PBIO 3080/5080 – STRUCTURAL BOTANY
FALL 2014
LAB 10: CORDAITES & CONIFERS

ORDER CORDAITALES

Cordaites are an important group of Carboniferous plants that are closely related to
conifers. Rudolf Florin (1951, 1954) was able to interpret that conifer cones are compound
structures by characterizing a transformational series of morphologies from the cordaitean cone
Cordaianthus, through Carboniferous and Mesozoic conifer cones, to the cone of Pinus. In this
lab we will briefly characterize one cordaitean plant, Cordaixylon dumusum, from its vegetative
organs and from its cones, which are placed in the genus Cordaianthus.

Examine the vegetative and fertile reconstructions of Cordaixylon dumusum (Rothwell
1993; Rothwell & Warner 1993). Note the overall morphology of the plant, and the positions
of attachment of the cones. While this species was a small shrub, some other cordaitean species
were mangrove trees along shorelines. Still others were giant canopy trees in the floodplain and
hillside floras of the Pennsylvanian and lower Permian.

Examine and draw the large, strap-shaped leaf with the genus name Cordaites. Is it
similar to the leaves of any living conifers? Examine and draw a cross section of these leaves.

Now examine cross sections of Cordaixylon and Mesoxyylon stems. Note the large pith,
endarch primary bundles (in Cordaixylon), wood, and cortex. Is there bark here?

Examine compressed and anatomically preserved specimens of pollen and ovulate
Cordaianthus cones. Find the primary axis, bracts, and secondary shoots with their vegetative
and fertile scales. Note the position of attachment of the pollen sacs in the pollen cones, and the
position of attachment of the ovules in the ovulate cones.

Also examine a pollen cone from the genus Emporia (= Lebachia). How does this
compare to that of Cordaianthus?

Now examine specimens and diagrams of the Pennsylvanian age ovulate conifer cone
Emporia, the Triassic cone Pseudovoltzia, and the modern Pinus cone. See pg. 407-408 in
Stewart & Rothwell (1993) as well as pgs. 425 and 430-431 of Gifford & Foster (1989), and
compare these diagrams to that of the cordaitean ovulate cone on pg. 402 (Stewart & Rothwell
1993) and pg. 450 (Gifford & Foster 1989). Diagram fertile secondary shoot (= cone scale of
Pinus) of each of these to make up a transformational series. Now, do you understand the
homologies of the conifer cone scale? Now exam a similar transformational series for the
evolution of Cupressaceae from the reprint on display (Rothwell et al., 2011). Note that both
transformational series show changes from Voltzia-type conifer cone scales to those of modern
genera.
**Order Coniferales**

Conifers are the most dominant and conspicuous gymnosperms in floras throughout the world. Included in this group are such widely cultivated and familiar trees as pine, spruce, fir, cedar, yew, and redwood. Conifers are also an extremely ancient group of seed plants that can be traced back as far as the Pennsylvanian, where the closely related Cordaitales were also an important component of the vegetation. With approximately 50 genera and 500-550 species, conifers represent the most successful and widespread group of extant gymnosperms. As illustrated in the figure below (from Rai *et al.* 2008), both morphological and molecular systematic have documented that the Pinaceae is the sister to all other living conifer families.
When extinct cordaites and conifers are added to the analyses, the transition from Paleozoic conifers like *Emporia*, through Triassic conifers like *Pseudovoltzia*, to the Jurassic and Cretaceous conifers of living families becomes apparent. The following tree, from preliminary work by Rothwell *et al.* (2009), does not resolve Cupressaceae completely, but it clearly reveals relationships among the oldest (Paleozoic) conifers as well as conifers that are assignable to modern families.

![Conifer Tree Diagram](image)

**Branching & Foliage**

Several representative forms are present in the laboratory. These have varying types of leaves and branching patterns, and include members of several major conifer families.

As you examine each specimen locate the leaves, distinguish them from the branches, and note any particular features such as leaf arrangement, the form of the leaf, and its size. Do any of these leaves remind you of *Cordaites*?
Leaf Anatomy

Examine a prepared slide of a transverse section of a *Pinus* leaf (= needle). Note the leaf form in the genus. Differences in leaf shape are often characteristic of genera in the Coniferales. Locate the central vascular bundle with xylem and phloem. This bundle is surrounded by **transfusion tracheids** of somewhat rectangular shape, and with circular bordered pits. An endodermis surrounds the transfusion tracheids.

The mesophyll of the leaf has cells with characteristically scalloped or involuted cell walls. A thick-walled epidermis is present in *Pinus*, with a thick layer of cutin on the outer surface. In addition, the stomata are usually sunken below the surface of the leaf. Beneath the epidermis will be found several layers of thick-walled **hypodermal** cells. Diagram the transverse section of the *Pinus* leaf, being sure to include the cellular components for a pie-shaped portion of the leaf.

Stem & Wood Anatomy

The conifers are generally woody plants and have the potential for abundant secondary tissue production. These are the plants for which the concept of **pycnoxylic wood** was derived. Several genera of conifers are important sources of timber, both in the Northern Hemisphere, where members of the Pinaceae are the most important, and in the Southern Hemisphere, where members of the Araucariaceae and Podocarpaceae assume this role as sources of timber. The term **softwood** is generally used to refer to these conifers and their wood, whereas the flowering plants are generally referred to as **hardwoods**. These terms are somewhat misleading since they do not necessarily reflect the actual hardness of the wood (i.e., some flowering plants have extremely soft wood). As these terms are used, hardwoods have vessels and usually have wood fibers of various types. In contrast, the softwoods lack vessels and usually have few or no fibers. The stem anatomy of conifers is fairly similar (although simpler) to the type that is found in woody eudicots.

Young *Pinus* stems have an endarch eustele with vascular cambium in each of the vascular bundles. Very soon after the initial maturation of the primary (1°) tissues produced at the apical meristem, the vascular cambium begins to produce secondary (2°) vascular tissue. Also, in the areas of parenchyma between the vascular bundles, by de-differentiation of the cells, additional areas of vascular cambium (**interfascicular** vascular cambium) develop. This leads to the presence of a continuous ring of vascular cambium in the stem cross section, and accounts for the continuous rings of secondary tissue subsequently produced.

Examine a transverse section of a *Pinus* stem that is several years old. In the center is the pith, which is surrounded by a ring of primary xylem strands. Outside of the primary xylem is a relatively broad zone of secondary xylem. Note the radiating rows of tracheids and wood rays. **Resin canals** are also present and are lined with secretory parenchyma. Annual rings should be
visible, each of which represents an annual increment of secondary xylem. Note the difference in the cells in the inner part of each ring as compared to the outermost cells of the ring. The inner cells represent spring wood; the outer cells make up the summer wood.

Outside of the secondary xylem is the vascular cambium. You should be able to find initial cells that produce tracheids of the secondary xylem; these are the fusiform initials. You should also be able to find ray initials that produce the cells of the rays. Note that the rays of the xylem continue across the cambial zone into the zone of secondary phloem, which lies to the outside of the cambium. The rays here are called phloem rays. Other cells in the secondary phloem include relatively large and empty-appearing sieve cells and cells of phloem parenchyma, which often have dark contents. Primary cortex is present outside of the phloem, and resin canals are present in this parenchymatous area.

An additional cambium, the cork cambium or phellogen, is present. This has arisen in the cortical tissue, and has produced cork tissue (phellem) toward the outside of the stem. You may find a few layers of old cortex and the epidermis outside of the cork in some areas. The cork and cork cambium, as well as any old primary cortex or secondary phloem between layers of cork, make up the periderm. The bark consists of everything outside of the wood. Is bark either all primary or all secondary tissue? Diagram the tissue of the stem of Pinus. How old is the stem you have?

Reproductive Structures

The characteristic reproductive structure produced by the sporophytes of the Coniferales is the cone. These cones are monosporangiate (i.e., a given cone produces either ovules or pollen, but not both). In general, conifers are monoecious in that a given plant will produce both ovulate or seed cones and pollen cones, but some species are dioecious like cycads and Ginkgo.

As characterized by Florin (1951, 1954), the ovulate cones of conifers are compound. They consist of a primary axis that bears modified leaves (bracts). In the axil of each bract there is a highly-modified and reduced shoot (secondary axis) called a cone scale. This forms a compound cone that can be compared to Cordaitanthus, the ovulate inflorescence of cordaiteans. Recall from earlier in this laboratory that the primary cone axis of Cordaitanthus bears bracts in the axils of which the fertile, short-shoots occur. The ovules of Cordaitanthus are borne at the tip of modified leaves that we call scales. Note that the “scale” of Cordaitanthus is a sporophyll while that of a conifer ovulate cone consists of the whole, highly-reduced axillary shoot. What are the homologies here? Examine a reconstruction of the primitive ovulate cone of Emporia lockardii to help you understand the homologies.

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In most genera of the conifers, the ovulate cones are obvious and correspond to the usual idea of a cone. However, some genera have ovulate reproductive structures that appear not to be cones when they are examined superficially. For example, the seed cone in genera of the Cupressaceae (such as Juniperus) becomes fleshy and berry-like when mature, and the single seed of Taxis (the yew) no longer reflects the compound nature of the ancestral cone structure.

As stressed above, the basic unit of construction of the ovulate cone is the cone scale. In
the Pinaceae the cone scale bears ovules on its adaxial (= upper) surface. Because it represents a modified axillary branch or short shoot, the cone scale is situated above (in the axil of) a bract. In the Araucariaceae the bract and scale are fused together forming a bract-scale complex. In this family the bract is large, and a small projection on its upper surface represents all that is left of a highly reduced cone scale. Note also that the only a single seed is embedded into the tissue of the bract-scale complex. In the families Taxodiaceae and Cupressaceae there also are bract-scale complexes, but in these families the bract-scale are more or less fused together. Therefore, it is difficult to distinguish individual complexes externally, and we speak of juniper “berries.” In the Podocarpaceae the ovule and cone scale are often fused, and indistinguishable externally. The cone scale, which encloses the ovule, is fleshy and the ovule appears to be terminal within the epimatium.

In the Taxaceae and Cephalotaxaceae, the ovules are terminal on short stalks that occur in the axils of vegetative leaves. The cone scale, as such, is either absent or consists only of the ovules proper.

The pollen cones of most conifers are simple, like those of cycads. The cone axis bears microsporophylls. This differs from the cordaites where the pollen-producing inflorescence, like the ovulate one, is compound. (We do not know yet how the simple pollen cones of living conifers relate to the type of inflorescence present in the cordaites.) What do you know about the basic construction of seed-plant shoots that may suggest such a relationship?

In this laboratory, we will emphasize the genus Pinus in regard to cone structure and details of the reproductive cycle. In general, each genus of conifer has somewhat distinct cone morphology and the structure of the cones is often an important aspect of differentiating the various genera. We are only going to deal with the rather broad range of variation of cone structure in a very general way in this course.

In the Pinaceae, the microsporophylls usually have two pollen sacs borne on the lower surface of the microsporophyll. The Taxodiaceae have 2 to 5 pollen sacs per sporophyll in a similar location. The Cupressaceae have 2 to 6, while the Araucariaceae produce sporophylls with as many as 15 pollen sacs per sporophyll. In the Araucariaceae this large number of pollen sacs is accompanied by a tendency for them to become more radially arranged about the sporophyll.

Examine a pollen cone of Pinus. Note the upturned ends of the sporophylls. Break or dissect the cone so that you can distinguish the cone axis and see how the sporophylls are attached. Note that bracts are absent. Examine an individual sporophyll. The pollen sacs are relatively large and extend along the lower surface. Draw an isolated microsporophyll of Pinus.

THE REPRODUCTIVE CYCLE OF PINUS

Having now considered some of the major features of the vegetative organs of the conifers and the general organization of the ovulate and pollen cones, the rest of this laboratory will deal with the detailed morphology of the reproductive structures and the sequence of events.
and structures among conifers, it is impossible to treat these in detail in the present course. Therefore, we will use Pinaceae to characterize conifers as a whole. *Pinus* or *Pseudotsuga* can be used as an example for the order. Illustrations of *Pseudotsuga* were used in illustrations presented in lecture, and *Pinus* will be used in the laboratory. You will note that the two are extremely similar.

The typical sequence of events in *Pinus* is as follows:

1) In the spring, as the shoots begin to initiate new growth and the new fascicles of leaves open and develop, the cones develop from primordia surrounded by bud scales. These cone primordia were produced the year before and remained dormant during the winter.

2) The pollen (= “staminate cones” of older literature) mature relatively(419,512),(476,538) rapidly, and by late spring or early summer they begin to dry out, releasing the pollen.

3) The ovulate cones are relatively small at the time of pollen release, when elongation of the cone axis separates the cone scales and allows the pollen to sift into the cones to enter the micropyles of the ovules. Pollination occurs with the aid of a pollination droplet during the spring or early summer of the first year.

4) After pollination, the ovulate cone closes. The megagametophyte and archegonia develop subsequently, while the pollen tube grows slowly through the nucellar tissue and toward the eventual position of the archegonium.

Usually, approximately one year elapses between pollination and fertilization. In some species the embryonic development commences quickly. In others, the seeds do not mature until an additional year or large part of a year elapses after fertilization. In some cases, therefore, two and a half years elapse from the appearance of an ovulate cone until it is mature and releases seeds. In other cases, nearly two years elapse.

**Mature Pollen Cone & Pollen**

Examine a prepared slide of a longitudinal section of a mature cone. Locate a pollen sac containing numerous winged pollen grains. Examine the pollen grains and note the stage(s) of development present. Draw a small portion of the pollen cone as it appears in longitudinal section. Draw the details of a single developing pollen grain.

**Young Ovulate Cone**

Examine a young ovulate cone at the approximate stage of development when pollination occurs. Locate cone scales, bracts and immature ovules. Note how the appearance differs from a typical mature ovulate cone.
Isolated cone scales bearing ovules are available. Examine one of these units. Draw the cone scale as it appears at the time of pollination.

Examine a demonstration slide bearing a longitudinal section of a young ovulate cone. Locate the cone scales and bracts. The bracts are relatively prominent at this stage of cone development, however, subsequent enlargement of the cone scale leads to its overshadowing the bract in the more mature cone. On the upper surface of the cone scales you will find the ovules.

By examining several ovules you should be able to distinguish the micropyle, integument, and nucellus region. Note that no megagametophyte is present as yet within the ovule. Pollen grains may be found in some of the micropyles and resting on the nucellus in the micropylar region. Draw the ovule and subtending cone scale.

Examine a demonstration slide of a median section through an ovule and cone scale at the stage of pollination. Note that deep within the nucellus there is megaspore mother cell that may be distinguished from the surrounding cells by its larger size. Add this megaspore mother cell to your drawing of the young ovule above. You now have the structure present at pollination.

**Megagametophyte Development**

Examine the demonstration slide of a section of an ovule having an early stage of megagametophyte development. This stage is the free-nuclear stage, prior to the formation of cell walls in the gametophyte. You will find a spherical area with relatively large nucellar cells surrounding the gametophyte, in which you will see several free nuclei in a common cytoplasm. Draw the free-nuclear stage of megagametophyte development.

Examine a prepared slide of a section through a relatively mature megagametophyte. Note how the ovule has increased in size. Within the ovule you will find the relatively massive, multicellular megagametophyte with archegonia near the micropylar end. The cytoplasm of the eggs is somewhat frothy in appearance. The egg nucleus may show. Diagram and label the section.

Examine a demonstration slide of a medially sectioned archegonium. Note the neck cells of the archegonium and the egg nucleus. Draw the mature, medially sectioned archegonium.

**Fertilization**

Examine a demonstration slide showing growth of a pollen tube through the nucellus, and in contact with the egg. This tube serves to transport two male gametes to the egg cell within the archegonium (*siphonogamy*).

Examine a demonstration slide showing two archegonia. In one of these there may be a single large zygote nucleus. In the other (near the lower part of the archegonium) there may be a pair of nuclei. Three two nuclei were produced as a result of the division of the zygote nucleus.
Their subsequent division will lead to the multicellular proembryo.

**Proembryonic and Embryonic Sporophyte**

Examine a prepared slide of a *Pinus* proembryo. Note the group of cells near the lower end of the archegonium. In pine, three tiers of cells develop as a proembryo, and the later stages of the embryo develop from the lowest tier of cells. Draw the proembryo of *Pinus*.

A slide of an isolated relatively mature embryo is also on demonstration. Diagram and label this embryo.

**The Seed**

Examine an intact seed. The wing consists of tissue of the cone scale that separates from the scale, and adheres to the mature seed.

**REFERENCES**


