At the present time there are competing hypotheses about the relationships among euphyllophytes. Some phylogenetic analyses that are based on only living species have yielded trees in which the seed plants are the sister group to all other euphyllophytes (i.e., Psilotopsida, Equisetopsida, and Pteropsida (= Filicopsida of some authors; Fig. 1). The large clade has been named Moniloformopaida as originally hypothesized from Devonian fossils by Kenrick and Crane (1997; Pryer et al., 2001). That hypothesis also predicts that the megaphyll has evolved only once among euphyllophytes and that both equisetophytes and psilotophytes are derived from a common ancestor that was a fern (Fig. 1).

Fig. 1 (Fig. 1 of Pryer, et al., 2001).
However, other phylogenetic analyses, including all those that also include extinct plants in the analysis, resolve a completely different pattern of relationships (Rothwell, 1999; Rothwell and Nixon, 2005). The fossil record, transformational series of morphologies, and more inclusive studies all reveal that Sphenopsida has a separate origin from trimerophyte grade euphyllophytes (Fig. 2). There is also growing evidence that the megaphyll has originated numerous times within the euphyllophytes (Tomescu, 2009; also see Fig. 3 of Lab. 6). Therefore, it is becoming increasing apparent that the “Moniliformopsida” does not reflect the overall pattern of euphyllophyte phylogeny. Rather, it is merely a reflection of restricted and inadequate (i.e., living species only) taxon sampling.

**Order Equisetales, Genus *Equisetum***

**General Features of Sporophytes**

*Equisetum* is the sole living genus of the Sphenopsida. About 15 species are recognized in The Flora of North America, and these occur in wide range of habitats. Species of this class are characterized by having articulated or jointed stems that bear whorled branches and leaves. The fertile structures of the sporophyte are usually aggregated into terminal strobili and consist of a stalked, peltate *sporangioaphore*. Each sporangioaphore bears several sporangia on the under surface, and the sporangia are *recurved* back...
toward the stem or cone axis. In some of the fossil members, whorls of sporangiophores alternate with whorls of leaves (called bracts in this instance), but in *Equisetum* the cone contains only sporangiophores. Probable sphenopsids are known from the Upper Devonian, but the class reached its zenith during the Carboniferous Period. Some of the fossil forms were arborescent and reached heights of twenty meters or more. Some of the extinct forms were heterosporous, and one species produced seed analogues with only one functional megaspore per sporangium. *Equisetum*, however, is homosporous. Of the various orders generally recognized in the Sphenopsida, we will deal with only one in laboratory, the Equisetales.

Examine material of *Equisetum arvense*, a species that is often found along railroad right-of-ways. This species produces aerial branching systems of two types; i.e., the branching is dimorphic. Very early in the spring, brownish fertile stems break through the soil and bear terminal cones. These cones are made up of sporangiophores, and the fertile stems are ephemeral. Later in the spring, the same rhizomes produce green, vegetative branching systems. These systems have whorls of scale leaves, and branches of several orders arise in whorls.

Note that this species has perennial rhizomes, but that the aerial shoots last only one year. Draw the growth form of *Equisetum arvense*. Be sure to include the dimorphic branching of the aerial shoots.

Now examine *Equisetum hyamale*, another native species. This species has perennial aerial shoots that are sparsely branched, and that have cones that are terminal. Sketch the growth form of *E. hyamale*.

**Anatomy of the Stem**

The stem of *Equisetum* contains very little vascular tissue and is entirely primary, even in the tropical forms that often reach 20 feet in height. Examine a stem longitudinal section to see the intercalary meristems, that are responsible for most of the elongation of the stem. Examine a cross-section of a stem and locate a ring of large canals in the cortex. These are the **vallecular canals**. An additional ring of canals is present deeper within the stem. These are smaller in diameter and mark the position of the first-formed xylem, or protoxylem, that became disorganized as the stem elongated after the cells matured. The resulting canals are called **carinal canals**. Metaxylem cells can be seen just outside of the carinal canals--two groups of cells per vascular bundle. These xylem cells flank a region of primary phloem.

Note that each vascular bundle is opposite a ridge on the outer surface of the stem. These ridges mark the location of sclerenchyma tissue in the cortex. The vallecular canals alternate in position with the carinal canals, a vallecular canal occurring opposite each of the furrows on the outer surface of the stem. Stomata generally occur in the furrows and are sunken below the surface. In most species the central portion of the stem (pith) becomes hollow in the internodes. Diagram the cross-section of the stem. Examine transverse sections of rhizomes and roots. How are they similar in anatomy to the stem?

**Structure of Strobilus**

Examine a longitudinal section through a cone that shows the structure of the cone units. Each of these units is a sporangiophore consisting of a stalk attached to the cone axis, a terminal fleshy head and a number of sporangia. The sporangia are pendant from the head, where they are attached to its inner surface and extend horizontally from the head toward the stem. These sporangia may be described as being recurved toward the stem. Note that the cone is homosporous and that the sporangia are relatively massive. Diagram a portion of this longitudinal section of the cone.

Using either fresh or preserved cone material, dissect out a single sporangiophore. Note the
appearance of the outer fleshy head. How are the sporangia arranged? What type of symmetry does this cone unit have? Does this appear to be a type of sporophyll? Draw the isolated sporangiophore.

Crush a sporangium onto a microscope slide. Note that the spore body is surrounded by coiled appendages called elaters, which are formed as thickenings of the perispore. As the spores dry out, the elaters will snap open violently, and the spores will separate and partially disperse. Would these elaters seem to have some adaptive advantage?

Gametophyte Phase

The gametophytes of *Equisetum* are potentially bisexual, but sequential development of the antheridia and archegonia generally ensures cross-fertilization. The mature gametophyte is lobed, green, and about 1/4 inch in diameter. Rhizoids anchor the plant to the substrate. Look at the gametophytes of *Equisetum* that are illustrated by Eames (1936; Page 100). How many sporophytes are produced by a single gametophyte. What does this suggest about the ancestral life cycle of vascular plants?

Life Cycle Exercise

Go to the “Equisetum Life Cycle” flash video on the course web site, and check to see how well you understand this plant.

Order Calamitales

The order Calamitales extends from the Missippian through the Permian, and is characterized by large, woody trees of the coal swamps. Calamitean plants are quite similar to *Equisetum*, but they are much bigger and probably lived for many years. They had leaves that were larger than *Equisetum*, and that were not fused to each other. Leaves are assigned to morphogenera, a common one of which is *Annularia*. The most common morphogenus of cones is *Calamostachys*, which had whorles of bracts that alternated with whorles of sporangiophores. How does this structure differ from the cones of *Equisetum*? Woody stems of the calamites are given several names, but the most commonly known one is *Calamites*, which also used for whole plants.

Examine the photographs of *Calamites* plants that are on display from the recent paleobotany textbook by Taylor, et al. (2009). Now examine the pith casts and woody stems of *Calamites*, compressed stems with *Annularia* leaves, and an anatomically preserved *Calamostachys* cone that are on demonstration. Compare these fossils to the figures on pages 200-203 of your textbook. If *Equisetum* is descended from the Calamitales, what changes would have occurred during the evolution of *Equisetum*?

References


