



Lab V. Early Land Plants and the Marattiales

A. Primitive Plants

Now that we have had a full dose of the lycophytes, it's time to look backward to the most primitive vascular plants of all. In this part of the laboratory, our principal goal is to get acquainted with three lineages of primitive plants, the Rhyniophytes, the Zosterophytes, and the Trimerophytes. As you work with the fossils in this lab, don't get frustrated. There is very little to see in these early land-plant fossils, so have as a goal understanding how little actual evidence we have from which to make inferences about the structure, function, and evolution of the earliest vascular plants. Although we know a lot about character state distribution among the primitive plants, most of our information comes from fossils that are more complete and/or better preserved than those we have to work with in the P BIO 108 lab. To supplement the notes and sketches you make in your lab notebook, take advantage of the references set out in the lab (e.g., Gensel and Andrews 1987; Gifford and Foster 1989; Stewart and Rothwell 1993).

***S1: For the first part of this lab sketch in detail one fossil plant from each of the major groups named below. Include the following for each fossil sketch: (1) Note what kind of fossil you are sketching, (2) put an approximate date and geologic time period, (3) write a short paragraph making paleobotanical observations about its morphology.**

***Supplement these with information taken from the lab manual and the references listed above and provided in lab. Label your sketch with morphological and anatomical features where possible.**

The three fossil groups and their defining features are:

1. **Rhyniophytes**: Vascular plants with no derived features
2. **Zosterophytes**: Vascular plants with exarch protoxylem, sporangia on short lateral stems, stem tips circinate, transverse dehiscence of the sporangium
3. **Trimerophytes**: Vascular plants with anisotomous branching and sporangia terminal in clusters of lateral branches, longitudinal dehiscence of the sporangium

1. Rhyniophytes and Zosterophytes

The fossils assigned to the Rhyniophytes share the following characteristics: cells that look like annular tracheids in a central cylinder, cuticle and epidermis, and isolated terminal sporangia with trilete spores. All of these characteristics are primitive, given that these are among the oldest vascular plants. Given our general understanding of how plants evolve, they make sense as primitive characters, since nothing is complicated, nothing is fused, and nothing is reduced and compacted into a new structure.

a. Rhynie Chert

Look at several pieces of Rhynie Chert. The object here is to see how fragmented and difficult to interpret the earliest plant fossils are. In this single rock sample from one locality, embedded at one time over 400 million years ago, you are seeing fragments of two divisions of vascular plants. Have your teaching fellow or someone who already knows point out the axes in the rocks to you.

- First, find *Rhynia* stem fragments. These have a simple, round or elliptical, dark vascular cylinder, a pale cortex, and a dark stem exterior. *Rhynia* is a member of the Rhyniophyta and the order Rhyniales.
- Then locate *Asteroxylon* stem fragments. These have a more complex, invaginated vascular cylinder. This fossil is a member of the Zosterophyte clade and the order Asteroxylales.

Here is a comparison of the two groups of fossil plants we've seen in the Rhynie Chert:

Rhyniophytes (A & C) Rhyniales	Zosterophytes (D - F) Asteroxylales
no dedicated sun-gathering structures, only photosynthetic stems or <u>axes</u>	small unvascularized projections (<u>enations</u>) for sun gathering
protoxylem centrarch	protoxylem exarch
haplostele	actinostele
<u>terminal sporangia</u>	<u>sporangia borne on short lateral stems</u>
<u>stem apex uncoiled</u>	<u>stems circinate</u>

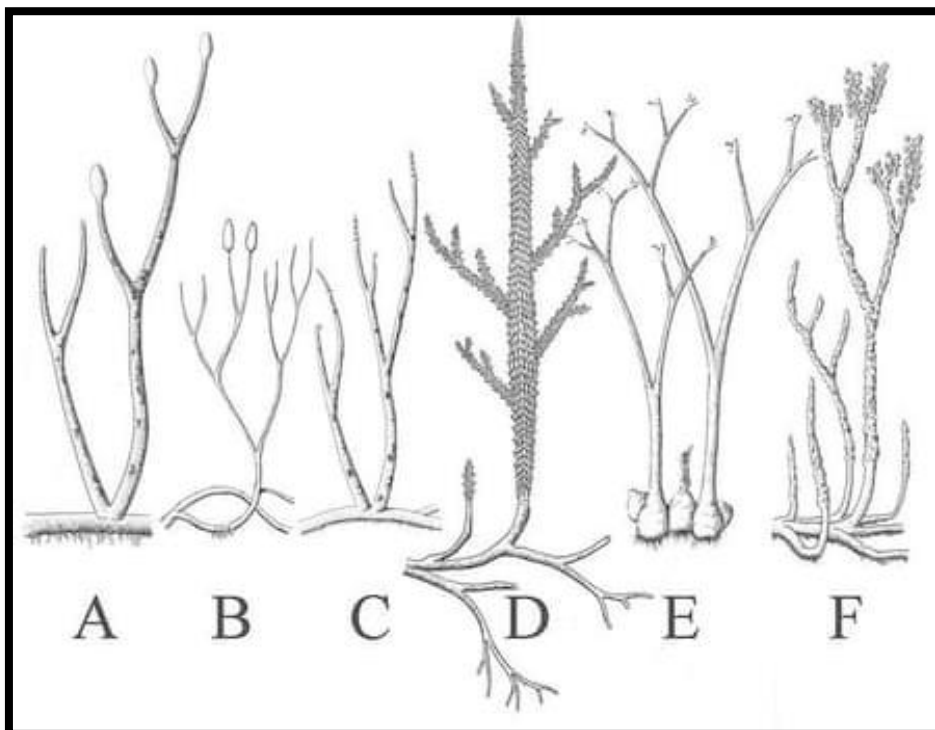


Figure 1. Artistic reconstruction of the Lower Devonian terrestrial plants from the Rhynie Chert. A. *Rhynia gwynne-vaughnii* B. *Aglaophyton major* C. *Ventarura lyonii* D. *Asteroxylon mackiei* E. *Horneophyton lignieri* F. *Nothia apophylla*

Illustration: Falconaumann

b. Paleobotanical observations: Zosterophyte example

Look at the other Zosterophytes on display in the lab. As you look, try to assemble some sort of basic feeling for the nature of these very primitive plants and for the difficulties of making inferences from fossils like these.

- i. First, look at compression fossils of *Sawdonia* in a sandy shale. Here, the main thing is to understand what you're seeing and how botanists interpret the fossils.

Possible observation:

"Black lines 3/8" wide with narrow dark lines like bristles on each side."

Palaeobotanical observation:

"Flattened stems or axes of a vascular plant as evidenced by the presence of cuticle, epidermis, and vascular cylinder with enations. These are not microphylls as there is no leaf trace present."

- ii. Compare with *Oricilla*:

Here you are looking for evidence of a distinctive feature of zosterophytes, circinate stems. Find the part of the fossil with a distinctive coiled look to the tip of an axis. Axis tips of these fossils all seem to have this feature, which suggests an unusual unrolling of the stem apex not known in any other group. (Ferns have leaves that do this, not stems.)

Make a palaeobotanical observation for yourself. What else do you notice compared to the rhyniophytes and other zosterophytes, like *Sawdonia* and *Asteroxylon*?

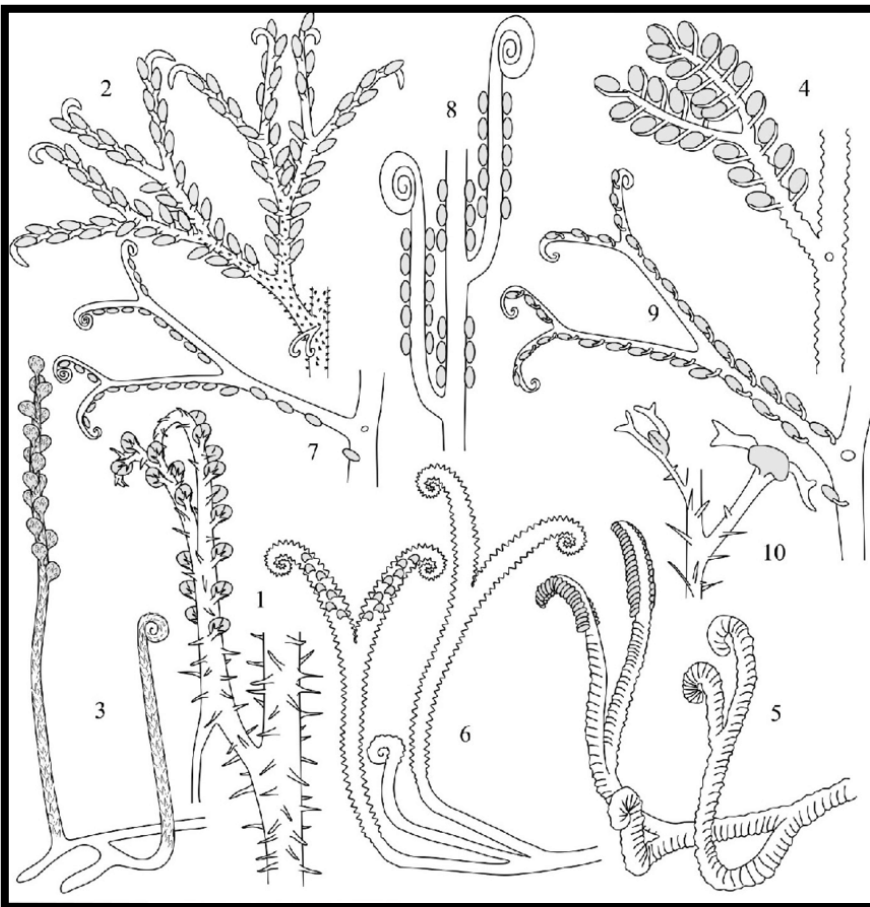


Figure 2. Leaf evolution in the subclass Ophioglossidae - Sawdoniales: 1. *Sawdonia ornata*; 2. *Deheubarthia splendens*; 3. *Discalis longistipa*; 4. *Crenatacaulis verruculosus*; 5. *Bathurstia denticulata*; 6. *Serrulacaulis furcatus*; 7. *Gosslingia breconensis*; 8. *Oricilla bilinearis*; 9. *Thrinckophyton formosum*. Modified after Rayner (1983)

2. Trimerophytes

Look at impression fossils of *Psilophyton* (order Trimerophytales) from the Trout Brook formation of north-central Maine. These fossils are in a darker, fine-grained shale than the others - presumably they were deposited in quieter waters where only fine mineral particles like mud were suspended in the water, allowing these fossils to be preserved in the sediments for millions of years.

a. *Psilophyton* Variation

Note that there are two *Psilophyton* morphologies here. See if you can pick them out.

- i. One has **projections** - not quite as prominent as those of *Sawdonia* - but they are there.
- ii. The other has no projections, but **ridges** are visible on the stems. What could those be for?

b. *Psilophyton* Axes

Look for branch points in the *Psilophyton* fossils. Break down the vegetative and reproductive characters when describing these plants in your sketches. This

Vegetative Characters:

Note that they are dichotomously branching with equal bifurcations (isotomous) in the pieces we have. These are minor parts of the branch systems; the major parts are characterized by unequal forking (anisotomous), so that there was a main, vertical axis to these plants with short lateral shoots.

Reproductive Characters:

The sporangia were borne in clusters on some of the side axes. Sporangia dehisced along a longitudinal slit. These psilophytans have characteristics that suggest they are the most primitive group of a large evolutionary lineage including horsetails, ferns, gymnosperms, and angiosperms.

These characteristics are:

- i. centrarch to mesarch protoxylem
- ii. sporangia in lateral clusters
- iii. pitted tracheids in some genera

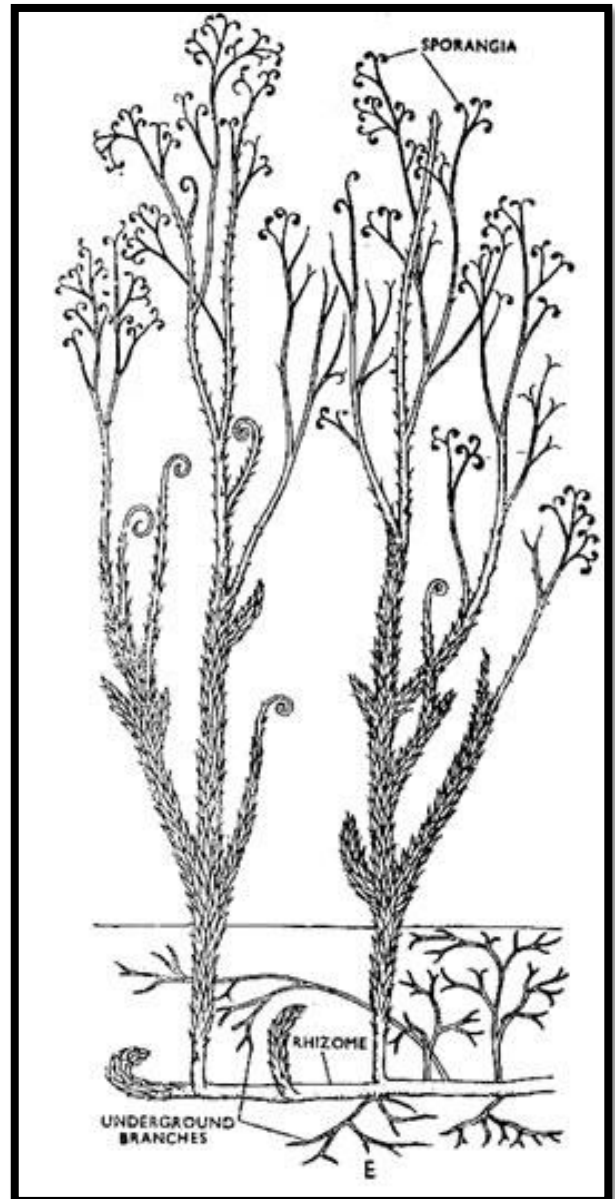


Figure 3. Trimerophyte *Psilophyton*. Note the circinate stems, and the combination of anisotomous and isotomous branching axes.



B. Monilophytes

As the sign says, we have now entered the monilophytes, the megaphyllous lineage sister to the lycophytes. We begin with a group of mostly large tropical ferns, order Marattiales. Like the rest of the monilophytes, these are spore-dispersed vascular plants with megaphylls and siphonosteles.

1. Marattiales, an Order of Eusporangiate Ferns

The Marattiales have a well-documented history. They first appear as tree ferns in the coal swamps right along with *Lepidodendron* and *Calamites*. The living species are prominent in some hot forests, both in tropical America and tropical Asia. These ferns are characterized by their arborescent habit, a distinctive stele and root structure, and a primitive thick-walled sporangium, called the **eusporangium**,

a. Living Plants

Go with your TA to the greenhouse to view the potted *Angiopteris*. The largest of the extant Marattiales, mature *Angiopteris* plants bear fronds up to 30 feet in length!

- i. These plants, like all ferns, have **megaphylls**. These megaphylls are divided into leaflets called **pinnae**, which are often divided even further into pinnules.
- ii. The leaflets are borne on stem-like axes called rachises (singular = **rachis**), which, as you can see, have swollen bases on some of the plants in the lab. These swollen bases, called **pulvinae**, are common in the Marattiales, but not elsewhere in the ferns.
- iii. You can also get an impression of the tops of the stems of these plants from looking in the pots. They are massive, mound-like stem tops, with short, blunt **stipules** at the leaf bases. Organs called stipules are common among flowering plants too: there they are homologous with whole leaves.
- iv. Typical fat, smooth **roots** are visible in the pot. These roots have neither root hairs nor mycorrhizae. Your teaching fellow will remove a length of the root to use for making sections.
- v. Back in the lab make a transverse section of the root with a razor and mount it on a slide without a cover slip. Add a drop or two of phloroglucinol and wait five minutes for the stain to develop. Note that a **pith** is present in these large roots. Also, the arrangement of their vasculature is more complicated than that of most roots.

***S2. Sketch the whole *Angiopteris* plant AND root in cross-section, with the detail of the vasculature. Is protoxylem exarch or endarch? Label the features described above and any cells and tissues you recognize in the root cross-section.**

b. Marattia: Stem in Transverse Section

i. A section of a modern-day Marattialean stem preserved in glycerine is on display in the lab. Here again you can see the typical roots of the Marattiales - some are even to be found in the deep interior of the stem. But what stands out about these sections is the complexity of the steles in the stems. Notice that there are numerous elongate vascular bundles in the transverse sections, and that they appear to be in several whorls from the inside to the outside of the stem. This is called a polycyclic.stele.

ii. Pairs of leaf traces arise from leaf gaps. Leaf gaps are interruptions in the vascular tissue such that the parenchyma of the pith is continuous with the parenchyma to the outside in the cortex. This interruption is typical of many more advanced plants. The leaf gap is commonly associated with the departure of the vascular bundles leading to a leaf in plants with large leaves such as the ferns and flowering plants. Two leaf traces should be visible distal to the leaf gap in the section.

*Root traces arise from sections of the stele as well, but they're hard to see in these complex stems.

***S3 Sketch the preserved stem in cross-section and label the features above.**

c. Reproductive Features of Marattiales

i. Unfortunately, the newly established *Angiopteris* plant in the greenhouse is not yet fertile. If it were, you could see its sori, looking very much like those in Figure 4. Note that the sporangia are arrayed in small groups on the abaxial surface (undersurface) of the megaphyll. This grouping of sporangia into aggregates called sori and the placement of sporangia underneath the leaf are typical features of ferns.

ii. Now compare the two slides of fertile leaves set up on the demonstration scopes in the lab. Note that Figure 4 shows the sorus of *Angiopteris*, a genus in which the sporangia are unfused. The other shows the sorus of *Marattia*, in which the sporangia are fused into a hot dog bun-shaped structure called a synangium.

***S4. Sketch the sorus of *Angiopteris* AND *Marattia* from a transverse section of leaf. Compare the different morphologies, and label the features above in each section.**



Figure 4. (A) *Angiopteris* - sporangia separate, unfused; (B) *Marattia* - sporangia fused into a synangium

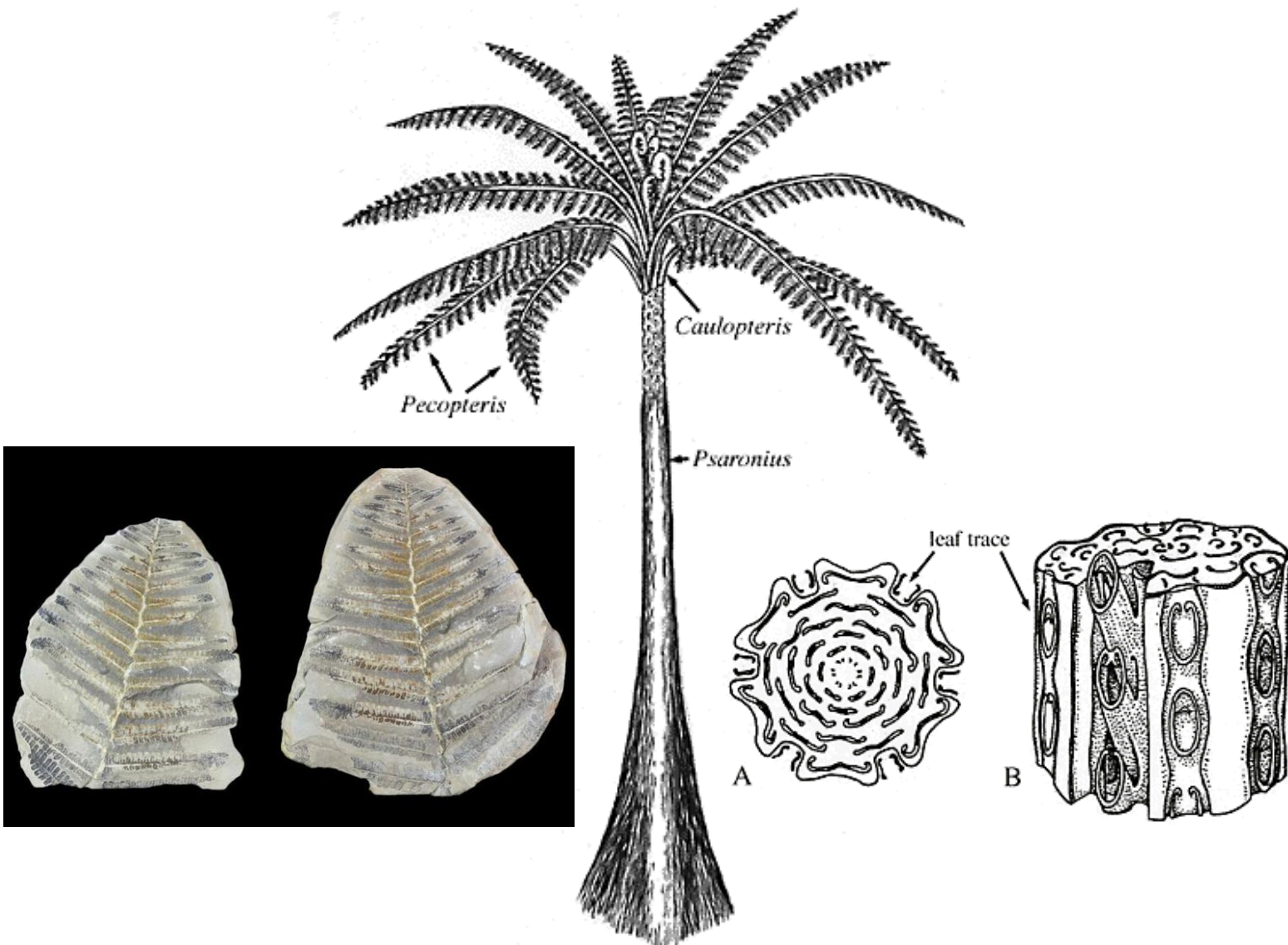
d. The Marattialean Genus *Psaronius*

i. *Psaronius* is an extinct Marattialean tree fern that lived during the late Carboniferous and the Permian. You will read about it in a forthcoming reading/writing assignment for PBIO 108. Keep today's images in mind as you take up that paper!

ii. Fossil leaves, form genus *Pecopteris*: Several large fragments of the *Psaronius* leaf are on display in the lab. Compare their features to those of present-day Marattialean leaves.

Transverse stem sections: Look at the peel of a *Psaronius* stem. The **polycyclic stele** without any secondary growth is very much like the living stem you just looked at a few minutes ago. Large roots reminiscent of the living roots you've seen today surround this fossil stem.

***S5. Sketch a pinna of *Pecopteris* AND a section of the *Psaronius* stem peel. Is it a piece of a pinna, or pinnule? Label parts of the leaf and the vascular system.**



Composite genus: *Psaronius*