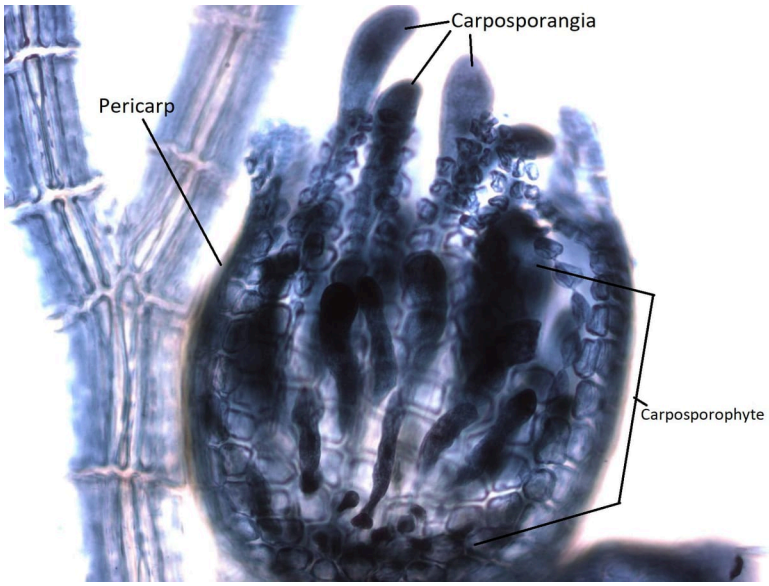


Figure 4.5.8: The image shows branches of the female gametophyte thallus on the left side. In the center, a globose cystocarp emerges from one of those branches. The cystocarp is composed of a haploid pericarp that forms the outside of the structure. The cells of the pericarp look blocky, almost scale-like. Within the pericarp, the tissues are diploid and belong to the carposporophyte. The carposporophyte is composed of many elongated carposporangia. Photos by Maria Morrow, CC-BY-NC.

Tetrasporophyte

The diploid carpospores are released into the ocean waters, where they will be carried on currents to another location. If a carpospore lands in an appropriate environment, it will grow by mitosis into a **tetrasporophyte** (2n).

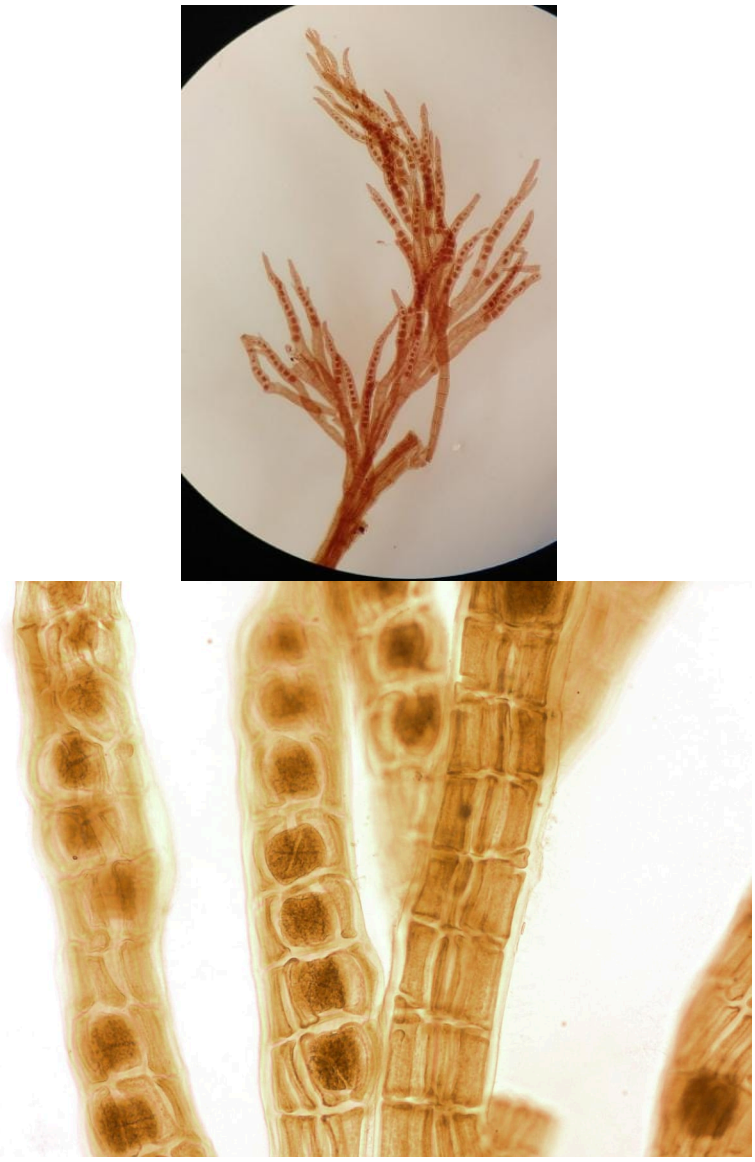


Figure 4.5.9: On the left, a full, unstained thallus of a tetrasporophyte is visible. It looks quite similar to both the male and female gametophytes, except the presence of round, darkened regions within the branches. These are the tetrasporangia, where meiosis will occur to produce haploid tetraspores. On the right, we see a magnified image of that same thallus and a more detailed view of the tetrasporangia within the branches. Photos by Maria Morrow, CC-BY-NC.

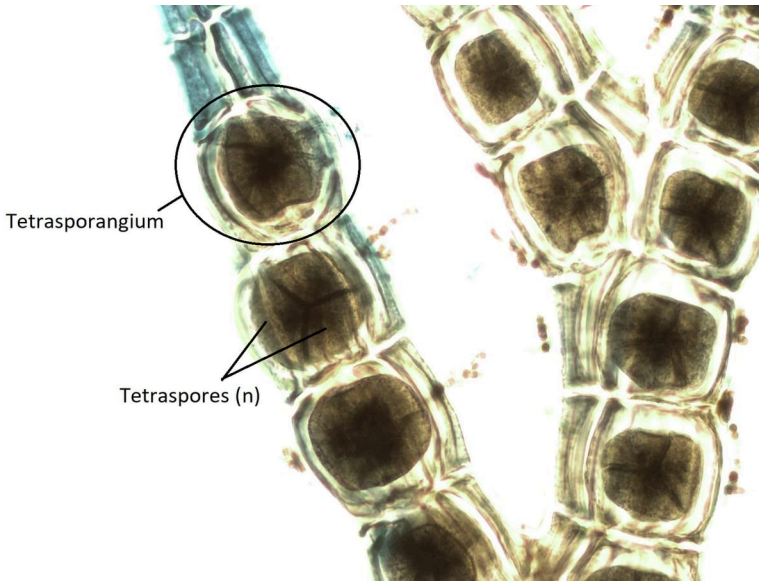


Figure 4.5.10: The image shows branches of the tetrasporophyte. Each of the compartments within the branches is filled with a globose tetrasporangium. In most of these, clear delineations can be seen where the tetrasporangium is dividing by meiosis into four distinct cells. These cells are haploid tetraspores. Photo by Maria Morrow, CC-BY-NC.

The tetrasporophyte produces **tetrasporangia** (2n) within the branches of the thallus. Each tetrasporangium produces four unique, haploid **tetraspores** by meiosis. Tetraspores (n) are released and will grow by mitosis into either male or female gametophytes, completing the life cycle.

Full Life Cycle Diagram

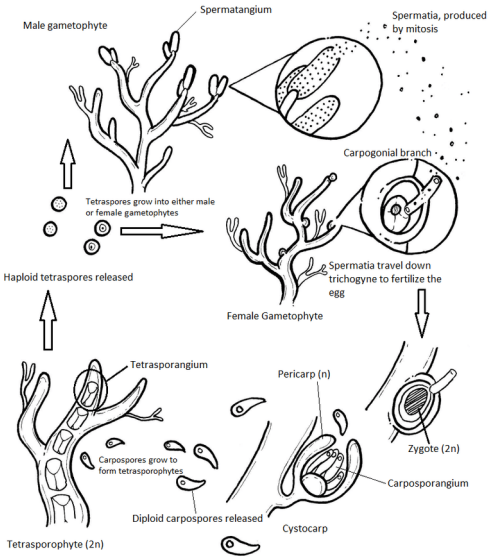


Figure 4.5.11: The alternation of generations life cycle of *Polysiphonia*. On the left side, in the center, there are four haploid tetraspores. These tetraspores grow by mitosis into haploid gametophytes, either "male" or "female". The male gametophyte produces spermatangia at the tips of its branches and these spermatangia produce haploid spermatia by mitosis. The female gametophyte produces carpogonial branches, which have an egg at the base and a long filament called a trichogyne that extends from the egg chamber. A spermatium fuses with a trichogyne and its nucleus travels down the trichogyne to fertilize the egg, making a diploid zygote. The zygote grows, still attached to the gametophyte, within a structure called the cystocarp. The cystocarp has an external layer called the pericarp that is formed from the female gametophyte's tissue (meaning it is haploid). Within the pericarp, the zygote has grown by mitosis into a carposporophyte making elongated carposporangia. Inside each carposporangium, diploid carpospores are produced by mitosis. Carpospores are released and grow by mitosis into tetrasporophytes. Within the branches of the tetrasporophyte, tetrasporangia are formed and undergo meiosis to produce four haploid tetraspores each. These tetraspores are released and we arrive back where we started. Diagram by Nikki Harris CC-BY-NC with labels added by Maria Morrow.

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4.6: Green Algae

The nature of the evolutionary relationships between the green algae are still up for debate. As of 2019, genetic data supports splitting the green algae into two major lineages: chlorophytes and streptophytes. The streptophytes include several lineages of green algae and all land plants. Streptophytes and chlorophytes represent a monophyletic group called Viridiplantae (literally "green plants"). Some green algal lineages have adapted to life on land, either inside of lichens or free-living (see Figure 4.6.1).



Figure 4.6.1: *Trentepohlia* is a genus of green algae that is found in terrestrial environments. It forms fluffy orange colonies on trees and is a photobiont in many lichens. One might not know they were looking at a green algae, due to the orange pigmentation. However, green algae have carotenoids. These terrestrial green algae produce an abundance of carotenoids, perhaps for protection from sun damage. Photo by Scott Loarie, CC0.

General Morphology

Similar to red algae, green algae can be unicellular or multicellular. Many unicellular species form colonies.

Unicellular

Unicellular species will have two whiplash flagella.

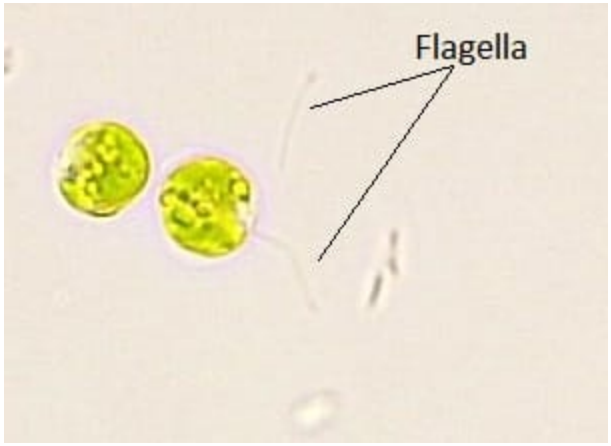


Figure 4.6.2: This image shows two unicellular green algae from the genus *Chlamydomonas*. They appear green due to the loss of phycobilins and evolution of chlorophyll b. They each have two whiplash flagella, though these are only visible on one of them in the picture. Photo by Melissa Ha, CC-BY-NC .

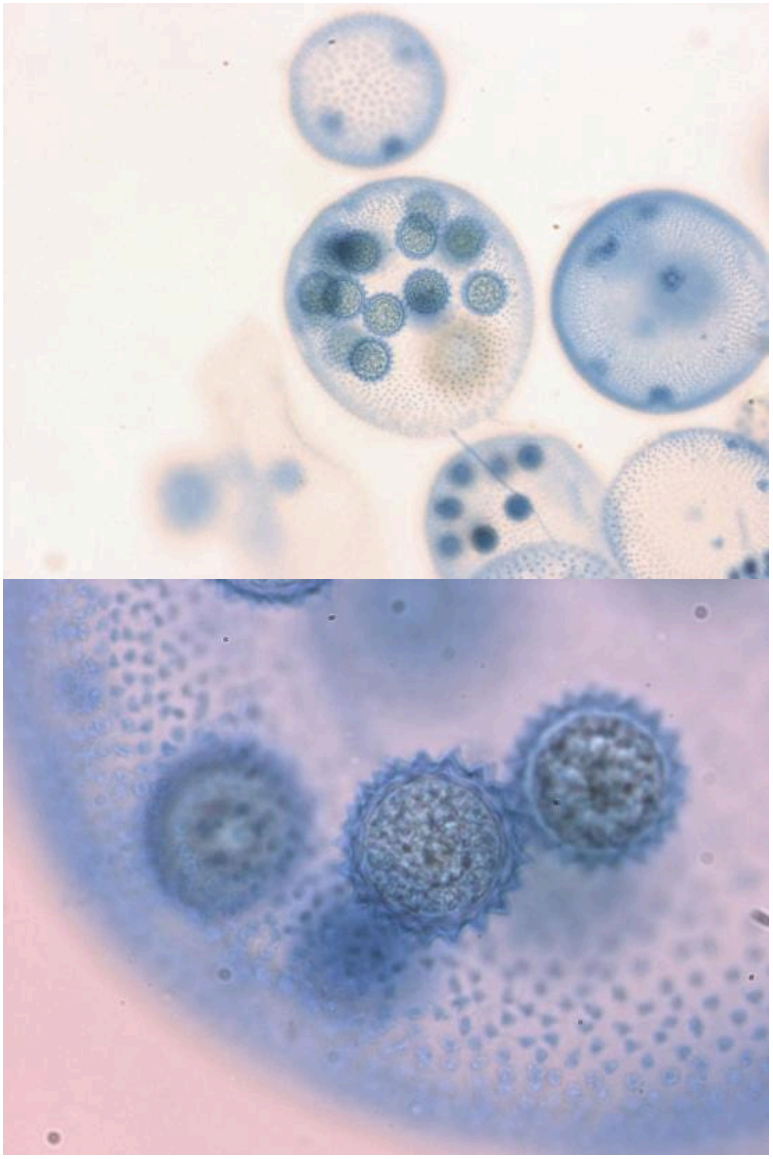


Figure 4.6.3: Volvox is a genus of unicellular freshwater green algae that form spherical colonies. Each individual beats its flagella to the exterior of the ball-like formation. Within the colony, new colonies can be formed by asexual reproduction. These internal colonies beat their flagella to the interior. When sexual reproduction occurs, a thick-walled, desiccation-resistant zygote forms, as seen in the image on the right. Photos by Maria Morrow, CC BY-NC.

YouTube Video

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

Video 4.6.1: This video shows how sexual reproduction occurs in the colonial green alga *Volvox*. Sourced from YouTube.

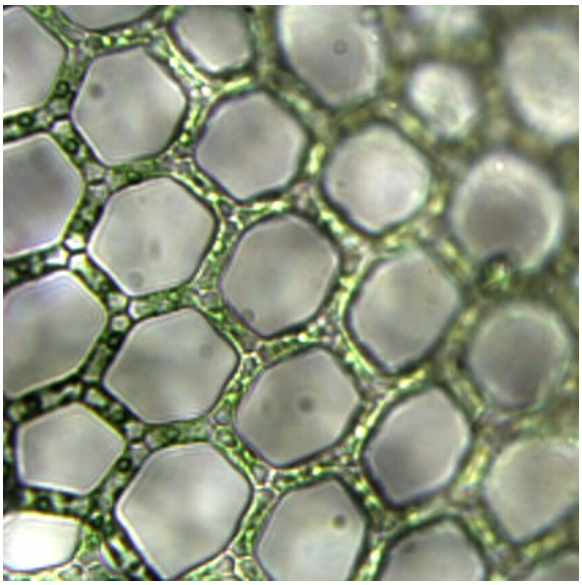


Figure 4.6.4: Hydrodictyon reticulatum is another colony-forming species. Individual, unicellular algae form together to create a complex colony structure. These algae are commonly called water nets. Photo by louiselewis, CC-BY-NC.

Multicellular

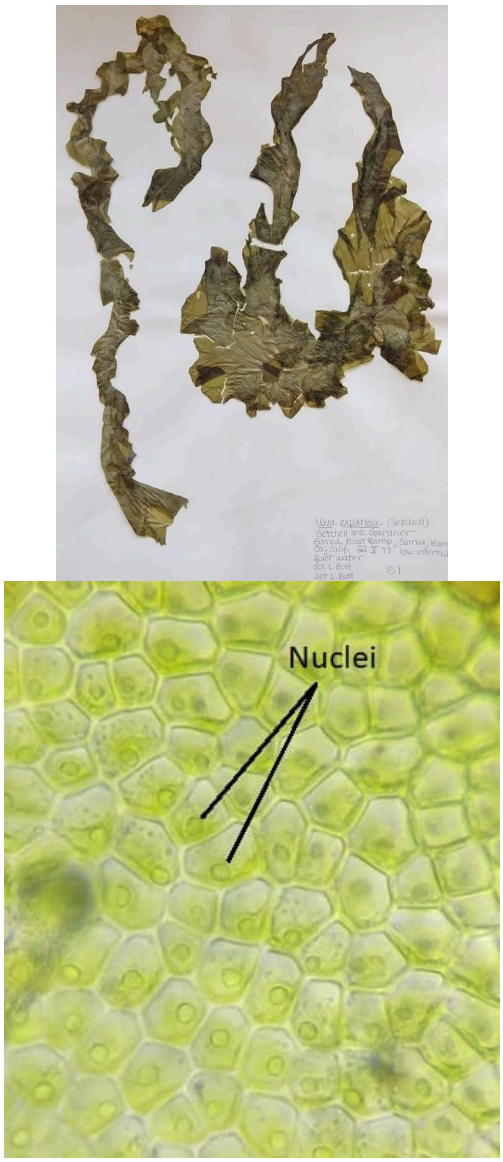


Figure 4.6.5: Ulva is a genus of multicellular marine green algae that forms flat sheets of cells. In the image on the left, there is a pressed sample of an *Ulva expansa* thallus that is serving as an herbarium specimen. In the image on the right, a piece of an *Ulva* thallus is being viewed through a microscope. Each cell contains green chloroplasts and a large nucleus, two of which are labeled in the image. Photos by Maria Morrow, CC BY-NC.



Figure 4.6.6: Chaetomorpha coliformis, a marine green alga formed from chains of cylindrical cells (commonly called sea emeralds). Photo by Svenjah Heesch, CC-BY-NC.

Oedogonium is a genus of filamentous green algae. Some species of *Oedogonium* are nannandrous. In nannandrous species, the antheridia are small, elongate filaments, usually produced on a different filament than the oogonium. Other species are macrandrous and the antheridia are produced as stacked cells within the same filament as the oogonium.

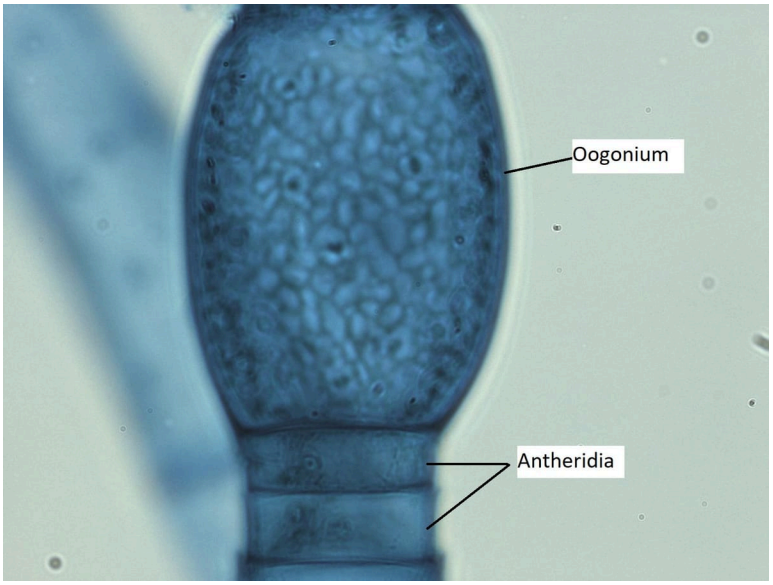


Figure 4.6.7: An oogonium and two antheridia of a macrandrous *Oedogonium*. The large, spindle-shaped oogonium is shown on top of the antheridia. This oogonium is not yet fertilized, so no oospore is visible. The antheridia are smaller cells within the filament, below the oogonium. Two can be seen in this image. Note: This is an image of a stained slide, so this normally green alga appears blue. Photo by Maria Morrow, CC BY-NC.

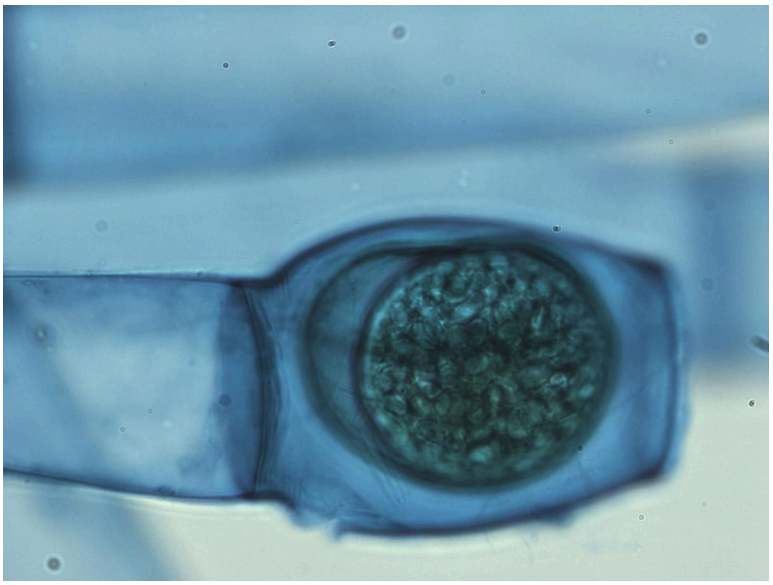


Figure 4.6.8: An oogonium of a macrandrous *Oedogonium* with a large, fertilized oospore inside. In an unfertilized oogonium, the inside looks evenly granular, as seen in Figure 4.6.7 above. Once it is fertilized, the contents resolve into a distinguishable, spherical structure: the oospore. Photo by Maria Morrow, CC BY-NC.

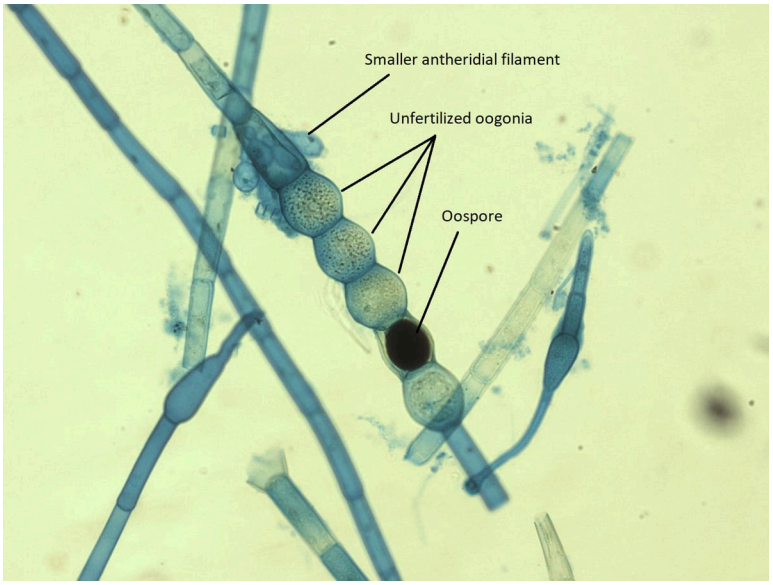


Figure 4.6.9: A nannandrous *Oedogonium* sp. There are several oogonia occuring in a row on a single filament. Many small antheridia are reaching toward those oogonia. The fourth of the five oogonia is fertilized and has a large, dark oospore inside. Photo by Maria Morrow, CC BY-NC.

Figure 4.6.10: A close up of the sexual structures of a nannandrous *Oedogonium* sp. The oogonium is located at the end of the filament and, in this case, is almost lemon-shaped. It is unfertilized, still appearing evenly granular throughout. Many small antheridia are reaching up to try to fuse with the oogonium to fertilize it. These can be seen on the sides of the filament below the oogonium and look like upside down blue bowling pins. Photo by Maria Morrow, CC BY-NC.

Spirogyra Life Cycle

Though green algae display a diversity of life cycles, many have a haplontic life cycle. A model organism for the green algae is *Spirogyra*. *Spirogyra* is a unicellular green algae that grows in long, filamentous colonies, making it appear to be a multicellular organism. Even though it is technically unicellular, its colonial nature allows us to classify its life cycle as haplontic. In the haploid vegetative cells of the colony, the chloroplasts are arranged in spirals, containing darkened regions called **pyrenoids** where carbon fixation happens. Each haploid cell in the filament is an individual, which makes sexual reproduction between colonies an interesting process.

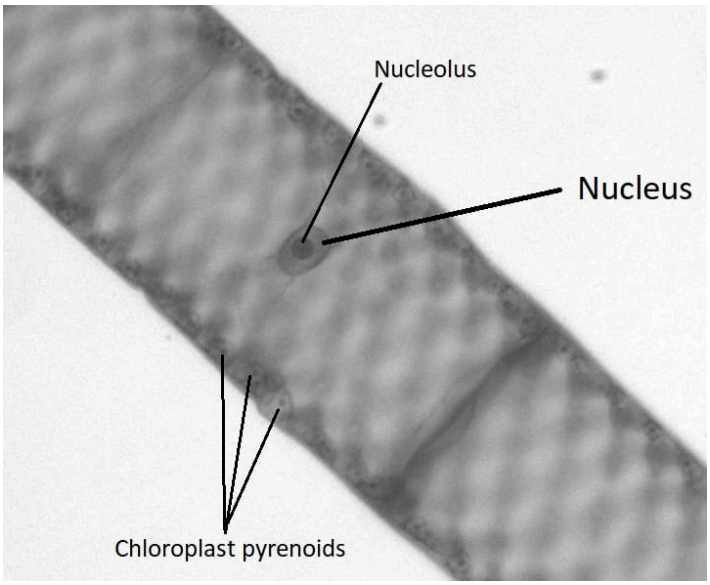


Figure 4.6.11: A vegetative cell in a *Spirogyra* colony. The nucleus is visible in the center of the cell, including a large, dark nucleolus. The chloroplasts are arranged in spirals around the cell and have dark regions called pyrenoids where carbon dioxide is fixed. Photo by Maria Morrow, CC BY-NC.

When two colonies of Spirogyra meet that are of a complementary mating type (+/-), sexual reproduction occurs. The two colonies align, each cell across from a complementary cell on the other filament. A **conjugation tube** extends from each cell in one colony, inducing formation of a tube on the cells in the other colony. The conjugation tubes from each colony fuse together.

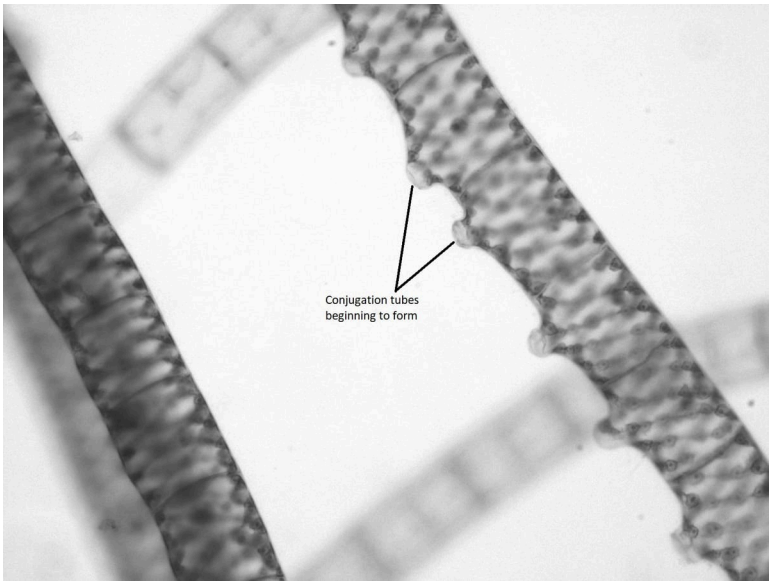


Figure 4.6.12: Spirogyra forming conjugation tubes. There are two vegetative colonies that are about to interact. The colony on the right has chemically sensed the presence of the colony on the right and has started to grow projections in the cell walls of each cell in the colony, extending them toward the other colony. These are the beginnings of conjugation tubes. Photo by Maria Morrow, CC BY-NC.

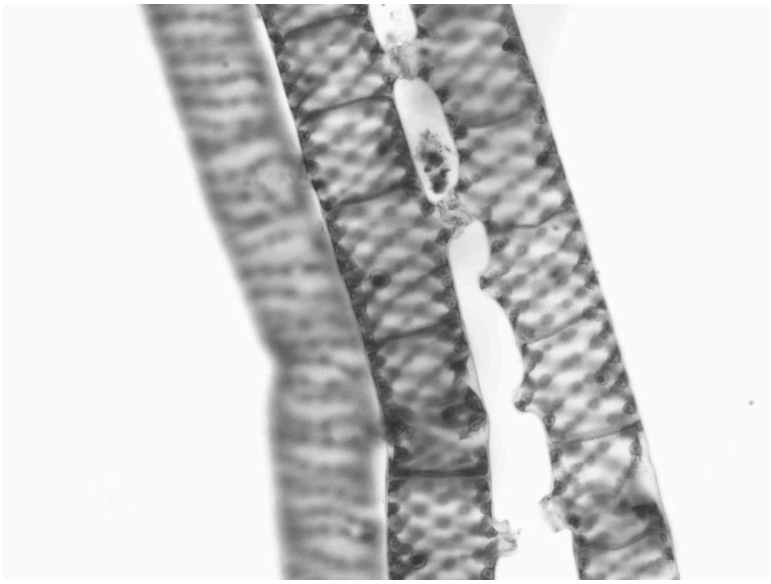


Figure 4.6.13: Spirogyra conjugation tubes meet. These two colonies are both forming conjugation tubes toward each other. Two sets of cells near the top of the image have successfully fused conjugation tubes, forming a connection between the two different organisms. Photo by Maria Morrow, CC BY-NC.

The contents of one cell will move through the conjugation tube and fuse with the contents of the complementary cell, resulting in a diploid **zygote**.

Figure 4.6.14: Movement of the cytoplasm from one colony to another in Spirogyra. The cytoplasm from one of the cells in the colony on the right has almost completely transferred through the conjugation tube and into the colony on the left. Photo by Maria Morrow, CC BY-NC.

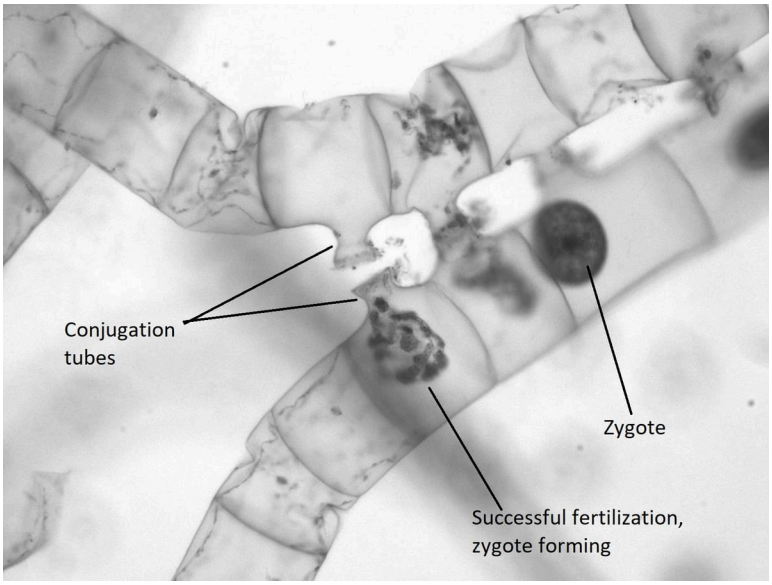


Figure 4.6.15: Cells in various stages of conjugation. Of the cells that have formed conjugation tubes and connected, the one farthest to the left has just recently finished the transfer and fusion of its cytoplasm, but the zygote hasn't fully formed yet. In the cell on the far right, there is a fully formed zygote. It is dark in color and has thick walls. The chloroplasts are not individually distinguishable within it. Photo by Maria Morrow, CC BY-NC.

The zygote appears as a large, egg-like structure contained within the complementary cell. It has a thick wall that provides resistance to desiccation and cold, allowing colonies of *Spirogyra* to overwinter, when needed. The other colony is now a filament of empty cells that will be broken down by some decomposer.

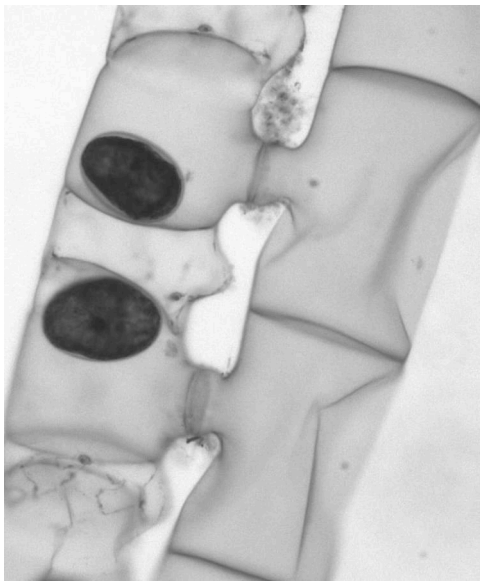


Figure 4.6.16: Completed conjugation in two sets of cells. There are two cells in the colony on the left with fully formed, thick-walled zygotes. The colony on the right now has two empty cells, because they have transferred their cytoplasmic contents into the colony on the left. Photo by Maria Morrow, CC BY-NC.

When conditions are right, the zygote undergoes meiosis to produce another vegetative colony of haploid cells.

Full Life Cycle Diagram

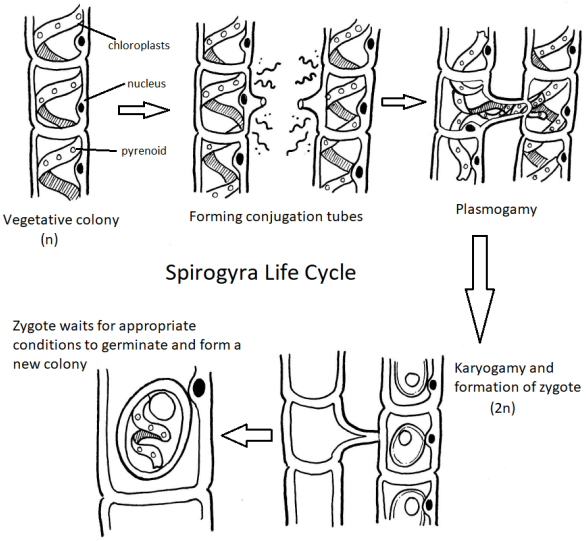


Figure 4.6.17: The haplontic life cycle of *Spirogyra*. Starting from the upper left corner and moving right, there is a single haploid vegetative colony of *Spirogyra*. The chloroplasts are drawn in as a single ribbon with circles representing pyrenoids. Each cell has a large, dark nucleus. Moving to the right, two colonies of complementary mating types begin to interact with each other through chemical signals and start forming conjugation tubes. In the next frame, the conjugation tubes have connected and the contents of one cell begins to transfer through the conjugation tube into a cell in the other colony. This is plasmogamy. Karyogamy occurs when the two nuclei fuse together and the diploid zygote is formed. This zygote waits for appropriate conditions to germinate, undergo meiosis, and form a new haploid colony. Diagram by Nikki Harris, CC BY-NC with labels added by Maria Morrow.

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5: BRYOPHYTES

Bryophytes arose in a period of Earth's history before soils had formed. The terrestrial surface was rocky and consisted primarily of crusts (microbial mats) composed of assemblages of prokaryotes. The exposure to sunlight would have been intense relative to the buffer provided by water. In addition, being surrounded by water would provide regulation of surrounding temperature and structural support. As green algae began to colonize the terrestrial surface, at least one of these lineages accumulated adaptations that were favorable to living on land--a waxy **cuticle** to prevent water loss, desiccation-resistant dispersal propagules called **spores**, and retention and feeding of the developing zygote. This lineage of green algae evolved into the ancestor of the bryophytes.

This evolutionary group includes liverworts, mosses, and hornworts. These plants do not have true roots to absorb water, nor do they have vascular tissue to transport that water to other regions of the plant. Because of this, bryophytes tend to grow prostrate (close to the surface they are growing on) and stay quite small. They do not have roots, but they have projections to anchor them to the surface, called **rhizoids**. They also tend to grow in moist areas where there is access to water and are reliant on water for the dispersal of gametes and fertilization. There are approximately 23,000 described species of bryophytes, most of them belonging to the mosses.



Figure 5.1: Liverworts, phylum Marchantiophyta, can be either leafy (like the one on the left) or thalloid (like the one on the right). First photo by Maria Morrow, CC BY-NC. Second photo by Иван Матершев, CC-BY-NC-SA.



Figure 5.2: Mosses, phylum Bryophyta, are always leafy. Photo by Maria Morrow CC BY-NC.



Figure 5.3: Hornworts, phylum Anthoceratophyta, are always thalloid. Male gametophyte of *Phaeoceros laevis*. Photo by georgeg, CC-BY-NC.



Figure 5.4: Root-like projections called rhizoids emerge from gametophytes. In the image, these are shown as transparent filaments extending from the underside of a green, thalloid gametophyte. Photo by Yuval, CC-BY-NC.

5.1: Hornworts

5.2: Liverworts

5.3: Mosses

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5.1: Hornworts

Hornworts, Phylum Anthocerotophyta



Figure 5.1.1: Hornworts growing in a cluster. The gametophytes are the leafy green material growing closer to the surface. The sporophytes are the emergent structures. The appearance of the sporophytes is what gives the hornworts their name. Photo by Maria Morrow, CC-BY-NC.

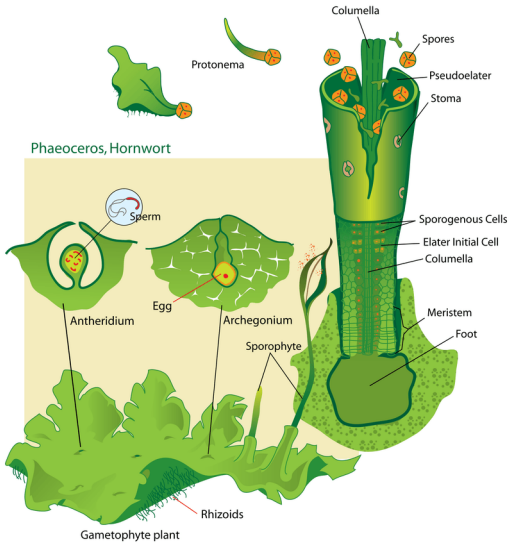


Figure 5.1.2: The *Phaeoceros* life cycle. The thalloid gametophyte is a flat flap of green, photosynthetic tissue with rhizoids extending from the underside. Within the thallus, an embedded antheridium produces sperm with two flagella and an embedded archegonium produces a single egg. When a sperm fertilizes an egg, a sporophyte composed of a single thin sporangium grows from the archegonium. At the base of the sporangium is a foot. A collumella extends up the center of the sporangium with long pseudoelaters aiding in spore dispersal. Notably, there are stomata on the sporangium. Diagram by derivative work: Smith609 (talk)Hornwort_life_cicle_svg_diagram.svg: Mariana Ruiz user:LadyofHats, CC BY 3.0, via Wikimedia Commons.

Gametophyte Morphology

Hornwort gametophytes are exclusively thalloid, often with compartments of mutualistic cyanobacteria from the genus *Nostoc*. Cells within the gametophyte are **monoplastidic**, containing one large chloroplast in each cell. On the exterior of the thallus,

simple pores allow for gas exchange (no guard cells, meaning pores are permanently open).

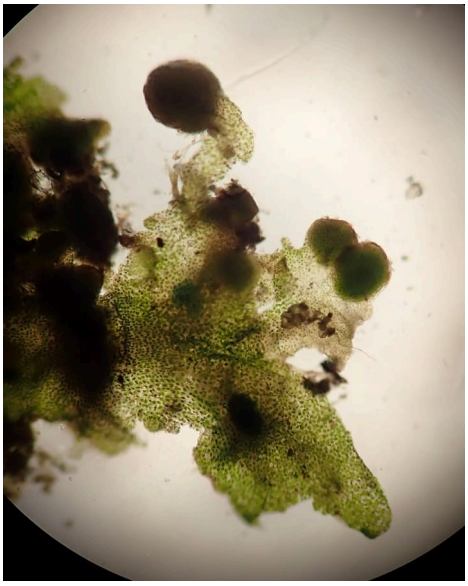


Figure 5.1.3: This image of part of a *Phaeoceros proskaueri* thallus shows the cells of the gametophyte each containing a single large plastid (monoplastidic). Photo by Amanda Heinrich, CC-BY-NC.

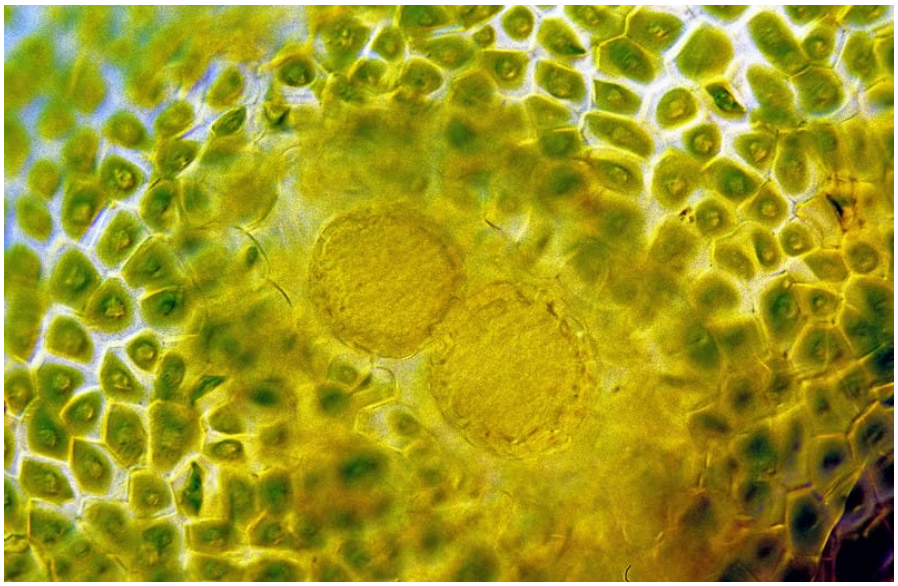


Figure 5.1.4: Antheridia on the male gametophyte of Phaeoceros. They are formed in a depression (crypt) within the thallus. Note the monoplastidic condition of the cells. Photo by George Shepherd, CC BY-NC-SA.

Sporophyte Morphology

Hornwort sporophytes are comprised of a linear sporangium that lacks a seta. It grows from a **basal meristem**, meaning the cells at the apex are the oldest. When you see the sporangia mature, this becomes more obvious, as the tip dries out first and dehisces (splits apart) to release the spores. Unlike the gametophyte, the sporophyte possesses true stomata for gas exchange.

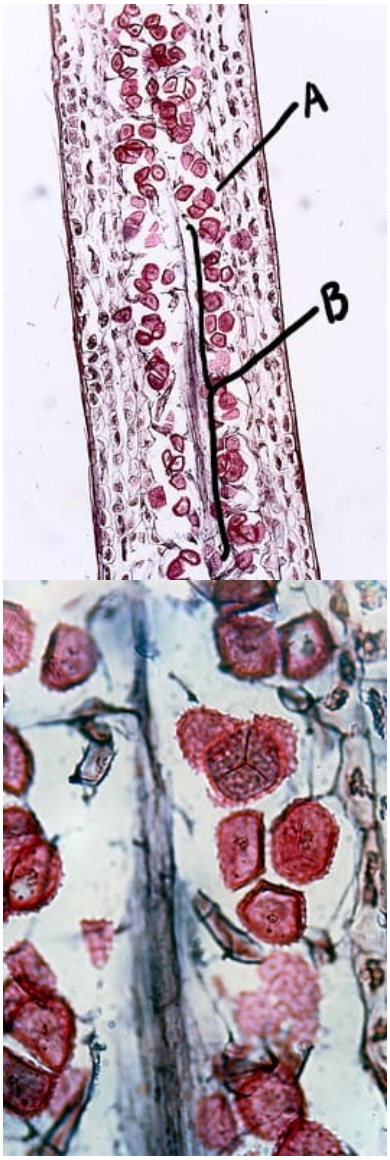


Figure 5.1.5: A cross section through an *Anthoceros* sporophyte. Spore tetrads (A) fill the sporangium and surround the central columnella (B). The second photo shows the spore tetrads at a higher magnification. Together, the four spores make a sphere. When separated, they have one rounded side and several flat sides Photos by George Shepherd, CC BY-NC-SA with labels added by Maria Morrow.

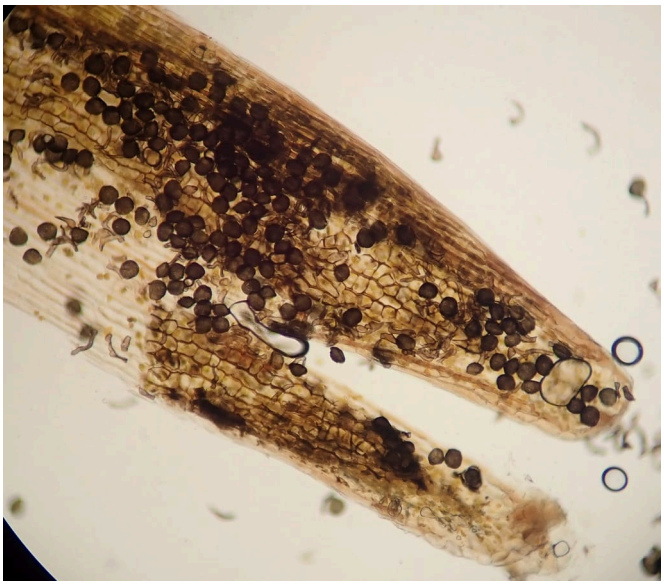


Figure 5.1.6: The tip of a sporophyte dehiscing (splitting down the center, here). There are many large spores visible inside the sporangium. Photo by Amanda Heinrich, CC-BY-NC.

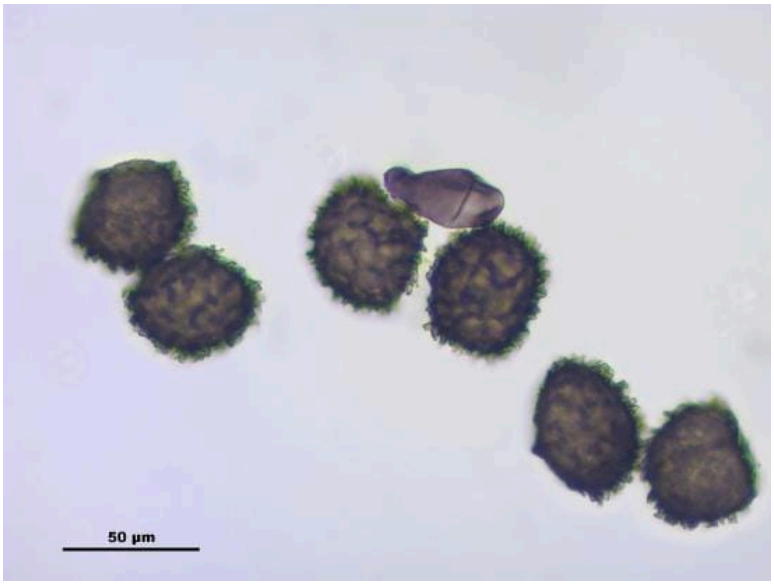


Figure 5.1.7: The large, ornamented spores of *Anthoceros agrestis*. Photo by HermannSchachner, CC0, via Wikimedia Commons.

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5.2: Liverworts

Liverworts, Phylum Marchantiophyta

Gametophyte Morphology

There are two distinct type of liverworts: leafy liverworts and thalloid liverworts. **Leafy liverworts** have leaves arranged in a flat plane with a set of smaller underleaves.



Figure 5.2.1: The leafy liverwort Porella has larger leaves running opposite each other down either side of the stem, making the liverwort look flat. The photo on the right shows a microscopic view of the leaves. Notice that there is no central rib on these leaves, which helps distinguish leafy liverworts from mosses. Photo on the left by Maria Morrow CC-BY-NC. Photo on the right by Rafael Medina, CC-BY-NC.

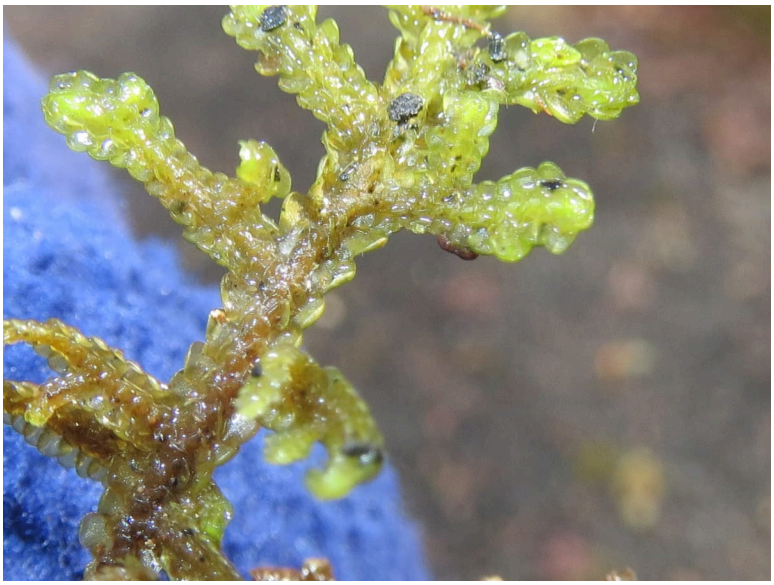


Figure 5.2.2: Another distinguishing feature of leafy liverworts are their underleaves. These are smaller, scale-like leaves that run along the center of the thallus on the underside. This image shows the underside of a *Porella navicularis* thallus covered with smaller underleaves. Photo by Howard Bruner, CC-BY-NC.

Thalloid liverworts have no leaves and their gametophytes look more similar to hornwort gametophytes. Another similarity to hornworts is the presence of simple pores for gas exchange (no guard cells, meaning pores are permanently open). Unlike hornworts, liverwort cells have multiple chloroplasts. Many liverwort gametophytes produce asexual clones called **gemmae**.



Figure 5.2.3: The thalloid liverwort Lunularia has crescent-shaped gemmae cups. Several of these are present in the image above. The small green pebble-looking structures within them are asexual clones of the thallus called gemmae. Liverwort gametophytes do not have stomata. Instead, the thallus is covered in raised bumps where simple pores are located. Photo by Maria Morrow CC-BY-NC.

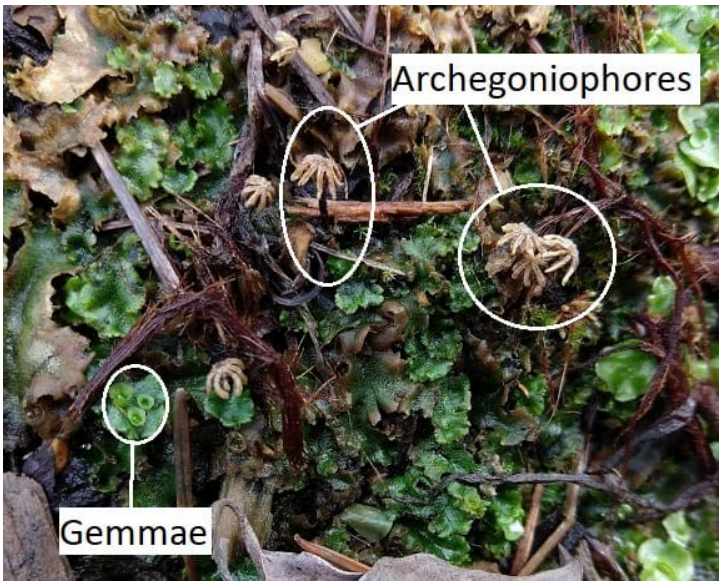


Figure 5.2.4: The thalloid liverwort Marchantia has many complex structures. A group of gemmae cups are circled in the lower left corner. There are several brown palm tree-like structures circled and labeled as archegoniophores. These are the part of the gametophyte where archegonia are produced. When fertilized, the sporophyte will grow within the archegonium and emerge on the underside of the archegoniophore. Photo by Maria Morrow CC-BY-NC.



Figure 5.2.5: This image shows structures from both gametophytes. The antheridiophore is on the left, with a flat surface that water can splash onto. This carries sperm from the embedded antheridia to other sufaces (hopefully, to an awaiting egg). On the right, there is a fertilized archegoniophore. The palmtree-like branches have lifted upward. Beneath them, yellow sporangia emerge at the tips of transparent setae. Photo by Felix Riegel, CC-BY-NC.

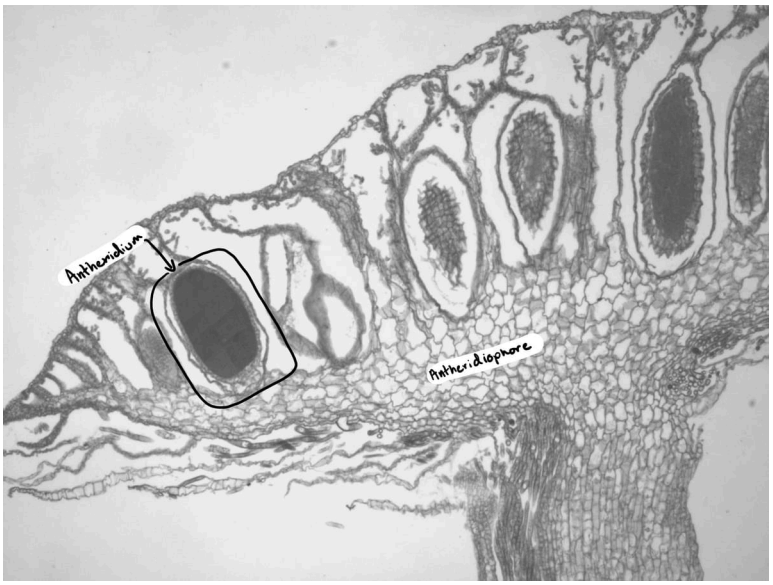


Figure 5.2.6: A micrograph showing a cross section through the top of an antheridiophore. An antheridium has been indicated with a black box. Inside the antheridium, sperm will be produced (in the darkened area), though none are visible here. Photo by Maria Morrow CC-BY-NC.

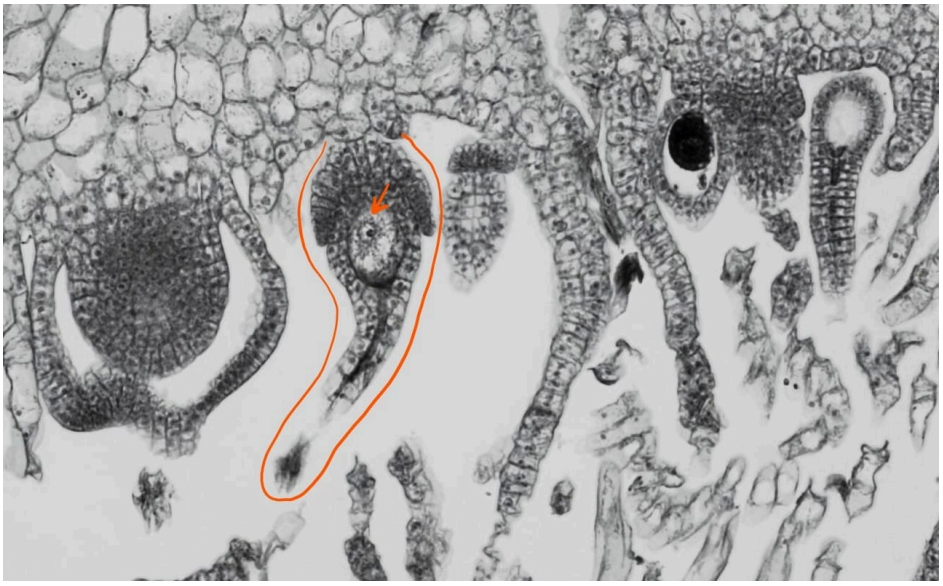


Figure 5.2.7: A close up of an archegonium (outlined in orange) on the underside of an archegoniophore. The egg within the archegonium has been indicated by an arrow. Photo by Maria Morrow CC-BY-NC.

Sporophyte Morphology

Liverworts produce a single sporangium (capsule) at the end of a seta, which is often fragile and transparent. The sporangium dehisces, splitting into four pieces. In thalloid liverworts, the sporophyte may emerge directly from the thallus or, as is the case with the genus Marchantia, from complex structures called antheridiophores and archegoniophores. In this case, the sporophytes emerge from the underside of the archegoniophore.

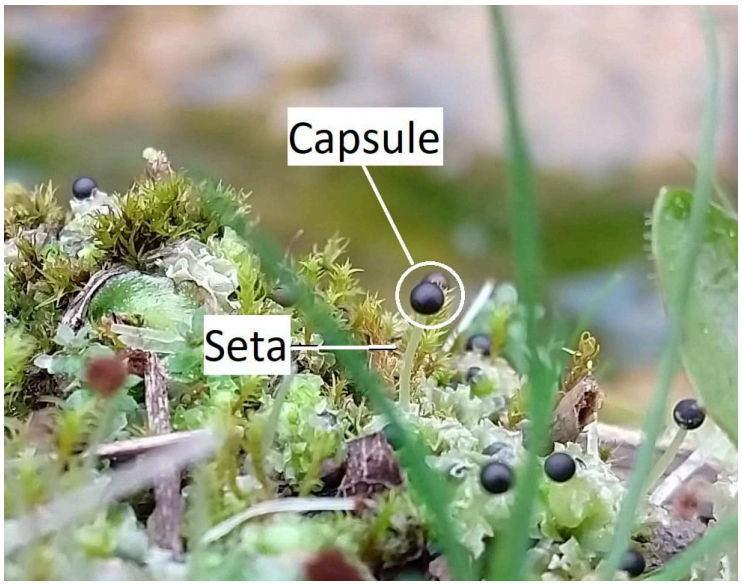


Figure 5.2.8: Liverwort sporophytes are comprised of a stalk called the seta and, at the top of the seta, a single capsule where spores are produced. In this liverwort (perhaps a Fossombronia), the sporophytes are short and stout with globose capsules. Photo by Maria Morrow CC-BY-NC.



Figure 5.2.9: Some liverwort sporophytes have long, transparent setae, making them look almost like molds. The capsules of the sporophytes in the image are also elongated. They will dry out and dehisce, pealing back into four triangular pieces and releasing the spores. Photo by Maria Morrow CC-BY-NC.

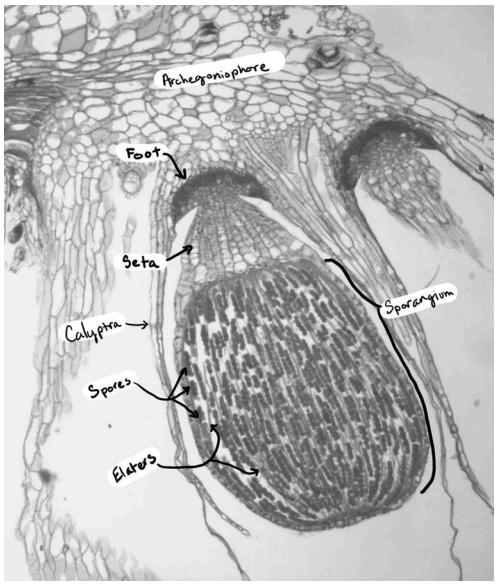


Figure 5.2.10: A sporophyte produced on the underside of an archegoniophore. It emerges upside-down and will eventually become more horizontal as the branches of the archegoniophore raise upward. The sporophyte attaches to the gametophyte at a region called the foot. It grows within the archegonium, now labeled as the calyptra. From the foot a short seta emerges, topped by a large sporangium. The sporangium is filled with rows of haploid spores produce by meiosis. Between these rows of spores, long elaters await the dehiscence of the sporangium to aid in spore dispersal. Photo by Maria Morrow CC-BY-NC.

Marchantia Life Cycle

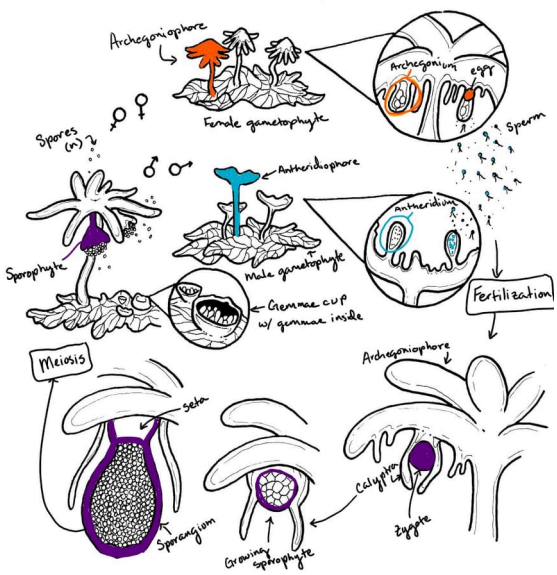


Figure 5.2.11: The *Marchantia polymorpha* life cycle. Starting with meiosis (left, center): Meiosis produces haploid spores which will grow by mitosis into either male or female gametophytes. Either of these gametophytes can produce **gemmae cups**--structures that hold asexually produced clones of the gametophyte (**gemmae**). Male gametophytes produce tall structures with flat tops called **antheriodiophores**. Many **antheridia** are embedded in the flat top of the antheridiophore. Antheridia produce biflagellate **sperm** by mitosis. Female gametophytes produce palm tree-like structures called **archegoniophores**. These archegoniophores produce **archegonia** on the underside of the 'branches', each with a single **egg** that was produced by mitosis. When water hits the flat top of the antheridiophore, it can splash sperm onto a female gametophyte. If the sperm are able to swim through the water to an egg, fertilization occurs producing a diploid **zygote**. The zygote grows into a **sporophyte** from within the archegonium. The remaining archegonial tissue is called the **calyptra**. A mature sporophyte will have a sterile stalk called a **seta** and a **sporangium** containing cells that will undergo meiosis to make haploid spores. Within the sporangium (not pictured), long twisted structures called **elaters** help disperse the spores aerially. Drawing by Nikki Harris CC-BY-NC with colors and labels added by Maria Morrow.

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5.3: Mosses

Mosses, Phylum Bryophyta

Gametophyte Generation

Mosses produce only leafy gametophytes. You can differentiate them from leafy liverworts because the leaves are arranged in a spiral and usually have a midrib-like struture called a **costa**. Like the other two groups of bryophytes, simple pores on the gametophyte allow for gas exchange (no guard cells, meaning pores are permanently open).



Figure 5.3.1: A cushion of moss gametophytes in the genus *Dicranum*. Moss sporophytes tend to look more "fuzzy" than leafy liverworts due to their spirally arranged leaves. Photo by Maria Morrow, CC-BY-NC.



Figure 5.3.2: A closer look at spiral leaf arrangement, this time with *Polytrichum commune,* the haircap moss. Note that leaves emerge from all directions of each gametophyte. Photo by Mizuki Maeda, CC-BY-NC.



Figure 5.3.3: Most mosses have leaves with a costa, a thickened line of cells that traverses the center of the leaf, much like a midrib. In this image, we are looking at a moss leaf under the microscope. The darker region that runs through the center of the leaf is the costa. Photo by Shane Hanofee, CC-BY-NC.



Figure 5.3.4: These moss gametophytes show spiral leaf arrangement and a distinct, tan costa running down the center of each leaf. Two of these are indicated by white arrows. In most mosses, the costae do not extend beyond the length of the leaf. Photo by Geoffrey Cox, CC-BY-NC.

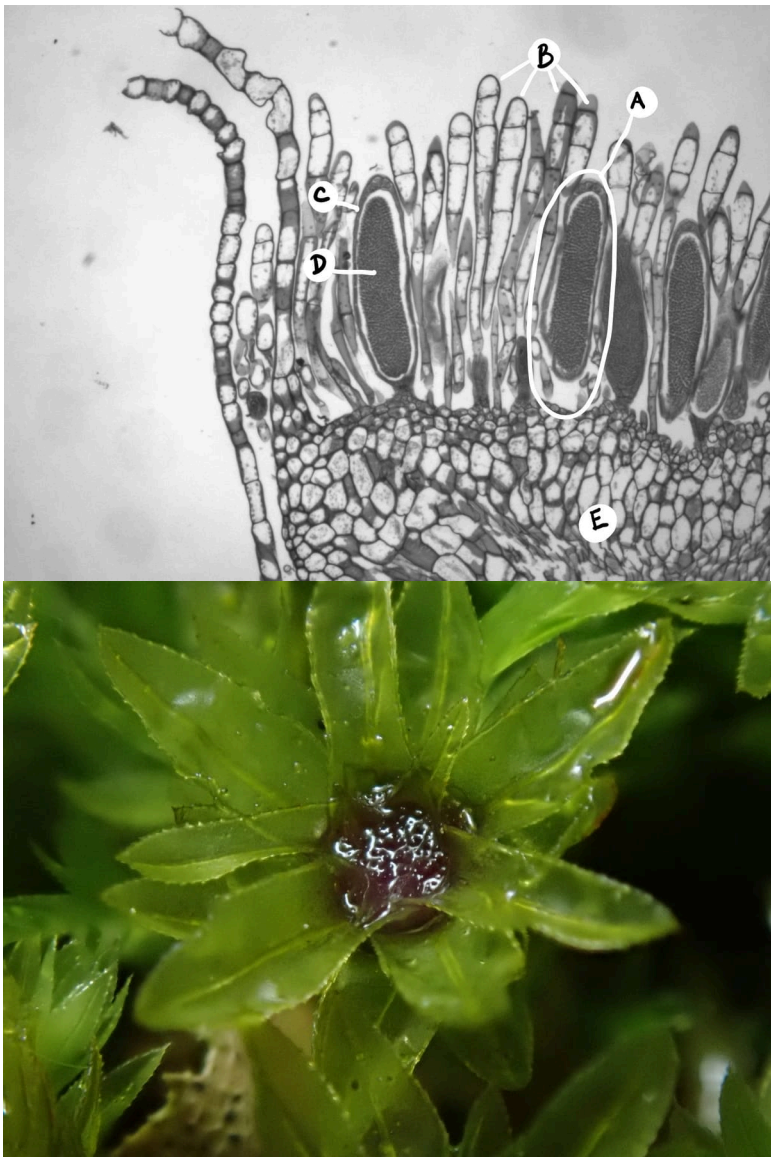


Figure 5.3.5: On the left is a labeled cross section of the antheridial head of a *Mnium* male gametophyte. On the right is an actual image of the splash cup (antheridial head) from a bird's eye view. The cross section is labeled as follows: A) An antheridium, B) paraphyses, C) sterile jacket of the antheridium, D) sporogenous tissue, E) male gametophyte. First photo by Maria Morrow, CC-BY-NC. Second photo by Bosmon, CC-BY-NC.

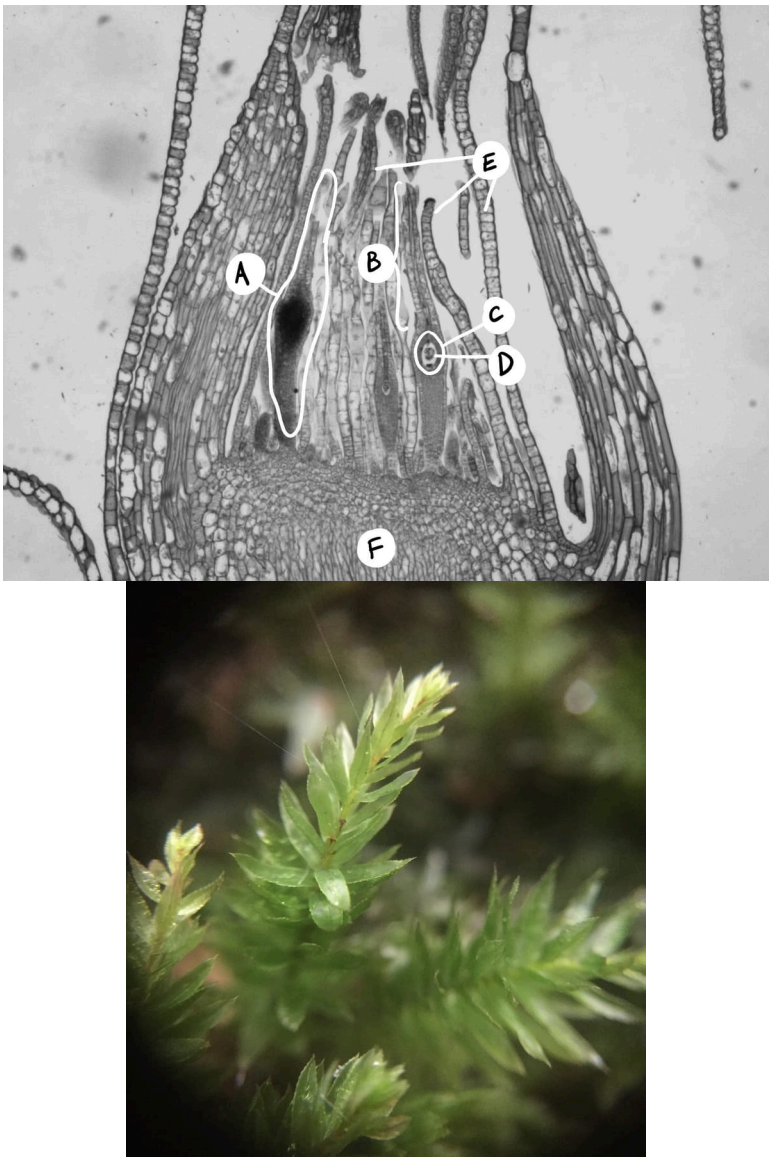


Figure 5.3.6: On the left is a labeled cross section of the archegonial head of a *Mnium* female gametophyte. On the right is an actual image of a female gametophyte. The cross section is labeled as follows: A) An archegonium, B) neck of the archegonium, C) venter, D) egg, E) paraphyses, F) female gametophyte. First photo by Maria Morrow, CC-BY-NC. Second photo by Tisrel, CC-BY-NC.

Sporophyte Generation

Moss sporophytes have a complex set of structures at the top of a seta. When the sporophyte emerges, it tears off a piece of the female gametophyte's archegonium, leaving a coating called the **calyptra**. Mosses have a **capsule**, where the sporangia are housed. This capsule has a lid-like structure called an **operculum**, which pops off when spores have matured. Depending on the moss, the sporophyte may have a **peristome** (teeth-like sheets of cells that aid in spore dispersal). True stomata are present for gas exchange.

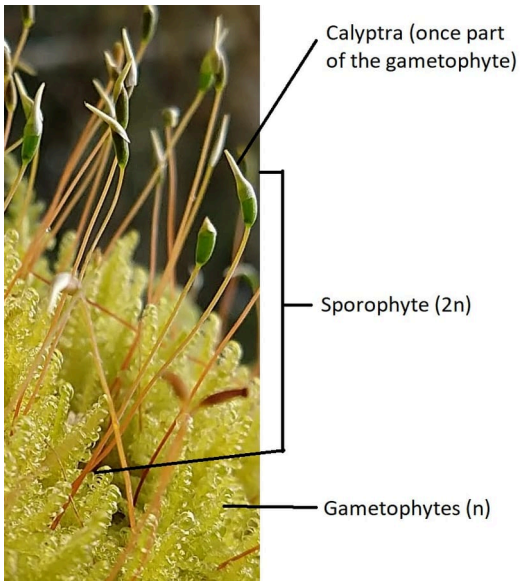


Figure 5.3.7: Moss sporophytes are composed of a seta and capsule, much like liverworts. When the sporophyte emerges from the archegonium, it brings a piece of that archegonium with it. This gametophyte remnant sits on the capsule like a cap, which is why it is called a calyptra. Photo by Maria Morrow, CC-BY-NC.



Figure 5.3.8: When the calyptra falls off, another feature of the sporophyte is visible: the operculum. This is a lid-like structure on the capsule that pops off when the spores are mature. All of the sporophytes visible in the two images above have a distinct operculum visible on the end of the capsule opposite the seta. Photos by Maria Morrow, CC-BY-NC.



Figure 5.3.9: The image on the left shows a moss sporophyte with a hairy calyptra covering the capsule. The sporophytes in the image on the right are from the same moss but are at a later stage in development. The calpytra and operculum have been shed, exposing a structure present in many mosses: the peristome. The peristome is a series of flaps that line the edge of the capsule opening and aids in spore dispersal. Photos by Maria Morrow, CC-BY-NC.

Mnium Life Cycle

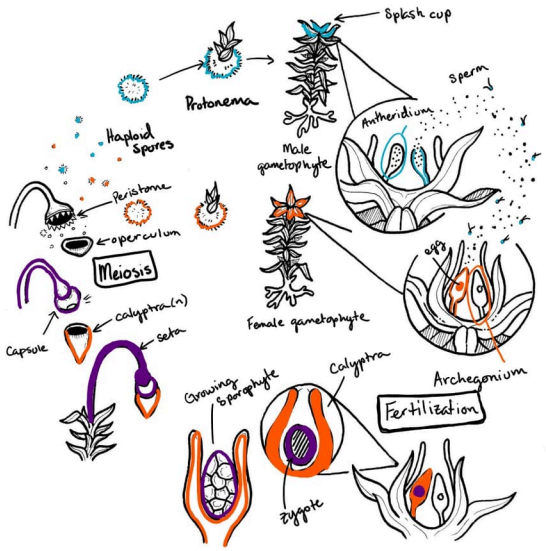


Figure 5.3.10: The *Mnium* life cycle. Starting with meiosis (left, center): Meiosis produces haploid spores which will grow by mitosis into either male or female gametophytes. Moss spores germinate and begin to grow into a chain of cells called a **protonema**. Male gametophytes are flat topped, called **splash cups**. Many **antheridia** are produced within the splash cup, surrounded by sterile cells called **paraphyses**. Antheridia produce biflagellate **sperm** by mitosis. Female gametophytes produce multiple **archegonia** at the top of the gametophyte. These are also surrounded by paraphyses. Each archegonium produces a single **egg** by mitosis. When water hits the splash cup, it can splash sperm onto a female gametophyte. If the sperm are able to swim through the water to an egg, fertilization occurs producing a diploid **zygote**. The zygote grows into a **sporophyte** from within the archegonium. The remaining archegonial tissue is called the **calyptra** and will remain on top of the sporophyte as a cap-like structure. A mature sporophyte will have a sterile stalk called a **seta.** Underneath the calyptra, there is a **capsule** containing cells that will undergo meiosis to make haploid spores. The capsule has a lid-like **operculum** that will pop off when the spores have matured. **Peristome** teeth along the opening of the capsule aid in spore dispersal. Drawing by Nikki Harris CC-BY-NC with colors and labels added by Maria Morrow.

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6: SEEDLESS VASCULAR PLANTS

As bryophytes began to colonize the terrestrial surface, they produced organic acids during metabolism that aided in the breakdown of the rocky substrate. When they died, their organic matter mixed with the weathered rock, forming the Earth's earliest soils. Formerly abundant to the first photosynthesizers to become terrestrial, access to sunlight became competitive as bryophytes expanded. This led to selection for individuals that could lift themselves higher and transport water throughout their tissues. Eventually, this selection resulted in the evolution of **vascular tissue** -- pipes that could bring water up from the ground so that parts of the plant could be raised upward, and those parts raised upward could transport their photosynthates down to the lower parts of the plant. The cells in the **xylem** (water-transporting vascular tissue) contained **lignin**, the tough, decay-resistant compound that wood is made out of. This rigid molecule in the vascular tissue allowed for structural support, allowing plants to grow taller -- some over 100 feet! The vascular system also allowed for the specialization of organs: **roots** for water absorption, **leaves** for photosynthesis, and **stems** for structural support.

Seedless vascular plants (SVPs) also began to rely more on the sporophyte stage. The sporophyte became the larger, nutritionally independent stage of the life cycle. **Branching sporophytes** offered more sites for meiosis to occur, resulting in increased opportunities for variation, which could be interpreted as more options in an increasingly competitive environment. There are approximately 20,000 known extant species, most of which are ferns.

6.1: Lycophytes

6.1.1: Lycopodium

6.1.2: Selaginella

6.2: Ferns and Horsetails

6.2.1: Horsetails

6.2.2: Ferns

6.3: Extinct SVPs

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6.1: LYCOPHYTES

Characteristics of Lycophytes

- **Microphylls**. Leaves have a single, unbranched vein of vascular tissue. Note: The term microphyll, confusingly, is not an indication of the size of the leaf.
- **Rhizomes**. Asexual propogation of the sporophyte through underground stems.
- **Homosporous or heterosporous**. Haploid spores grow into bisexual gametophytes in *Lycopodium*. In *Selaginella*, **microspores** develop into **microgametophytes** that produce sperm and **megaspores** develop into **megagametophytes** that produce eggs.

Extinct lycophytes like *Lepidodendron* and *Sigillaria* grew into tall trees, branching dichotomously and producing a moss-like canopy of microphylls. Some of these microphylls were several feet long! Lycophytes first appear in the fossil record over 400 million years ago. By the Carboniferous period (around 300 mya), the landscape was covered with lycophyte forests and shallow swamps. Much of the fossil fuels we use today are derived from these extinct arboreal lycophytes falling into swamps, slowing decomposition and creating layers of carbon-rich material that we now find as coal seams.

Extant lycophytes (those species still alive today) are represented by creeping forms, such as *Lycopodium* and *Selaginella*. Observe fresh specimens and prepared slides of *Selaginella* and/or *Lycopodium*. Draw and describe the important characteristics that differentiate these plants from bryophytes, including stem and leaf structure, below ground parts, and where spores are produced.



Figure 6.1.1: Lycopodium clavatum. The erect, tan structures are stalks with strobili at the top. The rest of the plant is green and growing more or less prostrate along the ground. Photo by David Bird, CC-BY-NC.

- Topic hierarchy

6.1.1: Lycopodium

6.1.2: Selaginella

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6.1.1: Lycopodium

Gametophyte Morphology

In seedless vascular plants, the sporophyte is the longer-lived, larger, leafy generation. This trend of sporophyte dominance throughout the evolutionary timeline of plants leads to continually smaller, less complex gametophytes. Gametophytes of this group are seldom seen. They are small and thalloid.

In *Lycopodium*, the gametophyte grows from a homospore and is bisexual, producing both antheridia and archegonia.



Figure 6.1.1.1: A preserved *Lycopodium* gametophyte. The flat thallus extending out to the right is the gametophyte. The sporophyte emerges from its left side, the root system developing downward and shoot system developing upward. This gametophyte would normally be green and photosynthetic, but the pigments were lost in the preservation process. Photo by Curtis Clark, CC BY-SA 3.0, via Wikimedia Commons

Sporophyte Morphology

Sporophytes branch dichotomously and have true roots and leaves due to the presence of lignified vascular tissue. The leaves, called **microphylls**, have a single, unbranched vein of vascular tissue. Note: The term microphyll, confusingly, is not an indication of the size of the leaf.

Figure 6.1.1.2: A *Lycopodium* sporophyte grows across a bed of feather mosses on the forest floor. Many branches stick upright and may develop strobili. Photo by Maria Morrow, CC-BY 4.0.



Figure 6.1.1.3: A closer view of the *Lycopodium* sporophyte shown above. The branches occur in Y-formations, showing dichotomous branching. There are many small, thin leaves (microphylls). Each one only has a single vein of vascular tissue, though this is not observable in this image. Photo by Maria Morrow, CC-BY 4.0.

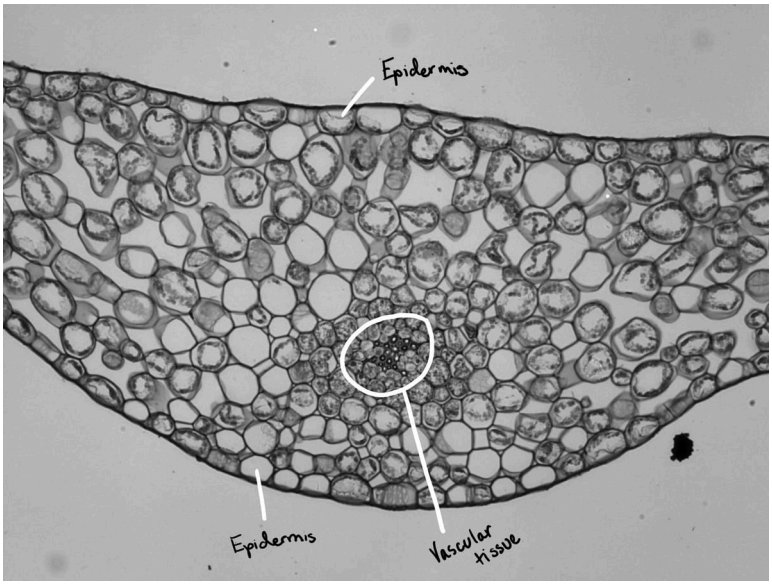


Figure 6.1.1.4: A cross section through a *Lycopodium* microphyll. There is a single vein of vascular tissue in the center and the leaves are now many cell layers thick (unlike most bryophytes). Photo by Maria Morrow, CC-BY 4.0.

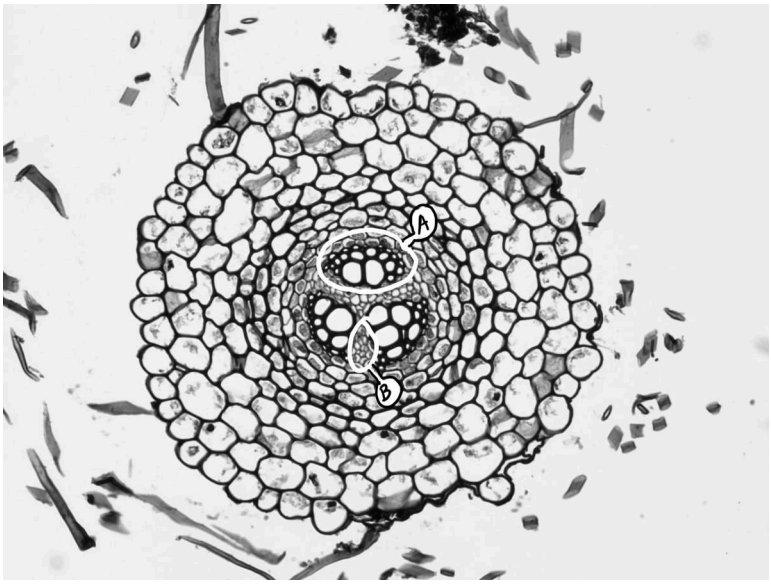


Figure 6.1.1.5: A cross section through a *Lycopodium* root. There is vascular tissue organized in the center with three columns of xylem (A) and phloem (B) between them. Photo by Maria Morrow, CC-BY 4.0.

Asexual propogation can occur via an underground stem called a **rhizome**. Homospores are produced in a structure called a strobilus that is produced at the end of a branch. A single plant can have many strobili.

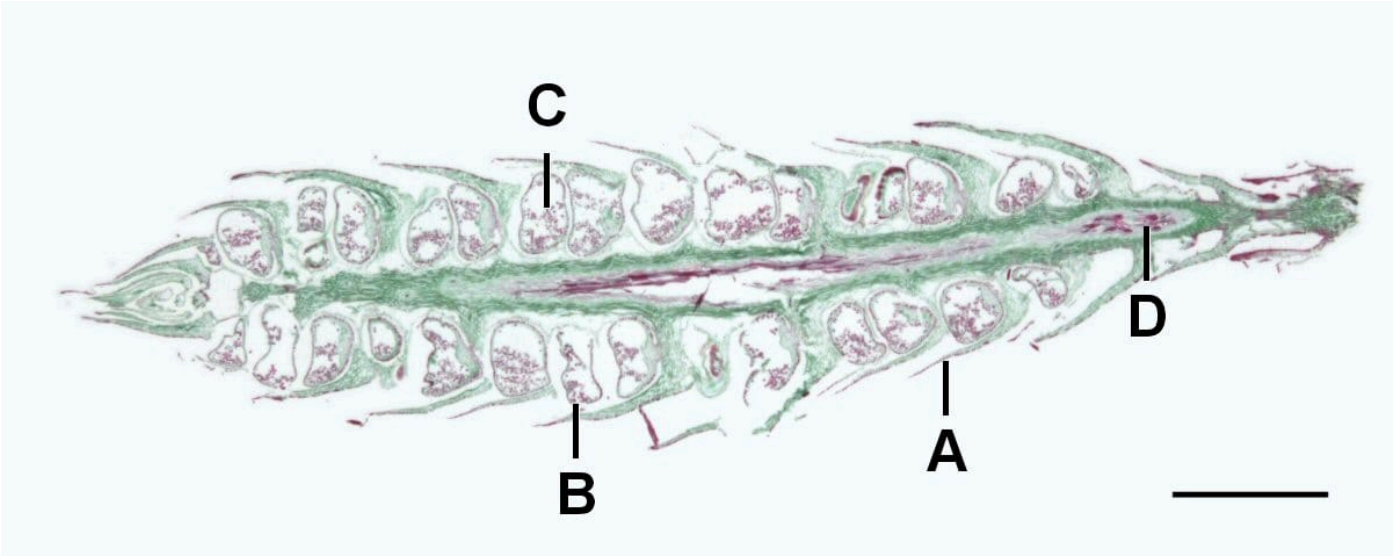


Figure 6.1.1.6: A longitudinal section of a *Lycopodium* strobilus, shown horizontally, and labeled as follows: A) sporophyll, B) sporangium, C) spores, D) cone axis. The sporangia and spores all look approximately the same size and shape. Each sporangium is attached to a leaf (sporophyll). These are arranged around a central axis. Scale bar represents 1.5mm Photo by Jon Houseman, CC BY-SA 3.0, via Wikimedia Commons

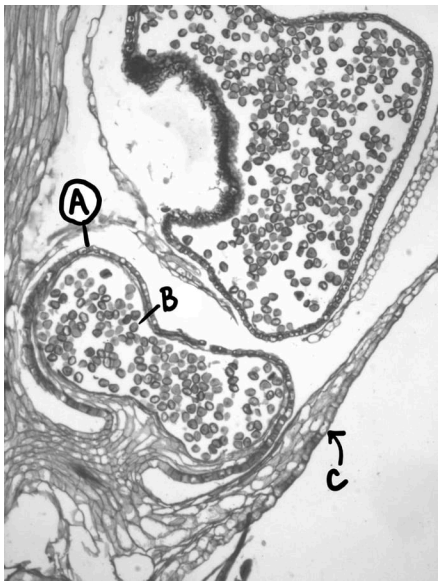


Figure 6.1.1.7: A closer view of a *Lycopodium* sporangium. Notice that the spores (homospores) are all approximately the same size in these sporangia and those shown in Figure 6.1.1.6. Labels are as follows A) sporangium, B) spores, C) sporophyll. Photo by Maria Morrow, CC-BY 4.0.

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6.1.2: Selaginella

Members of the genus *Selaginella* are heterosporous, meaning they produce two different types of spores.



Figure 6.1.2.1: In the first image, there are liquid-preserved strobili of *Selaginella*, showing mega- and microsporangia through translucent sporophylls. The second image is a cross section through a strobilus. Notice that the spores contained within the sporangia are quite different in size. Labels are as follows: A) cone axis, B) microsporangium, C) microspores, D) microsporophyll, E) megasporangium, F) megaspore, G) megasporophyll. Photo on the left is by Curtis Clark, licensed as noted, CC BY-SA 2.5, via Wikimedia Commons. Photo on the right is by Curtis Clark, CC BY-SA 3.0, via Wikimedia Commons with labels added by Maria Morrow.



Figure 6.1.2.2: Selaginella sporophytes have microphylls. These images show a *Selaginella* sporophyte spreading via dichotomous branching (first image) and the single, unbranched vein of vascular tissue present in each leaf (second image). Images by Sönke Bonde, CC0.

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6.2: FERNS AND HORSETAILS

Characteristics of Ferns and Horsetails

- **Megaphylls**. Leaves have branching veins of vascular tissue.
- **Rhizomes**. Asexual propogation of the sporophyte through underground stems.
- **Homospory**. Haploid spores grow into bisexual gametophytes that produce both antheridia and archegonia. Note: There is an order of aquatic ferns (Salviniales, to which the water fern genus *Azolla* belongs) that are heterosporous.



Figure 6.2.1: A fern gametophyte. The heart-shaped thallus has many long, thin rhizoids protruding from it. Photo by Curtis Clark, CC BY-SA 3.0, via Wikimedia Commons.

- Topic hierarchy

6.2.1: Horsetails

6.2.2: Ferns

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6.2.1: Horsetails

Horsetails are one of the most ancient lineages of plants and are relatively unchanged from the fossil record. If you look closely at the nodes of a green vegetative shoot**,** you will see that branches and leaves have not only switched roles, they have also switched places, with the photosynthetic branches emerging below the papery, non-photosynthetic leaves. The stems of horsetails are covered in silica, giving them the common name scouring rush, as they were formerly used to clean pots due to the abrasive nature of silicate granules. This is what gives the epidermis of the shoot its rough texture.

Gametophyte Morphology

Horsetail gametophytes are reduced and thalloid. Bisexual gametophytes grow from homospores and produce both antheridia and archegonia.

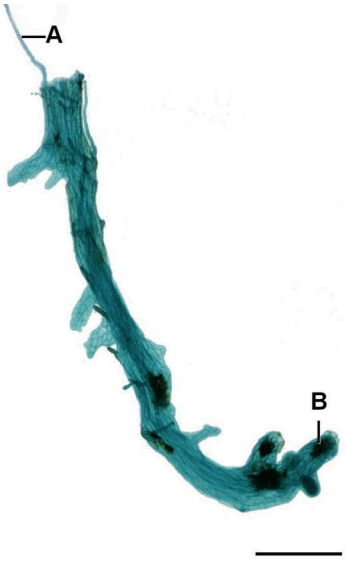


Figure 6.2.1.1: Whole mount of an *Equisetum* gametophyte. A indicates a long, thin rhizoid. B indicates one of several antheridia, each positioned on an extending lobe from the long, linear thallus. Scale=0.6mm. Jon Houseman, CC BY-SA, via Wikimedia Commons.



Figure 6.2.1.2: An *Equisetum* gametophyte with an antheridium indicated by the red box. This partial view of the thallus shows lobes on the edge where antheridia appear as darker, round areas. Within these, many sperm cells are produced. Photo by Bruce Kirchoff, CC BY 2.0, via Wikimedia Commons.

Sporophyte Morphology

Vegetative Shoots

On the sporophyte, the leaves are dark, papery and non-photosynthetic. Branches are photosynthetic and produced in whorls on the **vegetative shoot**. Shoots contain **silica**, which has an abrasive texture.



Figure 6.2.1.3: A vegetative shoot of *Equisetum*. There are rings of long, thin, green branches emerging from each node. Above each whorl of branches, a ring of pointy brown leaves are pressed up against the main stem. Photo by Maria Morrow, CC-BY 4.0

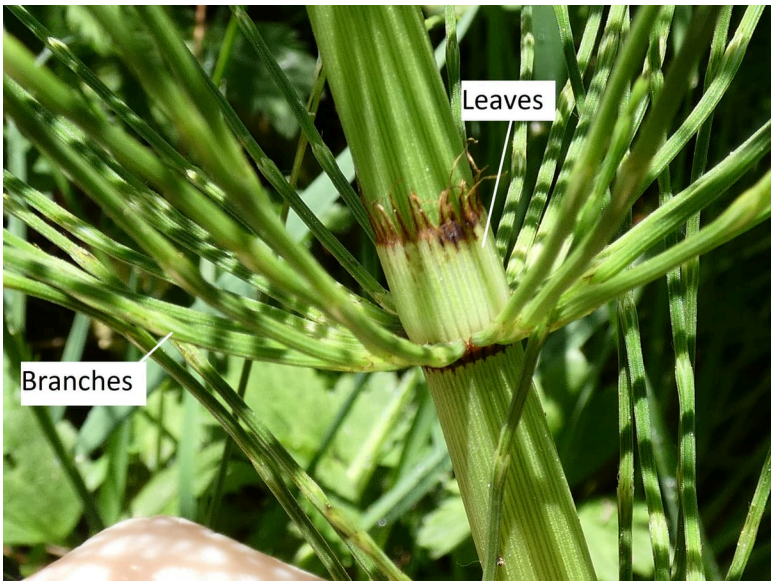


Figure 6.2.1.4: A close up of the vegetative shoot of *Equisetum*. In this image, you get a better view of the leaves. They start out as a united tube surrounding the main stem, then turn dry and brown, separating into individual, wispy points. The whorl of leaves looks a bit like a grassy crown encircling the stem. Photo by Maria Morrow, CC-BY 4.0

Reproductive Shoots

Sporangia are produced in a terminal strobilus on the **reproductive shoot**. In some species, this reproductive shoot lacks chlorophyll and is instead fed through the rhizome of connected vegetative shoots. Spores are photosynthetic and have four hygroscopic arms called **elaters.**

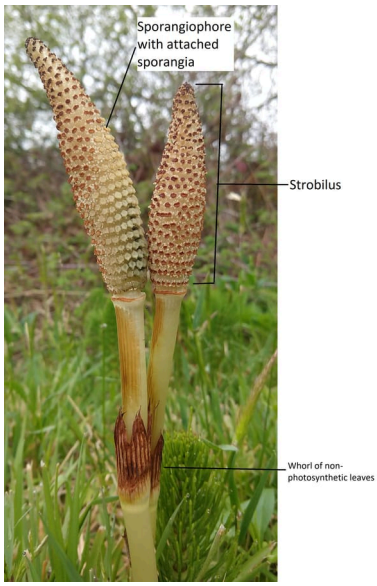


Figure 6.2.1.5: Two reproductive shoots of *Equisetum*. These shoots are a very pale yellow, lacking chlorophyll and unable to do photosynthesis. The leaves on the reproductive shoots still occur in whorls and are larger than on the vegetative shoots shown above. At the top of each shoot, there is an elongated structure that comes to a point and looks like it is covered in polka dots. These are the strobili. Each polka dot is the top of a sporangiophore, each of which bear many sporangia, perhaps visible to you as little white frills surrounding the polka dots. Photo by Maria Morrow, CC-BY 4.0

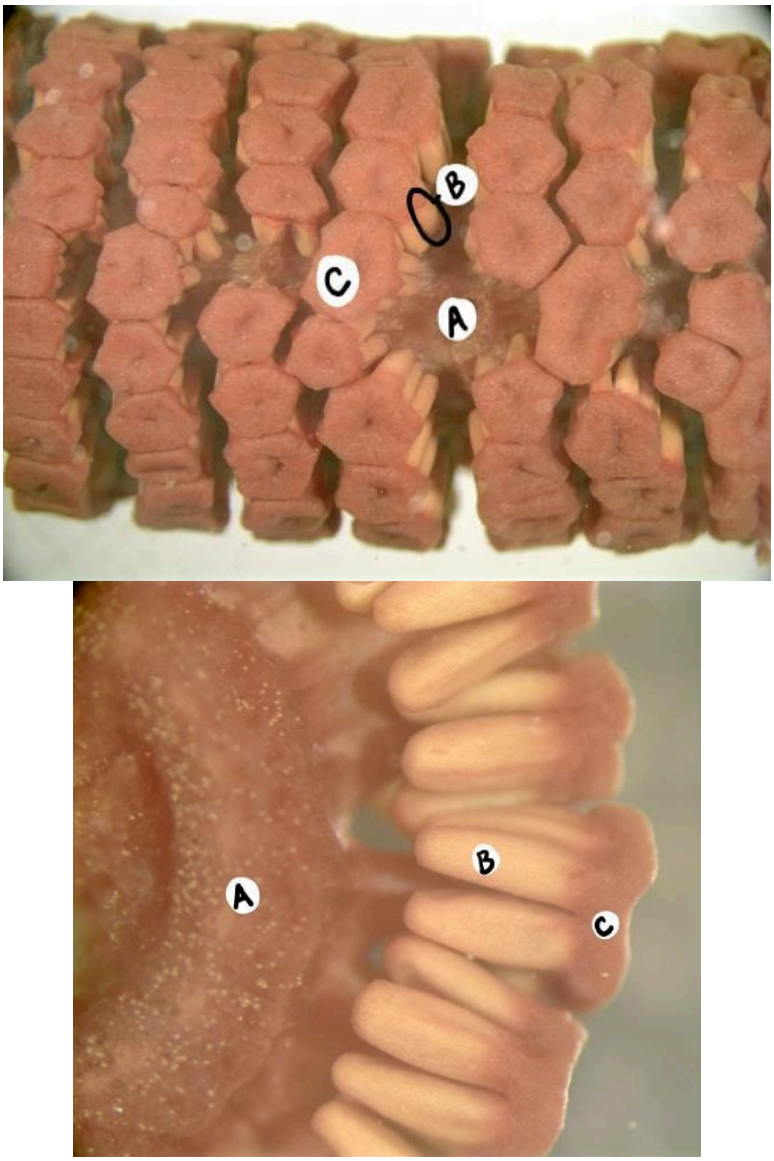


Figure 6.2.1.6: These images show a preserved *Equisetum* strobilus. In the first image, we are looking straight at the tops of the sporangiophores, but some sporangia are visible underneath them. There is a section where you can see the cone axis (labeled A). The second image is a cross section through the strobilus, viewing the sporangia dangling from the sporangiophores. In both images, the labels represent the same structures: A) cone axis, B) a sporangium, C) sporangiophore. Photos by Curtis Clark, CC BY-SA 2.5, via Wikimedia Commons with labels added by Maria Morrow.

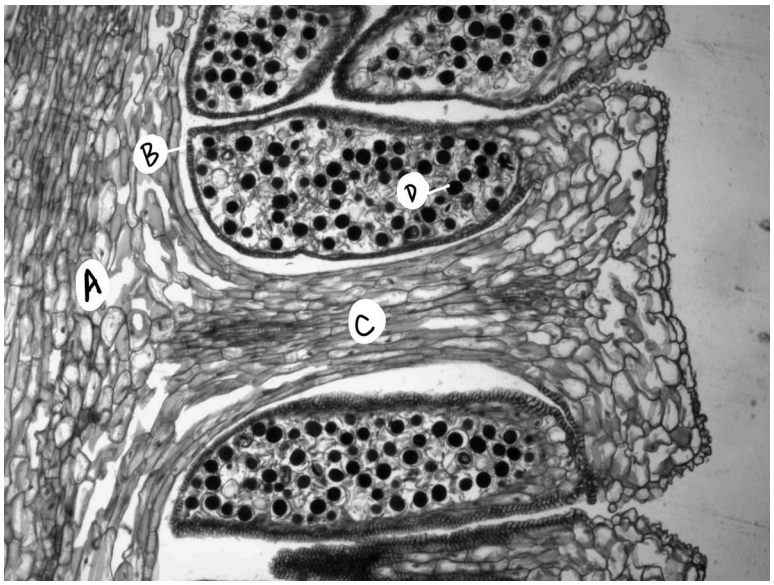


Figure 6.2.1.7: These images show a micrograph of a strobilus longitudinal section. The labels are as follows: A) cone axis, B) sporangium, C) sporangiophore, D) spore. Note that the spores are all about the same size (homospores) and are wrapped in thread-like structures. These thread-like structures are the elaters. Photo by Maria Morrow, CC-BY 4.0

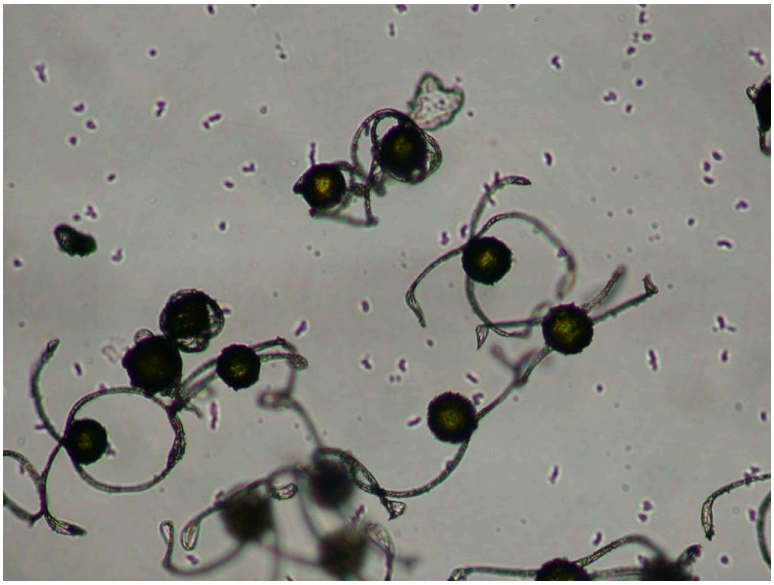


Figure 6.2.1.7: Equisetum spores under the microscope. The spores are green and photosynthetic. Each spore has four long, transparent arms extending out from it. Some of these arms (elaters) are wrapped around the spore. The elaters react to moisture, curling in around the spore when wet and extending outward when dry, to aid in spore dispersal. Photo by Keisotyo, CC BY-SA, via Wikimedia Commons.

YouTube Video

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

Video 6.2.1.1: This video shows how the elaters of *Equisetum* spores respond to changes in humidity. Retrieved from YouTube.

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6.2.2: Ferns

Gametophyte Morphology

Fern gametophytes are reduced, thalloid, and heart-shaped. They are often referred to as a prothallus or prothallium.

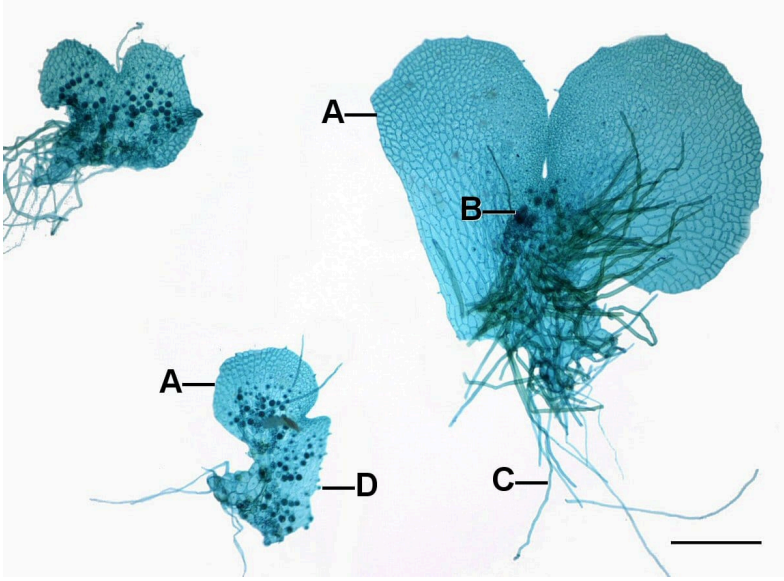


Figure 6.2.2.1: Three fern gametophytes that have been stained and so appear blue. The images are labeled as follows: A) Prothallus, B) Archegonium, C) Rhizoid, D) Antheridium. Scale=0.525mm. The rhizoids and archegonia emerge from the underside off the thallus. Descriptive text: A points to the flat, heart-shaped thallus, B points to structures with elongated necks close to the rhizoids, C points to long thin projections, D points to small dark structures spread across the thallus. Scale bar = 0.525mm. The rhizoids and archegonia emerge from the underside of the prothallus. Photo by Jon Houseman, CC BY-NC, via Wikimedia Commons.

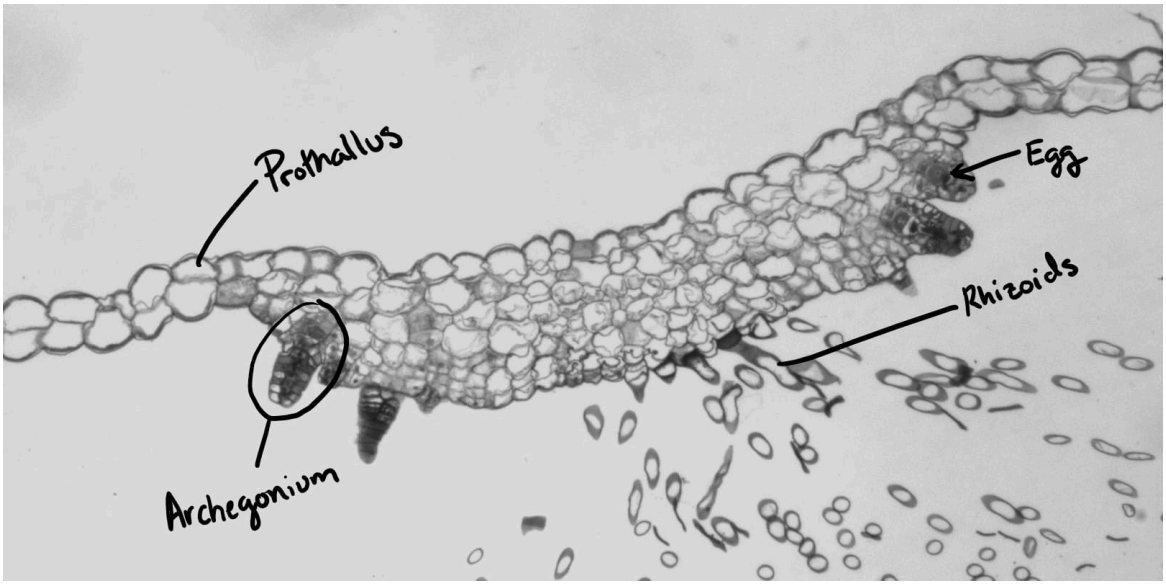


Figure 6.2.2.2: A section through a fern prothallus. The archegonia and rhizoids are located on the underside of the thallus. Each archegonium has a long neck. At the base of each archegonium, a single egg is housed. Photo by Maria Morrow, CC BY-NC.

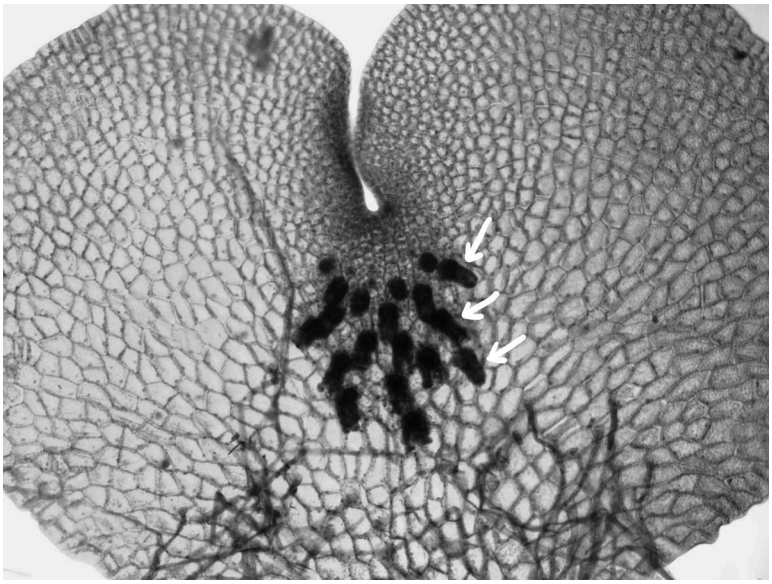


Figure 6.2.2.3: The underside of a fern prothallus viewed under a microscope. The long necks of the archegonia are visible and appear dark, protruding outward. Long, thin rhizoids emerge near them. Photo by Maria Morrow, CC BY-NC.

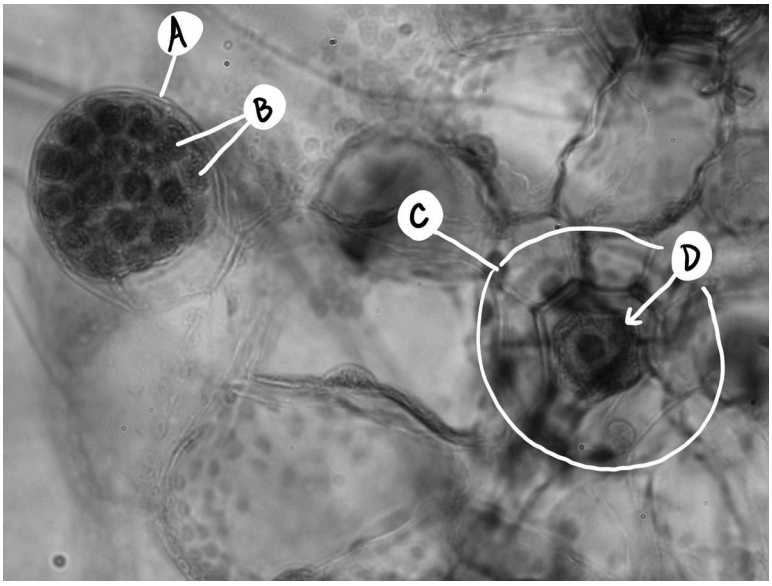


Figure 6.2.2.4: A magnified view of a fern gametophyte that has both antheridia and archegonia. The antheridium (A) has many sperm inside (B) and does not appear three dimensional. The archegonium (C) is surrounded by enlarged cells--we are looking straight down the neck. At the center of the archegonium, there is only a single egg (D). Photo by Maria Morrow, CC BY-NC.

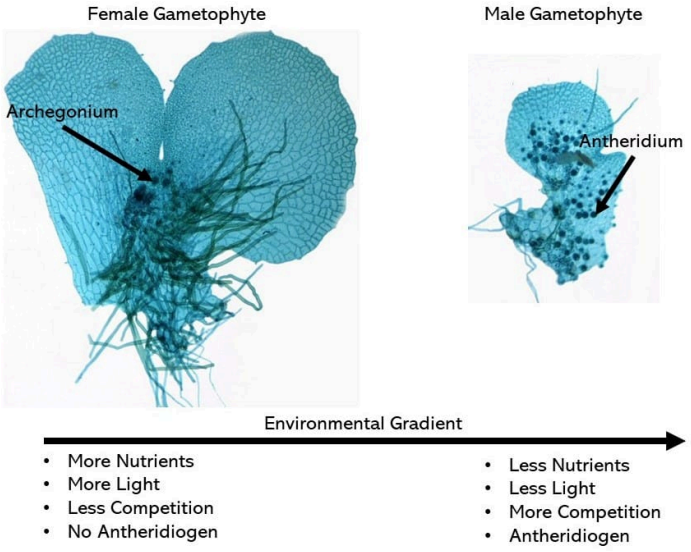


Figure 6.2.2.5: Fern gametophytes may develop either antheridia or archegonia based on environmental characteristics such as nutrients, competition, light, and antheridiogens. More nutrients, more light, less competition, and the absence of antheridiogen all select for the production of archegonia. Less nutrients, less light, more competition, and antheridiogen all select for the production of antheridia. Diagram by Jon Houseman, CC BY-NC, via Wikimedia Commons.

Sporophyte Morphology

Fern sporophytes are composed of megaphylls, often pinnately compound **fronds** that emerging as **fiddleheads** in the spring. Sporangia are produced in clusters called **sori** (sorus, singular) on the fronds.

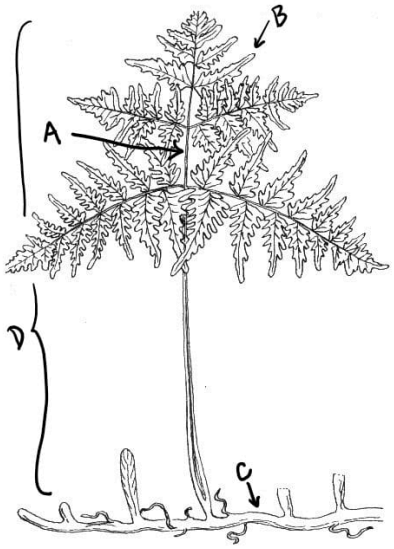


Figure 6.2.2.6: Anatomy of a fern. The fern frond (D) is emerging from an underground, horizontal stem called a rhizome (C). The frond is twice pinnately compound. The leaflets (B, also called pinnae) branch off of a central stem called a rachis (A). Drawing by Pearson Scott Foresman, Public domain, via Wikimedia Commons with labels added by Maria Morrow.

Circinate Vernation

Circinate vernation is a term used to describe the development of the fern fiddlehead into a frond. Because plants grow apically, it is important to protect the apical meristems in growing organs (as we have seen in both axillary and terminal buds with the evolution of bud scales). The fiddlehead is essentially a structure that tucks away the growing tips of the fronds. As the frond develops, it gradually unfurls, releasing the tips last.



Figure 6.2.2.7: The two images above show fiddleheads of two different types of ferns, a deer fern on the left and a sword fern on the right. Each has the same basic shape--a long stalk that transitions in a tightly coiled knot containing the developing leaf tissues. Photos by Maria Morrow, CC BY-NC.



Figure 6.2.2.8: The two images above show the same species of fern, a five finger maidenhair fern. In the first image, the leaflets are partially curled. They are midway through the process of uncurling, called circinate vernation. In the second image, you can see the mature form of that fern frond, after circinate vernation is complete. Photos by Maria Morrow, CC BY-NC.

Sori

A sorus (plural, sori) is a cluster of sporangia, often protected by an umbrella-like structure called the **indusium** as the spores mature. Each **sporangium** is lined by an inflated strip of cells called an **annulus**. When the spores have matured, the cells in the annulus begin to dry out, causing the cells to collapse and pull the sporangium open, releasing the spores.



Figure 6.2.2.9: The underside of *Polypodium* frond. Each fuzzy-look orange region is a developing sorus (a cluster of sporangia). These sori are not protected by an indusium. Photo by Maria Morrow, CC BY-NC.

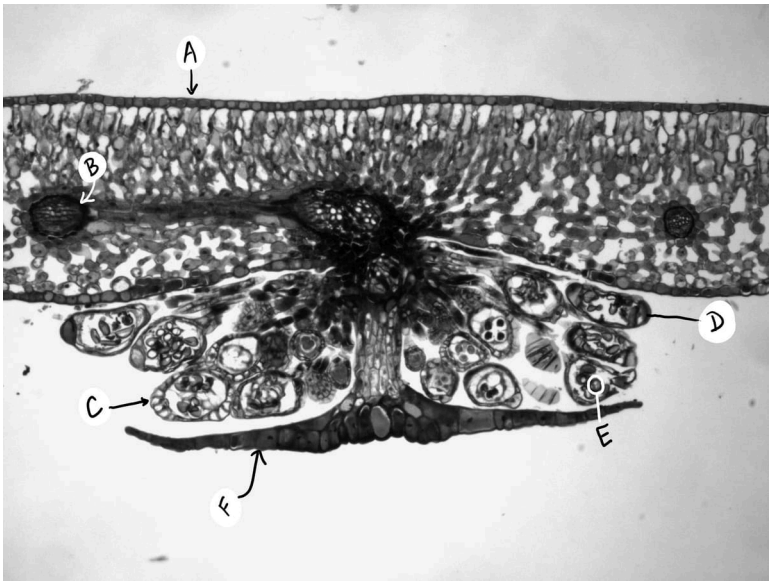


Figure 6.2.2.10: Cross section of a sorus. This cluster of sporangia is protected by a central umbrella-like structure called an indusium. Each sporangium is surrounded by a strip of inflated of cells called the annulus. When the cells in the annulus dry, it causes the sporangium to split open, releasing the spores. A=Epidermis, B=Vascular bundle, C=Annulus, D=Sporangium, E=Spore, F=Indusium. Photo by Maria Morrow, CC BY-NC.

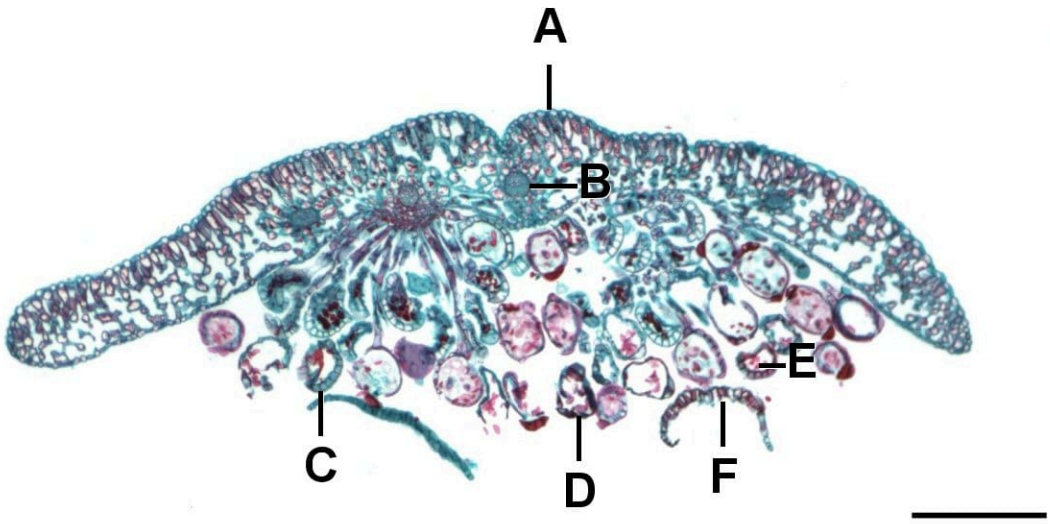


Figure 6.2.2.11: The epidermis of the leaf (sporophyll) is labeled A. A large vascular bundle (B) is located in the center, as well as several others located along the length of the leaf. Under the leaf, a cluster of sporangia (D) are forming a sorus. Each sporangium is surrounded by a thickened layer of cells, the annulus (C). Within the sporangia, spores (E) are produced. The entire sorus was once covered by the residual structures labeled F, the indusium. Photo by Jon Houseman, CC BY-NC, via Wikimedia Commons.

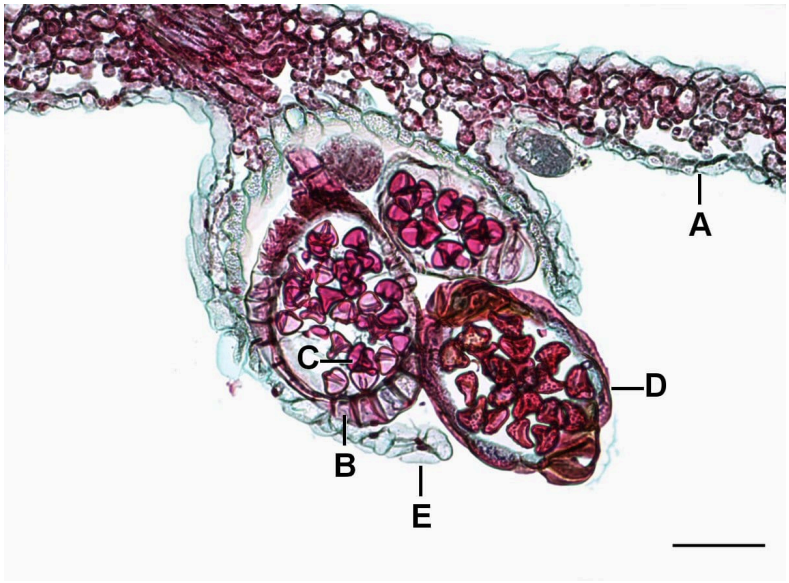


Figure 6.2.2.12: Cross section of a *Dicksonia* sorus. In this fern, the cluster of sporangia is enveloped by an extension of the leaf (E), a false indusium. A=Epidermis, B=Annulus, C=Spore, D=Sporangium, E=False indusium. Scale=0.1mm. Photo by Jon Houseman, CC BY-NC, via Wikimedia Commons.

Full Life Cycle Diagram

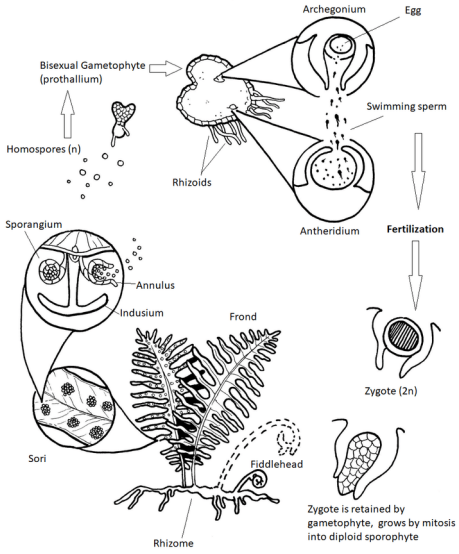


Figure 6.2.2.13: The diagram above shows the life cycle of a *Polypodium* fern. The gametophyte generation (n) is shown in the top half of the diagram and the sporophyte generation (2n) in the bottom half. Starting from the release of haploid homospores, these spores grow by mitosis into bisexual gametophytes. The gametophyte is heart-shaped, thalloid, and produces root-like structures called rhizoids. The antheridium produces many swimming sperm that are dispersed by water into an archegonium. A sperm swims down the neck/venter of an archegonium and fertilizes the single egg produced there. This produces a diploid zygote, which is retained on the gametophyte. The zygote grows by mitosis within the archegonium, producing a sporophyll (frond). When fully developed, the sporophyte will likely have multiple fronds and a rhizome. Fronds start as fiddleheads and uncoil by circinate vernation. The frond on the left is producing sori on the underside of the leaflets. Each sorus is a cluster of sporangia, which is protected by an indusium. Meiosis happens within the sporangia. Each sporangium has an inflated annulus to help release the spores when conditions are right. One of these has torn open to release its haploid homospores, which brings us back to the beginning. Diagram by Nikki Harris CC BY-NC with labels added.

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6.3: Extinct SVPs



Figure 6.3.1: In the first image there is fossil from a *Lepidodendron* tree on display at the State Museum of Pennsylvania. This extinct lycophyte genus was perhaps one of the dominant features in the landscape during the carboniferous period. The second image is an artist's reconstruction of *Lepidodendron,* showing dichotomous branching of the roots and shoots. Microphylls and pendant strobili emerge in the canopy. Photo of the fossil by Jstuby at en.Wikipedia, Public domain, via Wikimedia Commons. Artist's reconstruction by Tim Bertelink, CC BY-SA 4.0, via Wikimedia Commons.



Figure 6.3.2: In the first image there is fossil from a *Sigillaria* (possibly a root fragment) that is on display at State Museum of Pennsylvania. The second image is an artist's interpretation of what these plants looked like during the Carboniferous period. Photo of the fossil by Jstuby at en.Wikipedia, Public domain, via Wikimedia Commons. Artist's reconstruction by Tim Bertelink, CC BY-SA 4.0, via Wikimedia Commons.

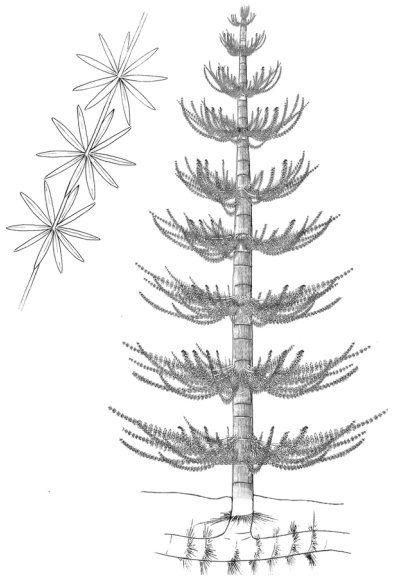


Figure 6.3.3: The first image shows fossils of *Calamites*, an extinct relative of *Equisetum*, from the Sedgwick Museum's collection. The second image is an artist's interpretation of what these plants looked like. There is a large rhizome under the surface of the soil. The tree-like horsetail might have been 60 feet tall and has whorled branches with small leaves. Fossil photo by Verisimilus, CC BY 3.0, via Wikimedia Commons. Artist's reconstruction by Falconaumanni, CC BY-SA 3.0, via Wikimedia Commons.

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7: GYMNOSPERMS

The plants that would become the gymnosperms evolved xerophytic leaves to prevent desiccation in the dry air. Some would have the ability to grow wider (and thus taller) via the production of a new layer of secondary xylem (wood) each year. These plants could also produce exterior layers of dead cells, unlike the living epidermis, called bark. Together, the production of bark and wood are part of a process called secondary growth. To increase the chances of fertilization in the absence of water, gametes began to be dispersed aerially via pollen. Perhaps most importantly, the zygote and female gametophyte were surrounded in a protective coating and dispersed as seeds. Both seeds and pollen develop within structures called cones (strobili).

The fossil record shows gymnosperms diversifying in a dry period called the Permian that followed the swampy Carboniferous period. Extant groups of gymnosperms include conifers, cycads (somewhat similar in appearance to palms), gnetophytes, and a single species from the ginkgophytes, *Ginkgo biloba*. Of the approximately 1,000 species of gymnosperms alive today, about 600 of these are conifers.

7.1: Cycads

7.2: Ginkgos

7.3: Gnetophytes

7.4: Conifers

7.4.1: Pine Life Cycle

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7.1: Cycads

Cycads are one of the more ancient gymnosperm lineages, appearing in the fossil record around 300 million years ago. Currently, many extant species are in danger of extinction in the wild. However, during the Jurassic period, these plants would have dominated the landscape. Though their large, compound leaves make them appear to be ferns at first glance, cycads can be classified as gymnosperms by the production of seeds instead of spores and xerophytic leaves. These plants share the following features:

- Dioecious. Male and female strobili on separate plants.
- Large compound, xerophytic leaves
- Insect pollinated



Figure 7.1.1: The first image is what might be considered a "typical" cycad. The leaves are long, tough, and pinnately compound with long, thin leaflets. Unlike a fern, the leaves look tough. The plant in the second image also shares these characteristics, yet it might not immediately stand out as a cycad. First: *Dioon holmgrenii,* photo by Daniela Fernandez y Fernandez, CC-BY-NC. Second: *Bowenia spectabilis,* photo by kerrycoleman, CC-BY-NC.



Figure 7.1.2: A cycad taking an arborescent form. It has a distinct, woody trunk and the leaves are emerging from the top of the trunk to form a small crown. *Cycas ophiolitica,* photo by Geoffrey Sinclair, CC-BY-NC.



Figure 7.1.3: Each leaf blade shown here is a leaflet from the larger, pinnately compound leaf. There are many parallel veins of vascular tissue traversing each leaflet and the rachis of the leaf looks woody. *Zamia integrifolia,* photo by John C., CC-BY-NC.



Figure 7.1.4: The large microstrobilus, the pollen-producing cone. This structure would be produced on a "male" plant and consists of many microphylls bearing microsporangia. It is called a microstrobilus, not because *it* is small, but because the pollen (and sperm inside the pollen) produced inside it are smaller than the seeds (and eggs) produced by in the megasporangium. Microstrobili are often larger than megastrobili in cycads. First: *Encephalartos villosus*, photo by Cultivar413 from Fallbrook, California, CC BY 2.0, via Wikimedia Commons. Second: Photo by BillyH, CC BY 3.0, via Wikimedia Commons.



Figure 7.1.5: A megastrobilus is composed of overlapping megasporophylls. Cycads are dioecious, meaning male and female strobili are produced on different individuals. These individuals are "female" and so produce a megastrobilus. Inside the megastrobilus, seeds are produced. These are visible in the second photo, the bright red structures that appear to be bubbling up from under the green megasporophylls. First: *Dioon merolae* Photo by Raul Ezequiel Gonzalez Trujillo, CC-BY-NC. Second: *Macrozamia macleayi,* photo by Blawson, CC-BY-NC.



Figure 7.1.6: From the megastrobilus, seeds are produced. The large red seeds can be seen still within the feathery megasporophylls of this megastrobilus. *Cycas revoluta,* photo by Kylelovesyou, CC BY 3.0, via Wikimedia Commons.

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7.2: Ginkgos

As of 2019, the most recent genetic studies have placed Ginkgos as the oldest of the extant gymnosperms. This does not mean that it was the first gymnosperm. From the fossil record, it seems that most early gymnosperms went extinct. The sole remaining species in this group, *Ginkgo biloba*, is a living fossil virtually unchanged from its fossilized ancestors. It is possible that this species was only kept alive due to cultivation efforts by Buddhist monks for its medicinal properties. This species is also long-lived, a single tree can live for thousands of years, and resistant to most pests. *Ginkgo biloba* can be recognized by the following features:

- Leaves deciduous, but tough, fan-shaped
- Dioecious (di- meaning two, oecious meaning house), with male and female strobili on separate plants. Females plants have paired ovules at the tips of branches, males have catkin-like structures that produce pollen.
- Wind pollinated



Figure 7.2.1: Ginkgo leaves have a distinctive shape that has remained relatively unchanged from their fossil record: a fan-shaped leaf that is often deeply dissected in the center. The fossil leaf on the right is around 60 million years old. First: *Ginkgo biloba* leaves, photo by Onidiras, CC-BY-NC. Second: Fossil Ginkgo leaf by Anders Sandberg from Oxford, UK, CC BY 2.0, via Wikimedia Commons.



Figure 7.2.2: Leaves of *Ginkgo biloba* are xerophytic and somewhat tough. However, they are deciduous. In fall, they turn a beautiful golden yellow before dropping from the tree. *Ginkgo biloba,* photo by Chocochan, CC-BY-NC.



Figure 7.2.3: Male *Ginkgo biloba* trees produce microstrobili that look a bit like inflorescences. Inside these structures, pollen is produced. Photo by Belvedere04, CC-BY-NC.



Figure 7.2.4: Female *Ginkgo biloba* trees produce fruit-like megastrobili as fleshy, paired ovules. Each globose structure contains a developing seed. Apparently, they can smell quite putrid. Photo by Kim, Hyun-tae, CC-BY.



Figure 7.2.5: Ginkgos can be quite long-lived. This ginkgo tree is approximately 750 years old. It bears burn scars from WWII and has a complex trunk structure. It is sometimes referred to as the inverted or upside down tree due to the numerous aerial roots growing steadily downward. *Ginkgo biloba* at Zenpuku-ji in Azabu. Photo by Belvedere04, CC-BY-NC.

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7.3: Gnetophytes

Gnetophytes represent an anatomically and genetically difficult group to classify. They have several traits in common with angiosperms, such as vessel elements in the xylem, double fertilization, and a covering over their seeds. Even their leaves are angiosperm-like, with netted venation. However, these traits are convergently evolved, meaning that angiosperms and gnetophytes each evolved these traits separately. Genetically, recent studies have placed the gnetophytes as a sister group to the Pinaceae (pine family) within the conifers. This would mean that pines, firs, and spruces are more closely related to strange gnetophytes like Ephedra than they are to other conifers like redwoods, cedars, and Pacific yew. However, the true nature of this evolutionary relationship remains murky and contentious.

Characteristics of Gnetophytes

- Angiosperm-like features: vessel elements, double fertilization, fruit-like ovule coverings
- **Dioecious**. Female plants have covered ovules, while male plants have pollen cones.
- Leaves xerophytic with **opposite arrangement**
- Primarily insect pollinated; brightly colored seeds are dispersed by birds

Notable Gnetophytes

Welwitschia mirabilis

This strange plant grows in the desert of Namibia. It has two large leaves that grow from a basal meristem.



Figure 7.3.1: In this small Welwitschia mirabilis, the two large leaves can be seen extending from the central, flat stem. The leaves grow from a basal meristem. The tips of the leaves are ragged, as these are the oldest parts. The leaves are shiny and the setting is dry, indicating their xerophytic nature. In the center, where the two leaves meet, branching stalks terminate in megastrobili. Photo by Waldier, CC-BY-NC.



Figure 7.3.2: A larger, older *Welwitschia mirabilis*. The leaves have split many times and have piled atop themselves. Photo by Alex Dreyer, CC-BY-NC.



Figure 7.3.3: Megastrobili of the female *Welwitschia mirabilis*. These magastrobili are composed of tightly overlapping megasporophylls. Seeds are produced within these structures. Note the short, woody stem at the base of the plant. Photo by Judd Kirkel, CC-BY-NC.



Figure 7.3.4: A closer view of a megastrobilus. Note the opposite arrangement of the megasporophylls. Photo by Christoph Moning, CC-BY-NC.



Figure 7.3.5: Male *Welwitschia mirabilis* plants produce microstrobili. These are smaller, a bit more red-to-pink, and thinner than the megastrobili. Photo by Luis Querido, CC-BY-NC.



Figure 7.3.6: Microstrobili of a male *Welwitschia mirabilis*. These cones are composed of many overlapping microsporophylls. Pollen is produced within microsporangia held on the microsporophylls. Photo by Peter Weston, CC-BY-NC.

Ephedra spp.



Figure 7.3.7: A thin stem of *Ephedra aspera* showing opposite leaf arrangement of two scale-like leaves. Photo by Fred Melgert / Carla Hoegen, CC-BY-NC.



Figure 7.3.8: Megastrobili of a female *Ephedra distachya*. These structures are swollen and red, making them appear fruit-like. Seeds are produced within these structures. Photo by Ramazan_Murtazaliev, CC-BY-NC.



Figure 7.3.9: Microstrobili of a male *Ephedra californica*. These small structures look like inflorescenses with anthers emerging. From between the microsporophylls, branching structures emerge, topped with yellow pollen. Photo by Fred Melgert / Carla Hoegen, CC-BY-NC.

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7.4: Conifers

Conifers

Conifers are the most species-rich lineage of gymnosperms. From the fossil record, we think there were over 20,000 species of conifers. However, their diversity declined with the dinosaurs. Currently, there are around 600 extant species. These amazing plants represent some of the oldest, tallest, and most massive organisms on the planet. Though currently low in diversity, these amazing plants make up 30% of Earth's forests. Conifers share the following characteristics:

- Monoecious. Plants produce both male and female strobili on the same plant.
- Wind pollinated with "winged" pollen (air sacs)
- Xerophytic leaves with a low surface area to volume ratio. Primarily evergreen, but some species are deciduous (ex. Dawn redwood and larch).

Note: The Pinaceae is currently the largest family of conifers, so many of our examples for this group of gymnosperms will be from the type genus *Pinus* (pines).

Seeds & Pollen

Seed Cones



Figure 7.4.1: The two images above show seed cones, also called megastrobili. The first shows a Douglas-fir cone shows off its sterile bracts, which are found below the ovuliferous scales and stick out quite far in this species. In the second image, a seed cone from a Jeffrey pine does not have visible bracts but it does showcase a pointy umbo (B) at the tip of the ovuliferous scale (A). Dual markings where two seeds developed on each scale (C). The area that we can see in the image is where the wing of the seed sat. Photos by Maria Morrow, CC BY-SA.

The megastrobilus, or seed cone, contains diploid megasporocytes that are produced within a megasporangium.

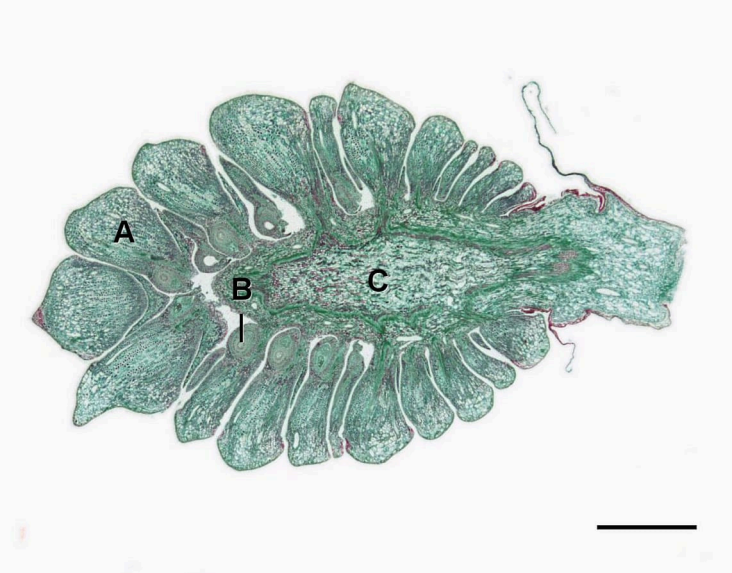


Figure 7.4.2: A micrograph of a longitudinal section through a yearling *Pinus* megastrobilus, labeled as follows: A=Ovuliferous scale, B=Megasporaphyll, C=Cone axis. Many ovuliferous scales surround the cone axis. Each scale has a megasporangium at its base, where it connects to the axis. Scale=1.0mm. Image by Jon Houseman, CC BY-SA, via Wikimedia Commons.

Each megasporocyte (also called a megaspore mother cell) undergoes meiosis. Only one of the four cells produced will survive to develop into a megagametophyte and the other three will die.

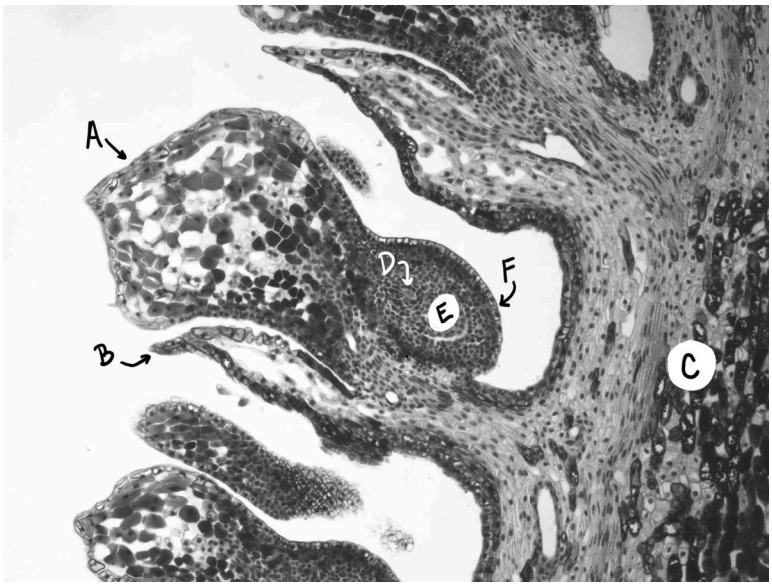


Figure 7.4.3: A long section through a megastrobilus allows us to see what is happening on each ovuliferous scale (A). The sterile bract (B) emerges below each scale. On top of the scale, toward the cone axis (C), the megagametophyte (D, this is likely in the megaspore mother cell stage, pre-megagametophyte formation) develops within the megasporangium (E). The megasporangium is surrounded by a protective layer called the integument (F). Photo by Maria Morrow, CC BY-SA.

The megagametophyte is part of the ovule and contains archegonia, each with an egg cell inside. The megagametophyte is retained within the megasporangium, which becomes the nucellus. Surrounding the nucellus is the integument, which is initially continuous with the ovuliferous scale and has a small opening called a micropyle.

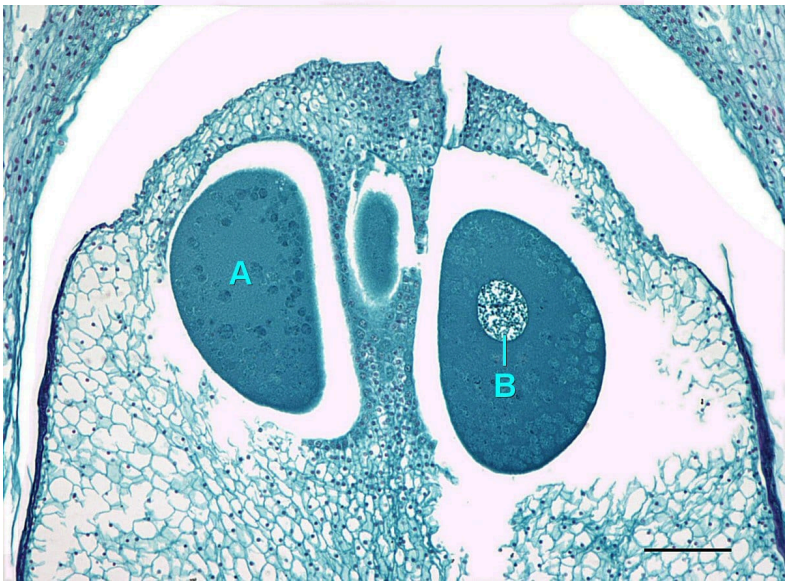


Figure 7.4.4: The first image is a micrograph of a *Pinus* ovule, labeled as follows: A=Gametophyte, B=Egg cell, C=Micropyle, D=Integument, E=Megasporangium. The integument lines the outside with a small hole at the tip (micropyle). Inside the integument is the megasporangium. The megasporangium surrounds the gametophyte, which has two egg cells within it, on the end closest to the micropyle. Scale=0.8mm. The second image is a closer view, showing the eggs within the megagametophyte, labeled as follows: A=Egg cell, B=Egg nucleus. The eggs are large and one has a nucleus visible. Scale=0.31mm. Images by Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

A grain of pollen will be transported on the wind and, if lucky, it will land on a seed cone. The seed cone has a drop of sugary liquid that it secretes, then retracts, pulling the pollen in toward the ovule. This stimulates the tube cell to germinate a pollen tube, while the generative cell divides by mitosis to produce two sperm. These sperm travel down the pollen tube, through the micropyle, and into an archegonium where one will fertilize an egg. When fertilization occurs, the micropyle closes and the integument becomes the seed coat.

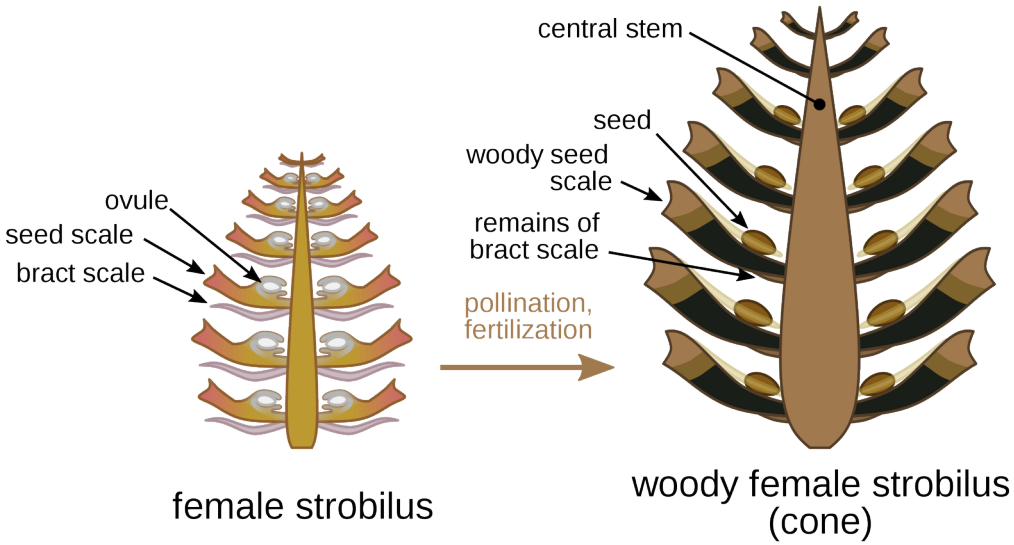


Figure 7.4.5: The megastrobilus before (left) and after (right) fertilization. In the unfertilized cone on the left, there is an ovule on top of each ovuliferous scale. In the fertilized cone on the right, the ovule has become a seed, the cone has become woodier, and the sterile bract has been reduced. Image by Nefronus, CC BY-SA, via Wikimedia Commons.

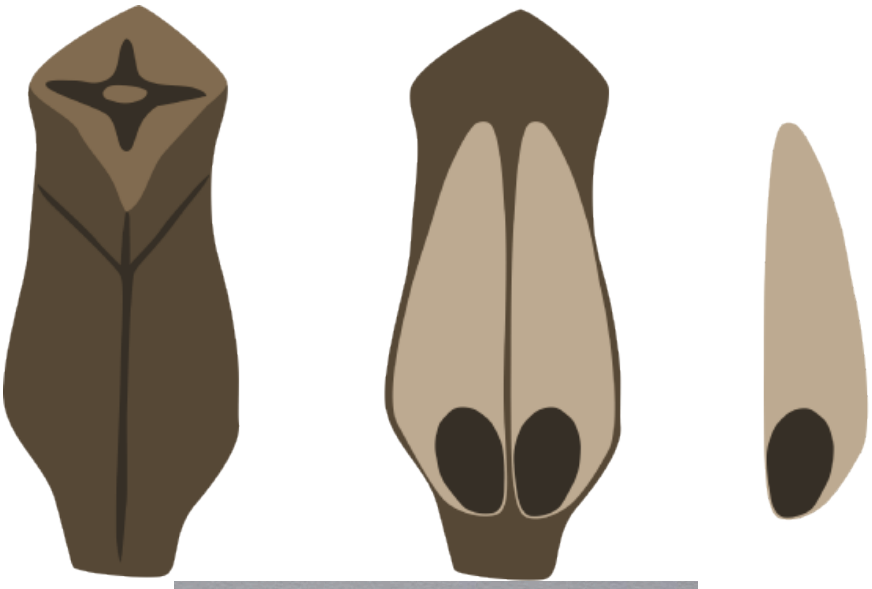


Figure 7.4.6: On the left is a drawing of an individual seed scale from a mature cone of the scots pine (*Pinus sylvestris*). Two winged seeds are located on each scale. In the image on the right, there are eight pine seeds from the same species. Just like in the drawing, the dark, oval region at the base is the seed and the rest of the tissue (tan) is the wing. First image by Dpaczesniak, CC BY-SA, via Wikimedia Commons. Second image is licensed under the Creative Commons Attribution-Share Alike 3.0 Unported license.

The zygote will grow and develop as an embryo, nourished by the megagametophyte tissue, as well as the nucellus. If you look in a long section of a pine seed, you can see the embryo's RAM and SAM. The seed will be dispersed by wind or animals and germinate to grow into a diploid pine tree once again.

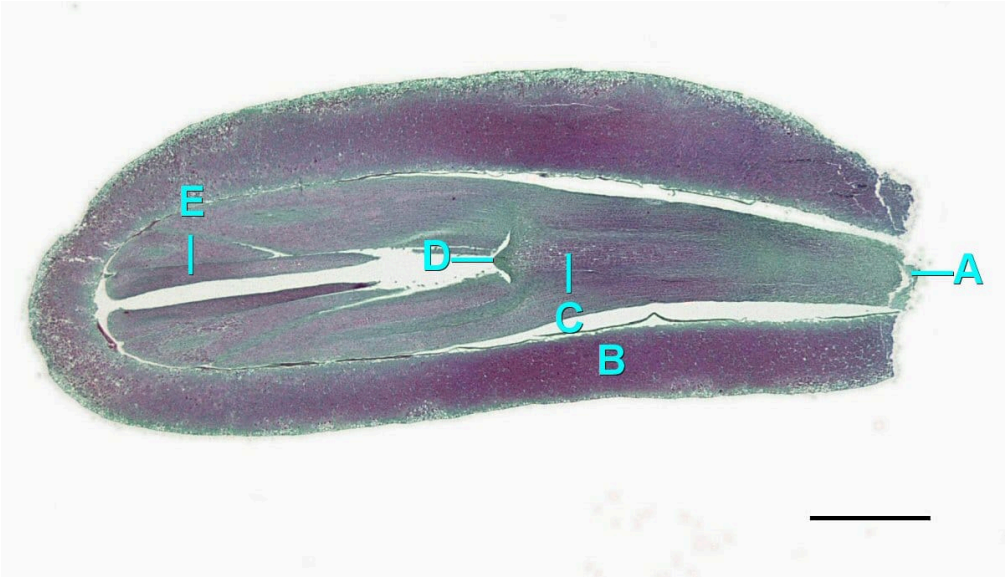


Figure 7.4.7: A longitudinal section through a fertilized pine seed. The embryo is developing within the integument, labeled as follows: A=Root cap, B=Integument, C=Hypocotyl-root axis, D=Shoot apical meristem, E=Cotyledons. The integument forms the outer layer, surrounding the embryo. The embryo has a root cap at one end, connected to the shoot apical meristem by the hypocotyl-root axis. Two arm-like cotyledons flank the shoot apical meristem. Scale=1.3mm. Photo by Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

Pollen Cones



Figure 7.4.8: Microstrobili on *Pinus sylvestris*. Unlike the woody seed cones, pollen cones are small, fragile, and ephemeral. Microgametophytes are formed within the microsporangia of the microstrobilus, or pollen cone. These structures are all diploid. Within the microsporangium, there are microsporocytes (also called microspore mother cells), diploid cells that undergo meiosis to produce haploid microspores. Microspores grow by mitosis into microgametophytes, AKA pollen. Author unknown (possibly Beentree), CC BY-SA.

The microgametophyte in gymnosperms is the four-celled, "winged" pollen grain. Within the pollen grain, you can distinguish the generative cell and the tube cell nucleus. The two prothallial cells are not apparent under the microscope. On either side of the pollen grain, two ear-like structures emerge. These air sacs may help orient the pollen grain toward the ovule.

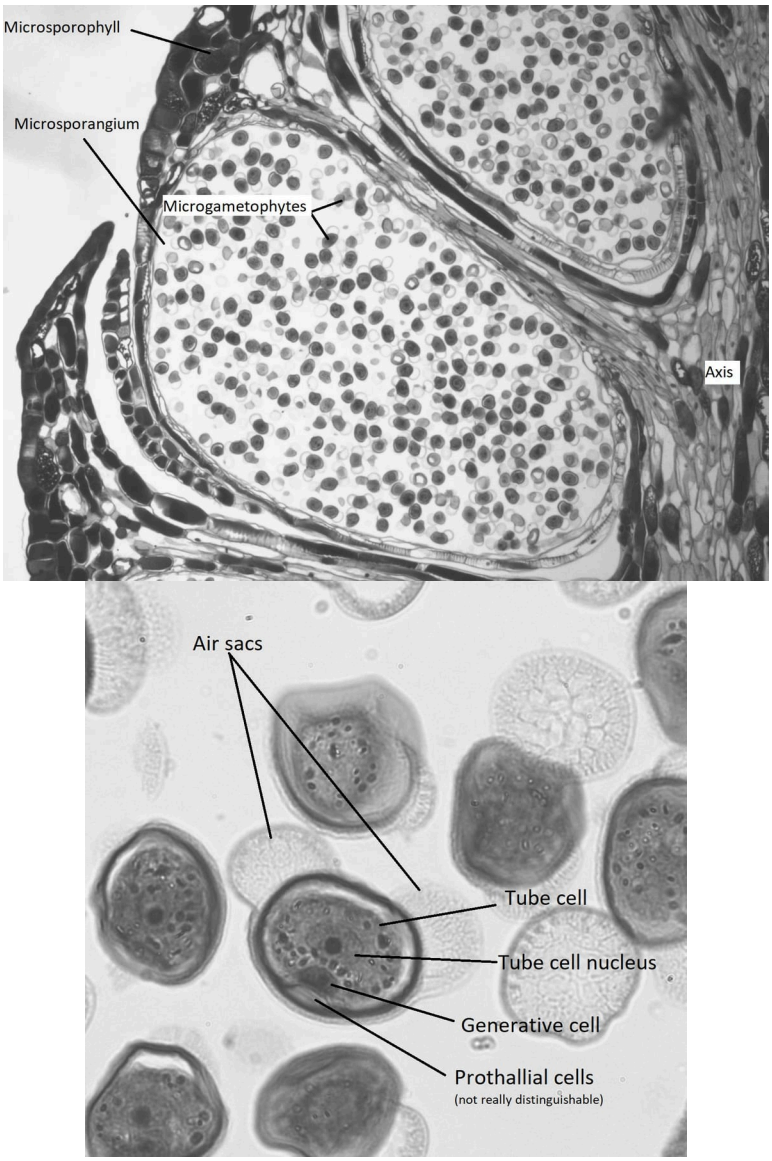


Figure 7.4.9: The first image is a long section through a pine microstrobilus that shows inside a microsporangium. Each microsporangium is produced on a leaf-like structure called a microsporophyll that emerges from the cone axis. Within the microsporangium, many mature pollen grains are visible. You can tell the pollen grains are mature at this magnification by the presence of the air sacs. In the second image, we see a closer view of pollen grains. The two ear-like air sacs flank the four cells enclosed in the center: the tube cell, generative cell, and two prothallial cells. The tube cell takes up most of the internal space and its nucleus is about the same size, if not a little bigger, than the entire generative cell. The two prothallial cells are squished against the edge opposite the air sacs and are not really distinguishable in this image. Photos by Maria Morrow, CC BY-SA.

Secondary Growth

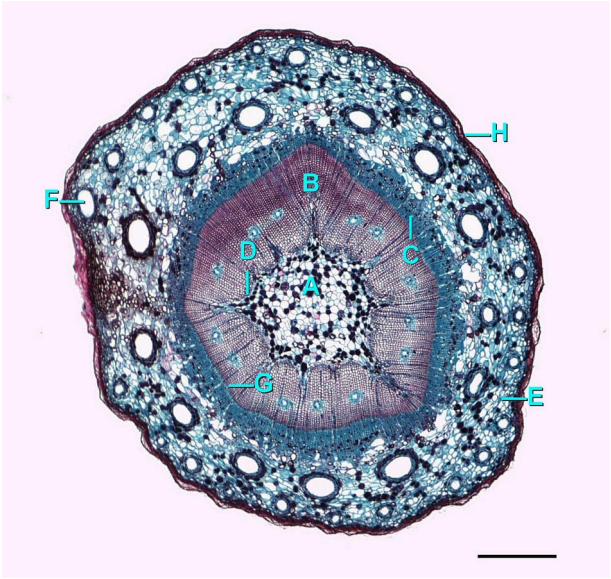


Figure 7.4.10: A cross section of a one-year *Pinus* stem undergoing secondary growth, labeled as follows: in the center is A=Pith, which is surrounded by B=Secondary xylem, C=Secondary phloem forms a ring around the secondary xylem (the vascular cambium would be found between these two layers). Some D=Primary xylem is found near the pith. A layer of E=Cortex surrounds the vascular tissue and pith, dotted with several F=Resin ducts. G=Vascular cambium, H=Epidermis, which is around the outside. Scale=0.625mm. Image by Jon Houseman, CC BY-SA, via Wikimedia Commons.

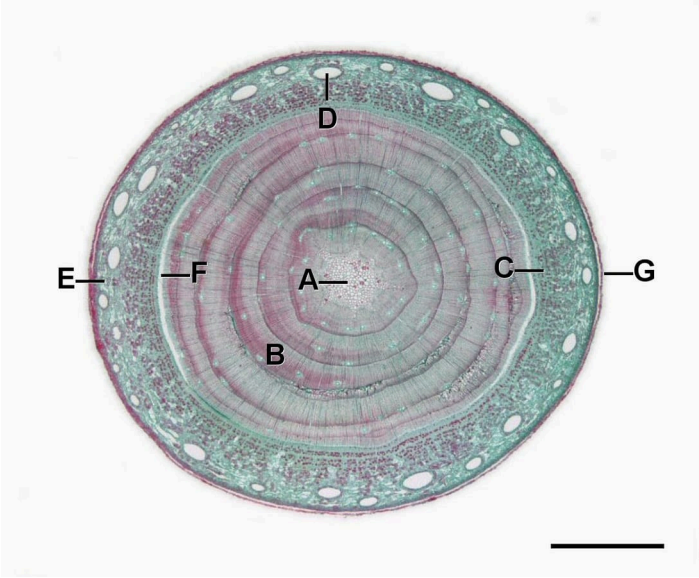


Figure 7.4.11: A cross section of a mature *Pinus* stem, labeled as follows: A=Pith, B=Secondary xylem, C=Primary phloem, D=Resin duct, E=Cortex, F=Vascular cambium, G=Epidermis. Scale=0.7mm. Image by Jon Houseman, CC BY-SA, via Wikimedia Commons.

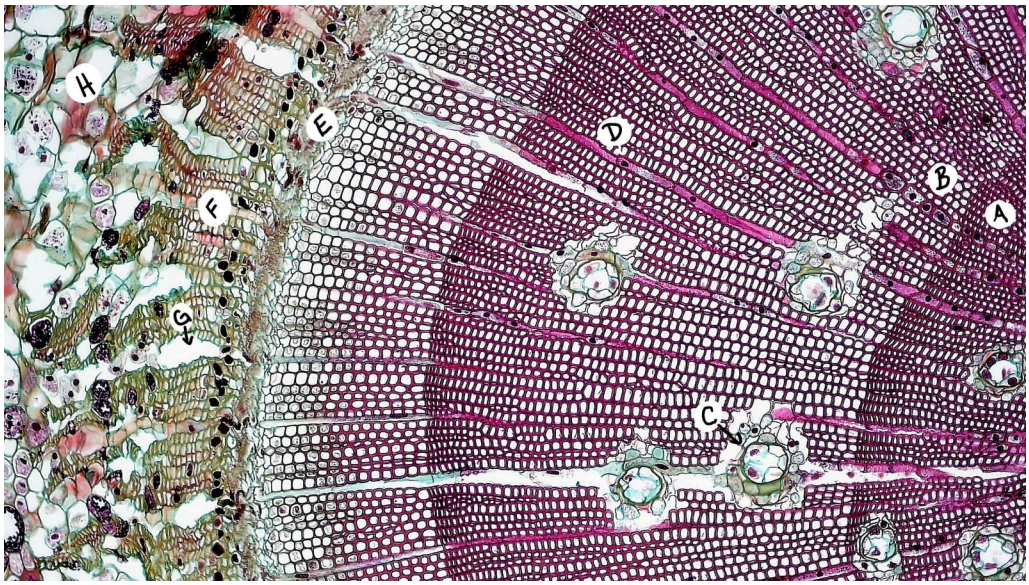


Figure 7.4.12: A closer view (100x) of some of the tissues in a mature *Pinus* stem cross section, labeled as follows: A and B are part of the secondary xylem, A=Late wood with densely packed, small tracheids, B=Early wood with larger diameter tracheids, C=Resin duct, D=Xylem ray, E=Vascular cambium, F=Secondary phloem, G=Phloem ray, H=Cortex. From the original figure caption: "During the first year of growth the cutinized epidermis is replaced by protective growth of cork rich periderm. The outer periderm consists of layers of cork cells, the phellem, which produces waterproofing suberin. Cork cells are dead at maturity. Deep to the phellem is a living layer of cork cambium or phellogen and beneath that, layers of cork parenchyma or phelloderm. Many cells in the periderm contain dark staining tannins. The cortex is divided into a thin outer hypodermis of lignified sclerenchyma cells and thicker inner cortex of thin walled parenchyma cells containing chloroplasts. Large resin ducts are surrounded by secretory parenchyma that produces resins and turpentines. Some cells enlarge into dark staining tyloses. Both endoderm and pericycle are inconspicuous. The vascular cylinder or stele in young stems consists of a ring of vascular bundles interspaced with medullary rays of parenchyma cells. Seasonal activity of the cambium replaces the isolated vascular bundles with well-defined annual rings of secondary phloem and xylem. Xylem is endarch with protoxylem found towards center of the stem and younger metaxylem towards the periphery of the stem. Protoxylem consists of annular and spiral tracheids with only tracheids found in metaxylem. True xylem vessels are lacking. Because of the greater production of xylem, the vascular cylinder is dominated by radially arranged rays of secondary xylem interspaced with medullary rays of parenchyma cells. Conspicuous resin ducts are present throughout the xylem. Phloem is endarch but annual growth the of stem makes it difficult to distinguish between older protophloem to the periphery and younger metapholem towards center of the stem. Phloem lacks companion cells, consisting entirely of sieve tubes and phloem parenchyma. Medullary rays in the secondary phloem include protein rich albuminous cells. A well-defined pith of parenchyma cells is occasionally interrupted by a few large resin ducts. Visit the BCC Bioscience Image featuring the Microscopic World of Plants. Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons with labels added by Maria Morrow.

Xerophytic Leaves

Xerophytic leaves are adapted to withstand drought conditions. In conifers, we see a wide range of xerophytic leaves with different morphologies that can be shaped by their local environment. Consider the leaves of the coast redwood and the giant sequoia, shown below. Though these two trees belong to different genera--*Sequoia* and *Sequoiadendron*, respectively--they are sister taxa. However, the coast redwood has adapted to life on the coast, where the giant sequoia has evolved in inland, higher elevation forests with much more extreme climatic conditions. How can this be seen in the structure of their leaves?



Figure 7.4.13: The image on the left shows the adaxial (upper) side and the image on the right shows the abaxial (under) side of coast redwood leaves. Note that, particularly in the photo on the left, the leaves look shiny. This is due to the presence of a thick cuticle. The stomata are also concentrated on the underside of the leaf, as indicated by the black arrow in the image on the right. They are clustered in two silvery rows on each leaf, called a stomatal bloom. However, for xerophytic leaves, these are relatively flat, with a fairly standard surface area to volume ratio. Photos by Maria Morrow, CC BY-SA.

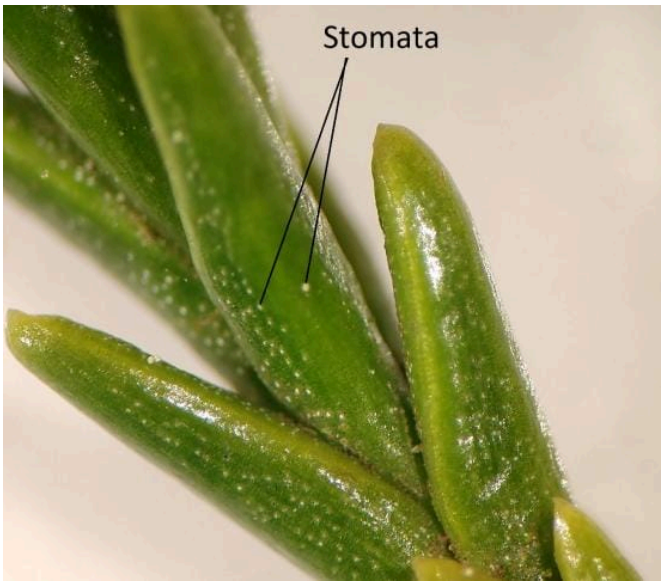


Figure 7.4.14: These giant sequoia leaves were retrieved from a tree planted in a coastal environment, so the differences here represent evolutionary history, alone. Much like the coast redwood, these shiny leaves have a thick cuticle. The big difference to note is the thickness of these leaves, maintaining a much lower surface area to volume ratio than the coast redwood. The second thing to note is the orientation of the leaves. They are held much more closely together, reducing exposure to the wider environment. Two stomata are indicated in the image, though there are many. They are present on both adaxial and abaxial leaf surfaces. Photo by Maria Morrow, CC BY-SA.

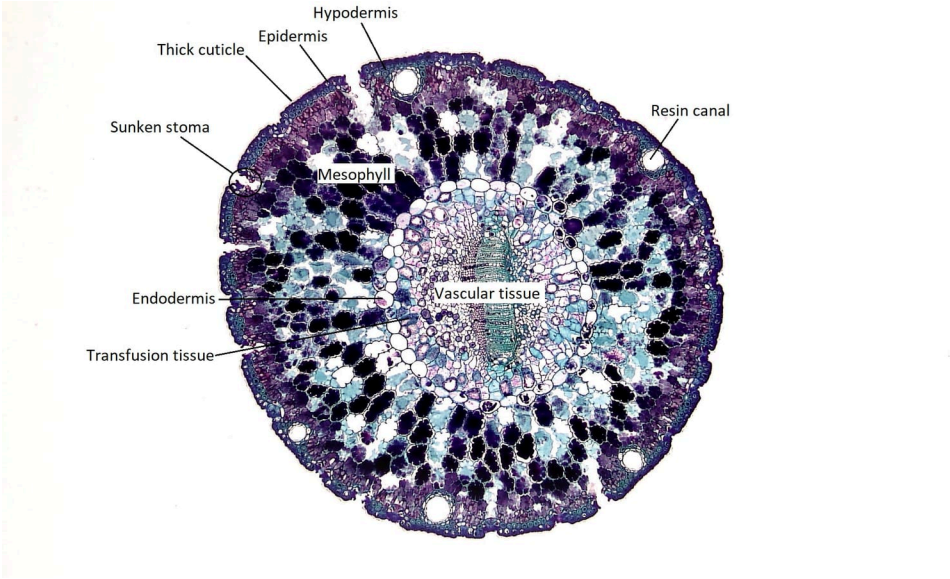


Figure 7.4.15: Most pine needles you see in botany are flat on one side, however, they also come in round. The tissues of this xerophytic leaf are labeled in the diagram. A thick cuticle surrounds the outside, coating the epidermis. Beneath the epidermis are several layers of tightly packed, small cells: the hypodermis. Stomata are sunken, located within the hypodermis. Under the hypodermis are the highly invaginated mesophyll cells. Further to the inside is a suberized ring of cells called the endodermis, just like in the root, which surrounds the vascular tissue. Transfusion tissue is located between the endodermis and the vascular tissue. There are also resin canals that ring the needle, appearing as holes surrounded by small cells. These secrete resin to protect the plant. Image by Fayette A. Reynolds M.S., Public Domain with labels added by Maria Morrow.

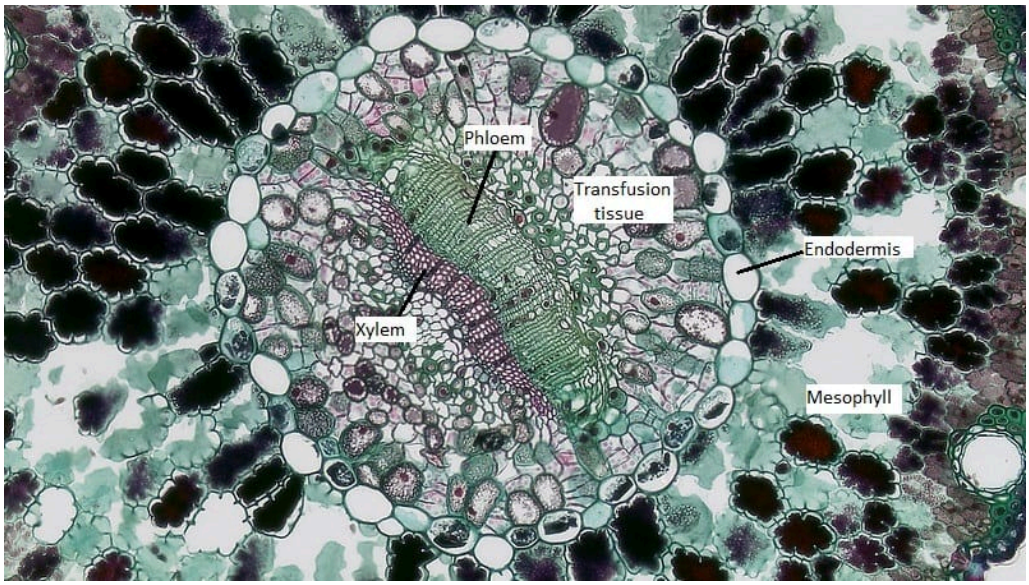


Figure 7.4.16: A close up of the vascular tissue from the image above. The xylem is composed of ranks of red-stained tracheids and is located to the left of the phloem. Image by Fayette A. Reynolds M.S., Public Domain with labels added by Maria Morrow.

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7.4.1: Pine Life Cycle

This video is an extremely helpful narrated animation of the pine life cycle. I recommend watching this video or some other walkthrough of the pine life cycle before attempting to interpret the complex diagram below.

YouTube Video

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

Video 7.4.1.1: A narrated video of the pine life cycle, sourced from YouTube.

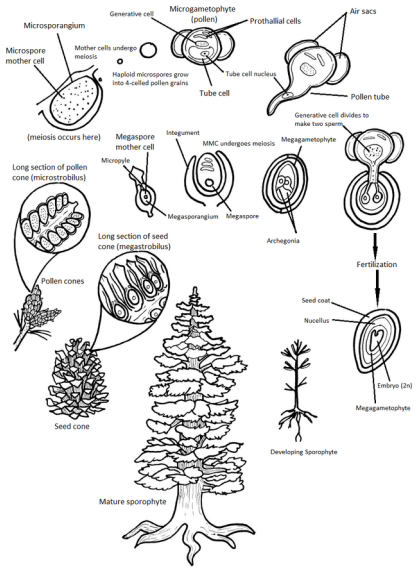


Figure 7.4.1.1: This is an illustrated diagram of the pine life cycle. Starting at the bottom of the image, there is a pine tree. This is the mature sporophyte (2n). It will produce both seed cones and pollen cones because it is monoecious. Seed cones will produce two megasporangia on each ovuliferous scale, each one surrounded by an integument. Within the megasporangium, a megaspore mother cell (2n) undergoes meiosis to produce four megaspores (n). Three die and one remains, developing by mitosis into the megagametophyte. The megagametophyte produces two archegonia, each with an egg. This trajectory occurs through the center of the diagram. Jumping back to the pollen cone, microsporangia are produced on each microsporophyll of the pollen cone. Initially, they are filled with microspore mother cells (2n) that then undergo meiosis to produce microspores (n). These microspores grow by mitosis (though only two rounds) into 4-celled microgametophytes: pollen. Each pollen grain is composed of two ear-like air sacs on the outside, a large tube cell, a small generative cell, and two tiny prothallial cells. The mature pollen grains are dispersed on the wind to seed cones where the tube cell will form a pollen tube into the megagametophyte by entering through a gap in the integument called the micropyle. The generative cell divides to produce to sperm cells, which travel down the pollen tube to fertilize an egg. Once fertilized, the integument closes, forming the seed coat. The embryo develops within the seed, consuming the megagametophyte and the megasporangium (now called the nucellus) as it grows. The seed is dispersed and, if in the right conditions, the embryo emerges from the seed coat and develops into a mature sporophyte. Diagram by Nikki Harris CC BY-NC with labels added.

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8: ANGIOSPERMS

The exact timing of the emergence of angiosperms is unknown, so it is difficult to relate their evolution to specific climatic conditions or other circumstances. However, there is relatively new fossil evidence of flowering plants as early as the Jurassic period, 174 mya. This was the age of the dinosaurs and coincides with the emergence of the first feathered dinosaurs -- birds! Angiosperms represent a single origin of related organisms, the phylum Anthophyta, that experienced an exceptional radiation in species. As of 2019, there are approximately 370,000 known extant species. Most of the plants that you see, eat, and otherwise interact with in your daily life are likely to be in this group.

Angiosperms can be distinguished from other plant groups by the production of **flowers**. These collections of modified leaves allowed angiosperms to attract pollinators and increase the chances of successful fertilization. Over time, angiosperms evolved different flower morphologies, smells, and colors that corresponded to their particular pollinators. These sets of characteristics, called **pollination syndromes**, allow scientists to predict the pollinators for different plants.

Once pollinated, the fertilized seeds are encased in a protective ovary whose structure can be specialized for different methods of dispersal, such as animal ingestion, animal attachment, flotation, or wind dispersal. This protective ovary and the encased seed(s) are more commonly called a **fruit**. Inside the developing seeds, angiosperms provide an additional food source to the developing zygote, the **endosperm**.

In the xylem, this group of plants evolved large diameter conducting cells for rapid water uptake called **vessel elements**, though this made them vulnerable to freezing conditions. In the phloem, sieve cells evolved into **sieve tube elements** with their associated **companion cells**, increasingly specialized for transportation of photosynthates.

8.1: Flower Anatomy

8.2: Flower Morphology

8.3: Monocots vs. Eudicots

8.4: Inflorescence Types

8.5: Fruits

8.6: Life Cycle

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8.1: Flower Anatomy

Flowers are composed of many distinct components: sepals, petals, stamens, and carpels. These components are arranged in whorls and attach to an area called the **receptacle**, which is at the end of the stem that leads to the flower. This stem is called the **peduncle**. In the case of an inflorescence, where multiple florets are produced in place of a single flower, the stems leading to the florets are called pedicels.

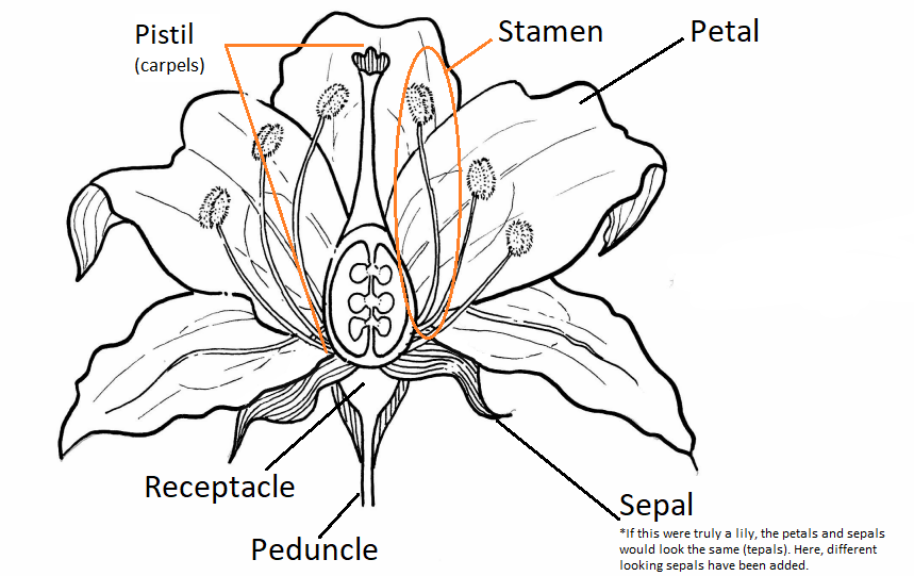


Figure 8.1.1: This diagram shows a long section through a flower. Starting from the bottom, there is a stem called the peduncle. The peduncle terminates in a region called the receptacle, where all of the parts of the flower are attached. Sepals are found on the outside of the flower, two are visible here, with petals located just within the ring of sepals. There are five petals visible. Inside the petals, six stamens encircle a central pistil (composed of fused carpels). Diagram by Nikki Harris CC BY-NC with labels added.

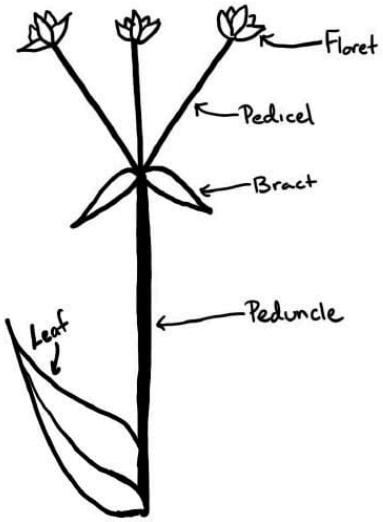


Figure 8.1.2: An image of an *Allium* inflorescense. Many small florets on stalks (pedicels) emerge from a central point at the tip of the peduncle. At this junction, papery leaves (bracts) can be seen. These features are labeled in a sketch shown to the right of the image. Photo by ramazan_murtazaliev, CC-BY-NC. Sketch by Maria Morrow, CC BY-NC.

Whorls

Flowers are composed of sets of highly modified leaves arranged in whorls. The outermost whorl of a flower is called the **calyx** and is composed of **sepals**. Inside the calyx is the **corolla**, which is composed of **petals**. The sepals are often smaller and less colorful than the petals, but this general rule can be misleading. For example, lilies often have identical sepals and petals. The only way you can distinguish between them is by location: Which whorl is on the outside?

Together, the calyx and corolla are called the **perianth** (peri- meaning around, anth- meaning flower).

The Perianth: Calyx and Corolla

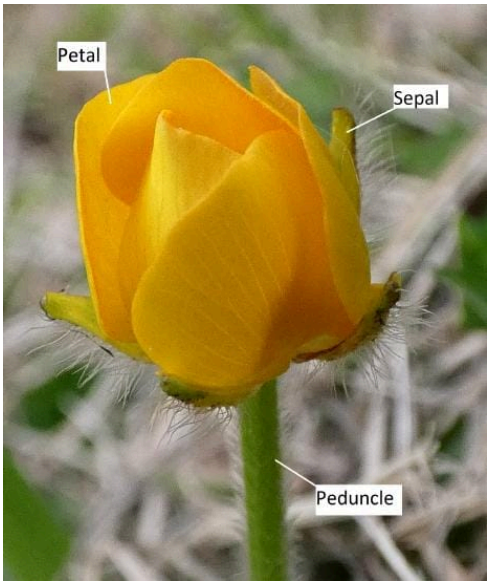


Figure 8.1.3: A closed buttercup (*Ranunculus* sp.) flower shows the entire perianth. The sepals are smaller and covered in long trichomes. There are four sepals visible. Inside the sepal whorl (calyx), there are five overlapping, yellow petals. These petals form the corolla. Photo by Maria Morrow, CC BY-NC.

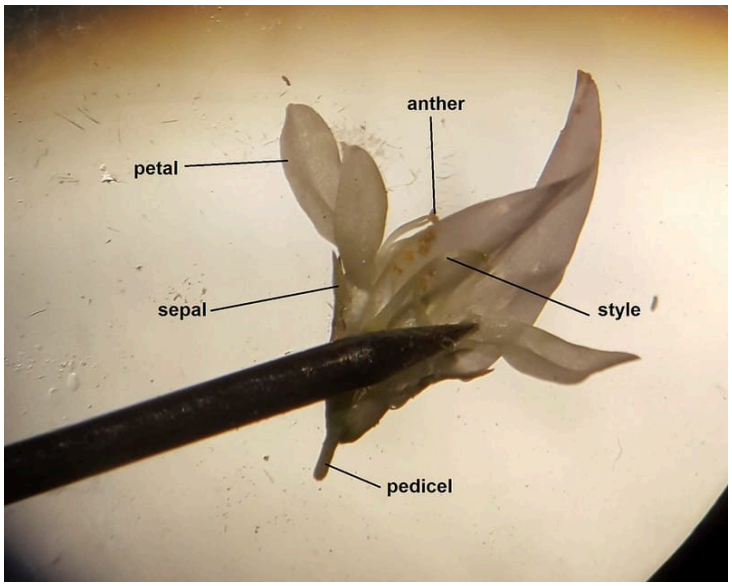


Figure 8.1.4: Dissecting a flower is often necessary to see all parts of the flower. This floret has been cut in half and is being held down by a sharp probe. The sepals are short and pointed, the petals are longer and rounded. Because this is a floret, the stem leading up to it is called a pedicel instead of a peduncle. Photo by Melissa Ha, CC BY-NC.

Reproductive Parts: Androecium and Gynoecium

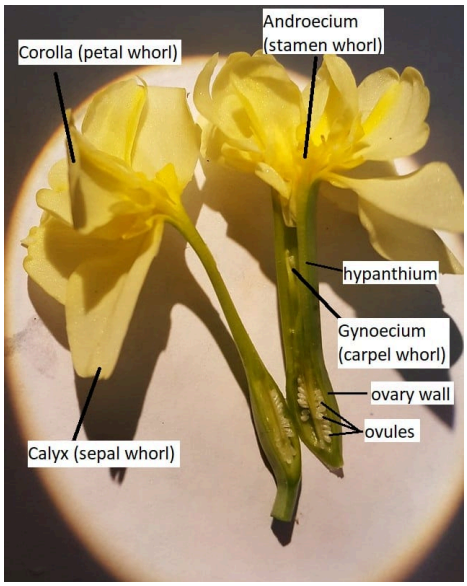


Figure 8.1.5: A dissected flower with all whorls labeled. The petals and sepals look the same, but can be distinguished by location. The stamens are similar in color to the perianth, located just inside the calyx. The gynoecium of this flower is located deep within a structure called a hypanthium, where all of the other floral whorls have fused together. The ovary is at the base of the hypanthium and is full of small, white ovules. Photo by Melissa Ha CC BY-NC with labels added.

Inside the perianth is the **androecium** (house of man), a whorl composed of **stamens**. Each stamen has a long **filament** holding up pollen sacs called **anthers**. Inside the androecium is the **gynoecium** (house of woman), which is composed of **carpels**. Each carpel has an **ovary** at the base where **ovules** are housed. The **style** emerges from the ovary and is topped by the **stigma**. Pollen grains land on the stigma and must grow a tube down the style to reach the ovule and complete fertilization.

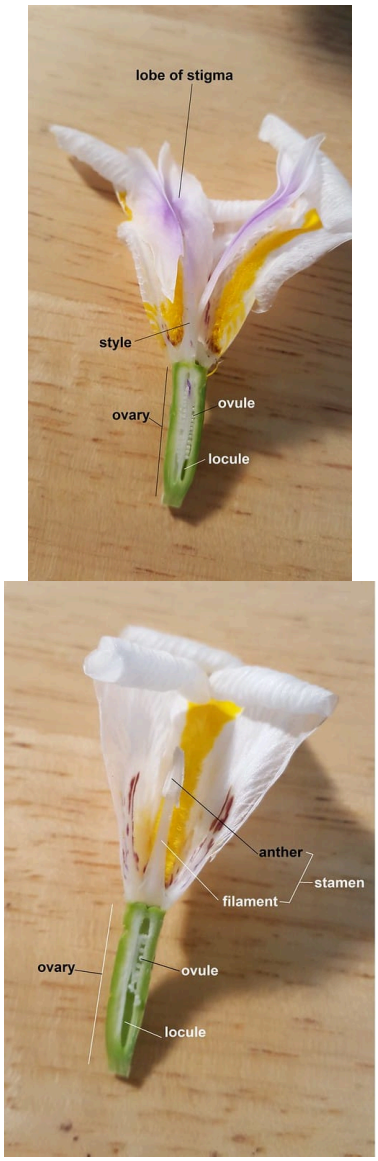


Figure 8.1.6: Here we see two sides of the same flower, which has been cut in half lengthwise. The first image shows the gynoecium, including two styles that fan out like wings toward the top where the stigma lobes are located. At the base of the styles, there is an elongated green ovary with many small white ovules inside. Each compartment of the ovary is called a locule. In the second image, the ovary is labeled, as well as the components of the androecium, including the anther and filament, which comprise the stamen. The anther is located at the end of the filament. Photos by Melissa Ha, CC BY-NC.

Androecium: The Stamen Whorl

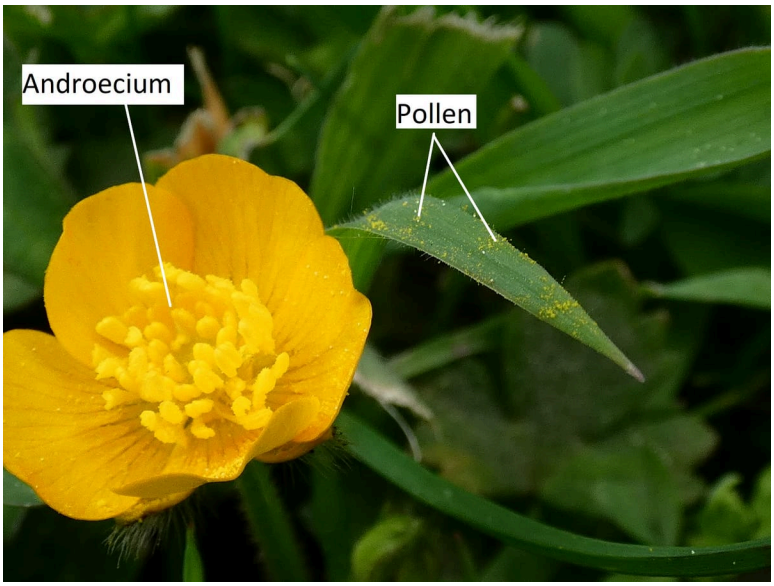


Figure 8.1.7: This buttercup has many stamens in the androecium. The anthers are flattened, long, and yellow. Yellow pollen grains produced within the anthers are scattered on the surface of an adjacent blade of grass. Photo by Maria Morrow, CC BY-NC.

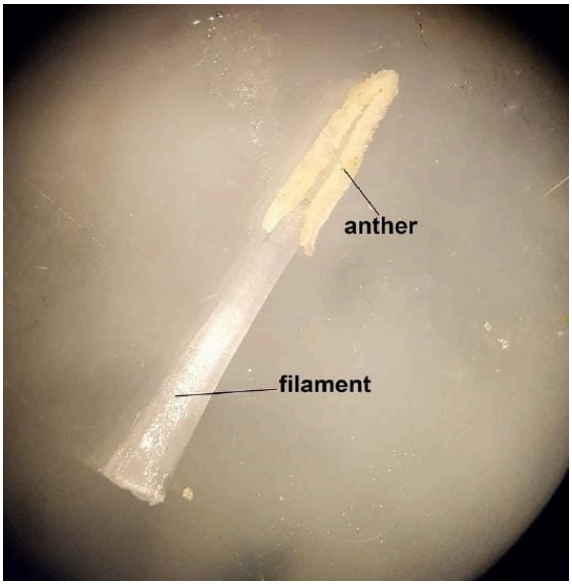


Figure 8.1.8: A single stamen that has been removed from a flower. The filament is long and flattened. At the end of the filament, there is an anther that has split partially open, releasing pollen grains. Photo by Melissa Ha, CC BY-NC .

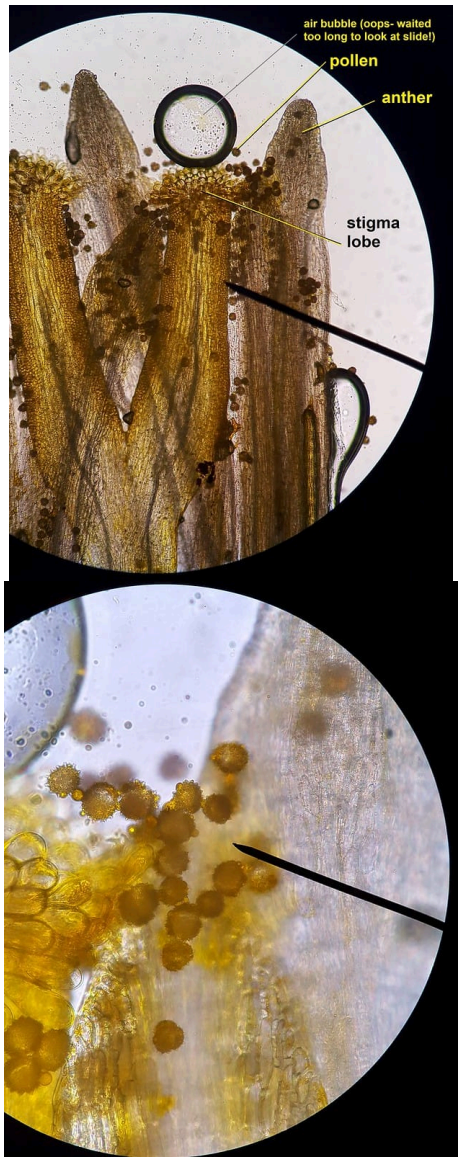


Figure 8.1.9: The image on the left shows two stigma lobes surrounded by anthers. The stigma lobes are covered in pollen. The image on the right shows the pollen at a higher magnification. The walls of the pollen are bumpy from ornamentation. Many species have characteristic pollen shapes and ornamentation that allow for identification of the plant species from the pollen grain, alone! Photos by Melissa Ha, CC BY-NC .

Gynoecium: The Carpel Whorl

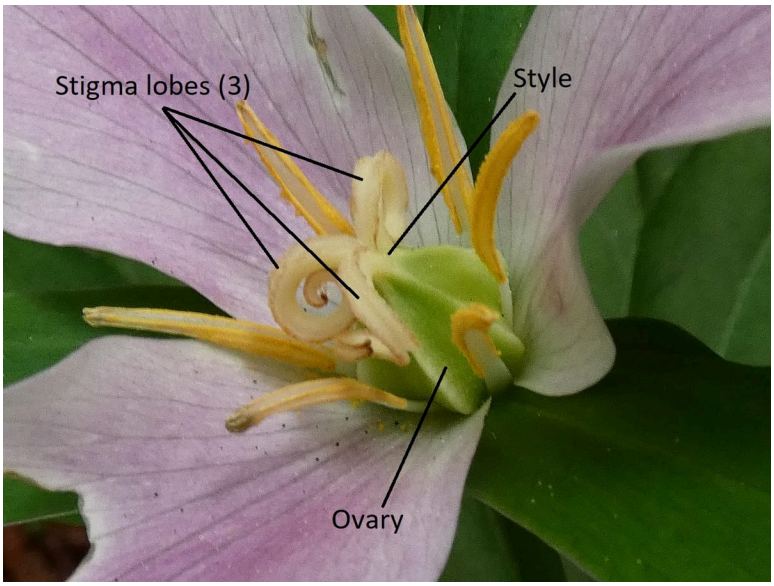


Figure 8.1.10: All of the whorls of this *Trillium* flower are visible in this picture. The sepals are on the exterior and green. The three petals are a light pink. There are six stamens, each with much longer anthers than filaments. The stamens encircle the enlarged ovary of this fertilized flower, which is grooved and beaked into an odd shape. A short style connects the ovary to three long, curling stigma lobes. Is this flower a monocot or eudicot? Photo by Maria Morrow, CC BY-NC.

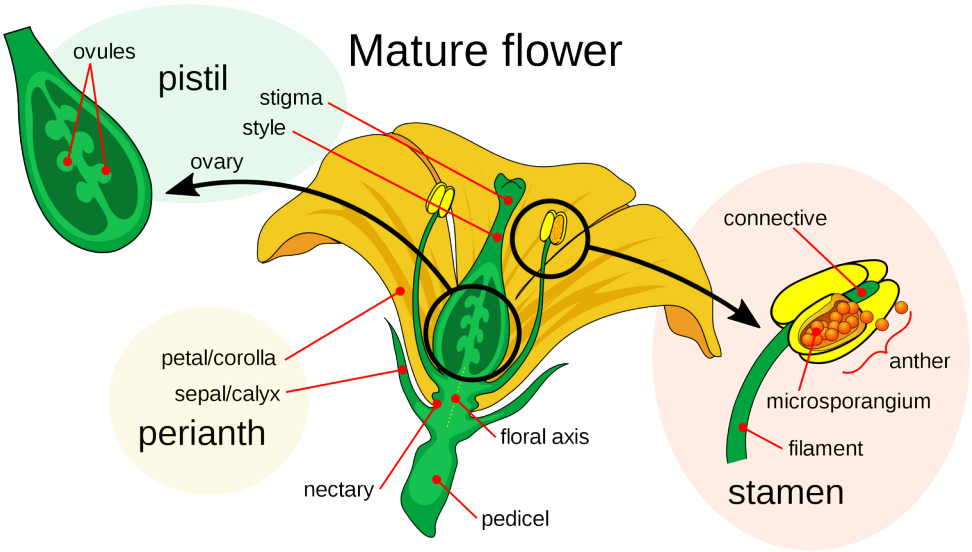


Figure 8.1.11: A syncarpous gynoecium in context. The gynoecium (whether composed of a single carpel or multiple "fused" carpels) is typically made up of an ovary, style, and stigma as in the center of the flower. Image by LadyofHats, Public domain, via Wikimedia Commons.

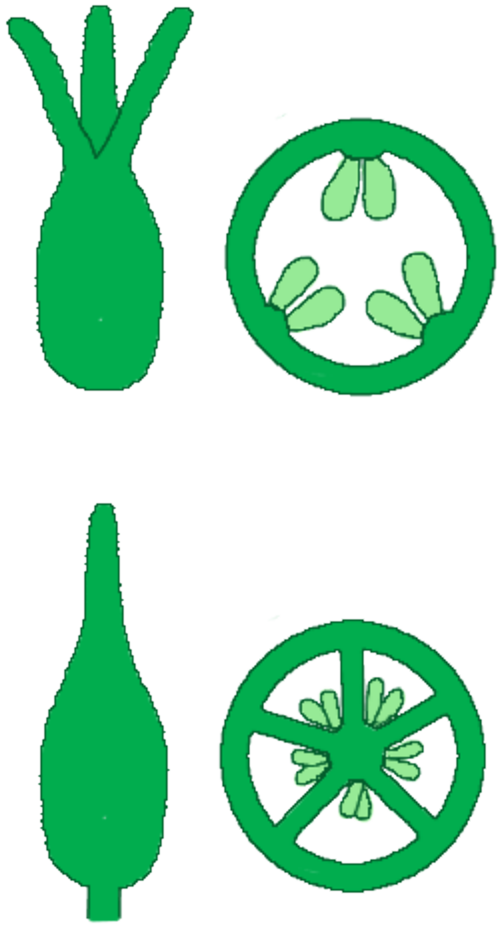


Figure 8.1.12: In an apocarpous gynoecium, the carpels are not fused together. The illustrated gynoecium on the left has three free carpels. A cross section of the ovaries shows the ovules inside. The gynoecium shown in the center is syncarpous, with fusion of the ovaries. A cross section of the ovary shows three sets of ovules. The gynoecium on the right is fully syncarpous with fusion of all parts (stigma, style, and ovary). The ovary cross section is divided into five distinct locules. Images by Michael G. Simpson. Redrawn and color: User:RoRo, Public domain, via Wikimedia Commons.

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8.2: Flower Morphology

Flowers are sets of highly modified leaves that function to attract a pollinator or, if no animal pollinator is used, to optimize spore dispersal in some way. Over the course of evolutionary history and coevolution, this has lead to an incredible diversity of shape, size, color, smell, and just about any other characteristic you can think of. Because most plants are angiosperms and because flowers are often so diverse, learning the terminology to describe flowers is a major step in learning to identify plants.

Floral Symmetry

Flowers that have multiple lines of symmetry (like a starfish) are **radially symmetrical**, also called actinomorphic. Flowers with only a single line of symmetry (like you) are **bilaterally symmetrical**, also called zygomorphic.

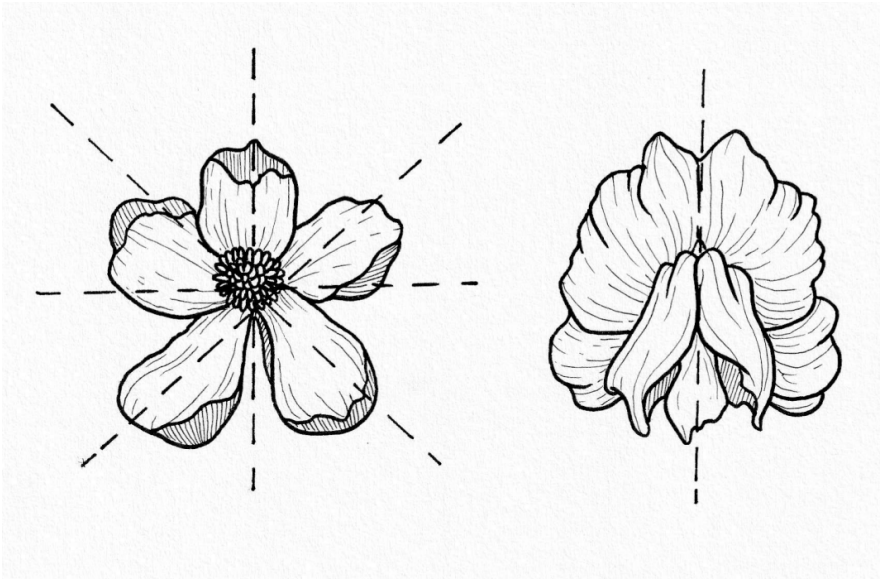


Figure 8.2.1: On the left is a picture of a radially symmetrical flower. It has five petals that all radiate out from a central point, like a star. We can draw many lines of symmetry through this flower, where if we folded the flower along that line, the two sides would line up with each other. (Note: There may be a line out of place here. Can you find it?) On the right is a bilaterally symmetrical flower. Only one line of symmetry can be drawn through this flower. Much like for humans, this flower is mirrored from side to side, but not top to bottom or any other direction. Diagram by Nikki Harris, CC BY-NC.

Radial Symmetry (Actinomorphic)



Figure 8.2.2: These are two duplicate images of the same flower. This *Trillium* flower has three lines of symmetry: one that travels from the tip of each petal down between the remaining two petals. The lines are drawn in on the picture on the right so you can compare. Photos by Maria Morrow, CC BY-NC.



Figure 8.2.3: Just as with the set of images above, these are two duplicate images of the same flower and the image on the right has lines of symmetry drawn in. This salmonberry flower has five lines of symmetry, though only three have been drawn in. Can you find the other two? Photos by Maria Morrow, CC BY-NC.

Bilateral Symmetry (Zygomorphic)



Figure 8.2.4: Again we have two duplicate images, but this one includes several florets. This cluster of bleeding hearts has two florets that each have a line of symmetry added in the image on the right. On each heart-shaped floret, the line travels from top to bottom, dividing it into two equal halves. There are no other lines of symmetry we could draw. Photos by Maria Morrow, CC BY-NC.



Figure 8.2.5: Again we have two duplicate images with the image on the right showing a line of symmetry drawn in. This violet has one larger petal on the bottom with two smaller petals winging out to either side. We can draw one line of symmetry through the center of the larger, lower petal and between the 4 smaller petals (as shown on the right). Due to the presence of the single, larger petal, there are no other lines of symmetry we could draw. Photos by Maria Morrow, CC BY-NC.

Whorls

Most flowers are composed of four whorls. If all whorls are present, a flower is said to be both **complete** and **perfect**. If any whorl is missing, the flower is **incomplete**. If one of those missing whorls is either the androecium (pollen-producing) or gynoecium (seed-producing), the flower is also **imperfect**.



Figure 8.2.6: This wild ginger flower (*Asarum caudatum*) has no corolla. It is incomplete, but it is still perfect. The hairy sepals are fused together at the base, then split into long, pointed tips that extend out like tendrils. These flowers are normally a deep wine red. Photo by mhays, CC-BY-NC.



Figure 8.2.7: This *Sirdavidia solannona* flower has no gynoecium, only tightly packed stamens at the center (a staminate flower). This flower is both imperfect and incomplete. Photo by Thomas L.P. Couvreur (Institut de Recherche pour le Développement , Montpellier, France), CC BY 4.0, via Wikimedia Commons.

Ovary Position

We can use the location of the ovary to further distinguish between flowers. If the other whorls of the flower meet below the ovary (the ovary or ovaries look a bit like an egg or eggs in a nest), the ovary is **superior** (on top of the rest of the flower). This means that the rest of the flower parts are below the gynoecium, so we can also call this flower **hypogynous** (below the gynoecium). The two terms both describe the same situation, but superior refers only to the ovary while hypogynous refers to the flower, in general.

Superior Ovary (Hypogynous Flowers)



Figure 8.2.8: A drawing of a hypogynous flower. The calyx, corolla, and androecium fuse to the receptacle below the gynoecium. The ovary sits on top of these other whorls, a superior ovary. Image by Gustav Hegi (1876–1932), Gustav Dunzinger, Public domain, via Wikimedia Commons.

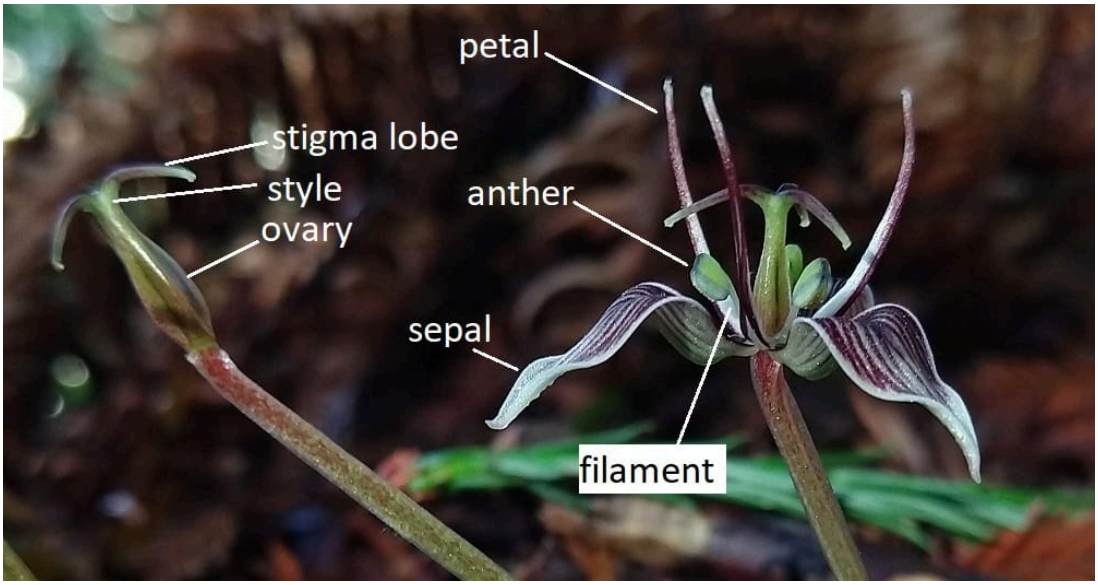


Figure 8.2.9: In the image above, we see two flowers (actually two florets of an underground umbel!) of a fetid adderstongue, *Scoliopus bigelovii*. The one on the left has shed all whorls except the gynoecium. This allows you to see what the gynoecium looks like and where it is positioned in the one on the right. In the complete flower, the sepals, petals, and stamens all meet below the ovary, which sits in the middle like one giant egg in an alien nest. Photo by Maria Morrow, CC BY-NC.

Inferior Ovary (Epigynous Flowers)

In the opposite situation, the other floral whorls join at a point above the ovary. In this case, the ovary is **inferior** and the flower is **epigynous** (on top of the gynoecium).



Figure 8.2.10: A drawing of an epiogynous flower. The calyx, corolla, and androecium fuse together above the gynoecium. The ovary sits below these other whorls, an inferior ovary. Image by Gustav Hegi (1876–1932), Gustav Dunzinger, Public domain, via Wikimedia Commons.

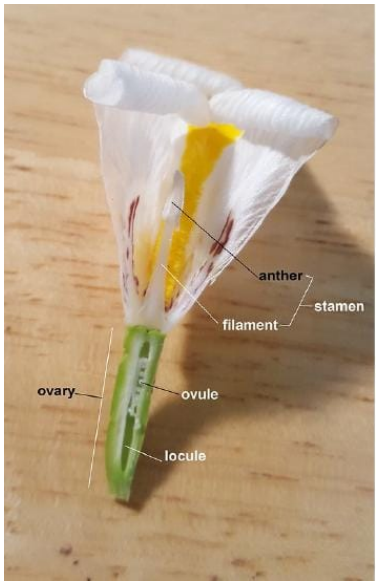


Figure 8.2.11: In this flower, the floral whorls are situated above the ovary, which is the elongated, green tube that contains the ovules. Photo by Melissa Ha, CC BY-NC.

Semi-inferior Ovary (Perigynous Flowers)

As always, there are less clear situations. In some flowers, as in the rose family, the floral whorls join together and fuse at a point above the ovary, then travel down, around, and below the ovary as a fused unit. This fused unit is called a **hypanthium**. The ovary is termed **semi-inferior**, as it is located below the unfused parts of the floral whorls. Because the floral whorls travel around the ovary as the hypanthium, the flower is **perigynous** (peri- meaning around).



Figure 8.2.12: A drawing of a perigynous flower. The calyx, corolla, and androecium fuse together to form a layer of tissue (hypanthium) that surrounds and fuses with the ovary. The ovary appears to sit below the other whorls, but is surrounded by the hypanthium (fused or not), a semi-inferior ovary. Image by Gustav Hegi (1876–1932), Gustav Dunzinger, Public domain, via Wikimedia Commons.

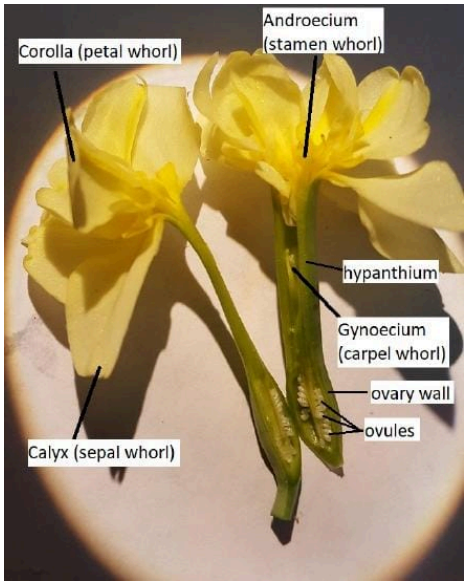


Figure 8.2.13: In this flower, the floral whorls join together where the petals and sepals seem to end. They then form a long, tubular hypanthium that looks much like an inferior ovary from the exterior. However, you can see the actually ovary (filled with ovules) is located only at the base of this structure. Photo by Melissa Ha, CC BY-NC.

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8.3: Monocots vs. Eudicots

Monocots



Figure 8.3.1: Monocots like the grass shown on the left produce only one cotyledon (mono- for one, -cot for cotyledons). Eudicots (on right), also called dicots, get their name from having two cotyledons. Cotyledons are the first, fleshy leaves that enveloped the embryo as it grew. Image from Pengo, CC BY-SA 2.5, via Wikimedia Commons.

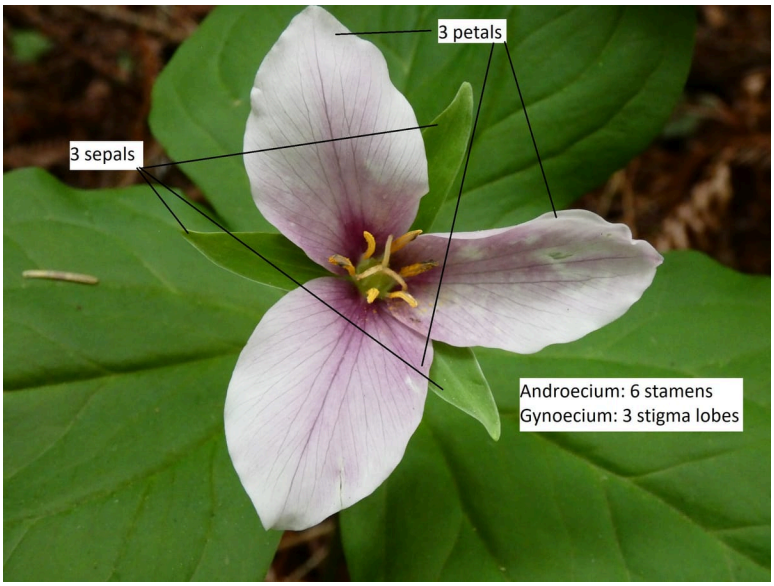


Figure 8.3.2: This Trillium is a monocot, which you can tell because it is 3-merous. There are three sepals, three petals, six stamens, and three stigma lobes visible in the gynoecium. Monocots have floral parts in sets of three (3-merous). Photo by Maria Morrow, CC-BY 4.0.

Eudicots



Figure 8.3.3: A eudicot seedling with two cotyledons. Photo by Maria Morrow, CC-BY 4.0.



Figure 8.3.4: Eudicot flowers tend to be 4-merous or 5-merous. The Clarkia flower (first image) is 4-merous. We cannot see the calyx, but there are four petals, 8 stamens, and 4 stigma lobes. The Flax flower (second image) is 5-merous. There are five sepals poking out between the five petals and 5 stamens (with blue anthers!). The number of stigma lobes is not distinguishable in this image. Photos by Maria Morrow, CC-BY 4.0.

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8.4: Inflorescence Types

Spathe & Spadix



Figure 8.4.1: In the image on the left, the spathe is shown wrapped around and enclosing the spadix (not visible). The spathe on a Calla lily looks like one large, funnel-shaped, white petal. In the image on the right, the top of the spadix is shown. This part of the spadix is covered with the male florets, making pollen. Photos by Maria Morrow, CC BY-NC.

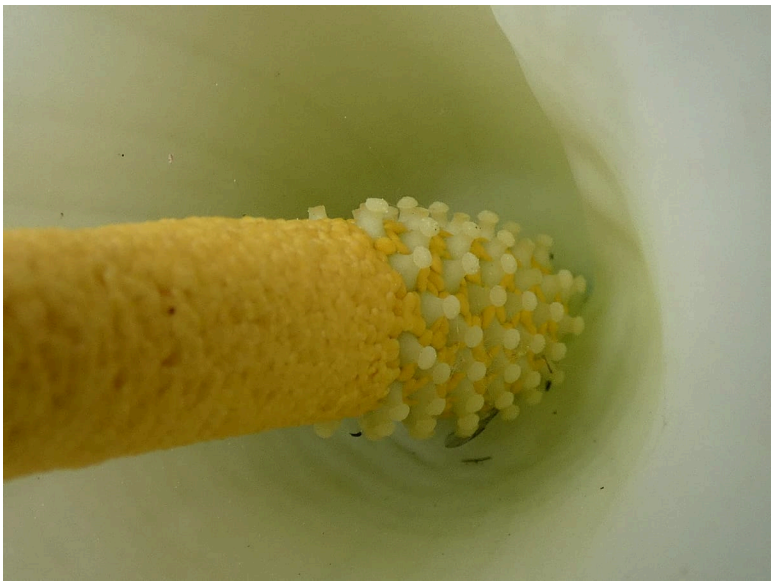


Figure 8.4.2: This is the base of the Calla lily spadix. It is covered with female florets. The gynoecium is shaped like a bowling pin, each with a large knob-like stigma at the top. Photo by Maria Morrow, CC BY-NC.

Head (also called a composite or capitulum)



Figure 8.4.3: A dandelion head inflorescence. Each "petal" is actually composed of five fused petals of a single floret. The tube-like structures emerging upward are the styles, each with two curled stigma lobes. Because this inflorescence has no disc flowers, it is called a ligulate head. Photo by Maria Morrow, CC BY-NC.



Figure 8.4.4: This oxeye daisy has a head inflorescence with two types of florets. In the center, there are yellow disc florets. These have five short petals and radial symmetry. Lining the outside of the inflorescence are white ray florets. These have several petals fused together in one long strap-like, bilaterally symmetrical corolla. The image on the right shows the bracts lining the outside of the inflorescence, called phyllaries. People commonly mistake these as sepals when considering this inflorescence as a single flower. Photos by Maria Morrow, CC BY-NC.



Figure 8.4.5: Clovers are quite beautiful, particularly up close. The fuzzy ball it produces is composed of many bilaterally symmetrical florets, typical of the flower morphology found in the legume family. These florets all attach to the same receptacle. Can you locate the calyx and corolla of each floret? Photo by Maria Morrow, CC BY-NC.

Spike



Figure 8.4.6: This *Plantago* inflorescence is a wind-pollinated spike. The florets have no showy perianth. The prominent structures seen here are the large anthers, located at the end of long, thin filaments. These florets are sessile, attached directly to the peduncle with no pedicels. Photos by Maria Morrow, CC BY-NC.

Raceme

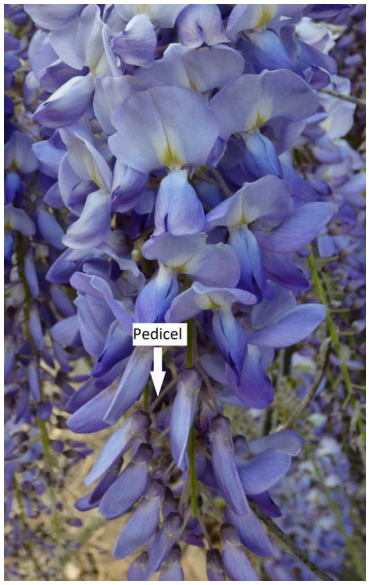


Figure 8.4.7: This Wisteria inflorescence is a pendant raceme. The florets are each attached to the peduncle by a short stem called a pedicel. One of these is indicated in the image with a white arrow. Wisteria is also in the legume family. Can you see the similarity between these florets and the ones in the clover inflorescence in Figure 8.4.5? Photo by Maria Morrow, CC BY-NC.

Catkin





Figure 8.4.8: Willows produce catkins. In the first image, there are several female catkins. There is no showy perianth or androecium, just a large gynoecium for each floret, giving the appearance of a spiky stick. In the second image, there is an androecium instead of a gynoecium. The yellow anthers are held out on thin filaments, making these male catkins look like yellow, fuzzy caterpillars. Photos by Maria Morrow, CC BY-NC.

Umbel

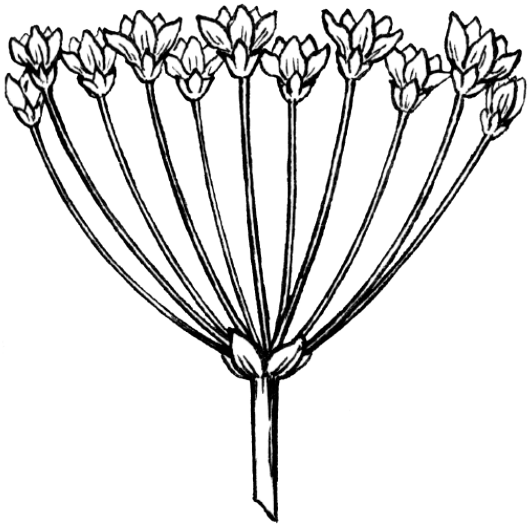




Figure 8.4.9: In an umbel, the pedicels all emerge from the top of the peduncle. The *Allium cernuum* inflorescence on the right is a drooping umbel. Drawing by Pearson Scott Foresman, Public domain, via Wikimedia Commons. Photo on the right by Steve Ganley, CC-BY-NC.



Figure 8.4.10: A compound umbel is when each pedicel then forms its own umbel. Drawing by H.M. Dixon, Public domain, via Wikimedia Commons. Photo of *Aegopodium podagraria* by Сергей, CC-BY-NC.

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8.5: Fruits

Ovary Anatomy

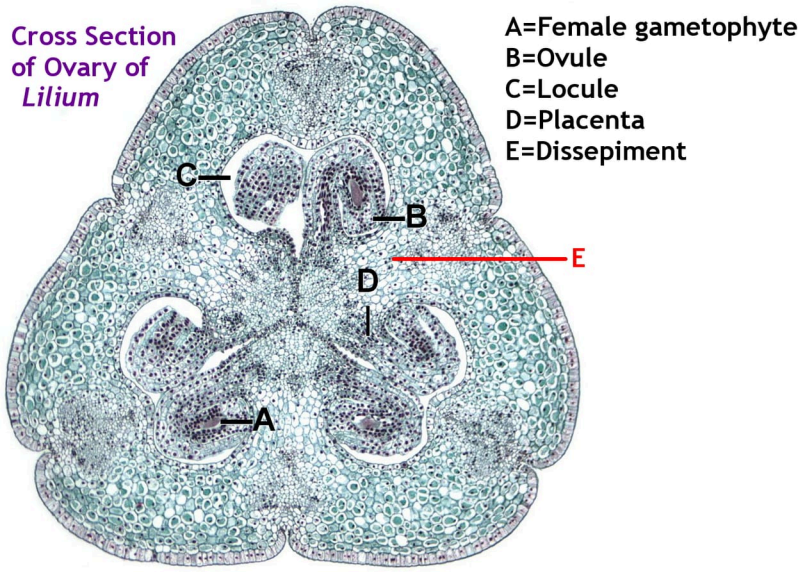


Figure 8.5.1: Cross section of *Lilium* ovary, showing A=Female gametophyte, B=Ovule, C=Locule, D=Placenta, E=Dissepiment. The label in red added to original contribution of File:Lilium ovary L.jpg provided by Jon Houseman and Matthew Ford. JonRichfield, CC BY-SA 4.0, via Wikimedia Commons.

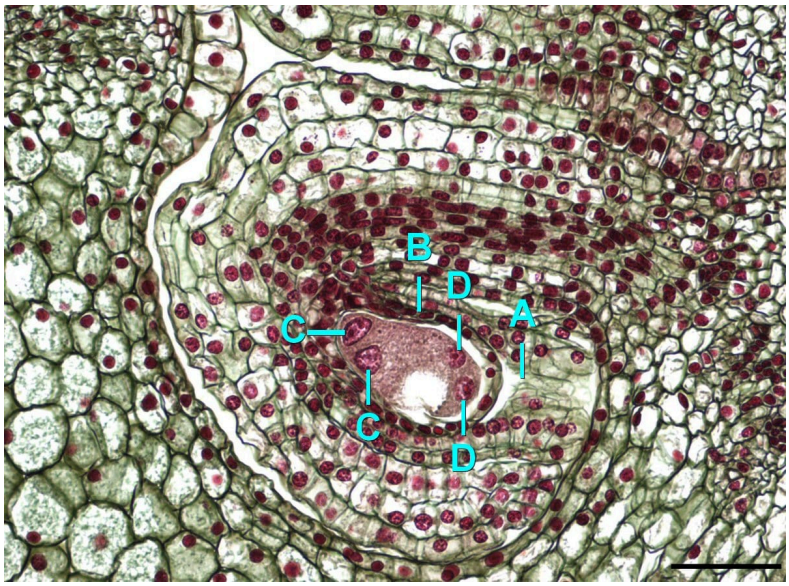


Figure 8.5.2: A *Lilium* ovary during the second stage of the four nucleate embryo. A-Micropyle, B-Integument, C-Antipodal cells, D-Synergid cells. Scale=0.1mm. Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

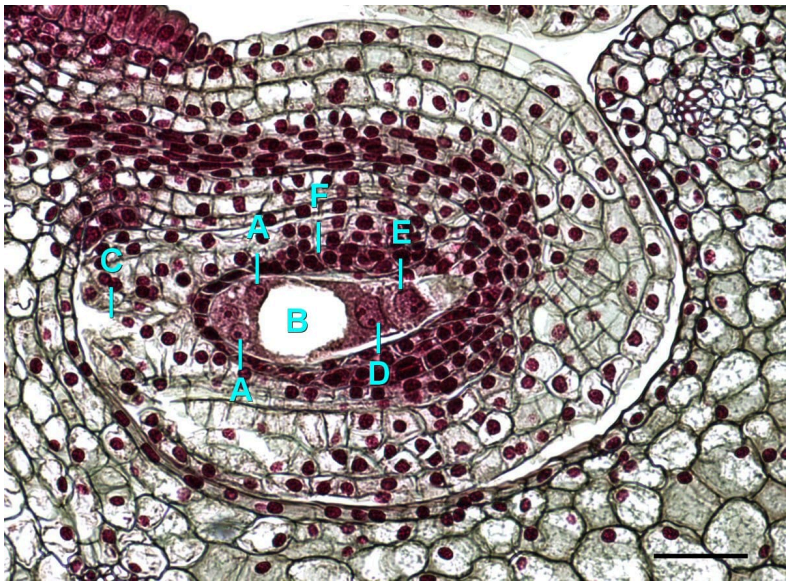


Figure 8.5.3: A *Lilium* ovary at the eight nucleate stage. A-Synergid cells, B-Vacuole, C-Micropyle, D-Polar nucleus, E-Antipodal cell, F-Integument. Scale=0.1mm. Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

Transitioning from Flower to Fruit



Figure 8.5.4: These two images show clusters of pear blossoms from the same tree. The cluster on the left is in an earlier stage of development. The corolla is still attached and the stamens are radiating outward to disperse pollen. In the image on the right, the corolla has fallen off and the anthers have shriveled. The calyx is still visible and, just below it, the semi-inferior ovary and hypanthium are beginning to swell. Eventually, these will swell to many times their current size and form the fruits we know as pears. Photos by Maria Morrow, CC-BY 4.0.



Figure 8.5.5: Salal (*Gaultheria shallon*) is a shrub in the same family as blueberries and madrone trees. Each pendant, urn-shaped corolla will fall off, leaving the calyx behind. The inferior ovary will develop into a berry. In this image, younger flowers are being produced on the left side at the end of the inflorescence, while older flowers develop into fruits on the right side. Photo by Maria Morrow, CC-BY 4.0.

Fruit Anatomy

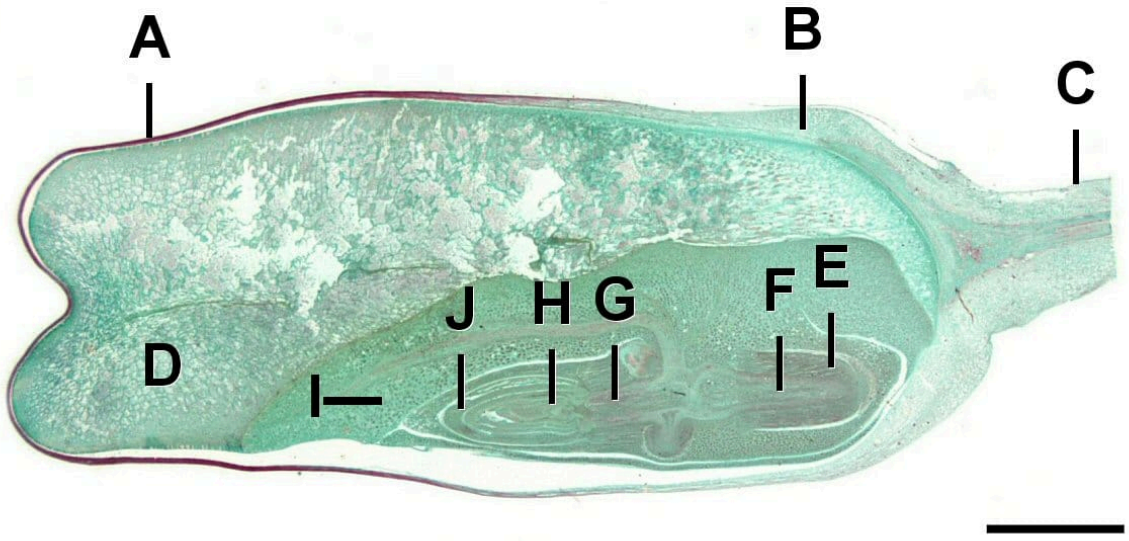


Figure 8.5.6: A *Zea mays* kernel. This fruit is a caryopsis, the seed coat is fused to the pericarp. Labels are as follows: A=Pericarp, B=Aleurone, C=Tip cap, D=Endosperm, E=Coleorhiza, F=Radicle, G=Hypocotyl, H=Plumule, I=Scutellum, J=Coleoptile. Scale=1.4mm. Jon Houseman, CC BY-SA 4.0, via Wikimedia Commons.

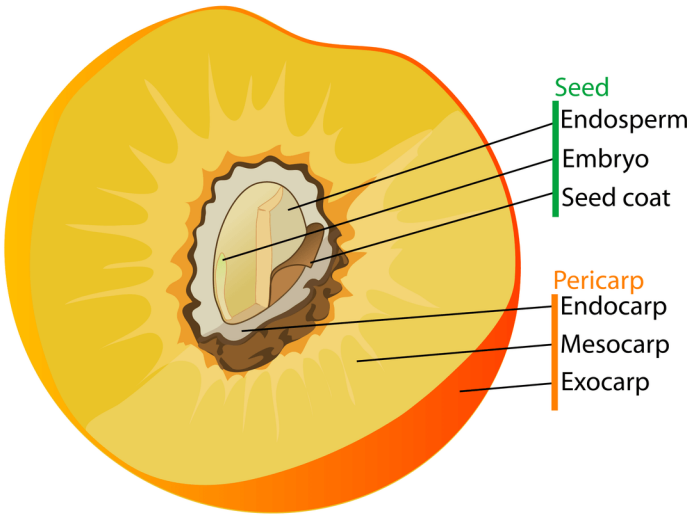


Figure 8.5.7: A diagram of a drupe. The pericarp of a fruit can be completely fused (as in Figure 8.5.7) or separated into distinct layers: the endocarp (innermost), mesocarp (middle), and exocarp (outermost). A drupe is a fruit type with a stony endocarp enclosing a single seed, a fleshy mesocarp, and a thin exocarp. Image by LadyofHats, Public domain, via Wikimedia Commons.

Some Common Fruit Types

Achene



Figure 8.5.8: These two images show the fruits produced from the head inflorescence of a dandelion. On the left, they are difficult to distinguish, forming a sphere around the receptacle. On the right, some of the fruits have been carried away on the wind, making the others easier to see. Each floret has produced an achene at the base (from an inferior ovary). Only the calyx remains, of the other floral whorls, and has formed into an umbrella-like structure for wind dispersal. Photos by Maria Morrow, CC-BY 4.0.

Berries

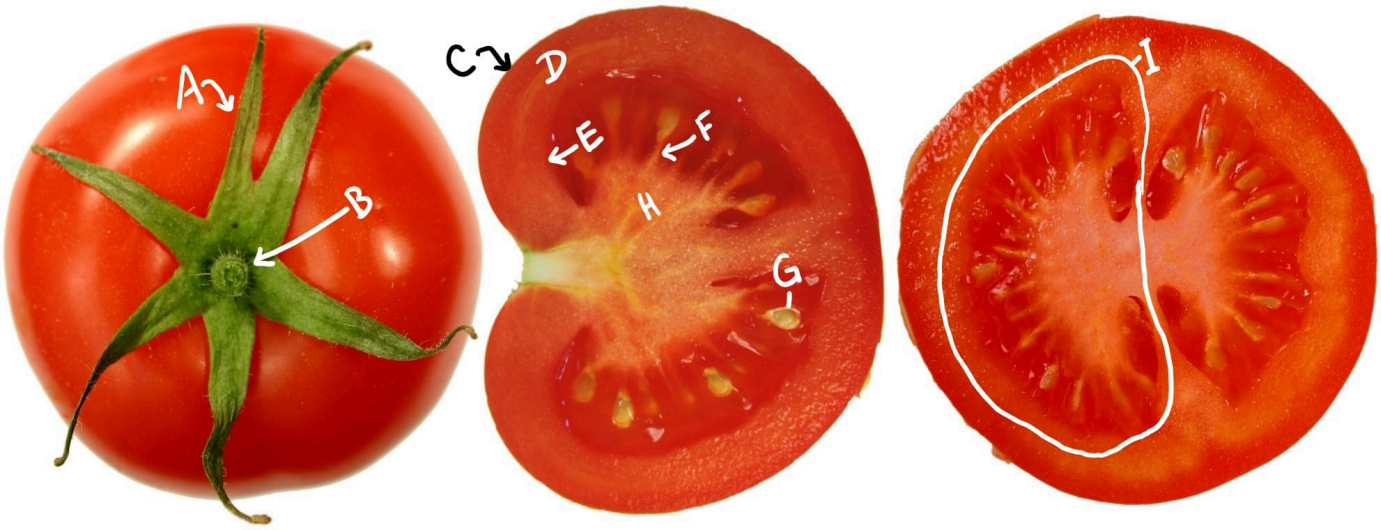


Figure 8.5.9: A tomato is a berry. The pericarp has distinct layers,but all are fleshy. The exocarp forms a thin skin around a fleshy mesocarp. There are many seeds. Labels are as follows: A=Calyx, B=Peduncle, C=Exocarp, D=Mesocarp, E=Endocarp, F=Funiculus, G=Seed, H=Placenta, I=Locule. Image of the tomatoes from © 2005 User:FoeNyx, CC BY-SA, via Wikimedia Commons with labels added by Maria Morrow.

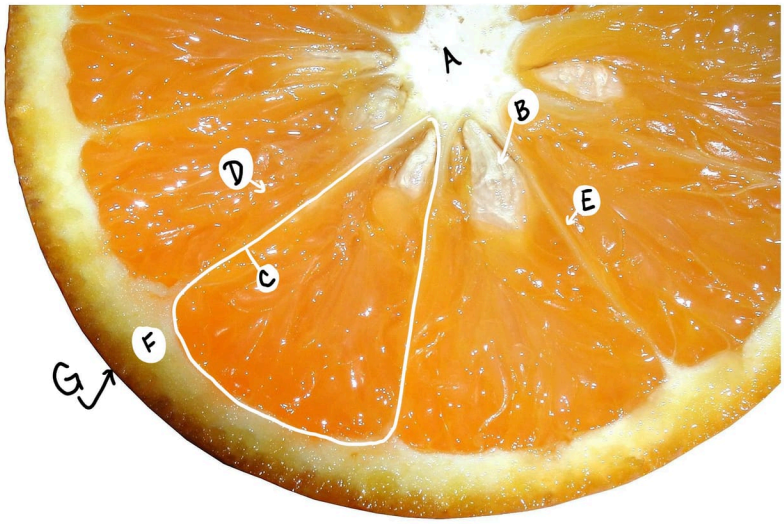


Figure 8.5.10: A hesperidium (citrus fruits) is a modified berry. The endocarp forms the skin around the segments, containing seeds and juice-filled trichomes. The exocarp forms an oily rind. A=Pith, B=Seed, C=Locule, D=Juice-filled trichomes, E=Endocarp, F=Mesocarp, G=Exocarp. Image of the orange slice from Paolo Neo, Public domain, via Wikimedia Commons with labels added by Maria Morrow.

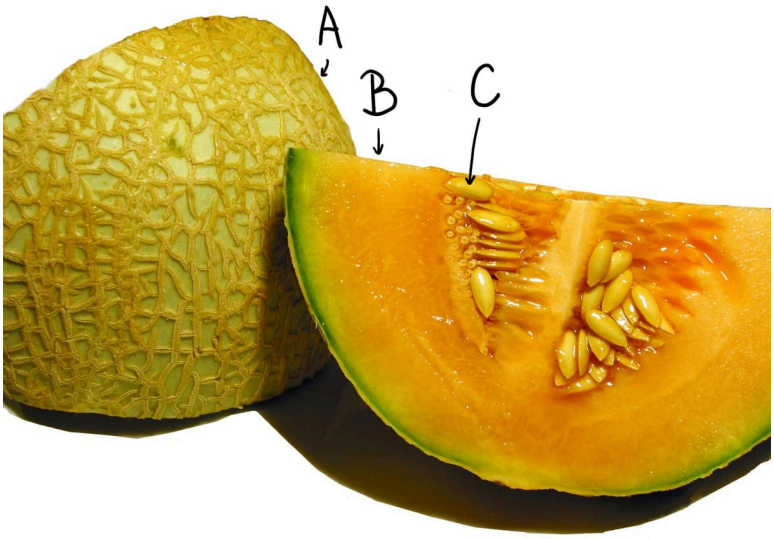


Figure 8.5.11: A pepo is another modified berry. The exocarp forms a (somewhat) tough rind (A). The mesocarp (B) is still fleshy. It contains many seeds (C). Image from User:Tomia, CC BY-SA, via Wikimedia Commons with labels added by Maria Morrow.

Accessory Fruits

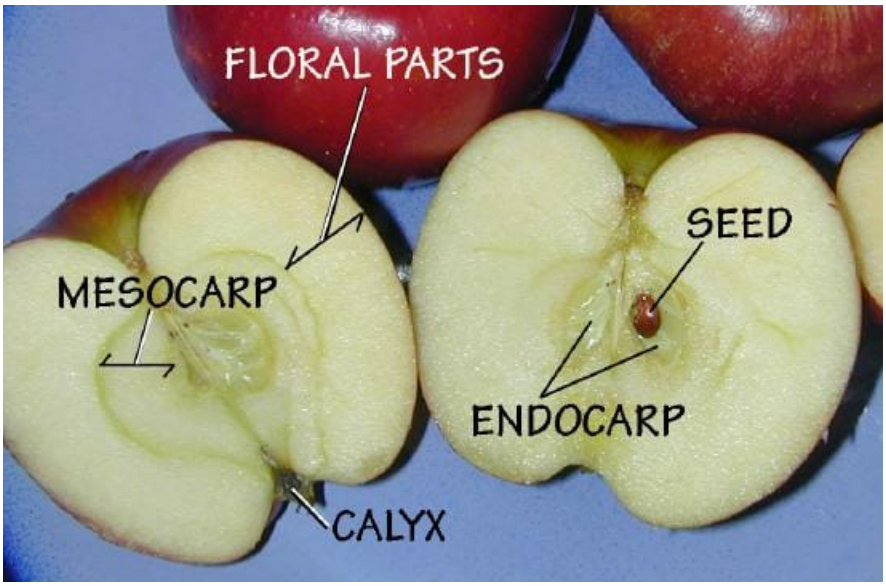


Figure 8.5.12: A pome is an accessory fruit made from a fleshy hypanthium. The papery core is the pericarp, which contains the seeds. Eric Guinther, CC BY-SA, via Wikimedia Commons.



Figure 8.5.13: Strawberries are accessory fruits formed from a swollen receptacle. The receptacle reddens and swells, pushing the developing fruits outward. The fruits are achenes that look like seeds, stuck to the outside of the receptacle. The calyx of the flower is the green, leafy part. If you look closely, you can see the styles attached to the achenes. Full strawberry photo author unknown, licensed under the Creative Commons Attribution-Share Alike 3.0 Unported license. Sliced strawberry photo by Paolo Neo, Public domain, via Wikimedia Commons.

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8.6: Life Cycle

Watch Video 8.6.1 to help untangle this complex life cycle.

YouTube Video

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

Video 8.6.1: A digital, narrated rendition of the angiosperm life cycle. https://youtu.be/0UEpq1W9C_E

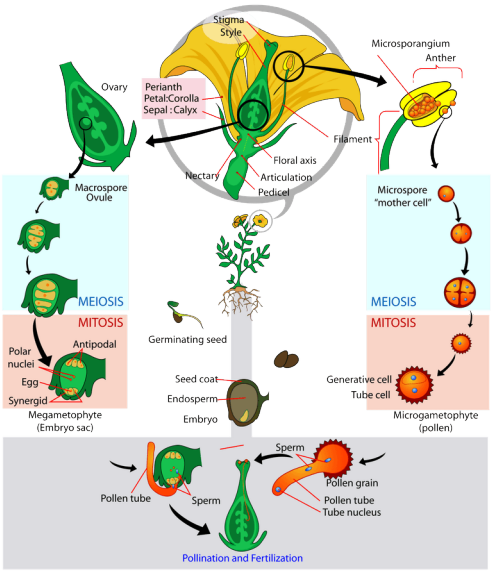


Figure 8.6.1: A diagram of the angiosperm life cycle. The formation of the ovule takes place on the left hand side, moving from top to bottom. The formation of the pollen grain takes place on the right hand side, again moving from top to bottom. At the center bottom of the image, pollination and double fertilization occurs, where the sperm cells fuse with the egg (forming a zygote) and polar nuclei (forming the triploid endosperm). The seed develops through the center of the image, transitioning into a mature sporophyte (the flowering plant). Diagram by LadyofHats, Public domain, via Wikimedia Commons.

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9: INTRODUCTION TO MICROSCOPY

Viewing microscopic structures is an integral part of the study of botany. Many life cycle features or anatomical characteristics used to differentiate between lineages of organisms can only be distinguished through a microscope. However, this affords you the opportunity to view that which most will never see!

The study of microscopic features of tissues is called **histology**. This study involves a variety of techniques for specimen preparation, including thin sections, squash mounts, heat treatments, and staining. Many tissues are colorless, making distinguishing features difficult. **Stains** can allow you to distinguish your specimen from the background (such as Congo Red for fungal hyphae, which stains the cytoplasm) or might have different chemical reactions with cellular compounds (such as Toluidine Blue for plant cells, which stains the primary wall purple and the secondary wall light blue). Some stains are carcinogenic, caustic, or are in some way hazardous, so be sure to follow the safety protocols when using them. Always avoid getting stains on yourself or your clothing (even when they are harmless, they still stain).

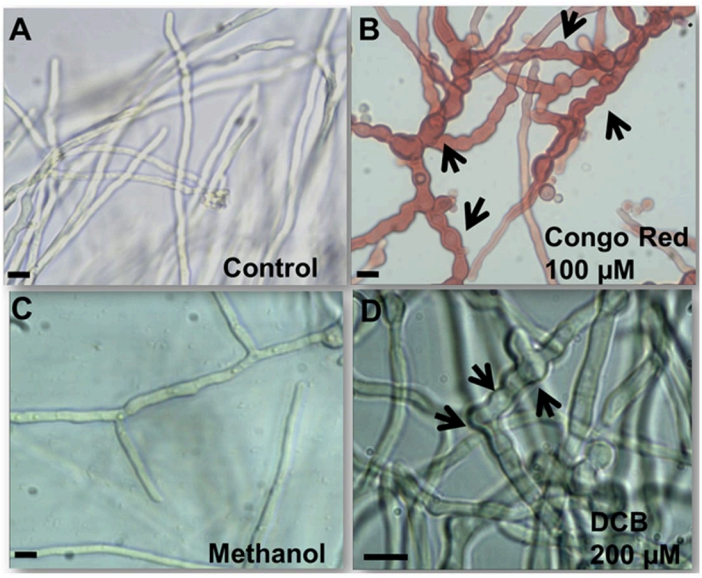


Figure 9.1: This image shows fungal hyphae without any stain (A) and stained with Congo Red (B). Notice how much easier it is to see the specimen. Scale bar=10 µm. Image retrieved from an open-access paper by Guerriero et al. (2013).

Microscopy is a skill that must be practiced. Like most skills, you might struggle with it at first--making good thin sections is particularly difficult. The more opportunities you have to practice, the better you'll get, and the more you'll be able to see in your specimens. Knowing how to apply stains and which are best for different types of specimens will dramatically improve your results. Keep notes!

This resource makes for an excellent additional companion for your adventures into histology.

9.1: Using Microscopes

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9.1: Using Microscopes

The Microscope

Dissecting Microscope

A dissecting microscope generally has lower magnification and uses incident light, meaning the light shines onto (not through) the specimen to view it.

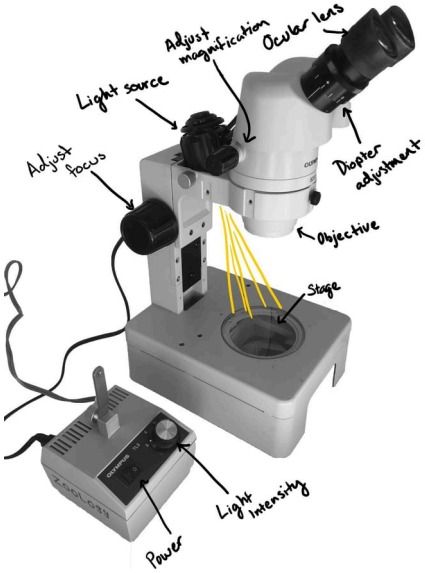


Figure 9.1.1: A labeled dissecting microscope. Two ocular lenses extend from the top with a diopter adjustment around the base of one. These are at the top of the stereo head. At the base of the head is the objective. On the side of the head is the magnification adjustment. A light source goes through the head and shines light onto the stage. The head is connected to the base by an arm where the focus adjustment is located. The light is connected by a cord to a separate device with a power switch and a knob to adjust light intensity. Photo by Sarah Greenwood via Wikimedia Commons with labels added by Maria Morrow. CC BY 4.0

Compound Microscope

A compound microscope is used for viewing small samples or pieces of a larger specimen at higher magnification. This type of microscope uses transmitted light, where the light must pass through the specimen to view it.

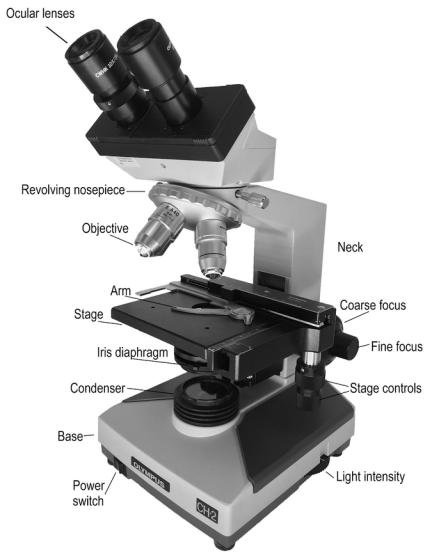


Figure 9.1.2: A labeled compound microscope, with the stage for the specimen located between the lenses and the light source (transmitted light). From top to bottom on the left side of the image, the labels read: Ocular lenses, revolving nosepiece, objective, arm, stage, iris diaphragm, condenser, base, power switch.From top to bottom on the right side of the image: neck, coarse focus, fine focus, stage controls, light intensity. Adapted from Compound Microscope by Sarah Greenwood via Wikimedia Commons. CC BY 4.0

Making and Staining Slides

There are many ways to make a slide. Preparation method and technique will vary, depending on your specimen and what you need to see. Below are some basic guidelines, but you should experiment with what works best for you and your specimen.







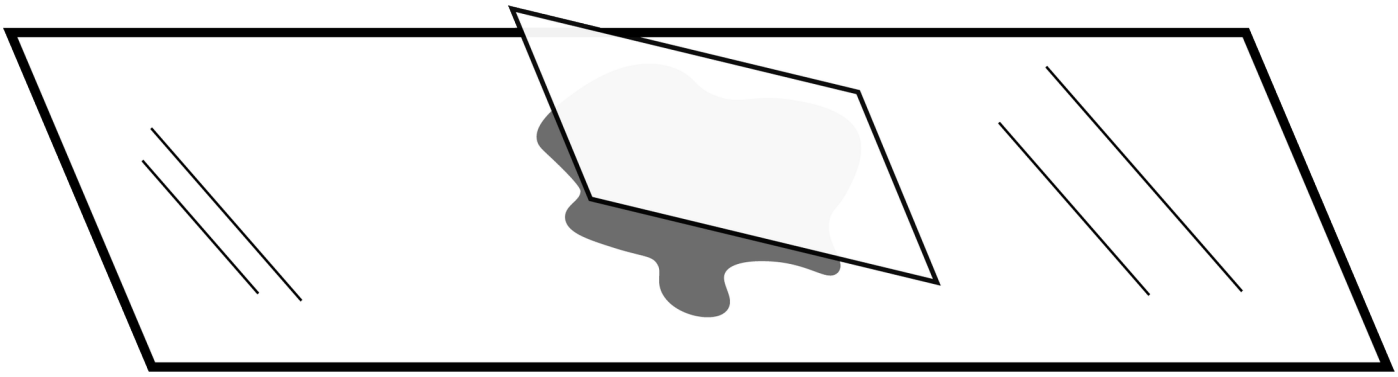


Figure 9.1.3: Preparing a wet mount. Add a few drops of liquid to the slide. Put your specimen onto the droplet of liquid. Add a cover slip. The best method for placing the cover slip is to touch it to the slide at an angle (see bottom image) and slowly bring it toward the droplet of liquid. Once the cover slip touches the liquid, lower it gently until flat. This method reduces the amount of air bubbles in your sample. First three images from WikiHow, CC-BY-NC-SA. Bottom image by Sarah Greenwood, CC BY 4.0, via Wikimedia Commons.

With compound microscopes, the light must pass through the specimen. For this to work, your prepared sample must be quite thin. Many prepared slides are made using a machine called a microtome to achieve the extremely thin, even sections needed to

see many anatomical features. As a human trying to perform this process, you'll need as much practice as possible to get a good thin section.

YouTube Video

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

Video 9.1.1: This video provides a demonstration of making thin cross-sections by hand for plant material such as stems and roots; includes a demonstration of staining the material using TBO (toluidine blue O), a metachromatic stain useful for many plant materials. [See Episode 6 for how to prepare TBO.] Sourced from YouTube.

Focusing with a Compound Microscope

YouTube Video

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View this YouTube Video online

Video 9.1.2: Dr. Patrick demonstrates the steps in focusing a compound light microscope from 10X to 100X. She shows you how the field of view changes with each lens. The use of immersion oil for the 100X lens is specifically shown. Sourced from YouTube.

Measuring Your Specimen

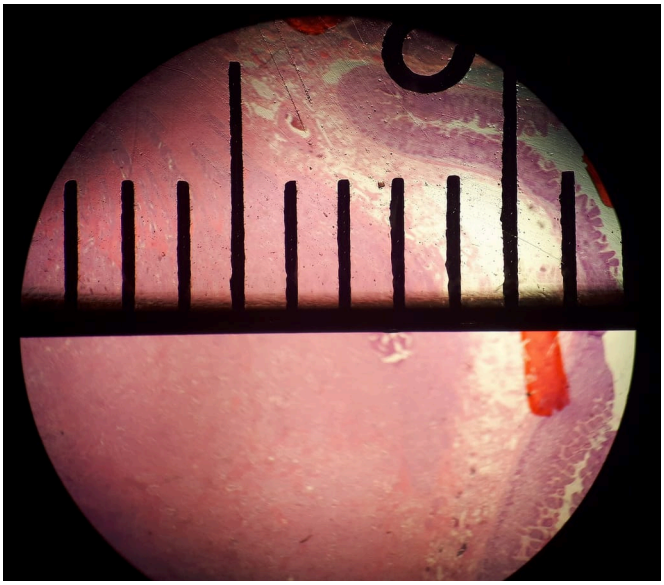


Figure 9.1.4: This image shows the field of view through a compound microscope. A ruler or reticle can be used to measure the field of view and/or the specimen you are viewing. The marks on the ruler in this image are millimeters. The diameter of the field of view at this magnification is approximately 11 mm. Photo by Mikael Häggström, M.D. - Author info - Reusing imagesConsent from the patient or patient's relatives is regarded as redundant, because of absence of identifiable features (List of HIPAA identifiers) in the media and case information (See also HIPAA case reports guidance)., CC0, via Wikimedia Commons.

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10: CELLS AND TISSUES

10.1: Plant Cell Structure and Components

10.2: Types of Plant Cells

10.2.1: The -enchymas

10.2.2: Specialized Cells

10.3: Cell Division

10.3.1: Interphase, Mitosis, and Cytokinesis

10.3.2: Meiosis

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10.1: Plant Cell Structure and Components

Plant Cells

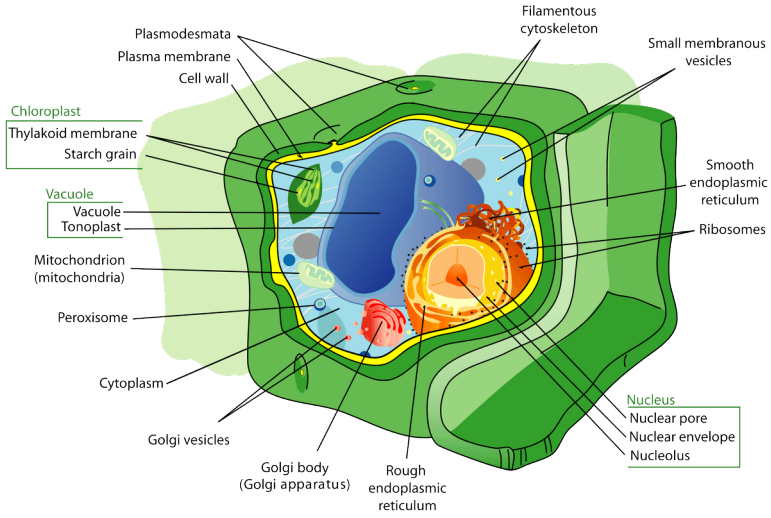


Figure 10.1.1: A diagram of a plant cell. Plants cells differ from animal cells in that they have a cell wall (which is glued to adjacent cells by the middle lamellae), a large central vacuole, and chloroplasts. Image by LadyofHats, Public domain, via Wikimedia Commons.

Plant Cell Components

Cell Wall, Plasma Membrane, and Middle Lamella

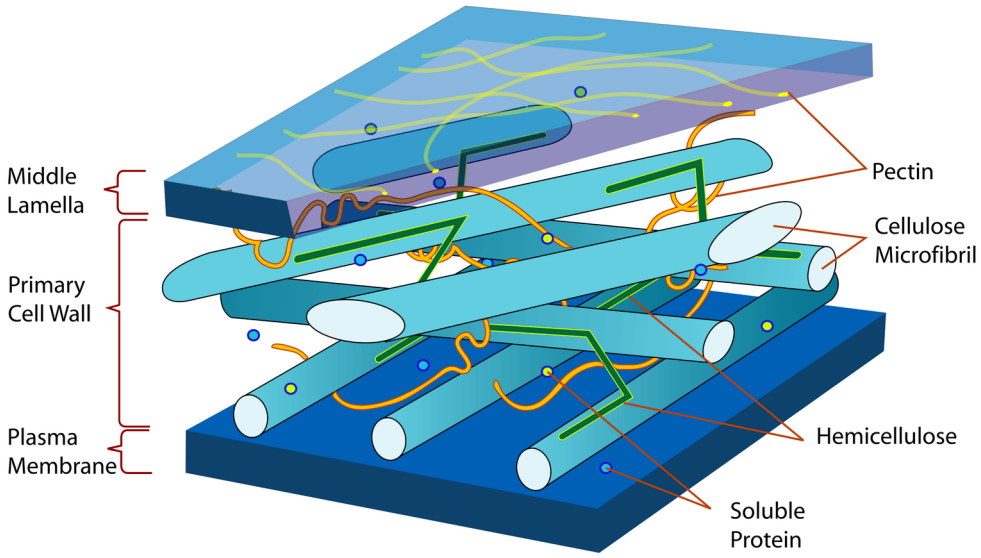


Figure 10.1.2: A diagram of the **primary cell wall**, including the plasma membrane and middle lamella. The primary wall is composed of crisscrossing cellulose and hemicellulose microfibrils. Strands of pectin and some soluble proteins are also in the mix. Diagram by LadyofHats, Public domain, via Wikimedia Commons.

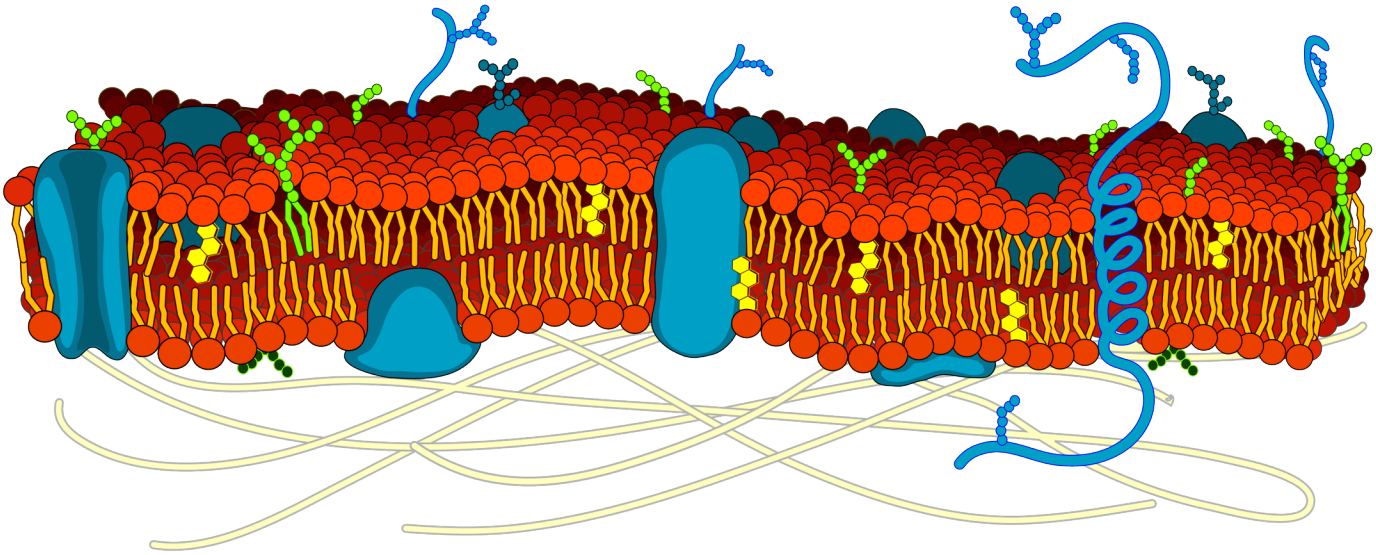


Figure 10.1.3: A generalized diagram of a plasma membrane. The cell membrane, also called the plasma membrane or plasmalemma, is a semipermeable lipid bilayer common to all living cells. It contains a variety of biological molecules, primarily proteins and lipids, which are involved in a vast array of cellular processes. It also serves as the attachment point for both the intracellular cytoskeleton and, if present, the cell wall. Diagram by LadyofHats, Public domain, via Wikimedia Commons.

Plasmodesmata are channels through the cell wall and middle lamella where the plasma membrane of adjacent cells (and therefore the cytoplasm) is connected.



Figure 10.1.4: The image above shows cells in the epidermis of a red pepper. Two locations are circled and labeled as plasmodesmata. In each of these circles, there is a section of the cell wall that appears to be missing. This is where a section of the plasma membrane traverses through a channel in the middle lamella and cell walls of both cells. Photo by Maria Morrow, CC BY-NC.

The Nucleus

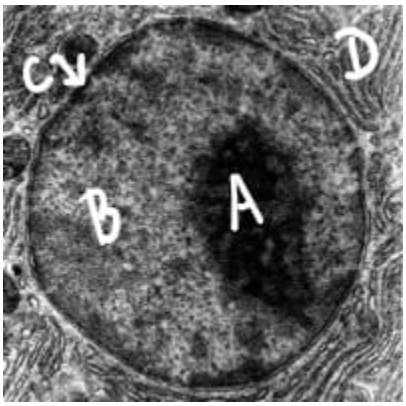


Figure 10.1.5: A micrograph of a cell nucleus. The nucleolus (A) is a condensed region within the nucleus (B) where ribosomes are synthesized. The nucleus is surrounded by the nuclear envelope (C). Just oustide the nucleus, the rough endoplasmic reticulum (D) is composed of many layers of folded membrane. Image from the public domain, via Wikimedia Commons, labels added by Maria Morrow.

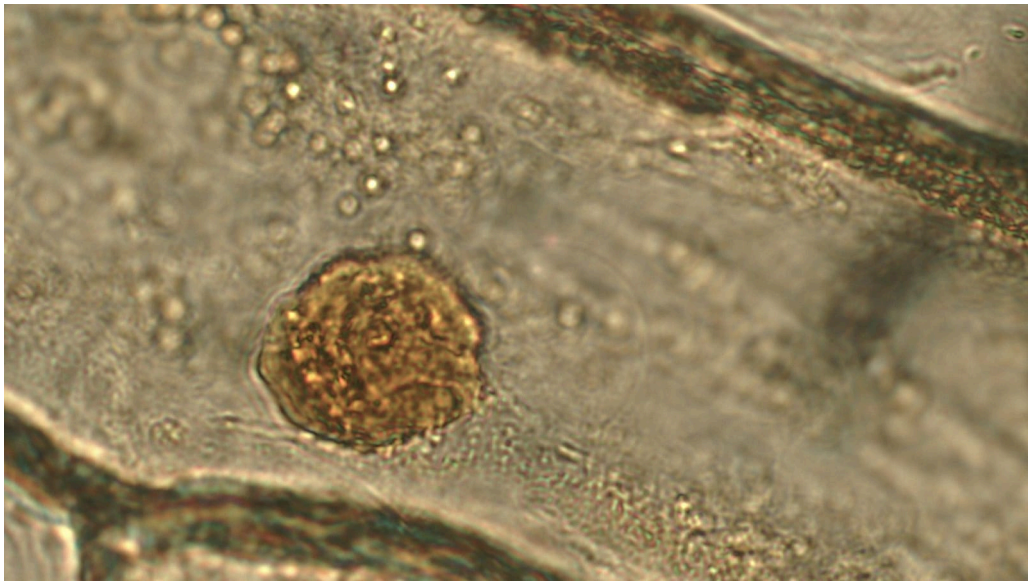


Figure 10.1.6: The large, golden, globose structure is an onion cell nucleus, magnification 3000x. Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons.

Plastids

Plastids are organelles that are the result of an endosymbiotic event in the evolutionary history of plants. In plants, plastids have two membranes.

Chloroplasts

Chloroplasts are plastids that contain green pigments called chlorophylls.

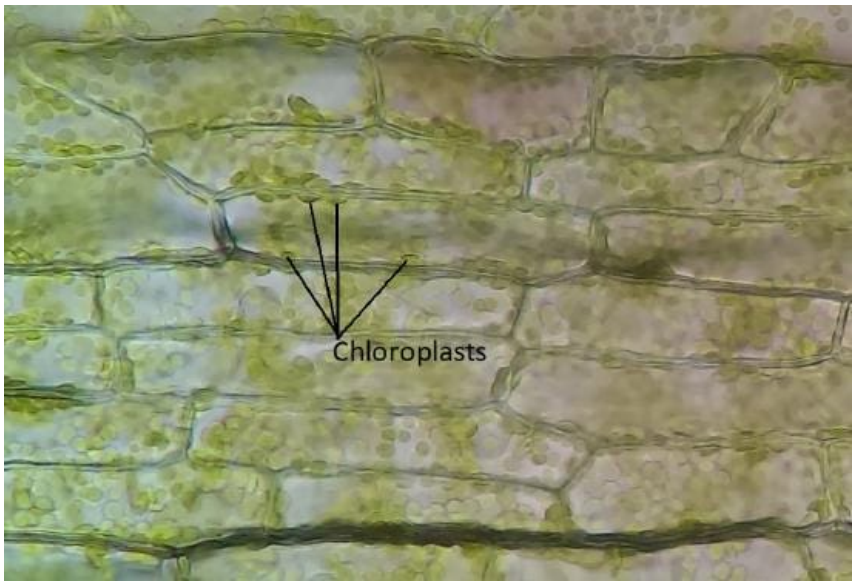


Figure 10.1.7: This image shows cells in the leaf of an aquatic plant, *Elodea*. Each cell is filled with small green discs which often appear to line the edges of the cell. These are chloroplasts (four are indicated and labeled in the image). Photo credit: Melissa Ha, CC BY-NC .

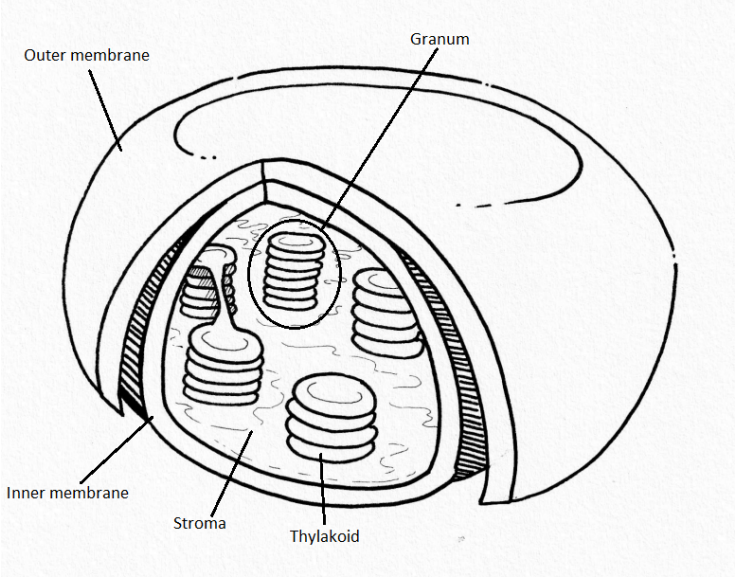


Figure 10.1.8: A diagram of chloroplast anatomy. There are two membranes, the outer and inner membrane, that enclose this structure. Within, there are stacks of flat discs. Each stack is called a granum and each individual disc is a thylakoid. The grana float within a jelly-like matrix called the stroma. Artwork by Nikki Harris, CC BY-NC .

Chromoplasts

Chromoplasts are plastids that do not contain chlorophyll, but do contain other pigments, such as carotenoids. Carotenoid pigments reflect colors like yellow, orange, and red.

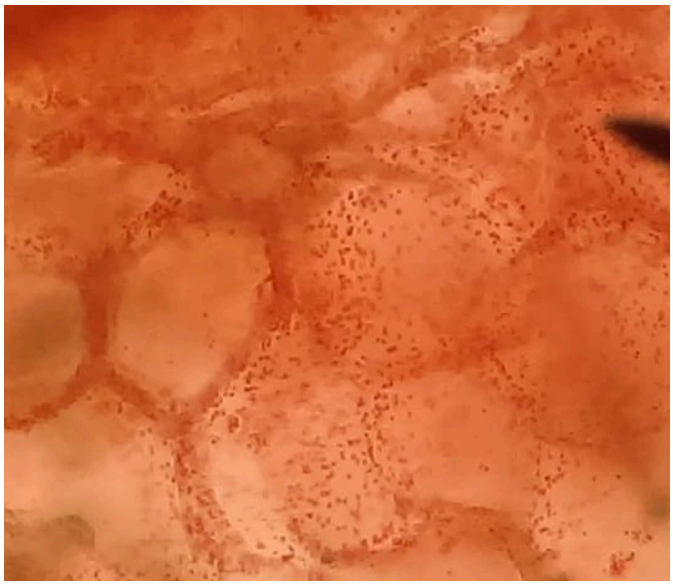


Figure 10.1.9: This image shows the cells of a red pepper. There are many small red dots floating within the cells. These dots are chromoplasts that contain carotenoids. The chromoplasts give the pepper its red color. Photo credit: Melissa Ha, CC BY-NC .

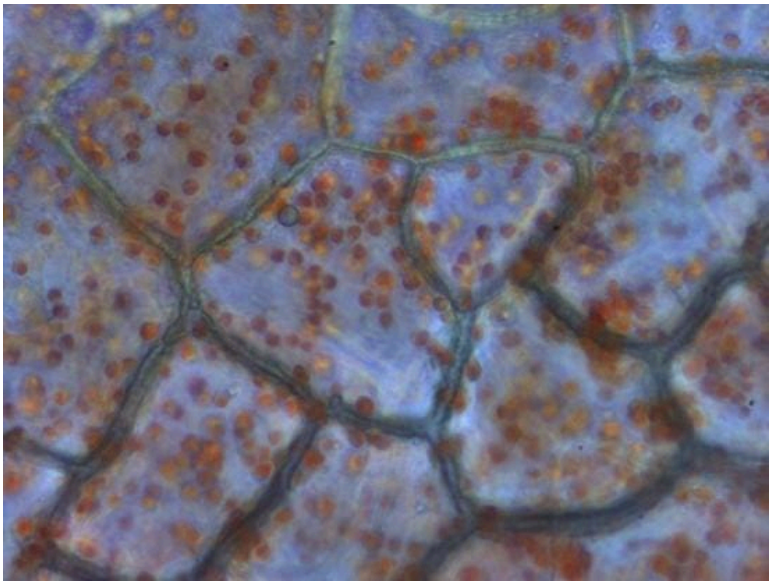


Figure 10.1.10: In this image of red pepper epidermal cells, the chromoplasts are larger and easier to distinguish. Each cell is filled with circular, red discs. These are chromoplasts that contain carotenoids. Photo by Maria Morrow, CC BY-NC.

Leucoplasts

Leucoplasts are plastids that do not contain pigments. The main function of leucoplasts is to store starches and oils. Leucoplasts that store starch are called **amyloplasts** (as in amylose).

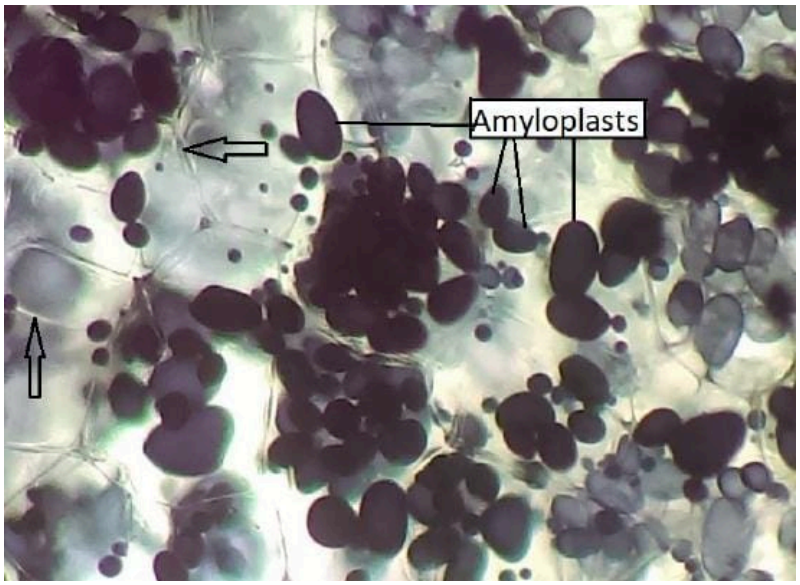


Figure 10.1.11: This image shows cells from a potato tuber that have been stained with iodine. When iodine interacts with starch, it turns a blue-black color. This helps us see the amyloplasts inside the cells, which would normally be transparent due to their lack of pigment. In the image, the cell walls of the potato cells can be seen as lighter lines (indicated by the arrows in two places). The amyloplasts are dark, pebble-like structures within the cells. Some of these are less opaque because they have not been in contact with as much of the iodine stain. Photo credit: Melissa Ha, CC BY-NC.

The Central Vacuole

The **central vacuole** is a large organelle that often fills most of the plant cell. It is filled with liquid and surrounded by a membrane called the **tonoplast**. Plants can alter the solute concentration in the central vacuole to influence cell structure and movement of water. It is also a place to store pigments, such as anthocyanins, or other secondary metabolites, such as phytotoxins.

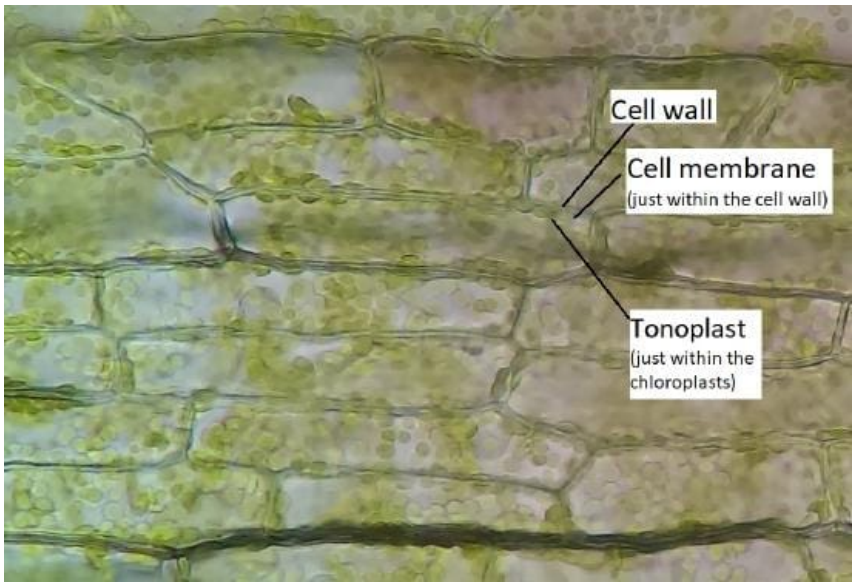


Figure 10.1.12: This image shows the same Elodea leaf cells again, this time with the cell wall, cell membrane, and tonoplast of one of the cells labeled. The cell walls are visible as thicker lines between the cells. The plasma membrane and tonoplast locations must be inferred. The plasma membrane is pushed against the cell wall, just to the inside of it. The tonoplast can be seen as the border between the chloroplasts the "empty space" within the cell, as the central vacuole pushes the cytoplasm to the edges of the cell. Photo credit: Melissa Ha, CC BY-NC .

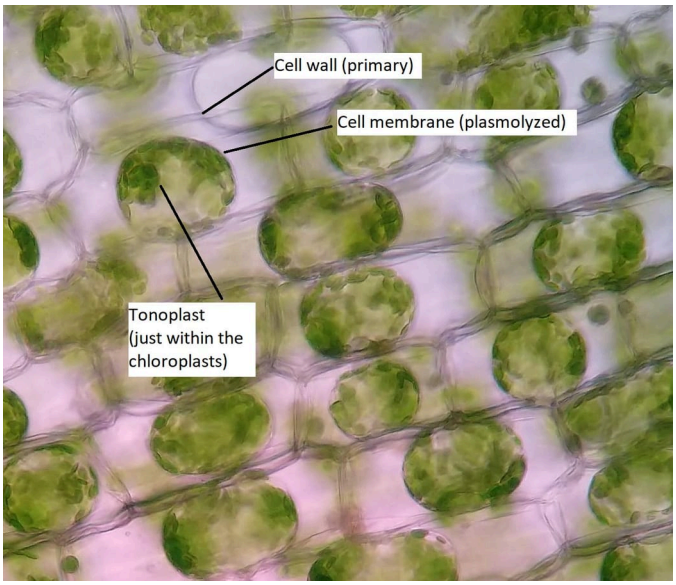


Figure 10.1.13: In this image, the *Elodea* leaf has been exposed to salt water. This helps us see the plasma membrane and tonoplast more distinctly, as much of the water has left the cell and the central vacuole has shrunk, causing plasmolysis. As the central vacuole shrinks, the plasma membrane collapses inward but the rigid cell wall remains in place. The plasma membrane is surrounding the outside of the chloroplasts, which have been clustered into a ball inside each cell. Just inside the shell of chloroplasts is the tonoplast. The nucleus will also be squished in there somewhere, though it is also transparent. Photo by Maria Morrow, CC BY-NC.

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10.2: TYPES OF PLANT CELLS

Plants have three primary cell types and these cell types compose tissues within the plant. These cells, as well as specialized cells formed from these general types, will be described in the pages of this chapter.

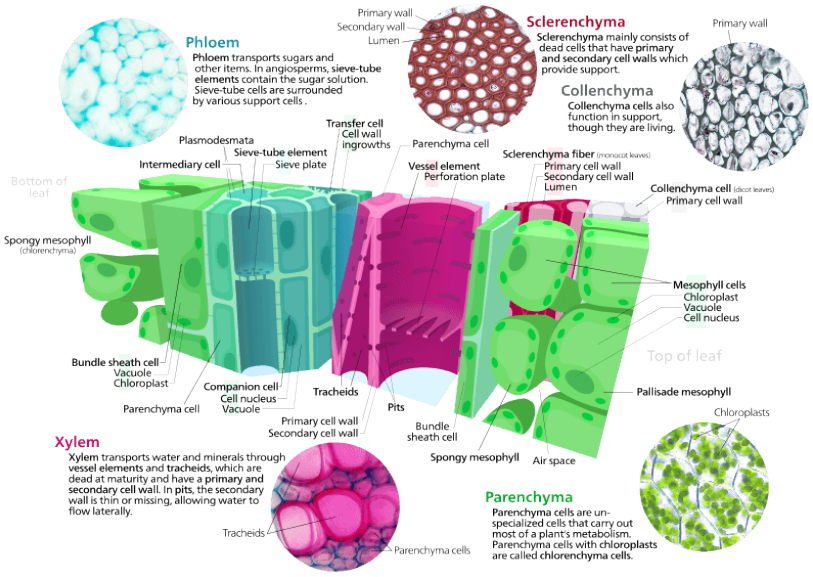


Figure 10.2.1: An amazing diagram of the cells and tissues present within a leaf. Image from Kelvinsong, CC BY-SA 3.0, via Wikimedia Commons.

- Types of Plant Cells

10.2.1: The -enchymas

10.2.2: Specialized Cells

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10.2.1: The -enchymas

There are three major cell types in plants that we can distinguish by differences in their cell walls. These three cell types are **parenchyma**, **collenchyma**, and **sclerenchyma**.

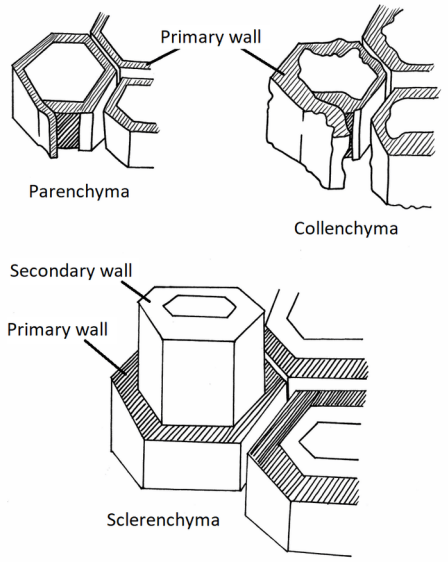


Figure 10.2.1.1: This diagram shows the three major cell types found in plants. In the upper left, parenchyma cells have an evenly thickened primary wall (shaded with stripes in the illustration). The primary wall of parenchyma cells is quite thin, though it has been widened in the diagram to make it easier to see. To the right of the parenchyma, collenchyma cells also have only a primary wall, but it is unevenly thickened, giving them a chunky appearance. Unlike parenchyma cells, the primary wall of a collenchyma cell is often quite thick. On the bottom half of the diagram, sclerenchyma cells are shown with a thick secondary wall (unshaded) that develops within the primary wall (shaded). Eventually, the primary wall of the sclerenchyma cells will die away. Artwork by Nikki Harris, CC-BY 4.0 with labels added by Maria Morrow.

Parenchyma

Parenchyma cells are characterized by an even, relatively thin primary wall.

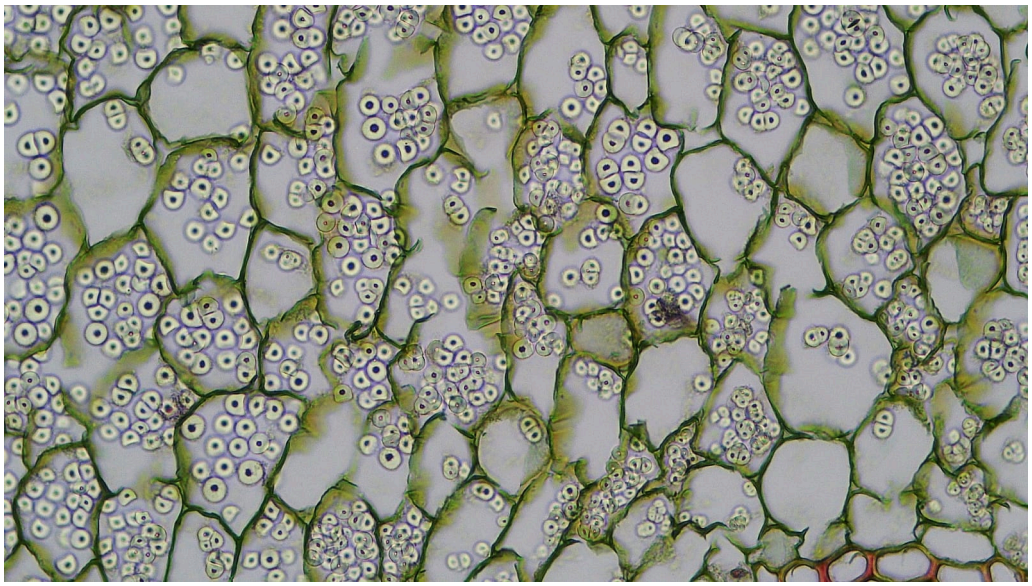


Figure 10.2.1.2: A cross section of a Ranunculus root showing parenchyma cells filling the cortex. Note the evenly thin cell walls. These cortex cells contain many starch grains. Photo by Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons.

Collenchyma

Collenchyma cells are characterized by an uneven, relatively thick primary wall.

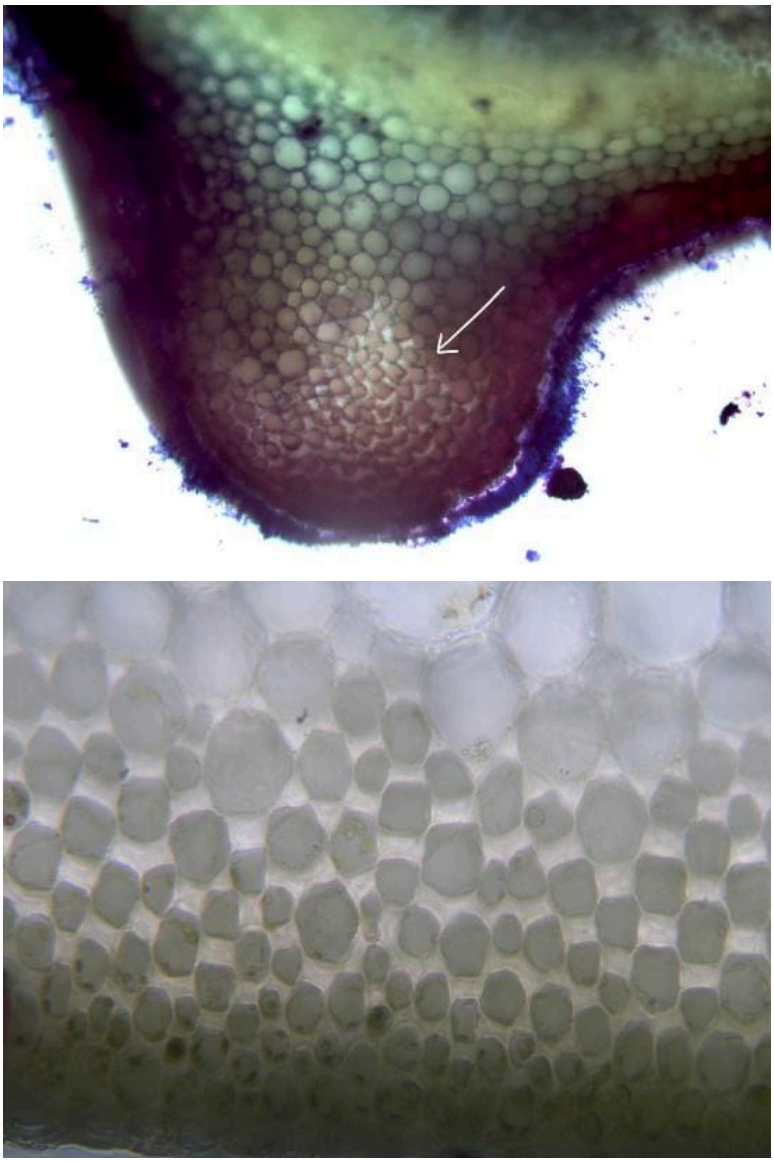


Figure 10.2.1.3: Collenchyma cells. Left: Angular collenchyma is a supportive tissue found in peppermint and other species like celery. 200X magnification. Taken in the Plant Lab at CU:Boulder. Photo by Spencer Llerandi, CC BY 4.0, via Wikimedia Commons with an added arrow by Maria Morrow. Right: Collenchyma tissue from celery. Photo from Clematis, CC BY-SA 3.0, via Wikimedia Commons.

Sclerenchyma

Sclerenchyma cells are characterized by the formation of a secondary wall composed of lignin. This secondary wall forms within the primary wall and eventually leads to the death of the cell. Sclerenchyma cells are dead at functional maturity.

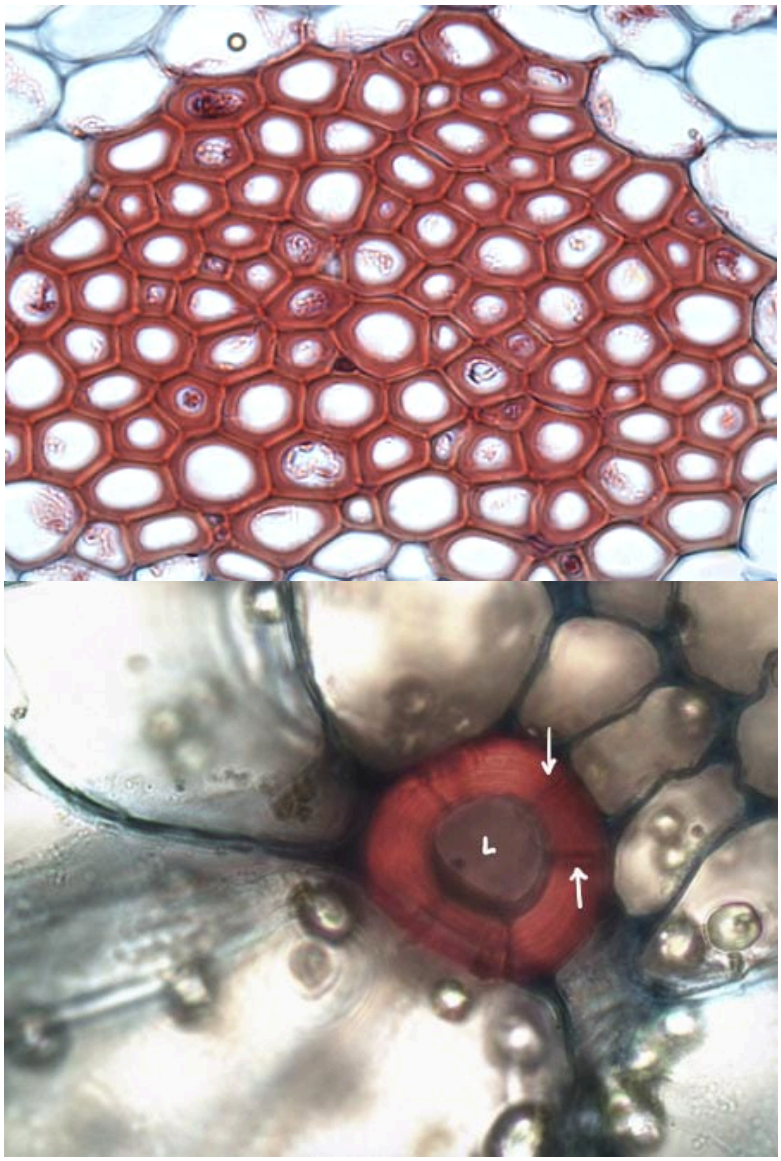


Figure 10.2.1.4: The first image is a cross section through a cluster of fiber cells (sclerenchyma). These cells have relatively evenly thick secondary walls that have stained red due to lignin. In the second image, there is a single fiber cell. The reddish donut is formed by its secondary wall. There are several gaps in this wall called pits, two are indicated by arrows. These are pits where plasmodesmata used to traverse the cell walls. The center (L) is the lumen, a now empty region where the cytoplasm used to be. First image: Snowman frosty at en.Wikipedia, Public domain, via Wikimedia Commons. Second image: Roland Gromes, CC BY-SA 4.0, via Wikimedia Commons with labels added by Maria Morrow.

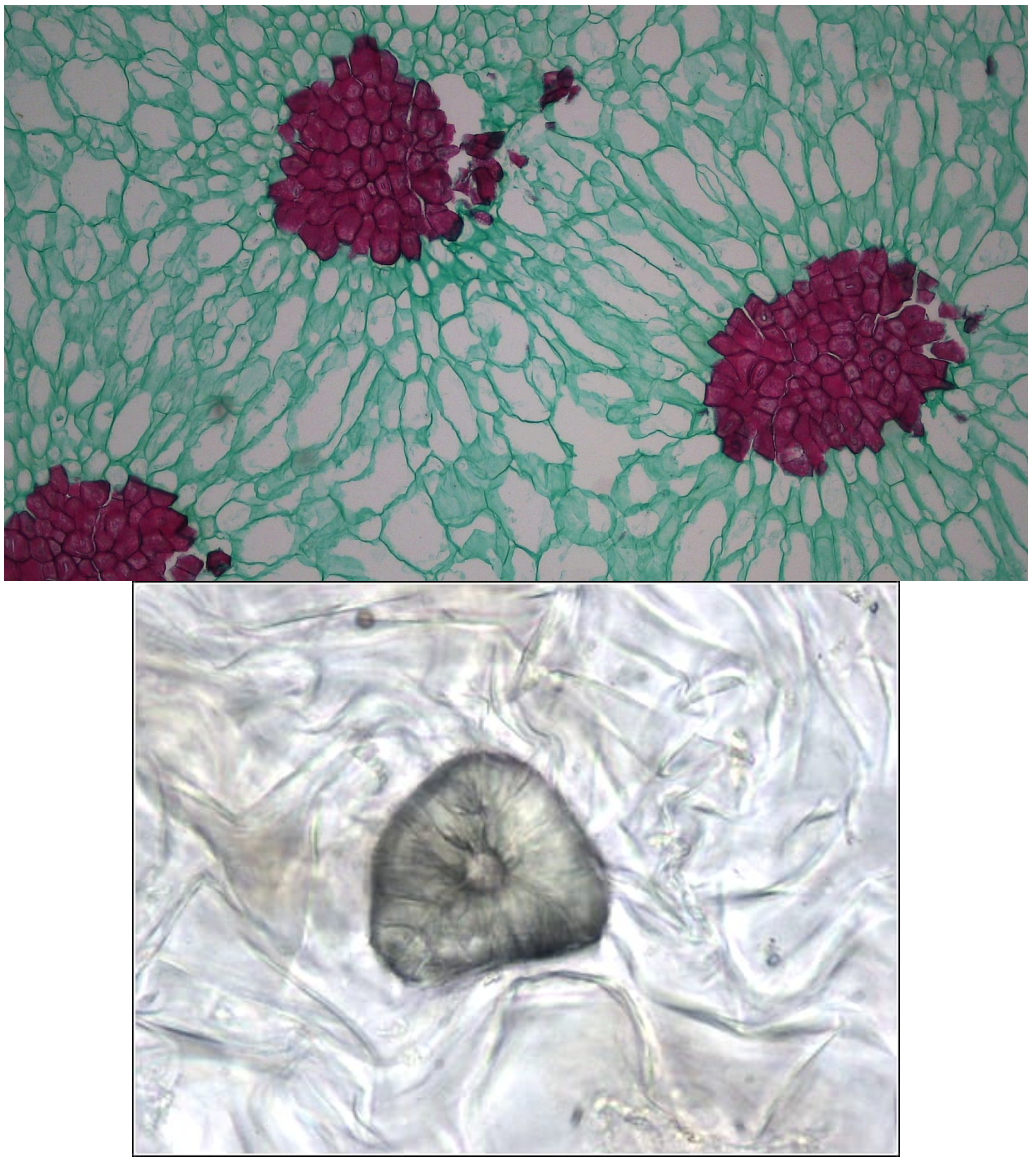


Figure 10.2.1.5: Sclereids are sclerenchyma cells found in pears. These woody cells give pears a gritty texture. In the first photo, the sclereids are stained a dark pink color and clustered into large groups, surrounded by parenchyma cells. In the second photo, a single sclereid is visible. It has a thick secondary wall with the channels of former plasmodesmata visible running through it, forming pits. First: Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons. Second: Snowman frosty at en.Wikipedia, Public domain, via Wikimedia Commons.

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10.2.2: Specialized Cells

Specialized Cells From the Protoderm

Guard Cells

Stomata are pores (holes) in the epidermis of plants. **Guard cells** are the pairs of cells, shaped a bit like parentheses or two sides of a donut, that flank the stoma. The guard cells regulate when the stoma is open or closed, which in turn regulates gas exchange with the environment and the rate of transpiration.

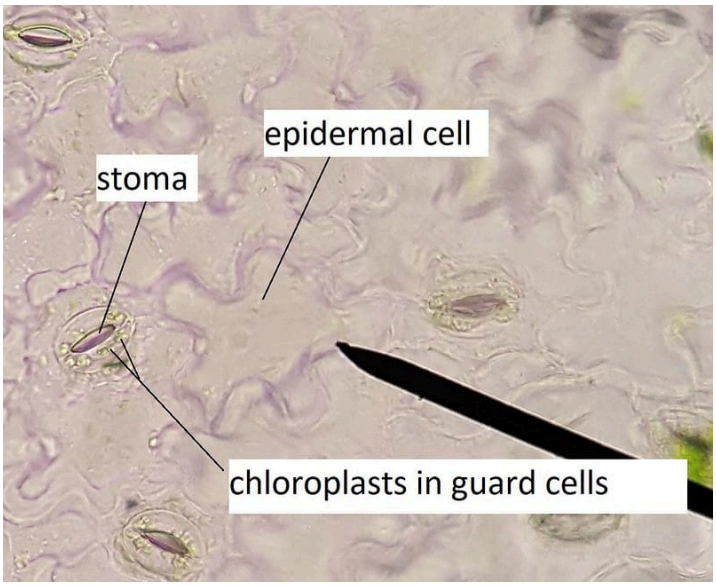


Figure 10.2.2.1: This image is of an epidermal peel. The epidermal cells look like transparent, interlocking puzzle pieces. Interspersed between these cells, there are stomata with guard cells. Each stoma looks a bit like a mouth, with one guard cell acting as the upper lip and another guard cell acting as the lower. Chloroplasts are visible within the guard cells. Photo by Melissa Ha, CC BY-NC .



Figure 10.2.2.2: There are two images above. The one on the left shows an open stoma, while the one on the right shows a closed stoma. Photo by Melissa Ha, CC BY-NC.

Trichomes

Trichomes are hairs composed of cells on the epidermis of a plant.



Figure 10.2.2.2: Trichomes on the underside (abaxial) of a leaf (left) and on a leaf margin (right). The trichomes in the photo on the left are long, fuzzy, and intertwining. The trichomes in the photo on the right are straight, separate from each other, and rigid-looking. The different appearance and texture of trichomes is one of the characteristics used to identify plants. Photos by Maria Morrow, CC BY-NC.



Figure 10.2.2.3: These nettle trichomes are structured much like a hypodermic needle. The long silica tip breaks off to inject a cocktail of stinging chemicals into any animal that brushes by it. Photo by Maria Morrow, CC BY-NC.

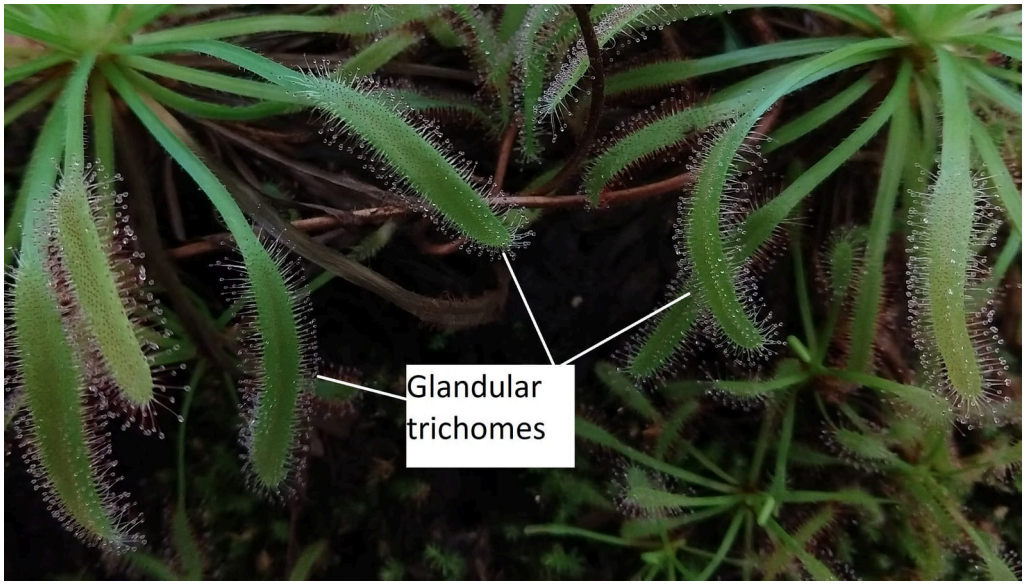


Figure 10.2.2.4: The ends of sundew (*Drosera* sp.) leaves are covered with glandular trichomes. Each trichome has a blob of sticky fluid at the tip. Insects are attracted to the fluid, becoming trapped in it, and the plant can slowly digest their bodies for the mineral nutrients that are lacking in their environment. Photo by Maria Morrow, CC BY-NC.



Figure 10.2.2.5: The underside (abaxial surface) of this sage leaf has two types of trichomes: glandular trichomes and peltate trichomes. The glandular trichomes are in tufts on raised bumps of the epidermis. Scattered amongst them are small white pearl-like structures (one is indicated by a black arrow). These are the peltate trichomes, which are disc-like instead of hair-like. Photo by Maria Morrow, CC BY-NC.

Specialized Cells From the Ground Meristem

Two types of specialized sclerenchyma cells that can be produced by the ground meristem are **sclereids** and **fibers**.

Sclereids

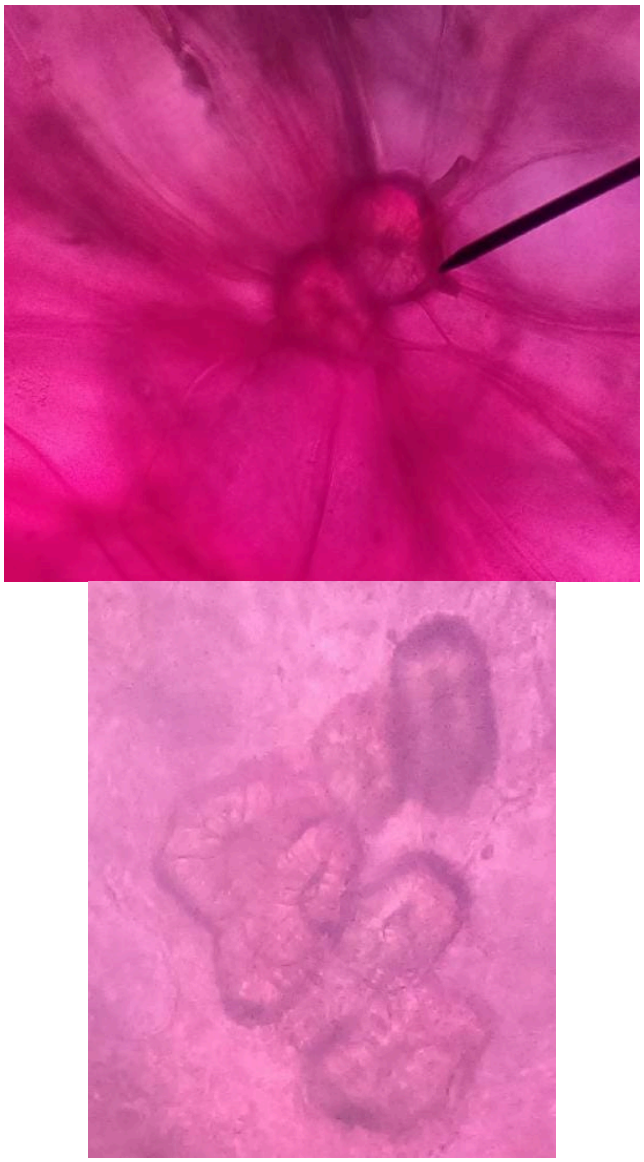


Figure 10.2.2.6: Sclereids are a type of sclerenchyma cell. These sclereids, called stone cells, are produced in the fruits of pears. In the image on the left, two stone cells are surrounded by many large parenchyma cells. There are plasmodesmata (not distinguishable) connecting the sclereids to these parenchyma cells. In the image on the right, there are 6 or 7 stone cells. They have a thick secondary wall with channels running through it (pits). These pits are the former locations of the plasmodesmata. Photos by Maria Morrow, CC BY-NC.

Fibers

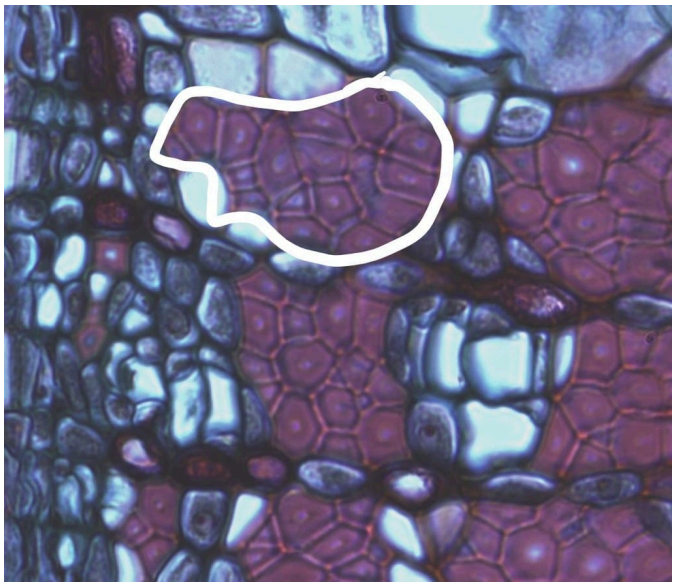


Figure 10.2.2.7: Clusters of fibers in the secondary phloem of a *Tilia* stem. Phloem cells are parenchyma, so they are not as rigid as xylem cells. A way for plants to strengthen and protect phloem tissue is to include bundles of fibers. One of these bundles has been circled in the image. Photo by Maria Morrow, CC BY-NC.

Specialized Cells From the Procambium

Tracheids and Vessel Elements

Tracheids and **vessel elements** are cells in the xylem that transport water. They have secondary walls with lignin and are dead at functional maturity.



Figure 10.2.2.8: All of these cells are dead and have secondary walls with lignin. The cell labeled A is a vessel element, with larger perforation plates on its ends and strange wall thickenings. B is a tracheid, thinner than a vessel element with rows of holes lining its sides (no perforation plates). C is a fiber, long and thin. Photo by Maria Morrow, CC BY-NC.

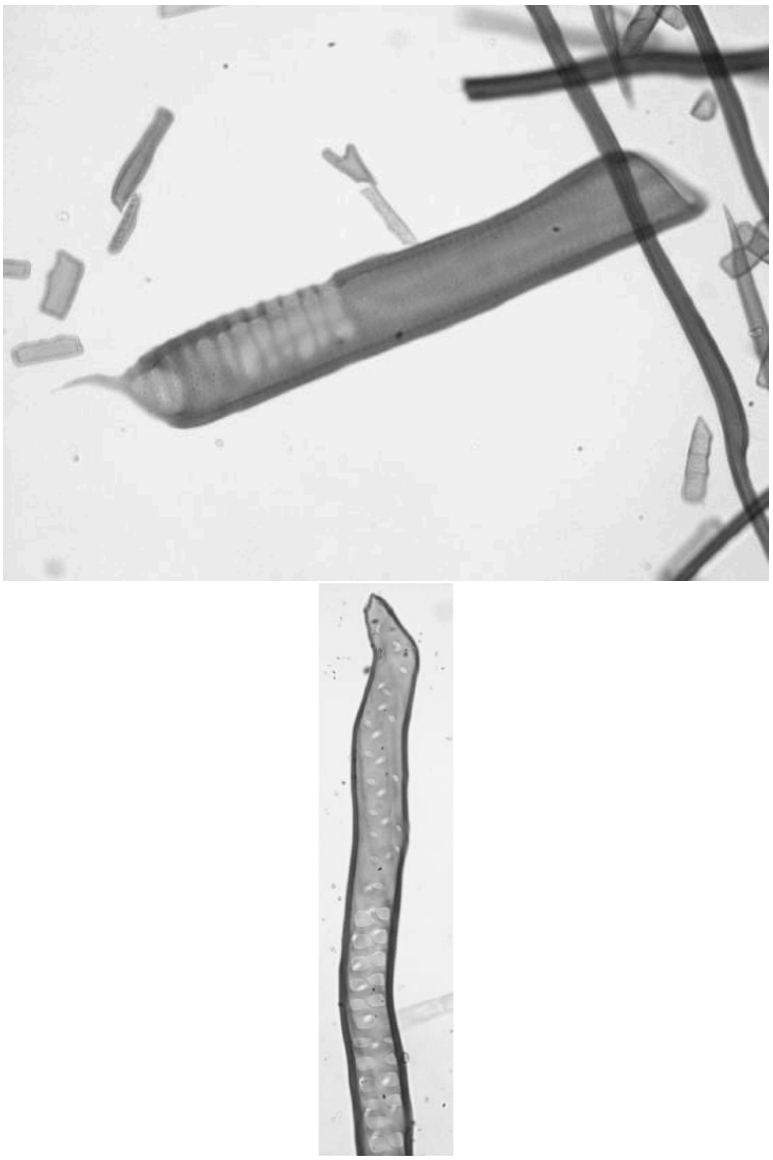


Figure 10.2.2.9: Conducting cells from the xylem. The first photo shows a vessel element with large openings at the ends. The second photo shows a tracheid, with tapered ends and sets of bordered pits along the length of it. Photos by Maria Morrow, CC BY-NC.

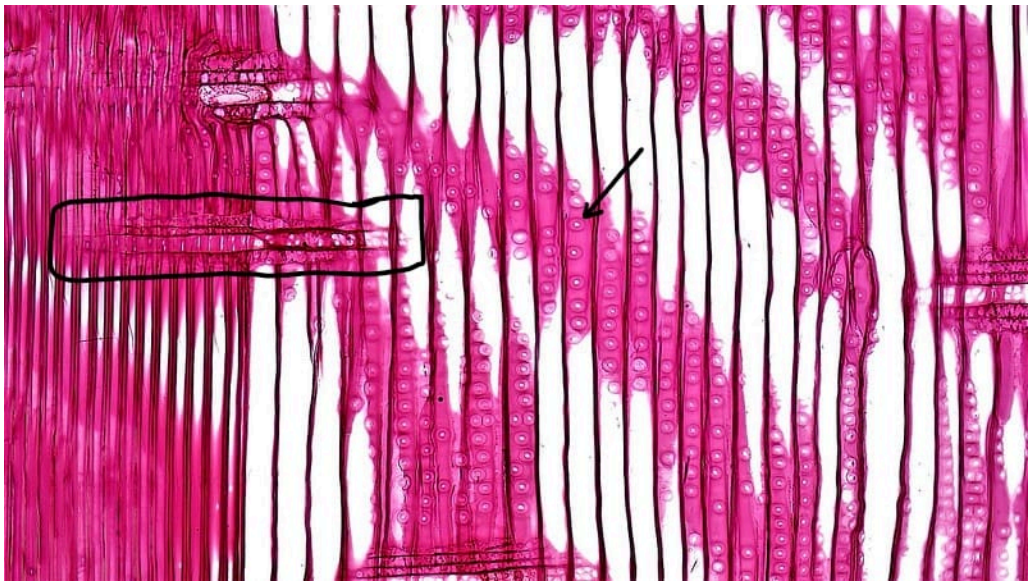


Figure 10.2.2.10: A longitudinal section through pine wood. "Gymnosperms like Pinus rely entirely on tracheids for water flow and mechanical support. True xylem vessels and wood parenchyma are lacking. While fibers are generally absent older stems may contain some fiber tracheids. The uniform wood of Pinus consists almost entirely of longitudinally oriented bands of narrow, pale staining tracheids interrupted by short bands of horizontally oriented xylem rays (indicated by box). Xylem rays, usually one cell thick and a few cells high, are composed of clear, thin walled parenchyma cells. The lumen of many tracheids is crossed by branched trabeculae. Tracheid side walls contain large circular bordered pits (indicated by arrow) that function to move water from tracheid to tracheid while preventing air flow from embolized tracheids. The membrane of each bordered pit is marked by a pale, thin, porous outer margo and a thicker, darker, inner torus. Large horizontally oriented resin ducts are lined with living secretory parenchyma that produce resins and many toxic terpenes including turpentines." Image and caption text from Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons. Labels added by Maria Morrow.

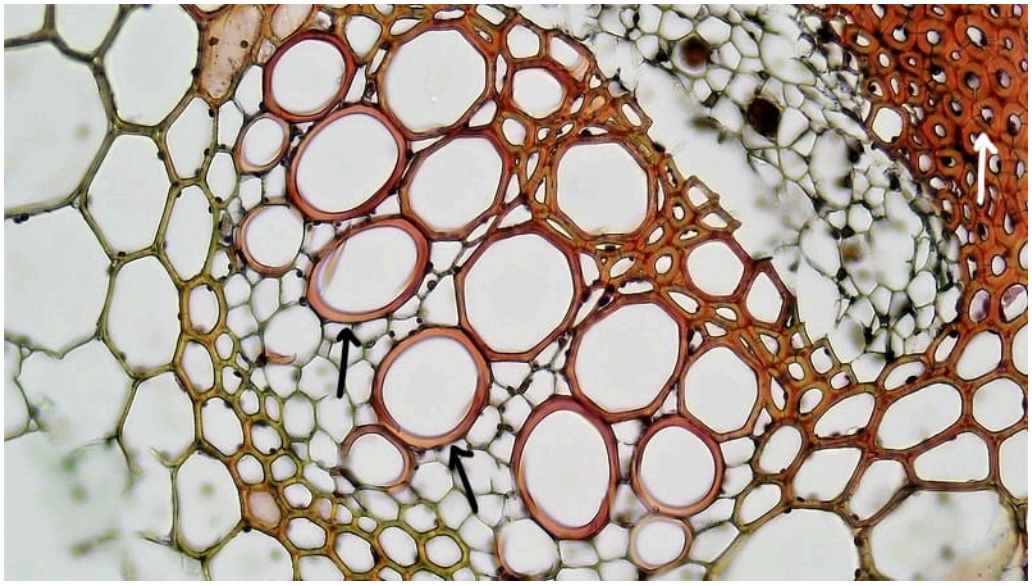


Figure 10.2.2.11: A cross section through a vascular bundle of *Helianthus*, 400x. "The highly lignified cells walls of xylem (black arrows indicate vessel elements) and mature sclerenchyma (white arrow indicates fibers) are stained red orange. These cells are dead at maturity and can also be distinguished by a heavy cell wall and absence of cytoplasm." Image and caption text from Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons. Labels added by Maria Morrow.

Sieve cells, Sieve Tube Elements, and Companion Cells

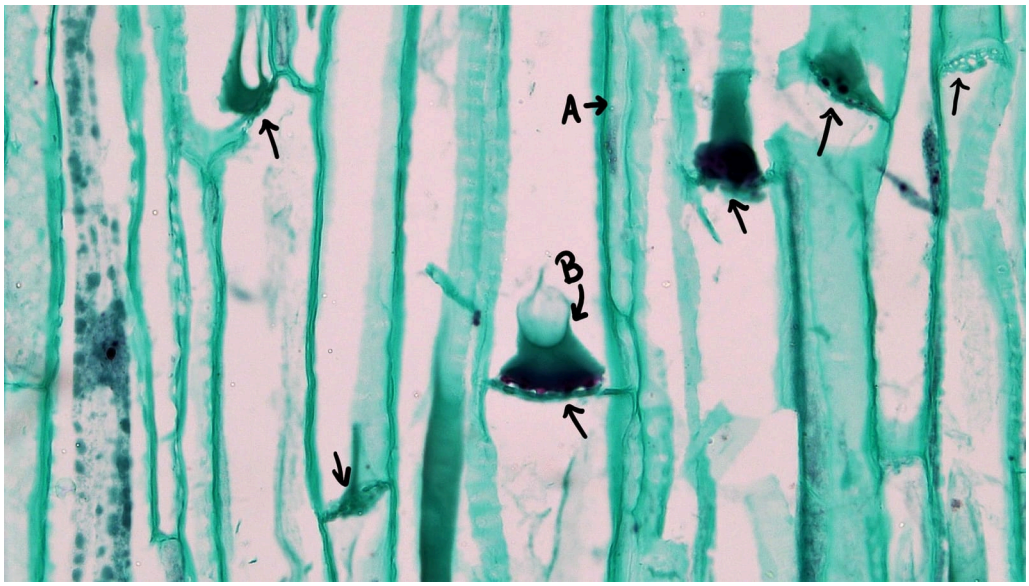


Figure 10.2.2.12: Longitudinal section through phloem. Most of the cells are sieve tube elements. The cells have sieve plates at the ends (marked by arrows). In the event of an injury, P-protein rushes to form a slime plug (B) and close the wound. Sieve tubes are alive but contain very little cell contents, they do not even have a nucleus. Instead, they are controlled by smaller companion cells (A). Photo by Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons. Labels added by Maria Morrow.

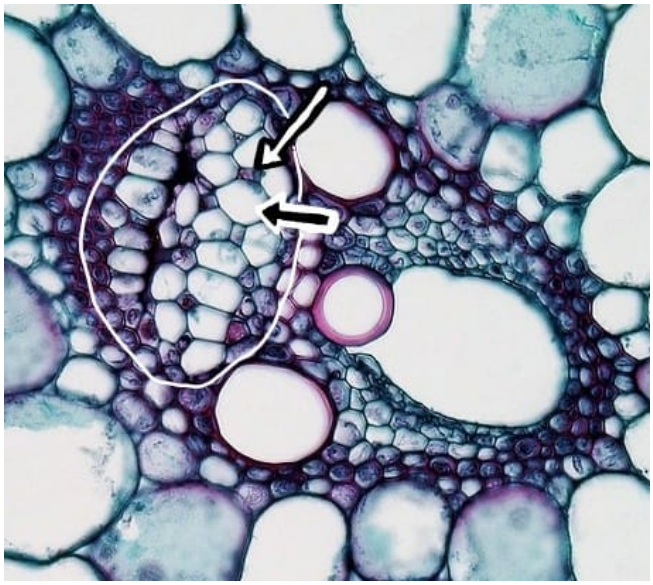


Figure 10.2.2.13: A cross section through a vascular bundle with the phloem circled (white). Within the phloem, there are two types of specialized parenchyma cells: the larger sieve tube elements (black arrow with white border) and the much smaller companion cells (white arrow with black border). Photo by Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons. Labels added by Maria Morrow.

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10.3: Cell Division

The Cell Cycle

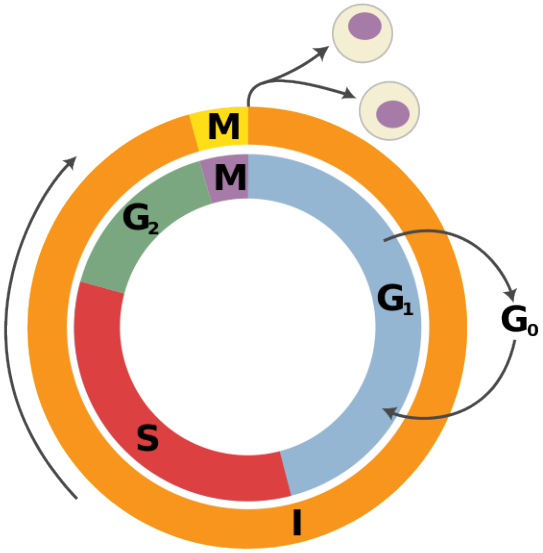


Figure 10.3.1: The cell cycle. Cells spend most of their time in interphase. If the cell will be specializing for a particular job, it will enter G0. If the cell will be dividing, it enters G1 (gap 1) during which the cell replicates organelles and cytoplasmic contents. During S phase (synthesis), the DNA is replicated. In G2, the cell checks that it is ready to divide. M is this diagram represents cell division. Here, mitosis is shown, resulting in two daughter cells. A second type of division, meiosis, is not depicted here but follows the same general progression. Diagram by Histidine, CC BY-SA 3.0, via Wikimedia Commons.

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10.3.1: Interphase, Mitosis, and Cytokinesis

Interphase

Cells spend most of their time in a stage called interphase. During this phase, the nuclear envelope surrounds the nucleus. There may be one or more nucleoli (dark, condensed regions) visible within the nucleus. The material around the nucleoli, contained within the nuclear envelope is DNA in the form of chromatin. This will not pick up a stain well and so will not appear as distinct shapes within the nucleus. Find these indicators of interphase in cell A in the image below.

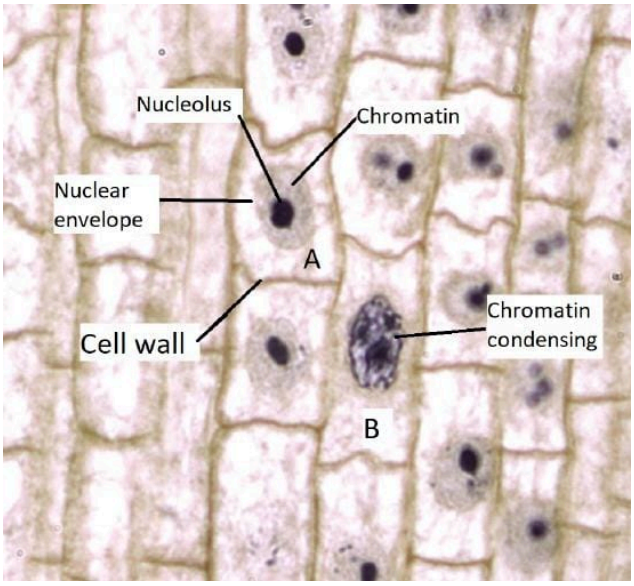


Figure 10.3.1.1: Cells in an onion root in interphase and prophase. Cell A has a large, dark nucleolus surrounded by greyish material (chromatin) that is enclosed within the nuclear membrane. A cell wall makes a box around each cell and the plasma membrane would be located just inside this box, though we cannot easily see it. In cell B, the chromatin is condensing and begins to look like dark, thick strands. It is still contained in the center of the cell, as the nuclear envelope has not finished dissolving. Photo by Maria Morrow, CC BY-NC.

In contrast, when a cell begins the process of division, the chromatin condenses into visible chromosomes that will pick up a stain and look like dark strings within the nuclear envelope, as seen in cell B in the image above.

In order to begin dividing, the cell needs to go through several processes that take place during interphase, including replicating the DNA (occurs in S-phase) and all of the cell contents.

Mitosis

Mitosis is the process of dividing the nucleus. To see cells in meiosis, we look in areas of a plant that would be actively growing. These areas where cells are actively dividing are called meristems, such as the root apical meristem.



Figure 10.3.1.2: A long section of an onion root tip. The edge of the growing tip has been outlined, attempting to show the location of the protoderm cells (located approximately on the black line) vs. the root cap, which would be located to the exterior of the black line. The root apical meristem is indicated by an arrow that points to the center of the U-shaped line. All cells in the root are derived initially from the root apical meristem. Photo by Maria Morrow, CC BY-NC.

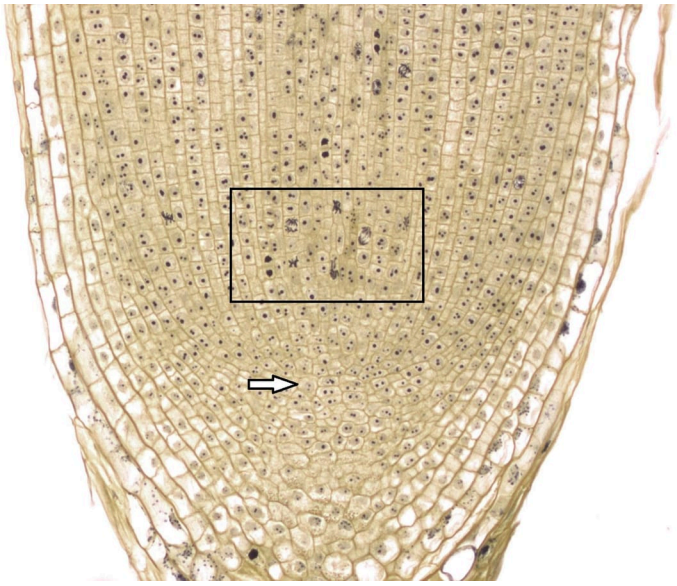


Figure 10.3.1.3: Cells in this onion root tip were caught in various stages of the cell cycle. The white arrow indicates the location of the root apical meristem. The box highlights an area where cells can be seen in most stages of mitosis. A stain has been used to show regions of dense nucleic acids, such as chromosomes and the nucleolus. Photo by Maria Morrow, CC BY-NC.

Prophase

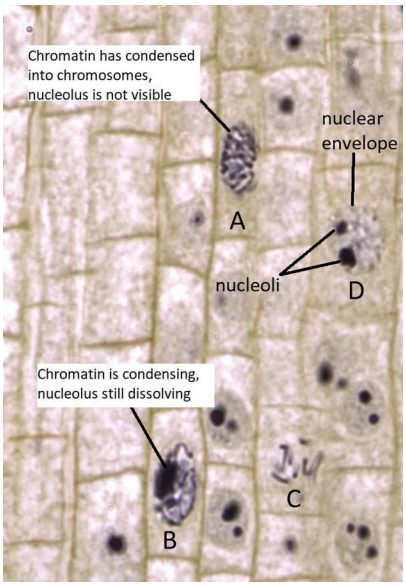


Figure 10.3.1.4: Cell A is in late prophase. The chromatin has condensed into visible chromosomes that form dark strands and the nucleolus is no longer visible. In cell B, the chromatin is condensing and some chromosomes are visible, but the nucleolus has not yet dissolved. In cell C, the nuclear envelope is gone, no nucleoli are visible, and the chromosomes are separating from each other. In cell D, the nuclear envelope and nucleoli are distinct and the chromatin has not yet condensed. Can you put these four cells in order by where they are in the process of mitosis? Photo by Maria Morrow, CC BY-NC.

Metaphase (including Prometaphase)

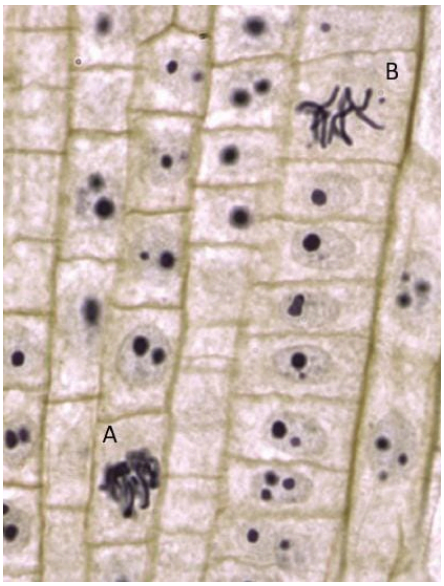


Figure 10.3.1.5: Cell A is in prometaphase. The chromosomes are no longer contained within a nuclear envelope. The spindle fibers are attaching to the kinetochores, but the chromosomes have not yet been pulled into a line. Cell B is in metaphase and the chromosomes are loosely aligned on the metaphase plate. Photo by Maria Morrow, CC BY-NC.

Anaphase

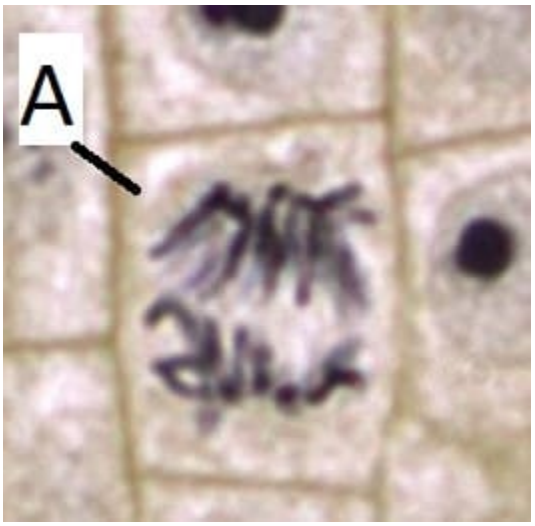


Figure 10.3.1.6: Cell A is in anaphase. The sister chromatids have been pulled apart and now there are two distinct groups of chromosomes on either side of the cell. Photo by Maria Morrow, CC BY-NC.

Telophase

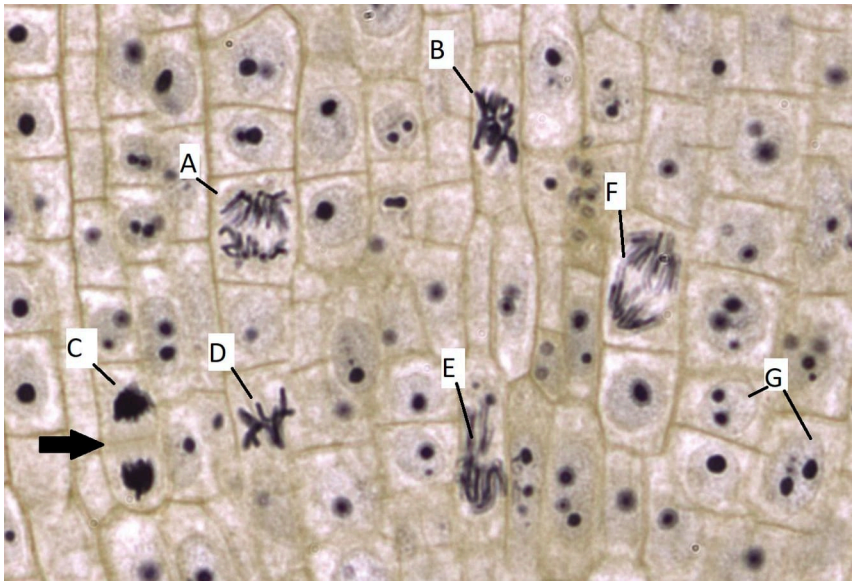


Figure 10.3.1.7: Cell C is in telophase. There are two dark regions where the chromosomes are clustered and decondensing, becoming indistinguishable from each other. A fuzzy line is forming between them, indicated by a black arrow, showing cytokinesis is happening as a new cell wall forms. Cell A is the same cell that is shown in Figure 10.3.1.6. In cell B and D, the chromosomes are grouped together in the center of the cell, though they appear much more orderly in cell D. In cells E and F, the chromosomes are in two distinct groups on either side of the cell, but are still distinguishable as individual strands. In the two cells indicated by G, there are distinguishable nucleoli and a clear nuclear envelope. Can you place these cells in order for where they are in the cell cycle? Photo by Maria Morrow, CC BY-NC.

Cytokinesis

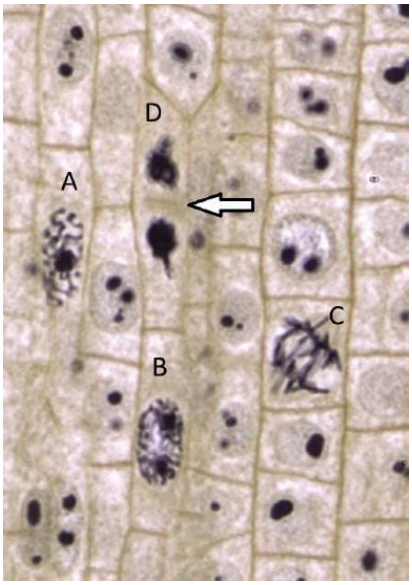


Figure 10.3.1.8: Cell D is in telophase. Cytokinesis is not part of mitosis, but happens concurrently with telophase. There are two dark regions where the chromosomes are clustered and decondensing, becoming indistinguishable from each other. A fuzzy line is forming between them, indicated by a white arrow, showing cytokinesis is happening as a new cell wall forms. Cell A has distinguishable chromosomes and a nucleolus. Cell B has partially condensed chromosomes, two nucleoli, and a clear nuclear envelope. Cell C has two groups of chromosomes being pulled to opposite sides of the cell. Can you place these cells in order for where they are in the cell cycle? Photo by Maria Morrow, CC BY-NC.

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10.3.2: Meiosis

Meiosis I

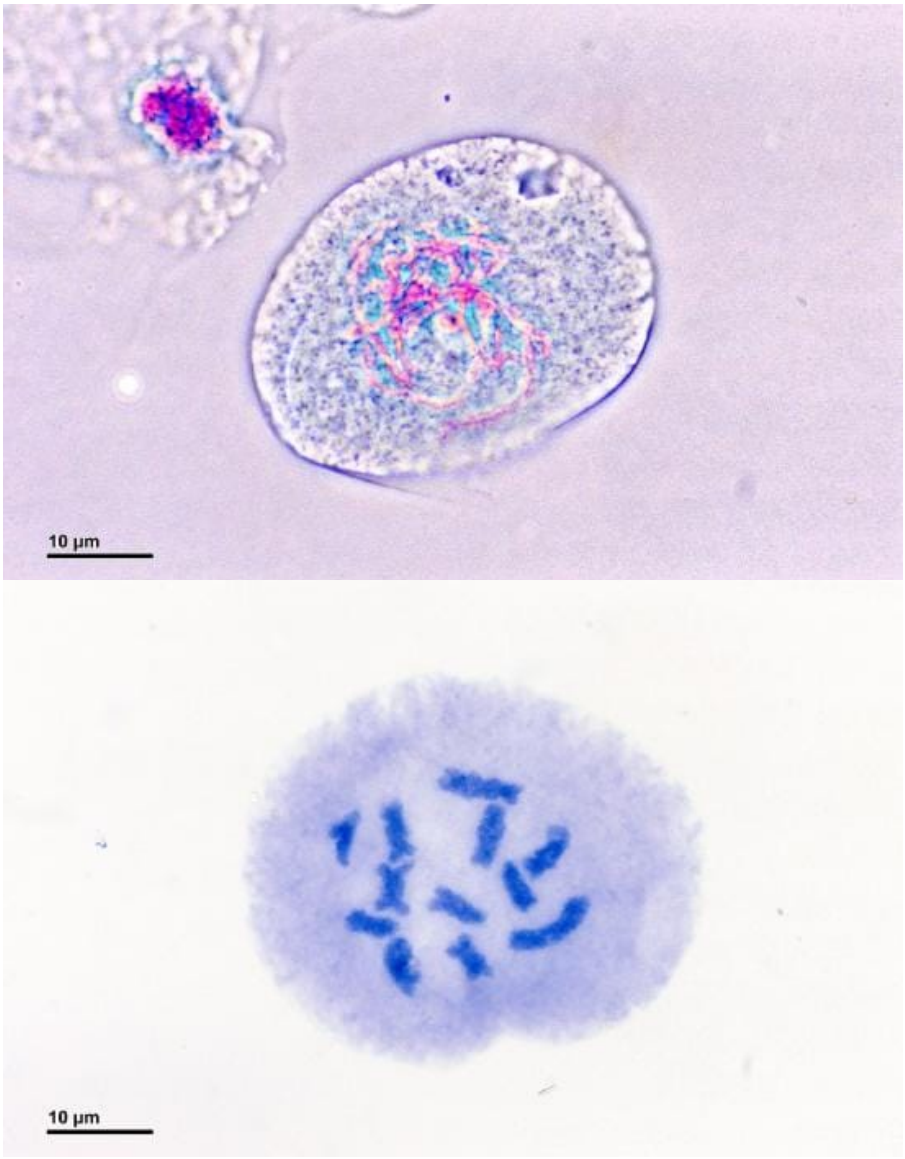


Figure 10.3.2.1: Dividing pollen mother cell, Prophase I. In the first image, the cell is in the early stages of prophase with the chromatin still condensing (appears neon pink). In the second image, twelve replicated chromosomes are visible, stained a deep blue. There is no visible nuclear envelope or nucleolus. Photos by Doc. RNDr. Josef Reischig, CSc., CC BY-SA 3.0, via Wikimedia Commons.

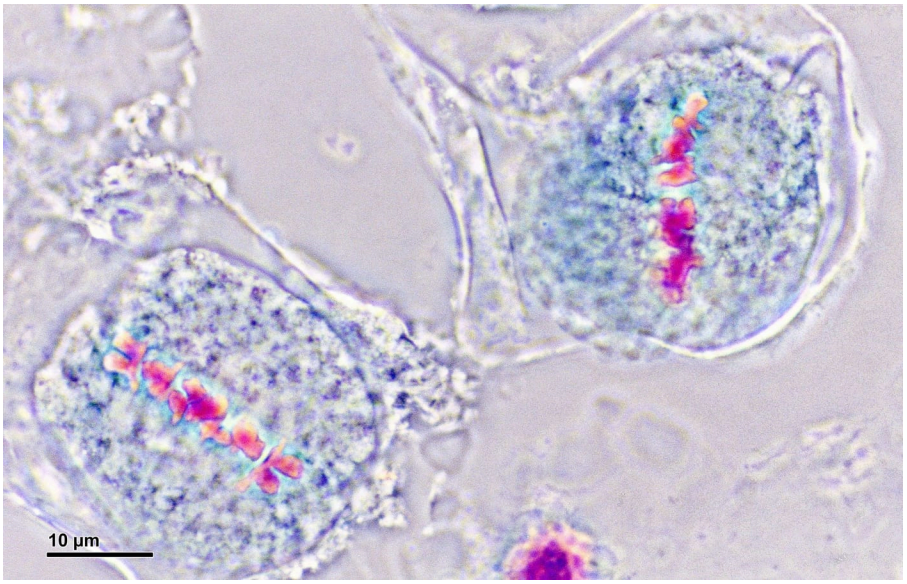


Figure 10.3.2.2: Dividing pollen mother cell, Metaphase I. The chromosomes in these two cells (appearing neon pink) are lined up across the center of the cell where the new cell wall will form. Photo by Doc. RNDr. Josef Reischig, CSc., CC BY-SA 3.0, via Wikimedia Commons.

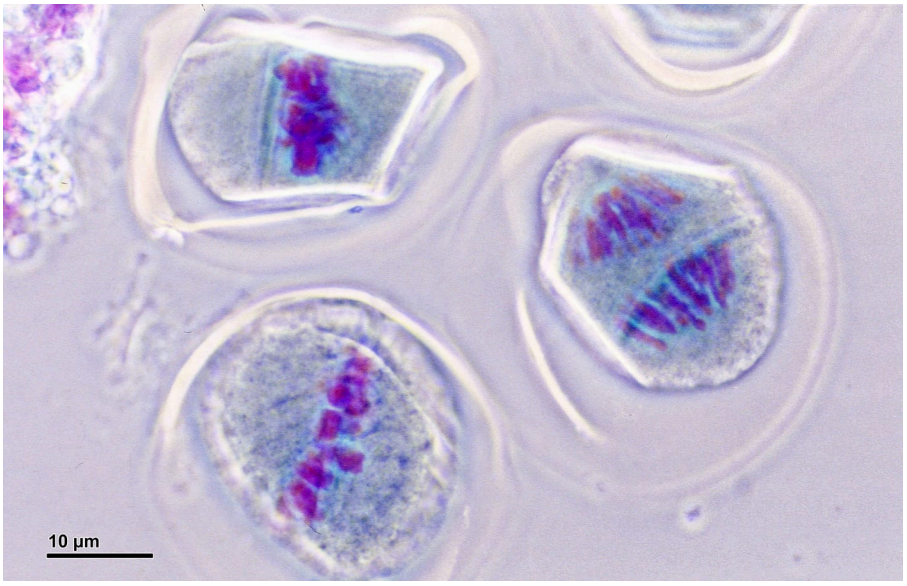


Figure 10.3.2.3: Dividing pollen mother cell, Metaphase I and Anaphase I. Here chromosomes are shown as stained bright pink. In the two cells on the left, the chromosomes are in the middle of the cell. The lower of these two cells is clearly in Metaphase I, with the chromosomes forming a distinct line across the cell. The cell on the right is in Anaphase I, sister chromatids (now each a chromosome) have been separated and pulled to either side. Photo by Doc. RNDr. Josef Reischig, CSc., CC BY-SA 3.0, via Wikimedia Commons.

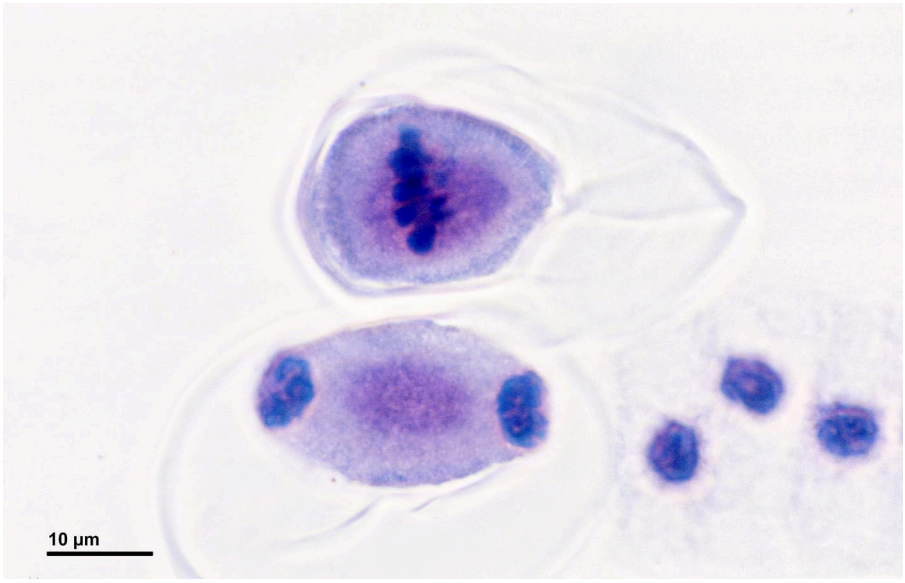


Figure 10.3.2.4: Dividing pollen mother cells, Metaphase I and Telophase I. The cell on the top is in metaphase I, while the cell on the bottom is in telophase I. In the lower cell, there are two reforming nuclei. Distinct chromosomes are no longer distinguishable. Photo by Doc. RNDr. Josef Reischig, CSc., CC BY-SA 3.0, via Wikimedia Commons.

Meiosis II

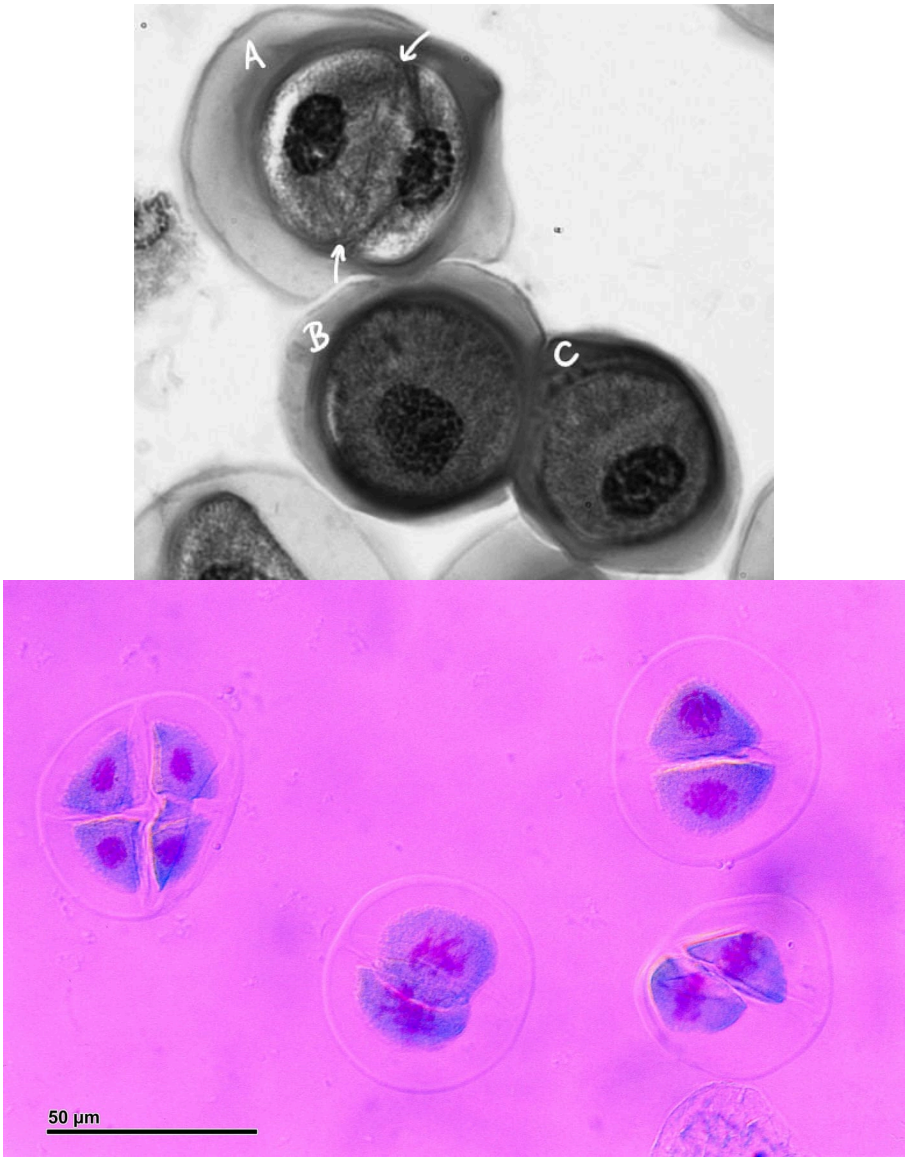


Figure 10.3.2.5: In the first image, cell A is clearly in prophase II. The white arrows point at the cell wall that formed during cytokinesis of meiosis I. There are two distinct nuclei with chromosomes condensing. Cells B and C are also in prophase II, but not clearly so (they appear to be in prophase I). This is because the second cell for each of these is under the first; the 3D nature of these structures makes it difficult to determine how many cells are present. In the second image, there are four dividing mother cells. The leftmost has four cells in it, while the other three have two. The three on the right are in prophase II, while the one on the left has completed meiosis. First photo by Maria Morrow, CC-BY 4.0 . Second photo by Doc. RNDr. Josef Reischig, CSc., CC BY-SA 3.0, via Wikimedia Commons.

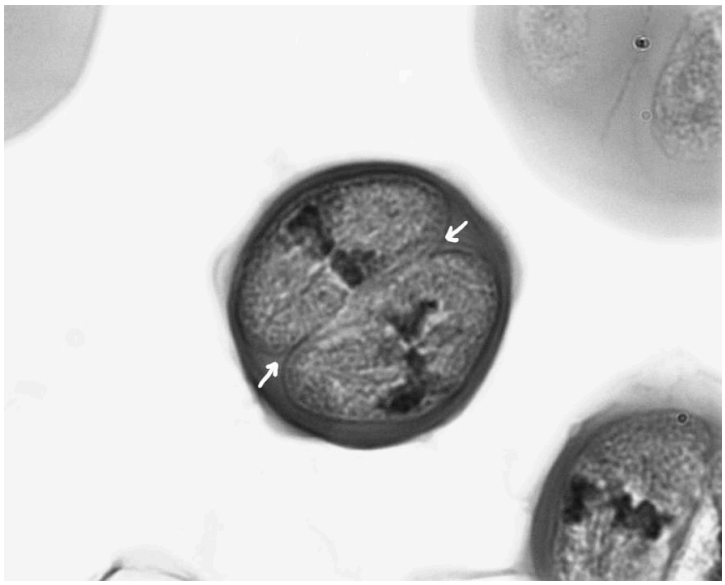


Figure \({10}{.}3{.}2{.}\eatSpaces{6\): A pollen mother cell in Metaphase II. There is a clearly formed cell wall (indicated by white arrows), formed during meiosis I. The chromosomes are lined up in the center of each newly formed cell. Photo by Maria Morrow, CC-BY 4.0.

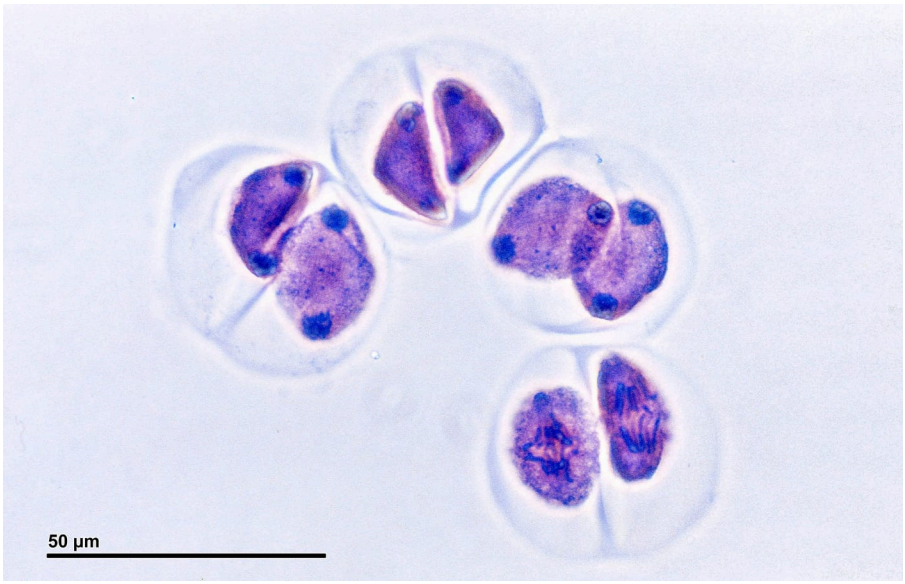


Figure Extra close brace or missing open brace : The three topmost cells are in telophase II, the lowest cell is in anaphase II. All four cells have a distinct cell wall. Photo by Doc. RNDr. Josef Reischig, CSc., CC BY-SA 3.0, via Wikimedia Commons.

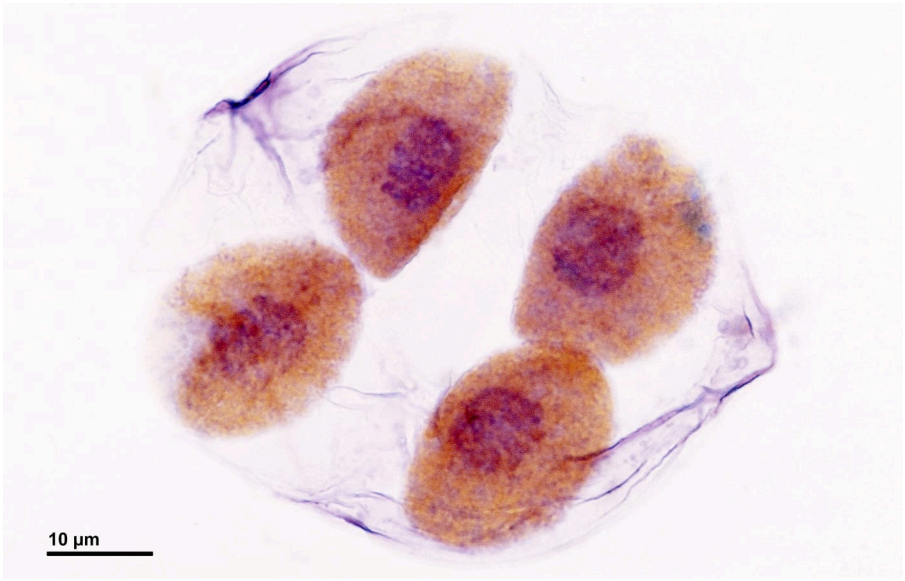


Figure 10.3.2.8: Four pollen grains. Each of these pollen grains is haploid and genetically distinct. Photo by Doc. RNDr. Josef Reischig, CSc., CC BY-SA 3.0, via Wikimedia Commons.

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11: ROOTS

The root system of a plant serves two primary functions: water absorption and anchorage. Roots with a higher surface area will be better adapted to absorbing water because they have more area to interact with the soil environment. Increased interaction with the soil environment can also contribute to increased anchorage, but there are always trade-offs. If roots become too fine, they will be easily broken and lose the anchorage function. Additionally, finer roots can also **lose** more water if the soil environment becomes dry. Alternatively, roots with more volume are able to store more water, starches, or other materials belowground. The balancing of these trade-offs with localized environments has resulted in a great diversity of root types and morphologies.

11.1: Primary Growth

11.1.1: Root Long Section (Zea mays)

11.1.2: Monocot Roots

11.1.3: Eudicot Root Cross Section (Ranunculus)

11.2: Secondary Growth

11.3: Root Systems

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11.1: PRIMARY GROWTH

All plant roots begin in primary growth, which is a lengthening of plant organs. Primary growth involves the root apical meristem, primary meristems, and primary tissues.



Figure 11.1.1: These wheatgrass seeds have recently sprouted, producing fresh root and shoot growth. This would be an excellent place to look for roots in primary growth. Note that, even though it is a tangled mess, the individual roots are not branching very much. Instead, they are growing like long, thin threads. At the tip of each of these threads, you would find a root apical meristem. Photo by Maria Morrow, CC BY-NC.

YouTube Video

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

Video 11.1.1: This video by Ben Montgomery provides a walkthrough of the internal structures and organization of plant roots, including lateral root formation. Sourced from YouTube.

- Primary Growth

11.1.1: Root Long Section (Zea mays)

11.1.2: Monocot Roots

11.1.3: Eudicot Root Cross Section (Ranunculus)

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11.1.1: Root Long Section (Zea mays)

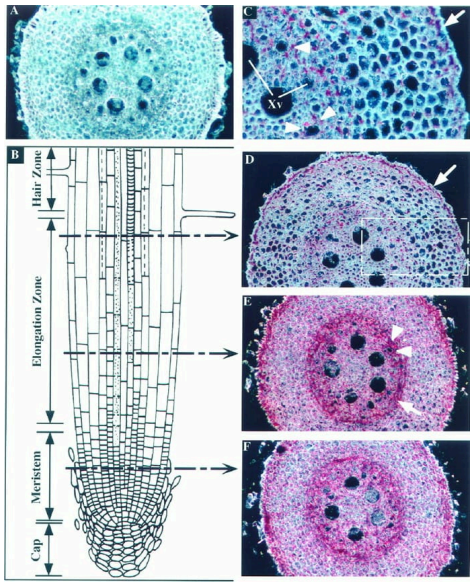


Figure 11.1.1.1: This figure is from a study exploring the expression of a particular mRNA in corn roots (shown as red in the images, but not important to understanding the anatomy). In B, we see a diagram of a longitudinal section through a growing root tip. The region labeled "Meristem" is the Zone of Division, covered by the root cap. The Elongation Zone is were cells get larger, and the region labeled "Hair Zone" is the Zone of Maturation, where cells are clearly differentiated and can start to specialize. D, E, and F show cross sections of the root in these zones. The large gaps in the cross sections are vessel elements, located within the vascular cylinder. Image retrieved from the open-access paper High Expression of the Tonoplast Aquaporin *ZmTIP1*in Epidermal and Conducting Tissues of Maize, Barrieu et al. 1998, published in Plant Physiology.

Figure 11.1.1.2: A diagram of a growing root tip. The tip of the root is covered by a cap of cells (C). Most of the root is covered by small projections (root hairs). The region of the root with hairs is labeled E. Between the area covered with hairs and the area covered by the cap, the root is labeled D. A=Root hair, B=Root cap, C=Zone of Division, D=Zone of Elongation, E=Zone of Maturation. Image from the public domain with labels added by Maria Morrow.

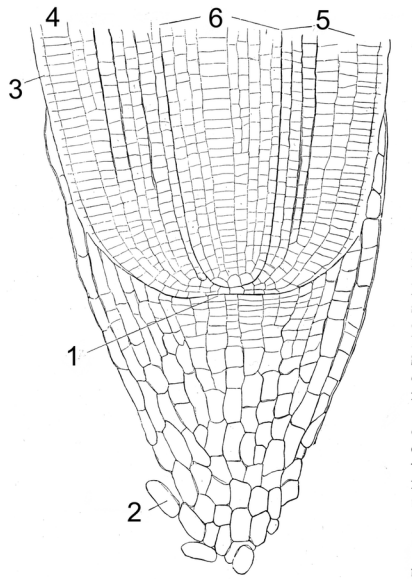


Figure 11.1.1.3: Anatomy of the root tip, zone of division. The first image is a *Zea mays* root tip. The second image is an illustrated diagram to show the tissues, labeled as follows: 1=Root apical meristem (RAM), 2=Root cap cell, 3=Rhizodermis (epidermis of the root), 4=Protoderm, 5=Ground Meristem, 6=Procambium. Photo by Maria Morrow, CC BY-NC. Illustration from de:Benutzer:Griensteidl, Public domain, via Wikimedia Commons.

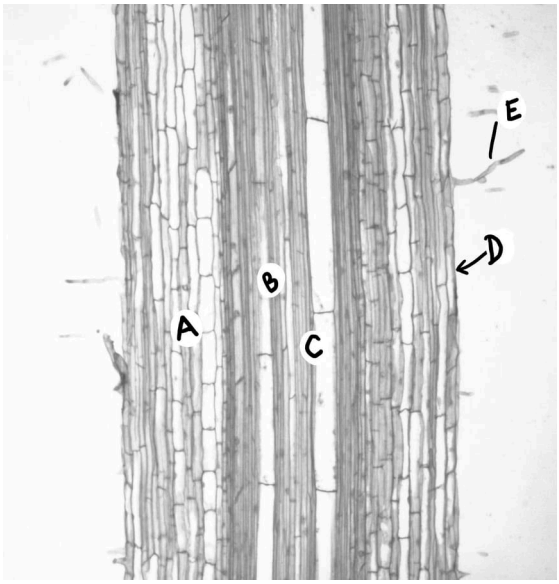


Figure 11.1.1.4: A longitudinal section through the zone of elongation. A=Cortex, B=Pith (or where the pith would be, this section may be slightly off center, capturing more of the vascular tissue), C=A vessel element in the vascular tissue, D=Epidermis, E=Root hair. Image by Maria Morrow, CC BY-NC.

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11.1.2: Monocot Roots

Zea mays

Zea mays (corn) is often used as a model organism for monocot anatomy.

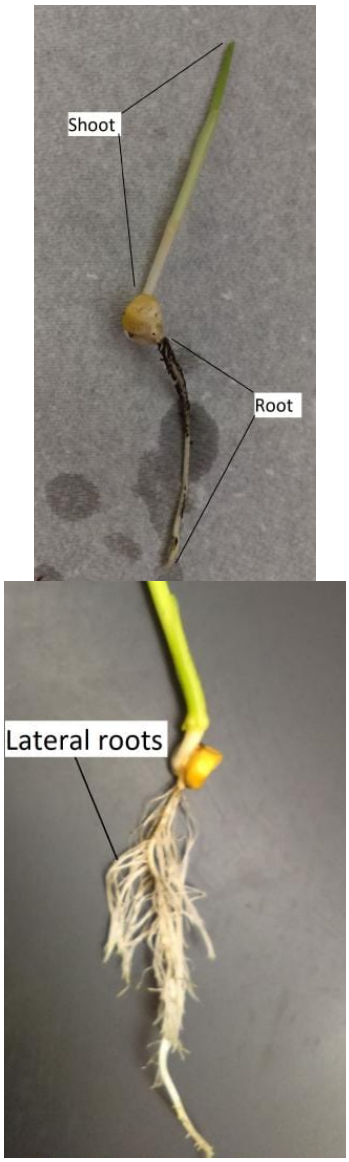


Figure 11.1.2.1: The images above show a corn seedling in two different stages of development. The first image is of the corn seedling at an earlier stage. It has produced a shoot (with one cotyledon) and a long root (radicle). In the second image, you can see that it has gotten larger by comparing the size of the seed coat from the corn kernel (caryopsis). The radicle has developed into a root system with many lateral roots branching off to the sides. Photos by Melissa Ha, CC BY-NC .

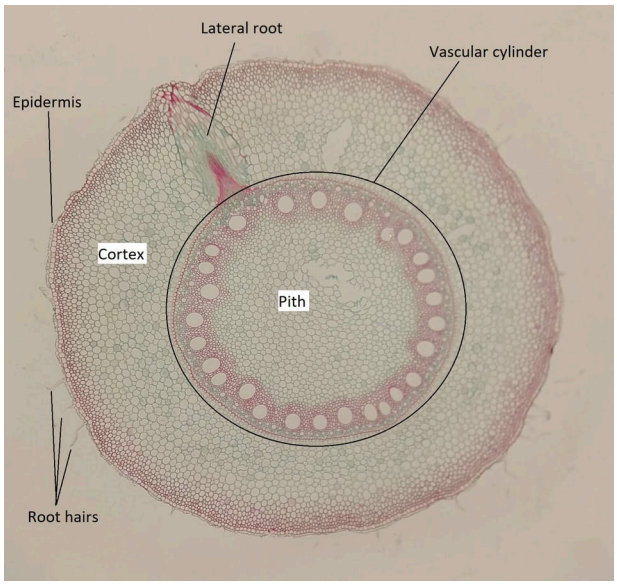


Figure 11.1.2.2: Corn root cross section. The major regions of the root are labeled in the cross section above. The epidermis is the outermost layer of cells and includes elongated cells called root hairs. The cortex is the region of cells between the epidermis and the vascular tissue. The pith is the region of cells contained within the cylinder of vascular tissue. A lateral root is emerging from the vascular cylinder. Photo by Maria Morrow, CC BY-NC.

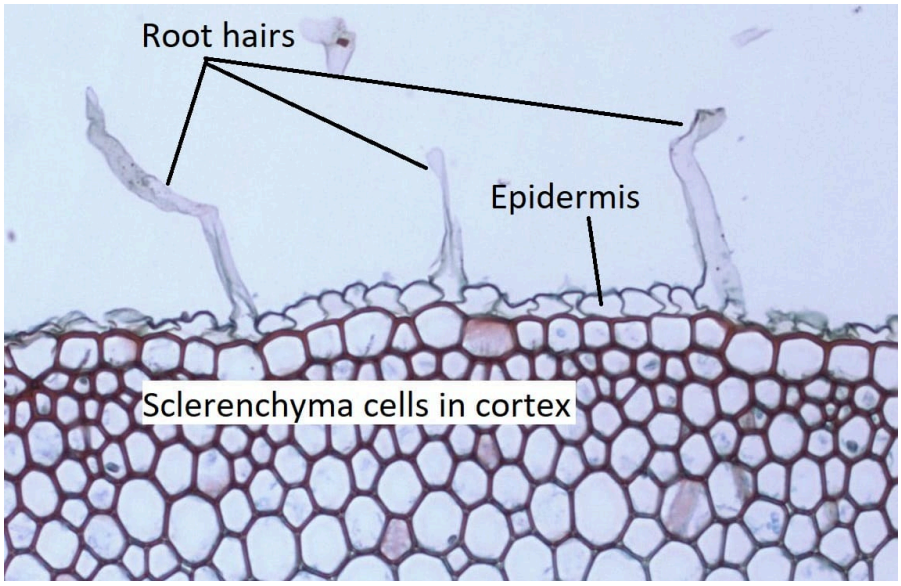


Figure 11.1.2.3: Corn root cross section, close up of epidermis and root hairs. The epidermis is the outermost layer of cells, produced by the protoderm. These are parenchyma cells. The epidermis includes long, thin cells that project outward called root hairs. Root hairs are specialized for absorbing water and will only be found in young, growing root tips. The cells below the epidermis are part of the cortex. Many of these have become sclerenchyma cells with thick secondary walls. Compare the cell walls found in the epidermis to those found in the cortex. Photo by Maria Morrow, CC BY-NC.

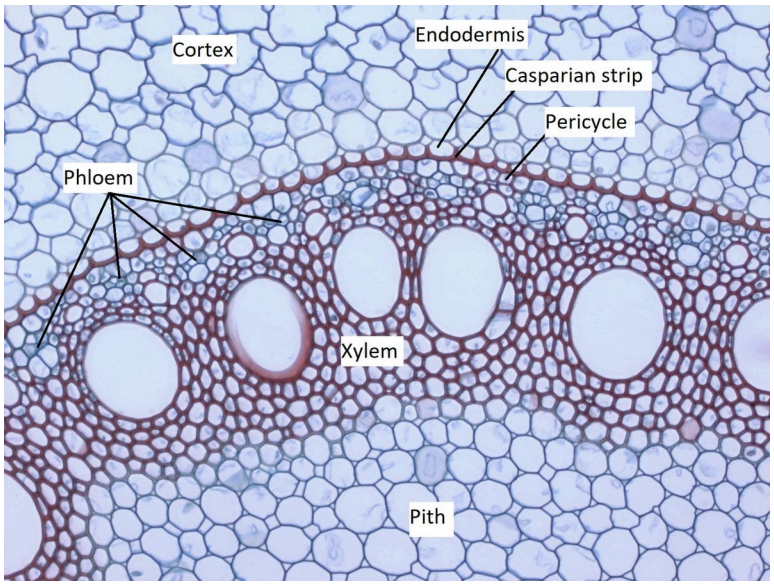


Figure 11.1.2.4: Corn root cross section, close up of part of the vascular cylinder. A band of cells travels across the center of the image, making a slight arc. This is a segment of the vascular tissue, which is arranged in a cylinder within the root. The vascular cylinder is within a suberized layer of cells that forms the border of the cortex, called the endodermis. The suberin wax layer coating the endodermal cells is the Casparian strip. Just inside the endodermis (below it, in this image orientation) is a layer of cells called the pericycle. This is where lateral roots are produced. The phloem tissue is composed of pockets of cells with thinner walls (stained blue). The rest of the cells in the vascular cylinder have thick secondary walls (stained red) and are part of the xylem tissue. When the cells begin to have thin, blue-stained walls again (in this image), you've reached the pith. Photo by Maria Morrow, CC BY-NC.

Smilax

The organization of tissues in a Smilax root is similar to that in a corn root.

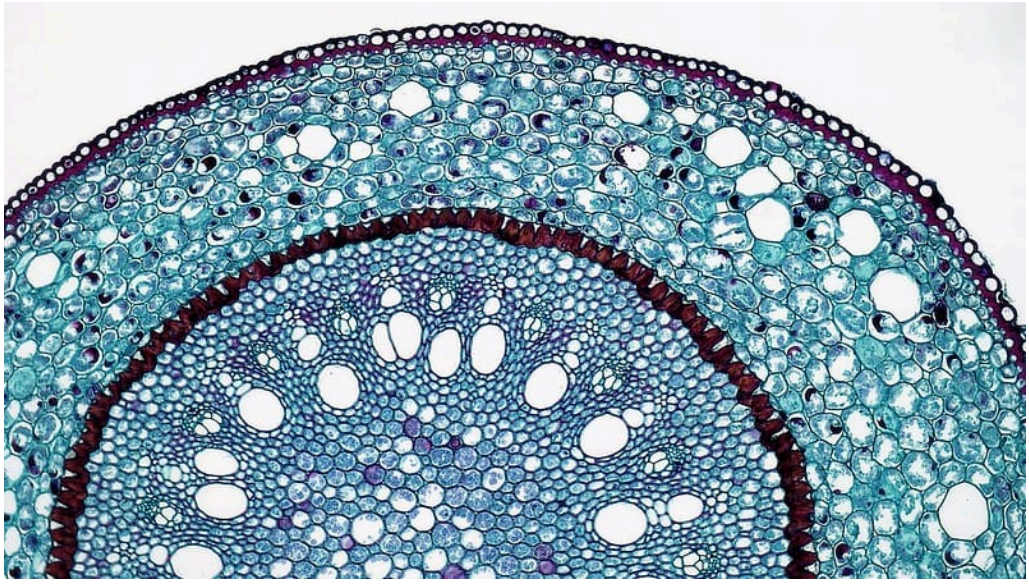


Figure 11.1.2.5: A cross section through a Smilax root. Compare this cross section to the corn root above. The staining is slightly different, so you cannot rely on color, alone. Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

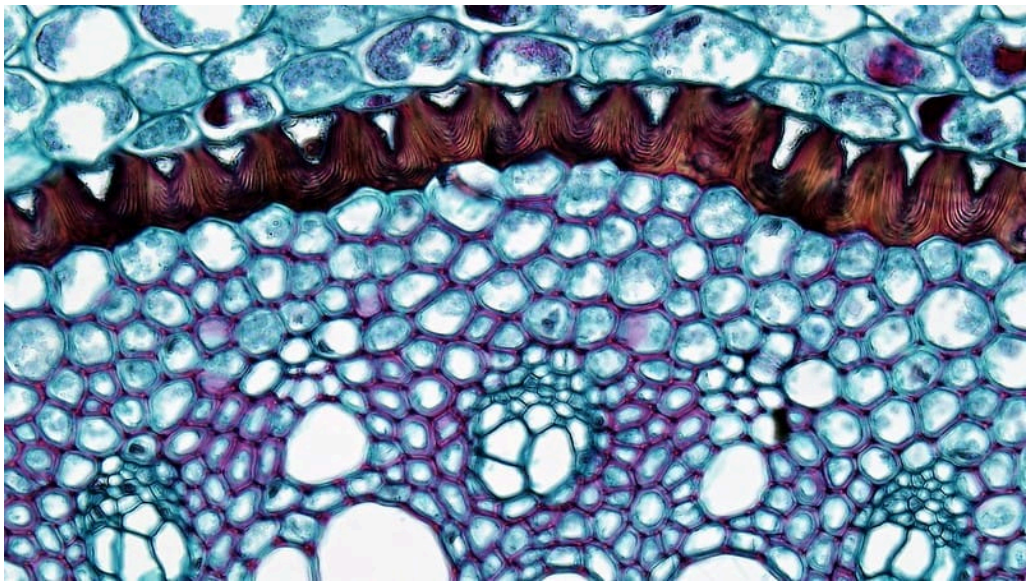


Figure 11.1.2.6: A close up on the multilayered Casparian strip of the Smilax root. The layers of Casparian strip look a bit like fingerprints or growth rings in wood, forming tightly packed layers surrounding each cell. Compare the thickness of this Casparian strip to the corn root. What would cause the difference in thickness? Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

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11.1.3: Eudicot Root Cross Section (Ranunculus)

Ranunculus

Figure 11.1.3.1: A cross section of a young *Ranunculus* root. The epidermis and cortex are in a similar arrangement as in monocots. However, the vascular cylinder has no internal pith region. Instead, it is composed entirely of vascular tissue with xylem at the center in a Y-shape and phloem filling the regions between the arms of the Y. Photo by Melissa Ha, CC BY-NC with labels added.

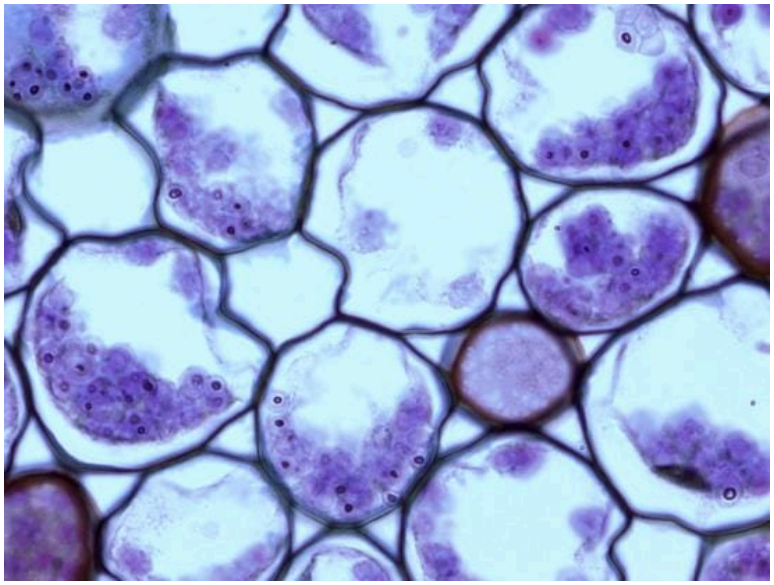


Figure 11.1.3.2: A close up on the cortex cells of the *Ranunculus* root. These cortex cells are also called storage cells because they contain many amyloplasts (stained purple) that store starch. Defined areas that do not contain amyloplasts are likely intercellular spaces (areas between cells). Photo by Maria Morrow, CC BY-NC.

Young Root

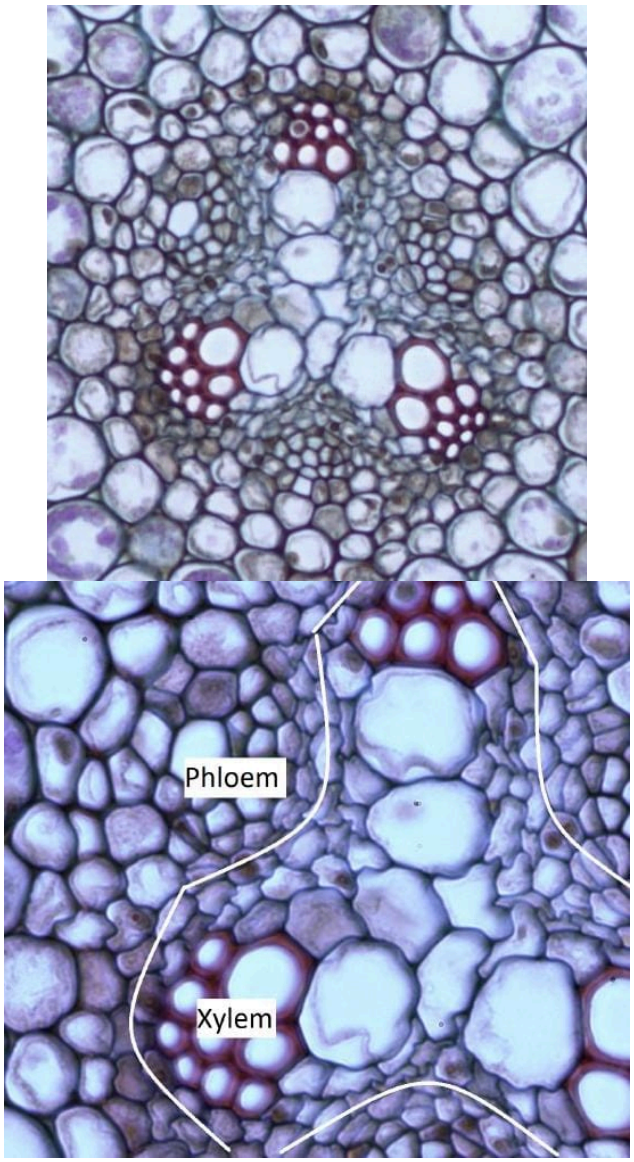


Figure 11.1.3.3: A close up on the vascular cylinder of the young *Ranunculus* root. At this stage, the vascular tissue does not have a well-defined boundary from the cortex (see the image on the left). Some of the xylem cells are stained red. These cells have developed their secondary walls and reached functional maturity. The others have only primary walls and are still developing. In the image on the right, the Y-shape of the xylem has been indicated by white lines. Those white lines represent the location of the procambium, which produces xylem to the inside and phloem to the outisde. One of the three pockets of phloem tissue is labeled. Photos by Maria Morrow, CC BY-NC.

Mature Root

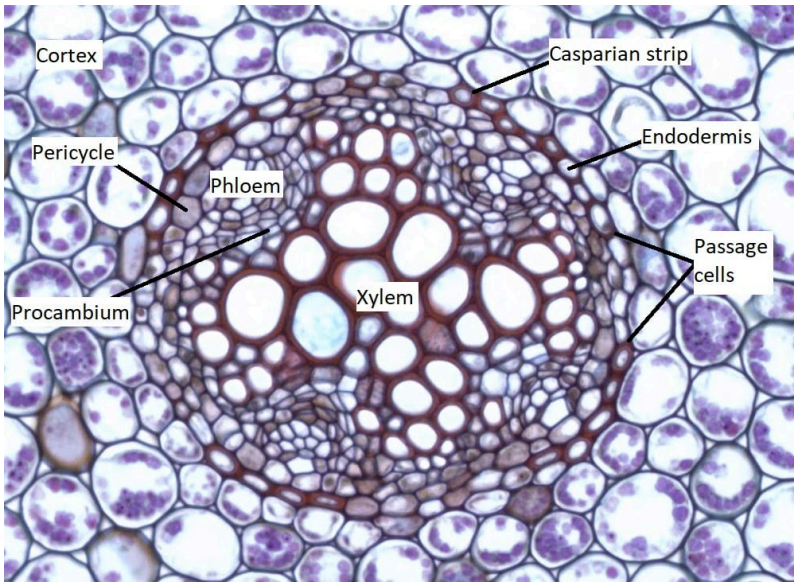


Figure 11.1.3.4: A close up on the vascular cylinder of a mature *Ranunculus* root. The vascular cylinder is now clearly defined by the boundary of the endodermis (the innermost layer of the cortex), which is beginning to be covered by Casparian strip (which stains red, making the covered cells look like they have a secondary wall, but they do not). There are regions of the endodermis that appear to have no Casparian strip or only have it between adjacent cells. These groups of cells, called passage cells, are located at the tips of the four xylem arms (which are in an X-shape, now). Eventually, all of the cells in the endodermis will be coated. Photo by Maria Morrow, CC BY-NC.

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11.2: Secondary Growth

In secondary growth, primary tissues and residual meristematic tissues produce secondary meristems, which then produce secondary tissues. Whereas primary tissues allow for vertical growth, secondary tissues allow for lateral growth: they allow stems and roots to become wider by producing **wood**. In addition to growing wider, secondary growth exchanges the living epidermis for a thick layer of dead, waterproofed cells called cork. The cork and a few other layers of tissue comprise something called the periderm, or perhaps more familiarly called **bark**.

This type of growth first evolved in gymnosperms. It is also present in many angiosperms. As a general rule, monocots do not undergo secondary growth (though some, like bamboo, have an analogous process).

Gymnosperms

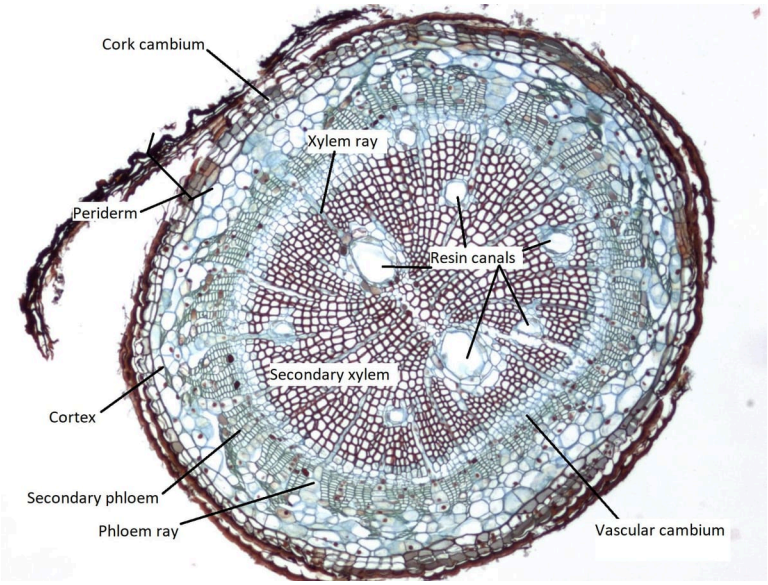


Figure 11.2.1: A cross section of a pine root in the early stages of primary growth. The first layer of periderm is forming, causing the epidermis to slough off. The periderm is currently the outermost layer, compose of a few layers of suberized cork cells, the cork cambium, and large cells called the phelloderm. The cortex is just inside the phelloderm and is getting smaller as the root grows. Ranks of cells just inside the cortex are secondary phloem cells (stained a blue-green color) which are being produced by the vascular cambium (a ring of cells stained light blue between the xylem and phloem). Just within the vascular cambium, making up the center of the root, is the secondary xylem (stained red, due to the secondary wall). There are large holes in the secondary xylem where resin canals are traveling through. Strings of parenchyma cells traverse laterally through the vascular tissue. These are called xylem rays and phloem rays, depending on their location within the vascular tissue. Image from Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons.

Angiosperms

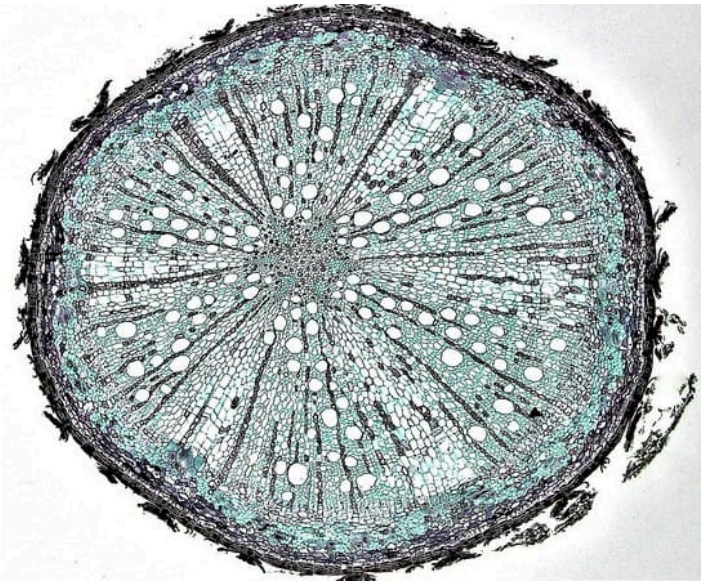


Figure 11.2.2: Older *Quercus* root, 40x. "In young roots, the vascular cylinder is surrounded by two rings of cells, the pericycle and endodermis, and above these layers the cortex and epidermis. In older roots underling activity of the cork cambium replaces the epidermal and cortical tissues with a protective zone of cork rich periderm. The outermost layer of periderm consists of layers of cork cells, the phellem, which produce the waterproofing substance suberin. Cork cells are dead at maturity. Deep to the phellem is a layer of living cork cambium or phellogen and just beneath that layers of cork parenchyma or phelloderm. Many cells in the periderm contain dark staining tannins. The vascular cylinder consists of an outer narrow ring of phloem,and deep to this, the vascular cambium. The vascular cambium remains active, producing annual growth of secondary phloem towards the outside of the root and secondary xylem towards center of the root. Because of greater production of xylem, the bulk of the vascular cylinder is dominated by radially arranged rays of secondary xylem interspaced with medullary rays of parenchyma cells. Annual growth rings of spring and summer wood is difficult to distinguish in roots. Both the pericycle and endodermis, which wrap vascular cylinder in younger roots, are lost due to seasonal growth of the vascular cylinder. The center of the root is made up of primary xylem." Caption text and image from Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons.

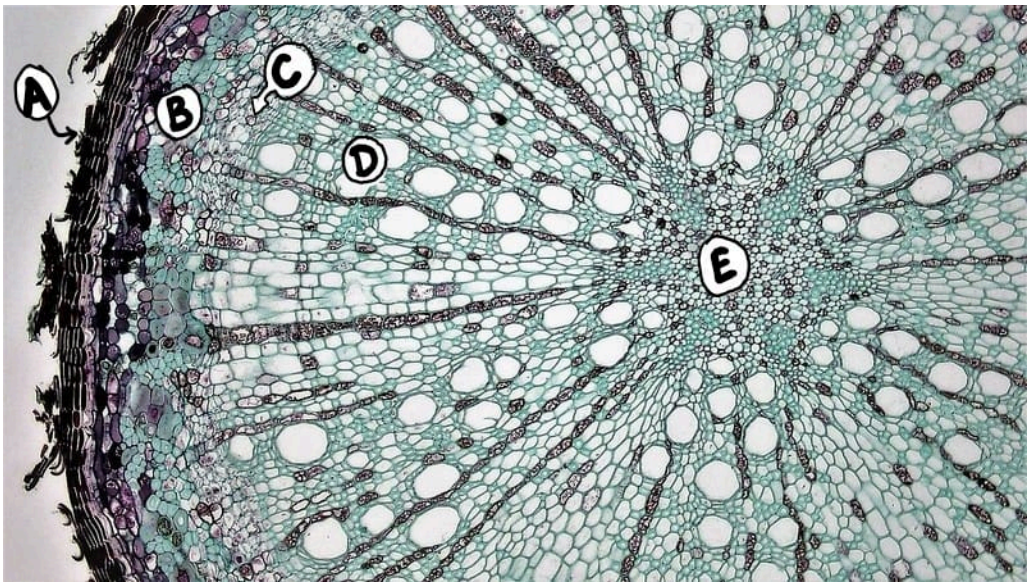


Figure 11.2.3: A labeled cross section through an older *Quercus* root, 100x. A=Periderms, B=Secondary Phloem, C=Vascular Cambium, D=Secondary Xylem, E=Primary xylem. Image from Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons. Labels added by Maria Morrow.

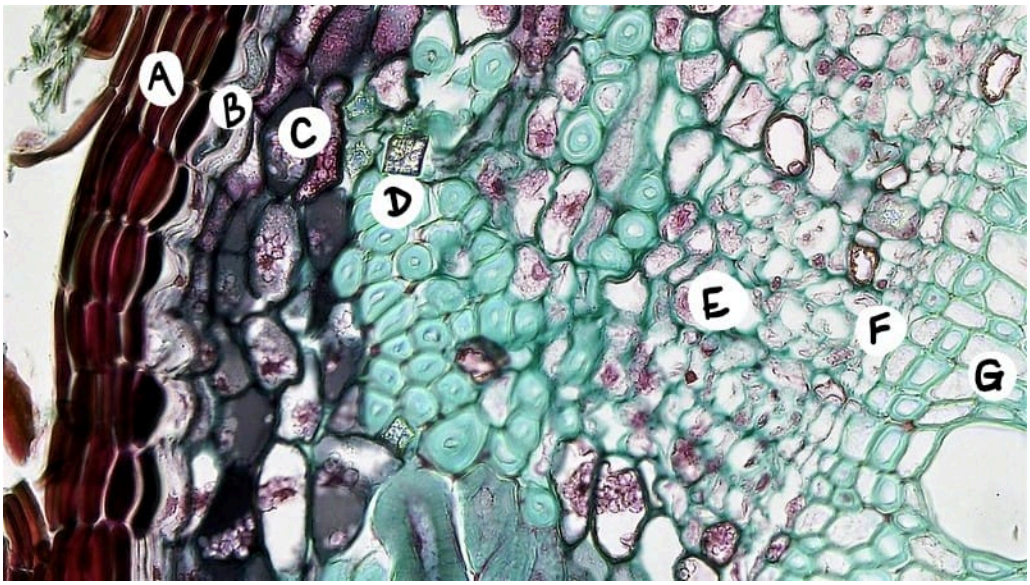


Figure 11.2.4: A labeled cross section through the outer tissues of an older *Quercus* root, 400x. A=Cork cells, B=Cork cambium, C=Phelloderm (A, B, and C=Periderm), D=Secondary phloem fibers, E=Secondary phloem, F=Vascular cambium, G=Secondary xylem. Image from Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons. Labels added by Maria Morrow.

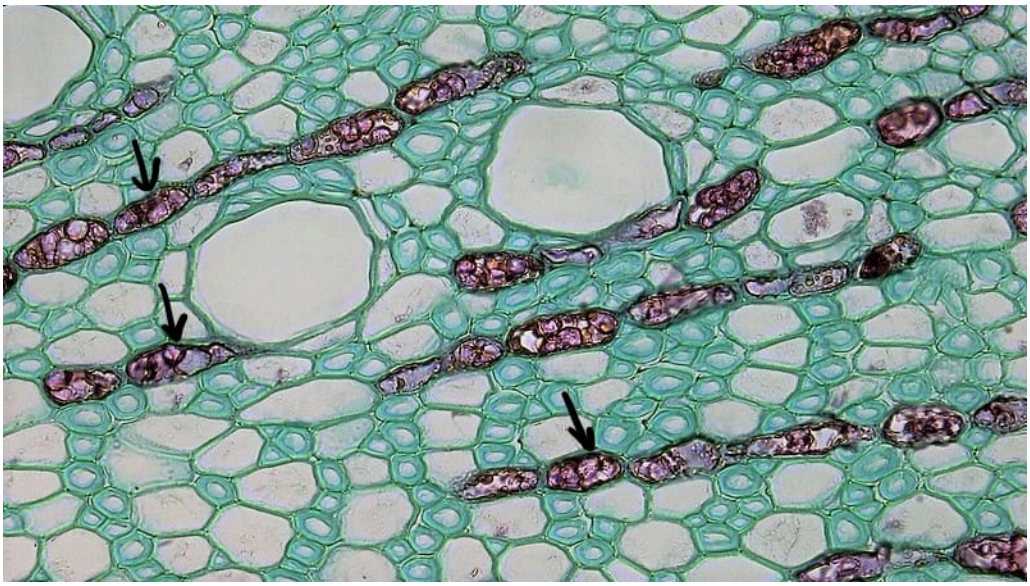


Figure 11.2.5: A cross section through the secondary xylem of an older *Quercus* root, 400x. The rows of darker cells (indicated by arrows) are parenchyma cells that traverse the secondary xylem and phloem. In the xylem, they are called xylem rays. In the phloem, they are called phloem rays. Image from Berkshire Community College Bioscience Image Library, CC0, via Wikimedia Commons. Labels added by Maria Morrow.

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11.3: Root Systems

Taproots

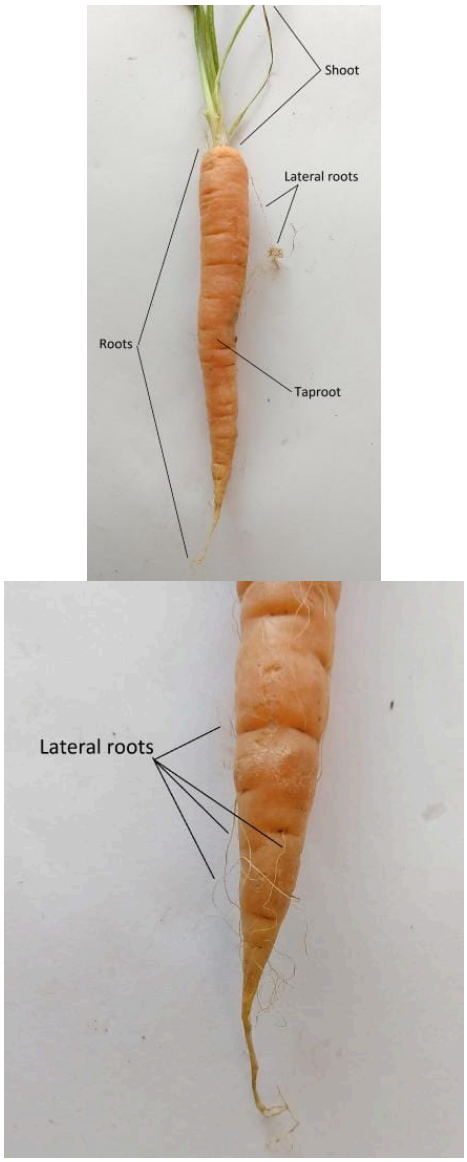


Figure 11.3.1: The carrot vegetable we eat is the taproot of a carrot plant. The large, central root (what we call a carrot) is a taproot and has many much smaller lateral roots that emerge from the sides. These are not root hairs, which would appear more like a microscopic fuzz at the ends of these lateral roots. Photos by Maria Morrow, CC-BY 4.0.



Figure 11.3.2: Some plants invest far more in their below ground tissues than their above ground ones. In this image, an enormous taproot of the small, prostrate plant *Abronia latifolia* (the yellow sand verbena) has been explosed as the dune sand has blown away from this area over time. How does investment in this taproot structure benefit this plant, considering the shifting, sandy environment? Photo by Maria Morrow, CC-BY 4.0.

Netted Roots

Figure 11.3.3: The netted root system of *Zea mays*. There are many roots of approximately the same diameter that then branch off into smaller roots. There is, distinctly, no one larger root. This is a netted root system. Photo by Maria Morrow, CC-BY 4.0.

Contractile Roots



Figure 11.3.4: The base of a dandelion rosette, showing a contractile root. The central root shown, where the leaves of the rosette meet at the base, looks like a compressed slinky. This is a contractile root, which can respond to seasonal changes in water availability to keep the dandelion plant at ground level. As water swells the soil, it can rise up. In response, this contractile root can swell with water, extending and allowing the plant to stay at the surface. In the case of a drought, the root can contract as the soil level drops. Photo by Melissa Ha, CC-BY 4.0.

Adventitious Roots



Figure 11.3.5: Adventitious roots of a kalanchoe plant. Many house plants reproduce themselves easily, lending to their cultivation and sale. The kalanchoe is extending a branch outward and producing new roots from its stem tissue. Notice the seven projections traveling down from the branch. These are adventitious roots, because they are produced by the stem. If this branch were cut off, it could be established as a new plant, due to the presence of these roots. Photo by Melissa Ha, CC-BY 4.0.

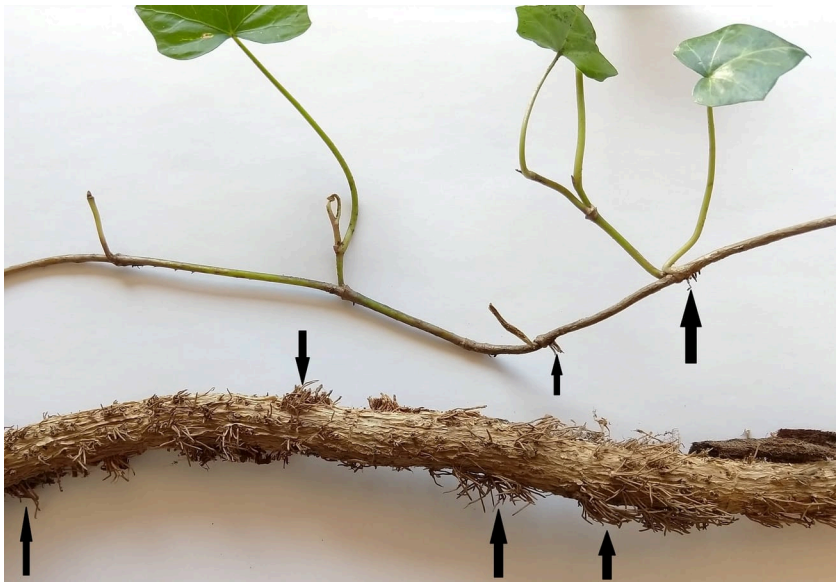


Figure 11.3.6: Vining plants frequently produce adventitious roots. This image shows two English ivy stems, a younger one on the top and a much older one on the bottom. The young stem has small clusters of adventitious roots emerging from the stem at nodes opposite to the leaves. Two of these are indicated by black arrows. On the older stem, adventitious roots emerge along the entire length, making it look hairy. There are a few particularly dense clusters, indicated by arrows. Photo by Maria Morrow, CC-BY 4.0.

Prop Roots.

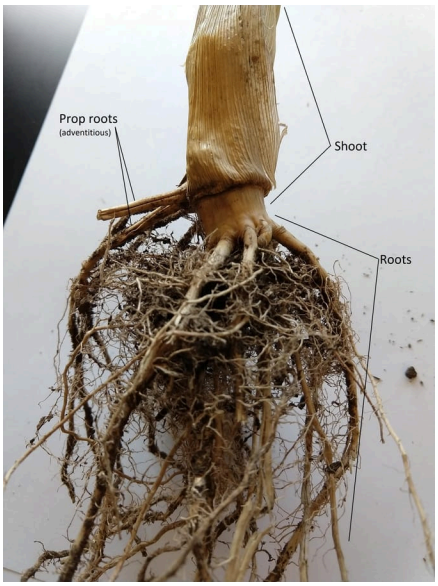


Figure 11.3.7: Zea mays also has prop roots that emerge from the stem. Above the netted root system, there is a short collar, then sheathing leaves emerge, indicating the transition to shoot tissue. At the base of these leaves, several prop roots are emerging. These prop roots, whose function is to give the plant extra stability from above ground, are also adventitious roots. Photo by Maria Morrow, CC-BY 4.0.

Pneumatophores



Figure 11.3.8: Mangroves grow in the intertidal zone where they spend much of the day inundated by water. Roots need to take in oxygen for cellular respiration. On strategy to gain access to oxygen is the development of aerial roots called pneumatophores (lung-bearers). The many pointed structures emerging from the soil under these *Avicennia* trees in Mumbai are pneumatophores. Photo by Dr. Raju Kasambe, CC BY-SA 4.0, via Wikimedia Commons.

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12: STEMS

The shoot of a plant is responsible for two major functions: photosynthesis and reproduction. In most plants, the leaves carry out **photosynthesis**, while the stems provide stability to elevate those leaves above potential competition. In annual plants, whose entire life cycle from germinate to death is completed in a single year, the epidermis on the stem is often photosynthetic, as well. All stems undergo primary growth. In gymnosperms and many angiosperms, stems will transition into secondary growth to form woody tissues.

12.1: Primary Growth

12.2: Secondary Growth

12.3: Woody Shoot Structures

12.4: Modified Shoots

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12.1: Primary Growth

Tissues in the shoot are derived from the shoot apical meristem (SAM). Just like in the root, the SAM produces three primary meristems, which produce the primary tissues:

- Protoderm → Epidermis
- Ground meristem → Cortex and pith (simply ground tissue in monocots)
- Procambium → Primary xylem and primary phloem

These primary tissues will then either differentiate into specialized cells or, as is the case in many eudicots, become meristematic and produce secondary tissues.

Coleus Stem Tip

Though it looks a bit alien, this is a section through a growing tip of a plant. In the center, where the alien's head might be, is a region of small, densely packed cells. This is the SAM of the apical bud. On either side of the SAM, like two upraised arms, are the leaf primordia. These are the early stages of developing leaves. Through the center of these leaf primordia is a darker region of small cells. This is the procambium, which will develop into the vascular tissue. Lining the outer edge of the SAM and the youngest portions of the leaf primordia is the protoderm. As the protoderm matures into the epidermis, it produces hair-like projections called trichomes. Between the protoderm and the procambium is the ground meristem.

On either side of the growing tip are two other darkened lumps of densely packed cells. These bud primordia will develop into axillary buds, producing either branches or flowers. Each bud primordium has its own SAM.

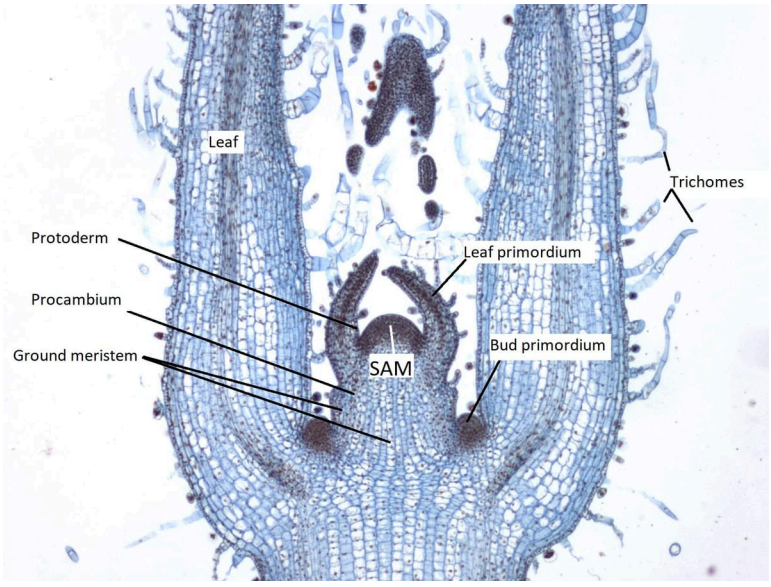


Figure 12.1.1: A partial view of a Coleus shoot tip long section. If we anthropomorphize it a bit and think of it as a humanoid with horns, it might be easier to conceptualize where the different parts are. The two "arms", held straight up into the air, are the leaves. Each leaf has many multicellular trichomes along its epidermis and a central strand of vascular tissue. Where the shoulders would be, there are two dark regions. These are bud primordia that will develop into axillary buds. They are dark in color because they are regions of intense cell division as they are rapidly growing. The "horns" are leaf primordia that will develop into leaves, much like the "arms". Between the two horns, at the top of the "head", is the shoot apical meristem (labeled SAM). All of the cells in the shoot are derived from this region. The protoderm runs along the exterior, near the SAM and leaf primordia. The procambium forms the vascular tissue and can be found in the center of the leaf primordia. The ground meristem forms the cortex and pith and can be found in the regions between the protoderm and procambium. Photo by Maria Morrow, CC BY-NC.

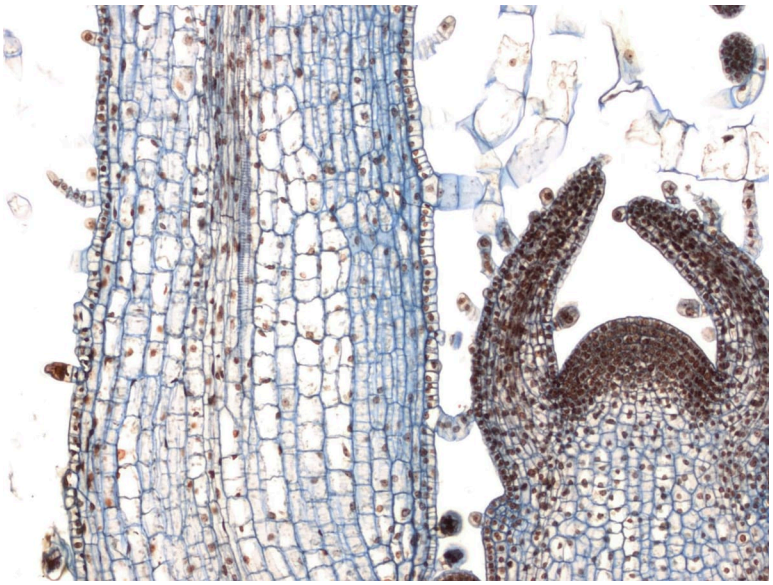


Figure 12.1.2: A closer view of the Coleus shoot tip long section. Can you locate the SAM and primary meristems? Look for regions of densely packed cells, as these are all meristematic tissues, actively dividing to produce more cells. Photo by Maria Morrow, CC BY-NC.

Monocots

Figure 12.1.3: A cross section of a *Zea mays* stem. The organization of tissues differs from the *Zea mays* root. Most notably, the vascular tissue is arranged in bundles, rather than a central cylinder. These bundles are densely packed toward the outside of the stem, then occur less frequently toward the inside. Because there is no distinct delineation of the tissues produced by the ground meristem, it is now called ground tissue (as opposed to cortex and/or pith). Photo by Maria Morrow, CC BY-NC.

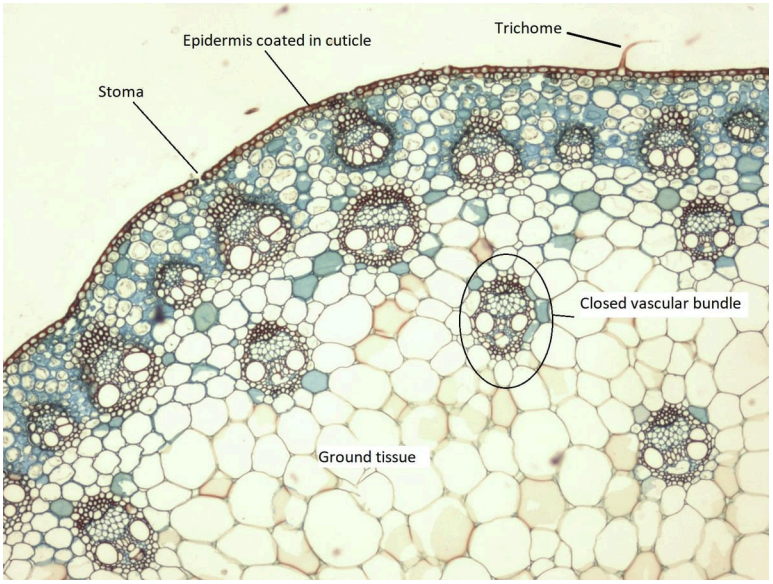


Figure 12.1.4: A closer view of a portion of the *Zea mays* stem. The epidermis is the outermost layer, coated in a thick cuticle that stains red. There are gaps in the epidermis where stomata are located, as well as a hair emerging (a trichome). The vascular bundles are situated within the ground tissue. Photo by Maria Morrow, CC BY-NC.

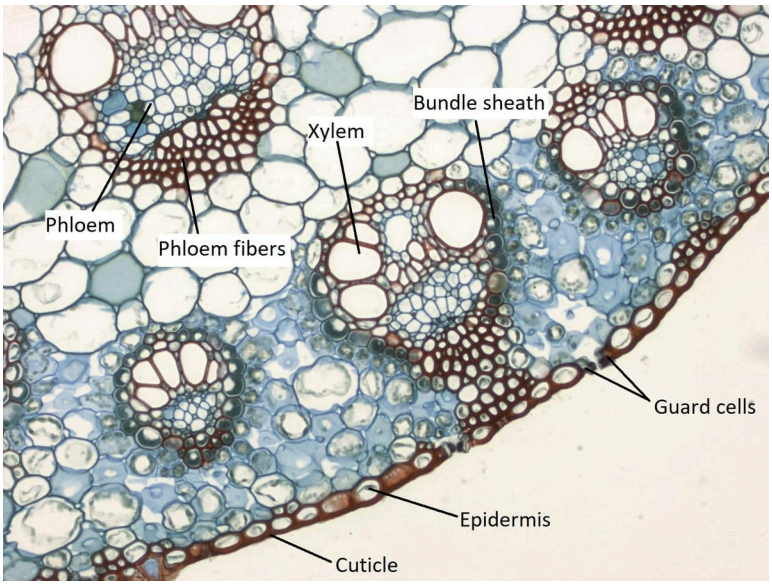


Figure 12.1.5: A cross section of a *Zea mays* stem highlighting the vascular bundles. In the epidermis, the cuticle and guard cells are easier to distinguish in this image. Vascular bundles are arranged close to the epidermis with the xylem (stained red) toward the interior of the stem and the phloem (stained blue) toward the exterior. Each bundle is surrounded by a layer of cells called the bundle sheath. Photo by Maria Morrow, CC BY-NC.

Eudicots

Helianthus

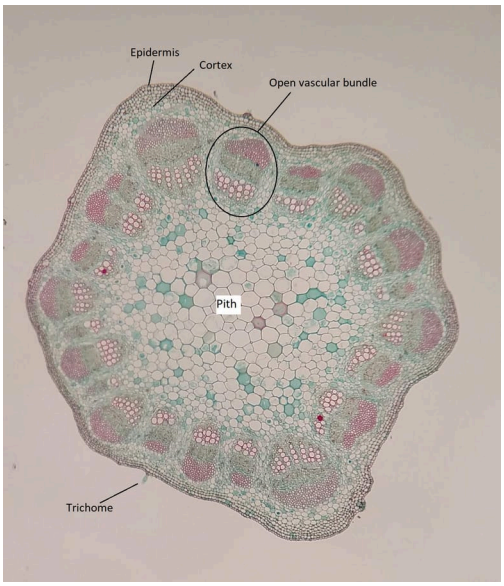


Figure 12.1.6: A cross section of a *Helianthus* stem. The outermost layer of cells is the epidermis. There is at least one trichome visible. Inside the epidermis is the cortex, which is composed largely of collenchyma in this plant. A ring of vascular bundles separates the cortex from the pith. Regions between the bundles are called pith rays. These vascular bundles are considered "open" because they have procambium tissue. Photo by Maria Morrow, CC BY-NC.

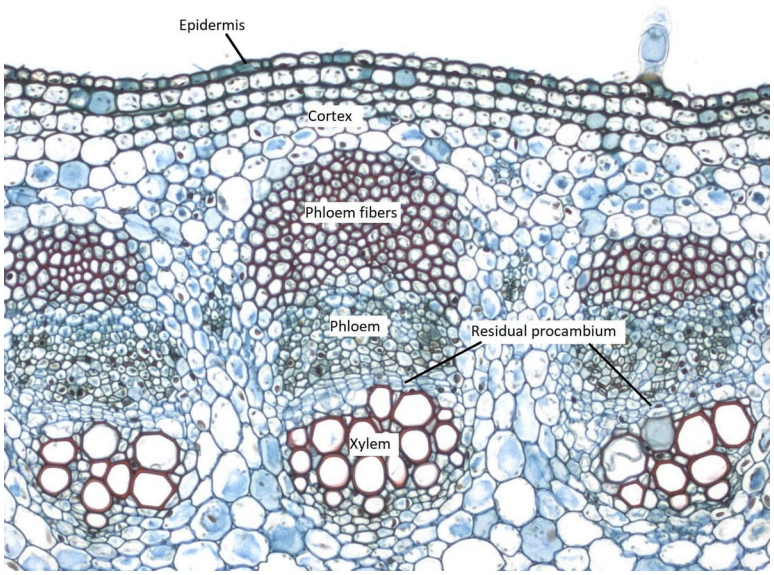


Figure 12.1.7: A closer view of a young *Helianthus* stem. The outermost layer of cells (in this image, the topmost) is the epidermis. There is a blue, light-bulb shaped structure emerging from the epidermis in the upper left. This is a trichome. Beneath the epidermis, three layers of densely packed collenchyma cells and several layers of parenchyma make up the cortex. Three large vascular bundles are shown. There is a large cluster of phloem fibers at the top of each bundle, stained red due to the secondary walls. Below that is the phloem, which is separated from the xylem (large, open cells that are stained red) by the residiual procambium (densely packed, light blue cells). Photo by Maria Morrow, CC BY-NC.

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12.2: Secondary Growth

Gymnosperms

Full Stem Cross Sections, *Pinus*

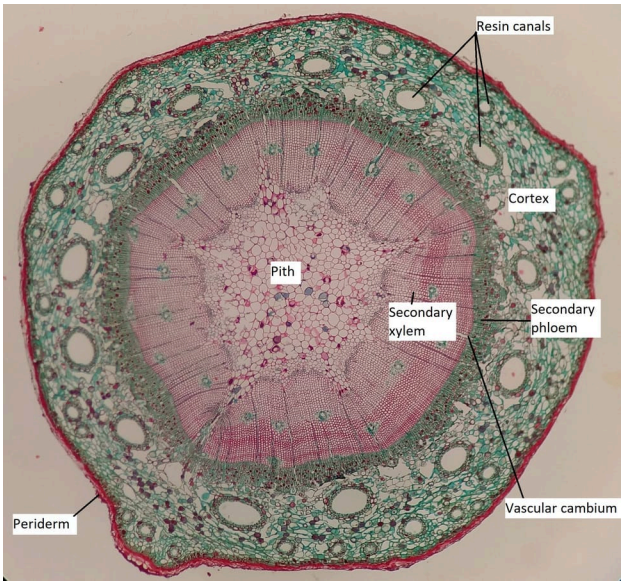


Figure 12.2.1: A cross section of a pine stem that is approximately one year old. The epidermis may still be present just outside the layer of periderm that has formed, but will soon slough off. Large (and small) resin canals are present in the cortex region. Just inside the cortex, a layer of more densely packed cells is the secondary phloem. This is separated from the secondary xylem by a thin layer of meristematic tissue: the vascular cambium. The secondary xylem, stained pink, has small blue-stained resin canals traversing it. Some of the cells in the xylem look darker than others. Within this layer of secondary xylem, at the center of the stem, are the large parenchyma cells of the pith. Photo by Maria Morrow, CC-BY 4.0.

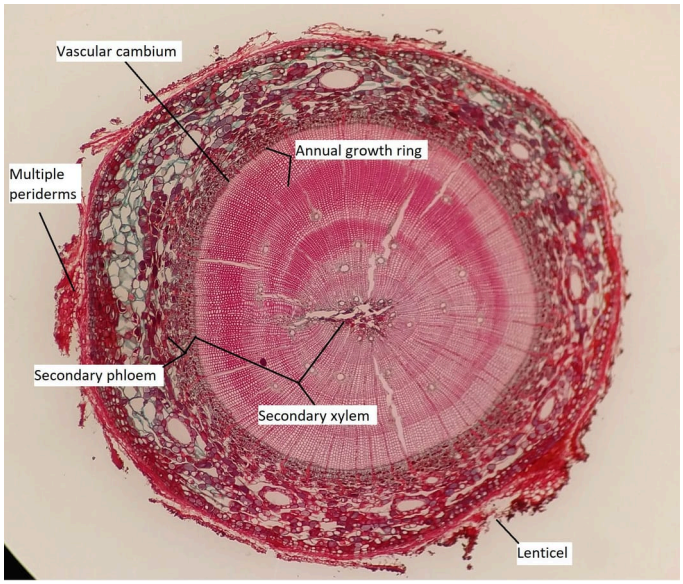


Figure 12.2.2: A cross section of a pine stem that is 4 years old. The epidermis is gone and several layers of periderm (outer bark) have formed around the outside of the stem. Tears in the periderm form lenticels. Inside the periderm is cortex with embedded resin canals. The secondary phloem is a thin ring of tissue surrounding the secondary xylem. Within the secondary xylem, several growth rings can be distinguished, with regions of more densely packed cells formed in the dry and/or cold season abutting larger cells formed in the following growing season. Photo by Maria Morrow, CC-BY 4.0.

Vascular Tissue

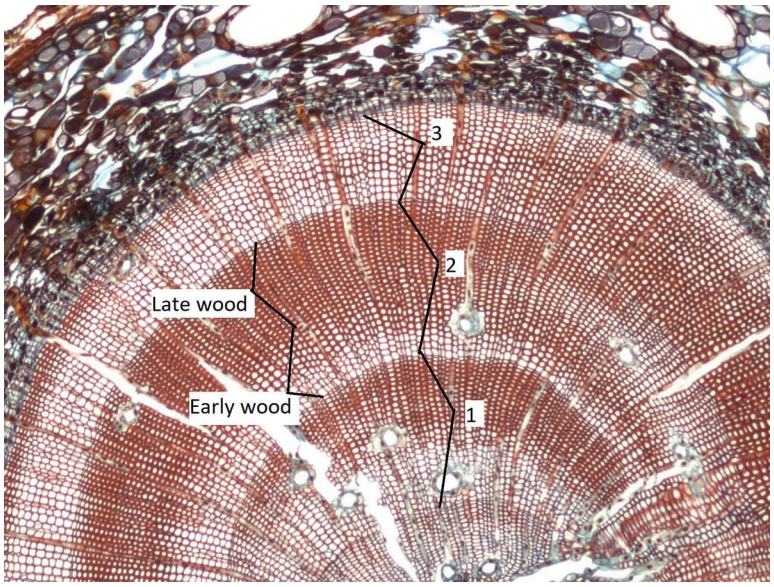


Figure 12.2.3: A close up on the annual growth rings formed in a pine stem. Within the secondary xylem, regions of more densely packed cells formed in the dry and/or cold season are called late wood. These alternate with rings of larger cells formed in the following growing season, called early wood. An annual growth ring is composed of the early wood and late wood formed in a single year. This stem has at least 3 annual growth rings. Photo by Maria Morrow, CC-BY 4.0.

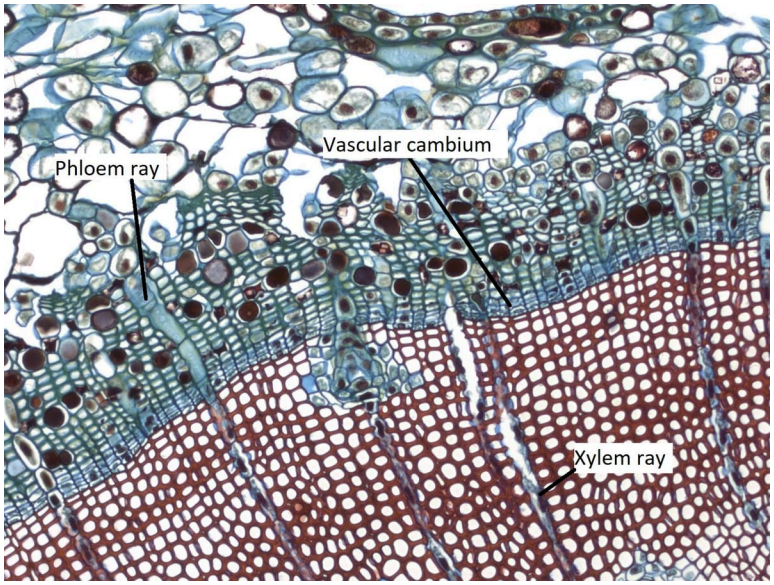


Figure 12.2.4: A magnified view of the vascular tissue and, specifically, the vascular cambium. The top of the image is composed of cortex cells. Quite abruptly, the cells become smaller and more tightly packed, appearing in columns. This is the secondary phloem tissue. The vascular cambium is below the phloem cells and appears as a line of flattened, light blue-stained cells. Just below the vascular cambium, the secondary xylem is composed of tracheids with red-stained secondary walls. Lines of parenchyma traverse the phloem (phloem rays) and xylem (xylem rays). Photo by Maria Morrow, CC-BY 4.0.

Periderm



Figure 12.2.5: A magnified view of the periderm (outer bark). The top of the image is composed of cork cells, which are empty and squished together. They are also coated in suberin. The cork cambium can be distinguished as one to two lines of small cells, all with visible nuclei. Just below the cork cambium, large cells that are filled with stained contents make up the phelloderm. These three layers comprise one periderm layer. Image from the Public Domain, sourced from Berkshire Community College Bioscience Image Library with labels added by Maria Morrow.

Wood



Figure 12.2.6: A driftwood stump found at the beach, with annual growth rings indicated by black arrows. This tree may have died from a fungal infection (*Leptographium wageneri*) that stained the wood. A black stain is present in the most densely packed cells of the late wood, making annual growth rings visible. At least 11 years of growth can be seen, potentially more. Photo by Maria Morrow, CC-BY 4.0.



Figure 12.2.7: The difference between sapwood and heartwood can sometimes be seen distinctly in where moss and algae grow on cut logs. These two logs both have algal growth (and moss, in the second image) in the sapwood region. Yet, it cuts off abruptly as it reaches the heartwood. What might cause this? Photos by Maria Morrow, CC-BY 4.0.

Angiosperms

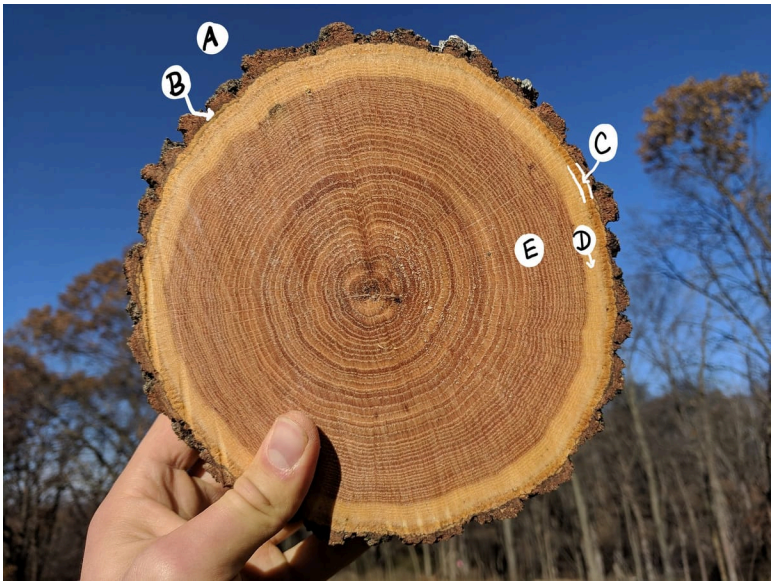


Figure 12.2.8: A section through an oak tree (*Quercus*). The outer bark is darker and jagged (A). Just under the outer bark is a thin layer of inner bark (C). B indicates the transitional zone between inner and outer bark. D and E are the wood, but D is still active in water conduction (sapwood). The vascular cambium would be located between C and D. A=Periderms (outer bark), C=Secondary phloem (inner bark), D=Sapwood (active xylem), E=Heartwood (inactive xylem). D+E=wood. Photo by Rbreidbrown, CC BY-SA 4.0, via Wikimedia Commons with labels added by Maria Morrow.

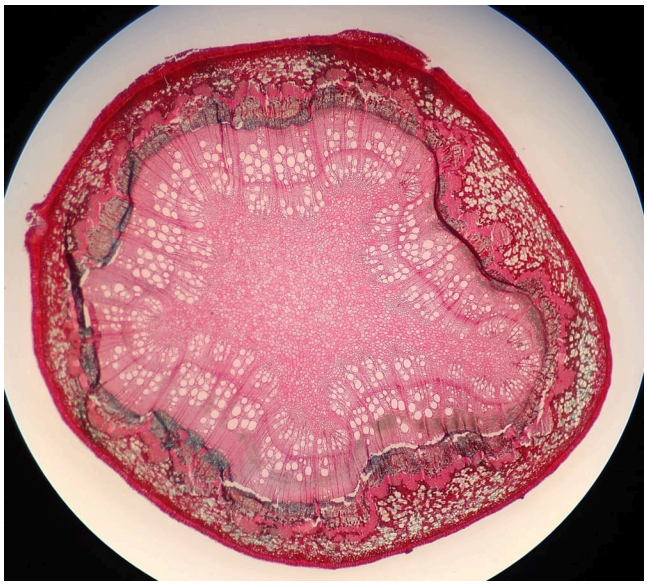


Figure 12.2.9: The arrangement of tissues in an angiosperm in secondary growth is similar to a gymnosperm. One way to determine whether you are looking at an angiosperm or gymnosperm cross section is to look for the presence of large, open cells in the xylem (vessel elements). Gymnosperms (excepting the gnetophytes) only have tracheids, whereas angiosperms have both tracheids and vessel elements. Can you tell how old this stem was by looking at the secondary xylem? Photo by Maria Morrow, CC-BY 4.0.

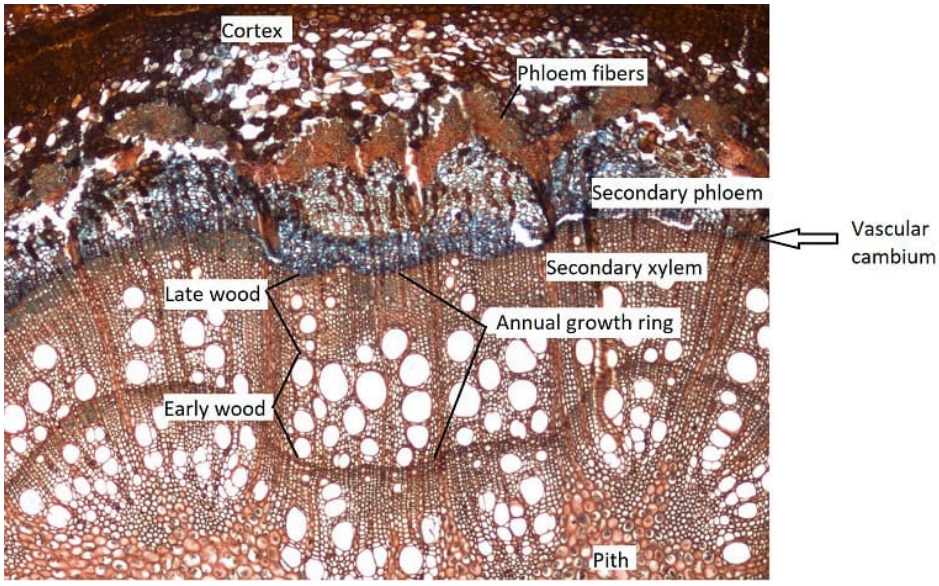


Figure 12.2.10: A cross section of the vascular tissue in a two year old oak stem. The cortex is separated from the secondary xylem by large bundles of phloem fibers. Below the phloem fibers are the conducting cells of the secondary phloem. The vascular cambium, indicated by the white arrow, separates the phloem from the xylem. In the xylem, there are two growth rings. A small bit of the pith can be distinguished at the bottom. Photo by Maria Morrow, CC-BY 4.0.

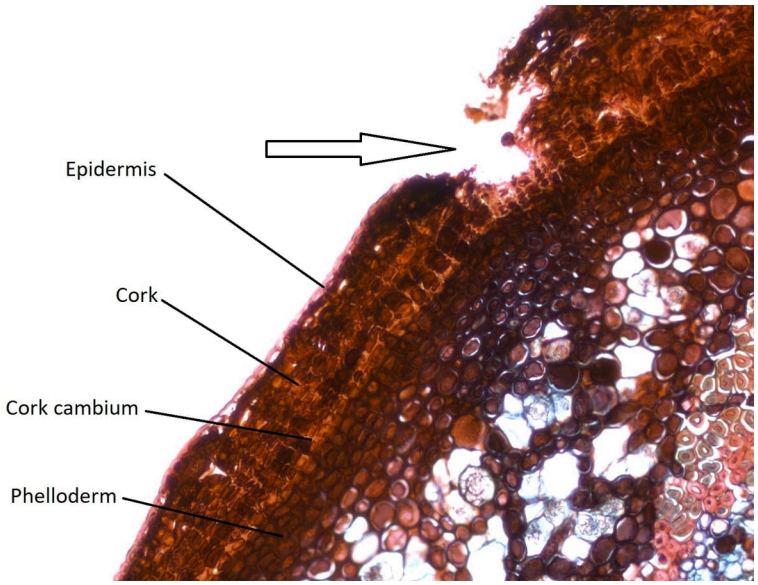


Figure 12.2.11: A lenticel in the periderm of an oak. The white arrow indicates a tear in the periderm, called a lenticel, that allows for gas exchange after the epidermis is lost. A thin layer of epidermis, coated in cuticle (stained pink), can be seen hugging the edge of the periderm. This will soon slough off. A lighter strip within the periderm cells (all stained an orange-brown) is the cork cambium. Image from the Public Domain, sourced from Berkshire Community College Bioscience Image Library with labels added by Maria Morrow.

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12.3: Woody Shoot Structures

Figure 12.3.1: A woody shoot and labeled scars. The most prominent scar on this shoot is the v-shaped leaf scar, which is lined with circular vascular bundle scars. Above the leaf scar, in the crotch of the v it forms, is a round axillary bud scar. Covering the bark are many small, circular scars. These are lenticels. Photo by Maria Morrow, CC BY-NC.



Figure 12.3.2: A piece of birch bark. The lenticels in birch bark form as long tears, as opposed to the circular ones in Figure 12.3.1. Photo by Maria Morrow, CC BY-NC.

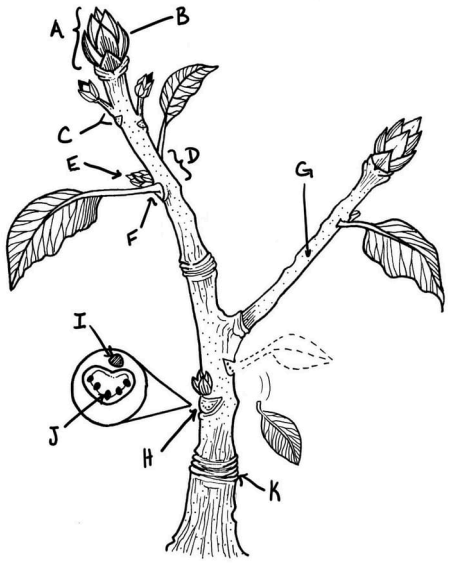


Figure 12.3.3: Diagram of a woody shoot (angiosperm). A=Terminal (or apical) bud, B=Terminal bud scale, C=Node, D=Internode, E=Axillary bud (in the leaf axil), F=Leaf, G=Lenticel, H=Leaf scar, I=Axillary bud scar, J=Vascular bundle scar (within the leaf scar), K=Terminal bud scale scars. The region between sets of terminal bud scale scars on a branch represents one year of growth. Diagram by Nikki Harris, CC BY-NC with labels added by Maria Morrow.

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12.4: Modified Shoots

Horizontal Stems

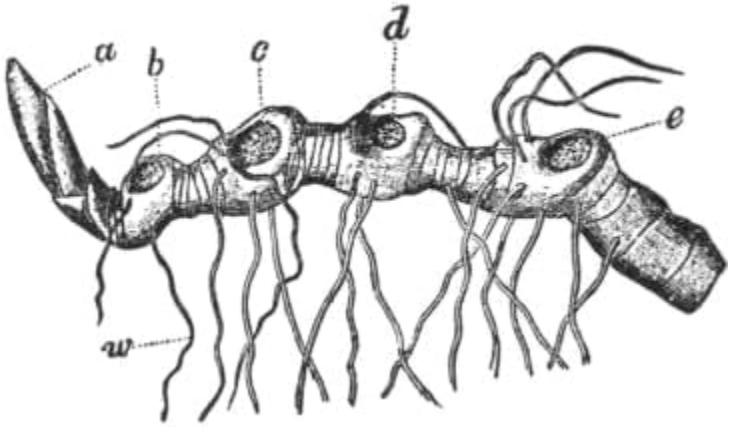


Figure 12.4.1: Rhizome of *Polygonatum multiflorum*. a=Bud of next year's aerial shoot; b=Scar of this year's, and c, d, e=scars of three preceding years' aerial shoots; w=adventitious roots. Diagram by AnonymousUnknown author, Public domain, via Wikimedia Commons.



Figure 12.4.2: Rhizome of *Alpinia purpurea*. Adventitious roots emerge from stem tissue that travels horizontally underground. Rhizomes can be distinguished from roots by the presence of nodes. Note the layers created by the sheathing, papery leaves of the rhizome. Below the stem, root like structures sprout out horizontally, but there are distinct sections or nodes to these structures (roots). Photos by Filo gèn', CC BY-SA 4.0, via Wikimedia Commons.

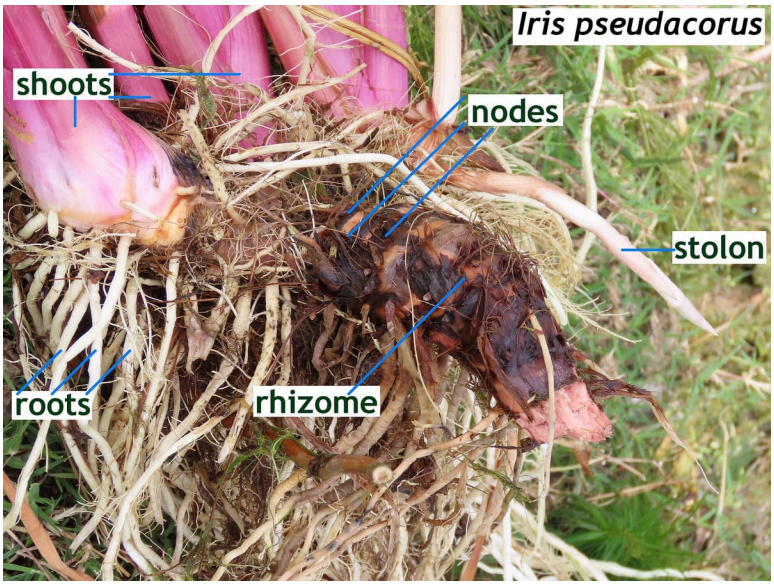


Figure 12.4.3: There is a lot going where these *Iris* shoots meet the roots. The shoots are emerging upward in the left hand corner, showing a pinkish hue from anthocyanin pigments. True roots emerge from the base of these shoots, pointing in the opposite direction and pigment-free. A large rhizome travels horizontally from the cluster of shoots and three nodes are indicated. A stolon (a horizontal above ground stem) emerges above the rhizome. Image by JonRichfield, CC BY-SA 4.0, via Wikimedia Commons.



Figure 12.4.4: Examples of horizontal stems. Ginger rhizomes are thick and belowground (top), and stolons of this spider plant are aboveground with long internodes (bottom). Top image by Sengai Podhuvan (CC-BY-SA), and bottom image by Eptalon (CC-BY-SA).

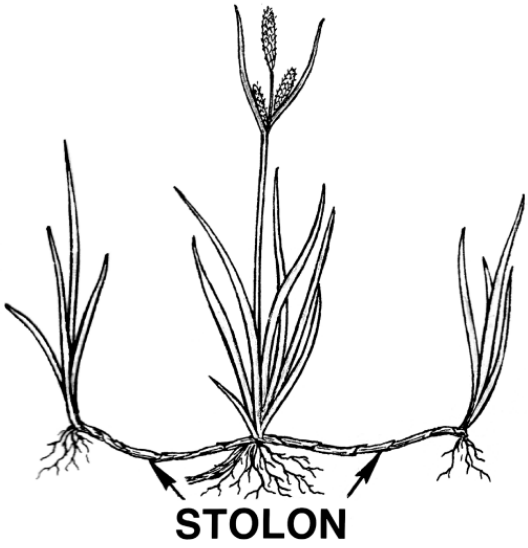


Figure 12.4.5: A stolon is an above ground horizontal stem. Some plants, such as strawberries (right) or the spider plant in Figure 12.4.4, use stolons to asexually reproduce clonal plants. Drawing on left by Pearson Scott Foresman, Public domain, via Wikimedia Commons. Photo on right by Amy Change, CC-BY-SA.

Storage Stems





Figure 12.4.6: Potato tubers are expanded, belowground stems modified for starch storage. Each "eye" on a potato is a node where a new shoot could emerge. First image by pxhere (public domain). Second image by Robin Corps and uploaded to flickr.com on January 23, 2006, licensed under the Creative Commons Attribution-Share Alike 2.0 Generic license.

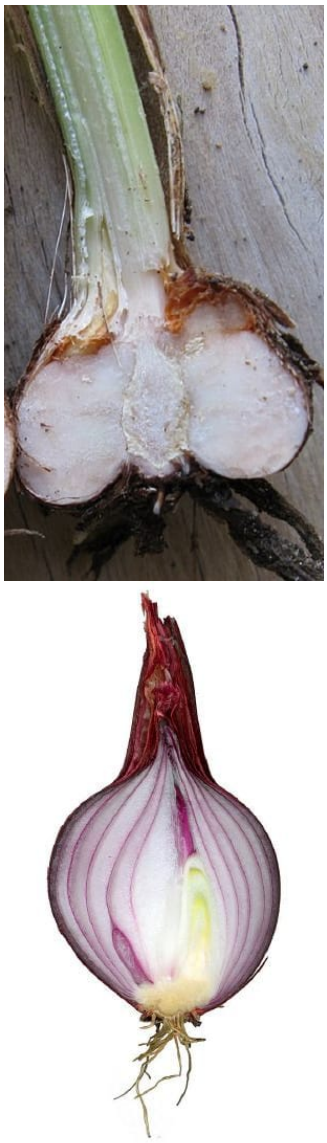


Figure 12.4.7: Both corms (left) and bulbs (right) are similar looking modifications for storage. The *Crocosmia* corm has a thick, expanded stem stores starch, and the leaves that surround it are non-photosynthetic and papery. The onion bulb has a relatively small stem surrounded by thick, fleshy leaves. Corm image by JonRichfield (CC-BY-SA), and onion image by Amada44 (CC-BY-SA).

Sharp Armaments





Figure 12.4.8: Thorns (first) and prickles (second). The thorns of the hawthorn are derived from the whole stem. They arise from axillary buds in the axils just above the leaves. The sharp projections on the rose stem are technically classified as prickles because they are derived from only the surface tissues of the stem. First image by Rasbak (CC-BY-SA), and second image by Ingrid Taylar (CC-BY).

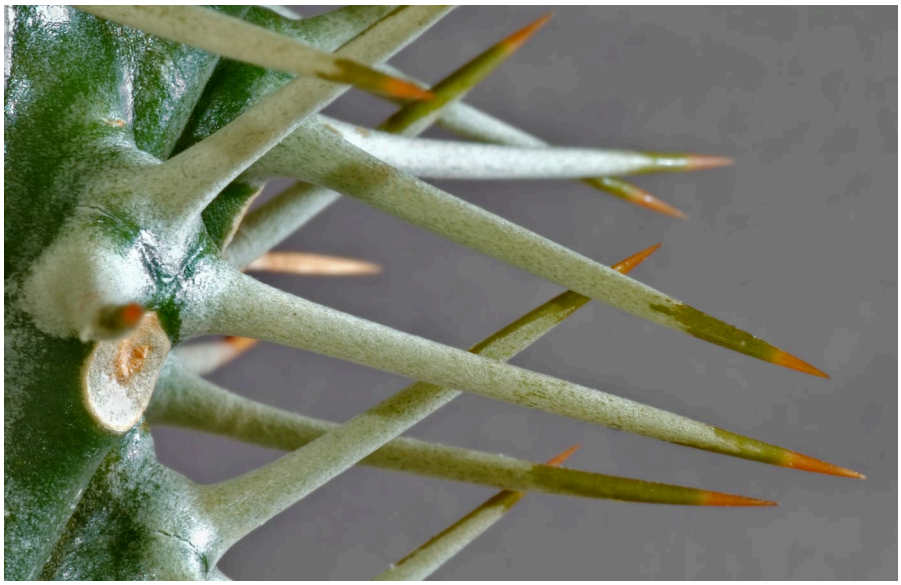


Figure 12.4.9: Cactus spines are not stems, but modified leaves. These spines have a thick cuticle and stomata can be seen as darker green areas within the pale white cuticle. Photo by André Karwath aka Aka, CC BY-SA 2.5, via Wikimedia Commons.

Climbing



Figure 12.4.10: The tendrils of the wild cucumber plant arise from stems. Other plants, such as *Lathyrus*, make tendrils from leaf tissue. Image by erwin66as (public domain)

Photosynthesis



Figure 12.4.11: Cladophylls in *Asparagus* (left) and actual leaves of young asparagus marked by black arrows (right). Left image by DenesFeri (CC-BY-SA), and right image by Sam Saunders (CC-BY-SA).



Figure 12.4.12: Cladophylls in butchers broom (*Ruscus*) are flattened like leaves. A flower arises from a node within the cladophyll. Image by Rosser1954 (CC-BY-SA).



Figure 12.4.13: Phylloclades in Christmas cactus. Image by Mokkie (CC-BY-SA).

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13: LEAVES

Leaves are specialized organs for performing photosynthesis. A leaf is often a relatively large, flat surface used to optimize sunlight capture. However, surfaces are areas that water can evaporate from, so a large amount of surface area exposed to sunlight results in increased transpiration. The anatomy of a leaf has everything to do with achieving the balance between photosynthesis and transpiration in the environment in which the plant grows. Plants that grow in moist areas can grow large, flat leaves to absorb sunlight like solar panels because sunlight is likely more limiting than water. Plants in dry areas must prevent water loss and adapt a variety of leaf shapes and orientations to accomplish the duel tasks of water retention and sunlight absorption. In general, leaves adapted to dry environments are small and thick with a much lower surface area to volume ratio.

13.1: Leaf Parts and Arrangement

13.2: Monocot Leaves

13.3: Eudicot Leaves

13.3.1: Adaptations to Water Availability

13.4: Modified Leaves

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13.1: Leaf Parts and Arrangement

In angiosperm anatomy, a leaf can be identified by where it emerges from the node. In a node, a leaf emerges below the axillary bud.

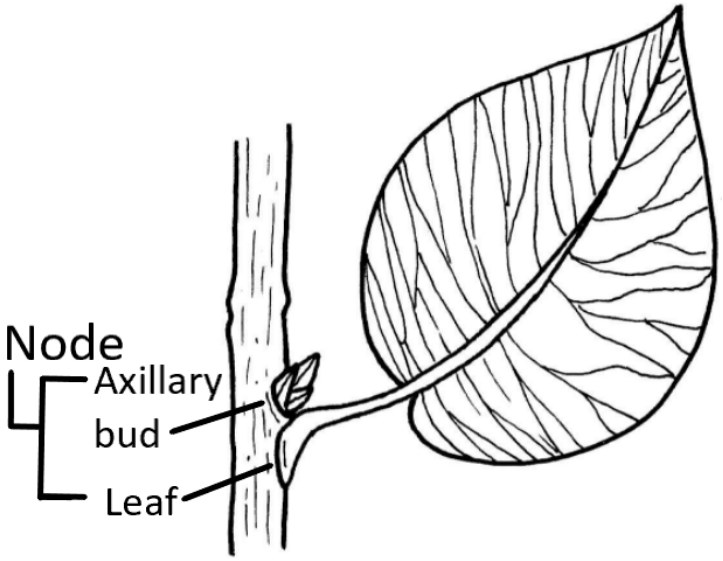


Figure 13.1.1: A diagram of a node. Each node is comprised of a leaf (on the bottom) and an axillary bud (on the top, located in the axil where the petiole meets the stem). Diagram by Nikki Harris, CC-BY 4.0 with labels added.

Leaf Parts

Leaves are generally composed of a few main parts: the **blade** and the **petiole**.

Figure 13.1.2: A leaf is usually composed of a blade and a petiole. The blade is most frequently the flat, photosynthetic part. The petiole is a stem that attaches the leaf blade to the main stem of the plant. As plants have radiated, diversified, and adapted to different environments, you'll see that there are many variations on this theme. The photo on the left is a palmate leaf, the diagram on the right is a pinnate leaf. Photo by Maria Morrow, CC-BY 4.0. Diagram on the right from Chapter 3.4.2, Botany, by Algiers, Ha, and Morrow.

The Leaf Blade and Vascular Arrangement

The leaf blade is (usually) the flat, photosynthetic part of the blade. In eudicots, the leaf will have a central midvein (also called the midrib), with smaller veins branching off from there. This type of vein organization is called **netted venation**. The edge of the blade is the **margin**.

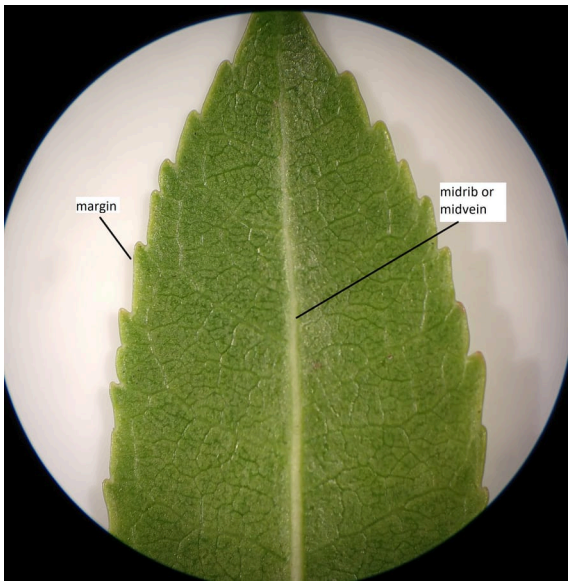


Figure 13.1.3: The adaxial (left) and abaxial (right) surfaces of a eudicot leaf blade. The margin is the edge of the leaf and its morphology can be useful for identification. This leaf margin could be described as serrate, much like a serrated knife. In the center of the leaf, a large central vein stands out. This is the midrib or midvein. Many smaller diameter veins branch out from the midvein. Photos by Maria Morrow, CC-BY 4.0.

In monocots, the veins may be all approximately the same size or there may be a larger midvein, but the veins run parallel to each other. This is called **parallel venation**.



Figure 13.1.4: A plantain (*Plantago* sp.) leaf. This monocot has several large veins that run parallel to each other, lacking any true midvein. Photo by Maria Morrow, CC-BY 4.0.

The Petiole

Most leaves have a stem that attaches the blade of the leaf to the rest of the plant. This is the petiole. However, in some plants, the leaves do not have a petiole and the blade is directly attached to the plant stem. These leaves are **sessile** (lacking a petiole).



Figure 13.1.5: The first image shows a branch of a tree with petiolate leaves. Each leaf blade is attached to the main branch by a short stem (petiole). In the second image, the leaf blades are attached directly to the main stem (sessile). Photos by Maria Morrow, CC-BY 4.0.

Stipules

Some plants will have paired appendages found at the base of the leaf. These are called **stipules**. Stipules can look leaf-like or take on other forms (e.g. spines or tendrils).

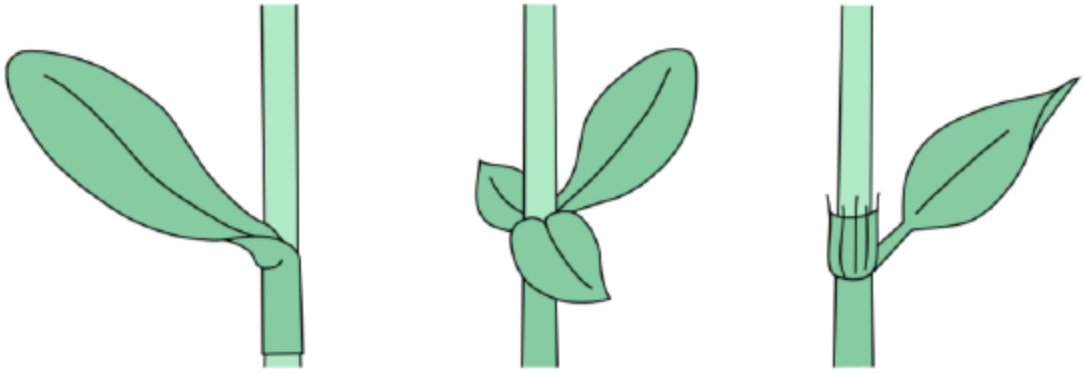


Figure 13.1.6: From left to right: sheath, stipules and ocrea. Diagram from Chapter 3.4.2, Botany, by Algiers, Ha, and Morrow.



Figure 13.1.7: Stipules of *Hibiscus*. Each leaf on this plant has two long, flat, green projections at the base. These are the stipules, adapted for photosynthesis (flat and green). Image by Nadiatalent, CC BY-SA 3.0, via Wikimedia Commons.





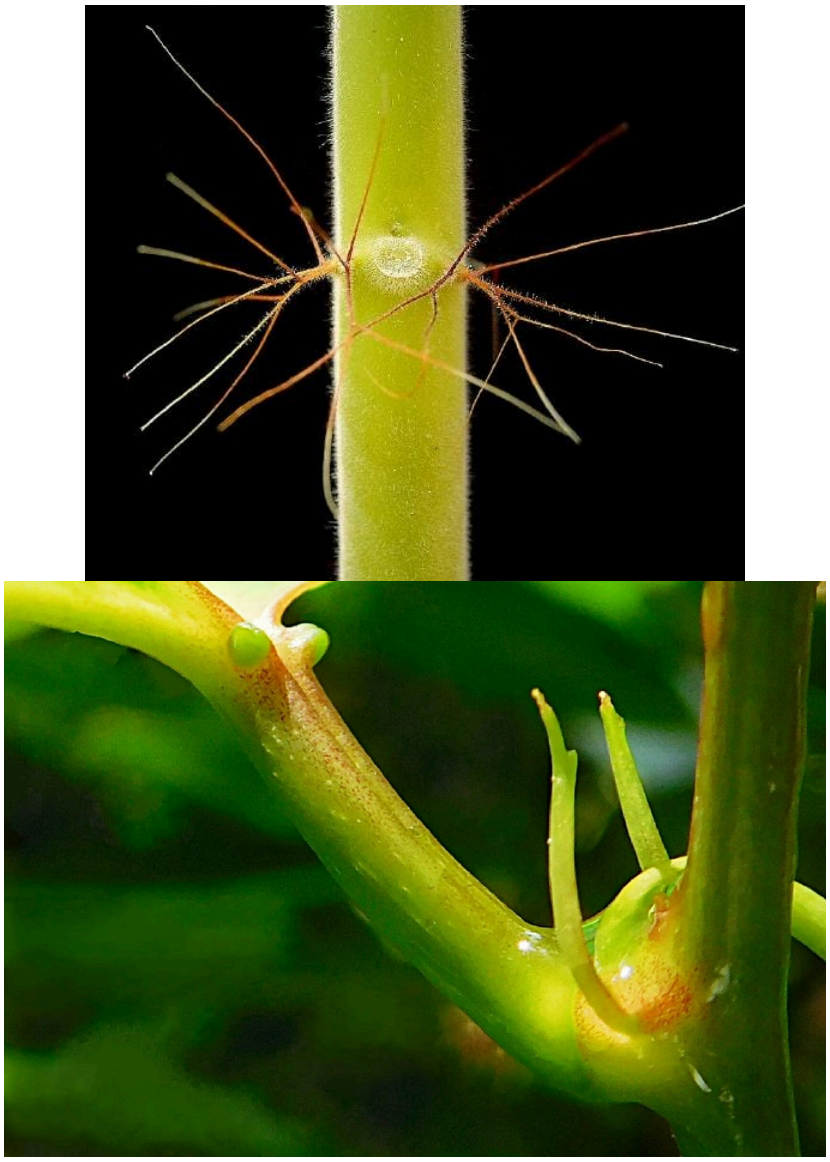


Figure 13.1.8: A variety of stipule morphologies. First image: Ton Rulkens from Mozambique, CC BY-SA, via Wikimedia Commons. Second image: Christian Fischer, CC BY-SA, via Wikimedia Commons. Third image: Frank Vincentz, CC BY-SA, via Wikimedia Commons. Fourth image: Filo gèn', CC BY-SA, via Wikimedia Commons.

Compound Leaves

A **compound leaf** looks like a branch with leaves emerging from it. However, these leaves are not accompanied by axillary buds (i.e. they do not emerge from a node). This branch is in fact a compound leaf composed of **leaflets**. Though there are no buds at the base of the leaflets, there will be a bud at the base of the compound leaf's petiole.

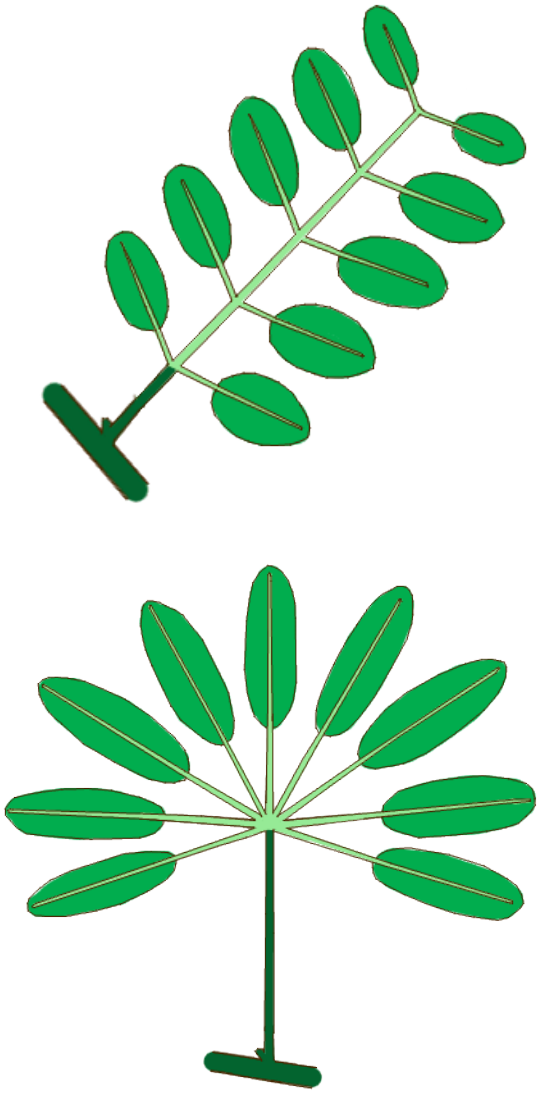


Figure 13.1.9: Compound leaves. The leaf on the left is pinnately compound, petiolules attach to a central rachis. The leaf on the right is palmately compound, petiolules all meet at the tip of the petiole and radiate outward. Diagrams by Michael G. Simpson. Redrawn and color: User:RoRo, Public domain, via Wikimedia Commons.

A compound leaf can be **palmate** or **pinnate**. In a pinnate compound leaf, the leaflets are attached to a central stem called a **rachis**. The leaflets can be sessile or may be attached to the rachis by **petiolules**. Compound leaves can be even more complex by being compounded multiple times.

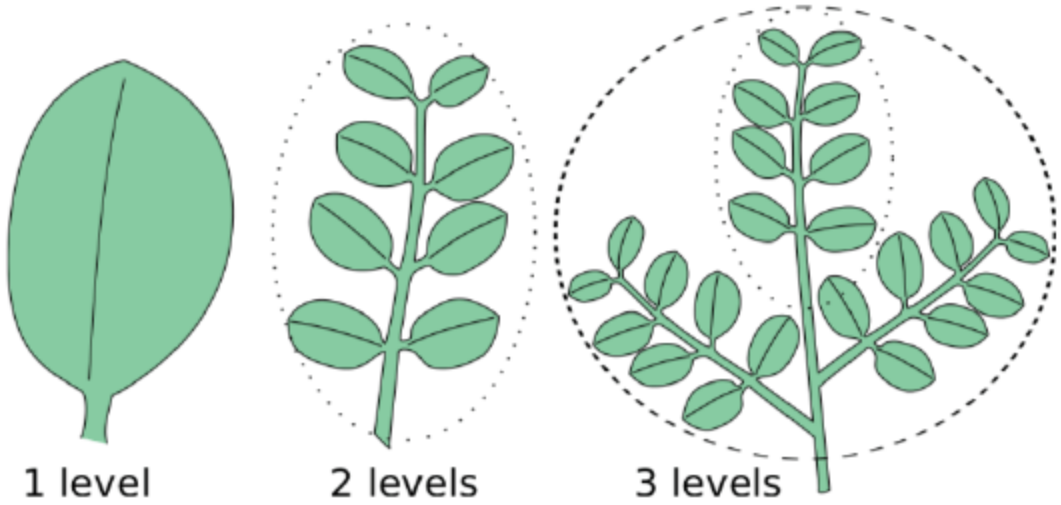


Figure 13.1.10: Leaves with one, two and three levels of hierarchy. Please note that the last leaf is ovate on the first and second level but circular on the third level of hierarchy. Diagram from Chapter 3.4.2, Botany, by Algiers, Ha, and Morrow.

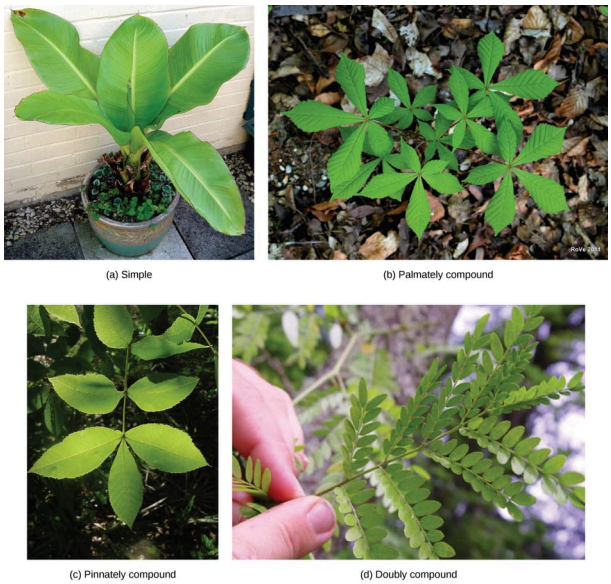


Figure 13.1.11: Leaves may be simple or compound. In simple leaves, the lamina is continuous. The (a) banana plant (Musa sp.) has simple leaves. In compound leaves, the lamina is separated into leaflets. Compound leaves may be palmate or pinnate. In (b) palmately compound leaves, such as those of the horse chestnut (Aesculus hippocastanum), the leaflets branch from the petiole. In (c) pinnately compound leaves, the leaflets branch from the midrib, as on a scrub hickory (Carya floridana). The (d) honey locust has double compound leaves, in which leaflets branch from the veins. (credit a: modification of work by "BazzaDaRambler"/Flickr; credit b: modification of work by Roberto Verzo; credit c: modification of work by Eric Dion; credit d: modification of work by Valerie Lykes).

Leaf Arrangement

In angiosperms, leaf arrangement is determined by how many leaves emerge per node.

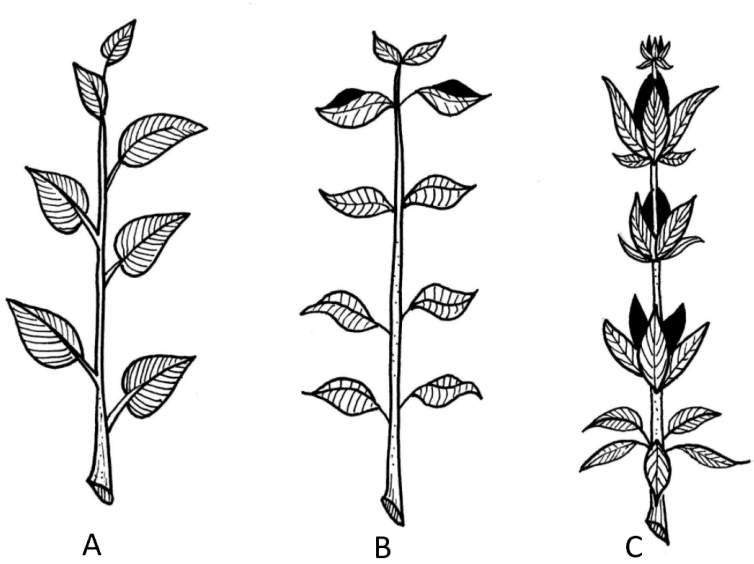


Figure 13.1.12: Types of leaf arrangement. In shoot A (far left), the leaves emerge one at a time. Shoot A has alternate leaf arrangement. In shoot B (middle), two leaves emerge per node, directly across from each other. Shoot B has opposite leaf arrangement. In shoot C, five leaves emerge at each node. Three or more leaves from a node is a whorled leaf arrangement. Diagram by Nikki Harris, CC-BY 4.0 with labels added.

Alternate Leaf Arrangement

In **alternate leaf arrangement**, one leaf emerges per node, giving the appearance of alternating leaves.



Figure 13.1.13: This salal (*Gaultheria shallon*) branch has alternate leaf arrangement. The leaves emerge with one per node. In this plant, a small bend occurs in the stem at each node, giving it a zig-zag shape. Photo by Maria Morrow, CC-BY 4.0.

Opposite Leaf Arrangement

In **opposite leaf arrangement**, two leaves emerge per node. Think of this as how your arms are opposite each other on your torso.



Figure 13.1.14: Both of the plants shown in the images above have opposite leaves, with two leaves emerging at each node opposite from each other on the stem. Photos by Maria Morrow, CC-BY 4.0.

Whorled Leaf Arrangement

In **whorled leaf arrangement**, three or more leaves emerge per node. I try to remember this as "around the whorled (world)", because the leaves often encircle the stem.



Figure 13.1.15: This member of the lily family has whorled leaves. There are between 5 and 8 leaves emerging at each node, making the plant look as if it were a tiered cake. Photo by Maria Morrow, CC-BY 4.0.

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13.2: Monocot Leaves

Macroscopic Features

Monocot leaves tend to have parallel venation, as opposed to the branching patterns seen in eudicots.



Figure 13.2.1: These two monocot leaves both have parallel venation. It is more obvious in the leaf on the right. However, if you look closely at the leaf on the left, you'll see that those veins do not cross each other. Instead, they travel in the same direction without overlapping, just as in the leaf on the right. Photos by Maria Morrow, CC BY-NC.

Microscopic Features

The model organism for monocots in botany is usually corn (*Zea mays*). Below, you'll see examples of corn leaf cross sections to demonstrate monocot leaf anatomy. Note that there are approximately the same number of stomata on either side of the leaf, that the vascular bundles are all facing you in cross section (because they run parallel to each other), and that the mesophyll is not divided into two distinct types. Note: There are exceptions. Many monocots will have a more specialized mesophyll arrangement.



Figure 13.2.2: A cross section of a corn (*Zea mays*) leaf. See the caption in Fig. 13.2.3 for a detailed description of the features present. Photo by Maria Morrow, CC BY-NC.

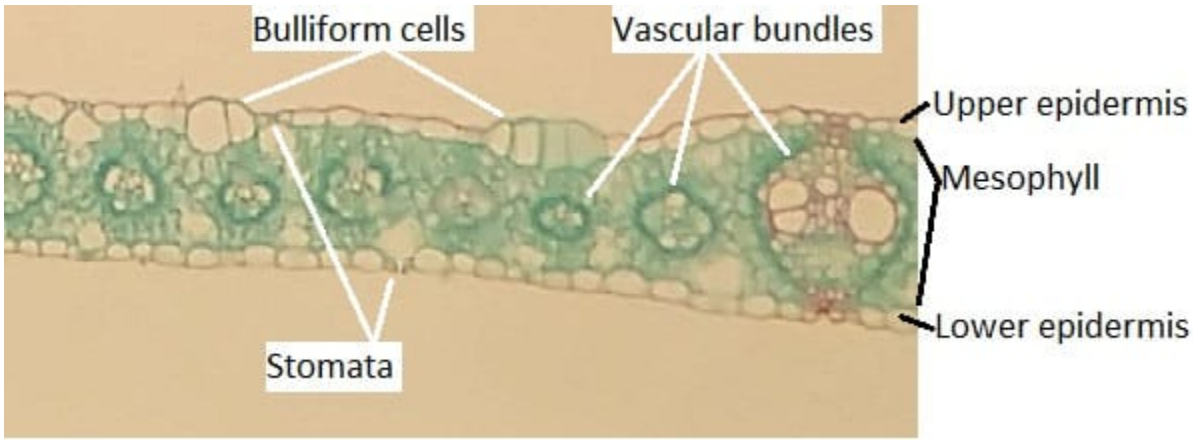


Figure 13.2.3: A cross section of a section of a corn leaf, labeled. The upper epidermis is composed of parenchyma cells that appear empty. There are two clusters of enlarged cells within the upper epidermis. These are bulliform cells and are not present in the lower epidermis. Stomata occur in approximately even numbers in both the upper and lower epidermis. Eight vascular bundles can be seen, the one on the far right is much larger than the others. In the larger vascular bundle, it is easier to distinguish the large, open vessel elements (stained red). Within the vascular bundle, the xylem tissue is closer to the upper epidermis and the phloem tissue is closer to the lower. Each vascular bundle is surrounded by larger cells with darkly-stained contents. These make up the bundle sheath. The tissue around the vascular bundles is the mesophyll. Photo by Maria Morrow, CC BY-NC.

Bulliform Cells

The bulliform cells present in the upper epidermis are not common to all monocots. This is an adaptation you can find in many grasses that are adapted to hot or dry environments. To avoid water loss, the bulliform cells can contract, causing the leaf to roll up and reduce surface area.

In the image below, you can see a leaf from the beach grass *Ammophila* rolled in on itself. Can you find the bulliform cells?

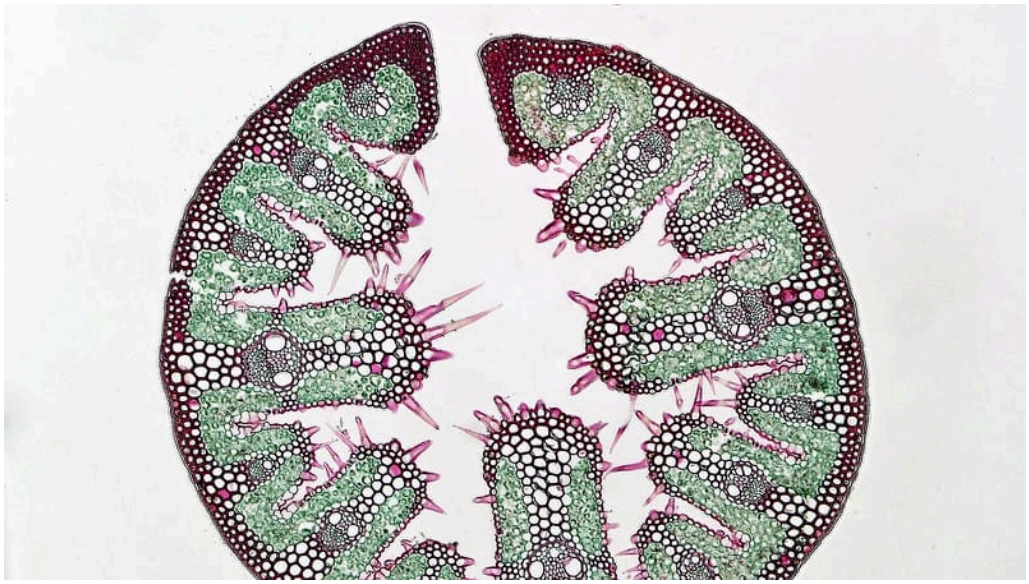


Figure 13.2.4: This European beach grass (*Ammophila arenaria*) leaf has rolled up due to shrinking of the bulliform cells. The upper epidermis is now highly invaginated and located on the inside of the rolled leaf. Image from the Public Domain, sourced from Berkshire Community College Bioscience Image Library.



Figure 13.2.5: This is a close up of the same European beach grass (*Ammophila arenaria*) leaf as above. The lower epidermis has a thick hypodermis (stained red). A thick cuticle can be seen coating the epidermis. On the right side of the image, there is a fold in the upper epidermis (which has many trichomes). At the folding point, several slightly larger cells can be seen. This is a region of bulliform cells, which allowed the leaf to fold and roll inward. Image from the Public Domain, sourced Berkshire Community College Bioscience Image Library.

Vascular Bundles

In the vascular bundle, the xylem will be on the top (adaxial side) and the phloem will be on the bottom (abaxial side). If you think about the way a leaf emerges from the plant, this matches the way the xylem and phloem are oriented in the stem, with the xylem toward the center of the stem and the phloem closer to the outside/epidermis.

The vascular bundle is often surrounded by inflated parenchyma cells that form a structure called a **bundle sheath**. In C4 plants, like corn, this is where the Calvin Cycle would take place.

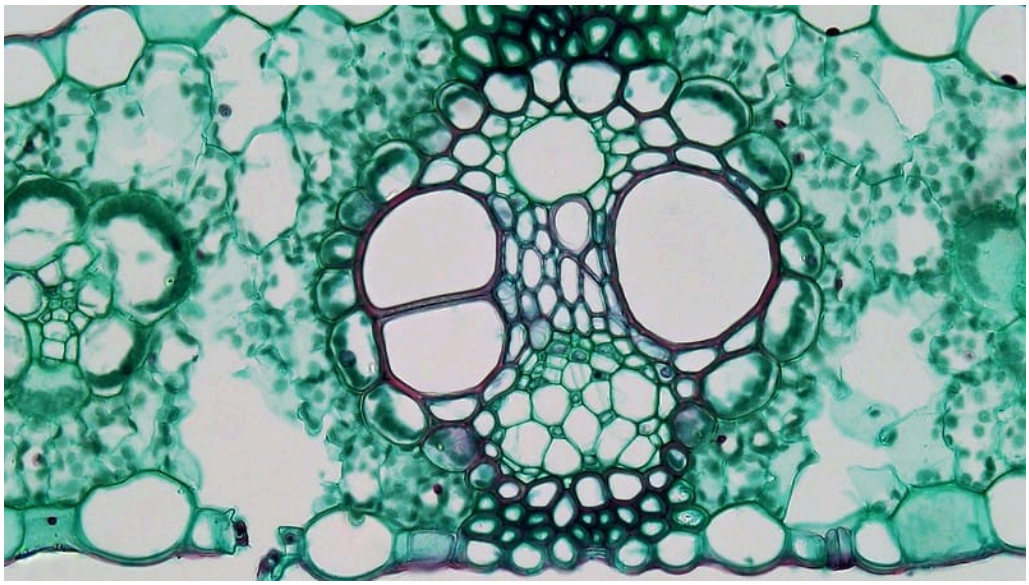


Figure 13.2.6: A vascular bundle of a corn (*Zea mays*) leaf. There are two vascular bundles in this image. The one on the left is difficult to distinguish and most of what you see are the enlarged bundle sheath cells. The larger vascular bundle on the right has less prominent bundle sheath cells, though they still form a distinct border between the vascular tissue and the mesophyll. The xylem tissue is located closer to the upper epidermis. You can locate it by searching for the large, open cells (vessel elements) with red-stained secondary walls. Below the xylem is the phloem tissue, which encompasses a smaller area. The larger cells in the phloem are sieve tube elements and the smaller ones are companion cells. Image from the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

Below is an image of a vascular bundle in another monocot, Yucca. This vascular bundle has large groups of sclerenchyma cells within it, a smaller group above the xylem and a much larger group below the phloem. How might you distinguish the sclerenchyma cells from the parenchyma cells? Consider the thickness of the cell wall(s) and how each cell type reacts to stains.

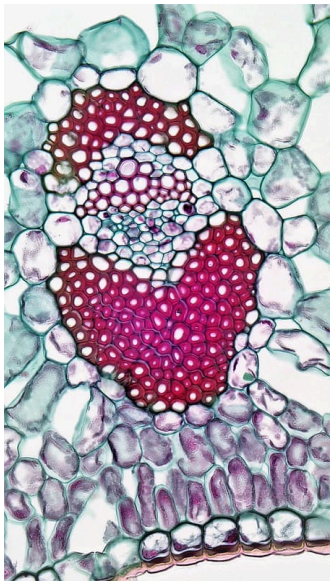


Figure 13.2.7: A vascular bundle from a Yucca plant (a monocot). The large groups of thick-walled, red-stained cells are sclerenchyma. These provide rigid support in the region of the vascular bundle. Image from the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

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13.3: Eudicot Leaves

Macroscopic Features

Eudicot leaves tend to have netted venation, with a larger central vein (the midrib or midvein) that branches off into a network of smaller veins. In the image below, you can see this branching pattern in a skeletal leaf.



Figure 13.3.1: A skeletal holly leaf shows the network of vascular tissue. The lignified xylem and phloem fibers break down far more slowly than the parenchyma cells of the leaf. As the rest of the leaf tissues decompose, the lignified vascular tissue is left behind. This reveals the netted pattern of increasingly smaller side branches found in eudicot leaves. Photo by Maria Morrow, CC BY-NC.

Microscopic Features

Eudicot leaves can usually be distinguished by netted venation at the macroscopic level, but they also differ at the microscopic level. Note the difference in organization between the tissues in the leaf below and the leaves shown in the monocot section.

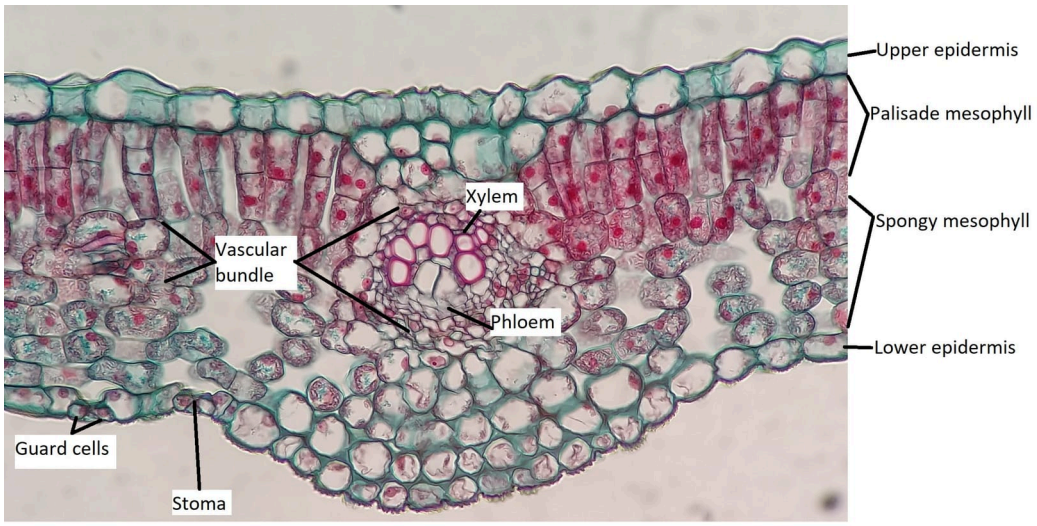


Figure 13.3.2: A cross section through a eudicot leaf. The upper epidermis is a single layer of parenchyma cells. There are no stomata present in the upper epidermis of this leaf. Below the epidermis, cells (appearing pink due to staining of the nuclei and chloroplasts) are arranged in columns, forming the palisade mesophyll. Beneath the palisade mesophyll is the spongy mesophyll. The cells are approximately the same size as the palisade mesophyll, but there are large intercellular spaces between them. The lower epidermis is another single layer of parenchyma cells, but several stomata (flanked by guard cells) are visible in this epidermal layer. A large vascular bundle is in the center of the leaf. The xylem (stained pink) is on the top and the phloem is on the bottom. Photo by Maria Morrow, CC BY-NC.

Cuticle

You will often see a waxy cuticle coating the surface of most plant tissues. In leaves, the location and thickness of the cuticle can give you clues about the environment that the plant has adapted to.

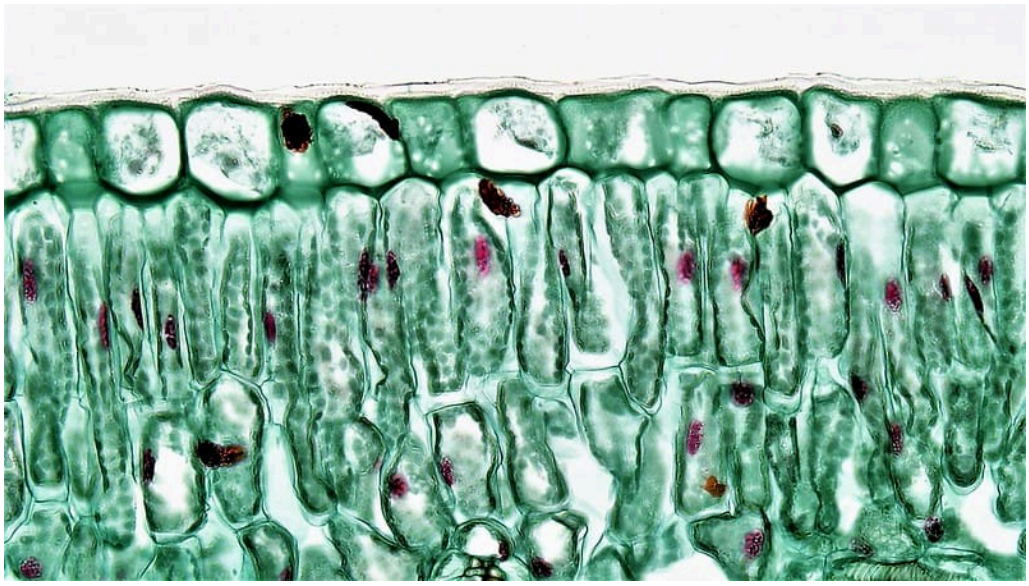


Figure 13.3.3: A cross section through the upper epidermis and palisade mesophyll. On top of the upper epidermis of this leaf, a transparent layer of cuticle is visible, sealing the top of the leaf. This waxy layer protects the leaf and forms a barrier to the movement of water. Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

Vascular Bundles

Seeing vascular bundles of eudicots in cross sections can be confusing. The organization of tissues in the much larger midrib vascular bundle is often spread out into a semicircle, still with xylem on the top and phloem on the bottom, but they can be

difficult to distinguish. In addition to this, the smaller veins are not oriented in the same direction, as they are in monocots.

In the image below, the vascular bundle just to the left of the midrib is coming more or less straight at us, so it is easy to distinguish the tissues. In contrast, the vascular bundle to the right of the midrib was moving diagonally and so was caught in an oblique section and looks more like a smear. Often with these oblique sections, you can distinguish the xylem cells by their strange secondary wall thickenings -- they look a bit like coiled springs.

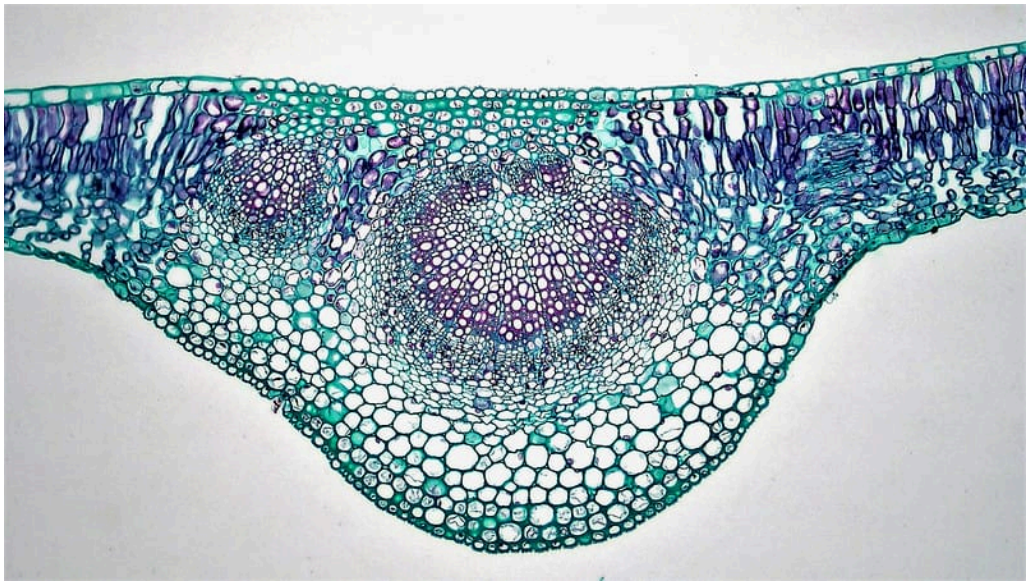


Figure 13.3.4: A cross section through the midvein of a eudicot leaf. The xylem tissue within the large vascular bundle is arranged in an arcing semi-circle, with phloem tissue in an arc traveling just below it. There are layers of collenchyma cells under the epidermis both above and below the midvein. What would be the function of these collenchyma cells? Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

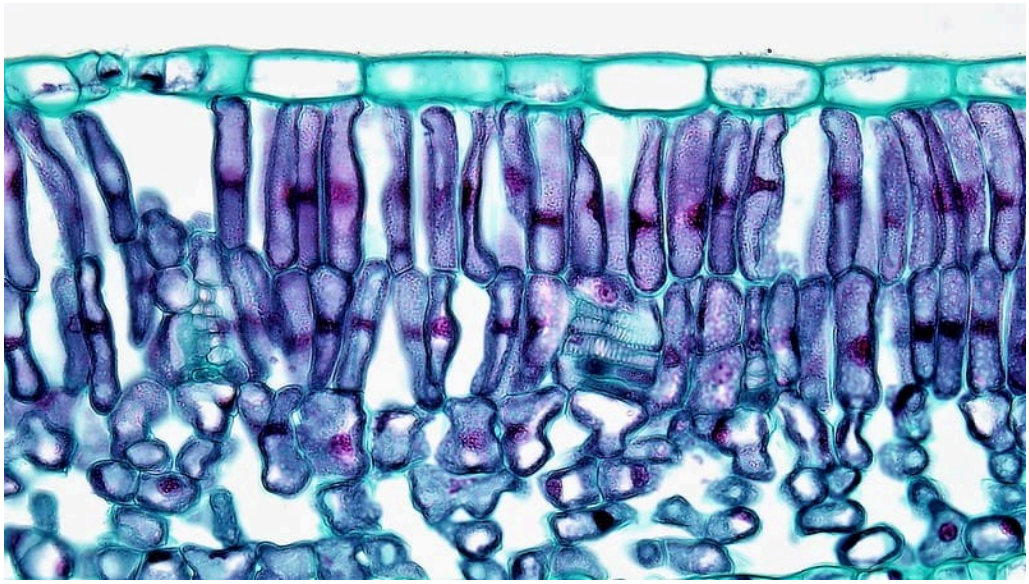


Figure 13.3.5: Just to the right of the center of this image, you can see the coiled spring appearance of the xylem vessel elements that have been caught in an oblique section. Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

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13.3.1: Adaptations to Water Availability

The morphology and anatomy of a leaf can allow you to predict the conditions that the plant is adapted to. In particular, what is the water availability in that plant's environment?

Mesophytic Leaves

A leaf in "normal" conditions is called **mesophytic** (meso- means middle), meaning it is not particularly adapted for either high or low water conditions.

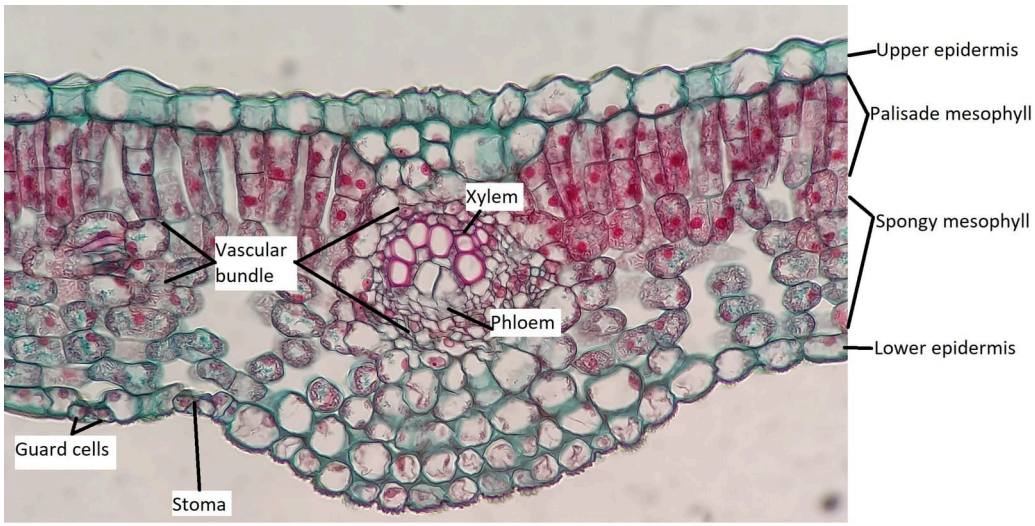


Figure 13.3.1.1: A cross section through a mesophytic leaf. The arrangement of tissues in a mesophytic leaf is as described in Fig. 13.3.2. As you look at adaptations to water availability, the arrangement of tissues in the leaf above will serve as the "standard" condition for leaves. Photo by Maria Morrow, CC BY-NC.

Hydrophytic Leaves

Hydrophytes (literally "water plants") are adapted to living in aquatic conditions.



Figure 13.3.1.2: A cross section through a dichotyledonous hydrophyte, *Nymphaea* (a water lily). The organization of tissues in this leaf is described in depth in Fig. 13.3.1.4. The important point here is to note the similarities between this eudicot leaf and the monocot leaf shown in Fig. 13.3.1.3. The similarities in tissue arrangement are due to convergent evolution to an aquatic lifestyle, as opposed to relatedness. Photo by Maria Morrow, CC BY-NC.

Below is an image of another hydrophytic leaf. This one is from a monocot, Potamogeton. Note the similarity to the Nymphaea leaf and the distinct differentiation between regions of mesophyll. A good example of convergent evolution to similar environmental pressures!



Figure 13.3.1.3: A cross section through a hydrophytic monocot leaf (Potamogeton). Note the similarity in internal anatomy to the hydrophytic eudicot Nymphaea shown in Fig. 13.3.1.2. Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

Tissue Organization

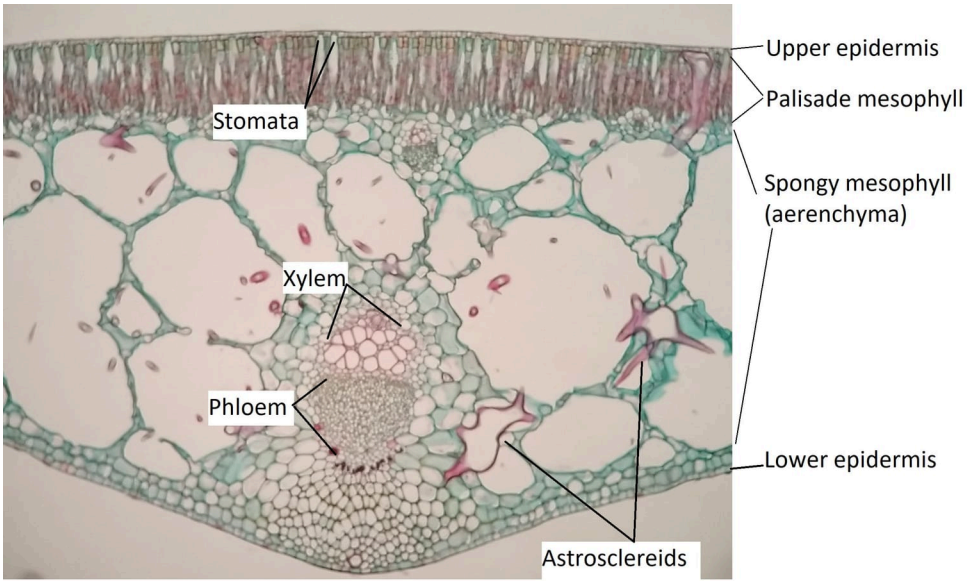


Figure 13.3.1.4: A cross section through a dichotyledonous hydrophyte, *Nymphaea* (a water lily). The upper epidermis is a thin layer of parenchyma with many stomata. Below each stoma, there is a chamber of air located within the palisade mesophyll (this makes them easier to find). Under the palisade mesophyll is a much larger region of spongy mesophyll than we would find in a mesophytic plant leaf. Most of the space is taken up by large air pockets, making this tissue aerenchyma. The lower epidermis has no stomata. Within the mesophyll, there are spiky, pink-stained astrosclereids that have been caught in strange views during the sectioning process. Photo by Maria Morrow, CC BY-NC.

Location of Stomata

Because *Nymphaea* is aquatic and sits on top of the water, the stomata are located only in the upper epidermis. You can locate them in the cross section by finding the gaps (stomatal pits) in the palisade mesophyll. Why wouldn't there be stomata in the lower epidermis?

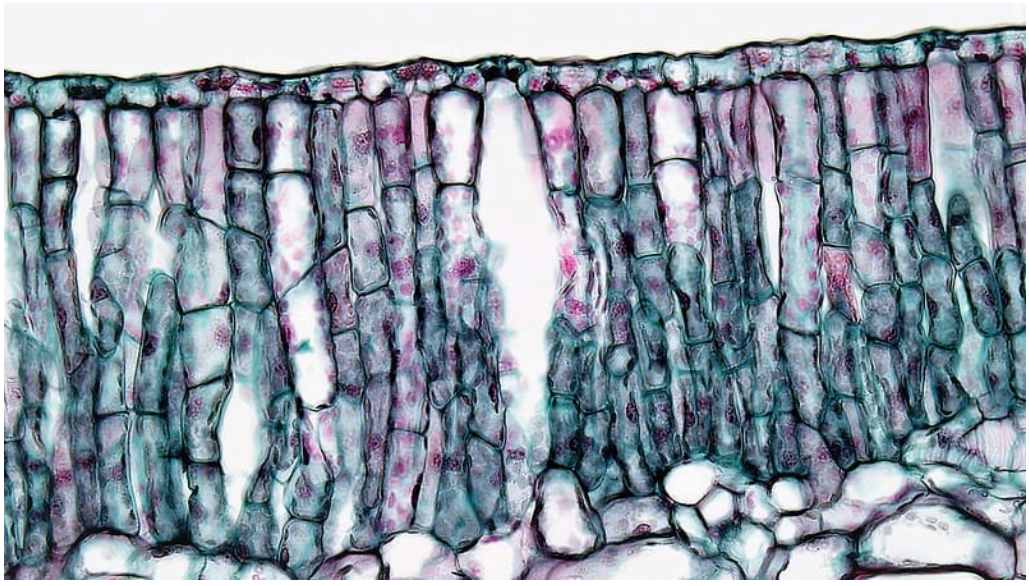


Figure 13.3.1.5: A close up of the stomata and stomatal chambers in *Nymphaea*. In the center of the image, there is an elongated empty space within the palisade mesophyll. At the top of this space, there are two guard cells flanking a closed stoma. At least three other stoma are present in the upper epidermis captured in this image, though the stomatal chambers haven't been captured as clearly in this section. Can you find them? Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

Other Features

If you see strange branching structures within your Nymphaea leaf cross section, you may be looking at an **astrosclereid** (astro- meaning star). This is a branching sclerenchyma cell with a thick secondary wall. What function might these cells have?

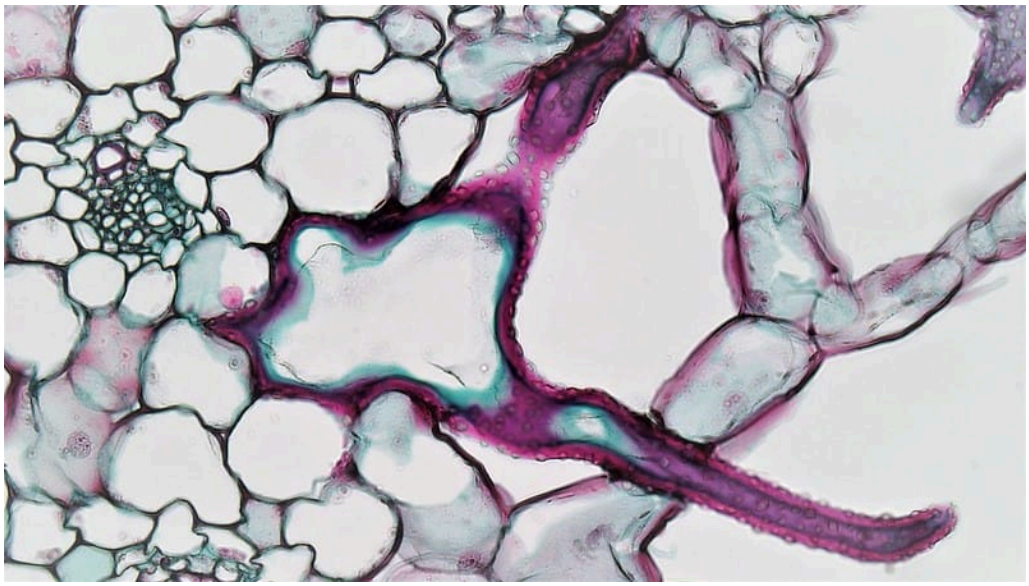


Figure 13.3.1.6: A close up of an astrosclereid found in a *Nymphaea* leaf, caught in partial section. These sclerenchyma cells are covered in pits and have long, sharp arms. Some span the entire width of the leaf. Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

Xerophytic Leaves

Xerophytes (literally "dry plants") are adapted to living in dry conditions with low water availability.



Figure 13.3.1.7: A cross section through a xerophytic leaf (*Nerium*). At first glance, the organization looks similar to a mesophytic leaf. However, there are several adaptations that allow this plant to lose less water (see Figure 13.3.1.8). Photo by Maria Morrow, CC BY-NC.

Tissue Organization

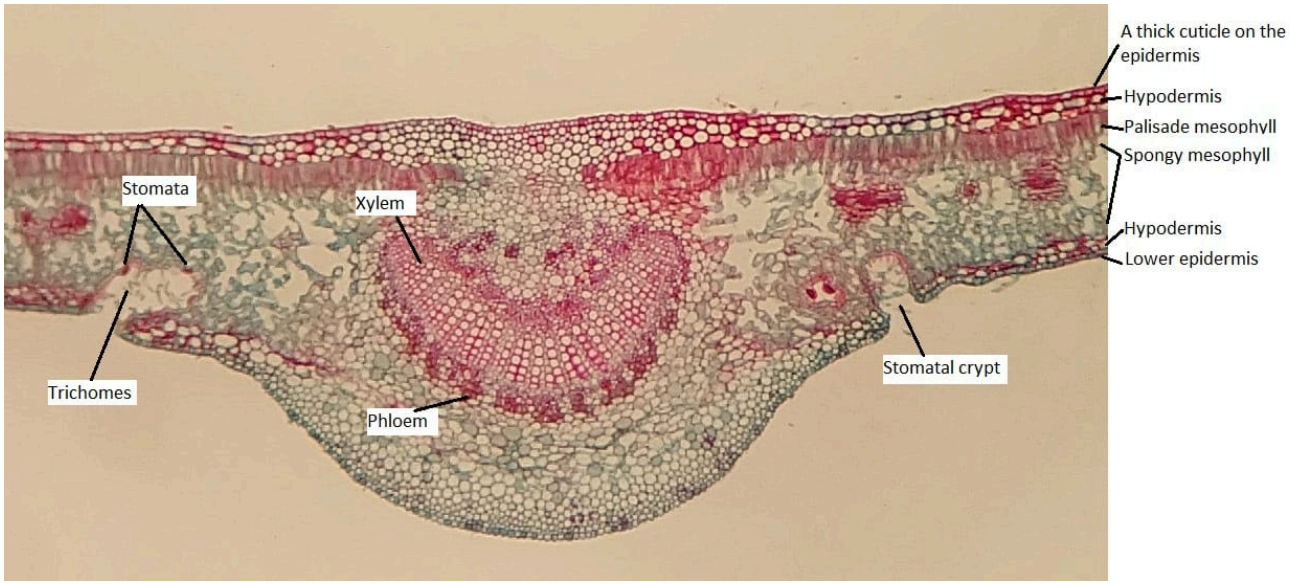


Figure 13.3.1.8: Tissue organization through a xerophytic leaf (*Nerium*). On the right side of the image, the layers of tissue are labeled from the upper surface of the leaf to the lower. The upper epidermis of the leaf is sealed by a thick, waxy cuticle. There are no stomata present in the upper epidermis. Just below the epidermis are several layers of tightly packed cells called the hypodermis. Beneath the hypodermis, the palisade and spongy mesophylls are arranged as in a mesophytic leaf. There are more layers of hypodermis between the spongy mesophyll and the lower epidermis. There are invaginations in the lower epidermis called stomatal crypts (see Figure 13.3.1.9). Stomata are located within these, surrounded by trichomes. Photo by Maria Morrow, CC BY-NC.

Cuticle Thickness

The image below shows the cuticle of the *Nerium* leaf. Notice how thick it is on the upper (adaxial) surface of the leaf and how it changes in thickness as it transitions to the lower (abaxial) surface.

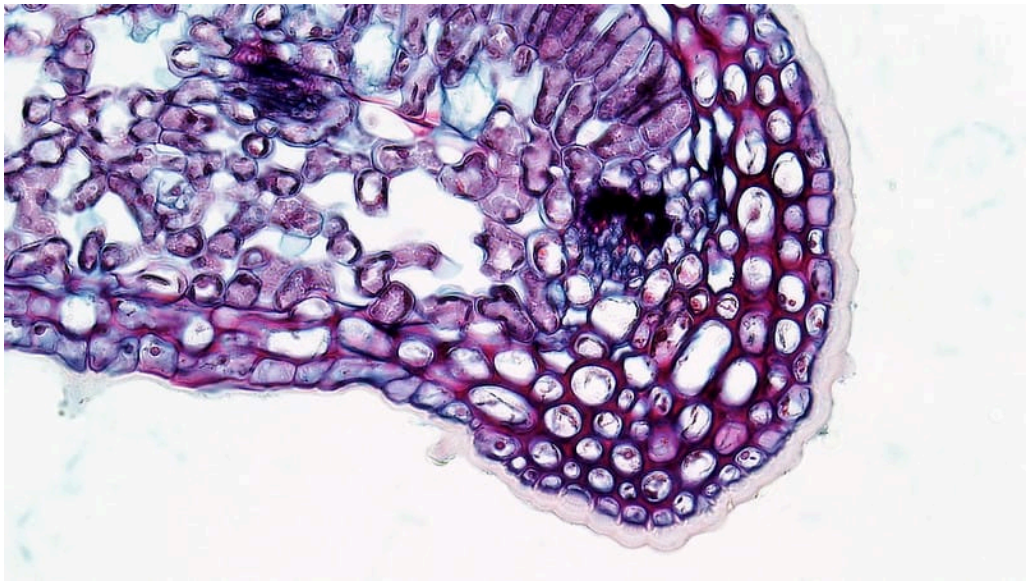


Figure 13.3.1.9: The margin of a xerophytic leaf. There is a thick cuticle on the upper epidermis (it looks like a transparent skin). The cuticle gets thinner as it transitions to the lower epidermis. Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

Location of Stomata

In xerophytic leaves, stomata tend to be located on the lower (abaxial) surface. This side of the leaf is usually cooler, as the upper (adaxial) surface is facing the sun. In extremely dry conditions, stomata might be further protected from the desiccating outer air by being located in **stomatal crypts**.

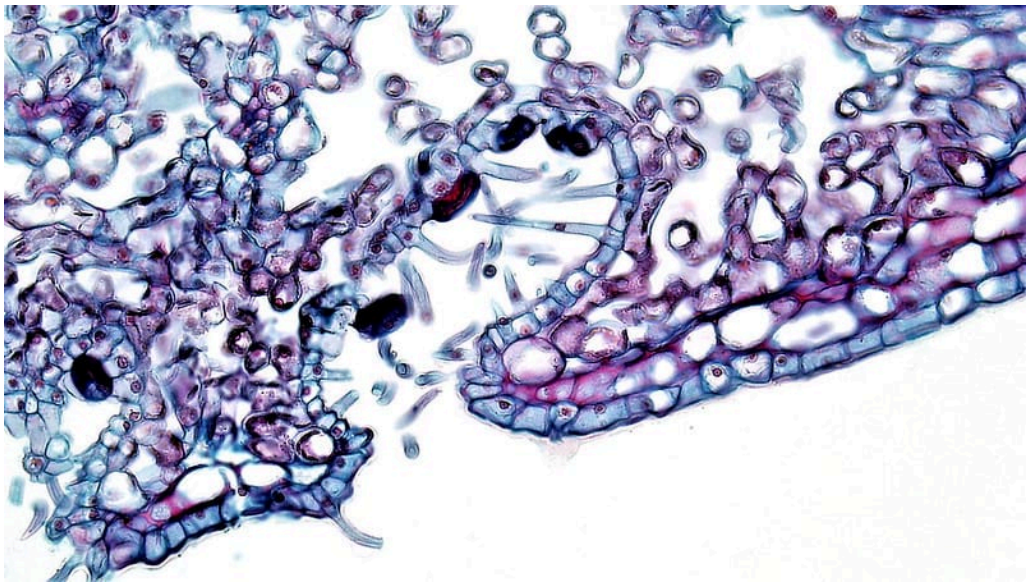


Figure 13.3.1.10: A stomatal crypt in the lower epidermis of a *Nerium* leaf. The epidermis folds inward, creating a small cave-like structure called a crypt. The stomata are located on the epidermis inside the crypt, surrounded by trichomes. Image is in the Public Domain, sourced from Berkshire Community College Bioscience Image Library.

Gymnosperms: The Original Xerophytes

Though pines are not angiosperms, they have xerophytic leaves (needles). Note the features this pine needle has in common with the *Nerium* leaf.

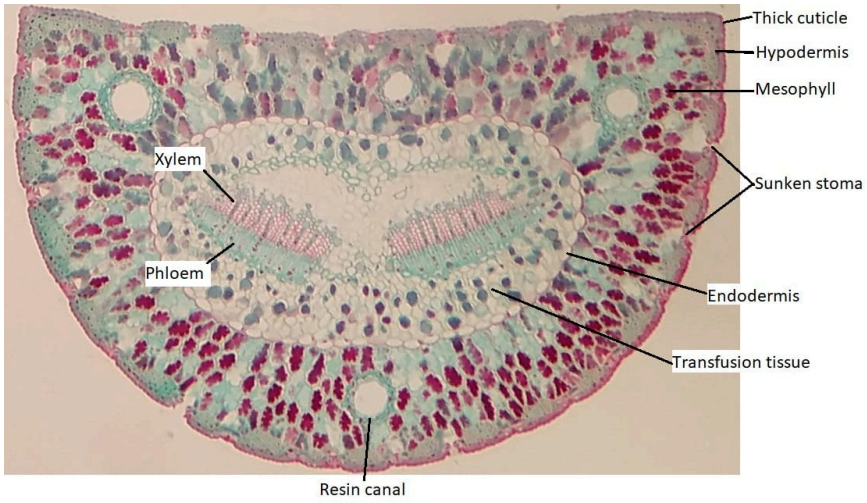


Figure 13.3.1.11: A cross section through a pine needle. Much like the *Nerium* leaf, this leaf is coated in a thick cuticle and there is a hypodermis below the epidermis (because this leaf is so round, there is not really a distinct 'upper' and 'lower'). There are no stomatal crypts, but the stomata are sunken, located in the hypodermis (see Figure 13.3.1.12). The leaf has a low surface area to volume ratio (more volume, less surface area), which decreases water loss. In the center of the leaf, There is a large region surrounded by an suberized endodermis (much look in a root). There are two vascular bundles within this region, surrounded by transfusion tissue. Photo by Maria Morrow, CC BY-NC.

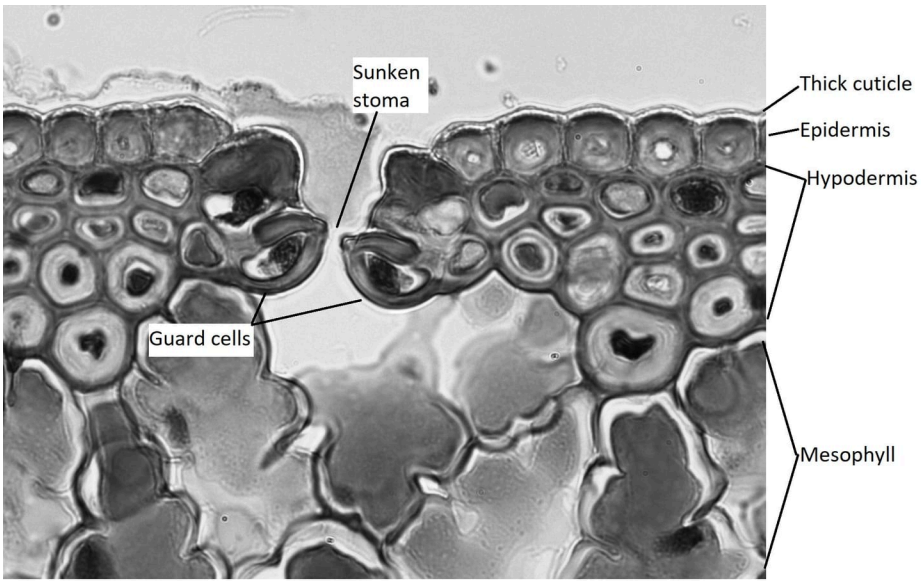


Figure 13.3.1.12: A closer view of a sunken stoma and the outermost layers of the pine needle. The thick cuticle is visible as a transparent layer coating the small epidermal cells. Each of the epidermal cells has a thick cell wall. The hypodermis is composed of 3-4 layers of small, tightly packed cells that also have thick walls (sclerenchyma). The guard cells of the stoma are located about 3 layers below the epidermis and the cuticle can be seen extending down over them. The stoma is open in this image. Below the stoma, there is a gap of air space, then highly invaginated mesophyll cells. Photo by Maria Morrow, CC BY-NC.

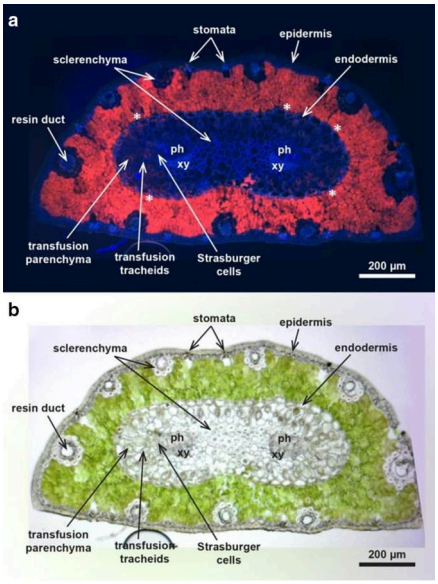


Figure 13.3.1.13: Two pine needle cross sections. In a) the mesophyll cells glow red (autofluoresce), in b) the mesophyll cells are green due to chlorophyll. Photosynthesis takes place in the mesophyll cells. "Scots pine needle cross-section photographed using a light microscope with UV excitation at 365 nm resulting in tissue autofluorescence (**a**), the same section photographed in the bright field (**b**). *x* xylem, *ph* phloem, asterisks indicate the radial thickening of the endodermal cells resembling the Casparian strip." Image and quoted caption text from the open-access paper Tissue-specific element profiles in Scots pine (*Pinus sylvestris* L.) needles. Pongrac, P., Baltrenaite, E., Vavpetič, P. *et al.* Tissue-specific element profiles in Scots pine (*Pinus sylvestris* L.) needles. *Trees* **33,** 91–101 (2019).

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13.4: Modified Leaves

The structure and function of a leaf can be modified over the course of evolution as a plant adapts to a particular environment. Some leaves may be converted to storage structures below ground (as with a bulb) or into plant defense structures (as with a spine). When function of the leaf blade is no longer primarily photosynthesis, some other plant part is usually modified to take its place. A **phyllode** is a petiole that has become flat and photosynthetic, looking much like a leaf blade.

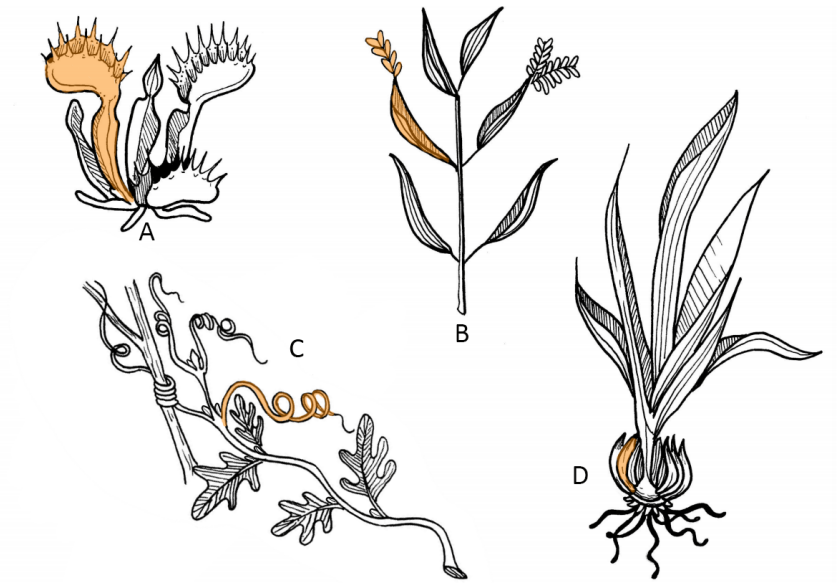


Figure 13.4.1: A diagram of leaf modifications. In each plant (A-D), one leaf has been shaded with orange. In A, the blade has been modified for a trap, the petiole is flattened into a phyllode. In B, the blade is a compound leaf and the petiole is flattened into a phyllode. In C, some of the leaves are tendrils (emerging below axillary buds). In D, the basal leaves are thick and fleshy with a short stem (a bulb). Diagram by Nikki Harris, CC-BY 4.0 with labels and color added by Maria Morrow.

Bulb



Figure 13.4.2: The onion bulb has a relatively small stem (tan tissue just above the roots) surrounded by thick, fleshy leaves. Image by JonRichfield (CC-BY-SA).

Succulent

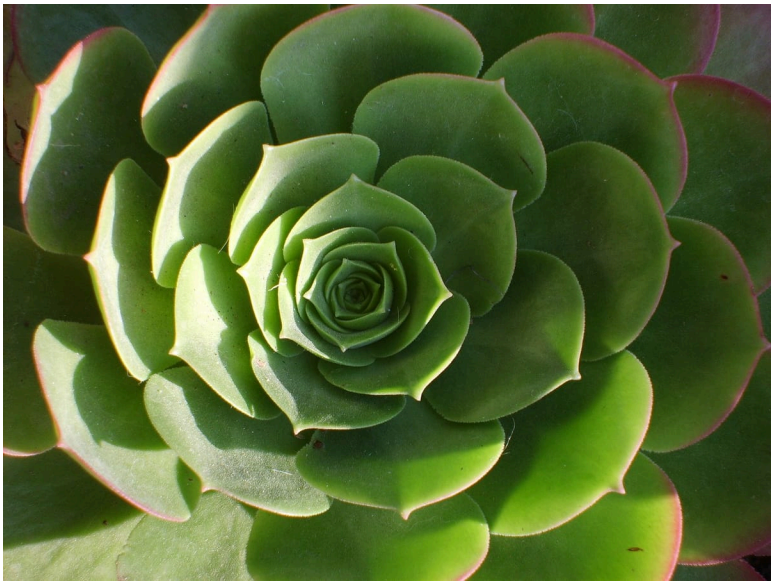
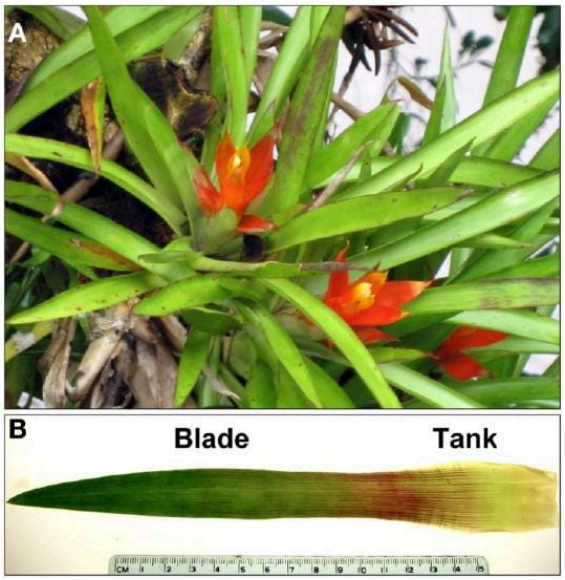


Figure 13.4.3: Succulent leaves are thickened for water storage. This water-storing tissue is called hydrenchyma (see Figure 13.4.4, bottom). Photo by Simon Burchell, CC BY-SA 4.0, via Wikimedia Commons.



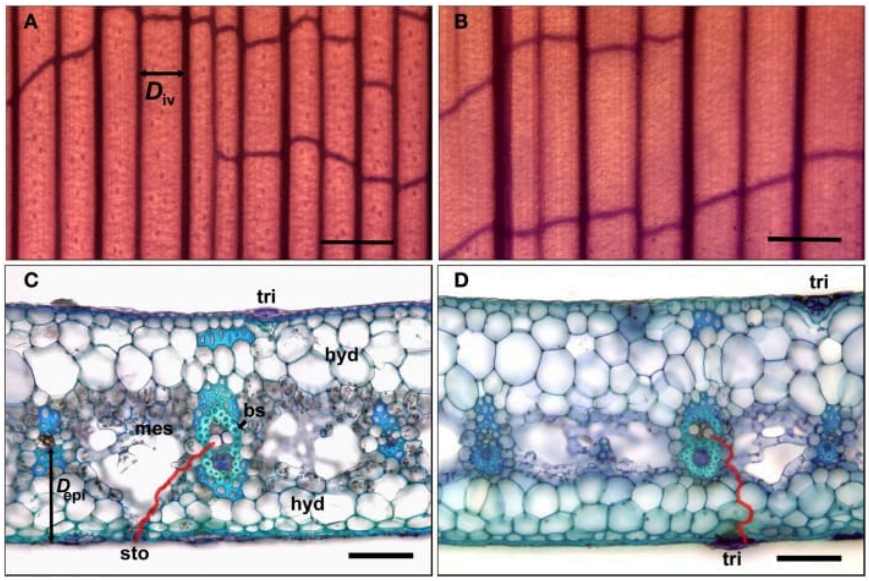


Figure 13.4.4: Top: "(A) Plants of *Guzmania lingulata* in the field at La Selva biological Station, Costa Rica, and (B) a single leaf of *G. lingulata* labeled with the two leaf regions examined." Bottom: "Sections of leaves of *G. lingulata* used to measure anatomical traits. Leaf clearings of the leaf blade (A) and tank region (B) used to determine interveinal distance (Div; black arrow); scale bars in (A) and (B) = 500 μm. Cross-sections of the leaf blade (C) and tank region (D); red lines indicate pathways for water between vein and abaxial surface (red line in (C) used to calculate Dmes; black arrow indicates distance between vein and epidermis Depi); scale bars in (C) and (D) = 50 μm. Abbreviations: bundle sheath cells (bs), hydrenchyma (hyd), mesophyll (mes), stomate (sto), and trichome (tri)." Figures and caption text from Leaf Hydraulic Conductance for a Tank Bromeliad: Axial and Radial Pathways for Moving and Conserving Water, North et al. 2013. Creative Commons Attribution 3.0 Unported.

Tendril



Figure 13.4.5: Many plants in the bean family (Fabaceae) produce leaf tendrils where all or part of the leaf forms a tendril. The first image is an illustration of a plant with compound leaves, some of the leaflets forming tendrils. The second image is of *Vicia villosa* with the terminal leaflets forming three tendrils. First image from Elsie Garrett Rice, Public domain, via Wikimedia Commons. Second image from Harry Rose from South West Rocks, Australia, CC BY 2.0, via Wikimedia Commons.



Figure 13.4.6: "Leaf tendrils: In weak-stemmed plants, leaf or a part of leaf gets modified into tendrils i.e., a green coiled threadlike structure which helps in climbing around the support. Gloriosa or Glory Lily has leaf tip modified into tendrils." Image and caption text by Krishna satya 333, CC BY-SA 4.0, via Wikimedia Commons.

Spine

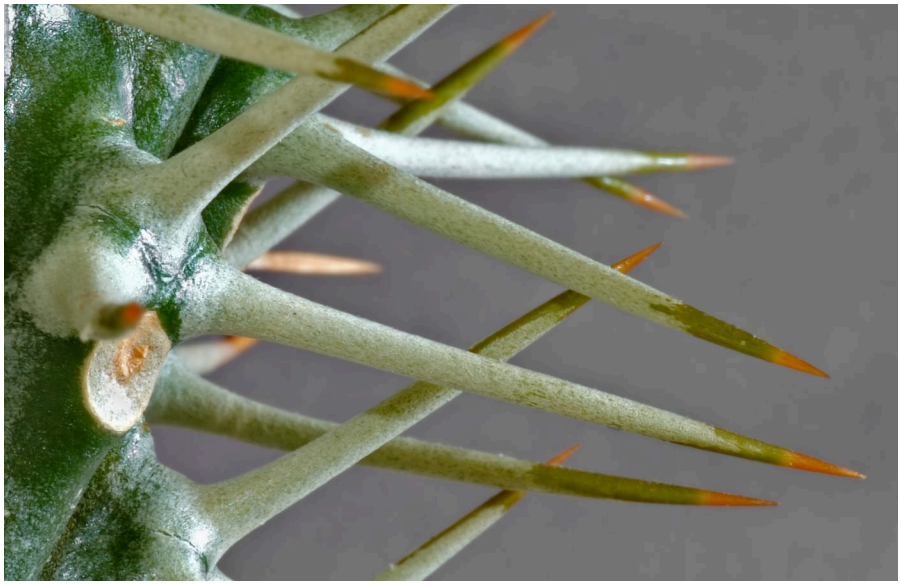


Figure 13.4.7: Cactus spines are not stems, but modified leaves. These spines have a thick cuticle and stomata can be seen as darker green areas within the pale white cuticle. Photo by André Karwath aka Aka, CC BY-SA 2.5, via Wikimedia Commons.



Figure 13.4.8: Ocotillo leaf petioles form into spines. Note the axillary buds present in the axil of each spine. Photographed by and copyright of (c) David Corby (User:Miskatonic, uploader) 2006. This file is licensed under the Creative Commons Attribution-Share Alike 3.0 Unported license.



Figure 13.4.9: Stipular spines of an *Acacia* sp. The paired sharp armaments subtend the leaves on this woody shrub. Dr Mary Gillham Archive Project, CC BY 2.0, via Wikimedia Commons.

Traps



Figure 13.4.10: The (a) Venus flytrap has modified leaves that can capture insects. When an unlucky insect touches the trigger hairs inside the leaf, the trap suddenly closes. The opening of the (b) pitcher plant is lined with a slippery wax. Insects crawling on the lip slip and fall into a pool of water in the bottom of the pitcher, where they are digested by bacteria. The plant then absorbs the smaller molecules. Top two photos by Maria Morrow, CC-BY 4.0. Last two photos credit a: modification of work by Peter Shanks; credit b: modification of work by Tim Mansfield, adapted from Botany by Algiers, Ha, and Morrow.

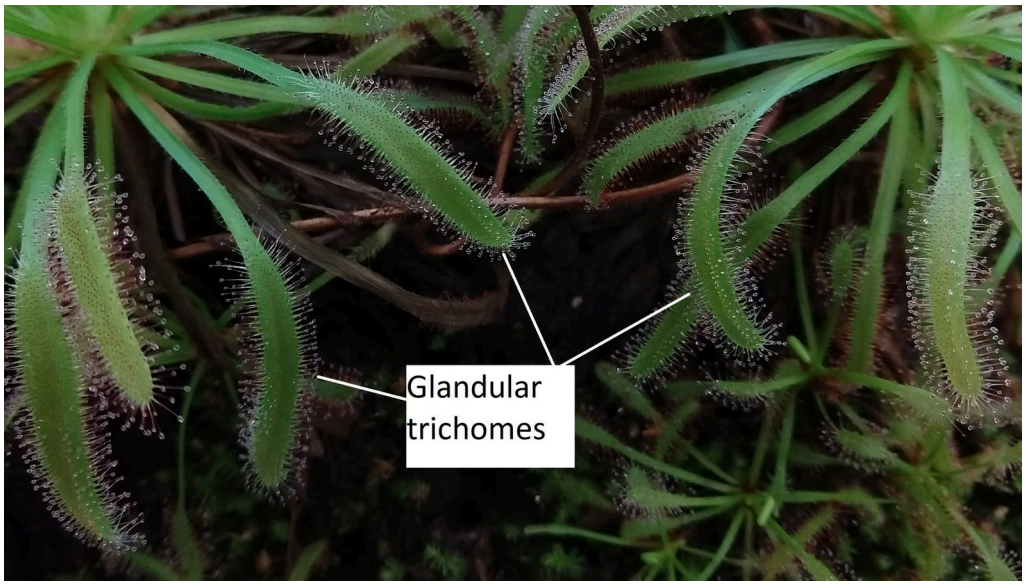


Figure 13.4.11: The ends of sundew (*Drosera* sp.) leaves are covered with glandular trichomes. Each trichome has a blob of sticky fluid at the tip. Insects are attracted to the fluid, becoming trapped in it, and the plant can slowly digest their bodies for the mineral nutrients that are lacking in their environment. Photo by Maria Morrow, CC-BY 4.0.

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14: ECOLOGY

Ecology is the study of the relationships among living organisms, including humans, and their physical environment. Ecology considers organisms at the individual, population, community, ecosystem, and biosphere level.

14.1: Pollination Syndromes

14.2: Dispersal Mechanisms

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14.1: Pollination Syndromes

Flowers have coevolved with their pollinators. The shape, color, smell, and many other features of a floral phenotype are adapted to their method of pollen dispersal. This set of characteristics is called a **pollination syndrome** and allows scientists to make inferences about the pollinator of a particular flower. Some of these are more obvious, while others, more cryptic. For example, humans do not see ultraviolet (UV) light, but many insects can (like bees). Flowers might be communicating with UV light in a way that might not be apparent to humans until you shine a UV light on them. In the *Malva assurgentiflora* flower (Figure 14.1.1), the pollen has UV fluorescence.



Figure 14.1.1: A *Malva assurgentiflora* flower in regular light (first photo) and ultraviolet light (second photo). In the first photo, the pollen looks a dull white and the petals are a vibrant fuschia pink. In the second photo, the petals appear dark burgundy purple, while the pollen is a glowing neon blue. The pollen of this flower has UV fluorescence; when the pollen absorbs UV light, it emits it at a different frequency and appears to glow. Photos by Alan Rockefeller, CC-BY-SA.

Pollination Syndromes and Vectors

Though flower phenotypes can also correlate to other environmental factors (e.g. Peach et al. 2020), we can connect pollination syndromes to pollen vectors, both biotic and abiotic (see Table 14.1.1).

Table 14.1.1: Pollination Syndromes (adapted from the US Forest Service).

Pollination Syndrome	Color	Structure	Scent	Nectar or Pollen
Wind	Dull, perianth often absent or reduced	Large feathery stigmas, large anthers	None	No nectar, large amounts of pollen
Birds	Reds and pinks	Often tubular or cupped	None	Lots of hidden nectar, moderate pollen

Pollination Syndrome	Color	Structure	Scent	Nectar or Pollen
Bees	Purples, blues, yellows, white, UV	Flat and shallow or tubular, with landing area	Sweet, fresh, mild	Pollen often sticky and scented, nectar usually present
Bats	White, dull green, or purple	Often bowl-shaped or pendant, anthers protruding	Musty or fruity, strong, emitted at night	Lots of hidden nectar
Moths	White, pale pink or purple	Often tubular or cupped, no landing pad	Strong and sweet, emitted at night	Lots of hidden nectar, limited pollen
Butterflies	Bright colors	Tubular, with wide landing pad	Faint, fresh	Lots of hidden nectar, limited pollen
Flies	Dark red, purple, brown	Shallow, funnel, or trap-like	Putrid, rotting	No nectar, moderate pollen



Figure 14.1.2: Trillium ovatum flowers are white until they have been pollinated, at which point they begin to turn pinkish-purple. In the image above, the flower on the left has been pollinated, while the one on the right has not. Photo by Maria Morrow, CC-BY 4.0.

Examples of Pollination Syndrome Characteristics

Bees, Bee-Like Flies, and Butterflies



Figure 14.1.3: The yellow color and surface for an insect to land and crawl around on in this head inflorescence are characteristic of bee pollination. However, this flower does not smell particularly fresh or sweet. Instead, the odor is more astringent and a bit unpleasant. Photo by Maria Morrow, CC-BY 4.0.



Figure 14.1.4: These foxglove florets are purple and bell-shaped. The lower petal serves as a landing pad for bees, with a speckled pathway (nectar guide) to lead the bee to the nectar at the center of the flower. The anthers are visible on the lowest full floret, dangling above the entrance to deposit pollen on the bee's back as it crawls in. Photo by Maria Morrow, CC-BY 4.0.



Figure 14.1.5: This *Iris* flower has a bee pollination syndrome. The primary colors are purple and yellow. There are nectar guides leading the bee to the center of the flower. To get there, the bee must crawl under the stigma first, then under the anthers. This flower has a pleasant, sweet smell. Photo by Maria Morrow, CC-BY 4.0.



Figure 14.1.6: This *Delphinium* flower has a butterfly pollination syndrome (this also works for long-tongued bees). The color is purple, there is a lipped petal that serves as a landing pad, and there is a long nectar spur extending from the back of the flower. This flower has a pleasant, sweet smell. Photo by Maria Morrow, CC-BY 4.0.

Birds



Figure 14.1.7: These flowers have a bird pollination syndrome. The *Fuschia* (left) is pink and purple, pendant, and relatively odorless. The nectar is located deep within the flower at the base of a hypanthium. The *Castilleja* (right) is bright red with many tubular flowers (these could also be butterfly pollinated). First image by Peter Clarke, CC BY-SA 3.0 via Wikimedia Commons. Second image by Maria Morrow, CC-BY 4.0.



Figure 14.1.8: A hummingbird pollinating red, tubular flowers. The anthers and stigma extend below where the hummingbird enters, rubbing it on the chin and chest when it goes in for nectar. Photo by VJAnderson, CC BY-SA 4.0 via Wikimedia Commons.

Flies and Beetles



Figure 14.1.9: Fritillaria flowers are often fly pollinated. The dark red splotches on the petals and overall unpleasant smell fit a fly pollination syndrome. Check out this page to see Fritillaria species being pollinated by flies. Photo by Maria Morrow, CC-BY 4.0.



Figure 14.1.10: These flowers have a beetle pollination syndrome. Beetles prefer white to green flowers with a large place to land. First image from Pollinator at the English language Wikipedia, CC BY-SA 3.0 via Wikimedia Commons. Second image by Sweetbay_Magnolia_Magnolia_virginiana_Flower_Closeup_2242px.jpg: Photo by and (c)2008 Derek Ramsey (Ram-Man). Co-attribution must be given to the Chanticleer Garden.derivative work: Bff, CC BY-SA 3.0 via Wikimedia Commons.

Wind



Figure 14.1.11: Wind pollinated flowers have a reduced or absent perianth, large anthers, and feathery stigmas. This grass spike has large pinkish anthers dangling from long filaments. Feathery stigmas can be seen emerging from some of the florets. Photo by Maria Morrow, CC-BY 4.0.

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14.2: Dispersal Mechanisms

Ballistic



Figure 14.2.1: A cluster of dwarf mistletoe berries (first image). The seeds are shot out (second image, B) when turgor pressure builds up within the berry. Dwarf mistletoe seeds have velocities of about 24 m/s and may travel over 10 meters. The seeds are covered with a sticky substance (viscin) and occasionally are dispersed by birds, either by being eaten or getting stuck to them. First image by Maria Morrow, CC BY-SA 3.0. Second image from the open-access paper Mistletoes: Pathology, Systematics, Ecology, and Management (Mathiasen et al. 2008), Plant Disease.

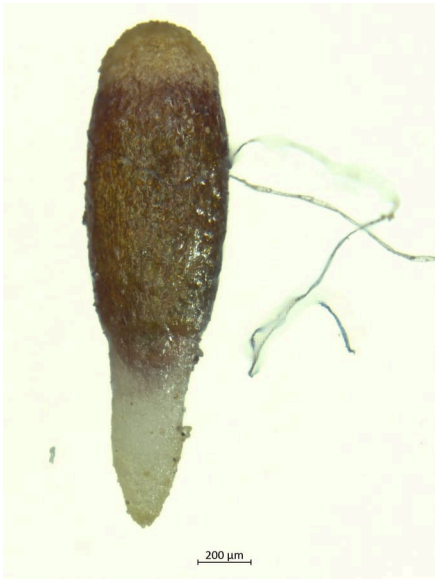


Figure 14.2.2: "The sticky seed of juniper dwarf mistletoe (Arceuthobium oxycedri (DC.) M. Bieb) from the Crimean Peninsula–a semi-parasitic species of Holarctic Cupressaceae hosts parasitizing Eastern prickly juniper, Juniperus deltoides R.P. Adams, Greek juniper, J. excelsa M. Bieb. and Oriental thuja, Platycladus orientalis (L.) Franco. Among the unique features of Arceuthobium spp. are ballistic seed dispersal primarily achieved through a hydrostatically controlled explosive discharge mechanism and thermogenesis. Seeds of A. oxycedri are ~0.9–1 mm long and ~0.4–0.5 mm wide, with an elongated pedicel on the proximal (acuminate) apex. A. oxycedri seeds are covered by a sticky viscin ("birds glue") forming a snow-white cap on the distal (roundish) apex and thin layer on the surface of the seed. After the hydration viscin forms sticky stands required for parasite attachment to the host branch and/or sporadic ornithochory. The picture was taken using stereomicroscope Axio Zoom.V16 (Carl Zeiss, Germany). Seeds are from Mt. Malyi Sokol, Sudak territory Autonomous Republic of Crimea, Ukraine." Image and caption text by Yuliya Krasylenko, CC BY-SA 4.0 via Wikimedia Commons.

YouTube Video

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

Video 14.2.1: Watch this fun video of different plants utilizing ballistic seed dispersal. Sourced from YouTube.

Wind





Figure 14.2.3: Samaras are winged achenes adapted to wind dispersal. The maple samaras in the first image are also schizocarps, breaking apart at maturity into two separate fruits. First image by Gmihail at Serbian Wikipedia, CC BY-SA 3.0, via Wikimedia Commons. Second image by Marco Schmidt [1], CC BY-SA 3.0 via Wikimedia Commons.

Water



Figure 14.2.4: Lotus seeds are water dispersed. This lotus fruit is bouyant and has many seeds embedded within it. As it matures, it dries, the seeds are released and sink into the water to germinate. Photo by Bouba, CC BY-SA 3.0 via Wikimedia Commons.

YouTube Video

This interactive element is not available in this format. Visit the link or scan the QR code to access it online.

View this YouTube Video online

Video 14.2.2: Watch this clip to see more water-dispersed seeds and fruits. Sourced from YouTube.

Animal Attachment & Ingestion



Figure 14.2.5: Animal attachment. Fruits of *Xanthium*, cockleburrs, have hooked spikes that allow them to attach to passing animals. Photo by Muséum de Toulouse, CC BY-SA 3.0 via Wikimedia Commons.



Figure 14.2.6: Animal ingestion. Fruits that we think of as fruits are generally adapted for animal ingestion. These red raspberries might be eaten by birds, the seeds excreted in some new locale. Photo by Juhanson, CC BY-SA 3.0 via Wikimedia Commons.



Figure 14.2.7: Habanero chiles (and other spicy peppers) have specially adapted for bird dispersal. They contain a compound called capsaicin that is incredibly spicy to most mammals but does not bother birds. Photo from The original uploader was Fir0002 at English Wikipedia., CC BY 2.5 via Wikimedia Commons.

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GLOSSARY

A

Abiotic | nonliving

Abscission | the natural detachment of plant parts, such as with leaves in the winter

Accessory fruit | a fruit where the fleshy material is not derived from the ovary. Ex. A strawberry or rose hip

Achene | a dry fruit with a single seed surrounded by a pericarp that can be peeled away. Layers of the pericarp are not distinguishable with the naked eye. Ex. A sunflower seed.

Actinomorphic | See “Radial symmetry”

Adhesion | attraction between dissimilar molecules or substances (such as tape to paper)

Adventitious root | a root that emerges from stem tissue

Aerenchyma | parenchyma tissue with large air pockets for flotation

Aggregate fruit | a fruit derived from a flower with multiple free carpels. Ex. A blackberry.

Akinete | a form some cyanobacteria can take. Larger, thick-walled cells that tend to be more granular in appearance. Akinetes store large amounts of lipids and carbohydrates so that they have enough energy to begin a new colony if conditions become too cold or too dry for survival. Formation of akinetes can be triggered by dry or cold conditions.

Alcohol fermentation | a form of fermentation performed by yeasts that converts pyruvate into ethanol and CO_2 to replenish NAD+

Alternate (leaf arrangement) | one leaf emerges at a node

Alternation of generations | See “Haplodiplontic”

amylo | starch (amylose)

Amyloplast | a type of plastid that produces and stores starch. An amyloplast is a type of leucoplast, which are plastids that do not contain pigment.

Anaphase | the stage of mitosis where spindle fibers pull sister chromatids to either side of the cell, splitting them into two separate chromosomes

Anaphase I | the stage of meiosis I where spindle fibers pull homologous chromosomes to either side of the cell

Anaphase II | the stage of meiosis II where spindle fibers pull sister chromatids to either side of the cell, splitting them into two separate chromosomes

andro | male, man

Androecium | the floral whorl composed of stamens

angio/angium | vessel

Annual growth ring | a light and dark region of secondary xylem that forms in response to environmental conditions. The light portion of the ring is composed of larger cells, formed when water is abundant (also called early wood). The dark portion of the ring is composed of smaller diameter, densely packed cells, formed when water becomes more scarce (also called late wood).

Annulus | a ring-like structure. In fungi, this refers to the partial veil remnants left around the stipe. In ferns, it refers to the ring of inflated cells around the sporangium that dries and pulls the sporangium open, releasing the spores.

anth | flower

Anther | pollen sacs in flowering plants

Antheridiophore | a structure that bears antheridia

Antheridium | a multicellular structure on the gametophyte that produce sperm by mitosis

Antipodals | three haploid cells in the embryo sac located on the opposite end of the micropyle

Apical growth | growth extending from the tips (such as the tips of roots or shoots in plants)

Apothecium | a (usually) cup-shaped fruiting body produced by some ascomycetes

Arbuscule | a highly branched structure formed by endomycorrhizal fungi on the plasma membrane of plant root cells. The increased surface area increases the ability to exchange materials.

Archegoniophore | a structure that bears archegonia

Archegonium | a multicellular structure on the gametophyte that produce an egg by mitosis

Ascocarp | a fruiting body (sexually reproducing structure) produced in the fungal phylum Ascomycota

Ascospore | a haploid spore produced by meiosis, then mitosis, within the ascus of an ascomycete

Ascus | a sac-like structure where meiosis occurs to produce spores in ascomycetes. Asci, plural.

Asexual reproduction | a form of reproduction that produces identical copies of the parent cell (e.g. mitosis, binary fission, and budding)

Astrosclereid | a sclereid cell that transverses the leaves of *Nymphaea* and forms star-like shapes

ATP | (adenosine triphosphate) a high energy molecule with three negatively charged phosphate groups. ATP can "donate" a phosphate group to a reaction, breaking a high energy bond and releasing energy. This process is called phosphorylation. Most work done in cells is powered by ATP.

ATP Synthase | an enzyme that uses the flow of H+ ions back down their concentration gradient (secondary active transport) to phosphorylate ADP into ATP.

auto | self

Autotroph | an organism that forms organic molecules from inorganic molecules. This can also be thought of as an organism that makes its own food (self-feeding).

Auxospore | an enlarged spore produced by diatoms during sexual reproduction (and apparently sometimes through asexual reproduction)

Axillary bud | a structure located in the axil of the leaf that produces a branch, flower, or inflorescence

B

Bark | layers of periderm (phelloderm, cork cambium, and cork) form the outer bark, while the secondary phloem forms the inner bark.

Basal meristem | meristematic tissue located at the base of a structure. Most plants grow from apical meristems, producing new tissue at and elongating from the tips. Basal meristems produce tissue where the tips are the oldest parts.

Basidiocarp | a fruiting body (sexually reproducing structure) produced by some basidiomycetes

Basidiospore | a haploid spore produced by meiosis within the basidium

Basidium | a (usually) club-shaped structure that produces spores in the basidiomycetes

Benthic | at the bottom of a body of water

Berry | a fleshy fruit with a thin exocarp, fleshy mesocarp, and one to many seeds not enclosed within an endocarp derived from the ovary wall

bi | two

Bilateral symmetry | having one line of symmetry

Binary fission | a form of asexual reproduction used by prokaryotic cells where the original cell expands as internal contents are replicated, then a new cell wall forms in the middle, dividing into two new, identical cells

bio | life

Bioavailable | a form that can be absorbed by and assimilated into an organism.

Biotic | living

Blade | the (usually) flat, photosynthetic portion of the leaf located at the end of the petiole. In brown algae, this is the leaf-like structure (or structures) on the thallus.

Bud primordium | the early developmental stage of the axillary bud

Bud scar | the scar left behind on a stem where the axillary bud has fallen off via abscission

Budding | a form of asexual reproduction used by yeast where a smaller cell is made from the original cell, leaving a bud scar. The smaller cell grows to normal size after separation from the parent cell.

Bulb | a rosette of fleshy leaves modified for storage, surrounding a short stem

Bulliform cells | enlarged cells in the epidermis that respond to water loss by collapsing, causing the leaf to roll or fold and reducing sun exposure

Bundle scars | scars left behind inside a leaf scar where the vascular bundles of the leaf travelled into the stem

Bundle sheath | the ring of cells that surround a vascular bundle. This could be in the stems of monocots or in the leaves of either group.

C

C3 | the "standard" and most energy efficient form of photosynthesis

C4 | a form of photosynthesis performed by plants adapted to hot weather. RuBisCO is located in the bundle sheath cells, where CO2 is actively transported in the form of an acid to keep concentrations high. This occurs when stomata close to prevent water loss, limiting CO2 intake.

Calvin cycle | the light independent phase of photosynthesis where RuBisCO fixes CO2 and the end product is glucose. This process occurs in

the stroma of the chloroplast.

Calyptra | tissue from the female gametophyte that is carried on top of the developing sporophyte in the bryophytes

Calyx | the floral whorl composed of sepals

CAM | Crassulacean acid metabolism. This is a form of photosynthesis performed by plants adapted to dry weather. Stomata close during the day to prevent transpiration and open at night to let in CO2. The CO2 is actively transported into the central vacuole and converted into an acid. During the day, it is converted back into CO2 so photosynthesis can occur.

Cap (pileus) | the top of a mushroom. The spore producing surface is on the underside of the cap (usually).

Capillary action | the tendency of a liquid to rise or fall as a result of surface tension

Capsule | a dry fruit with multiple fused carpels that open at maturity. Ex. Cotton. Note: this term is also often used to describe the structure that encases the sporangia in mosses.

Carotenoids | red, orange, and yellow pigments found in plants, green algae, and photosynthetic heterokonts. These are often used to protect from sun damage or to signal ripening in fruits, as well as absorb some of the green parts of the spectrum of light.

carp | of the fruit or fruiting body

Carpogonium | a structure produced on the red algae female gametophyte. It consists of the egg and the trichogyne and may also be called the carpogonial branch.

Carposporangium | a structure that produces carpospores

Carpospore | a diploid spore that is identical to the zygote in the red algae life cycle. Carpospores grow by mitosis into a tetrasporophyte.

Carposporophyte | a multicellular diploid phase in the red algal life cycle that produces clones of the zygote called carpospores

Caryopsis | a dry fruit similar to an achene, but the pericarp is fused to the seed. This fruit type is produced by members of the Poaceae (grass family). Ex. A corn kernel.

Casparian strip | a layer of suberin that coats the endodermis in roots. This layer forms in patches, leaving passage cells at the xylem poles.

Cell wall | a rigid structure that encloses the plasma membrane. The presence and composition of the cell wall are useful features in classifying and identifying organisms.

Cellulose | a polysaccharide found in plant cell walls. Cellulose is also found in the cell walls of oomycetes and red, green, and brown algae.

Central cell | a cell in the embryo sac containing two polar nuclei

Central vacuole | a (generally) large, fluid-filled organelle enclosed by a membrane (the tonoplast). The central vacuole often takes up the majority of a plant cell and is responsible for storage of compounds (ex. toxins, anthocyanins, and salts) and turgidity of the plant cell, which contributes to rigidity of the entire plant.

Centric | (a diatom) with radial symmetry

Centromere | the central region of a chromosome where sister chromatids are attached (in replicated chromosomes)

Chemical energy | energy stored in the bonds between atoms within molecules

Chemiosmosis | the movement of ions from areas of high concentration to low concentration across a semipermeable membrane. This happens with H+ flow through ATP synthase in both cellular respiration and photosynthesis.

Chemosynthesis | a cellular process that uses chemical energy derived from oxidizing (stealing electrons from) inorganic compounds to build organic molecules. In this process, the inorganic compound is the electron donor. The waste product will depend on what the initial inorganic compound is (for example, if hydrogen sulfide is used, sulfur and water could be produced as waste products).

Chitin | polysaccharide (carbohydrate) found in fungal cell walls and arthropod exoskeletons

Chlorenchyma | parenchyma cells with chloroplasts for photosynthesis

Chlorophyll | a photosynthetic pigment that reflects light in the green portion of the spectrum. These molecules can harvest energy from the blue and, to a lesser extent, red part of the spectrum of light by emitting an electron after absorbing a photon. All photosynthetic organisms covered in this class contain chlorophyll a, which is the primary molecule involved in the light-harvesting portion of photosynthesis.

Chloroplast | a double-membrane bound organelle derived from bacterial endosymbiosis that contains chlorophyll and is responsible for photosynthesis. Chloroplasts can be converted into chromoplasts or leucoplasts, when needed.

Chromatin | DNA wound around histone proteins

chromo/chroma | color

Chromoplast | a double-membrane bound organelle derived from bacterial endosymbiosis that contains pigments other than chlorophyll, such as carotenoids. Often found in ripening fruits to attract animals with the red hues.

Chromosome | chromatin that has been tightly packaged in preparation for cell division

Chytrid | an aquatic fungus with swimming spores (zoospores)

Circinate vernation | the process by which fern fiddleheads unfurl in the spring

Citric acid cycle | a process that takes place in the matrix of a mitochondrion during cellular respiration. ATP, NADH, and FADH2 (as well as some CO2) are produced.

Cladode | a stem that has been modified for photosynthesis, often green with increased surface area

Clamp connection | a rounded structure that forms on the side of a basidiomycete hypha as nuclei divide

Classification | a system of categorizing organisms into like groups

Cleistothecium | an enclosed, microscopic fruiting body produced by some ascomycetes

Coenocytic | this can refer to fungal hyphae with no septations (cross walls) or, more generally, to any cell with many nuclei

Coevolution | the linked evolution of two interacting species

Cohesion | attraction between like molecules (for example the attraction of a partial positive charge on the hydrogen atom of one water molecule to the partial negative charge on the oxygen atom of another water molecule)

Collenchyma | cells with unevenly thickened primary walls, often involved in flexible support in young growing tissues

Community | multiple interacting populations living in the same area at the same time

Companion cell | a cell with a nucleus paired with a sieve tube element. The companion cell acts as the command center for that sieve tube element.

Complete (flower) | a flower containing all four floral whorls

Complex septation | also called a dolipore septum. The walls around the pore in the septum are swollen and two structures that look like parentheses (aptly called parenthesomes) flank the pore.

Conceptacle | a chamber inside the Fucus receptacle that houses the gametangia

Cone | see “strobilus”

Conidiophore | a structure that bears conidia

Conidium | a spore produced by mitosis (asexual reproduction) in molds

Conjugation tube | a structure produced in Spirogyra that allows mating to occur between compatible colonies. Cell contents are transferred through the conjugation tube.

Consumer | an organism that eats other organisms as an energy source. A primary consumer eats producers, a secondary consumer eats primary consumers (though it may also eat producers), and a tertiary consumer eats secondary consumers (though it may also eat both primary consumers and producers, as well).

Cork | suberized cells that are dead at functional maturity produced in the periderm during secondary growth. Cork cells form the outermost layer of stems and roots in secondary growth.

Cork cambium | the secondary meristem that produces cork to the outside and phelloderm to the inside

Corm | a stem that has been modified for storage. Nodes on the corm produce papery leaves.

Corolla | the floral whorl composed of petals

Cortex | tissue produced by the ground meristem, located between the vascular tissue and the epidermis

Costa | the central “vein” in a moss leaf. Note: mosses do not have true vascular tissue, particularly not in the gametophyte.

Cotyledon | the first leaf or leaves to appear as a seed germinates

Crossing over | during prophase I of meiosis, homologous chromosomes align and can swap regions of DNA, resulting in increased genetic variety within an organism’s gametes.

Crustose | a lichen that is completely appressed (stuck up against) what it is growing on. Cannot be (easily) removed from this substrate.

Cuticle | a waxy layer made of the lipid cutin that coats the epidermis in plants

cyan | blue

cyst | a sac or bladder containing fluid

Cystocarp | a structure produced on the female gametophyte of red algae. The carpogonium enlarges and the zygote develops inside, growing by mitosis into the carposporophyte. Female gametophyte tissue (the pericarp) surrounds the carposporophyte. These two components together comprise the cystocarp.

cyto | cell, cellular

Cytokinesis | division of the cytoplasm through the formation of a new cell wall during mitosis and meiosis, which happens concurrently with telophase.

Cytoplasm | everything inside the plasma membrane, excluding the nucleus. This term is often confused with the term cytosol, which refers to

the jelly-like matrix that fills the cell and surrounds the organelles, if present.

Cytoplasmic streaming | movement of the cytoplasm around the cell to transport nutrients, organelles, or other materials

D

Decomposer | an organism that breaks down dead organic matter, transforming the molecules trapped within those organisms into forms that are released into the environment and their respective nutrient cycles. This term is synonymous with the terms saprobe and saprophyte.

Dehiscent | a dry fruit that opens on its own at maturity, usually to disperse the seeds

Dendrochronology | a process used to determine the order and timing (chronology) of events using information in tree rings

Dependent variable | the variable(s) in a scientific experiment that you record data on during and/or after your experiment

di | two; double

Diffusion | the tendency of particles to move from areas of high concentration to areas of lower concentration due to random movements and entropy

Dikaryon | a dikaryotic fungal thallus

Dikaryotic | having two unfused, haploid nuclei per cell (n+n)

Dioecious | male and female reproductive structures are produced on different plants

Diploid | having two sets of chromosomes (2n)

Diplontic | a life cycle where the multicellular stage is diploid

Dispersal agent | in angiosperms, the organism or phenomenon that aids in dispersal of the seeds

Double fertilization | the fertilization of both the egg (producing a zygote) and the polar nuclei (producing the endosperm) in the angiosperm life cycle. A form of double fertilization also occurs in gnetophytes, but the result is two fertilized eggs.

Drupe | a (typically) fleshy fruit with a thin exocarp, fleshy mesocarp, stony endocarp, and (typically) a single seed. Ex. A peach.

E

Ecosystem | the biotic and abiotic components of an environment and the interactions between these components

Ectomycorrhizal | a mycorrhizal association formed by some Ascomycota and Basidiomycota (and at least one zygomycete) around the cells of plant roots, forming a fungal sheath around the roots and a hartig net within the roots. See “mycorrhizal” for more information.

Egg | the haploid cell produced by the megagametophyte that must fuse with a sperm to produce a zygote

Elaters | elongate structures that promote spore dispersal by interacting with moisture in the air (hygroscopic movement). Found on the spores of Equisetum and in the sporangia of bryophtyes.

Electromagnetic energy | energy that travels as a wave and does not require a medium. For example, light is a form of electromagnetic energy because it can travel as a wave through the vacuum of space. Sound, even though it travels as a wave, is not a form of electromagnetic energy because it requires a medium, such as air or water, to transmit it. Sound does not travel in space! So, laser gun battle in space = totally silent.

Electron transport chain | a series of protein complexes that transfer electrons between each other. The energy from the electrons allows some of these protein complexes to pump H+ across the membrane.

Embryo | a zygote that is retained and nourished by the female gametophyte.

Embryo sac | the mature megagametophyte of an angiosperm, containing 7 cells and 8 nuclei

endo | inside, internal, inner

Endocarp | the innermost layer of the pericarp in a fruit. In a peach, the endocarp is the stony pit enclosing the seed.

Endodermis | the innermost layer of the cortex in the root (also present surrounding the transfusion tissue in a pine needle)

Endogenous | formed from within

Endomycorrhizal | fungi that penetrate between the cell wall and plasma membrane of plant roots, establishing a mutualistic exchange of materials. This is a trait shared by all of Glomeromycota.

Endosperm | the result of a sperm fertilizing the polar nuclei (central cell) in the embryo sac. This triploid tissue is consumed by the growing zygote in an angiosperm seed.

epi | on top of

Epidermis | the outermost layer of the plant, composed of a single cell layer. These cells are parenchyma and often include specialized cells, such as trichomes or guard cells.

Epiphyte | growing on a plant

eryth | red

eu | true

Eudicot | (alternatively called dicot) flowering plants that produce two cotyledons

Eukaryote | an organism that can be unicellular or multicellular, but each cell with contain a nucleus (though this may be lost in some plant cells). Eukaryotes have linear DNA that is stored inside the nucleus and their cells contain membrane-bound organelles like mitochondria and the endoplasmic reticula.

exo | outer

Exocarp | the outer layer of the pericarp in a fruit. In a peach, the exocarp is the fuzzy skin.

Exogenous | formed on the exterior

F

Fascicular cambium | residual procambium within vascular bundles that joins with the interfascicular cambium to form the vascular cambium in eudicots

Fermentation | a process that occurs after glycolysis to restore NAD+, such as the production of lactate or ethanol

Fiber | an elongated sclerenchyma cell with tapered ends whose function is structural support

Fiddlehead | a frond that has yet to unfurl via circinate vernation

Filament | (in flowers) the stem-like structure that holds the anthers aloft

Flagellum | a long projection that can be present on both prokaryotic and eukaryotic cells that is used for movement

Floret | a flower in an inflorescence

Floridean starch | the form of starch used by red algae as a storage carbohydrate

Flower | a set of modified leaves that promote fertilization (pollination)

Foliose | leaf-like. In lichens, a flattened thallus with two distinct sides (can be removed from substrate).

Follicle | a dry fruit composed of a single carpel that splits open along a single seam at maturity

Food | compounds your body can break down to get energy, usually carbohydrates

Food web | an interconnected network of organisms participating in the flow of energy through an ecosystem. A food web involves primary producers, consumers, and decomposers. At each transition in a food web from one organism to another, about 90% of the available energy is lost as heat.

Foot | the base of the sporophyte seta, where it attaches to the gametophyte

Frond | the megaphyll of plants in subclass polypodiidae in the Ferns

Fruit | the swollen ovary and enclosed seeds produced by angiosperms

Frustule | the silica cell wall of diatoms, composed of two valves

Fruticose | a lichen that is three dimensional, but without two distinct sides. Often called “busy” or “shrubby”

Fucoxanthin | a carotenoid found in photosynthetic heterokonts

Funiculus | transitional tissue between the angiosperm ovary and the developing ovule, much like an umbilical cord

G

G0 | the stage of the cell cycle when a cell ceases to divide and specializes

G1 | the stage of the cell cycle when cytoplasmic contents are duplicated

G2 | the final stage of the cell cycle, where a cell is verified to be ready for division

Galactans | sulfated polysaccharides present in the cell walls of red algae

Gametangium | a structure that produces gametes

Gamete | a haploid cell that must fuse with another haploid cell to form a zygote

Gametophyte | a haploid, multicellular generation that produces gametes by mitosis

Gametophyte dominant | a life cycle where the gametophyte is larger, longer-lived, and nutritionally responsible for the sporophyte

gamy | union, marriage

Gas bladder | a pocket in the thallus of brown algae that traps gases to act as a float

Gemma | an asexual clone of plant tissues, such as in thalloid liverwort gametophytes (gemmae, plural)

Gemmae cup | a cup-like structure where gemmae are produced

Generative cell | the haploid cell in pollen grains that divides to produce sperm

Gills (lamellae) | structures in some mushrooms where the spore producing basidia are located

glyco | relating to sugar (often glucose)

Glycogen | a polysaccharide (carbohydrate) used to store sugars in fungi, animals, and other heterotrophs

Glycolysis | the first stage in cellular respiration or fermentation, where glucose is broken down into two molecules of pyruvate. This occurs in the cytoplasm.

Granum | a stack of thylakoids in a chloroplast (grana, plural)

Gravitropism | movement or growth with respect to the pull of gravity (toward or away from)

Ground meristem | the primary meristem that produces ground tissue, cortex, and pith. In the root, it also produces the endodermis (the innermost layer of the cortex).

Ground tissue | tissue produced by the ground meristem with no particular organizational structure, such as in the stems of monocots.

Guard cell | a parentheses-shaped parenchyma cell in the epidermis of a plant that regulates the opening and closing of a stoma, depending on water availability

gyn | female, woman

Gynoecium | the floral whorl composed of carpels

H

H+ | a hydrogen atom that is missing an electron. A hydrogen ion. A proton.

Haplodiplontic | a life cycle where there is a multicellular haploid phase and a multicellular diploid phase (also called alternation of generations or, occasionally, sporic meiosis)

Haploid | having one set of chromosomes (n)

Haplontic | a life cycle where the multicellular phase is haploid

Head (flower) | an inflorescence where florets are directly attached to the receptacle. There can be ray florets and/or disc florets present. Also called a capitulum.

Heartwood | secondary xylem that is no longer conducting water. Often darker in color and is located in the center of the stem.

Heliotropism | movement or growth with respect to the sun

Hesperidium | a modified berry with a leathery rind. Locules are filled with juicy trichomes. Ex. An orange.

hetero | other

Heterocyst | a form some cyanobacteria can take. Heterocysts are larger, round, thick-walled cells that can appear yellow and have two polar bodies, one on each end where they attach to other cells in the colony. These individuals are involved in nitrogen fixation and so cannot perform photosynthesis.

Heterosporous | producing two different spore types: microspores and megaspores

Heterotroph | an organism that consumes other organisms, living or dead, as a carbon source.

Holdfast | a structure at the base of brown algal thalli that attaches the thallus to a surface

homo | same

Homologous chromosomes | chromosomes from different parental origin that contain the same genes in the same order. For example, you have homologous copies of chromosome 1, one from each parent.

Homosporous | producing a single spore type that grows into a bisexual gametophyte

hydro | water

Hydrophyte | a plant adapted to aquatic environments (or high water levels)

hyper | over, above

Hypertonic | a solution with a higher ratio of dissolved solutes to water than the solution on the other side of a semipermeable membrane

Hypha | a walled, thread-like cellular structure that fungal body plans are composed of

hypo | under, below

Hypodermis | a layer or multiple layers of cells just under the epidermis

Hypothesis | a proposed explanation for a phenomenon that is both testable and falsifiable

Hypotonic | a solution with a lower ratio of dissolved solutes to water than the solution on the other side of a semipermeable membrane

I

Imperfect (flower) | a flower containing either an androecium or gynoecium, but not both

Incomplete (flower) | a flower missing at least one floral whorl

Indehiscent | a dry fruit that does not open on its own at maturity

Independent assortment | an event in meiosis that results in increased genetic diversity. During metaphase I, homologous chromosomes line up randomly on either side of the metaphase plate, resulting in different combinations of chromosomes in each meiotic event.

Independent variable | the variable in a scientific experiment that you change between treatment groups

Indusium | an umbrella-like structure in a fern sorus that protects the developing sporangia

Inflorescence | a compound flower composed of multiple florets

Inner bark | secondary phloem

Integument | the protective layer surrounding a developing ovule in seed plants. After fertilization, it becomes the seed coat.

Interfascicular cambium | cells in the pith rays that join with the fascicular cambium to form the vascular cambium in eudicots

Intermembrane space | the area between two membranes, such as between the inner and outer membranes in a mitochondrion

Internode | the region of the plant stem between nodes

Interphase | cells spend most of their time in this part of the cell cycle. It is broken into three distinct phases that prepare a cell for division.

iso | same

Isomorphic | sharing the same overall form

Isotonic | two solutions on either side of a semipermeable membrane that have the same ratio of dissolved solutes to water

K

karyo | seed (in biology, this term refers to the nucleus)

Karyogamy | fusion of two nuclei

Kinetochore | a region on the centromere of a chromosome where spindle fibers attach during cell division

Krebs cycle | see “citric acid cycle”

L

Lactic acid fermentation | a form of fermentation performed by animal cells and bacteria that converts pyruvate into lactate to replenish NAD+. H+ are produced as a byproduct, hence the name lactic acid.

Latex | a compound produced by some groups of plants that often serves a protective function. It can contain toxic compounds and/or gum up the mouthparts of insects

Leaf | a plant organ with lignified vascular tissue that emerges from a node in the position of the leaf, below the axillary bud (away from the growing tip of the branch)

Leaf axil | the area formed in the angle between the petiole of the leaf and the stem

Leaf primordium | the early developmental stage of a leaf

Leaf scar | the scar left behind on a stem where the leaf has fallen off or was removed

Legume | a dry fruit composed of a single carpel that splits open along two seams at maturity. This is the fruit of plants in the Fabaceae (bean family). Ex. A lupine pod or a peanut.

Lenticel | a tear in the periderm of woody plants that allows for the exchange of gases with the exterior environment

leuco | white or colorless

Leucoplast | a double-membraned organelle derived from bacterial endosymbiosis that does not contain pigment. Leucoplasts synthesize and store lipids or starch, such as in amyloplasts.

Lichen | a symbiotic relationship between a fungus and an alga and/or a cyanobacterium

Life cycle | a summary of the major events in a species’ development, including fertilization, growth, and reproduction

Lignin | a tough, complex polymer in the secondary walls of sclerenchyma cells. A primary component of wood, along with cellulose.

Link reaction | the transportation of pyruvate from the cytoplasm of the cell into the matrix of the mitochondrion. In the process, pyruvate is converted to acetyl-CoA.

Locule | a compartment of an angiosperm ovary representing one carpel

lyse | to break apart

M

Mannitol | a type of carbohydrate produced by fungi involved in lichen symbiosis

Matrix (mitochondrion) | the fluid-filled area enclosed by the inner membrane in a mitochondrion

Megagametophyte | a haploid, multicellular stage in heterosporous alternation of generations that produces eggs by mitosis

Megaphyll | a leaf with branching vascular tissue

Megaspore | a haploid cell produced via meiosis of the megasporocyte. This cell grows by mitosis into a megagametophyte.

Megasporocyte | a diploid cell produced by the sporophyte that will divide by meiosis to produce the megaspore(s) that grow into megagametophyte(s)

Megastrobilus | a structure on the sporophyte that produces the megagametophytes

Meiosis | a type of cell division that halves the number of chromosomes and results in 4 genetically distinct daughter cells. For example, one diploid cell could go through meiosis to produce 4 haploid cells. This type of division is used for sexual reproduction.

Meristem | a region of cells that divides by mitosis to produce new tissues

meso | middle

Mesocarp | the middle layer of the pericarp in a fruit. In a peach, the mesocarp is fleshy.

Mesophyll | the tissue in a leaf between the upper and lower epidermis that is not the vascular tissue

Mesophyte | a plant adapted to moderate environmental conditions

Metaphase | the stage in mitosis where chromosomes align in the center of the cell

Metaphase I | the stage in meiosis I where homologous chromosomes align across from each other in the center of the cell. The alignment is random, so each time meiosis occurs, there can be a different arrangement of chromosomes on either side. See “independent assortment”.

Metaphase II | the stage in meiosis II where chromosomes align in the center of the cell

Metaphase plate | a region in the center of a dividing cell, equidistant from the poles, where chromosomes line up

Microgametophyte | a haploid, multicellular stage in heterosporous alternation of generations that produces sperm by mitosis

Microphyll | a leaf with a single, unbranched vein of vascular tissue

Micropyle | a gap in the integument where the pollen drop is secreted and pollen grains (or tubes) can access the ovule

Microspore | a haploid cell produced via meiosis of the microsporocyte. This cell grows by mitosis into a microgametophyte.

Microsporocyte | a diploid cell produced by the sporophyte that will divide by meiosis to produce the microspore(s) that grow into microgametophyte(s)

Microstrobilus | a structure on the sporophyte that produces the microgametophytes

Middle lamella | a pectin-rich layer between plant cell walls

Middle lamella | a pectin-rich region between adjacent cells

Mitosis | a type of cell division that results in two identical daughter cells, both identical to each other and to the parent cell. This type of division is used for growth, repair, and asexual reproduction. Mitosis refers strictly to the division of the nucleus, while cytokinesis is the division of the rest of the cell contents.

Mitosporangium | a structure that produces spores by mitosis, such as in asexually reproducing *Rhizopus*

Mold | asexually reproducing mycelial fungus

mono | one, singular

Monocot | flowering plants that produce a single cotyledon

Monoecious | male and female reproductive structures are produced on the same plant

Monomer | a molecule that can bind to other molecules of the same type and form a polymer. A repeating subunit of a larger molecule.

Monoplastidic (cell) | a cell having only a single plastid, such as the single large chloroplast in the cells of Anthocerophyta

morph | form

Multicellular | an organism composed of multiple interacting cells

Multiple fruit | a single fruit that is composed of many florets from the same inflorescence. Ex. A pineapple.

Mutualism | a type of symbiosis in which both partners get a net benefit from the interaction.

Mycelium | the fungal body, composed of hyphal filaments

myco | fungus

Mycobiont | the fungal partner in a lichen

Mycorrhizal | a type of mutualistic relationship between plants and fungi. The fungus enters the plant through the roots and takes sugars from the plant. In exchange, the plant takes water and dissolved nutrients (particularly nitrogen and phosphorus) from the fungus.

N

NADH | a molecule that carries two high energy electrons from glycolysis or the citric acid cycle to the electron transport chain in cellular respiration

NADP+ reductase | reduces (adds electrons to) a molecule of NADP+ to create high-energy NADPH. The H+ is added to balance the negative charge from one of the added electrons.

NADPH | a molecule that carries two high energy electrons from the electron transport chain to the Calvin cycle in photosynthesis

Negative control | a group in your experiment that should show no change from initial conditions. If change occurs in the negative control, your experiment could have false positives.

Netted root system | a root system where there is no central, larger root. Most roots are relatively the same diameter.

Nitrogen fixation | the process of converting atmospheric nitrogen (N2) into bioavailable forms, such as ammonia (NH3). This process is carried out by certain bacteria using the enzyme nitrogenase and by the action of lighting ripping through the atmosphere, splitting molecules apart.

Node | the region on a stem where a leaf and axillary bud emerge. The axillary bud emerges on the side of the node closest to the growing tip of the stem.

Nonpolar | a type of covalent bond that is equally shared, resulting in no residual charges on the atoms. Nonpolar compounds “like” to interact with other nonpolar compounds.

Nucellus | the nutritive tissue provided by the megasporangium to the growing embryo in seed plants

Nuclear envelope | a double-membraned structure composed of phospholipids that encloses the genetic material of the cell

Nucleoid | a region in prokaryotes that contains all or most of the genetic material. A nucleoid is not surrounded by a membrane.

Nucleolus | a dense region within the nucleus that often appears as a dark dot. A single nucleus can contain several nucleoli. This region is where ribosomes are synthesized and contains a large amount of RNA.

Nucleus | a double-membrane bound organelle in eukaryotes that contains the organism’s genetic material. The nucleus is often referred to as the command center of the cell, both DNA replication and transcription occur within this organelle. In multicellular organisms, some eukaryotic cells may lack a nucleus at maturity, such as sclerenchyma.

Null hypothesis | an “anti-hypothesis” that predicts no relationship between the dependent and independent variables

Nut | a dry fruit with a stony pericarp encasing a single, large seed. Ex. An acorn.

O

Oogonium | a structure in heterokonts where the eggs are produced

Oospore | a thick-walled zygote produced in the oogonium of oomycetes

Operculum | a cap-like structure that covers the opening of the moss capsule until the spores are ready to be dispersed

Opposite (leaf arrangement) | two leaves emerge at a node

Organ | a collection of tissues working toward the same function, such as a leaf, stem or root

Osmosis | the diffusion of water across a semipermeable membrane

Ostiole | a small opening, such as at the top of a *Fucus* conceptacle

Outer bark | periderm or layers of periderm

ova | egg

Ovary | a structure that encloses the ovules in angiosperms and will develop into the pericarp when fertilized

Ovule | a structure in seed plants that contains the megagametophyte and will develop into a seed when fertilized

Ovuliferous scale | a cone scale in the megastrobilus of conifers where seeds develop

P

Palisade mesophyll | tissue in eudicot leaves that is composed of elongated cells that look like columns, full of chloroplasts photosynthesizing

Panicle | a branched raceme inflorescence

Parasitism | a type of symbiosis in which one partner gets a net benefit, while the other gets a net negative impact.

Parenchyma | cells with an even, thin primary wall and no secondary wall that are alive at functional maturity.

Passage cells | cells where the xylem is closest to the endodermis in the root where the Casparian strip forms last. This allows water to be transported into the xylem from root hairs.

Pedicel | the stem that attaches to a floret

Peduncle | the stem that attaches to a flower at the receptacle

Pennate | (a diatom) with bilateral symmetry

Pepo | a modified berry with a tough, rind-like exocarp. Ex. A pumpkin.

Peptidoglycan | a substance found in bacterial cell walls that consists of interlinked carbohydrates and polypeptides. Antibacterials like penicillin work by inhibiting the formation of peptidoglycan.

Perfect (flower) | a flower containing both an androecium and a gynoecium

Perforation plate | an opening at the end of a vessel element that allows for the passage of water and dissolved nutrients from cell to cell.

peri | around

Perianth | the outer whorls of a flower, composed of the calyx and corolla

Pericarp (fruits) | tissue that develops from the ovary wall in angiosperms and encloses the developing seeds. The pericarp is composed of the exocarp, mesocarp, and endocarp.

Pericarp (Rhodophyta) | the female gametophyte tissue that surrounds the carposporophyte in the cystocarp

Pericycle | a layer of meristematic tissue in the root, just inside the endodermis, that produces lateral roots and secondary meristems

Periderm | an exterior layer produced during secondary growth composed of phelloderm, cork cambium, and cork. Also called outer bark.

Peristome teeth | sheets of cells that look like papery teeth that interact with moisture in the air (hygroscopic movement) to help spores disperse from the capsule in some mosses

Perithecium | a microscopic, flask-shaped fruiting body produced by some ascomycetes

Petiole | the structure that attaches the leaf blade to the stem. Some plants lack petioles and these leaves are called sessile.

phaeo | dusky (often refers to organisms with golden brown hues)

Phagocytosis | to consume by engulfing. The process of engulfing creates a compartment called a phagosome, where acids or other digestive fluids can be secreted for breakdown of the engulfed material.

Phelloderm | large storage cells produced to the inside of the cork cambium in secondary growth

Phloem | the conducting tissue in plants that transports sugars produced during photosynthesis.

Phloem fibers | clusters of fibers located in the phloem that provide structural support (other phloem cells lack a secondary wall).

Phloem rays | parenchyma cells that connect the secondary phloem to the secondary xylem

phore | bearer of

photo | light

Photobiont | the photosynthetic partner in a lichen, such as green algae or cyanobacteria

Photon | a particle of light

Photorespiration | a process that occurs when RuBisCO binds to oxygen instead of CO_2; no glucose is made and energy is wasted in the process. This occurs when concentrations of CO_2 are low.

Photosynthesis | a cellular process that uses electromagnetic energy (sunlight) to assemble molecules of glucose from carbon dioxide. Water is used as an electron donor and oxygen is produced as a waste product (in oxygenic photosynthesis). Chemical formula: $6CO_2 + 6H_2O$ --(in the presence of sunlight)--> $C_6H_{12}O_6 + 6O_2$

Photosystems I & II | complexes containing chlorophyll, located in the thylakoid membrane, that absorb photons during photosynthesis.

Phototropism | movement or growth with respect to a light source

Phycobilins | polar pigments found in red algae and cyanobacteria

Phycocyanin | a blue phycobilin, more prominent in cyanobacteria

Phycoerythrin | a red phycobilin, more prominent in red algae

phyll | leaf

Phyllode | a modified petiole that is flattened to function like a leaf

Phylogeny | a hypothesis on the evolutionary relationships between organisms depicted as a branching tree diagram

phyte/phyto | plant

Phytoplankton | microscopic, photosynthesizing organisms in aquatic environments

Pilus | a projection from a prokaryotic cell that is used to interact with other cells. Pili, plural.

Pinnae | leaflets on a pinnately compound leaf (pinna, singular), such as a fern frond

Pit connection | a connection of the cytoplasm between adjacent cells formed due to incomplete cytokinesis. Found in Rhodophyta.

Pith | tissue produced by the ground meristem that is enclosed by vascular tissue

Placenta | a region of tissue in the ovary wall that supplies nutrition to the developing ovule and then seed through the funiculus

Planktonic | free-floating; wandering

plasm | living substance, tissue

Plasma membrane | a semi-permeable membrane composed of a phospholipid bilayer and a fluid mosaic of proteins, lipids, and associated carbohydrates that encloses the cytoplasm. In general, plasma membrane controls what enters and exits the cell. Nonpolar molecules like oxygen and carbon dioxide, and small molecules like water, can freely diffuse across. Molecules that are too large or too polar (charged) must be transported across.

Plasmid | a small loop of DNA that can be transmitted between organisms. Antibiotic resistance genes are often carried on plasmids.

Plasmodesma | a tube of plasma membrane that traverses the cell wall and middle lamella, connecting the cytoplasm of adjacent cells (plasmodesmata, plural).

Plasmogamy | fusion of the cytoplasm of two cellular structures

Ploidy | the number of sets of chromosomes an organism has

Pneumatophore | a root that has been modified to grow above ground and access oxygen for plants that live in flooded environments, e.g. mangroves

Polar | a type of covalent bond that is unequally shared, resulting in partial charges on the atoms. Polar compounds are partially charged and "like" to interact with other polar or ionic (charged) compounds.

Pollen | the microgametophyte of gymnosperms and angiosperms. Pollen grains deliver the sperm to the egg.

Pollen cone | see "microstrobilus"

Pollination | the successful transfer of pollen from one plant to another. This process is often mediated by insects, wind, or other vectors.

Pollination syndrome | a set of floral characteristics that have evolved in response to a particular pollinator

Pome | a fleshy fruit encased in a swollen hypanthium, the papery endocarp forms a "core". Ex. An apple.

Population | individuals of the same species living in the same environment at the same time

Positive control | a group in your experiment that should show normal/expected results. If no change occurs in the positive control, your experiment could have false negatives.

Prickle | a modified region of the epidermis that functions as a sharp armament for protection

Primary consumer | an organism that eats primary producers, often called herbivores.

Primary endosymbiosis | an evolutionary process by which, in this case, a photosynthetic cyanobacterium was engulfed by a heterotrophic ancestor of the red algae. The cyanobacterium was not digested and evolved into a double membrane chloroplast. This process also occurred with mitochondria.

Primary meristem | a region of cells produced by the apical meristem that divides to produce primary tissues

Primary phloem | phloem tissue produced by the procambium

Primary producer | an organism that uses some external, abiotic energy source, such as electromagnetic or chemical energy, to build organic molecules. Example: plants use energy derived from sunlight to molecules of glucose.

Primary tissue | a region of cells produced by a primary meristem that collaborate toward a shared function

Primary wall | a semi-rigid structure that surrounds the plasma membrane. All plant cells have a primary wall composed of cellulose.

Primary xylem | xylem tissue produced by the procambium

pro | before

Procambium | the primary meristem that produces the primary xylem and primary phloem. In the root, it also produces the pericycle.

Prokaryote | a unicellular organism that lacks a nucleus or membrane-bound organelles. The DNA in a prokaryote occurs as a single, circular chromosome. Prokaryotic cells are surrounded by a cell wall, though the composition can vary depending on whether it is a bacterium or an archaean.

Prop root | an adventitious root used to provide stability or to attach onto other organisms

Prophase | the first stage of mitosis, where the nuclear envelope and nucleoli break down, spindle fibers form, and chromatin condenses into chromosomes

Prophase I | the first stage of meiosis I, where the nuclear envelope and nucleoli break down, spindle fibers form, and chromatin condenses into chromosomes. Homologous chromosomes pair and crossing over occurs.

Prophase II | the first stage of meiosis II, similar to prophase of mitosis. In meiosis of a diploid cell, cells are haploid when prophase II begins.

Protoderm | the primary meristem that produces the epidermis

Pyrenoid | a dense region where carbon fixation happens within chloroplasts of many groups of algae and hornworts

Pyruvate | a three carbon compound formed from the breakdown of glucose during glycolysis

R

Raceme | an inflorescence where florets are attached to a central axis by pedicels

Rachis | the central stem in a pinnately compound leaf, where the leaflets attach

Radial symmetry | multiple lines of symmetry can be drawn

Random fertilization | reproductive propagules (such as eggs and sperm) are not individually selected by the parents for the production of offspring, but are paired on chance

Raphide | a needle-like crystal of calcium oxalate that forms in the tissues of certain plants

Receptacle | in flowers, the point where all of the whorls attach to the peduncle. In *Fucus*, the swollen ends of the thallus.

Residual procambium | procambial tissue (the primary meristem that forms the vascular tissue) remaining between the xylem and phloem of eudicot vascular bundles in primary growth

Resin | a sticky substance produced in some gymnosperms and angiosperms that works to seal wound damage and prevent infection and herbivory

Resin canal | a channel that runs through the tissues of some gymnosperms and angiosperms to secrete and transport resin

rhiz | root

Rhizoid | a root-like structure that lacks vascular tissue and has the function of anchorage

Rhizome | a modified stem that travels horizontally below ground, producing new shoots and adventitious roots at nodes, resulting in asexual reproduction of the shoot

Ribosomes | complexes of proteins and RNA that function as an enzyme. This enzyme reads RNA to build proteins during a process called translation. The ribosome forms a peptide bond between amino acids, releasing a water molecule in the process. This is why proteins are called polypeptides.

Root | a plant organ whose function is anchorage and water absorption. Roots have a specific sequence of development and organization of tissues that is different from stems and leaves.

Root apical meristem (RAM) | the meristem responsible for producing the primary meristems in the root. All cells in the root ultimately derive from this meristem.

Root cap | cells that are produced by the RAM to the outside of the root and sloughed off continually. These cells protect the growing tip, lubricate its journey through the soil, and interact with microbes in the vacinity of the root.

Root hair | a single epidermal cell that elongates to maximize surface area. Root hairs are only produced at the growing tips of the root system.

RuBisCO | Ribulose-1,5-bisphosphate carboxylase/oxygenase. This enzyme fixes CO2 during the Calvin cycle of photosynthesis. If CO2 concentrations are low, it may bind to oxygen instead, causing photorespiration.

S

S | phase - the stage of interphase where DNA is replicated

Samara | a winged achene. Ex. A maple helicopter is both a samara and a schizocarp.

sapro | death, decay

Saprobe | see “Decomposer”

Saprophyte | see “Decomposer”

Sapwood | secondary xylem that is still actively conducting water. Often lighter in color than the heartwood

Schizocarp | a fruit that breaks into multiple pieces (separate carpels) when mature

scler | hard, tough

Sclereid | a sclerenchyma cells that (generally) serves a protective function. In pears, these cells dominate unripened fruits, making them difficult to eat.

Sclerenchyma | a cell with a secondary wall that is dead at functional maturity

Secondary consumer | see “Consumer”

Secondary endosymbiosis | an evolutionary process by which, in this case, a red alga was engulfed by a heterotrophic oomycete. The red alga was not digested and evolved into a four membrane chloroplast. This type of endosymbiosis has occurred multiple times.

Secondary growth | the production of secondary tissues, resulting in lateral growth. Occurs in gymnosperms and some angiosperms

Secondary phloem | phloem tissue produced by the vascular cambium. Also called inner bark.

Secondary wall | a wall in plant cells that is formed within the primary wall. The secondary wall contains lignin, providing structural support, but its formation kills the cell eventually. This cell wall is present in sclerenchyma cells.

Secondary xylem | xylem tissue produced by the vascular cambium. Also called wood.

Seed | a structure produced by gymnosperms and angiosperms that houses the growing embryo and supplies nutrition via the nucellus and the megagametophyte.

Seed coat | the integument forms the seed coat after fertilization of the egg. This structure surrounds and protects the seed.

Seed cone | see “megastrobilus”

Septum | division; divider. For example, the cross walls between cells in hyphae.

Serpentine | a mineral that, when present in soils, results in low Ca:Mg ratios and often contains heavy metals

Seta | a stem-like structure that holds up the sporangium in the sporophytes of some bryophytes (setae, plural)

Sexual reproduction | production of offspring through the fusion of cells that were produced during meiosis

Shoot apical meristem (RAM) | the meristem responsible for producing the primary meristems in the shoot. All cells in the shoot ultimately derive from this meristem.

Sieve cell | a conducting cell in the xylem

Sieve tube element | a conducting cell in the xylem of angiosperms that lacks a nucleus

Simple pore | a hole in the epidermis that is not regulated by guard cells

Simple septation | in ascomycetes, the cross walls between cells have a hole in the center

Sister chromatid | one of two replicated, attached, identical chromosomes

som(e) | body

Sorus | a cluster of sporangia, such as on a fern frond (sori, plural)

Sperm | a gamete that fuses with an egg. Generally smaller than the egg and often with flagella.

Spermatangium | a structure that produces spermatia

Spermatium | the nonmotile male gametes of red algae. This term is also used to describe a stage in the life cycle of rust fungi.

Spike | an inflorescence where florets are sessile, attached directly to a central axis

Spindle | a network of microtubules that organizes and separates chromosomes during cell division

Spine | a leaf that has been modified into a sharp armament for protection

Splash cup | the head of a male gametophyte in mosses, where antheridia await raindrops to splash sperm out

Spongy mesophyll | tissue in eudicot leaves that is full of air pockets for gas exchange during photosynthesis, located below the palisade mesophyll

Sporangiophore | a structure that holds up sporangia (such as the T-shaped projections on Equisetum strobili)

Sporangium | a structure that produces spores

Spore | a propagule that grows by mitosis (it does not fuse with another propagule)

Sporophyll | a leaf where spores are produced

Sporophyte | the multicellular, diploid phase of the plant life cycle that produces spores by meiosis

Sporophyte dominant | a life cycle where the sporophyte is larger, longer-lived, and nutritionally independent from the gametophyte

Stamen | a floral structure composed of anthers and a filament

Standardized variables | variables in your experiment that are kept the same across all treatment groups and control groups

Stem | a plant organ with lignified vascular tissue that emerges from a node in the position of the axillary bud (toward the growing tip of the branch)

Sterigma | a projection from a basidium that the basidiospore sits atop in phylum Basidiomycota. Sterigmata, plural.

Stigma | the pollen receiving part of the carpel, located at the end of the style

Stipe | the stem-like structure in brown algae and fungi

Stipular spines | stipules modified as sharp armaments for a protective function

Stipules | paired appendages at the base of a leaf

Stolon | a stem that grows horizontally above ground, producing new shoots and adventitious roots at nodes, resulting in asexual reproduction of the shoot

Stoma | an opening in the epidermis of a plant that is flanked by two guard cells, allowing for regulated gas exchange with the exterior environment.

Stomatal crypt | a cavity in the lower epidermis of a leaf where stomata are located

Storage root | a root modified to store water or carbohydrates

Strobilus | a structure where gametophytes are produced in most SVPs and gymnosperms. The strobilus is composed of sporophylls (or similar structures) and sporangia.

Stroma | the fluid inside a chloroplast, much like the cytosol of a cell

Stromatolite | a formation created by the layering of photosynthetic bacteria, mucilage, and calcium carbonate. The first widely agreed upon evidence of life can be found in fossilized stromatolites.

Style | the structure that the pollen tube grows down to reach the ovary, located between the ovary and stigma

Suberin | a waxy lipid that forms the Casparian strip and is present in cork cells

Succulent | a plant or swollen tissue that stores water and can use this water for metabolic purposes during periods of drought

Sunken stoma | a stoma located in a depression in the epidermis to prevent water loss

Surface tension | a property caused by the attraction of partial charges between molecules in a liquid. This property minimizes surface area.

sym | shared

Symbiosis | when two or more organisms of different species live in close proximity to one another, sharing some aspect of their life cycle.

Synergids | two haploid cells that flank the egg in the embryo sac

synthesis | to form or put together

T

Taproot | a root system that has a larger central root with smaller lateral roots, such as a carrot or a turnip.

Telomere | the region at the end of a chromosomal arm

Telophase | the stage of mitosis where the chromosomes decondense into chromatin, the spindle breaks down, and the nuclear envelope and nucleoli reform. Cytokinesis happens during this stage of mitosis.

Telophase I | the stage of meiosis I where the chromosomes decondense into chromatin, the spindle breaks down, and the nuclear envelope and nucleoli reform. Cytokinesis happens during this stage of meiosis, resulting in two haploid cells.

Telophase II | the stage of meiosis II where the chromosomes decondense into chromatin, the spindle breaks down, and the nuclear envelope and nucleoli reform. Cytokinesis happens during this stage of meiosis, resulting in four haploid cells.

Tendril | a modified leaf or branch used for attachment and/or climbing

Terminal bud | the bud at the end of a stem where the next year's growth is formed

Terminal bud scale scars | scars left behind on a stem where the terminal bud scales have fallen off after the new tissue emerges. The distance between terminal bud scale scars indicates one year of growth (in a temperate climate).

Terminal bud scales | modified leaves (bracts) that cover and protect the developing terminal bud

Tertiary consumer | see "Consumer"

Tetrasporangium | a structure that produces tetraspores

Tetraspore | a haploid spore produced by meiosis in the red algae life cycle. Tetraspores develop into either male or female gametophytes.

Tetrasporophyte | the multicellular diploid that undergoes meiosis in the red algae life cycle

Thalloid | having a thallus for a body plan

Thallus | a body composed of undifferentiated tissues

Thigmotropism | movement or growth in response to touch

Thin layer chromatography | a process used to separate substances by polarity

Thorn | a stem modified as a sharp armament for protection

Thylakoid | a high surface area structure in chloroplasts with chlorophyll molecules in the membrane. This is where the electron transport chain of photosynthesis occurs.

Thylakoid space | the internal area of a thylakoid

Tissue | a collection of cells working toward the same function

Tonicity | the amount of dissolved solutes in the solution relative to another solution on the other side of a membrane. This can also be thought of as osmotic potential.

Tonoplast | the membrane that encloses the central vacuole in plant cells.

Tracheid | a long, narrow sclerenchyma cell in the xylem with tapered ends and bordered pits. These cells conduct water in the xylem tissue.

Tracheophytes | plants that have lignified vascular tissue. This group includes seedless vascular plants, gymnosperms, and angiosperms.

Transfusion tissue | tissue that surrounds the vascular bundles in some xerophytic leaves, located within the endodermis

Transpiration | the evaporation of water from plant tissues

Trap | a leaf that has been modified to capture organisms, most often insects, to digest for nutrients missing from the plant's environment

Treatment group | a group in your experiment where you have made some modification to the independent variable

trich | hair

Trichogyne | a slender tube that the spermatium travels through to get to the egg in the red algal life cycle

Trichome | a parenchyma cell that projects outward as a hair from the epidermis

troph | feeding

Trumpet hyphae | sugar-conducting cells present in some brown algae

Tube cell | the cell in pollen grains that grows the pollen tube to the ovule for the sperm to travel down

Tuber | an underground stem modified for storage that can produce new shoots from nodes called "eyes"

Turgid | the state of being filled to swollen, such as with plant cells

U

Umbel | an inflorescence where pedicels converge on a single point where they attach to the peduncle

uni | singular, one

Unicellular | an organism composed of a single cell. Unicellular organisms can be prokaryotic or eukaryotic.

Universal veil | some mushrooms start out covered by a material called a universal veil. As they grow, they break through this veil, often leaving remnants in areas of the mushroom.

Universal veil scales (warts) | remnants of the universal veil on the cap of a mushroom

V

Vascular cambium | the secondary meristem that makes the secondary xylem to the inside and secondary phloem to the outside

Vascular cylinder | when the vascular tissue forms a ring that divides the ground tissue into two distinct regions. This is present in monocot roots and eudicot stems.

Vascular tissue | composed of xylem tissue that conducts water and dissolved nutrients, and phloem tissue that conducts photosynthates

Vegetative | a cell, organ, or life stage of an organism that is not actively involved in reproduction. When referring to cyanobacteria, the vegetative cells are the individuals that are performing photosynthesis for the colony. For *Spirogyra*, the vegetative cells are those that are not undergoing sexual reproduction to form a zygote. In plants, vegetative parts (you might call them vegetables) are anything that is not a fruit or flower.

Vessel element | a wide sclerenchyma cell in the xylem with perforation plates at each end. These cells conduct water in the xylem tissue of angiosperms and gnetophytes.

Volva | remnants of the universal veil at the base of a mushroom

W

Whorled (leaf arrangement) | three or more leaves emerge at a node

X

xanth | yellow

xero/xeric | dry

Xerophyte | a plant adapted to dry environmental conditions

Xerophytic leaf | a leaf that has specifically adapted to dry conditions

Xylem | the lignified, water conducting tissue in a plant

Xylem rays | sheets of parenchyma cells that traverse the secondary xylem

Y

Yeast | a unicellular fungus

Z

Zone of division | a region in the growing root tip where the RAM and primary meristems are located. Generally, this zone ends around where the root cap stops.

Zone of elongation | a region in the growing root tip where cells exit the cell cycle and begin to get larger

Zone of maturation | a region in the growing root tip where cells differentiate into specialized cells or tissues

zoo | animal

Zoosporangium | a structure that produces zoospores

Zoospore | swimming spore (has at least one flagellum)

zygo | can mean yoke-shaped, paired, or joined

Zygomorphic | see “bilateral symmetry”

Zygosporangium | a large, ornamented structure where both fertilization and meiosis occur in some lineages of early fungi (formerly classified as the Zygomycota)

Zygote | the first diploid cell in an organism’s life cycle

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