

## Topic #9: Ferns<sup>1</sup> and Fern Allies<sup>2</sup>

**REQUIREMENTS:** Powerpoint presentation, coal balls

### *Objectives*

1. What is paleobotany? Discuss the difficulties of identifying particular extinct groups.
2. For each of the following primitive characteristics found in evolutionary lines "leading" to angiosperms, name the corresponding advanced characteristic: dominance of haploid generation, homosporous, flagellated gametes, lack of seeds.
3. Name several adaptations required before plants could make the transition to land.
4. Why would you say that the anatomy of the dicot root is more primitive than that of the dicot stem?
5. What is the difference between a microphyll and a megaphyll? Briefly, how is each presumed to have arisen evolutionarily?
6. How do ferns and their allies differ from bryophytes? From gymnosperms and angiosperms? (Consider only extant groups.)
7. Discuss evolutionary advances seen in the seedless vascular plants.
8. Draw the life cycle of a fern. Compare it to that of a moss.

### *Lecture*

**POWERPOINT SLIDES:** A series of slides that provide phylogenetic orientation, the relationship among extant plants and extinct plants, and the focus of BOT 3015.

### *Paleobotany*

Ferns and fernlike plants were the major life forms during the Carboniferous Period (ca.  $350 \times 10^6$  YBP—dates must be considered approximate). Vascular plants (which include ferns) arose perhaps as early as  $600 \times 10^6$  YBP (but clearly by  $400 \times 10^6$  YBP). The remains of many of these plants are used as coal.

---

<sup>1</sup>Leatherleaf fern production brought Florida about \$64 million in 2000. The total sales value of Florida foliage, floriculture, and cut greens in 2001 was more than \$700 million. See <http://www.nass.usda.gov/fl/rtoc0h.htm>.

<sup>2</sup>The technical term is pteridophyte (literally, fern plant), which refers to seedless, vascular plants.

**POWERPOINT SLIDE:** Vascular plants of the Carboniferous (Fig. 33.17 of Starr and Taggart).

In general (and specifically for the coal deposits found in Illinois, which form the basis for most of this discussion), these seedless, vascular plants grew in areas that were alternately large swamps just above sea level and shallow seas. (Earth's geography was much different back then. E.g., at the beginning of the Carboniferous, Europe and North America had collided, leaving no North Atlantic Ocean.) The debris accumulated as peat, which subsequently became coal. Coal balls are masses of plant debris that were impregnated by dissolved minerals seeping through the peat before it had become coal. As the minerals crystallized, the result was a nodule of rock: the coal ball. Although the plant contents of a coal ball may be well preserved, generally, the remains are fragmentary and distorted. Unfortunately, they are also monotonous—the same plants appear again and again.

The method used for examining these fossils is (A) to slice through one; (B) to polish the surface; (C) to expose the surface briefly to acid (which etches away the rock (calcite), leaving the plant remaining in relief); (D) to overlay the surface with an acetate film, which has been liquefied with acetone; (E) when the acetone dries, to lift the film off, along with the relief; and (F) to examine the film under a microscope.

**POWERPOINT SLIDE:** Coal ball (courtesy of Tom Phillips, University of Illinois)

**POWERPOINT SLIDE:** Peel (Fig. 2, p. 4 of Phillips) and interpretation (p. 5 of Phillips).

This is one of the best peel sections that one can make. (Scientists, like most people, like to put their best feet forward.)

(A) The material is mostly the same; coal balls are found throughout the world, yet only 100 genera have been described, and many of these are descriptions of the same plant.

(B) The reason for name duplications is that, when a scientist finds a new structure, he or she assigns it a name. Thus, a leaf may be assigned one name and a root another. Later, it may become clear that these "organ genera" were different parts of the same plants. For example, *Stipitopteris* is the foliar member of *Psaronius*. Another complication is that the term "species" is difficult to apply to extinct organisms. By the historical definition, "species" refers to a group of organisms that form a (potential) breeding population. Obviously, this test can be applied only to extant (sexual) organisms.

The next slides show a fossil and interpretations.

**POWERPOINT SLIDE:** Schematic cross section of *Psaronius* stem (Fig. 21-22 of Scagel) and whole-plant representation (artist's concept, Fig. 7-6 of Delevoryas).

The point clearly emerges that a great deal of detective work is required to make reconstructions.<sup>3</sup>

#### *Uses of Fossil Plants*

**POWERPOINT SLIDES:** A series of slides on the impacts of the conversion of fossil hydrocarbons to CO<sub>2</sub>, and suggestions for limiting consumption without diminishing quality of life.

#### *Summary of Evolutionary Advances in Plants*

**POWERPOINT SLIDE:** Reproductive trends—shift from dominance of haploid generation, homospority, isogamy, gamete motility, absence of seeds.

(A) As I have mentioned repeatedly, in general, as plants evolved, the dominant role shifted from the haploid generation (the gametophyte) to the diploid generation (the sporophyte). Plants, some algae, a few Protista related to *Allomyces* (a chytrid), and some insects are the only organisms to show this alternation of generations. *Chlamydomonas* does not display alternation of generations; it exhibits the phenomenon of zygotic meiosis. In the center panel, the life cycle is reminiscent of that of mosses—two multicellular generations are obvious. Finally, the third panel is typical of angiosperms—a small haploid generation and a dominant diploid generation.

(B) Heterospority as seen in angiosperms is easy to define. It is the situation in which (a) one kind of spore (e.g., microspore) is formed in one type of sporangium and this spore germinates to form a unisexual gametophyte (e.g., male) and (b) a second kind of spore (e.g., megaspore) is formed in a second kind of sporangium and this second kind of spore germinates also to form a unisexual gametophyte (e.g., female). The textbook definition of homospority is also simple (“one kind of spore”), but the situation is somewhat more complex than this brief definition would suggest. Bryophytes, recall, have only a single sporangium per sporophyte, and a single kind of spore is formed. By a morphological definition, therefore, bryophytes are homosporous, but functionally some (not discussed in this course) are heterosporous because spores are genetically different; one forms a male and another forms a female gametophyte. (In some cases, whether archegonia or antheridia

---

<sup>3</sup> Take some comfort in knowing that expert interpretation is sometimes not. In one extreme case, a “jellyfish” fossil was re-interpreted years later as a frond!!!

predominate is controlled by the environment, e.g., by hormones released from a nearby plant.) As mentioned in a footnote to the master table at the end of this topic, a contrived terminology (“physiological heterospory”) is used to describe such organisms. In many or most homosporous plants, the germinating spore breaks open, and a gametophyte grows out of it. In most heterosporous plants, the gametophyte develops within the spore wall (undergoes “endospory”) if a wall is present. This type of gametophyte development is necessary for the evolution of seeds.

(C) Isogamy (in which the gametes are indistinguishable) is primitive. The species of *Chlamydomonas* that we studied was an example. Oogamy, in which the gametes differ in size, was pointed out as the pinnacle of the dead-end volvocine line, *Volvox*. Bryophytes, too, are oogamous.

(D) Having motile gametes is the primitive condition. On the evolutionary line leading to angiosperms, most male gametes retain flagella as in the bryophytes and the ferns and fern allies. Even some gymnosperms have motile gametes, but it is not the common condition. Obviously, terrestrial organisms that depend on external motility by flagellated gametes are amphibious. Angiosperms lack flagellated cells altogether.

(E) The development of the seed was a major evolutionary advance. In brief, the seed is an embryo (i.e., an immature sporophyte), a nutritive reserve (in the form of the persistent female gametophyte, endosperm, or cotyledons), and a protective cover (the seed coat). It is an effective means for propagation because it can remain dormant and germinate when suitable conditions prevail. The food reserve "helps the young plant get off to a strong start."

Seed formation requires that the megaspore (haploid) remain on the sporophyte and germinate there and that the resulting female gametophyte produce a gamete that is fertilized there. Recall, e.g., that the moss spore germinates after being released from the sporophyte, whereas the angiosperm female gametophyte is surrounded by and nourished by the sporophyte. Therefore, no free-living female gametophyte exists in seed plants. Angiosperms and gymnosperms produce seeds. Other organisms do not (except "seed ferns"  $\approx$  gymnosperms). Seed plants replaced nonseed plants as the dominant organisms about 300 million years ago.

(F) The transition to land required several adaptations:

**POWERPOINT SLIDE:** Evolution of other traits that provided adaptability to a terrestrial life style.

(F1) Development of a cuticle or waxy layer covering terrestrial plants, as we have seen, e.g., in angiosperms. (Some bryophytes also have a poorly developed ("inapparent") cuticle.) The elaborated cuticle is virtually impervious to water and therefore conserves water, usually the most limiting resource for terrestrial plants. Some authorities also emphasize the importance of the cuticle in

absorbing harmful UV radiation.<sup>4</sup> When plants ascended to land, the atmosphere contained less O<sub>2</sub> (<50% of current levels, but the exact figure is debated). Less O<sub>2</sub> should have meant less ozone to absorb some of the sun's UV. (The extent to which a diminution of ozone from anthropogenic sources affects Earth UV flux is an important current field of inquiry. What inspires most rancor among the principals is the debate over whether the increased UV will result in significant crop loss.)

(F2) Development of stomata, which first appeared on the sporophytes of some advanced bryophytes (some mosses and hornworts; in both taxa, stomata are sometimes not functional). Stomata are lacking on bryophyte gametophytes—but, (nonadjustable) pores are found on the liverwort thallus, and some fossil gametophytes appear to have functional stomata. These plants—unlike living plants—had an isomorphic alternation of generations (i.e., the gametophyte and sporophyte generations looked identical.) As discussed elsewhere, the emphasis is placed on the role of stomata in conserving water, but transpiration through them pulls required nutrients up into the shoot, and the position and clustering of stomata on early land plants are consistent with their evolution to fulfill this role.

(F3) Development of vascular tissue, required to supply water to parts of the plant that are distant from a water source, and development of a water-absorbing organ, the root.

(F4) Development of mechanisms for coping with stress (an aquatic or a marine environment is relatively constant in temperature and water activity). During the course, we have discussed several such mechanisms (e.g., development of the seed and staggered germination). Many, many other mechanisms exist, some of which are obvious to you (e.g., shedding of leaves in the winter, shedding of leaves in response to drought). Such mechanisms take all forms. To give you a flavor of the ubiquity and diversity of these mechanisms, I will list a few examples: (a) All spores that are released by land plants have very elaborate, desiccation-resistant walls. (b) Land plants produce spores over a relatively long period. (c) The first land plants completed their life cycles over short periods. (d) Primitive “dioecious” land plants with motile gametes have sometimes evolved a simple but “clever” mechanism to ensure the proximity of the gametophytes: the tetrad of spores produced meiotically does not fall apart—two germinate to form female gametophytes and the other two germinate to form male gametophytes. Obviously, this strategy is counterproductive for outcrossing, but it does promote survival. (e) Land plants have evolved elaborate stress-signaling systems, which we can only partially explain presently. One of these, e.g., transduces the drought signal in roots to stomatal closure in leaves.

(F5) Development of photoprotective mechanisms. As mentioned, the cuticle absorbs UV light, but land plants have evolved a battery of redundant mechanisms (e.g., accumulation of UV-absorbing

---

<sup>4</sup>Kraus and his colleagues (*Plant Cell Environ* 20:1079) have shown that the cuticle can absorb an enormous amount of UV to protect the tissues underneath. An extreme example is the cuticle of *Cydonia oblonga* (the

flavonoids in the epidermis; movements) to absorb damaging light or dissipate excess light. (Land plants, it must be noted, are not the only organisms to have developed photoprotective mechanisms. E.g., some exposed algae accumulate high levels of nonprotein amino acids that absorb UV.)

(F6) Development of support tissues (an adaptation that coevolved with vascular systems).

To emphasize the significance of the development of the vascular system, I stress three areas: (1) the root, which contains a central core of xylem; (2) the stem, whose discrete vascular bundles are more advanced than the root's central core of vascular tissue; and (3) the leaf. Not all stems have the complicated vascular structure indicated by this dicot cross section, however. Stems of some primitive vascular plants have a structure similar to that of the dicot root. Some types of vascular anatomies, the different types of steles (= vascular cylinders), are shown in the next slide.

**POWERPOINT SLIDE:** Vascularization (Fig. 16-7 of Raven, Evert, and Curtis).

**POWERPOINT SLIDES:** A series of slides that review dicot anatomy, primary growth (root, shoot, leaf).

The most primitive type of stele, the protostele, is shown on the left. It is a solid core of vascular tissue. This type of stele is found in the primary growth of most dicot roots (as you have already seen), and as you will see, it is found in shoots of some seedless plants. (Although we will not be concerned with such arrangements, the relationship between the xylem and the phloem in the central core of the protostele can be different from what you have seen.) The siphonostele, shown at the center, comprises vascular tissue surrounding a central pith; you have not seen this arrangement before, and it is found in the steles of some vascular seedless plants. In the siphonostele, both the xylem and the phloem form a ring, and phloem may be outside the xylem or on both sides. The eustele, right, is found in the stele of many seed plants (recall the dicot shoot, primary growth). The siphonostele and the eustele evolved independently from the protostele, so extant seed plants (with eustele) did not arise from extant seedless vascular plants (with siphonostele). For more information, see the chart at the end of this topic.

Recall the difference between the development of a leaf (at the meristem) and the development of roots (from the pericycle). By definition, leaves contain vascular tissue, so the "leafy" lateral appendages of mosses are not leaves, although in informal discussions, that word is used for convenience.

---

quince), which permits only 0.02% of 300-nm radiation to penetrate.

**POWERPOINT SLIDES:** Microphyll and megaphyll evolution (Fig. 16-8 of Raven, Evert, and Curtis).

Restrict your attention to the bottom portion of the slide, which emphasizes leaf vascularizations and serves as a reminder that:

(G) Simple and equal dichotomous branching is the primitive condition. One sees how unequal branching results in more complex structures.<sup>5</sup>

(H) Although the structure of roots is primitive, their very presence is an advanced condition.<sup>6</sup> gametophytes do not develop true vascularized roots (though they do form absorbing structures, rhizoids).

(I) The presence of true leaves is advanced.

---

<sup>5</sup>Additional information about types of leaves is found in the chart at the end of this topic.

<sup>6</sup>Sporangia are always part of the shoot system, and plants are sexual creatures, ergo the “requirement” for a shoot but not a root.

*Ferns and Fern Allies*

Characteristic	Whisk Fern <sup>a</sup>	Club Moss	Horsetail <sup>b</sup>	Fern <sup>c</sup>	Gymnosperms <sup>d</sup>	Angiosperms <sup>d,e</sup>
Vascular tissue	all					
True roots, leaves	-(+)	+	+	+	+	+
Large leaves	-	-	+(-)	+	-/+	+
Gametophyte retained in sporophyte	-	-	-	-	+	+
Sperm w/o flagella	-	-	-	-	+(-)	+
Production of seed	-	-	-	-	+	+
Flowers/fruit	-	-	-	-	-	+

<sup>a</sup>No roots. <sup>b</sup>Articulated, "reduced" megaphylls. <sup>c</sup>Real leaves. <sup>d</sup>Seeds. <sup>e</sup>Flowers.

We will discuss several examples of extant seedless vascular plants. **Focus** on the evolutionary trends that are seen in each, as pointed out in the preceding table. Do not miss the point by considering it so much information to commit to memory. A master table<sup>7</sup> also follows this topic for your convenience. Although I will provide an exposure to the various seedless vascular plants listed in the table, the emphasis will be on ferns themselves.

As noted, our focus will be on ferns. Altogether, we will briefly look at four groups, in part because of tradition and in part because of morphology. **In a formal treatment, three of these are condensed into one phylum and the club mosses remain unique. If you wish, more information can be found in your textbook.**

Whisk Fern

**POWERPOINT SLIDE:** *Psilotum* (Botanical Garden, University of Tübingen).

This group is tropical and subtropical and is represented by only two living genera. The distinguishing characteristic is that they are the only extant vascular plants that do not have roots (*Psilotum* lacks true leaves, but the other living genus, *Tmesipteris*, has microphylls (each has only a

---

<sup>7</sup>**IMPORTANT:** do not consider the master table at the end of this topic simply something else to memorize—that is not its purpose. You will not be responsible for any information that appears ONLY in the master table. You will, of course, be responsible for anything mentioned in lecture, in the normal text, or in the objective questions.

single vein) arranged spirally. The shoot has a simple contiguous vascular system (like the dicot root), which is not dissected into bundles. Both genera have primitive dichotomous branching. They are homosporous—they have only one type of spore (sporangia are borne in "axils" of "leaves"), which forms a bisexual subterranean gametophyte—the gametophyte (reminiscent of the moss protonema) is associated with a fungus. Like some bryophytes, the Psilophyta evolved from more complex ancestors.

#### Club Moss

**POWERPOINT SLIDE:** *Lycopodium* (club moss) (Botanical Garden, University of Tübingen).

Although this plant is small, fossil lycophyte trees exhibited secondary growth and were among the dominant plants of the coal-forming forests.

The Lycophyta include only five living genera, which range from the arctic to the tropics. The plant forms a rhizome (underground stem) from which aerial branches and adventitious roots arise. The leaves are borne spirally (one vein per leaf, so they are microphylls). Species are homosporous or heterosporous. Sporangia are on the upper surfaces of the microphylls *or* are borne in "cones" at the top of the plant. The gametophyte is subterranean. Heterospory is thought to have evolved in the lycopods and independently in several other lines. The vascular tissues may or may not be dissected into bundles. Depending on genus, the sperm are biflagellate or multiflagellate.

#### Horsetail

**POWERPOINT SLIDE:** *Equisetum* (Botanical Garden, University of Tübingen).

The Sphenophyta include only one genus (*Equisetum*). Its distinguishing characteristic is its conspicuously jointed stems with whorled leaf arrangement at the nodes. (No other plant looks like this.) The Sphenophyta have leaves, which are usually interpreted as megaphylls. Having only one vein, the leaves look like microphylls, but the current consensus is that these leaves have evolved through reduction to their present state. Ferns were the first extant plants to have evolved complexly vascularized leaves (i.e., megaphylls). Like the lycopods, sphenophytes usually have roots. They are homosporous(?). (A degree of heterospory is apparent—two size classes of spores are formed, one giving rise mostly to male gametophytes and the other to bisexual gametophytes; both are very small, about the size of a pinhead.) Sporangia are born on terminal "cones." They have discrete vascular bundles.

Ferns

**POWERPOINT SLIDE:** Fern body (Fig. 24-2 of Wilson, Loomis, and Steeves).

Ferns are diverse in habit and include some plants that look unfernlike:

**POWERPOINT SLIDE:** Mexican tree fern (*Cibotum schredei*) (U.S. Botanical Garden, Washington).

**POWERPOINT SLIDE:** Australian tree fern (U.S. Botanical Garden, Washington).

**POWERPOINT SLIDE:** Brazilian tree fern (*Dicksonia* sp., Rio Grande do Sul, Brazil).

**POWERPOINT SLIDE:** Staghorn fern (*Platycerium vassei*) (U.S. Botanical Garden, Washington).

**POWERPOINT SLIDE:** Bear's paw fern (*Aglaomorpha meyeniana*) (U.S. Botanical Garden, Washington).

**POWERPOINT SLIDE:** Himalayan maidenhair fern<sup>8</sup> (*Adiantum microphyllum*) (U.S. Botanical Garden, Washington).

**POWERPOINT SLIDE:** Bird's nest fern (*Asplenium nidus*) (U.S. Botanical Garden, Washington).

In contrast to the previous groups, the ferns comprise many living species (about 12,000, that is, many more than gymnosperms). Their distinguishing characteristic is that they are the only seedless vascular plants with obvious megaphylls ("normal" leaves). Leaf development is distinctive; the frond unfolds spirally, as shown in the slide.

---

<sup>8</sup>In the beginning of this course, I emphasized the importance of plants as sources of medicinals. As a means of noting that seedless plants were also part of the herbalist's stock, I take this quote from D. Brown o.c.: "Medicinal uses of the maidenhair fern have been recorded since Classical times. Dioscorides mentioned 'adianton' for asthma; Culpeper valued it as 'a good remedy for cough, asthmas, pleurisy, etc., and on account of its being a gentle diuretic also in jaundice and other impurities of the kidneys'; and Gerard claimed it was a hair restorative. It was once popular as *sirop de capillaire*, a cough mixture made from rhizomes and fronds, flavored with orange blossoms. The hardier *A. pedantum* from America and Japan is used in similar ways. *A. aethiopicum*, which occurs in Australia, has been used by Aborigines to sooth bronchial complaints. *Capillus-veneris* means 'Venus' hair' and may refer to the Roman goddess of love, who rose from the waves with miraculously dry hair."

The fern embryo—unlike that of other seedless vascular plants—does produce a root, but it withers. In short, the roots of all seedless vascular plants (when roots are present) are adventitious, unlike the general situation in gymnosperms and dicots.

Usually, seedless vascular plants lack a vascular cambium (which gives rise to secondary growth), but several extant (e.g. *Isoetes*, in the Lycopphyta) and fossil vascular plants do have a vascular cambium, and some fossil species reach the proportions of trees.

**POWERPOINT SLIDE:** Fiddlehead, unfolding to become a leaf (north Leon County, Florida).

Ferns are usually homosporous. Spores commonly form in sporangia (sori) on the undersurfaces of leaves (called fronds in ferns).

**POWERPOINT SLIDE:** Sori (north Leon County).

The vascular arrangement depends on species.

**POWERPOINT SLIDE:** Life cycle of ferns (custom).

(A) Haploid spores (at 11 o'clock) are formed in the sporangium. Clusters of these sporangia are the sori (singular, sorus) as seen previously.

(B) A special layer of cells in the sporangium deform, bending the top back and taking most spores with it in the "cap."

(C) The spore germinates (11 o'clock), giving rise to a bisexual, rootless, independent *green* gametophyte—often heart-shaped and one cell layer thick. An important point: although ferns are homosporous and form bisexual gametophytes, the archegonia and antheridia of a particular gametophyte do not mature at the same time. Therefore, gametes of a single gametophyte do not undergo syngamy. If they did, the sporophyte would be homozygous, which is undesirable.

(D) The multiflagellate sperm (2 o'clock) swims to the archegonia and down the neck canal and fertilizes the egg, forming the embryo. (Some ferns develop archegonia and antheridia at different times, ensuring outcrossing.)

(E) The resulting zygote divides; depends on the gametophyte for some time; differentiates into root, stem, and leaf; and finally develops into the mature sporophyte.

**CHART: SOME GENERAL CHARACTERISTICS OF 4 EXAMPLES OF EXTANT, SEEDLESS, VASCULAR PLANTS**

(As mentioned in the narrative, three of these four groups are now considered to be in one phylum while Lycophyta remains separate.)

Group	Leaves	Roots	Stele <sup>a</sup>	Body organization
Psilophyta Example: <i>Psilotum</i>	NONE (spiral scales) <sup>b</sup> (distinguishing characteristic)	NONE (rhizoids) <sup>c</sup>	protostele	unbranched or dichotomously branching; sporangia at "elbows" of leaf-like scales; homosporous <sup>d,e</sup>
Lycophyta Examples: <i>Lycopodium</i> ( <i>Isoetes</i> ) ( <i>Selaginella</i> )	MICROPHYLLS (distinguishing characteristic)	true roots present (also rhizomes with adventitious roots)	protostele	(usually) spirally arranged small leaves; reclining rhizome with erect branches; sporophylls sometimes grouped into cones; homo- and heterosporous
Sphenophyta <sup>g</sup> Example: <i>Equisetum</i>	single-veined, but usually interpreted as reduced megaphylls	occasionally present (adventitious arising at some nodes)	siphonostele (modified)	conspicuously jointed stem; whorls of scale-like leaves (distinguishing characteristic) interpreted to be reduced megaphylls; sporophylls grouped into cones; homosporous  (. . .)
Pterophyta "ferns"	megaphylls; complex—with palisade +spongy	root formed by embryo withers; adventitious roots on rhizome	various	diverse, including unfernlike representatives; sporangia commonly in clusters, called sori (singular: sorus); homosporous (except . . .)

<sup>a</sup>A protostele is more or less a core of vascular tissue, like the primary growth of a dicot root. A siphonostele is a "tube" of xylem, with cortex outside and pith inside. Phloem is located just external of the xylem and sometimes internally also. A eustele is a ring dissected into vascular bundles (e.g., as in primary growth of the dicot stem). Other, finer distinctions exist (e.g., monocot shoot) but we will disregard them. Generally, secondary growth is absent in extant seedless vascular plants.

<sup>b</sup>We speak broadly here and ignore the interpretation given to *Tmesipteris*, a genus that is closely related to *Psilotum*.

<sup>c</sup>A rhizome is an underground stem, which is recognized from anatomical features (i.e., presence of nodes, surficial origin of lateral appendages, organization of apex (w/o cap), and vascular organization). For our purposes, we will use rhizoid as a diminutive, which in extreme was the single-celled rhizoid of the liverwort gametophyte.

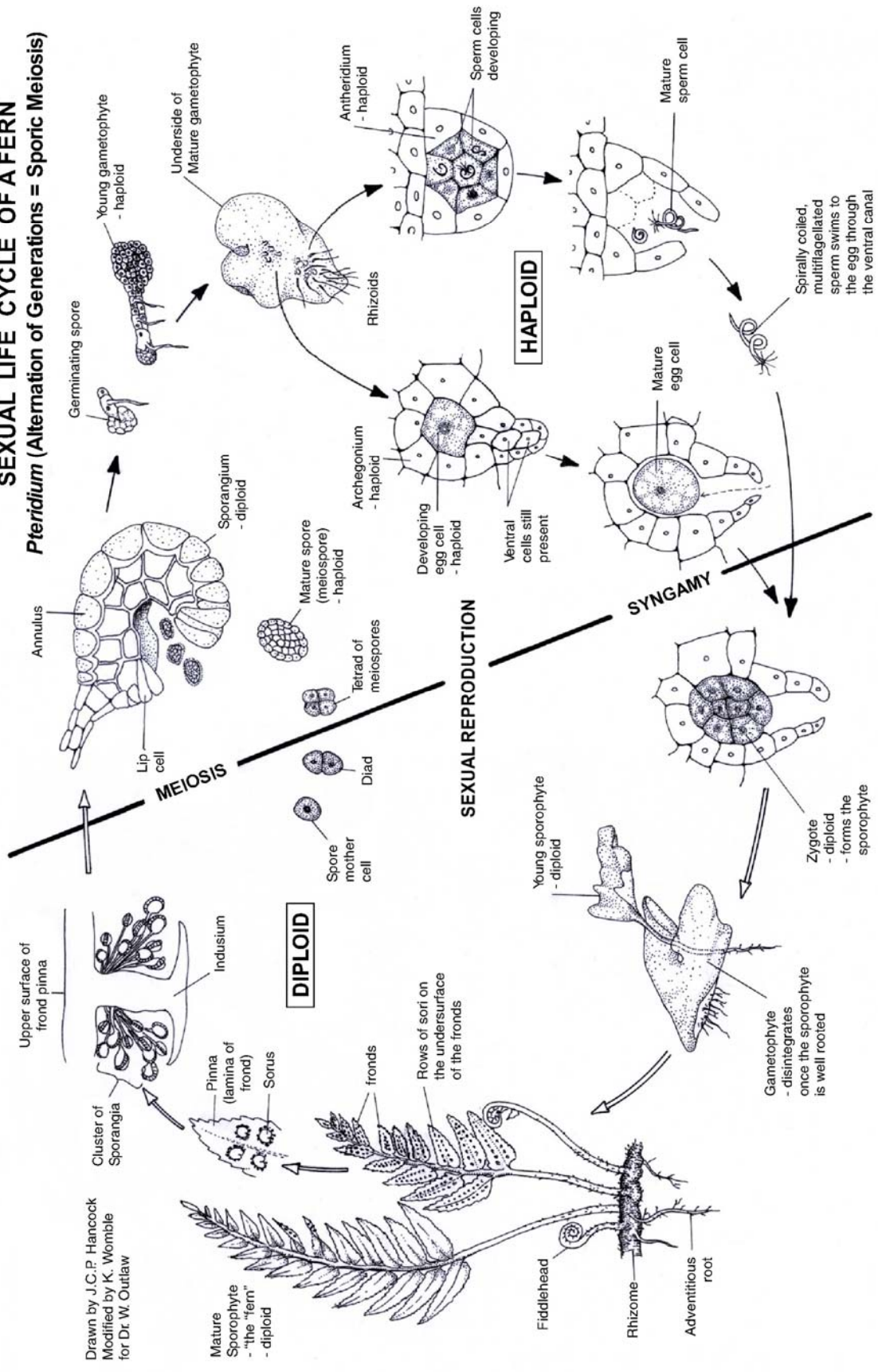
<sup>d</sup>Homosporous means having haploid spores that are not morphologically distinguishable. (Heterosporous is the opposite.) Heterosporous plants have distinct male and female gametophytes. (Though often invoked, the converse of this statement does not necessarily hold and leads to some contrived terminology such as "physiological" heterospory, but that is beyond this course.)

<sup>e</sup>Traits may arise independently, and a seemingly advanced characteristic may be found in primitive organisms. E.g., vessels—more advanced tracheary elements—are found in angiosperms and some seedless plants but not in gymnosperms (except . . .). Similarly, heterospory apparently arose more than once. Perhaps less intuitive is that some biochemical traits, such as C<sub>4</sub> photosynthesis (known only among angiosperms), arose several times. As an aside, CAM (which also has multiple origins) is known among seedless plants (*Isoetes* sp.).

<sup>f</sup>The microphyll, a primitive type of leaf, has but a single vein. It is presumed to have evolved as an outgrowth ("thorn") from a protostele-type stem. Megaphylls, usually but not always larger than microphylls, have a more complex venation pattern. These latter are presumed to have evolved from branches across which a ground and dermal system spread. Megaphylls are usually associated with either a siphonostele or a eustele.

<sup>g</sup>Interestingly, a "common" name for sphenophytes, articulates, reflects their most striking feature (viz., jointed stems).

# SEXUAL LIFE CYCLE OF A FERN Pteridium (Alternation of Generations = Sporic Meiosis)



Drawn by J.C.P. Hancock  
Modified by K. Womble  
for Dr. W. Outlaw

Mature Sporophyte - "the fern" - diploid

**DIPLOID**

**HAPLOID**

**SEXUAL REPRODUCTION**

**MEIOSIS**

**SYNGAMY**