VI. Ferns I: The Marattiales and Vegetative Features of the Polypodiids

We now take up the ferns, order Marattiales - a group of large tropical ferns with primitive features - and subclass Polypodiidae, the leptosporangiate ferns. (See the PPG phylogeny on page 48a: Susan, Dave, and Michael, are authors.) Members of these two groups are spore-dispersed vascular plants with siphonosteles and megaphylls.

A. Marattiales, an Order of Eusporangiate Ferns

The Marattiales have a well-documented history. They first appear as tree ferns in the coal swamps right in there with Lepidodendron and Calamites. (They will feature in your second critical reading and writing assignment in this capacity!) The living species are prominent in some hot forests, both in tropical America and tropical Asia. They are very like the leptosporangiate ferns (Polypodiids), but they differ in having the common, primitive, thick-walled sporangium, the eusporangium, and in having a distinctive stele and root structure.

1. Living Plants

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

a. These plants, like all ferns, have megaphylls. These megaphylls are divided into leaflets called pinnae, which are often divided even further. The feather-like design of these leaves is common among the ferns, suggesting that ferns have some sort of narrow definition to the kinds of leaf design they can evolve.

b. The leaflets are borne on stem-like axes called rachises, 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.

c. 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.

d. 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.

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.

2. Marattia: Stem in transverse section (sections in glycerine)

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 sort of a complex stele is termed polycyclic.

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.
3. Reproductive Features of Marattiales

a. Study a piece of *Angiopteris* leaf (Fig. 13) with sori under the dissecting scope. Most importantly, the sporangia are in small groups on the abaxial surface (is 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.

b. Finally, compare the two slides of fertile leaves set up on the demonstration scopes in the lab. Note that one shows the sorus of *Angiopteris,* a genus in which the sporangia are unfused. The other shows the sorus of *Marattia* (Fig. 14), in which the sporangia are fused into a hot dog bun-shaped structure called a *synangium.*

*Angiopteris* - sporangia separate, unfused
*Marattia* - sporangia fused into a synangium
4. The Marattialean Genus Psaronius

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

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.

B. Polypodiidae, the Leptosporangiate Ferns: Vegetative Features

Now that you have gotten a feeling for the eusporangiate ferns, it's time to focus on the leptosporangiate ferns, subclass Polypodiidae. Polypodiids, the largest and most diverse clade of ferns, includes about 10,000 species in seven orders, the largest and most diverse of which is Polypodiales. The group has a fossil record going back at least to the Permian period, but its living representatives present ample evidence that present-day speciation is continually yielding new evolutionary entities.

*Features shared by the eusporangiate ferns (Marattiales) and the leptosporangiate ferns (Polypodiids):*

- megaphylls, circinate vernation, sporangia abaxial on megaphyll (or a transformation of this feature), no secondary growth, spores dispersed (not retained to germination), homospory

*Features unique to the leptosporangiate ferns:*

- leptosporangia (tapetum plus one wall layer, versus two wall layers) with few spores per sporangium, stalk long and slender, antheridia few-celled, protruding (not sunken in the tissues of the gametophyte)
1. Vegetative Features of the Polypodiids

You are virtually surrounded by a diversity of megaphyllous, non-woody, leptosporangiate plants in the subclass Polypodiidae. Look at the leaf design of the various types to appreciate their variety. DIAGRAM two different leaves. Label the diagrams indicating the dissection and venation type of each leaf.

a. Phlebodium aureum - Use this plant to focus on basic leaf design and the boundary between stem and leaf. The stem of this plant is covered with papery, tan scales, which are thought to have a role in the retention of water around the stem axis. This creeping stem, called a rhizome, gives rise to leaves and adventitious roots as it grows.

The leaves have green stalks called petioles. The petioles may at first appear like stems, however their vasculature is bilaterally symmetrical, like leaves, not radially symmetrical, like stems. The leaf blade itself, called a lamina, is deeply dissected - we speak of this leaf design in Phlebodium as once-pinnatifid. Note that the venation of the lamina is anastomosing: the veins diverge and then come together again in a net-like pattern.

b. Now compare Phlebodium with several other ferns in the lab to gain an idea of the diversity of leaf design within the limits apparently imposed on ferns.

   i. Cyrtomium: once-pinnate, the pinnae broad and their veins anastomosing like Phlebodium, not free like Pteris.

   ii. Pteris: once-pinnatisect (note the pinnae or leaflets are completely separated from the midrib of the leaf only at the base); basal segments of the pinnae strongly developed, resembling the rest of the pinna

   iii. Microsorum: leaves entire (undivided).

c. Many ferns have specialized means of producing new plants asexually, that is without meiosis and syngamy: look at three other examples in the lab:
i. **Asplenium**: plantlets arise on leaf axes

ii. **Tectaria**: same

iii. **Nephrolepis**: thin, leafless stems called stolons grow away from parent plant to establish new sporophytes.

d. Stems and Steles

Now is the time to make your own personal sections of a stem in order to get a firsthand understanding of the typical fern stele, in this case a siphonostele with overlapping leaf gaps (otherwise known as a *dictyosteles*). Use the living stems of *Onoclea sensibilis* (sensitive fern) available in the lab. Make sure you choose a section at least 2 inches long that includes at least two leaf bases.

i. Identify the surface features: remnants of last year's leaves, branching roots, and a cluster of young, coiled leaves — fiddleheads, or more formally, *croziers*— at the stem apex (you may not get an apex, so look around until you see one.)

ii. Make a clean transverse section through an internode with a new razor blade. You should be able to see a broad pith, a group of vascular bundles in a cylinder near the periphery, a narrow cortex, and a darkened outer region.

iii. Now make a series of similar sections up through the attachment point of a leaf. Lay them out in a series on a microscope slide, so that you know both the order and the orientation of the sections. (It will be easier to keep your sections in the proper orientation if you notch the top of each one with a razor blade.) There will be little difference between adjacent sections, but changes add up. Your teaching fellow will explain the method in more detail.

iv. Once you have your sections, DIAGRAM about six in order, in the same orientation, in your lab book. The goal here is to trace the changes in the vascular bundles, leaf traces, and root traces from section to section, so position is critical for your diagram. You also need to be able to tell vascular bundles from leaf traces from root traces. Here are some hints:
- Make a couple petiole sections in order to learn the appearance of the leaf traces - they usually come in pairs.

- Root traces are single, and they are in longitudinal section in your sections, because they are placed more or less perpendicular to the stem axis.

- The vascular bundles lie in one ring in the stem center.

Now look at prepared slides of *Polypodium* rhizome transverse sections, in order to see cell detail in one of these stems. Focus on a single vascular bundle (Fig. 15) in the stem at medium or high power.

i. Identify the tracheids: angular cells that have red-staining, lignin-rich cell walls.

ii. Surrounding this xylem is a complete ring of phloem: these bundles are *amphiphloic*.

iii. An endodermis is clearly visible around each vascular bundle.

iv. Locate the *leaf gaps*. (Reread the next to the last paragraph on page 43 to remind yourself what a leaf gap is.)

Make a DIAGRAM of a whole stem section. Be sure to label leaf gaps and leaf traces. Now make a DRAWING showing a close-up of a vascular bundle.

![Fig. 15](image)