VASCULAR PLANT MORPHOLOGY
LABORATORY 4

Class Lycopsida

Members of the Lycopsida have true stems, leaves and (usually) roots. Their sporangia are borne on the adaxial surface of (or in the axils of) sporophylls, and they may or may not resemble the vegetative leaves. In the "lycopods" branch gaps are present in the stele, but no leaf gaps occur in the xylem. Therefore, when the stele has parenchyma at the center, it is a medullated protostele. The leaves (with only one or two exceptions) have a single vascular strand and appear to have arisen phylogenetically from superficial emergences or enations. The extant orders of Lycopsida are: Lycopodiales, Selaginellales, and Isoetales. Fossil orders sometimes include the Protolepidodendrales, Lepidodendrales, and Pleuromeiales. However, in this course the Protolepidodendrales are included in the Lycopodiales and the Pleuromeiales are included in the Isoetales. A comprehensive evaluation of lycophytes was published in the Annals of the Missouri Botanical Garden in 1992 (Vol. 79: 447-736), and the included papers bring up to date much of the current knowledge of the group.

Order Lycopodiales

Members of the Lycopodiales are homosporous, herbaceous, eligulate, isophyllous, and they have true roots. Traditionally, approximately 400 species of two extant genera have been recognized and assigned to the family Lycopodiaceae. More recently, however, (Lycopodium) has been subdivided such that seven or more genera and three families are now recognized. Classifications are as follows (from Wagner and Beitel, 1992).

For the purposes of (examinations in) this course we well continue to recognize only two genera. In lecture and lab we will also use the segregate genera Huperzia and Diphasiastrum, and for those who wish to learn about the diversity among this group the paper by Wagner and Bietel (1992) will be an instructive tool. Lycopodium s.l. is the more common of the two and forms a ground cover in woodlands. There are approximately 400 species of Lycopodium and a considerable number of them are tropical although some species are found in arctic and alpine areas. The second genus of the order, Phylloglossum, is monotypic and is restricted in its distribution to New Zealand, Tasmania, and the extreme southeast of Australia. Material of Phylloglossum is virtually unobtainable, so our laboratory work will be restricted to the genus Lycopodium.

Lycopodium s.l. - The sporophyte plant generally has dichotomously (isostomously) or pseudomonopodially branching stems, clothed with many small, closely spaced and helically arranged leaves (microphylls). Some species have prostrate or creeping stems and upright branching systems, while others do not show much specialization of the shoot system. In the simplest case, sporangia are borne in the axils of essentially unmodified leaves, while in other species the sporophylls, are aggregated into strobili (= lax cones) or compact cones, are confined to the branch tips, and lack chlorophyll. In other species the cones are borne on elongated stems that have relatively few, small leaves.

Adventitious roots arise behind the growing tip, but they traverse the stem for some distance before emerging near the bases of aerial stems, or all along the length of the horizontal stems. Roots can, therefore, sometimes be seen within the cortex in cross sections of the stem. The roots branch dichotomously at times.

Examine the sporophyte of L. (= Huperzia) lucidulum, a form that lacks cones. Find a zone of sporophylls. Draw a habit sketch of this plant.

Examine either L. annotinum or L. obscurum. Is a cone present? Where does it occur and what is the nature of the stem that bears it? Draw a cone and the tip of the branch that bears it.

Examine L. (= Diphasiastrum) digitatum. What type of stem or stem system bears the cones? Draw the part of the plant bearing cones, and a few cones.

Lycopodium--anatomy of the stem.

Species of the genus are generally protostelic and may have **actinosteles**, **haplosteles**, or steles in which the xylem is dissected into a series of plate-like anastomosing strands (**plectosteles**). The leaf traces, which are small, arise from the tips of the xylem lobes. No interruption in the vascular system occurs above the point where the leaf trace leaves the stele; that is to say, no leaf gaps are present.

Examine a transverse section of a plectostelic Lycopodium stem. Locate the xylem, phloem, and limit of the stele. Find a leaf trace and bases of leaves and sections of leaves if any are present. Diagram this cross section of the stem.

A word should be said at this point concerning the development of the xylem in the stem of Lycopodium. All of the tissues of this stem are primary, i.e. they are composed of cells produced at the apical meristem of the stem. Look at the xylem of the stem. Note that as one proceeds from the inner part of the xylem toward the outside, the diameters of the xylem elements decrease. The xylem elements (tracheids) with the smallest diameter are located toward the outer edge of the xylem. These cells represent the first cells of the xylem that matured and are called protoxylem. The inner cells matured later and are called metaxylem. The xylem, therefore, has matured centripetally, i.e. toward the center of the stem.

Xylem development of this type is said to be exarch. Exarch development of the xylem is common in lycopods. It also characterizes the roots of seed plants. There are other patterns of xylem development in later laboratories.

Lycopodium--structure of the sporophylls and cones.

Tease out a sporophyll from a preserved strobilus (cone). Note the position of the sporangium on the leaf. What is the technical word used to describe the location of the sporangium in this case? Note the form of the sporangium. Draw the sporophyll and sporangium from the adaxial side.

Examine a longitudinal section of a Lycopodium strobilus on a prepared slide. Note the sporangia, subtending sporophylls, and the pads of sterile tissue projecting into the spore masses. This is the subarchesporial pad. Note also that one type of sporangium and one type of spore are present in the cone. What is the technical term used to describe this feature of Lycopodium? Near the tip of the cone you may see the spores in adhering tetrads or clusters of four. Diagram a part of this longitudinal section of the cone.

Order Selaginellales

The genus Selaginella is the only living member of this order. There are approximately 700 species of Selaginella, the vast majority of which live in tropical or subtropical areas and in shady and very moist environments. Some species live in temperate regions. Some of the tropical forms reach a considerable size and may superficially resemble ferns. The temperate forms are generally small and have a tufted growth form. In all cases, sporophylls are aggregated into strobili. Selaginella is herbaceous and ligulate. Moreover, the genus is heterosporous in that two types of spores are produced in sporangia each of which has a different appearance. The spores differ in size; the smaller type (microspore) develops a male gametophyte and is produced in relatively large numbers within the sporangium. The larger type (megaspore) is usually produced in smaller numbers per sporangium and develops a female gametophyte. Unlike Lycopodium, the gametophyte phase is retained within the spore wall (**endosporic**), developing there rather than as a free-living individual. Additional aspects of this heterosporous mode of reproduction will be discussed below. Selaginella is further characterized in having a structure known as the **ligule**, a flap-like process arising from a small pit on the adaxial surface of the leaf.

Selaginella - Examine preserved material of a relatively small and prostrate species such as S. kraussiana. Notice the dorsi- ventral appearance of the stems due to the occurrence of two size classes of leaves in definite series. The two types of leaves are generally present in four rows. This condition of having more than one type of leaf is called anisophylly. Coming off of the stem you may see leafless axes which branch at their tips. These are the so-called **rhizophores**, while the branches at the tip are roots.

Locate a slide showing cross sections of a Selaginella stem and rhizophore. How do they compare? Note the stelar structure of each. Locate the leaf traces and leaf bases. What type of stele do you find in the stem and rhizophore? How is the endodermis constructed? Draw the stem in transverse view.

Examine the preserved material for strobili, which occur at the tips of branches and are generally four angled. These strobili are made up of sporophylls of two types. One type is a microsporophyll, the other is a megasporophyll. Their relative numbers and distribution in the strobili vary a great deal from species to species. Draw a portion of a Selaginella plant to show the vegetative and fertile portions of the plant.

Using either fresh or preserved material of strobili, detach a microsporophyll. This is usually recognized by the spherical shape of the sporangium. A large number of microspores may be seen within this sporangium. Draw the microsporophyll and its sporangium as they appear from the adaxial side.

If you wish you may crush the sporangium and examine the microspores with the microscope. You should be able to see a triradiate mark on the surface.

Using the same cone material, dissect out a megasporophyll. This generally may be recognized by the lobed shape of the sporangium.

Draw the megasporophyll and its attached megasporangium from the adaxial side.

Crush the megasporangium in water on a slide and note the appearance and number of megaspores present. Draw a typical megaspore showing its sculptured wall and the prominent triradiate mark.

Examine a longitudinal section of a strobilus. Locate the megasporophylls and microphylls. What process occurs in the production of the spores? You should also locate flap-like structures, the ligules, one of which arises from the adaxial surface of each sporophyll distal to the stalk of the sporangium. Selaginella is, therefore, ligulate. Was this the case in Lycopodium? Many fossil lycopods were ligulate, including most of the Lepidodendrales.

In the strobilus note the single nucleus in the microspores, the nature of these spores, and the nature of the megaspore. Examine the interior of the megaspore and you may see the developing megagametophyte. This megagametophyte becomes multicellular and archegonia develop. Diagram a part of the longitudinal section of the strobilus.

On a demonstration slide observe sectioned megaspores in which megagametophytes may be found in varying stages of development. You should be able to locate some gametophytes in which cells have been formed at the region of the triradiate mark. You may also be able to locate archegonia, either mature or immature.

After examining the megagametophytes make a composite sketch of a megagametophyte with an archegonium.

Review the essential features of the reproductive cycle of Selaginella making sure you understand this heterosporous plant as compared with the homosporous condition. Where do each of the following events occur in Selaginella? Meiosis. Development of the gametophyte phases? Fertilization? Development of the embryonic sporophyte?

Order Isoetales

The Isoetales may be characterized as heterosporous, ligulate, woody and isophyllous plants with no true roots. Instead, the bottom of the plant body (the **corm** of Isoetes) is a reduced shoot that has been modified for rooting (the **rhizomorph**). The order has only one living genus, Isoetes. Some people also recognize a second genus Stylites, but its member species are more probably only a growth variant of Isoetes. The plants appear to represent descendants of some of the Carboniferous arborescent lycopods included in the order Lepidodendrales (e.g., Lepidodendron and Sigillaria). Plants intermediate between Sigillaria and Isoetes include the Pennsylvanian genus Chaloneria, the Triassic genus Pleuromeia, the Lower Cretaceous Nathorstiana, and the Upper Cretaceous and Eocene Isoetites. This fossil record documents one of the most convincing reductional series known for any vascular plants. In addition, it allows us to better understand the curious and traditionally puzzling morphology of Isoetes.

Examine a whole plant of Isoetes. Note that the squat or flattened stem is bilobed and resembles a fleshy corm such as one might find in some flowering plants. Arising from the upper surface you will find numerous narrow, elongate leaves which superficially resemble those of a grass. These leaves are borne spirally, and from the lower lobed part of the stem you will find numerous roots which are also produced in a spiral arrangement. Sketch this whole plant of Isoetes to show its habit.

Examine a prepared slide of a longitudinal section of the stem. You should be able to locate the apical meristem and developing leaf primordia, as well as older leaves. If the section is near median you will also see the centrally placed protostele from which both leaf and root traces depart. An apical meristem is also present at the base of the corm, and this produces roots in a precise arrangement (curved rows), that is modified from a spiral. Make a sketch of the overall organization of the plant from this section.

Examine prepared slides bearing microsporophylls and megasporophylls. On the microsporophyll locate the **velum**, the **ligule** and the massive sporangium that is filled with microspores. Note also the **trabeculae**, plates of sterile tissue which project from the sporangium wall into sporangial cavity Remember the **trabeculae** of Selaginella? How are they similar to, and how are they different from those of **Isoetes**?

Examine a megasporophyll on the same slide. Note the difference in spore size and find the parts corresponding with those you saw on the microsporophyll. Diagram this megasporophyll as it appears in longitudinal section.

In Isoetes the initial stages in the development of the gametophytes occur within the old spore walls while the spores are still in the sporangia on the parent plant. As the sporophylls decay, the spores are freed and dispersed. In some cases the spores do not develop any further until the next growing season.

Extinct Representatives of Lycopsida

Of the extinct lycopods, the Lower and Middle Devonian representatives are the oldest and most primitive. Although they are sometimes placed in their own order, Protolepidodendrales, they are structurally comparable to the Lycopodiales. We include them with the Lycopodiales in this course, and will concentrate on the Lepidodendrales, and on representatives of the Isoetales that traditionally have been placed in the Pleuromeiales (= Pleuromeiaceae of the Isoetales) in this lab.

Order Lepidodendrales

The Lepidodendrales extend from the Mississippian to the Permian, and include many dominant forms of the Paleozoic coal- swamp floras. It is from these floras that the organic material in our Ohio coals was compressed. The order is characterized by heterosporous plants that are ligulate, woody, isophyllous and that have no true roots. Like Isoetes, the entire rooting system of these plants, the **rhizomorph** is a shoot that has been modified for rooting. Since the Middle Pennsylvanian, this clade has undergone a continuous reduction in diversity as well as in size of the largest members. Relationships among the rhizomorphic lycophytes have been evaluated by Bateman, DiMichele and Willard (1992), and a summary cladogram from this paper is presented below.

Paralycopodites (= Lepidodendron of old classifications)

This is one of the most common genera of the order. Its stem is distinguished in having rhombic or diamond-shaped leaf bases (that are taller than wide) on its outer surface. Names are given to the isolated plant parts since it was not known that the remains all belonged to the same type of plant when originally described.

Examine a demonstration specimen showing the outer surface of a stem of Paralycopodites. The prominent leaf bases, each of which bears a leaf scar (area of leaf attachment), persisted after the distal portions of the leaves abscised. Sketch this specimen.

Examine a transverse section of a preserved stem of Paralycopodites. A pith is present in the center of the stele and is surrounded by primary xylem. This is surrounded by secondary xylem in older stems. A zone of phloem occurs outside of the xylem. A broad cortex is present outside the stele, and some periderm is present in the outer part of the cortex. You may be able to see a ligule embedded in a leaf base.

The underground parts of lepidodendraleans consisted of modified shoots (the **rhizomorph**) that bore "rootlets" (= modified microphylls) in a spiral arrangement. The rootlet-bearing axis is very commonly found as a cast. The name given to this portion of the plant is Stigmaria.

Examine a cast of a Stigmaria axis. Note the scars where the rootlets were attached. Examine transverse sections of Stigmarian rootlets. Is the anatomy of these roots similar to other vascular plant roots? What order of vascular plants?

Sporophylls were aggregated into distinct cones in Paralycopodites. These cones are bisporangiate, with megasporophylls at the base and microsporophylls apically. Examine the specimen of Flemmingites (the old name Lepidostrobus, is still used by some authors) on demonstration, one of the genera of lepidodendralean cones. Note the cone axis and the sporophylls bearing horizontally elongate sporangia. How are the sporophylls arranged?

The leaves of Paralycopodites were narrow and varied greatly in length. Some species bore leaves in excess of three feet long. Examine a small branch bearing leaves.

Sigillaria - This genus of the Lepidodendrales is characterized by sparsely branched (one or two times) stems and by having leaf bases or leaf scars in vertical rows on the stem. Often, the stems are also vertically ridged. Examine a specimen showing the external features of the stem, and the plant reconstruction on demonstration.

Family Chaloneriaceae (Isoetales)

Perhaps the best known of all fossil lycophytes is Chaloneria cormosa, a Pennsylvanian species that is structurally quite similar to representatives of the Mesozoic Pleuromeiaceae. This plant was probably the Typha latifolia of the Paleozoic. It was unbranched with a terminal fertile zone, and grew in dense patches in marshy areas. The base of the plant was similar to the base of the corm in Isoetes.

Examine the reconstruction of Chaloneria to get an idea of its overall morphology. Draw the plant habit of Chaloneria. Now examine a cross section of the vegetative stem and a cross section of the stem in a fertile zone. Note the similarity of the stem to that of Lepidodendron. Are there trabeculae in any of the sporangia? What does this suggest about relationships among the Lepidodendrales and Isoetales?

Now examine a longitudinal section of the base of the stele. Note how it swells and truncates like the base of Isoetes. What does this suggest about relationships among the Lepidodendrales and Isoetales?

Family Pleuromeiaceae (Isoetales)

This family of extinct lycopods is made up of several Mesozoic genera and is allied to the Isoetaceae. You will note a distinct similarity of Pleuromeia to Chaloneria. However, the Pleuromeiales are not known from anatomically preserved species, so our knowledge of them is somewhat more limited than for Chaloneria.

Pleuromeia - Examine the reconstructions in Gifford and Foster (Pages 147 & 166). Note the columnar stem, long leaves, and the large terminal strobili. Also note the underground parts and how this lower part of the plant resembles Isoetes. Pleuromeia, which is from the Triassic Period, is structurally intermediate between the Paleozoic genus Sigillaria and the Cretaceous genus Nathorstiana. Pleuromeia reached three to four feet in height.

Nathorstiana - Examine the reconstruction of this genus in Gifford and Foster (Page 166). The plant looks much like Isoetes but was about 12 or so inches in height. Note that a distinct stem region is still present. In addition, note the similarity of the leaves to those of Isoetes, and the similarity between the lower part of the stem and the base of the Isoetes plant.

Think about relationships among the various lycophytes we have studied. Do you recognize the possibility of both a clade with adventitious roots and one with no true roots (i.e., a rhizomorph instead)? What features of the fossil forms allow us to understand the highly unusual structure of Isoetes. What is the significance of heterospory among the lycophytes?

References

Bateman, R.M., W.A. DiMichele and D.A. Willard. 1992. Experimental cladistic analysis of anatomically preserved arborescent lycopsids from the Carboniferous of Euramerica: An essay on paleobotanical phylogenetics. Ann. Missouri Bot. Gard. 79: 500-559.

Wagner, W.H., Jr. and J.M. Bietel. 1992. Generic classification of modern North American Lycopidiaceae. Ann. Missouri Bot. Gard. 79:676-686.