

Evolution of Plants

What is a plant? It's really the simple questions in biology that are the most difficult to answer. You might reply plants contain chlorophyll and undergo photosynthesis. That's true for most plants but there are several which do not contain chlorophyll; they are parasitic on other plants. You might say all are eukaryotic in their cellular makeup but plants share this characteristics with protists, fungi, and animals. You might say plants contain cellulose. However, many protists have cellulose, some fungi do and even humans have some cellulose associated with their skin. So you see, it's not easy to define plants. However, here's a stab at it. **Plants are multicellular, eukaryotic organisms which typically are autotrophic and have cell walls composed of cellulose.**

Most plants are terrestrial, but many are aquatic in characteristics, a throw-back from the time all organisms had some aquatic existence. Some plants moved from the aquatic environment early on and then moved on to the land only to return later to an aquatic environment.

The move to a terrestrial existence proved to be as difficult for plants as it did for animals. The terrestrial environment is a harsh environment with many extremes: temperature, moisture, oxygen concentration, and others. Plants had to cope with these problems. To prevent drying out, they evolved a waxy cuticle to protect them from desiccation (as well as protection from bacteria, insects, and fungi). To allow for gas exchange, plant evolved stomata. To support themselves, plants produced cell walls which often become lignified (strengthened). Different forms of storage products evolved as well.

Alternation of Generations

Plants, like animals, go through a cycle of generations based on mitotic and meiotic divisions. This is based on whether their stage of growth (as opposed to their reproductive stages) is diploid ($2n$) or haploid (n). In most higher plants, the plant body is diploid. The only haploid part of the cycle occurs when meiosis takes place to produce sperm or eggs. Therefore, the life cycle alternates from haploid (sperm and eggs) to diploid (plant body) back to haploid (sperm and eggs) with the majority of the time in the diploid state (for higher plants).

Plants lower on the evolutionary scale, on the other hand, spend most of their life cycle in the haploid stage and only a small amount of time is spend in the diploid stage (when the egg is fertilized by the sperm).

The diploid stage of the life cycle is referred to as the **sporophyte** stage and the haploid part of the life cycle is called the **gametophyte** stage. Plant life cycles alternate between the two stages. Nonvascular plants spend the predominance of their life cycle in the haploid or gametophyte stage.

Evolution of Higher Plants

Campbell (1993) suggests four major periods of plant evolution. The first major period was the origin of terrestrial plants from aquatic ancestors, some 4.25 million years ago during the Silurian period of the Paleozoic era. Plants needed to evolve some protections when they emerged to land. To prevent water loss to the terrestrial environment, a waxy cuticle was produced. Primitive aquatic plants often released their sperm or egg into the water for fertilization. This approach would not work on land. Terrestrial plants developed multicellular jackets around the gametes and embryos. Water has a great buoyant effect. The move to land required greater support of their bulk and a more efficient means of transporting nutrients. The answer to this was specialized tissue for the conduction of food (**phloem**) and water (**xylem**). Collectively, phloem and xylem are called **vascular tissue**.

The earliest terrestrial plants that seem to have some form of specialized tissue are in some moss species (most mosses lack this). Specialized tissue in some mosses called **leptoids** and **hydroids** are found which seem to have some role in food and water conduction; however, whether these tissues are homologous to higher vascular plant tissue is still under debate.

The second stage of plant evolution as outlined by Campbell (1993) was the spread of vascular plants during the Devonian period of the Paleozoic era, approximately 400 million years ago. Many of the earliest, successful vascular plants were the ferns and a group we call the fern allies.

The third period stated by Campbell (1993) was when vascular plants began the production of seed. Many of the dominant forms of plants in the early Devonian, as the ferns and fern allies, produced spores for reproduction. Near the end of the Devonian, approximately 360 million years ago, the first seed producing plants arose. Some are still around today in the form of cycads and other primitive gymnosperms. The term **gymnosperm** literally translates as naked seed. Gymnosperms do not enclose their seeds in protective structures such as fruits. Instead, they are exposed on structures called **cones**. Gymnosperms are on the decline today and are often artificially maintained by tree farms. This artificial maintenance is called **disclimax**.

Campbell's (1993) last highlight in the evolution of plants occurs with the rise to dominance of flowering plants during the early Cretaceous period of the Mesozoic era, some 130 million years ago. Flowering plants are those plant which produce flowers which mature into fruits which "cover" the seed. These are the dominant plants on the planet today and by far, the most successful.

Plant Taxa

One of the first things about botany you need to learn is botanists like to be different. In zoology, the next largest category in the taxonomic hierarchy after kingdom is the taxon called **Phylum**. Botanists prefer the term **Division**. Depending upon which botanist you talk to, there are 10 or more divisions of plants. We will detail 12 divisions.

Table 1: Taxonomic Scheme of Plants.

Taxon	Common Name	Approximate Number of Extant Species
Nonvascular Plants Division Hepatophyta Division Bryophyta Division Anthoceroophyta	Liverworts Mosses Hornworts	6,500 10,000 100
Seedless Vascular Plants Division Psilophyta Division Lycophyta Division Sphenophyta Division Pterophyta	Whiskferns Club mosses Horsetails Ferns	10-13 1,000 15 12,000
Gymnosperm Seed Plants Division Coniferophyta Division Cycadophyta Division Ginkgophyta Division Gnetophyta	Conifers Cycads Ginkgo <i>Gnetum</i> , <i>Welwitschia</i>	550 100 1 70
Angiosperm Seed Plants Division Anthophyta	Flowering Plants	235,000

Nonvascular Plants

Nonvascular plants are defined as not having specialized tissue for the conduction of food and water. Additionally, they do not have true roots or true leaves. These are the most primitive of the land plants, indeed, often having a somewhat amphibious existence - able to survive both in and out of water. The most primitive of the nonvascular plants are considered to be members of the division Hepatophyta.

Division Hepatophyta - the Liverworts

Liverworts are some of the most primitive of land plants, never venturing too far from their aquatic existence. Some liverworts remain entirely aquatic while others are somewhat amphibious. Others have developed into fairly successful terrestrial plants. However, they all still have the need of water for reproduction.

Liverworts are so named because earlier naturalists seemed to recognize some resemblance to the human liver. It is, at best, a tenuous similarity. Early herbalists subscribed to a concept known as Doctrine of Signatures where plants often indicated a use by their appearance. Hence, liverworts were considered a good cure for liver ailments. Interestingly, some of these old beliefs do have some soundness in modern medicine. Probably 80% of all drugs today are plant or fungal derived.

In any case, the basic design of the liverwort body (**thallus**) is a lobed structure, often with dichotomous branching. Growth of the thallus occurs at the tip.

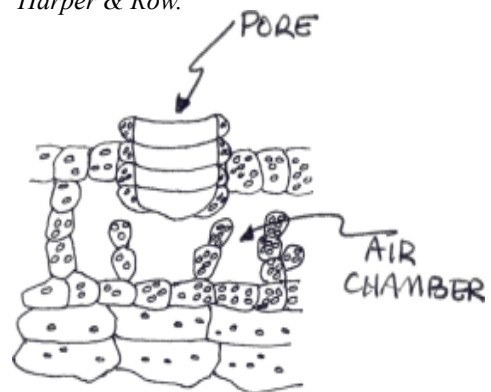
The Genus *Marchantia* (after N. Marchant, French Botanist)

□ Observe the specimen of the genus *Marchantia*. *Marchantia* is a **dioecious** liverwort, meaning it has male and female plants. You find this plant in damp, shady areas growing on muddy flats. Note the dichotomous branching of the thallus. Since growth occurs from the tip, the plant often decays and decomposes as the new growth occurs. The upper portion of the plant is separated into large polygonal **air chambers**. Opening to the surface from each chamber is a central **pore**. Some biologists believe these openings are the forerunners of stomata of higher plants.

Rhizoids are found in abundance on the ventral surface. There are two types: **smooth** and **pegged**. Smooth rhizoids penetrate the substrate and anchor the plant. Most of the smooth rhizoids are found toward the center of the underside of the thallus. Pegged (or tuberculate) rhizoids run horizontally along the ventral surface of the thallus and are often held in that position by **scales**. Scales differ from rhizoids in that rhizoids are multicellular but only a single cell thick while scales are multicellular and several cells in thickness. Scales and pegged rhizoids seem to be involved in the capillary conduction of water.

The thallus is composed of two distinct layers when viewed in cross section. The upper layer contains the air chambers which are formed from **parenchyma** cells in which are abundant chloro-

Figure 1: *Marchantia* section through pore. From Bold HC. 1973. Page 241 in *Morphology of plants*, 3rd ed. New York: Harper & Row.



plasts. This is overlaid by an epidermis which also contains chloroplasts. The upper layer, therefore, serves as the photosynthetic layer of the plant. The lower layer is also composed of parenchyma cells; however, few chloroplasts are located there and this layer seems to be concerned with storage. The pores which open into the air chambers are composed of 4 or 5 tiers of cells forming a raised platform. It functions as a stoma would with the exception the pore is not capable of closing. Instead, only the lower tier of cells close.

□ Look for the male form of the plant with raised splash platforms. These structures, along with their stalks are called **antheridiophores**. The sperm are found in packets, surrounded by a sterile layer of cells called the **antheridium**. There are numerous antheridia along the top of the antheridiophore, buried within. When a drop of rainwater splashes on the flat surface, it first releases the sperm which ooze to the surface. The next drop of rainwater splashes the sperm over to the female plant thallus.

□ Observe the female thallus. It looks like umbrellas without the cloth, or some suggest they look like miniature palm trees. On the undersurface of these “umbrella ribs” called **archegoniophores** are egg containing structures called **archegonia**. They point downward, along with the ribs of the umbrella-like structure. When sperm splash over to them, the ribs serve to pull water (and sperm) upward to the archegonia via capillary action. Sperm then swim into the neck of the archegonium and fertilize the egg.

After the egg is fertilized, a series of mitotic and meiotic divisions occur to produce a **capsule** with **spores** inside. The spores are released when the capsule matures and splits open. Hygroscopic devices, called **elaters**, uncoil and help spread the spores. The spores germinate into a gametophyte plant which you recognize as the male or female thallus. The sporophyte stage is very short-lived in that it is the

Figure 4. *Marchantia elater*. From Bold HC. 1973. Page 247 in *Morphology of plants, 3rd ed.* New York: Harper & Row.



Figure 2. *Marchantia antheridiophore*. From Bold HC. 1973. Page 244 in *Morphology of Plants, 3rd ed.* New York: Harper & Row.

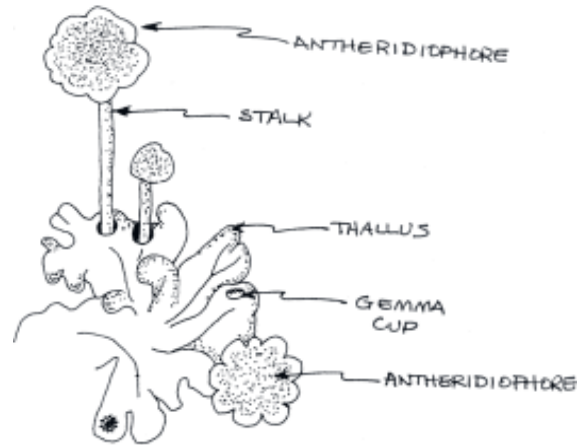


Figure 3. *Marchantia archegoniophore*. From Bold HC. 1973. Page 243 in *Morphology of plants, 3rd ed.* New York: Harper & Row.

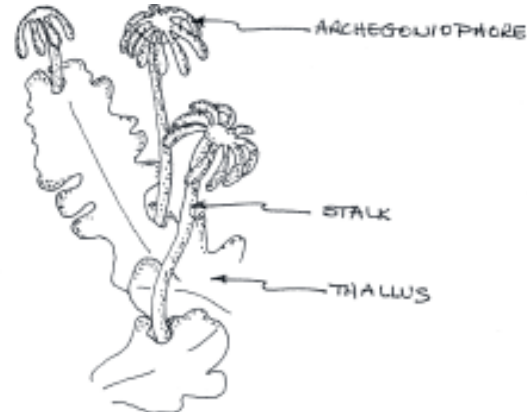
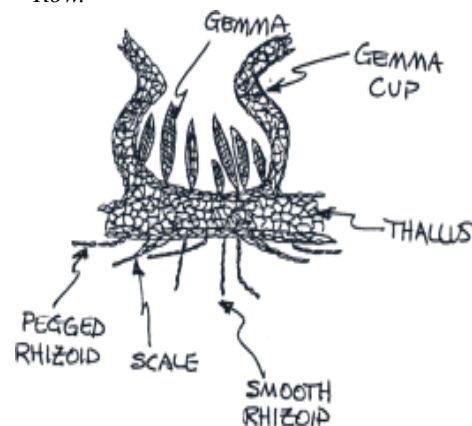


Figure 5. *Marchantia gemma cup*. From Bold HC. 1973. Page 242 in *Morphology of plants, 3rd ed.* New York: Harper & Row.



stage where the egg is fertilized and the part that forms the capsule and elaters.

□ Note the mature sporophyte part of the plant attached to the gametophytic thallus. The ribs have been raised upward to reveal swollen sporophytic capsules.

Sexual reproduction in *Marchantia* is controlled by light. After 30 days growth under an incandescent lamp set for 16-hour days, reproductive structures begin to appear.

Marchantia may also reproduce asexually by fragmentation or by the production of **gemmae**. Gemmae are buds which are found within a structure called the **gemma cup**. Rainwater will splash the gemmae out where they will land and germinate to produce new thalli.

□ Observe the prepared slide of *Marchantia* antheridiophores showing the antheridia. Look for the **sterile jacket** of cells surrounding the **spermatogenous** cells in the center. Spermatogenous cells will eventually undergo additional mitosis to produce biflagellate sperm cells. Sperm are released from the antheridia when a drop of water hits the flat splash platform. They begin to ooze out upon the flat surface and the next water droplet splashes the sperm, hopefully to a female plant.

□ Observe the prepared slide of *Marchantia* archegoniophores. The archegonia are found on the undersurface of the umbrella-like arms. The archegonium is composed of a series of sterile cells which form an urn or vase-like structure. The base of the vase is called the venter and the neck itself is simply called the neck. The neck is plugged with a series of cells called the neck canal cells. Inside the venter is tissue which will develop into the egg and ventral canal cell. The ventral canal cell and neck canal cells degenerate to form a slimy mucous which allows sperm to swim down the neck of the archegonium and fertilize the egg.

□ Note the **archegonium**, the **egg cells**, the **venter**, the **neck**, the six rows of **neck canal cells**, and the **ventral canal cell**. You will probably not be able to see all these structures within one archegonium, so scan the entire slide.

Once sperm fertilize the egg, you establish the diploid condition and thus the sporophytic part of the plant. The zygote undergoes mitosis to produce a series of transverse and longitudinal

Figure 6. *Marchantia* antheridia. From Bold HC. 1973. Page 244 in *Morphology of plants, 3rd ed.* New York: Harper & Row.

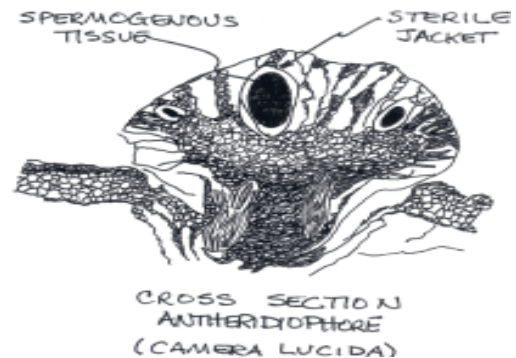


Figure 7. *Marchantia* archegonia. From Bold HC. 1973. Page 245 in *Morphology of plants, 3rd ed.* New York: Harper & Row.

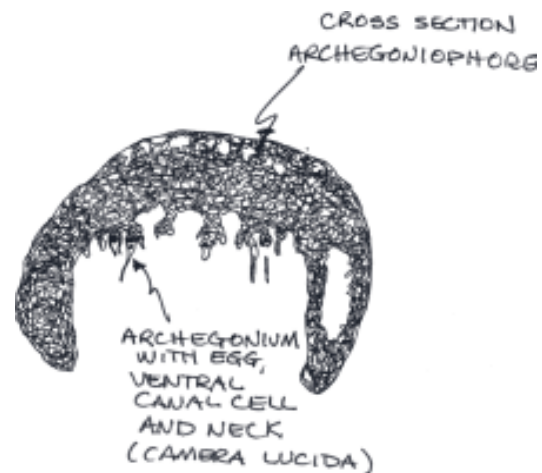
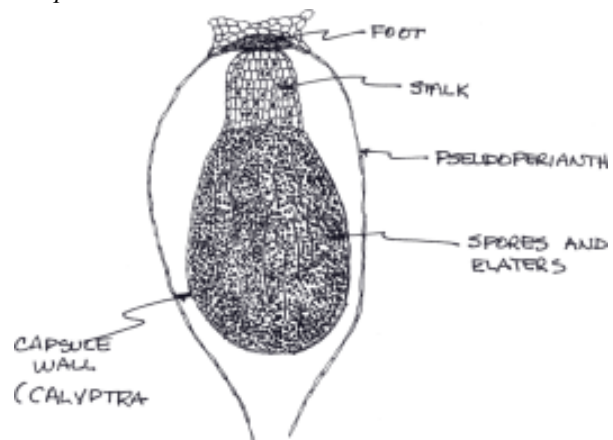
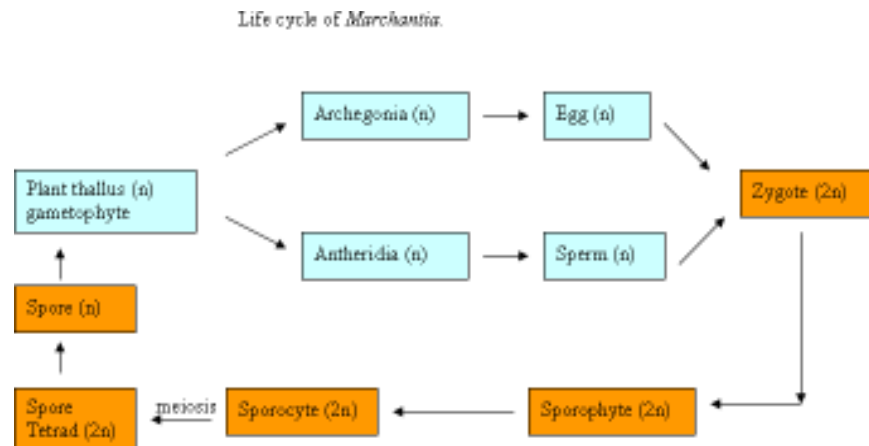


Figure 8. *Marchantia* capsule. From Bold HC. 1973. Page 248 in *Morphology of plants, 3rd ed.* New York: Harper & Row.



divisions. As the diploid tissue increases, the archegonium keeps pace with the growth. The venter paces its growth with the sporophyte to produce the **calyptra** or covering of the sporophyte. In addition, extra growth from the stalk of the archegonium forms a **pseudoperianth**. It has no real function but is analogous to the development of petals in

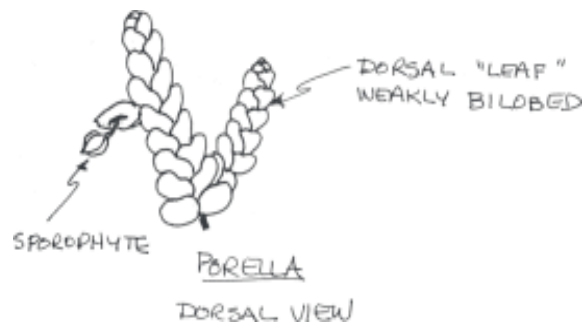
Figure 9. *Marchantia* life cycle.



flowering plants. Differentiation now begins to take place in the sporophyte with three regions of cells forming: the **foot**, the **seta** and the **capsule**. The foot grows down into the archegonium and archegoniophore, anchoring the sporophyte into the gametophyte. The capsule differentiates two areas of cells: one forms the wall of the capsule and another forms a mass of cells called **sporocytes**. Some sporocytes will undergo meiosis and produce tetrads of spores. A second group of sporocytes will form structures called **elaters**. These are hygroscopic and aid in spore dispersal by alternately lengthening and contracting. Sporocytes undergo meiosis to produce **tetrads** of spores. The tetrads break apart to produce individual haploid spores. These haploid spores are discharged when the capsule ruptures and may germinate to produce either a male or female thallus. The cycle then begins again.

Observe the prepared slide of a mature sporophyte of *Marchantia* and try to recognize as many of the structures as possible. Be sure you can differentiate which parts of the structure are diploid and which are haploid.

Figure 10. *Porella*, a leafy liverwort. From Bold HC. 1973. Pages 263-264 in *Morphology of plants*, 3rd ed. New York: Harper & Row.



The Genus *Porella*

Marchantia is often referred to as a **thallose** liverwort. Other liverworts, at least superficially, may resemble the next group, the mosses. Their leaf-like structures are arranged in two rows, with a double row of bilobed leaf-like appendages on top and a ventral row of single leaf-like appendages. The leaf-like structures (they are not true leaves) are a single cell thick. The ventral row of leaves are different in shape and size from the dorsal rows. This difference is referred to as **anisophylly**.

Unlike the thallose liverworts, these leafy liverworts don't have an abundance of rhizoids so the water absorption function of these is probably limited. Rhizoids are probably more involved in anchorage (Bold 1973).

Observe the preserved specimen of *Porella* and look for the difference in the ventral and dorsal "leaves."

Division Bryophyta - the Mosses

Most people have some familiarity with mosses. Some even think they only grow on the north side of trees (untrue). What many people refer to mosses are not mosses at all. Spanish moss is a true vascular plant which produces flowers. In any case, like the liverworts, they do not have true leaves or true roots. They date from the Carboniferous period and are thus younger evolutionarily speaking than the liverworts.

There are three classes within the division:

Class Sphagnopsida - peat mosses

Class Mnionopsida - “true” mosses and

Class Andreaeopsida - granite mosses.

We'll restrict our study to the first two.

The Genus *Sphagnum* (Gr. *sphagnos* = kind of moss)

The Class Sphagnopsida is represented by a single genus, *Sphagnum*. *Sphagnum* is found in fresh water pools, bogs, swamps, and along the shores of lakes. It has an unbelievable ability to hold water due to special “dead” cells found in the leaf-like structures. Some reports indicate it has the ability to hold up to 16 to 26 times its weight in water.

Sphagnum may form large floating mats, sometimes called “quaking” bogs which can support the weight of a human. The term quaking comes from the fact the mat is really floating atop a pool of water. As the moss dies, it falls to the bottom and becomes a major sediment. Dried *Sphagnum* in this form is called peat, a major fuel source and an important component in the plant nursery industry for its water holding capabilities.

Sphagnum is often found in very acidic aquatic environments. The acidity can be significant enough to retard the growth of bacteria and fungi. Some early pioneers used *Sphagnum* as a dressing for wounds because of its high acid, low bacterial count. Since it grows in such acidic conditions, it is a great preservative. Human bodies and cloth dated over 2000 years have been recovered from peat bogs in Denmark.

The “stem” of *Sphagnum* terminates in dense apical branches. There are two other types of branching occurring on the stem: ascendant and pendulous. Ascendant branches project outward from the stem and horizontally. Pendulous branches are found tangled about the axis of the stem and some suggest they serve a capillary function.

Figure 11. *Sphagnum*. From Bold HC. 1973. Page 291 in *Morphology of plants*, 3rd ed. New York: Harper & Row.

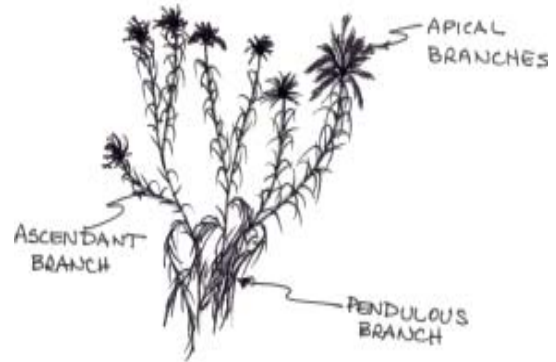


Figure 12: *Sphagnum* with photosynthetic and “dead” cell. From Bold HC. 1973. Page 292 in *Morphology of plants*, 3rd ed. New York: Harper & Row.

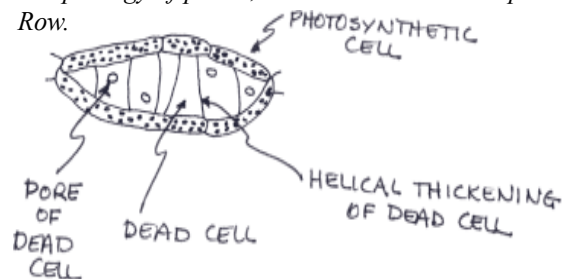
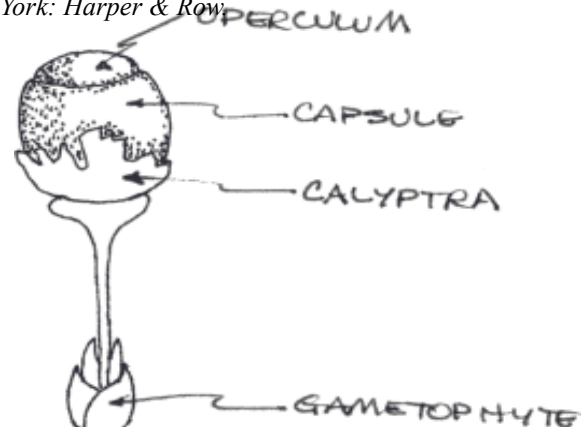


Figure 13. *Sphagnum* capsule. From Bold HC. 1973. Page 295 in *Morphology of plants*, 3rd ed. New York: Harper & Row.



Mature plants of *Sphagnum* have no rhizoids; they absorb through their “leaves” and stems. There are two types of cells in their leaf-like appendages: photosynthetic and colorless (dead) cells. In reality, dead cells are only dead at maturity.

□ Observe the living or preserved *Sphagnum* with sporophytes (the small round black structures). The sporophyte is a capsule of spores. Remove a leaf from this and make a wet mount. Look for large, “dead” cells surrounded by smaller, living, photosynthetic cells. The dead cells open to the environment by pores and are responsible for the plant’s water holding capability.

□ Demonstrate the water retaining ability of *Sphagnum* by immersing a handful of peat in water. Now, see how much you can squeeze out of the sample.

Sexual reproduction pretty much follows the pattern in the liverworts.

The Genus *Polytrichum* (Gr *polytrichos*, very hairy)

The Class Mnionopsida comprises those plants known as the true mosses. The term “true” is a little misleading - *Sphagnum* is no less a moss although it is found in a separate class. There are numerous genera and species in the Mnionopsida, including the genus *Mnium* from which the class name is derived. However, we’ll concentrate our study on the genus *Polytrichum*, sometimes commonly called haircap moss. The common name comes from the “hairy” cap found on top of the capsule (sporophyte). Of course, it’s not real hair but simply remnants from a part of the archegonium called the **calyptra**.

Polytrichum is found worldwide. There are male and female plants (gametophytes), thus it is dioecious. There are some curious features to the anatomy of the “stem” of the plant. Stems in mosses are typically differentiated into three regions: **epidermis**, a thick **cortex**, and a **central strand**. The strand is composed of two layers of cells called **leptoids** and **hydroids**. Hydroids conduct water and leptoids seem to protect this region. Hydroids are thus analogous to the vascular tissue in the higher plants and mosses are considered to be the evolutionary forbearers of vascular plants.

The life cycle of a moss begins with a germinating spore (n). The growth which results from the spore is called a **protonema**. The protonema begins to rapidly branch. At first, the protonema looks like a green algae, but it may be distinguished from this group of plants by

Figure 14. *Sphagnum* sporophyte section through capsule. From Bold HC. 1973. Page 294 in *Morphology of plants, 3rd ed.* New York: Harper & Row.

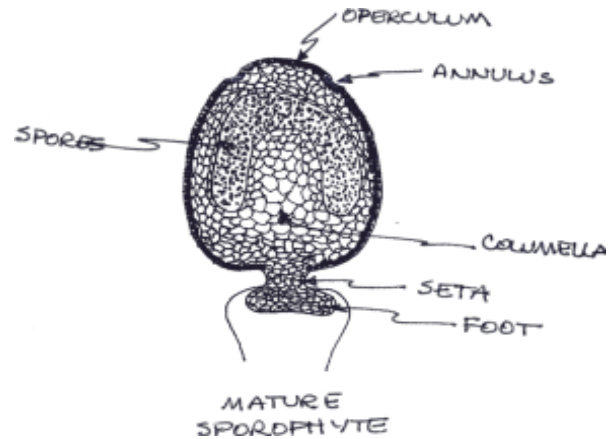


Figure 15. *Polytrichum* male and female gametophytes. From Bold HC. 1973. Page 302 in *Morphology of plants, 3rd ed.* New York: Harper & Row.



Figure 16. *Polytrichum* protonema. From Bold HC. 1973. Page 297 in *Morphology of plants, 3rd ed.* New York: Harper & Row.



lens-shaped chloroplasts. The protonema eventually forms the mature male or female gametophyte plant (n).

□ Observe the prepared slide of a protonema. Try to distinguish the lens-shaped chloroplasts. To which green algae would you consider it to be similar?

The female gametophyte does not have any real distinguishing characteristics other than a spiral arrangement of leaf-like structures around the stem. Remember, there are no true leaves in nonvascular plants.

□ Observe the preserved or living specimen of the female gametophyte of *Polytrichum*. The leaf-like structures are a single cell in thickness except for a multicellular thickness along the midrib. Archegonia eventually differentiate at the apex of the plant.

□ Obtain a prepared slide of *Polytrichum* archegonia. This slide is a longitudinal section through the female gametophyte. Look for the archegonia at the apex. Note the **archegonia** with the long **necks**, the **venters**, egg cells, the **stalk** which supports the archegonium and the sterile hairs of **paraphyses**.

□ Observe a living or preserved specimen of the male gametophyte of *Polytrichum*. The male gametophyte of *Polytrichum* has a flattened apex which serves as a splash platform in a similar way of that of *Marchantia*.

□ Obtain a prepared slide of a longitudinal section through the male gametophyte. Note the **antheridia**

composed of a **sterile jacket** of cells and **spermatogenous** tissue. Antheridia are mature when they turn orange.

They produce biflagellate, corkscrew-shaped sperm which are released by water. Also note the **paraphyses** in between the antheridia.

The sporophytic plant of *Polytrichum* remains attached to the gametophyte and is dependent upon it for a period of time for nutrition. After fertilization of the egg, mitotic divisions occur and a **foot**, **seta**, and **capsule** differentiate. The foot firmly embeds itself in the gametophyte, the seta elongates to form the stem and the capsule differentiates into a **capsule wall**, a **sterile columella**, and **sporogenous** tissue. The sporogenous tissue (2n) undergoes meiosis to produce a tetrad of spores (n). After the spores develop and mature, the calyptra either decays or is blown away. A covering, called the **operculum**, fits over the top of the capsule.

□ Obtain a living or preserved sporophyte and carefully remove the calyptra and operculum and look into the capsule. Spores are further protected by a row of hygroscopic teeth called the **peristome**. In dry

Figure 17. *Polytrichum archegonium*. From Bold HC. 1973. Page 305 in *Morphology of plants*, 3rd ed. New York: Harper & Row.

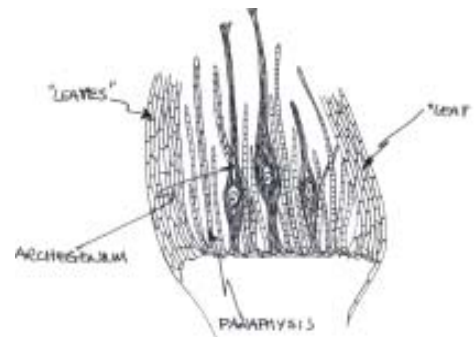


Figure 18. *Polytrichum* male and female gametophytes. From Bold HC. 1973. Page 303 in *Morphology of plants*, 3rd ed. New York: Harper & Row.

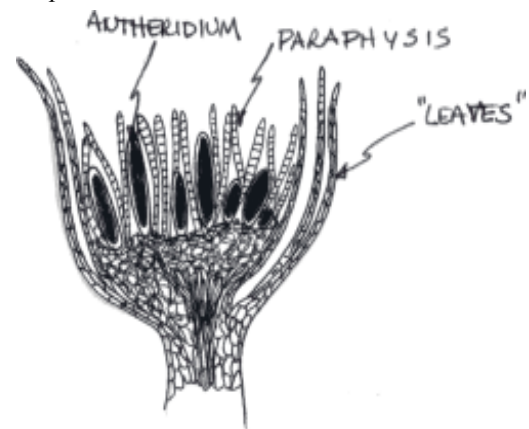
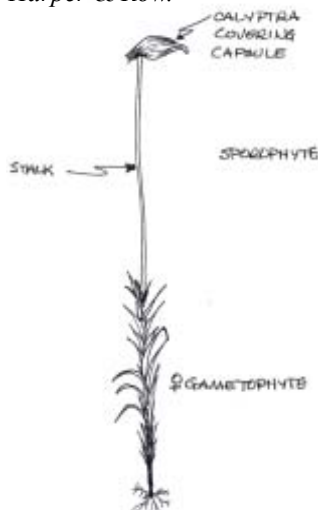


Figure 19. *Polytrichum* male and female gametophytes. From Bold HC. 1973. Page 302 in *Morphology of plants*, 3rd ed. New York: Harper & Row.



weather, the peristome opens and spores may be released. In wet weather, the peristome closes. Demonstrate this by placing a capsule under a dissecting scope and allowing it to dry. Then touch it with a pipette of water from an eyedropper. Note the changes.

□ Observe a prepared slide of a longitudinal section through the capsule. Try to identify **spores**, **columella**, **seta**, and perhaps **operculum** and **peristome**.

Division Anthocerophyta - the Hornworts

These are similar to the liverworts but distinctive enough to be placed in their own division. The male and female reproductive structures are not nearly as well pronounced as in the liverworts or mosses. The main interest in the hornworts is in the sporophyte stage. The sporophyte of *Anthoceros* is an elongated capsule that more closely resembles the sporophyte of mosses. Several differences do occur, however. The sporogenous tissue which develops after the zygote formation differentiates into two regions: a sterile column of tissue called the **columella** and a sterile layer that undergoes meiosis to produce tetrads of spores. The **seta** is much reduced but the **foot** firmly anchors the sporophyte to the gametophyte. One additional peculiarity is the development of stomata on the epidermis of the capsule.

Observe the preserved or living specimen of *Anthoceros*, a representative genus. Note the gametophytic and saprophytic portions of the plant. How do you think the spores are freed from the plant?

Observe the prepared slide of a longitudinal section through the capsule of *Anthoceros*. Look for the **columella**, the **spores**, the **foot**, and **stomata**.

Figure 20. *Polytrichum* male and female gametophytes. From Bold HC. 1973. Page 312 in *Morphology of plants*, 3rd ed. New York: Harper & Row.

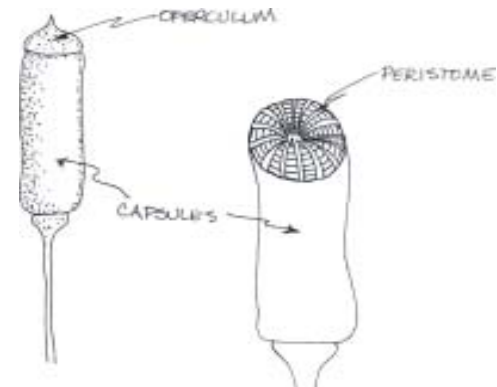
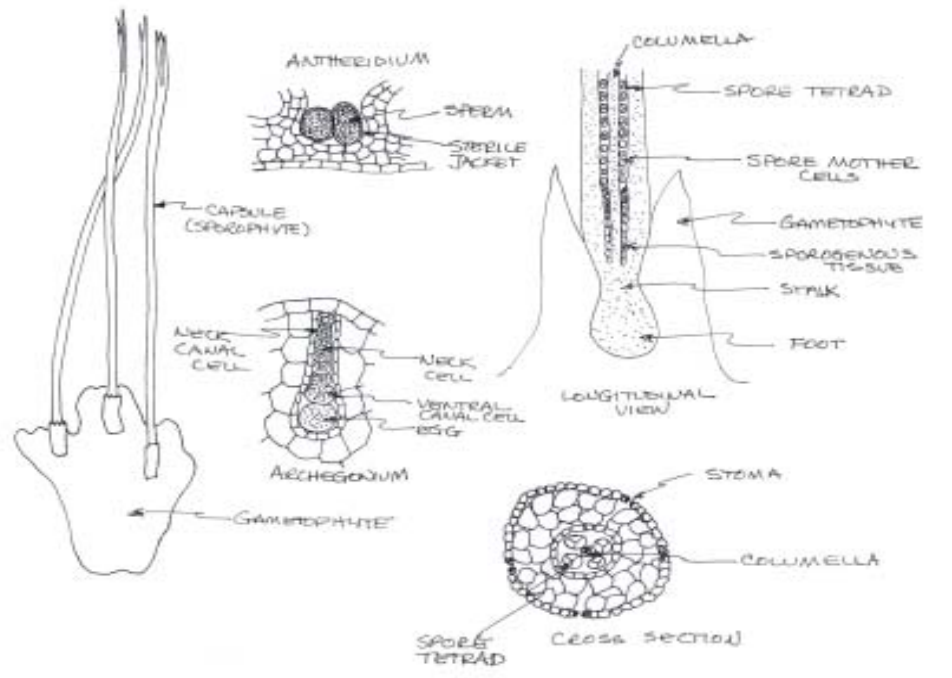


Figure 21. *Anthoceros*. From Bold HC. 1973. Page 274-278 in *Morphology of plants*, 3rd ed. New York: Harper & Row.



References Cited

Bold HC. 1973. Pages 241 *in* Morphology of plants, 3rd ed. New York: Harper & Row.

_____. 244.

_____. 243.

_____. 242.

_____. 247.

_____. 244.

_____. 245.

_____. 248.

_____. 263-264.

_____. 291.

_____. 292.

_____. 295.

_____. 294.

_____. 302.

_____. 305.

_____. 303.

_____. 302.

_____. 312.

_____. 274-278.

Campbell NA. 1993. Pages 560-561 *in* Biology, 3rd ed. Redwood, CA: Benjamin Cummings.

_____. 560-561.

_____. 560-561.

_____. 560-561.