VASCULAR PLANT MORPHOLOGY
LABORATORY 3

Simplest and Earliest Land Plants

At one time all of the most ancient (i.e., fossils of the Silurian and Devonian) and simple vascular plants were placed in the class Psilopsida. The Psilopsida now has two living genera; Psilotum and Tmesipteris. Three additional classes, the Rhyniopsida, the Zosterophyllopsida and the Trimerophytopsida were proposed by Banks in the 1960s to include most of the ancient (Silurian and early Devonian) vascular plants see #1, below). Many people regard the Psilopsida as having descended from the Rhyniopsida, however, no connection occurs in the fossil record. Others regard the similarities between these two groups as being the result of convergent evolution. More recent cladistic studies have demonstrated that none of the classes of anticent fossil plants is monophyletic (see #2, below). Nevertheless, they continue to serve as a convenient framework for presenting an introduction to the material.

Included within these classes are homosporous plants with no true stems, leaves or roots. The sporophyte plant body shows little organ differentiation and is generally considered to be made up of axes. Superficial enations occur on the aerial parts of some species. The axes usually branch dichotomously, and the resulting axes may be **equal**, **unequal**, or form a **pseudomonopodial** system. The sporangia are either clearly terminal on branches, or in an apparently lateral position. In the latter case, some sporangia appear to be actually terminal on much reduced lateral branches. The axes of the plants usually form two systems, an underground and an aerial one. The underground system serves for anchorage and absorption of materials via rhizoids. The aerial system serves in photosynthesis, in support of the reproductive structures, and in conduction of materials (via the stele).

1) Generalized Phylogenetic Relationships of Tracheophytes (Traditional Representation from Knoll and Rothwell, 1981)

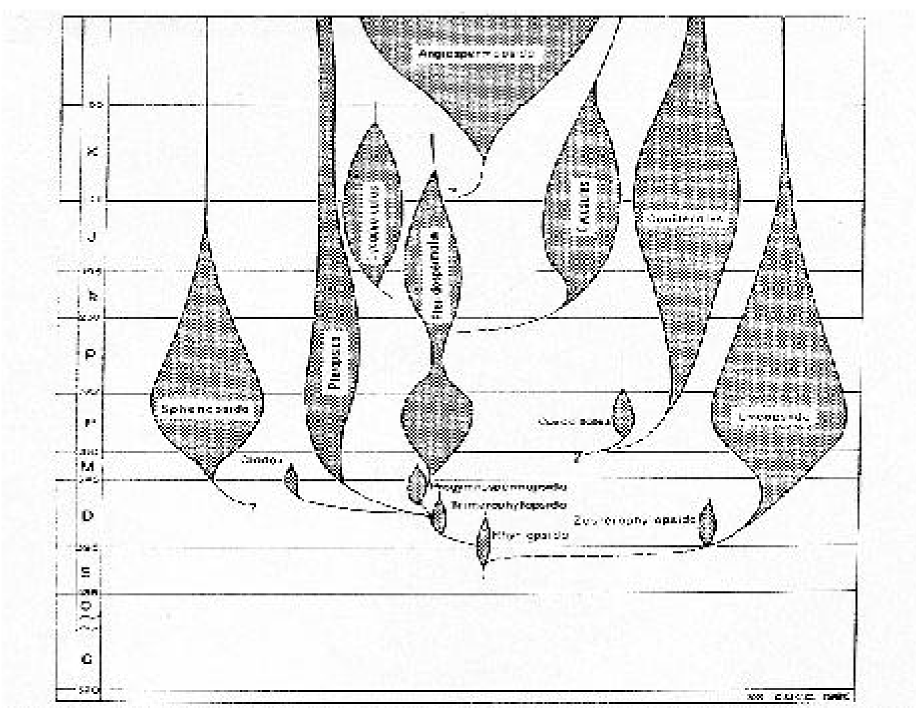
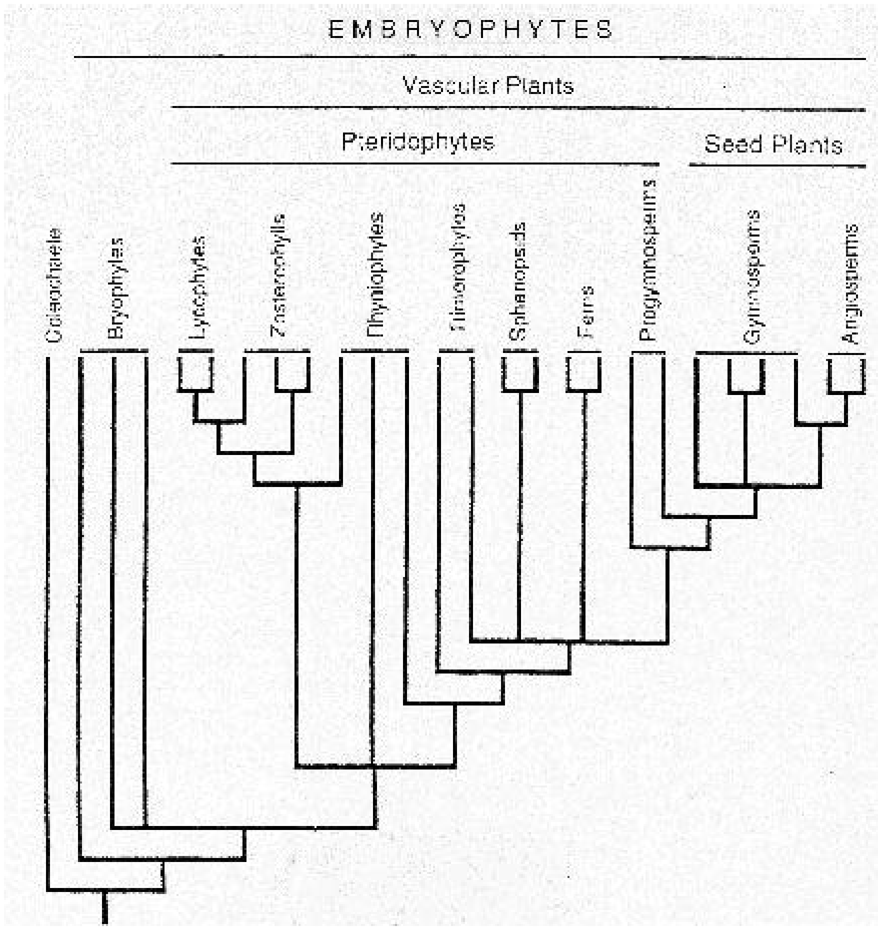


FIGURE 2. Generalized phylogenetic relationships of major vascular plant groups as understood in 1980. Contrast with Fig. 1, which shows relationships as understood in 1960. See Fig. 1 for further explanation of the figure.

2. Cladistic Representation (from Rothwell, 1994; as modified from Crane, 1990)



The Simplest Living Pteridophytes

Class Psilopsida

Genus <u>Psilotum</u>
*Examine a potted plant of <u>P</u>. <u>nudum</u> to familiarize yourself with the overall habit of this sporophyte phase. Obtain a piece of the plant having an aerial branching system arising from a portion of the underground system of axes. Note the dichotomous branching of both systems. Are the aerial axes completely naked? Why are the scale-like structures on these axes not considered to be leaves by most people? Note synangia and below these, forked enations.

Examine the underground system. How does it branch? Are roots present?

Sketch a portion of the plant to show these basic external features of the sporophyte.

Cut free-hand sections of the underground axes and examine with the microscope. Note that the vascular tissue is in an extremely simple arrangement. Xylem in the very center, surrounded by phloem and endodermis. Note the rhizoids arising from the epidermis and the parenchymatous cortex. As is characteristic of vascular plants, these rhizoids are unicellular.

Diagram this axis cross-section.

Now examine prepared slides of the aerial axis in transverse section. Locate the xylem and phloem. The xylem has arm-like projections, and the center of the vascular cylinder may have parenchyma present. Note the various regions of the cortex. Do these zones appear to have different functions on the basis of their cellular makeup?

The epidermis contains numerous stomata. Locate a stoma and note its basic features. Note also the thick layer of cutin (the cuticle) on the surface of the aerial axis. What type of functions does this axis appear to carry out in the life of the plant?

Diagram a cross-section of the aerial axis.

Draw a stoma as it appears in cross-section.

Examine the synangia on the living plant of Psilotum. Are any external indications present that this apparently single structure may consist of more than one part? How many parts? Is the synangium sessile or is it stalked?

Examine prepared slides of transverse sections of the synangium. Determine the internal organization from these planes of section. How many spore-producing areas (sporangia) are present? What is their arrangement? Does this fertile structure have a vascular system? Draw a spore. Is it trilete or monolete?

Draw a synangium of Psilotum as it appears in transverse section.

Genus Tmesipteris

The only other genus of the Psilopsida is Tmesipteris, a plant of the southern hemisphere. This plant may often be found epiphytic upon other vascular plants such as tree ferns. Examine the photographs of Tmesipteris in Gifford and Foster, p. 96 & 97, and the preserved specimen on demonstration. Note the leaf-like appendages (enations?) that are vascularized in this genus. Unlike Psilotum, where the synangia are borne on stalks just above a bifid enation, the synangia of Tmesipteris are attached at the base of the bifid enation. Also, there are only two sporangia per synangium in Tmesipteris, rather than three as in Psilotum.

Draw a small portion of the Tmesipteris plant.

Examine transverse sections of the aerial axis of Tmesipteris. Note its similarities to that of Psilotum.

Draw a section of Tmesipteris axis.

Examine the synangium of Tmesipteris as it appears in section view (prepared slide). How does it compare to the synangium of Psilotum?

Draw the synangium of Tmesipteris.

Review the life history of Psilotum and Tmesipteris, being sure that you understand the nature of both sexual and asexual phases of the life cycle, the place where meiosis and spore formation occur, and the place where fertilization occurs. Where does the embryonic sporophyte develop? Is water necessary for fertilization?

Evolution and Fossil Pteridophytes

The fossil record provides the only known evidence for the origin and early evolution of vascular plants. As figured on diagram #1 above, the earliest evidence for tracheophytes occurs in late Silurian sediments (consult your geological time scale if you don't remember the age of the Silurian), and several groups of primitive vascular plants were present by Lower Devonian time. Rhyniopsida is the oldest and simplest group, and the group that gave rise to both Zosterophyllopsida and Trimerophytopsida. Zosterophyllopsida probably gave rise to Lycopsida early in the Devonian, and Trimerophytopsida is thought to have given rise to all of the other groups of living vascular plants during the mid-Devonian.

The laboratory that follows is designed to give you some familiarity with the earliest vascular plants and also to familiarize you with the types of evidence we use to interpret major systematic relationships among vascular plants. See Kenrick and Crane (1997) for the most up to date systematic analysis of the most primitive land plants. Throughout the laboratory keep in mind the structural and reproductive similarities of each group to the others.

Class Rhyniopsida

The earliest known tracheophytes are assignable to the Rhyniopsida. They first appear in the Upper Silurian, but are most common in the Lower Devonian. They are characterized by naked, (equally) dichotomously branched axes with terminal sporangia. Internally they have a tiny haplostele with no differentiation between protoxylem and metaxylem tracheids.

Genus Aglaophyton (segregated from Rhynia)

Examine a slide of a cross section of Aglaophyton major, the larger of the two species previously included in the genus Rhynia. Note the central xylem cylinder and surrounding zone of phloem (the **stele**), the broad cortex, and the epidermis. Stomata are present in the epidermis and you may be able to locate one. What kind of stele is this? Do you find protoxylem? Why or why not?

Diagram this cross section of Aglaophyton major.

Examine a demonstration slide illustrating the "tracheids" of Aglaophyton. Are these tracheids? Why or why not?

Genus Rhynia A demonstration slide of Rhynia gwynne vaughani shows numerous axes in cross section. Apparently the plants were buried and preserved in situ. These are smaller than Aglaophyton, but otherwise look similar. What **major** difference is there between these two genera?

The sporangia of Rhynia were borne terminally on the aerial axes. These are extremely rare. Examine the spores from a broken sporangium; on demonstration. Draw a spore. Examine the illustrations A. major and R. gwynne-vaughani.

Class Zosterophyllopsida

This subdivision consists mainly of Lower Devonian representatives. Plants have equal or unequal branching, and are clothed by small, unvascularized leaf-like processes called enations. The sporangia occur on the sides of the axes and may be subtended by an enation. Internally they exhibit an exarch actinostele. These plants may have evolved from among the Rhyniopsida, and are thought to have given rise to the Lycopsida.
*Examine a specimen of Sawdonia and note the spiny axes. These spines are non-vascularized enations. Sketch a branch of Sawdonia. Where would you expect to find the sporangia if they were present?

*Examine the compressed axes, and a slide of Renalia fertile axes. This plant is intermediate between Rhyniopsida and Zosterophyllopsida in that it has sporangia like Zosterophyllopsida, but they are terminal on axes like those of the Rhyniopsida. Are there enations on Renalia? Draw a sporangium. Be sure to note its shape and mode of dehiscence. This distinctive type of sporangium also is characteristic of the zosterophylls figured on page 110 of Gifford and Foster. What does this plant imply about the relationships of Rhyniopsida, Zosterophyllopsida and Lycopsida?

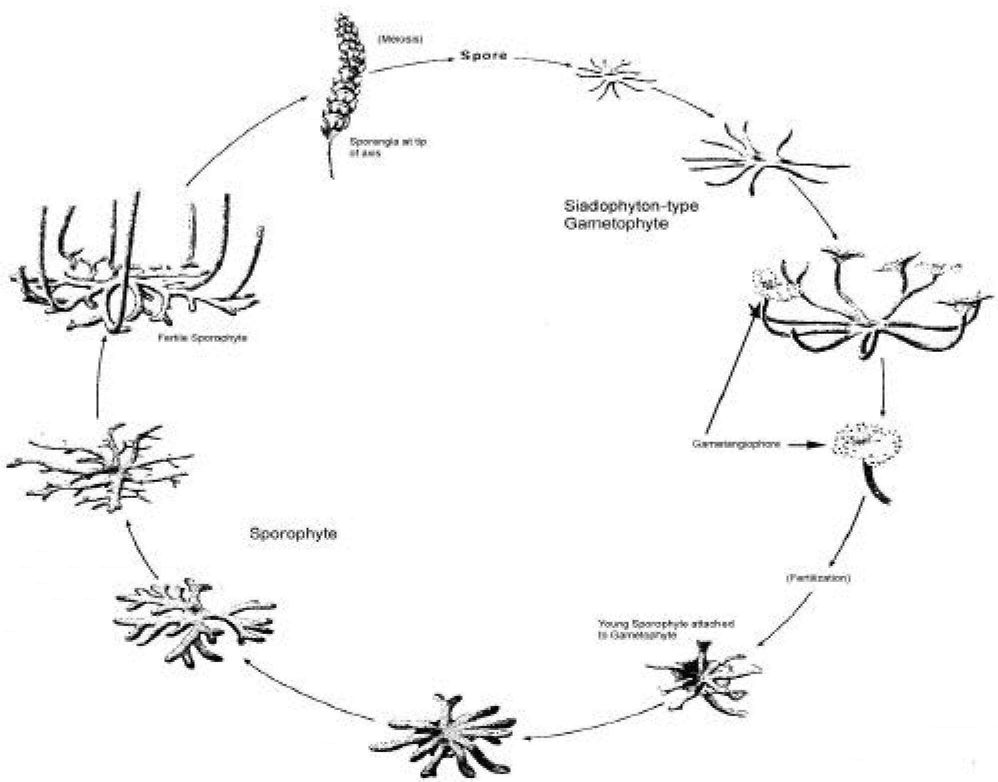
Class Trimerophytopsida

Members of the Trimerophytopsida were most abundant during the Lower and Middle Devonian. They are larger and have more specialized branching than plants of the Rhyniopsida, but like the later group have terminal sporangia. Some representatives have enations like those of the Zosterophyllopsida, but others have naked axes. Internally, they exhibit a centrarch or mesarch protostele that is much more prominent than that found in the Rhyniophytopsida.

Examine a fertile specimen of Psilophyton. How are the sporangia arranged? Draw the specimen.

Gametophytes of the Most Ancient Vascular Plants

Figure 3. Life cycle of <u>Zosterophyllum</u> from Schweitzer, 1990.



In the past few years we have discovered the gametophyte phase of the life cycle for several of the most ancient vascular plants. Contrary to expectations, these gametophytes are relatively large, much branches and complex plants. They are assigned to several genera that are known from both compressions that show plant morphology, and from anatomically presrved specimens that show vascularization of the axes and anatomical features of both archetonia and antheredia. Even immature sperm are preserved in some specimens!

Examine compression specimens that are assignable to the genus <u>Sciadophyton</u>. Note that the plant consists of axex that branch from a central disk. As is demonstrated by the specimens figured by Remy,Gensel and Hass, 1992, some axes branch and others terminate in gametangiophores. Some gametangiophores bear archegonia, while others produce antheridia. Note the outstanding preservation of immature sperm in some.

Review the features of the plants found in Psilopsida, Rhyniopsida, Zosterophyllopsida and Trimerophytopsida. What are the relationships of each of the groups to one another?

Review the life cycle of Psilotum and Tmesipteris. Compare it to the life cycle of an ancient land plant, to that of a filicalean fern, and to that of a moss. Compare the structure of the conducting tissue in Aglaophyton to that of a moss and to that of a typical vascular plant. What do these comparisons reveal about our traditional conception of differences between bryophytes and vascular plants?

Examine the life cycle of the ancient plant Zosterophyllum as reconstructed by Schweitzer (1990; see Figure 3, below). Be sure that you understand what is sporophyte (diploid), what is gametophyte (haploid), and how the sporophyte and gametophyte interact. Is this life cycle more like that of a fern or a moss? Why? What phase of the life cycle does Sciadophyton represent?

References

Crane, P.R. 1990. The Phylogenetic context of microsporogenesis. In, Microspores: Evolution and ontogeny. Academic Press, London.

Graham, L.E. 1993. Origin of land plants. J. Wiley & Sons, Inc., New York. 287 pp.

Kenrick, P. and P.D. Crane. 1991. Water-conducting cells in early fossil land plants: Implications for the early evolution of tracheophytes. Bot. Gaz. 152: 335-356.

Kenrick, P. and P.D. Crane. 1997. The origin and early diversification of land plants, a cladistic study. Smithsonian Institution Press, Washington, 441 pp.

Knoll, A.J. and G.W. Rothwell. 1981. Paleobotany: Perspectives in 1980. Paleobiology 7: 7-35.

Remy, W., P.G. Gensel and H. Hass. 1993. The gametophyte generation of some early Devonian land plants. International Journal of Plant Science 154: 35-58.

Rothwell, G.W. 1994. Phylogenetic relationships among ferns and gymnosperms; an overview. Journal of Plant Research, 107: in press.

Schweitzer, H.J. 1990. Pflanzen erobern das Land. Kleine Senckenberg-Reihe, Nr., Frankfurt, 18: 1-75.