An excerpt from

BOTANY READINGS

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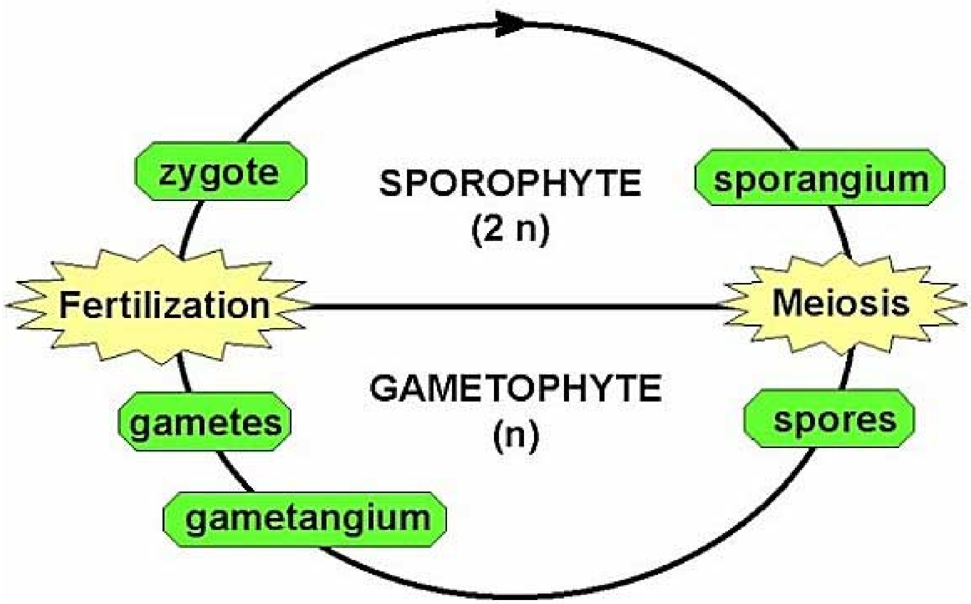
https://botany4u.neocities.org/readings/

How Do Plants Differ?

To summarize the sequence of the major events in the life histories of plants, we can use the stylized diagram that is below the following terms.

- **sporophyte**: diploid plant that produces spores through meiosis
- **sporangium (-a)**: structure on a plant where meiosis occurs and spores are produced
- **spore**: haploid meiotic product in plants, the first cell in the gametophytic generation of plants
- **gametophyte**: haploid plant that develops from a spore, produces gametes
- **gametangium (-a)**: structure on a gametophyte that produces gametes
- **antheridium (-a)**: gametangium that produces male gametes (sperm)
- **archegonium (-a)**: gametangium that produces female gametes (eggs)
- **meiosis**: division that produces cells with nuclei with the haploid chromosome number from a diploid cell
- **fertilization**: the fusion of gametes and their nuclei to form a zygote
- **zygote**: a fertilized egg, the first cell in the sporophytic generation of plants



This diagram is generally considered to depict the "life cycle" of a plant. By using the term "life cycle," we are looking at how a plant starts out at one point, such as the zygote, and goes through a developmental sequence that eventually gets the plant to a stage where it contributes to the formation of new plants that are at the same stage of development from which the original plant started.

Using the pea plant as an example, it started when an egg was fertilized by a sperm to form the diploid zygote. The zygote divided mitotically to form two cells; those two cells divided to form four cells; those four divided to form eight, and so on and so forth until we could see a multicellular plant that we recognize as a pea plant with roots, stem, leaves, and flowers. This is the sporophyte, with each cell containing the **2n** number of chromosomes. For the pea this is 14. We will look at the next things that happen in more detail in the reading about the flowering plants, but for now we want to note that in the flowers are the sporangia. The sporangia contain cells that go through meiosis to produce spores. The spores develop into microscopic, haploid plants, the gametophytes. The gametophytes produce the eggs and sperm, which will fuse to form a new zygote. We have just completed the life cycle of a pea plant!

The following readings about plants include details of the life cycles of the major groups of plants. As you go through the readings and see how sexual reproduction is similar, yet different, for the different groups, you hopefully will gain a better understanding of the importance of well-known plant structures such as flowers

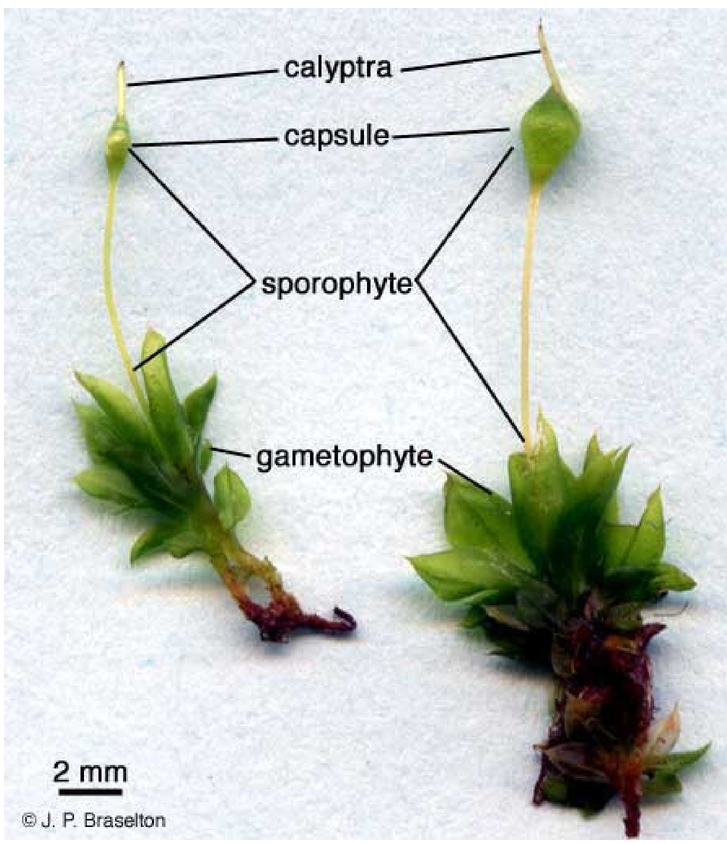
Bryophytes

The bryophytes are plants that do not have vascular tissues (xylem and phloem). Bryophytes are small plants, generally only several centimeters in height. Also, they usually grow only in moist areas. The major groups within the bryophytes are the **mosses**, **liverworts**, and **hornworts**. Since mosses are the most common bryophytes, and you probably already have come in contact with mosses, we use mosses as our example for bryophytes in general.

The dominant phase of the life cycle is the **gametophyte**—viz., the part of the life cycle we see the most is the gametophyte. The gametophyte is haploid (i.e., has the n number of chromosomes) and produces the gametes. In the case of most mosses, one individual gametophyte will produce only male gametes, sperm. Another individual will produce only female gametes, eggs. Each female moss gametophyte will have a structure, the **archegonium**, in which an egg is produced. Each male moss gametophyte will have some **antheridia**, the structures in which sperm are produced. Archegonia and antheridia collectively are termed **gametangia**. The female gametangium is the archegonium; the male gametangium is the antheridium.

Fine, greenish or light reddish-brown, filamentous structures, approximately 1-5 centimeters in length, stick out of some of the gametophytes. They are the **sporophytes** growing out of the gametophytes.

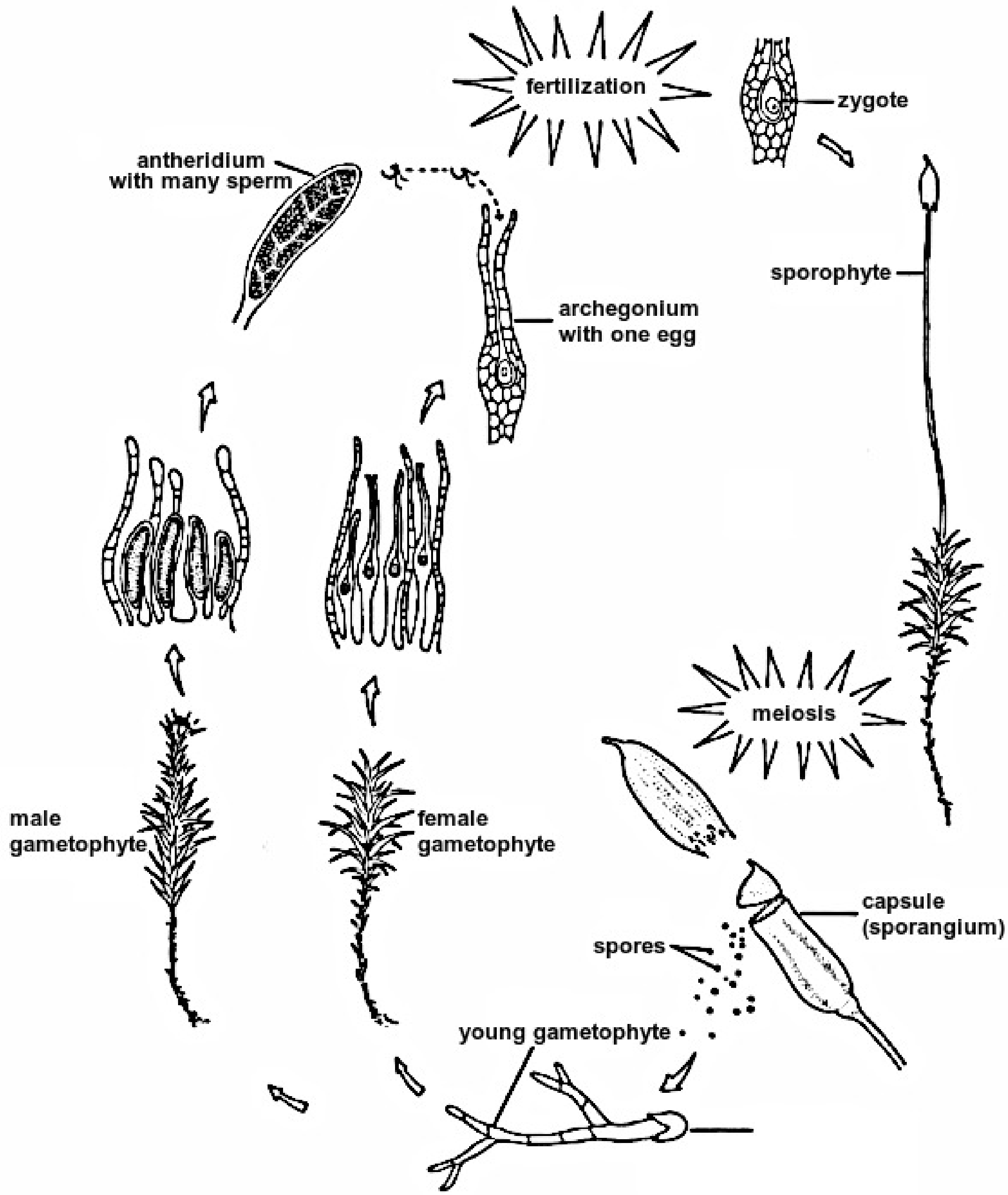
Swellings at the tips of the sporophytes are **sporangia**, the **capsules**. A cap covering the capsule is the remnant of the archegonium and known as the **calyptra**. The sporophytes of mosses are less noticeable than the gametophytes. Also, they are dependent on the gametophyte for much of their nutrition.



Meiosis in the sporangium produces spores, the first cells in the haploid (**n**) phase of the life cycle. Spores germinate and develop into gametophytes. Some gametophytes have antheridia that produce sperm; other gametophytes have archegonia that produce eggs. Sperm swim from the antheridium of one gametophyte to the archegonium of another gametophyte and fertilize the egg. The fertilized egg is the **zygote**, the first cell in the diploid (**2n**) phase of the life cycle. The zygote divides and after a series of cell divisions develops into the mature sporophyte which remains attached to the gametophyte. A sporangium (capsule) develops at the tip of the sporophyte, meiosis occurs and spores are produced.

Note that there is only one type of spore produced in the sporangium. The term for this is **homospory**. Mosses, therefore, are **homosporous**.

Life Cycle of a Moss



Pteridophytes: Ferns

Pteridophytes are a large group of plants that have vascular tissue but do not produce seeds. The most common pteridophytes are the ferns, so we use ferns in this set of readings as our only example of a pteridophyte—the non-seed vascular plants.

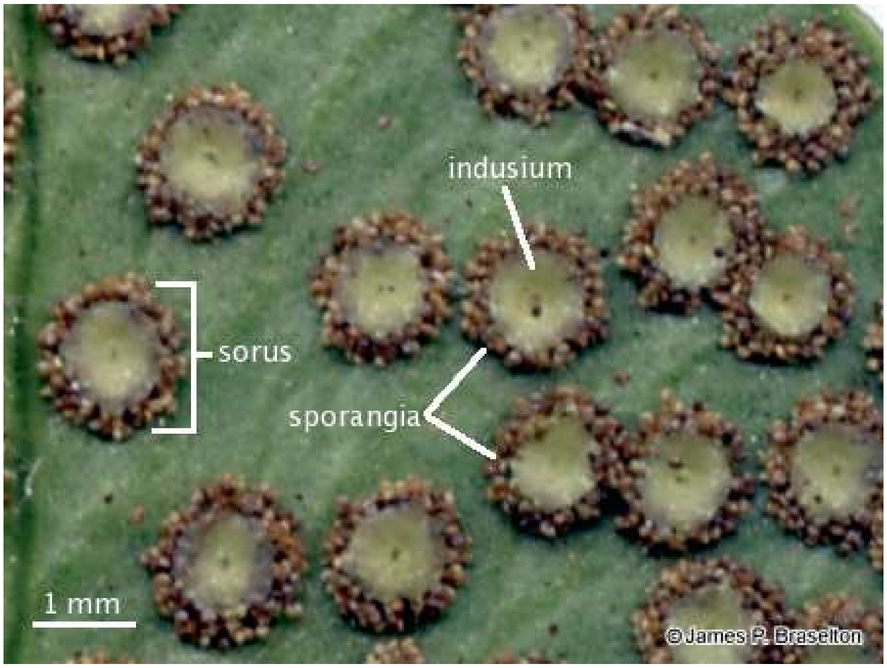
Ferns are beautiful plants recognized mostly by their graceful leaves. The leaves botanically are referred to as **fronds**. The veins of the fronds are vascular bundles, hence ferns are classified in the vascular plants. The fronds are part of the sporophyte, each cell, therefore, is diploid (**2n**).

Many ferns spread by horizontal underground stems, the **rhizomes**. At the nodes of rhizomes fronds grow up; roots grow down from the nodes. Young fronds are shaped like a shepherd's crook or **crosier**, and, therefore, are called crosiers. Another term often applied to crosiers is **fiddlehead**.

Sporophytes produce spores through the process of meiosis within sporangia. The little dots on the underside of fern fronds are collections of sporangia—the collections are known as **sori** (**sorus** is the singular). Sori may be circular, oblong, or linear, depending on the species of fern.

Sori on the undersides of leaflets of fern leaves (fronds). Mature sori on the left (large arrow); very young sori on the right (small arrow).

The shapes of the sori are characteristics used by many botanists to classify ferns. In some ferns, each sorus has a little cap known as the indusium.



Higher magnification of sori on the underside of leaflet of fern leaf (frond). This species of fern has indusia. Sporangia can be seen sticking out from under the indusium of each sorus.

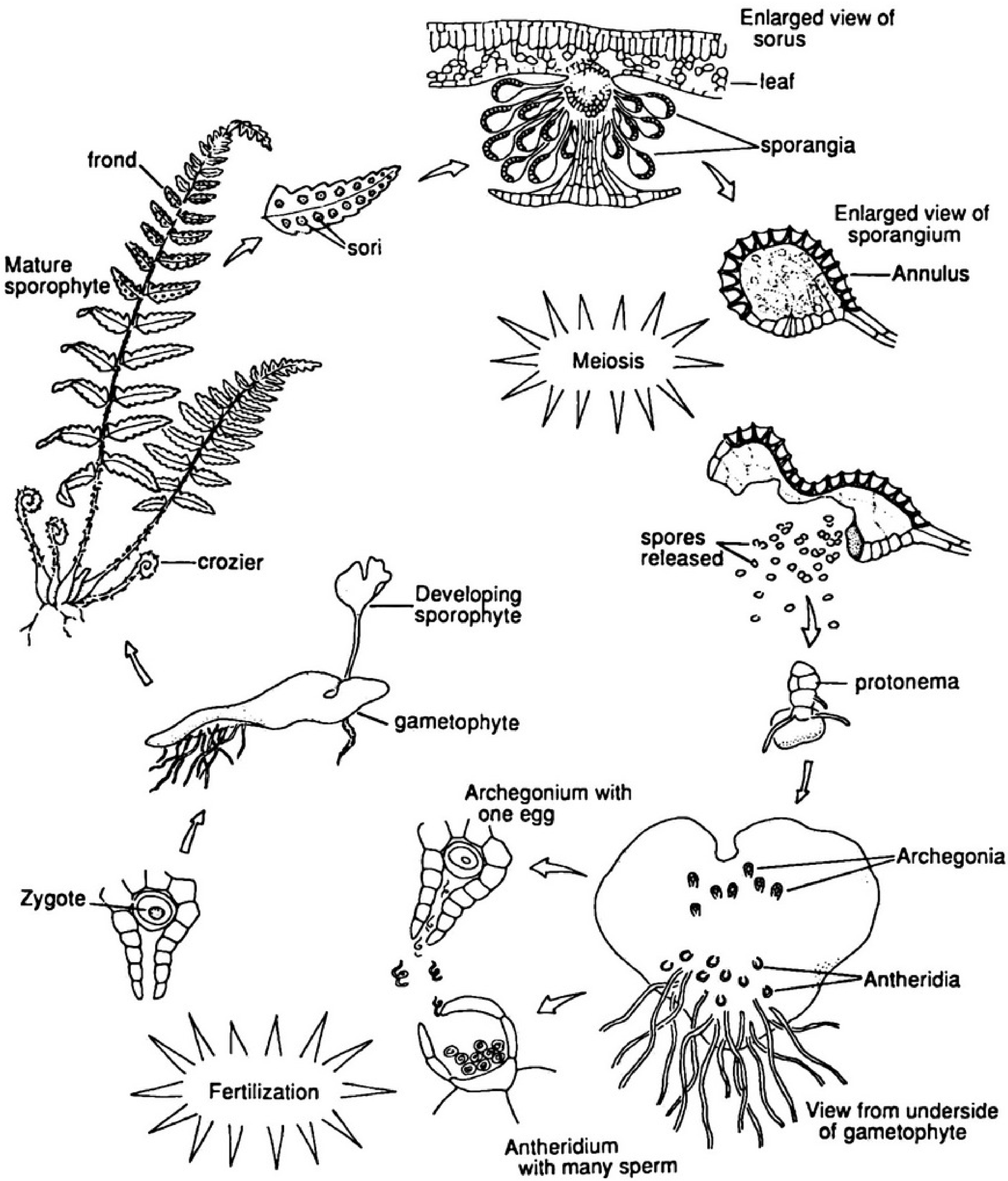
Meiosis occurs in each sporangium within the sorus, producing haploid (n) spores. Only one type of spore is produced in fern sporangia. Ferns, like mosses, are **homosporous**. Each sporangium has a group of specialized cells, the **annulus**, that straighten out at maturity and rip apart the sporangium. When this occurs spores are released into the air.

Each spore that lands on a suitable, moist site germinates. First a filamentous structure, the **protonema**, is formed. The protonema is the immature gametophyte. As the protonema develops into the mature gametophyte (**prothallus**), it becomes heart-shaped. Note that the fern gametophyte is green (i.e., photosynthetic) and free-living from the sporophyte. It is also much smaller than the sporophyte. A typical fern gametophyte is about the size of a fingernail. Each cell of the gametophyte is haploid (n).

On the underside of a mature fern gametophyte are the sperm-producing **antheridia** and egg-producing **archegonia**. Sperm swim from the antheridia to the archegonia. One sperm swims up the neck of an archegonium and fuses with the egg to form the diploid **zygote**, the first cell in the sporophytic generation.

The zygote divides, and after a series of cell divisions the young sporophyte can be seen growing from the gametophyte. The young fern sporophyte is not dependent on the gametophyte. Instead, the fern sporophyte gets larger than the gametophyte, eventually obscuring or crushing it. The sporophyte grows at the apical meristem of the stem.

Life Cycle of a Fern



Gymnosperms

Gymnosperms are one of the two groups of seed plants. The flowering plants (angiosperms), are the other. In going from mosses and ferns to the seed plants, we see a very significant difference in plant life cycles. In mosses and ferns the propagating units for new individuals are spores. In the seed plants, gymnosperms and angiosperms, the propagating units for new individuals are seeds. Spores are single, haploid cells, and develop into gametophytes. Seeds, in contrast, are complex structures that contain an immature sporophyte, the embryo.

The remainder of this reading is concerned with how a seed is formed. Although seeds of gymnosperms and angiosperms have similarities, this and the reading for angiosperms make several important distinctions between seeds of gymnosperms and angiosperms. A major difference between gymnosperms and angiosperms is how the seeds are attached to the plant. Seeds of gymnosperms are not enclosed; instead, they are open to the surrounding environment. This type of unprotected seed is a **naked seed**. The name gymnosperm means "naked seed." In contrast, seeds of angiosperms are enclosed in a special structure that at maturity is called the fruit.

There are going to be more new terms for you to learn as development of seeds of gymnosperms and angiosperms is considered. Be patient and try not to get bogged down with the new terminology. An important point to keep in mind is that you already know the basic stages in the life cycles of gymnosperms and angiosperms. Look back at readings for bryophytes and ferns, draw a circle, and fill in the words **gametes**, **sperm**, **egg**, **fertilization**, **zygote**, **sporophyte**, **sporangium**, **meiosis**, **spores**, **gametophyte**, **antheridium** and **archegonium**.

Gymnosperms are a diverse group of plants, one group of which has cones involved in reproduction. The cone-producers, botanically called **conifers**, are the gymnosperms most commonly seen. Pines, spruces, and firs are conifers. Since you probably are most familiar with pines, we use them for our example of a gymnosperm life cycle.

The pine tree that you and I recognize as a pine tree is the sporophyte. The sporangia of conifers are contained in special structures, the **strobili** (**cones**). Upon close examination of a pine tree, we see that there are two types of strobili: 1) the large woody strobilus that most people call a "pine cone"; and 2) a much smaller, delicate, yellow strobilus. Each type of strobilus produces its own type of spore; there are two types of spores produced by conifers.

This condition where two types of spores are produced is referred to as **heterospory** as opposed to **homospory** as occurs in mosses and ferns. Gymnosperms, therefore, as exemplified by pine trees, are **heterosporous**. A major distinction we can make between seed plants (gymnosperms and angiosperms) and the non-seed plants (mosses and ferns) is that seed plants are heterosporous and non-seed plants are homosporous. Back to the example of a gymnosperm, the pine tree.

The smaller strobili of a pine tree occur in clusters at the tips of branches. The smaller strobili properly are called staminate strobili, but many people, including botanists, often refer to them as "male cones" or "male strobili." Think of each male strobilus as a very shortened branch, and each scale-like leaf with two sacs attached to the underside. The sacs are the sporangia. Within each sporangium meiosis occurs in many cells; many haploid spores are produced.

A cluster of male strobili (cones) of pine at the tip of a branch in early spring prior to the release of pollen.

The spores produced in the sporangia of the male strobili are smaller than the spores produced in the larger strobili. The smaller spores are called **microspores**. Each microspore develops into a gametophyte that itself is very small. The small gametophyte is called the **microgametophyte**. Microgametophytes also are called **pollen**. Each pollen at maturity consists of only a few cells. Two cells are the sperm. Note that each cell of the microgametophyte, including the two sperm, is haploid. Also, there is no antheridium in which the sperm are produced.

In the spring, pine trees produce millions of pollen grains. If you are one of those unfortunate individuals who is allergic to pine pollen, you will sneeze a lot when pollen is being released from sporangia in male cones. If you have a pine tree near your house, you will dust up a lot of yellow dust, the pine pollen, from your furniture.

The larger strobilus of the pine tree is what most people think of as a pine cone, sometimes referring to it as the "female cone" or "female strobilus." In the female cone is a structure, the **ovule**, that contains the megasporangium. If you think of a pine cone as a shortened branch, each scale-like leaf contains two ovules on the topside of the leaf. The integument of the ovule protects the megasporangium. An opening in the integument, the **micropyle**. A space between the micropyle and the megasporangium is called the **pollen chamber**. Both micropyle and pollen chamber have important roles in the pine life cycle.

Only one cell in each **megasporangium** goes through meiosis. In addition, only one haploid **megaspore** is produced by meiosis in each megasporangium. The single megaspore develops into a multicellular **megagametophyte**. Within the megagametophyte are several **archegonia**, each with an **egg**. Note that all of this development has occurred within the ovule sitting on the leaf-like scale in a pine cone.

To complete the life cycle, a sperm will fuse with an egg to form a zygote, the first cell in the diploid, sporophytic generation. For this to eventually happen, the first step is for the pollen to float through the air and land on top of a scale in the female cone. The transfer of pollen from the male cone to the female cone is **pollination**. When an ovule is receptive, a drop of sticky fluid is produced and fills the pollen chamber; some fluid exudes through the micropyle. Pollen sticks in the fluid exuding from the micropyle. As the fluid dries, it and the stuck pollen are drawn in through the micropyle. The micropyle grows shut, entrapping pollen in the pollen chamber.

The pollen germinates and a tube digests through the megasporangium and into the megagametophyte. Eventually the pollen tube grows close to an archegonium and ruptures, releasing a sperm into the egg. The fused sperm and egg is the diploid **zygote**, the first cell in the sporophytic phase of the life cycle.

Remember that all of this has been happening inside the ovule! The zygote goes through cellular division, and after many divisions an immature sporophyte is developed within the ovule and is surrounded by the megagametophyte. The immature sporophyte is an **embryo**. While this is happening the outermost layer of the ovule, the integument, develops into the seed coat. We now have a mature pine seed.

A seed is a matured ovule. In this example of a gymnosperm, the pine, the matured ovule consists of a **seed coat, megagametophyte, and embryo**. This is a very complex structure if you pause to think about it. The seed coat is diploid tissue from the original parent sporophyte. The megagametophyte is a haploid plant that developed from a megaspore produced by the original sporophyte. The embryo is a new diploid sporophyte. Looking at it another way, a pine seed really is a combination of three different plants.

Female strobili (cones) of pine: the one on the left a young cone several weeks after pollination, the cone on the right a year after pollination.

A mature female pine cone is woody. The scales separate and the seeds drop off the scales. Most pine cones you pick up during a walk in the woods already have released their seeds. But if you look carefully at the topside of one of the scales you can see two oblong indentations where the ovules (seeds) were attached. To see younger stages of pine cones, look on the tree. Since it takes two years for a cone to develop to maturity, you often can find pine cones of different stages of development on the same tree. If you want to see what a pine seed looks like, or even taste one, go to a fine food store and buy a jar of "pine nuts" —they are pine seeds.

Female strobili (cones) of pine: the one on the left a young cone a year after pollination, the right a mature cone that has opened and released the seeds.

Upon germination of the seed, the young sporophyte begins to grow. It may take several to many years before the new sporophyte has matured enough to produce cones, thus completing the life cycle.

In summary of the gymnosperm life cycle as exemplified by pines, gymnosperms are heterosporous vascular plants with naked seeds. Microspores are produced by meiosis in male strobili and develop into pollen (microgametophytes). Megaspores are produced within ovules in female cones and develop into megagametophytes. The matured ovule (seed) consists of a seed coat, megagametophyte, and embryo.

The Flowering Plants

The flowering plants (*aka* angiosperms) are the most common plants on earth at the present time. For this reason most people think of flowering plants when they think of plants in general.

Oak trees and maple trees are flowering plants. Likewise, the grasses are flowering plants even though their flowers are not as showy as those of the great white *Trillium*, the red bud tree, or the wild crabapple. Some plants have flowers with all the parts (pistil, stamens, petals, and sepals), i.e., the flowers are complete. Other plants have flowers with just pistils, petals and sepals on one individual (imperfect flowers); and flowers with just stamens, petals and sepals on other individuals (also imperfect flowers). Some flowering plants, the annual herbs, take only one growing season to complete their life cycle (go from seed-to-seed). Others such as the oak trees take many years.

There is no one angiosperm that would serve as an example that could represent the entire group. So this discussion of the life cycle we use an idealized plant, one that in principle represents the major features of the group.

The flowering plants that we observe day-in-and-day-out are the sporophytic phase of the life cycle. The two main structures involved in the life cycle and seed formation are the stamens and pistil. Angiosperms, like gymnosperms, are heterosporous, producing two types of spores.

Meiosis within many cells within the anther of the stamens produces many microspores. Microspores are haploid and develop into microgametophytes. Microgametophytes also are called pollen. Up to now in general terms the development of pollen in flowering plants is similar to pollen development of gymnosperms. But pollen of angiosperms is much simpler at maturity than gymnosperm pollen. A mature angiosperm pollen grain consists of three cells: A large cell called the tube cell contains within it two smaller cells, the sperm.

At maturity, the anther splits and pollen is released. Depending on the plant, pollen is then transferred to the pistil either by wind or an animal such as an insect or bird. The transfer of pollen from anther to pistil is pollination.

The pistil consists of stigma, style, and ovary. Pollen lands on the stigma portion of the pistil. We leave the pollen sitting on the stigma and concentrate for the moment on the ovary.

Within the ovary are ovules. This is an important difference between gymnosperms and angiosperms: ovules of angiosperms are enclosed within an ovary! The number of ovules within an ovary varies with species. We are going to jump ahead just a little: the ovary will develop into a fruit; ovules develop into seeds. Think of some fruits and the seed inside and you should get the idea of how ovules are arranged within ovaries. A peach has one seed; only one ovule was within the ovary. A watermelon has many seeds; many ovules were within the ovary. More about fruits later. Let's get back to development within the ovule and how an ovule develops into a seed.

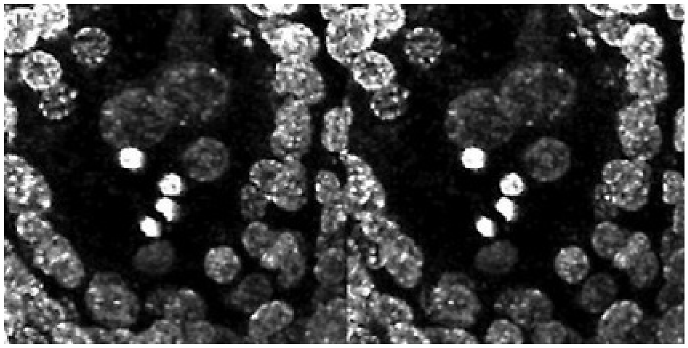
The outer layer of the ovule is the integument. There is an opening at one end of the integument, the micropyle. The interior of the ovule is the megasporangium which contains one cell that goes through meiosis. Only one haploid megaspore results from meiosis.

The megaspore develops into a megagametophyte. There is a big difference, however, between megagametophytes of gymnosperms and angiosperms. The mature megagametophyte of angiosperms is called the embryo sac and consists of seven cells with a total of eight nuclei. The large, central cell contains two nuclei, the polar nuclei. At the micropylar end of the embryo sac is the egg nestled between two cells. Some botanists consider the two cells adjacent to the egg as a very small archegonium.

Remember the pollen we left sitting on top of the stigma? While we were watching the megaspore develop into the embryo sac the pollen germinated. A pollen tube started growing down through the stigma and style, and through the ovary wall. As the tip of the pollen tube grew through the stigma, style, and ovary, the two sperm were carried right behind the growing tip of the pollen tube. We now have found the pollen tube growing right up into the micropyle.

A lot of exciting things happen! First, the pollen tube ruptures. As this occurs the two sperm are discharged into one of the cells next to the egg. One sperm passes through this cell and fuses with the egg and the diploid zygote is formed. We knew that would happen. But the other sperm also passes through the cell and goes into the large central cell. Here the second sperm fuses with the two polar nuclei! This fusion product contains three nuclei, hence three sets of chromosomes. The second fertilization forms a triploid (**3n**) nucleus called the primary endosperm nucleus. More about the primary endosperm nucleus in a little while.

First let's review what has just happened. One sperm fused with the egg to form the zygote. The second sperm fused with the polar nuclei to form the primary endosperm nucleus. We now have seen something that is unique to flowering plants: **double fertilization**.



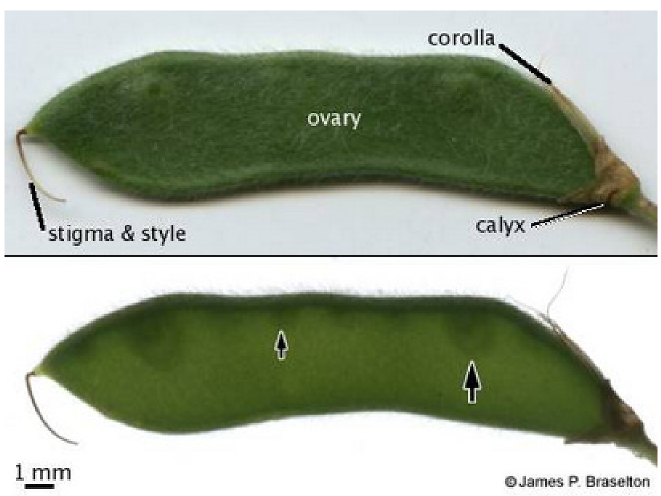
Stereo pair of intact ovule showing the moment of double fertilization in potato. One sperm nucleus is near the two polar nuclei and the other sperm nucleus near the egg nucleus. The other two bright objects are known as "x-bodies," one the remnants of the vegetative (tube) nucleus and the other the nucleus of the degenerated cell that the pollen tube entered.

The confocal scanning laser microscopy images are presented so that the two side-by-side images form a stereo pair for viewing with a standard stereo viewer or map-reading device, or by relaxing and crossing your eyes until the right and left images of each pair fuse into one.

Reference: Braselton, J. P., M. J. Wilkinson, & S. A. Clulow. 1996. Feulgen staining of intact plant tissues for confocal microscopy. Biotech. & Histochem. 71: 84-87.

A seed is a matured ovule. The integument of the ovule develops into the seed coat. The zygote develops into an immature sporophyte, the embryo. The primary endosperm nucleus divides and after many divisions fills the seed around the embryo with a triploid tissue called the endosperm. The mature angiosperm seed consists of old sporophyte (seed coat), a new sporophyte (embryo), and another product of fertilization, the endosperm.

Recall that the ovule is contained within an ovary. While the ovule is maturing, so is the ovary. The ovary matures into a fruit.



Two views of a fruit (legume) of Scotchbroom. In the upper photo, remnants of all floral parts are present. In the lower photo which had strong light shining through the fruit, the unfertilized ovules are small (small arrow) whereas the fertilized ovules (large arrow) will matured into seeds.

We essentially have completed the life cycle of an angiosperm. If the seed is put in the right environment it will germinate. If it is the seed for an annual plant, the seedling will rapidly develop into a mature plant that will flower and produce seeds and fruit within one growing season. Examples of annuals are beans, peas, and corn. Seeds of biennial plants germinate and grow into a fairly mature plant the first year; the plant will not flower and form fruits and seeds, however, until the second year. If the seed is of a perennial plant, the seedling will develop into a larger plant that may take many years to mature before it flowers and produces seeds and fruits.

Monocots and Dicots

Let us now turn our attention to some basic variations in seed structure of angiosperms. In other readings the terms monocot and dicot were used to distinguish between the two major groups of flowering plants. Several differences in flower structure, stem structure, and leaf structure have been mentioned. What ultimately distinguishes monocots from dicots, however, is structure of the embryo within the seed.

An embryo is a miniature plant, consisting mainly of an axis with an embryonic shoot and embryonic root. Near the junction of the embryonic root and shoot is attached a leaf-like structure that is called either a seed leaf or cotyledon. Embryos in seeds of monocots have only one cotyledon, hence the designation monocotyledon (one cotyledon). All the flowering plants with seeds that have embryos with a single cotyledon are placed in the Class Monocotyledonae. Another term for the single cotyledon is scutellum.

Two cotyledons are attached to the embryo in the dicots. All the flowering plants with embryos with two cotyledons are placed in the Class Dicotyledonae.

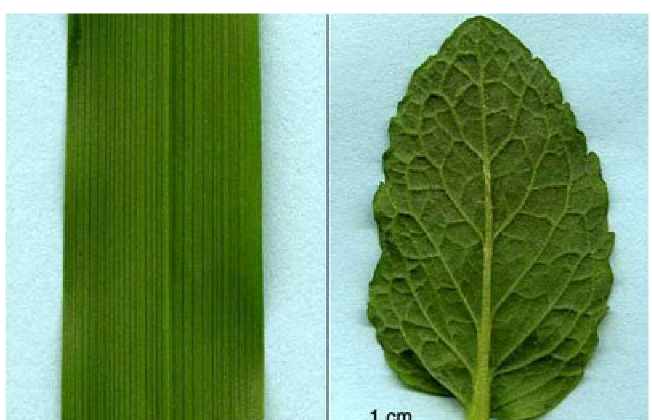
Another major difference generally occurs between seeds of dicots and monocots, but it is not a definitive characteristic. Monocot seeds generally have endosperm present at maturity. The endosperm serves as a food source for the embryo when it starts to grow during germination of the seed. Dicot seeds generally do not have endosperm present. Instead, food from the endosperm was transported into and stored within the two cotyledons during maturation of the seed. The two cotyledons take up most of the bulk of the dicot seed. As the embryo starts to grow upon germination of the seed, food stored in the cotyledons is used for the initial source of energy for the young plant.

In addition to seed structure, there are four other differences between monocots and dicots. (Keep in mind that the definitive difference between the two groups is the number of cotyledons attached to the embryo.)

- Flowers of monocots generally have the parts in threes or groups of three. For example, a monocot flower may have three sepals, three petals, six stamens, and a pistil with three chambers. Flowers of dicots generally have the parts in fours or fives, or multiples of four or five.

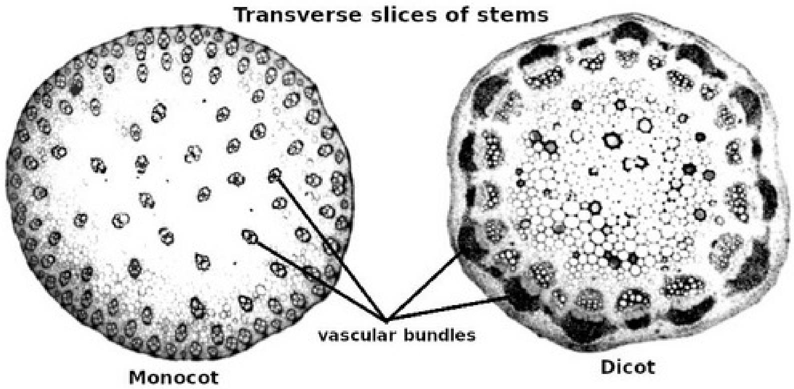
Monocot vs. dicot flowers: left is spiderwort, a monocot; right is phlox. a dicot.

- Leaves of monocots generally have parallel venation whereas leaves of dicots generally have netted venation.



Monocot vs. dicot leaves: left is daylily, a monocot; right is mint, a dicot.

- When viewed in cross section, vascular bundles in primary growth of stems of dicots occur in a ring between the pith to the interior and the cortex to the exterior. Vascular bundles in monocots generally are scattered throughout the stem.



- Dicots that have secondary growth do so with a vascular cambium. Monocots generally do not have secondary growth and hence do not have vascular cambium.