Introductory Botany
The 'Bryophytes'

What plants are and what they are not: plants are the bryophytes, ferns and fern allies, angiosperms, and gymnosperms. Algae are not plants.

True plants are also called embryophytes, because they produce an embryo that becomes multicellular while protected by parental tissues. All embryophytes also have gametangia (though in seed plants, gametangia may have been lost by evolutionary reduction) and spores with walls containing sporopollenin. The bryophytes, ferns and fern allies are free-sporing (seedless) plants. Gymnosperms and angiosperms are the seed plants.

As with the algae, the 'bryophytes' are not a natural group of organisms: altogether they are not descendent from a single common ancestor. The discovery that they are three distinct lineages rather than one is a triumph of modern studies of evolution, using both morphological and molecular data in cladistic analyses. Altogether, there are about 20,000 species of bryophytes, making them second in species richness only to the angiosperms.

The fossil record of the group is generally poor, especially in their existence in the Paleozoic. But we know they were present then, because nearly all analyses of modern plants tell us that bryophytes are the oldest remaining lineages of plants.

Some Terminology:

mosses
liverworts
hornworts
embryophyte
nonvascular plant
sporopollenin
heteromorphic alternation of generations
gametophyte, gametangium
monoicous, dioicous
protonemata
sporophyte, sporangium
spore tetrad
matrotrophy
capsule, seta
peristome
antheridia
archegonia
free-sporing
homosporous
thallus
rhizoids
polkilohydry
desiccation tolerance
cryptogamic crust
peat

Major Groups of Bryophytes:

The bryophytes include the hornworts, liverworts and mosses. All are found in New Jersey, but mosses are the most conspicuous part of the flora. The moss genus *Sphagnum* (peat mosses) is represented by nearly 50 species in New Jersey, making the state the region with the highest species richness of any comparable area in North America. The differences among these groups are beyond the scope of this course.

Common Features of Bryophytes:

Heteromorphic alternation of generations (as with all true plants)
Gametophyte-dominated life cycle, with the sporophyte usually short-lived and existing while attached to the gametophyte. Are there advantages to this type of life cycle?
Produce gametes in archegonia and antheridia
Simple sporophyte, usually with a stalk and always with a single sporangium
Free-sporing and homosporous
Extensive asexual reproduction (by fragmentation or specialized structures = gemmae)
Why is asexual reproduction so common in the bryophytes?
How does asexual reproduction influence our concept of an individual?
Rootless and Nonvascular (no true xylem or phloem)
Why are bryophytes so successful, despite the absence of roots and vascular tissue?
Poikilohydry - the variation of water content with water available from the environment
What are the advantages and disadvantages of poikilohydry?
Desiccation tolerance - physiological adaptation to nearly complete drying of tissues

Ecology of Bryophytes:

The familiar stereotype of bryophytes is that they occur in moist, shaded habitats. Certainly many do. Bryophytes contribute a substantial portion of the photosynthetic biomass within epiphytic communities of temperate and tropical rain forests. However, they also comprise much of the plant biomass in boreal and arctic regions and in peatlands, and are important in soil formation in arid regions, where they form a portion of cryptogamic crusts (a cryptogam crust contains lichens, bryophytes, algae or cyanobacteria). They survive in habitats that no seed plants can tolerate. I have personally seen bryophytes in caves, on roofs, in old shoes, on dung, on bones, on otherwise bare lava rock, and on soils contaminated with heavy metals (as from mining). One place they are rare is along the seashore, because few are tolerant of salt spray.

True plants are terrestrial plants that must overcome the problems of being a photosynthetic, sessile organism in an aerial environment. What are the problems of being a plant, as compared to an alga? It has been said that the vascular plants (all plants but bryophytes) overcome the problems of life on land by structural adaptations such as lignin, a thick cuticle, vascular tissue, and a well-developed root system. Paradoxically, bryophytes have none of these adaptations, yet are very successful in terms of their species richness. What explains their success despite a lack of these adaptations?

Many species of bryophytes produce abundant, tiny sexual spores from sporangia. It has been suggested that because of this and the fact that bryophytes are very ancient, that the geographic range of many bryophytes should be large --- either intercontinental or across continents. Some species have such broad ranges, but many have geographically restricted ranges and are endemic to only one particular region. Thus, although bryophytes as a group are found in nearly all terrestrial habitats, individual species are not.

Economic and Ecological Impact:

Though their stature is small and we don't utilize bryophytes as food, it would be foolish to assume bryophytes have no economic utility or ecological importance.

1. Bryophytes are model systems for understanding vascular plants. Bryophytes tell us about seed plants --- how they might have originated, and what major transformations took place to lead to the modern flora. Recent work in biotechnology, such as the development of drought-resistant crops, is based on comparisons of bryophytes and angiosperms. Similarly, the control of flower production (which is the basis for fruit formation) can be better understood by comparing the genes regulating reproduction in bryophytes and angiosperms.

2. Peat moss. The genus *Sphagnum* is the principal component of peat in cool regions. Peat is combustible, and produces more energy per mass than wood (though less than coal or oil). Peat is also useful in gardening, because the shoots of *Sphagnum* include a network of porous dead cells that store water, giving wet peat a sponge-like property. The cell walls of *Sphagnum* cause acidification of the water in the environment by cation exchange. This process can be very effective, in some cases lowering the pH to 3.0 - 4.0. This can be useful in the cultivation of plants requiring acid soils (acidophiles). In recent history, peat has been used as both a surgical dressing and in sanitary napkins for women. Can you say why?

3. Conservation biology. Some bryophytes are sensitive indicators of human disturbance or pollution. As such, they can be used to monitor the past, present and future impacts of humans. The National Forest and Park Services are currently interested in having trained specialists with a knowledge of bryophytes conduct botanical surveys of their lands.

4. Pharmaceutical applications. The liverworts in particular are characterized by diverse secondary chemistry. There are several research programs across the globe dedicated to identifying useful chemical extractions from liverworts. Much remains to be done.

5. Decorative materials. Certain species of feather mosses (a description of the appearance of several species, not a taxonomic group) are utilized as decorative materials in crafts such as nativity scenes. Unfortunately, the harvest of bryophytes for such purposes appears to be a major cause of extinction or rarity of certain mosses. Do you think it is ethical to purchase such products?

6. Control of global climates. Bryophytes are a substantial portion of the vegetational biomass in cooler regions of the world. Soils in cold region contain an enormous amount of trapped carbon, much of which is derived from dead bryophytes. There is much concern that a slight increase in global temperatures will lead to a further increase in global temperatures because cold region soils will release additional carbon into the atmosphere. What is the mechanism for this?

7. Bryophytes are a large fraction of the biomass and/or species richness in certain biomes. Aside from cold climate regions (6 above), they are also of substantial ecological importance in temperate and tropical rainforests, deserts, and some freshwater lakes.

8. Cryptogamic crusts. In arid environments, cryptogamic crusts --- which include lichens, bryophytes, algae and cyanobacteria --- are important in soil formation.

Plant Diversity
The Pteridophytes

The pteridophytes include the monilophytes and lycophytes, and are free-sporing (seedless) plants, as are the bryophytes. Historically, pteridophytes have been called the vascular nonseed plants, to distinguish them from both the bryophytes and seed plants. Altogether, pteridophytes are not a natural group of organisms (they are nonmonophyletic), because collectively they are not descendent from a single common ancestor.

The fossil record indicates that monilophytes and lycophytes were present in the Late Devonian Period, nearly 400 million years ago, and well before the origins of dinosaurs or mammals. Many extinct lineages of pteridophytes are recorded from the Paleozoic Era, including arborescent (tree) forms that contributed to the so-called Coal Swamp Flora from the Carboniferous Period (280 - 345 mya). Pennsylvanian Coal is largely derived from fossilized monilophytes and lycophytes. The tree forms that dominated the Carboniferous Period are now extinct.

Some Terminology:

pteridophytes
monilophytes: true ferns, horsetails, whisk ferns
lycophyte: club mosses, spike mosses, quillworts
coal swamp
Paleozoic Era
Carboniferous Period
sporophyte-dominated life cycle
free-sporing
homosporous; heterosporous
polysporangiate
rhizome
frond = compound leaf
petiole (leaf stalk), blade
sorus (plural: sori)
fiddlehead
vascular tissue (xylem, phloem)
thallus
antheridia, archegonia
epiphyte
strobilus (plural: strobili)
megasporangium; megaspores
microsporangium; microspores

Major Groups of Pteridophytes:

The true ferns are monilophytes, and are the most familiar concept of pteridophytes. Most species of true ferns have plants with large, compound leaves, and underground rhizomes. Other monilophytes include the horsetails (sphenopsids) and whisk ferns. Lycophytes represent a different major lineage of plants than the monilophytes, and includes the club mosses, spike mosses and quillworts. Despite the separate origins of monilophytes and lycophytes, they have common features in their life histories, so that it is reasonable to make some generalizations about the reproductive biology of all pteridophytes.

Common Features of Pteridophytes:

Heteromorphic alternation of generations, as with all true plants
Sporophyte-dominated life cycle, with the sporophyte usually perennial (although the

stem may be underground) and independent of the gametophyte at maturity
Development of the gametophyte occurs independently of the sporophyte
Question: What might be advantages of the fern type of life cycle? Disadvantages?

Polysporangiate - with many sporangia produced per sporophyte
Question: How is a fern sporophyte different than the sporophyte of a bryophyte?

Question: Does having many sporangia per sporophyte increase the genetic variation in spores produced by a sporophyte? Explain.

Gametophytes produce gametes in archegonia and antheridia --- as with the bryophytes.
Free-sporing and homosporous (in simple terms, seedless)
only a few, such as *Azolla*, *Selaginella* and *Isöetes*, are heterosporous like seed plants
Extensive asexual reproduction --- in the sporophyte, by growth of a rhizome,
or in gametophyte generation, by specialized structures called gemmae
Roots and Vascular Tissue (true xylem and phloem) in the sporophyte
Question: The gametophyte generation lacks roots and vascular tissue. Are there any disadvantages to having roots and vascular tissue?

Ecology of Pteridophytes:

The familiar stereotype of pteridophytes, largely based on ferns of our region, is that they occur in moist, shaded habitats such as forests or ravines. Certainly many pteridophytes do occur in these habitats. However, they also found in rock outcrops in deserts and treeless mountain slopes, in grasslands, along roadsides, and submerged in freshwaters (none are marine). In the tropics, a large number of species are epiphytes, living on other plants. Some tropical species have a tree growth form, reaching more than 50 feet in height. Forests dominated by tree ferns occur in Australia, New Zealand and South America. Several species are weeds, found in fields and open, disturbed sites. Some survive in extremely dry conditions, as on barren lava or sandstone outcrops.

Economic and Health Impact:

Although there are many examples of uses of pteridophytes in traditional cultures, they are not abundantly used in modern western cultures except in landscaping. One reason they have limited economic potential is that they do not produce wood --- they have no vascular cambium.

- Landscaping and horticulture. For aesthetic and practical reasons, ferns are popular in landscaping. Many have striking fronds, and the rhizomatous growth of many species leads to dense colonies that are desirable in gardens. Some local species such as Christmas Fern (the genus *Polystichum*) have evergreen fronds and remain one of the few plants species with leaves during the winter months.

- A few ferns are used in cuisine. Canned fiddleheads (young leaves) were once commonly available in the eastern U.S. and Canada. They are said to taste like artichokes, crisp asparagus or broccoli. Some species, such as cinnamon fern (*Osmunda cinnamomea*; locally common) and ostrich fern (*Matteuccia struthiopteris*) are edible and apparently safe. Fiddleheads are considered to be a "good" source of potassium; they also contain vitamin C, niacin and iron.

- The fiddleheads of other species such as bracken fern (*Pteridium aquilium*; locally common) contain carcinogens, and consumption can lead to stomach cancer. It is noteworthy that cattle avoid eating bracken fern.

- Arborescent fossilized ferns and fern allies are a major component of coal. In this way, ferns and fern allies are responsible for much of our energy resources. On the other hand, coal is not a renewable resource --- it is used more rapidly than it is replaced ---- and is in part responsible for global warming.

- *Azolla*, an aquatic floating fern, is capable of nitrogen fixation, and is commonly used in the cultivation of rice.

- Several pteridophytes are considered to be among the most problematic weeds of the world, including *Equisetum arvense* (common horsetail), *Salvinia molesta* (water fern) and *Pteridium aquilinum* (bracken fern).

Summary of Major Groups of Pteridophytes:

True Ferns (Polypodiophyta)
The largest group of ferns and fern allies, with about 12,000 species
Sporophytes of many species have rhizomes and compound leaves called fronds
Young leaves are called fiddleheads
Sporangia in most species are produced on the undersurface of leaves
Gametophytes are photosynthetic and are a thallus, without stems, leaves or roots

Horsetails; Scouring Rushes (Sphenopsids; *Equisetum*)
Horsetails include 15 species, but some have a widespread distribution
Sporophytes have highly reduced leaves; some species have much-branched stems
Sporangia are produced in cones (strobili); all species are homosporous
Silica deposits in the cell walls give stems a rough texture --- Native Americans used stems as scouring pads for cookware

Whisk Ferns (*Psilotum* and *Tmesipteris*)
A small group of monilophytes (< 5 species), found in the southern U.S. and subtropical or tropical climates.
Oddly, the sporophyte of *Psilotum* lacks leaves; photosynthesis occurs in the stems
Gametophytes are subterranean and heterotrophic
Current molecular evidences suggests a near relationship to basal lineages of true ferns, although the plants have no leaves

Lycophytes: Club Mosses, Spike Mosses and Quillworts
Includes about 1,100 species, most of which are tropical
Lycopodium (club moss), *Selaginella* (spike moss) and *Isöetes* (quillworts) are all in the local flora; (*Lycopodium* is known locally as ground pine or ground cedar)
Sporophytes of *Lycopodium* and *Selaginella* both have small leaves, but the latter is heterosporous

Some species produce sporangia in cones (strobili), but these cones have an independent origin of those found in gymnosperms, and so are not evidence of a relationship to gymnosperms.
Lycophytes are a distinct lineage of plants from the monilophytes

Question: What is heterospory? What are its advantages and disadvantages?