

Topic 16. Secondary Growth

Introduction: Secondary growth results from the cell division at lateral meristems called **cambium**. To properly understand secondary growth, one must first be familiar with primary structure of the stem and the root. Specifically you should have an understanding of the organization of the primary tissues in the two stems we have studied (*Medicago* and *Coleus*) and of the *Ranunculus* root. It may be a good idea to review both "Cells and Tissues of the Plant Body", "The Root", and "The Shoot" before proceeding.

Some Important Definitions:

Primary tissues: Tissues generated from the growth of an apical meristem.

Cambium: A lateral meristem consisting of a sheet of cells. Growth of these cells increases the girth of the plant organ involved.

Secondary tissues: Tissues generated from the growth of a cambium.

Vascular Cambium: A cambium that gives rise to secondary xylem to the inside, and to secondary phloem to the outside.

Periderm: A structure that consists of a cork cambium (phellogen), producing cork tissue (phellem) to the outside, and in some cases, a layer of cells to the inside called phelloderm. Periderm functions to limit dehydration and block pathogens after the epidermis is disrupted by the onset of secondary growth.

Cork (phellem, you need know only the term "cork"): Tissue, dead at maturity generated from a **cork cambium**. The cell walls of the tissue are impregnated with suberin. This waterproofs the tissue. The cork used to seal wine bottles is cork tissue harvested from a species of oak. The cell theory was first proposed by Robert Hooke in 1665 after microscopic examination of a slice of cork.

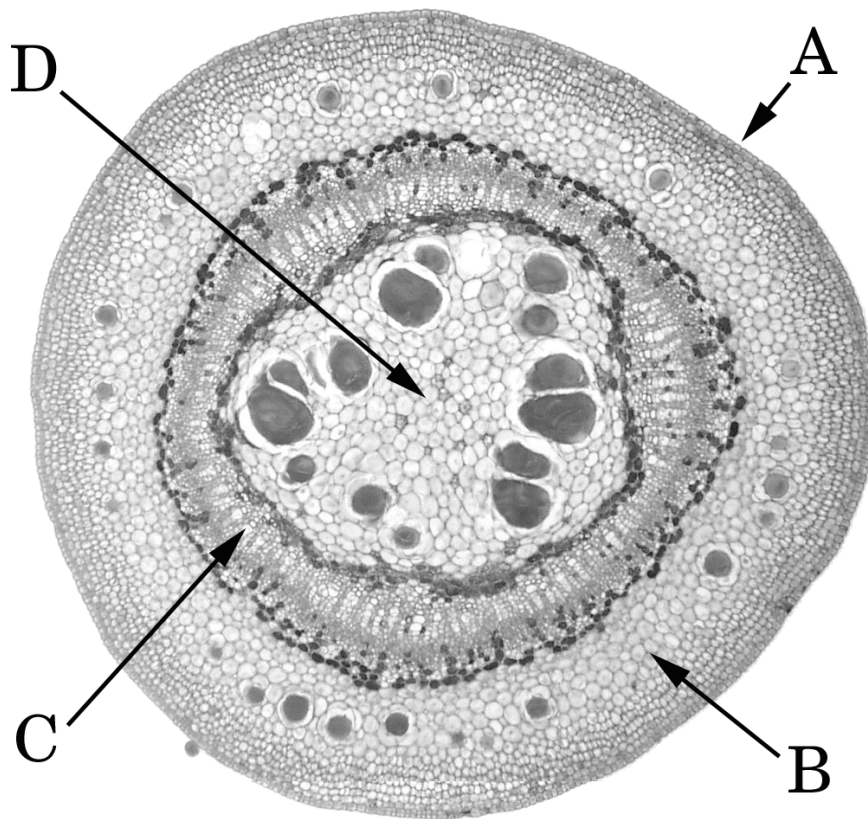
Cork Cambium: A cambial layer that functions to produce cork, and in some cases, phelloderm. In roots it is derived initially from pericycle. In stems it is first derived from the cortex. Unlike the vascular cambium, these cambial layers do not persist for the duration of the life of the plant organ. Over time, one cork cambium will be supplanted by another generated from parenchyma cells further inside.

Phelloderm: In some periderms the layer of living secondary tissue is generated by the cork cambium to the inside. We will not consider the phelloderm in the following exercise.

I. The Primary Structure of the *Tilia* Stem

Take the prepared slide of the cross section of a *Tilia* (basswood) stem at the end of primary growth and survey the slide with your microscope at 40x. Identify the three tissue systems. This stem differs from that of *Medicago* or *Coleus*. In *Tilia*, the interfascicular regions of ground tissue between the vascular bundles are only one cell layer wide and the primary vascular tissue appears as an almost continuous ring. As in both *Coleus* and *Medicago*, the primary xylem lies inside the phloem. As in the stems studied earlier, the ground tissue is segregated by the vascular tissue into pith and cortex. The dermal tissue consists of an epidermis. This stem will be transformed by the growth of two cambiums: the vascular cambium, which forms between the primary xylem and primary phloem, and by the cork cambium that will form in the cortex and will supplant the epidermis.

Label the figure



Cross section of *Tilia* Stem at the end of primary growth

A = _____

C = _____

B = _____

D = _____

Draw the intact epidermis.

Draw a primary vessel element.

II. Secondary Tissues of an older *Tilia* Stem

Take the prepared slide of the cross sections of *Tilia* (basswood) stems: 1, 2 and 3-year sections on the same slide. Survey the section of the 1-year old stem with your microscope at 40x. Starting in the middle of the stem, identify the following: **pith; xylem tissue, phloem tissue, cortex, periderm, and epidermis.**

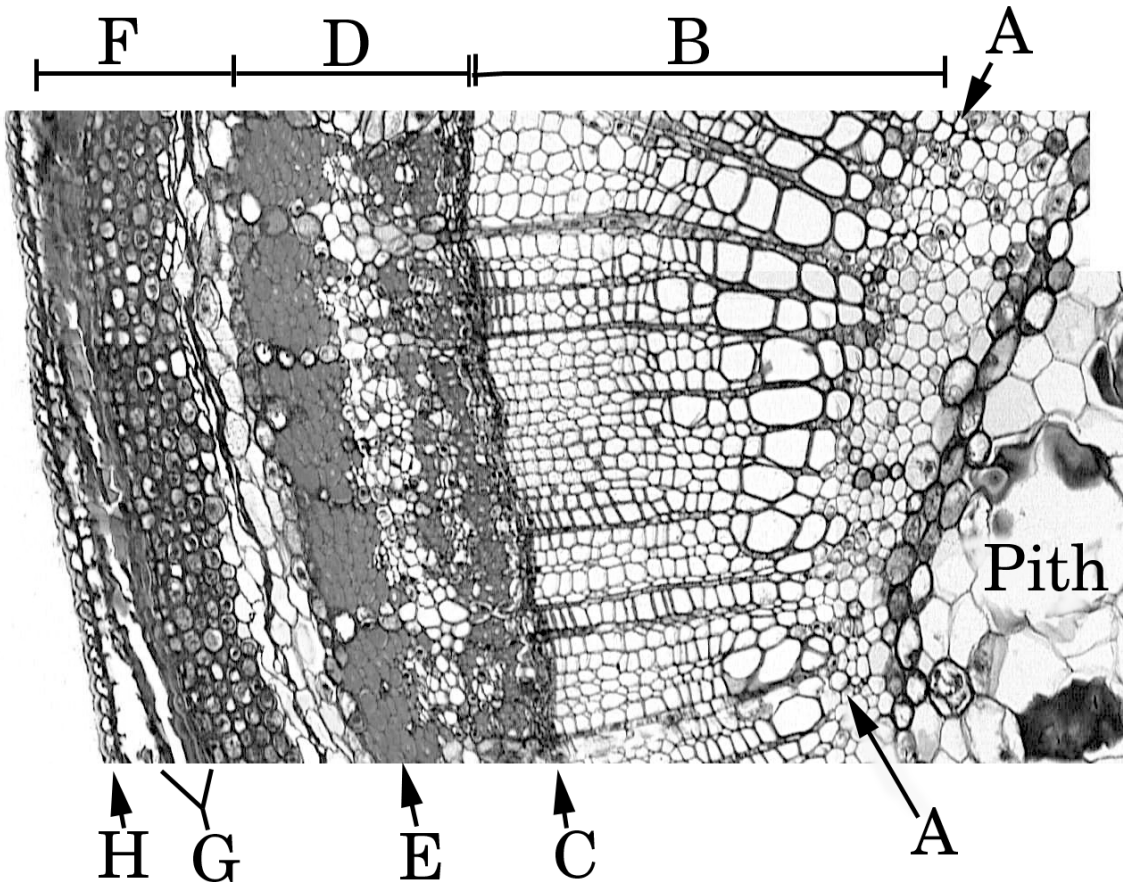
Now switch to 400x. Carefully study the boundary of the xylem with the pith. The innermost xylem is primary. The outermost is secondary. The boundary between the two is subtle: the secondary xylem starts where the **xylem rays** begin. Xylem rays are areas of parenchyma of the secondary xylem running radially through the stem. Starting at the outside of the cylinder of xylem, locate a ray and follow it towards the pith. Where it ends marks the location of the primary xylem.

Study the boundary between the xylem and the phloem. This marks the location of the **vascular cambium**. Note that on either side of the vascular cambium are the youngest secondary tissues. The farther the tissues lie from the vascular cambium, the older the tissue. This means that **as we move outward through the xylem we move progressively from older to younger xylem.** However, **as we move outward through the phloem we move progressively from younger to older phloem.**

The outermost phloem is the protophloem and is marked by a continuous ring of fibers. These fibers differentiated from cells in the primary phloem that matured after the onset of secondary growth.

Outside of the phloem is the cortex. In the cortex a periderm has formed to the outside. The periderm consists of a cork cambium together with the cork tissue derived from that cambium. Note the epidermis being sloughed off the stem.

Label the figure



Cross Section of a One-year Old *Tilia* Stem

A = _____

E = _____

B = _____

F = _____

C = _____

G = _____

D = _____

H = _____

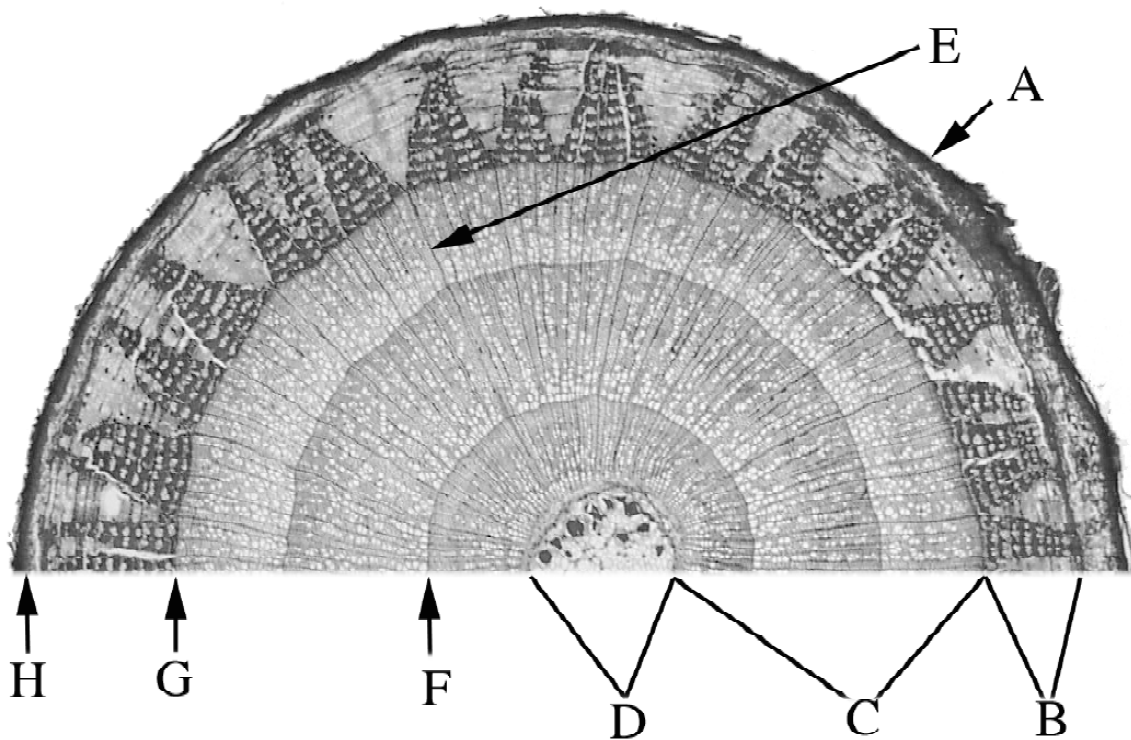
Section After Three Years Growth.

Switch back to 40x and survey the 3-year old *Tilia* section. The obvious changes visible here are the growth rings present in the secondary xylem, and the growth of certain rays in the phloem forming wedge-shaped regions of parenchyma. The sequence of tissues outlined before are the same from the center outward: pith, primary xylem, secondary xylem, vascular cambium, secondary phloem, primary phloem, cortex, and periderm.

Switch to 400x and carefully study a growth ring of the secondary xylem. The growth increments are areas where smaller thick-walled vessel elements border larger thin-walled vessel elements. The smaller cells make up late summer's growth and the larger cells early spring growth. By observing this boundary you should be able to tell in which direction is the pith. You will need to make this determination for one question on the lab exam. The rays in the xylem are continuous with those in the phloem.

The enlargement of some of the phloem rays serve to relieve the tension on the phloem created by the expanding cylinder of xylem. This stress tends to create longitudinal rips in the phloem which would destroy its integrity. The expansion of these rays (they are called dilated rays) prevents these tears. The phloem outside of this ray tissue consists of bands of fibers alternating with areas containing sieve-tube elements and companion cells.

Label the figures.



A = _____

E = _____

B = _____

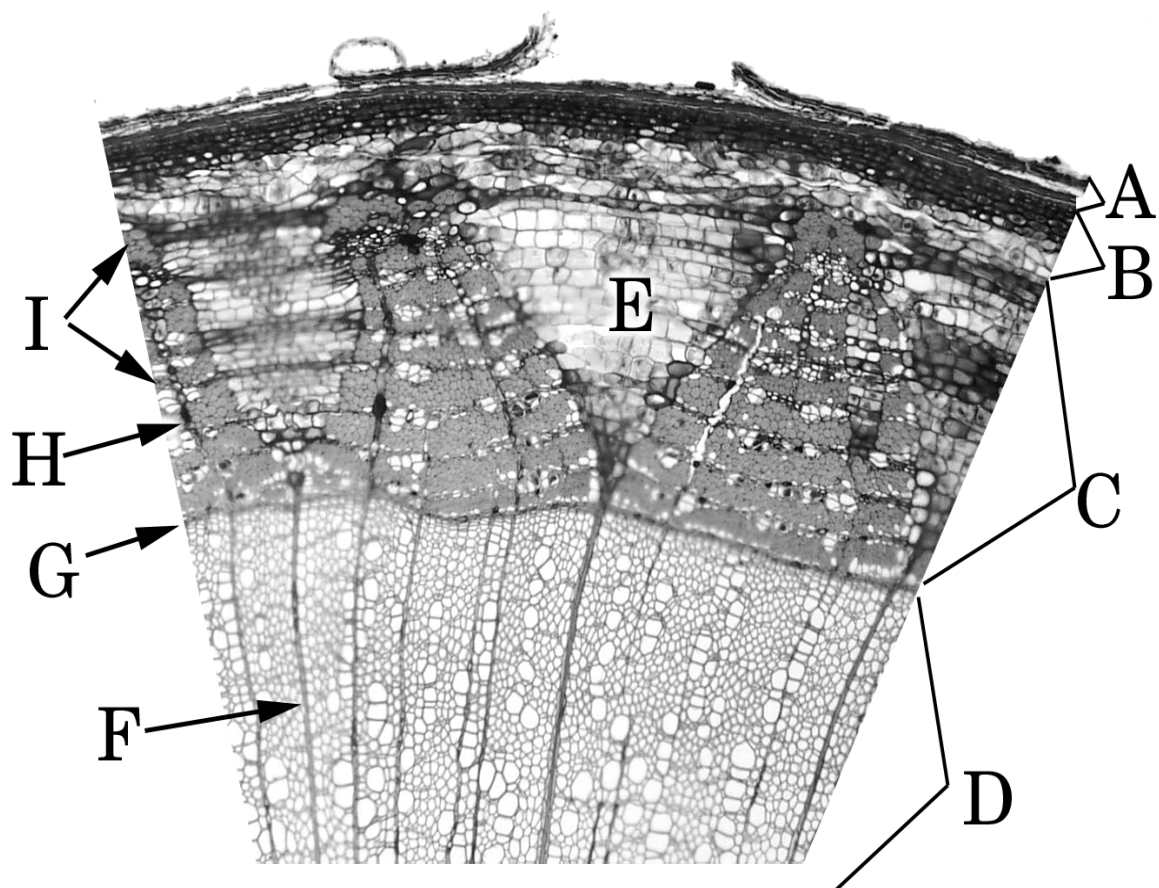
F = _____

C = _____

G = _____

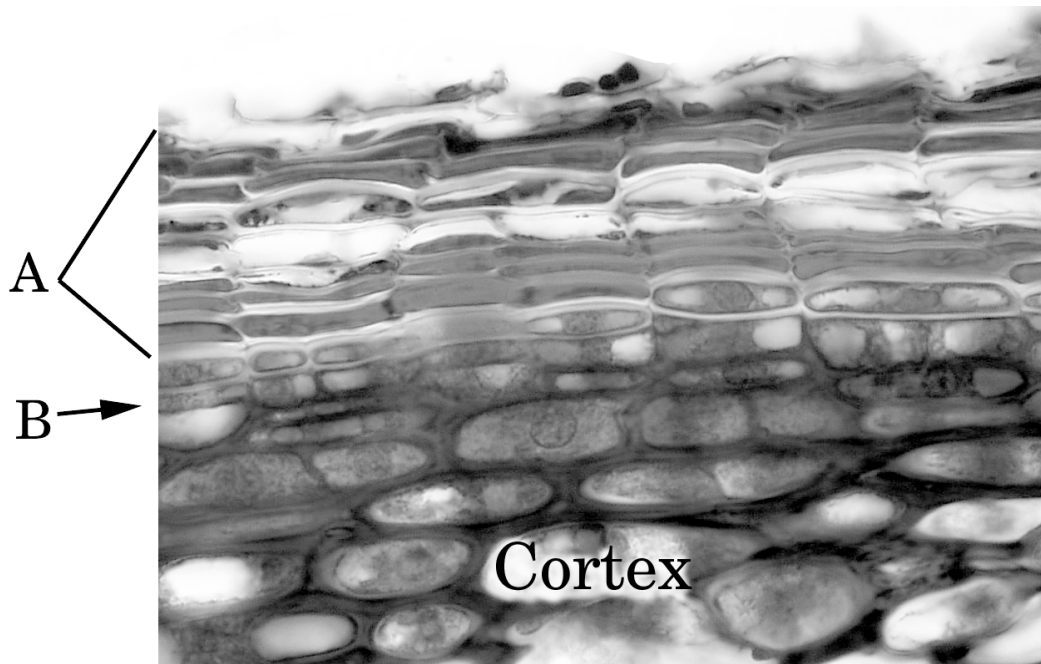
D = _____

H = _____



A = _____
 B = _____
 C = _____
 D = _____
 E = _____

F = _____
 G = _____
 H = _____
 I = _____



Periderm of an older *Tilia* stem

A = _____

B = _____

Drawings: Draw the following of a woody *Tilia* stem below and on the next page.

a phloem fiber

sieve-tube element
with companion cell

cork cells
with cork cambium

adjacent vessel elements across
a growth ring

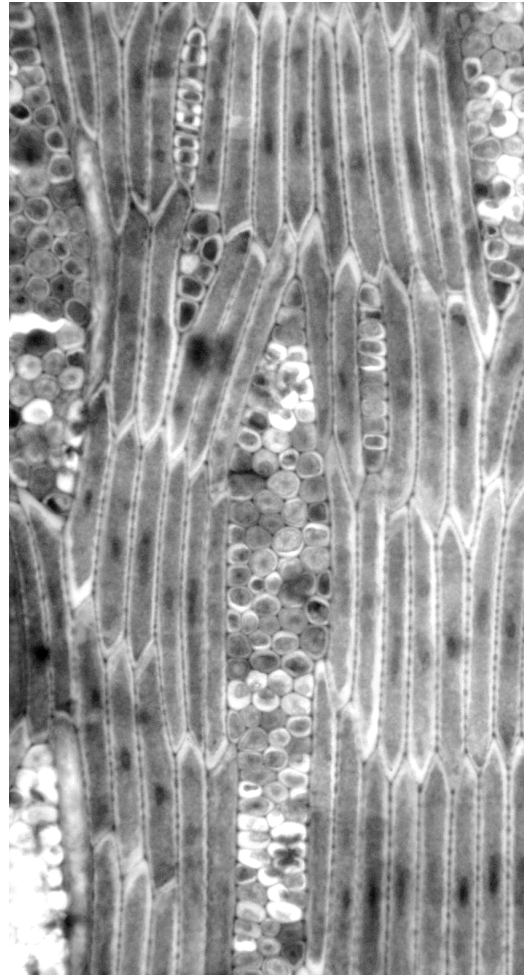
Parenchyma in
a xylem ray

Parenchyma in a
non dilated phloem ray

III. Face View of a Vascular Cambium

The vascular cambium is a hollow cylinder of actively dividing cells. In cross sections of stems, this dimensional aspect of the structure isn't apparent. To see the cambium as a sheet of tissue, one must observe a longitudinal section of a woody stem through the cambium. This type of section is a tangential section. The cut is made following a plane tangential to the cylinder of the cambium.

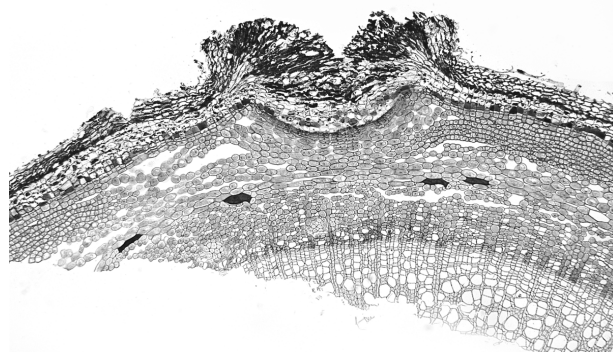
Observe the demonstration slide of the tangential section of the cambium of *Robinia* (black locust). Note that there are two types of cells each with a different orientation. One type of cell is arranged vertically and are termed **fusiform initials**. These go on to form tracheary elements in the wood, or, if incorporated into the phloem, sieve-tube elements, companion cells or fibers. The other cells are arranged horizontally and are called ray initials. These go on to form the rays both in the secondary xylem and secondary phloem.



Vascular Cambium of *Robinia*

IV. Lenticels

Lenticels are tears in the bark. They allow for the diffusion of gases to and from the living tissues in the woody stem. Observe the demonstration slide at the front of a section of a lenticil in *Sambucus*.



Lenticel of *Sambucus*

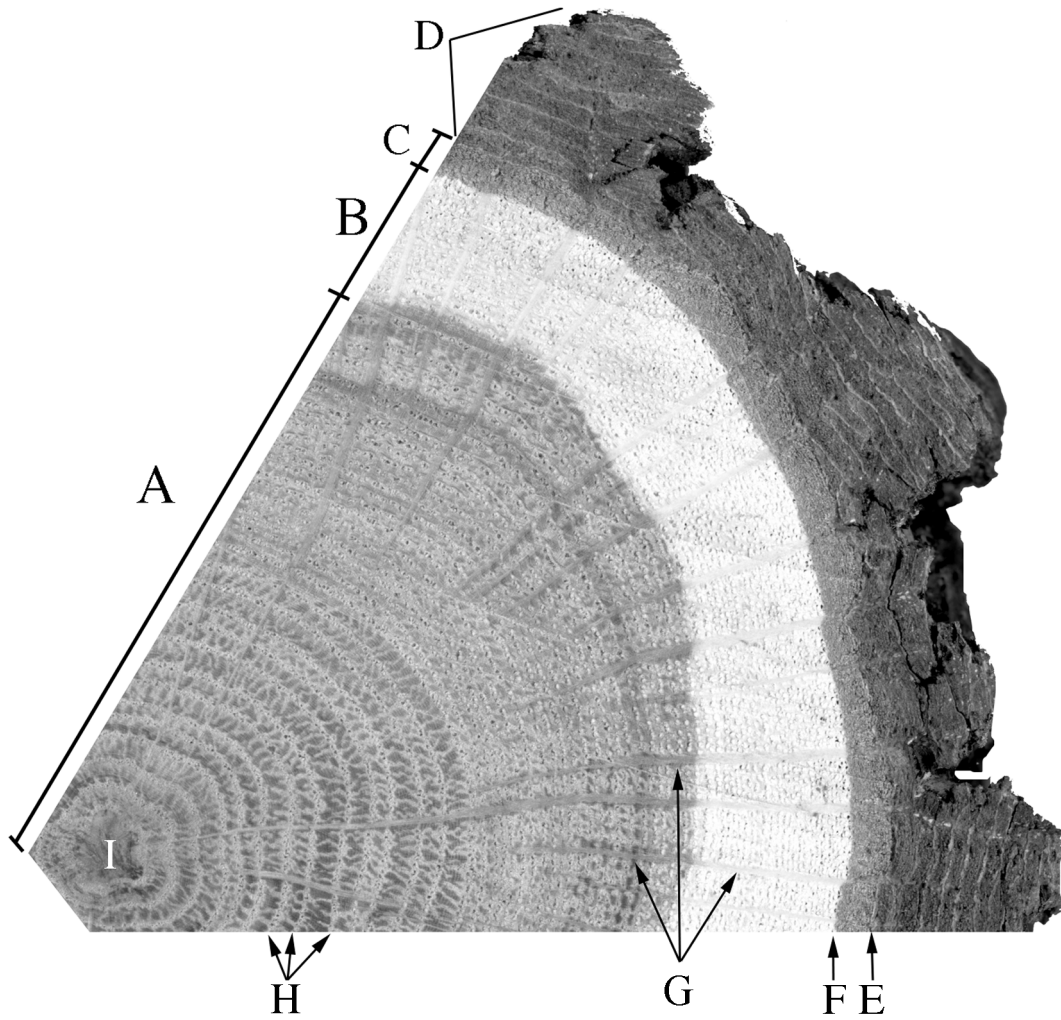
V. Gross Structure of Woody Stems

Woody stems are mostly secondary xylem (wood) surrounded by bark. The xylem may include heartwood and sapwood. Heartwood is darker. While its cells are all dead and the tracheary elements are nonfunctional, the tissue still provides support. The sap wood is lighter. In the sap wood the tracheary elements (tracheids and vessel elements) are functional and the tissue includes living parenchyma cells. The boundary between the bark and wood marks the location of the vascular cambium.

The bark itself is divided into two regions by the cork cambium: the living area inside the cork cambium is the inner bark, and the dead tissue outside is the outer bark. Evidence of earlier cork cambia can be easily discerned in some woody stems.

Take a section of oak wood from the front bench and identify the following: **pith**, **heart wood**, **sap wood**, **vascular cambium**, **xylem rays**, **inner bark**, and the **outer bark**. If you can't locate these all of the above, ask your TA for help.

Label the Figures.



Cross Section of Bur Oak Stem

A = _____

E = _____

B = _____

F = _____

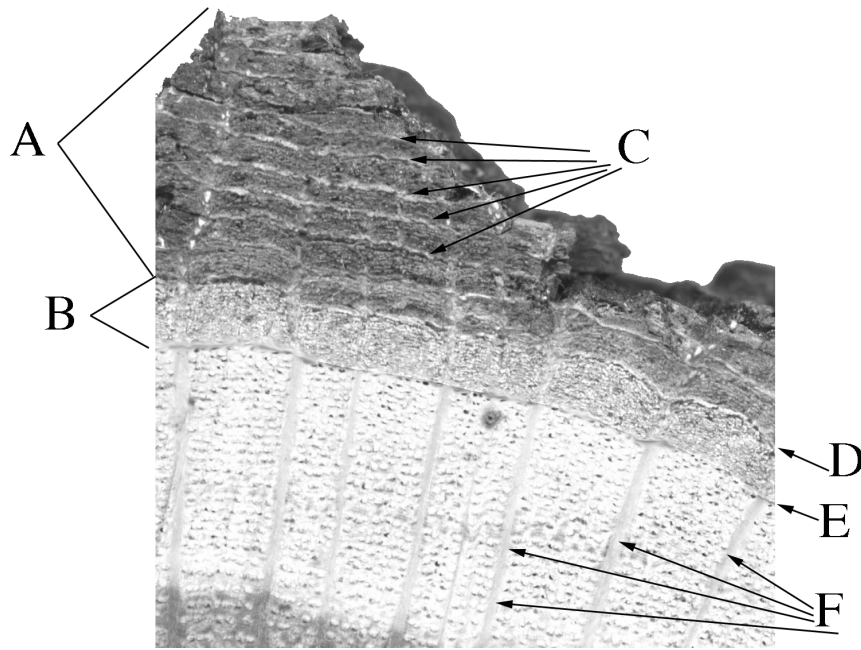
C = _____

G = _____

D = _____

H = _____

I = _____



Detail of the Bark of Bur Oak

A = _____

D = _____

B = _____

E = _____

C = _____

F = _____

VI. Secondary Growth in Roots

The onset of secondary growth in roots is somewhat different than that in stems. This is well illustrated in your text on page 601 in figure 25-16. The pericycle plays an important role in secondary growth. It both forms the periderm and also splices together the pieces of vascular cambium at the protoxylem poles where it is discontinuous. Because the first periderm is formed by the pericycle, all the tissues outside and including the endodermis are sloughed off immediately with the onset of secondary growth.

Via. Secondary Growth in *Tilia*: Locate the prepared slide of *Tilia* root and observe with your microscope. Identify the vascular cambium, secondary xylem, and secondary phloem. Can you identify the star-shaped mass of primary xylem inside this root? Identify the periderm, vascular cambium, primary xylem, secondary xylem, and secondary phloem.

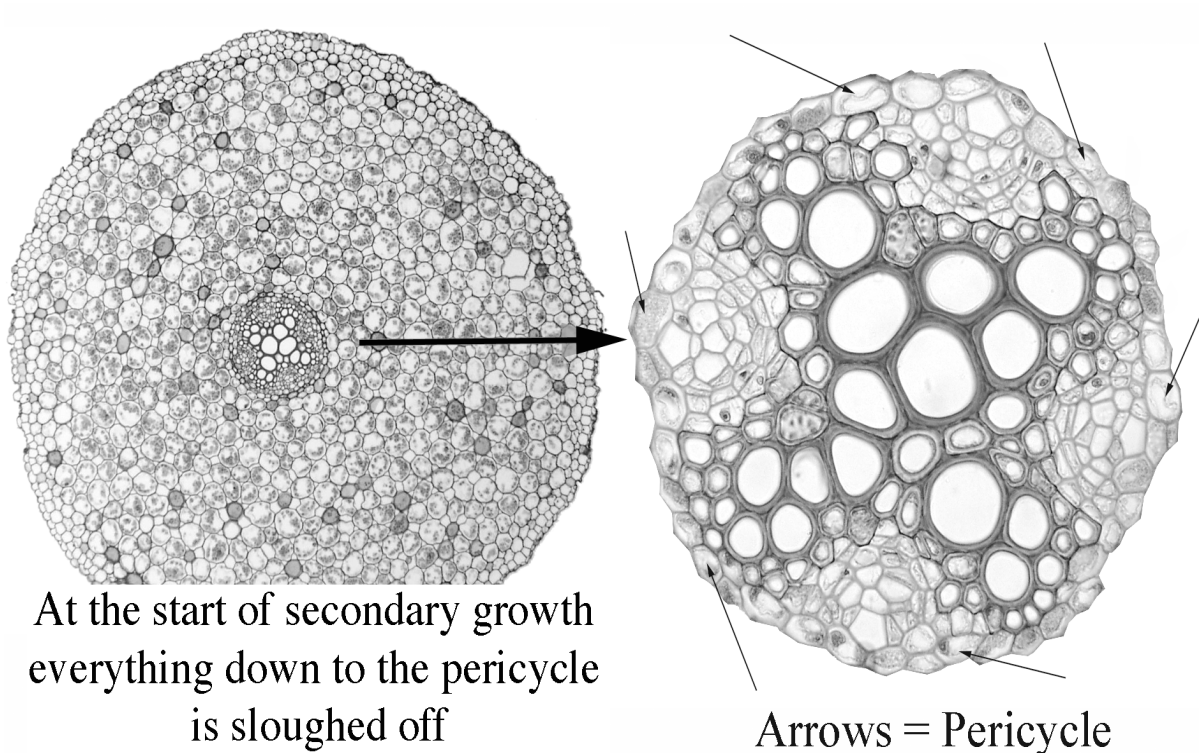
From what primary tissue is the secondary tissue surrounding the phloem derived?

Vlb. The carrot: Carrots are roots with lots of secondary growth. At their core, they are composed of xylem tissue surrounded by phloem tissue. Make a cross section of a carrot and observe it with a dissection microscope. Note the rays which are indicative of secondary tissues. Identify the vascular cambium, primary xylem, secondary xylem, and secondary phloem.

From what primary tissue is the secondary tissue surrounding the phloem derived?

Draw a vessel element in your carrot section.

Oak wood and the inner core of carrots are both examples of xylem tissue. Why is one hard and tough while the other is crisp and delicious? Can you relate this to the different functions of roots vs. stems?



Cross Section of a *Ranunculus* Root at the End of Primary Growth (Left).

At the onset of secondary growth in the root, only the vascular cylinder with the pericycle is retained (right).