VIII. Equisetophytes: The Horsetails

A. Equisetum

The horsetails are the only living members of the Equisetophytes. The genus Equisetum, in which all the horsetails are classified, contains a small number of species from diverse geographic sources and ecological habitats. A small, unbranched species reaches the Arctic Circle in wet areas. A tall, robust species some 10 or more feet high and nearly an inch in diameter grows in wet areas of the tropics. Equisetum hyemale, a species you will examine in this laboratory, thrives on seepy hillsides in our part of the world. Distinctive whorls of fused leaves and sometimes branches characterize Equisetum.

1. Basic Morphology of the Sporophyte

Fig. 8

a. Study a fresh aerial axis of Equisetum hyemale (Fig. 8)

i. Each node stands out, since it has a sheath of minute leaves. These leaves, technically microphylls because each has a single vascular bundle, are fused together for half their length or more. Nevertheless, you should be able to pick out the individual leaves that together make up the whorl.

ii. Notice that the leaves are in whorls – that is to say in sets radiating from nodes. Whorled leaves and branches (present in many of the species, though not this one), are a diagnostic feature of the Equisetophytes.

iii. The internodes of these horsetails have characteristic ridges.

b. Look at a piece of internode from the scouring rush, Equisetum

hyemale, under the dissecting `scope.

i. Under the scope the ridges look bumpy: what you are seeing is an encrustation of silica on the surface cells. Equisetum is unusual among plants in having silica. Silica is very hard - harder than steel in fact. It's said that scouring rush was used like a scouring pad for scrubbing pots in the old days - no wonder!

ii. Between the ridges are two minute lines of glistening dots. These are the lines of sunken stomates that lie in the grooves between the ridges.

2. Anatomy of the Internode

Look at a prepared slide of the Equisetum arvense sterile stem transverse section (x.s., internode). DIAGRAM the section as you work - make a DRAWING of a single sector including at least one vascular bundle. Under lowest power, the ridges in the stem stand out, as do the several rings of large cavities in the interior of the stem.

a. Search for sunken stomates in the grooves between the ridges, out at the exterior of the stem. They are sunken in that the guard cells are not right at the surface, but set into a pit in the surface of the stem.

b. These stomates open inward into the first ring of large cavities. These irregular cavities are for gas exchange - the stem cortex of the horsetails is where most photosynthesis takes place, since the leaves are so small.

c. The next ring of cavities are called *vallecular canals*, which lie in the inner part of the cortex. There has not been a function demonstrated for these canals.

d. Just interior to the vallecular canals and alternating with them are the *carinal canals*. Survey these under higher power. These carinal canals were formed during the elongation of the internode by the stretching and destruction of the protoxylem. Look for remnant protoxylem cells in one or two of the carinal canals. Use these hints:

i. They usually stick out a bit into the canal.
ii. They have slightly thicker walls than the cells around them.
iii. They have enough lignin to stain a bit pink.

The carinal canals function in water transport.

e. Now investigate the vascular bundle, the group of small cells just outside of each carinal canal. The phloem makes up the vast majority of each vascular bundle. The inner limit of the phloem is the carinal canal itself; the outer limit is the endodermis, a layer of cells that runs around the entire group of vascular bundles.

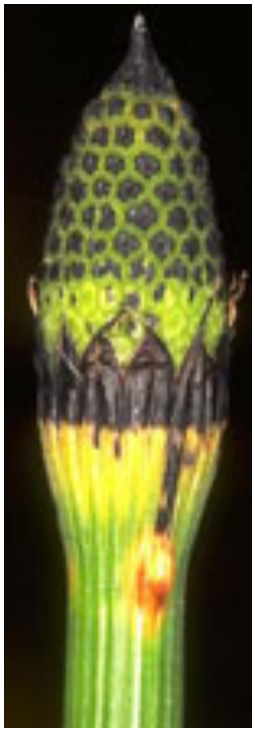
To identify the endodermis, look at the layers of cells just outside the vascular bundle under medium power. The first layer of cells that is noticeably larger than the cells of the vascular bundles is the endodermis. The cell walls of the endodermis are fairly thick, except for a small region in each radial wall, which is thin and transparent. This small, transparent zone, actually an area of cell wall impregnated with a waxy compound called suberin, is the casparian strip. The casparian strip functions as a waterproof "gasket," making it impossible for water to flow between the vascular cylinder and the cortex by passing between cells. To flow from one region to another, water must move *through* the endodermal cells, a process that the cell can regulate. The casparian strip is present in the roots, rhizomes, and often even the aerial stems of most vascular plants.

f. Now look back at the vascular bundle. To each side of the phloem mass are one or two larger, empty cells with thicker, slightly pink cell walls. These are the metaxylem elements of the vascular bundle. Think about it; a canal has most of the water-conducting capacity of this plant - the xylem is of little importance, at least in the internode. (In the nodes, there are no cavities and the xylem remains functional.)

g. At the very center of the stem is the *pith cavity*. Originally filled with parenchyma, the innermost part of the stem was disrupted during internode elongation. The original parenchyma cells have been destroyed, and all that remains is space.

3. Dissection of an Equisetum strobilus.

Take a strobilus from one of the jars of pickled material available in the lab. Put the strobilus on the stage of your dissecting microscope and begin by looking at its general features.



a. Note that the surface of the strobilus is made up of whorls (rings) of more or less hexagonal sectors. The theme of whorled design is repeated in the strobilus (Fig. 9).

b. Now use probes to break open the strobilus and figure out how it is constructed. You should be able to see that the hexagonal sectors are at the tips of the lateral axes (called sporangiophores), each attached to the main stem. Attached under the tips of the sporangiophores are sets of sporangia. Think of the sporangiophore as an umbrella and the sporangia as balloons hanging from beneath the shelter of the umbrella.

c. Examine the longitudinal section of the Equisetum strobilus to see how the sporangiophores are arrayed relative to one another and to the strobilus axis.

Fig. 9

d. Next choose a single sporangiophore with sporangia and isolate it on the surface of the 'scope stage. Break open the sporangia and spill their contents on the stage. Watch as the contents dry. At highest power you should be able to see the spores gradually dry out and start to writhe and gesticulate - through the action of spore-wall features called *elaters*. To see the elaters of your spores, mount them on a microscope slide and look at them under the microscope.

4. Transverse section of a mature Equisetum arvense strobilus.

Look at this section under low power. You should be able to see the

basic features of the strobilus again, only more neatly prepared. DIAGRAM the section as you work. Make sure your diagram shows the relationship between the sporangia and the sporangiophore that bears them. Label both the sporangiophore axis (this feature may not be visible insections) and the terminal flange.

a. The sporangia stand out because they are full of spores, brilliant red. Presumably, the dense red substance in the spore interior is fat or oil serving as stored nutrients for the beginning of gametophyte growth. The elaters are visible as little turquoise threads surrounding the spores.

b. The sporangium wall at maturity consists of two layers of cells, a small inner one and a larger outer one with helical secondary-wall thickenings. These thickenings play a role in the support and dehiscence of the sporangium. As the sporangium dries, these cells dry out. The cells change shape as they dry because of the thickenings, so that the sporangium wall is distorted and ruptures.

c. Note that the sporangia are attached underneath a terminal flange of the sporangiophore.

d. Look at the vascular cylinder in the center of the strobilus axis. Contrast the design here with that of the internode - the basic difference is that these cells have not been disrupted by extensive elongation of the internode, so that the canals are for the most part missing and the vascular bundles are intact.

i. Only a poorly developed pith cavity is present: it looks much more as if it was the product of the tearing apart of parenchyma cells.

ii. The vascular bundle has a substantial number of metaxylem cells, perhaps a few protoxylem cells, and little or no carinal canal.

iii. You may be able to see that there is an endodermis with a casparian strip even here in the strobilus - it's hard to see.

5. Equisetum shoot apical meristem.

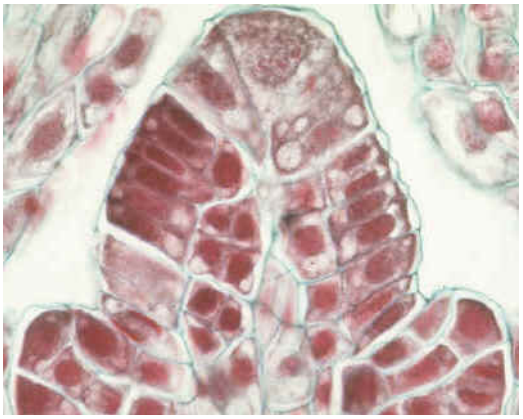


Fig. 10

Look at the demonstration slide of the Equisetum shoot apical meristem. You will see one very important additional detail of vegetative structure. The apical meristem in this slide shows one of the best examples of a single tetrahedral apical initial we will see in the course (Fig. 10). This sort of meristem is typical of many spore-dispersed vascular plants. Mitosis, packets of cells derived from a single derivative, primordia, differentiating tracheids, and opening canals are all visible in this slide.

6. Equisetum Gametophytes

Look at the prepared slides of Equisetum gametophytes. These independent gametophytes are quite different from those of Lycopodium: they are made up of *lamellae*, which are delicate, flat growths of photosynthetic cells, with gametangia attached. The antheridia are located up toward the tips of the lamellae, whereas the archegonia are often hidden down at the base of the lamellae. Ordinarily, the archegonia and antheridia are located on different gametophytes, though antheridum-bearing lamellae can sometimes develop on old archegoniate gametophytes. DIAGRAM a gametophyte with antheridia.

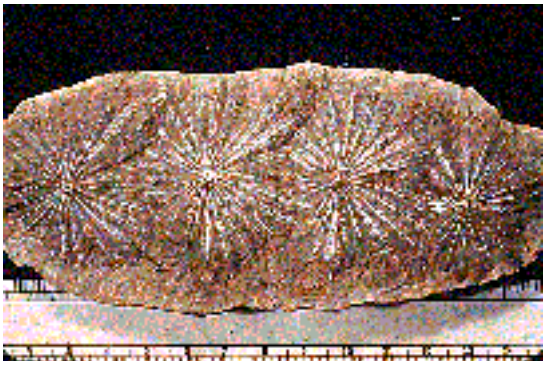
B. The giant fossil horsetail, Calamites

In the same swamp with Lepidodendron was a horsetail that grew to 30 feet or more high. Stem structure looks weak enough so that most botanists accept the idea that these Calamites plants grew in thickets and held one another up. They are placed in the Equisetales, the same order as the living horsetails.

Three form genera are important to us:

Annularia: small stems with leaves

Asterophyllites: small stems with leaves
Calamites: petrifactions and casts of large stems



1. Look at the two form genera of leaves. Notice that both are whorled. We now think that the differences in the rock represent real differences in the arrangement of leaves on the original shoots – Annularia (Fig. 11) leaves tilted to one side, whereas Asterophyllites had its leaves arranged symmetrically around the stem.

Fig. 11

If we are right about the arrangement, then the branches that held the two form genera of leaves were probably at different angles to the main stem - think about it.

2. Look at a stem peel of Calamites. Most important to note is the broad layer of secondary xylem - these plants had cambia. Inside the secondary xylem is a pith cavity, and between the two is a zone with separate little vascular bundles (same as in the living stem) protruding out into the pith cavity. (These are not preserved all the time, so look carefully around the pith cavity to see them.)

Contrast the peel with a pith cast. The pith cast is the mud that lay in a pith cavity now turned to stone, so that the furrows in the surface of the pith cast correspond to the vascular bundles of the original primary body of the Calamites stem.

Make DIAGRAMS of both the cast and the peel and label them to make comparison of the two clear.

C. Fossils of Sphenophyllum, Order Sphenophyllales

Look at compression fossils of Sphenophyllum (Fig. 12). You can see a few things just from these compressions, which have been likened to fossil

butterflies.

1. Notice that the stem of this plant is very delicate. It's thought that these plants were scrambling vines that grew up onto other plants rather than standing erect, mostly because these stems look too weak to stand alone.

2. Notice that the leaves are whorled, just as in the other Equisetophytes.

3. However, you should be able to see that the venation in the leaves is complex - it divides over and over again. This sort of leaf, which is called a megaphyll, is thought to be very different in its origin from microphylls. Strobilus structure of these plants was very specialized as well.

We'll have more to say on Sphenophyllum in class. For the moment, the important thing to remember is that this genus has a few superficial Equisetophyte features (like whorled leaves), but many more fundamental features that distinguish it from the Equisetophytes. In fact, some botanists question whether Sphenophyllum is very closely related to the true horsetails at all!

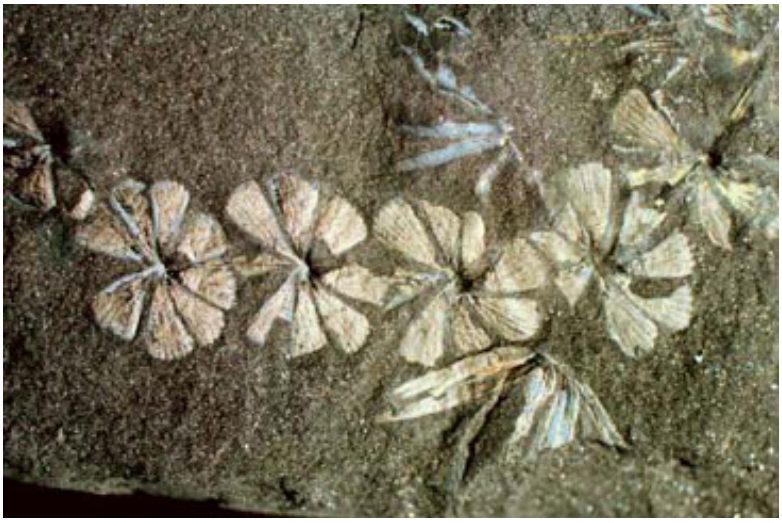


Fig. 12