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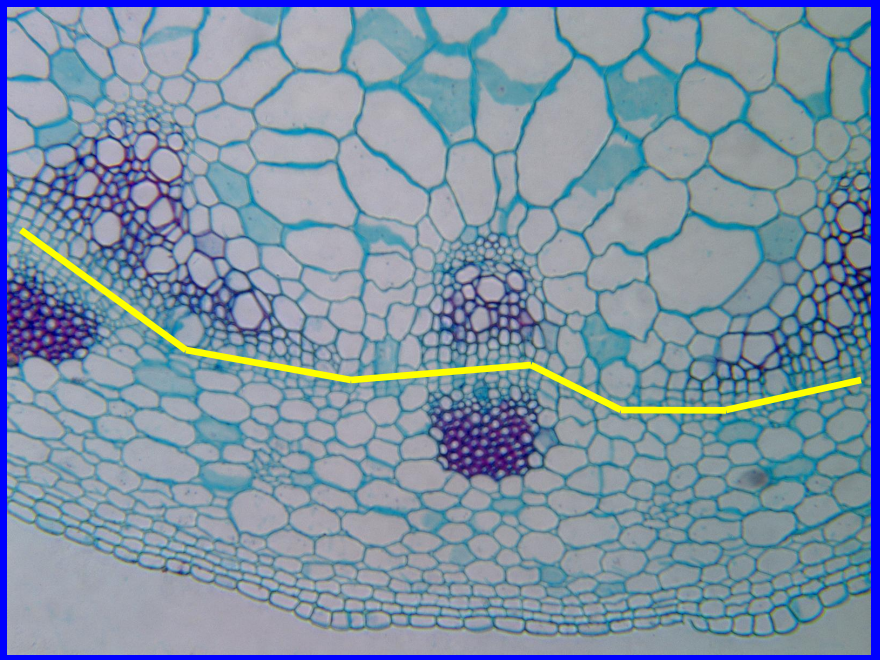
V. Secondary growth and secondary structure of the stem



(I) Secondary structure of the dicotyledons stem

1. Origins and activities of vascular cambium

(1) Origins

① Fascicular cambium: A layer of tissue having potential meristematic ability is left between the primary xylem and primary phloem of vascular bundle when procambium generates the vascular tissue, which is called the vascular cambium.

② Interfascicular cambium: Some cells having restored meristematic ability corresponding to cambium portion in the parenchyma of medullary ray constitute the interfascicular cambium.

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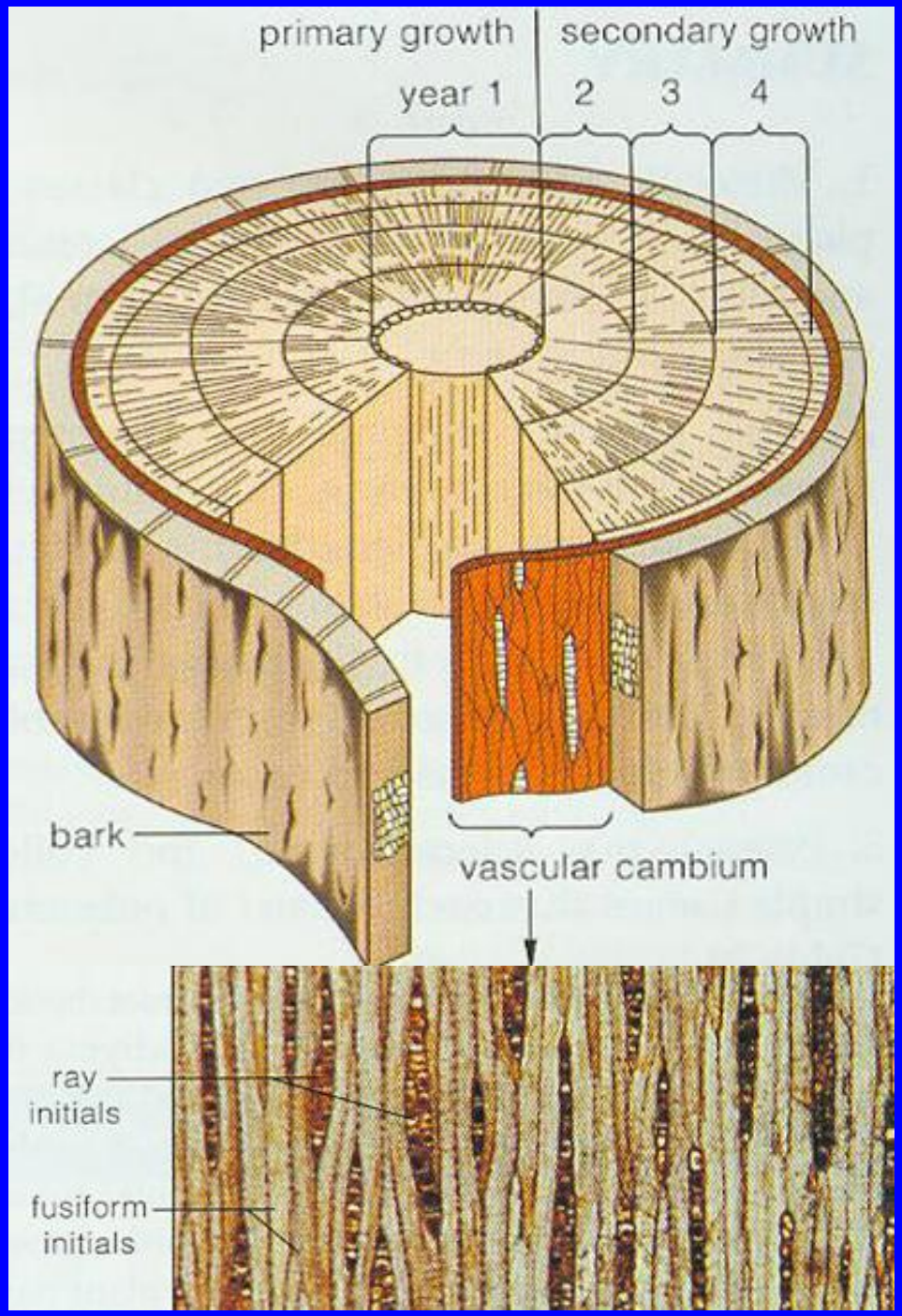

A view of vascular cambium in an older stem showing secondary growth.

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③ Structural characteristics of the procambium and fascicular cambium cells:

The procambium, located under the apical meristem, with very small cell and thick plasma and without large difference in the cells, is homogeneous tissue, which is totally transformed to primary vascular tissue.

The fascicular cambium, located between the primary xylem and primary phloem, having cells with different size and length and being vacuolized, is non-homogeneous tissue.

④ Cambial activity: The cambial cells undergo tangential division, forming the blast cell of secondary phloem outward, divided as the secondary phloem, and adding inside the primary phloem; which forms the apical cell of secondary xylem inward and adds outside the primary xylem.

⑤ Medullary ray and vascular ray: Division of the medullary ray cell elongates thr original medullary ray; and generates new vascular rays inside the secondary phloem and secondary xylem.

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(2) Cell composition, division mode and derived cell development of vascular cambium

①Fusiform initial cell: It is shaped as fusiform with both sharp ends. Its length is several or many times larger than its width, the tangential plane is wider than the radial plane, and the long axis is parallel with that of the stem, which forms the longitudinal system. Its derivative cells are divided into secondary xylem, secondary phloem and new fusiform initial cells.

② Ray initials: Ranging from slightly elongated shape to that of near equal diameter, similar to parenchyma, perpendicular to the long axis of stem, forming the transverse system. Its derivative cells are divided into ray cells and new ray initials.

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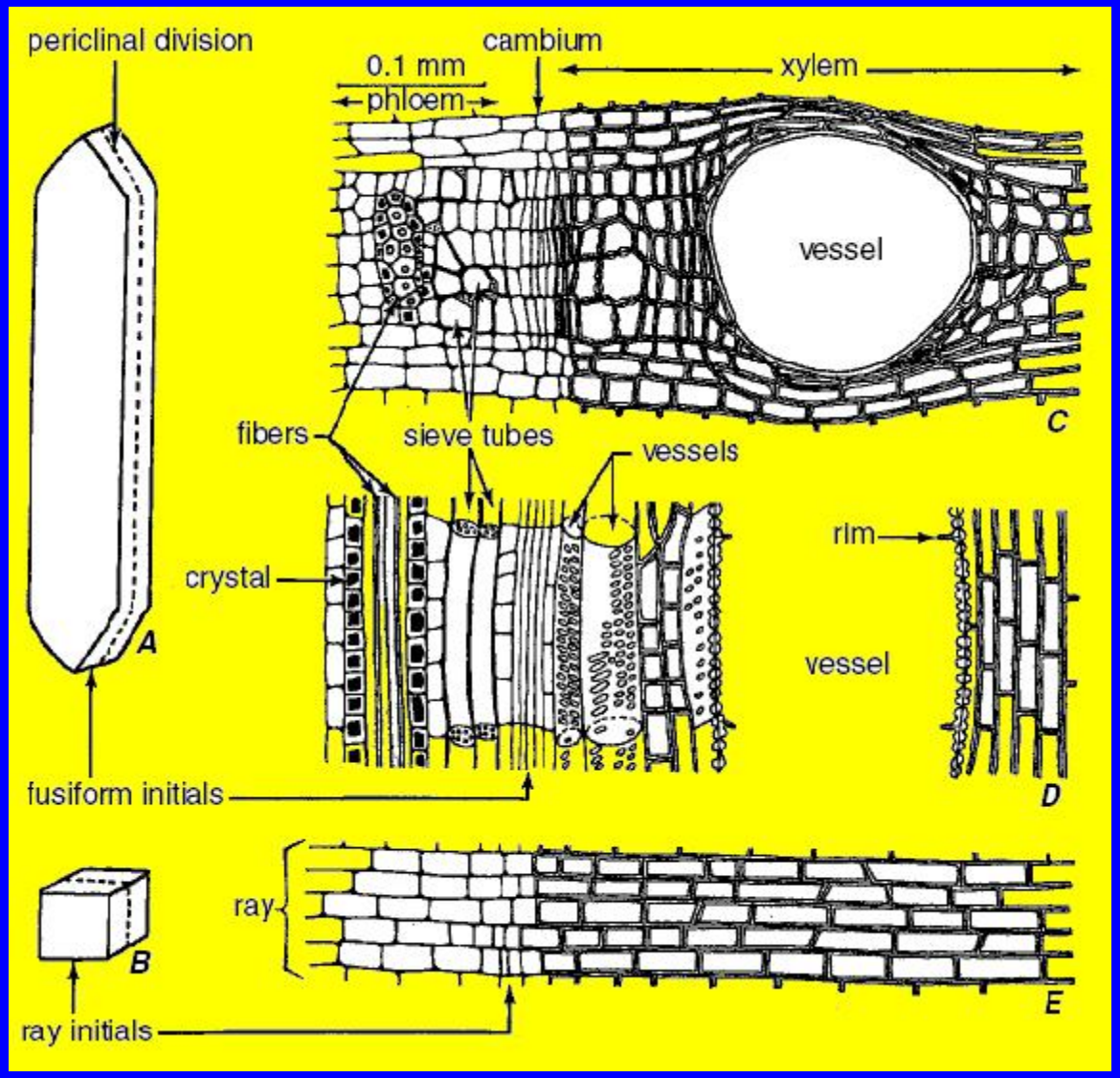

Vascular cambium in relation to derivative tissues. A, diagram of fusiform initial; B, of ray initial. In both, orientation of division concerned with formation of phloem and xylem cells (periclinal division) is indicated by broken lines. C, D, E, *Robinia pseudoacacia*; sections of stem include phloem, cambium, and xylem. C, transverse; D, radial (axial system only); E, radial (ray only). (From Esau, 1977)

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③ Cambial zone: Generally a zone composed of the initial cells and derivative cells that are not differentiated yet but under periclinal division is called cambial zone.

④ Secondary xylem:

a. The number of xylem formed by the cambium is much more than that of the phloem;

b. The composition is similar to the xylem, but having different degree of lignification;

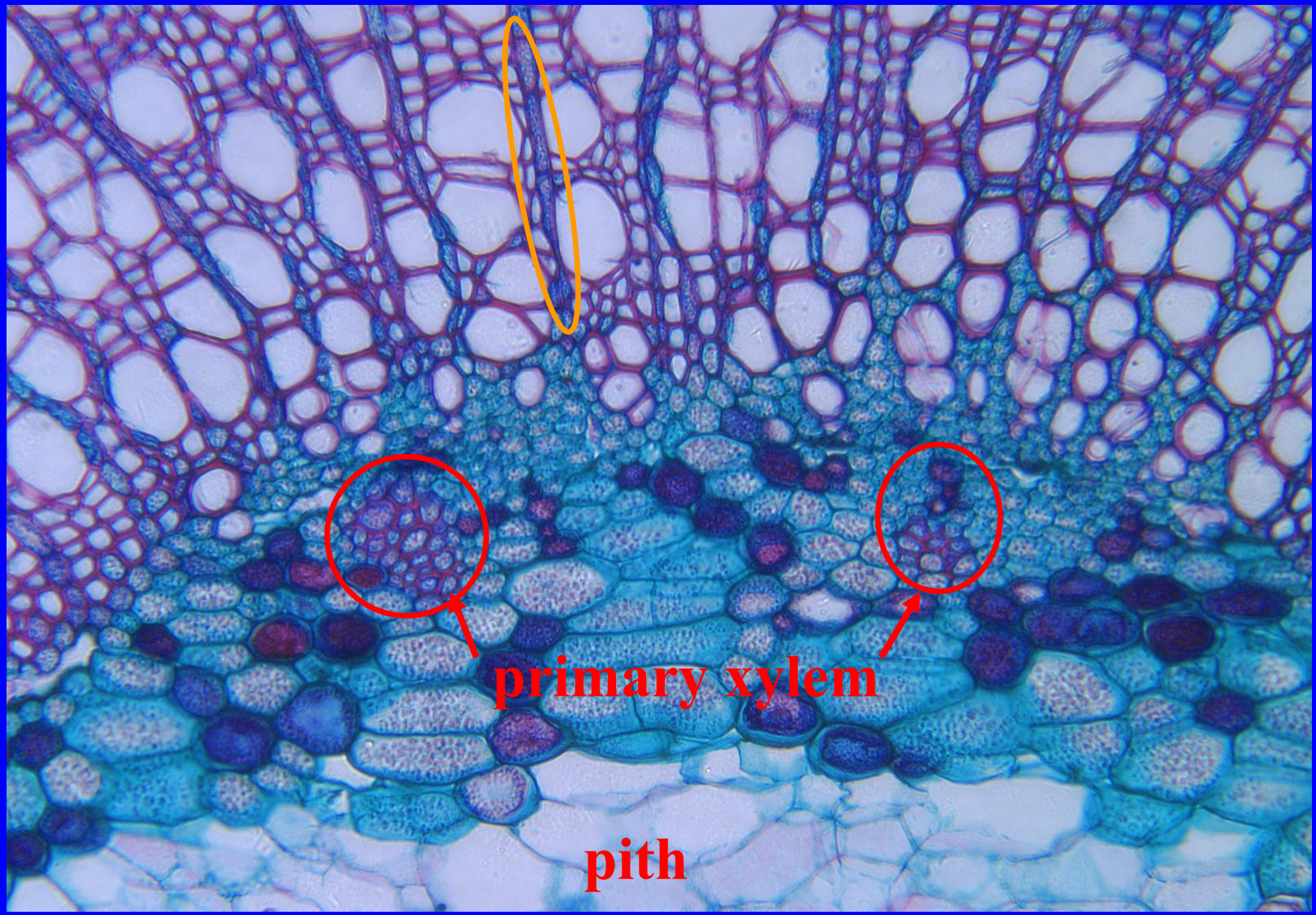
c. The most common is the pitted vessel while there is few scalariform and reticulated ones;

d. Having xylem parenchyma running through in fascicles or layering;

e. The number of xylogen is much higher than that of the primary xylem. Its composition is inferior to that of the vessel;

f. The xylem ray is developed from cells grown inwards by the ray initials, elongated and arranged radially, which is parenchyma, usually lignificated, forming the radial system of stem. It is a structure specific to the secondary xylem.

Secondary xylem of poplar stem.



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⑤ Secondary phloem:

a. The composition is similar to that of the primary phloem, sometimes having stone cells, but with different quantity, shape and distribution.

b. Phloem ray is formed by radial elongation of cells derived from the ray initials towards the secondary phloem. The wall will not be lignificated, and the shape is not regular as the xylem ray. It is a structure specific to the secondary phloem.

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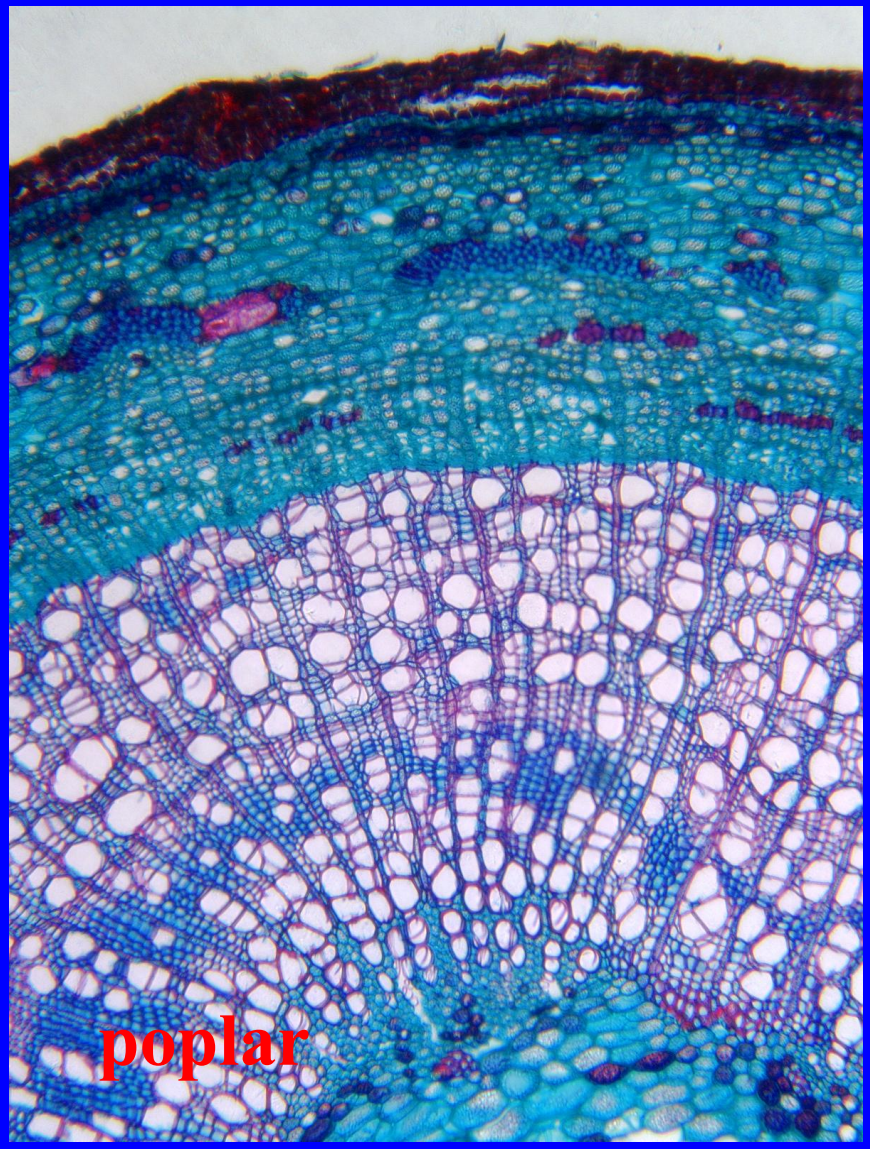
⑥Vascular ray:

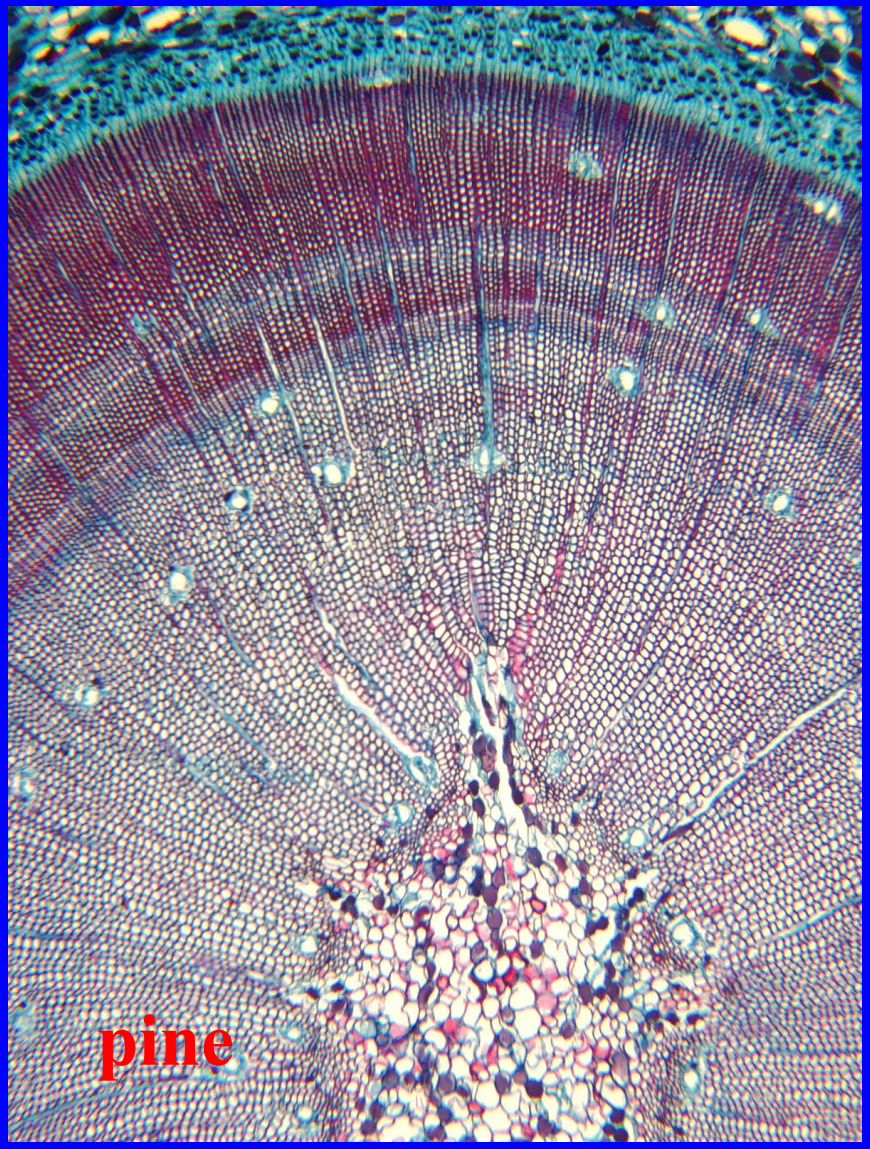
a. Phloem ray constitutes the vascular ray by connecting with xylem ray in the secondary xylem via ray initials of the vascular cambium.

b. It run through the secondary xylem and secondary phloem transversally, which is transverse conducting tissue as well as storage tissue.

c. With respect to the medullary ray, it is a secondary ray with unfixed quantity, which shall be increased as formation of new vascular tissues and thickening of the stem.

Vascular ray of poplar and pine stems.





⑦Expansion of cambial circumference:

a. The fusiform initial cell is divided into two daughter cells radially and anticlinally, which grows tangentially to widen the tangential plane;

b. The fusiform initial cell generates a new cell by lateral and anticlinal division, growth of which also widens the tangential plane;

c. Slant and anticlinal division of the fusiform initial cell nearly resembles to the transverse division, and the two generated daughter cells grow to be in parallel state through lengthwise immersion, which increases both length of the cambial initial cells and width of the tangential plane;

d. Proliferation, division and cell enlargement of the ray initials plays a certain role in increase of the cambial circumference.

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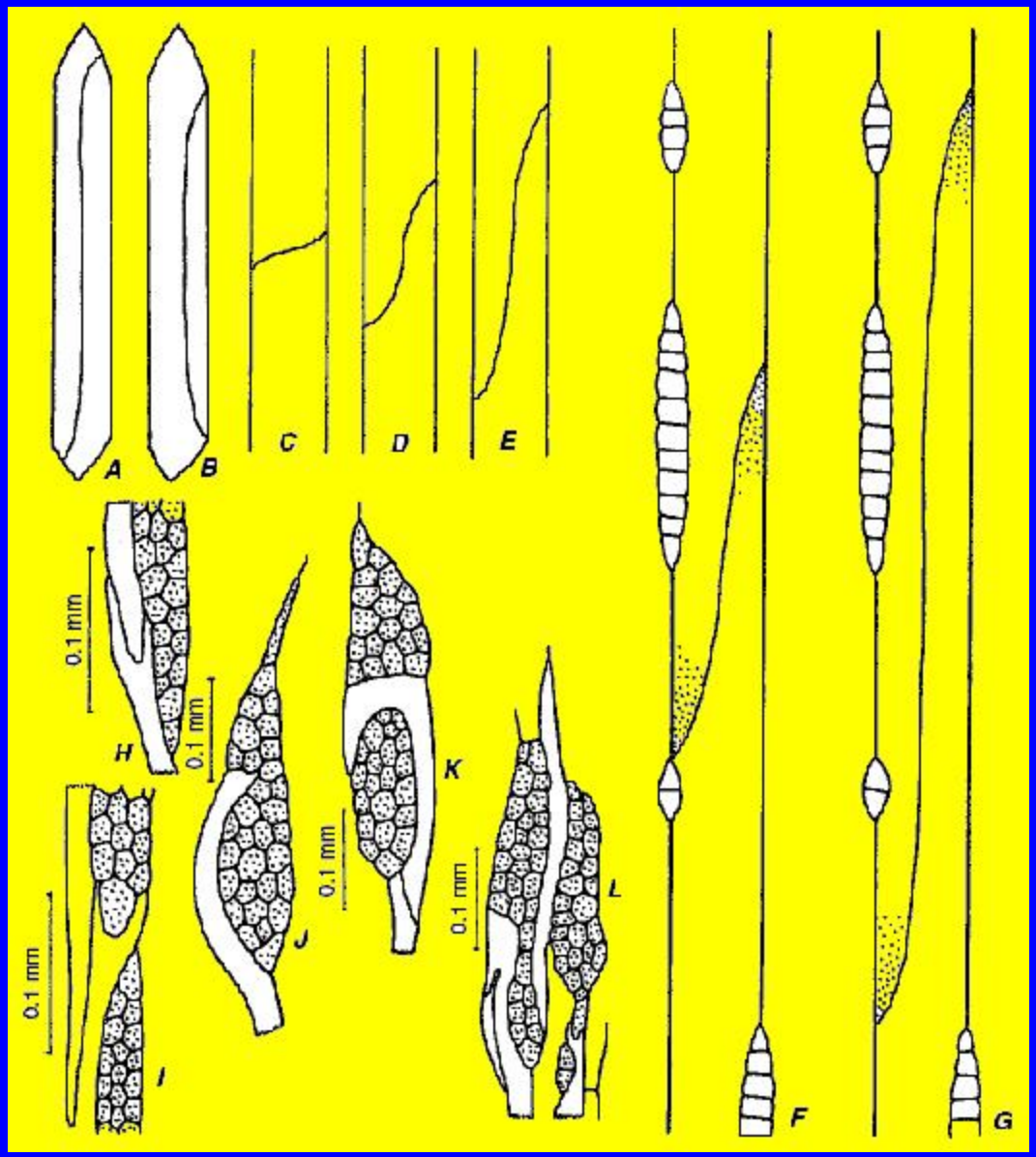
Division and growth of fusiform initials. Initial divided: A, by radial anticlinal wall; B, by lateral anticlinal wall; C-E, by various oblique anticlinal walls. F, G, oblique anticlinal division is followed by apical intrusive growth (growing apices are stippled). H, I, forking of fusiform initials during intrusive growth (*Juglans*). J-L, intrusion of fusiform initials into rays (*Liriodendron*). (All tangential views) (From Esau, 1977)



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⑧ Activities of the ray initials:

a. The fusiform initial cell generates a part laterally from the middle to form the ray initials;

b. The fusiform initial cell splits a ray initial transversally near the top;

c. A half or the whole fusiform initial cells are split into uniseriate ray initials;

d. The fusiform initial cell is gradually shortened due to degeneration, forming ray initials;

e. A ray initial is split into a series of ray initials;

f. The uniseriate ray initial is anticlinally split into double or multiple series, and the later one can be combined to become wider.

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(3) Seasonal activities and growth ring of the vascular cambium

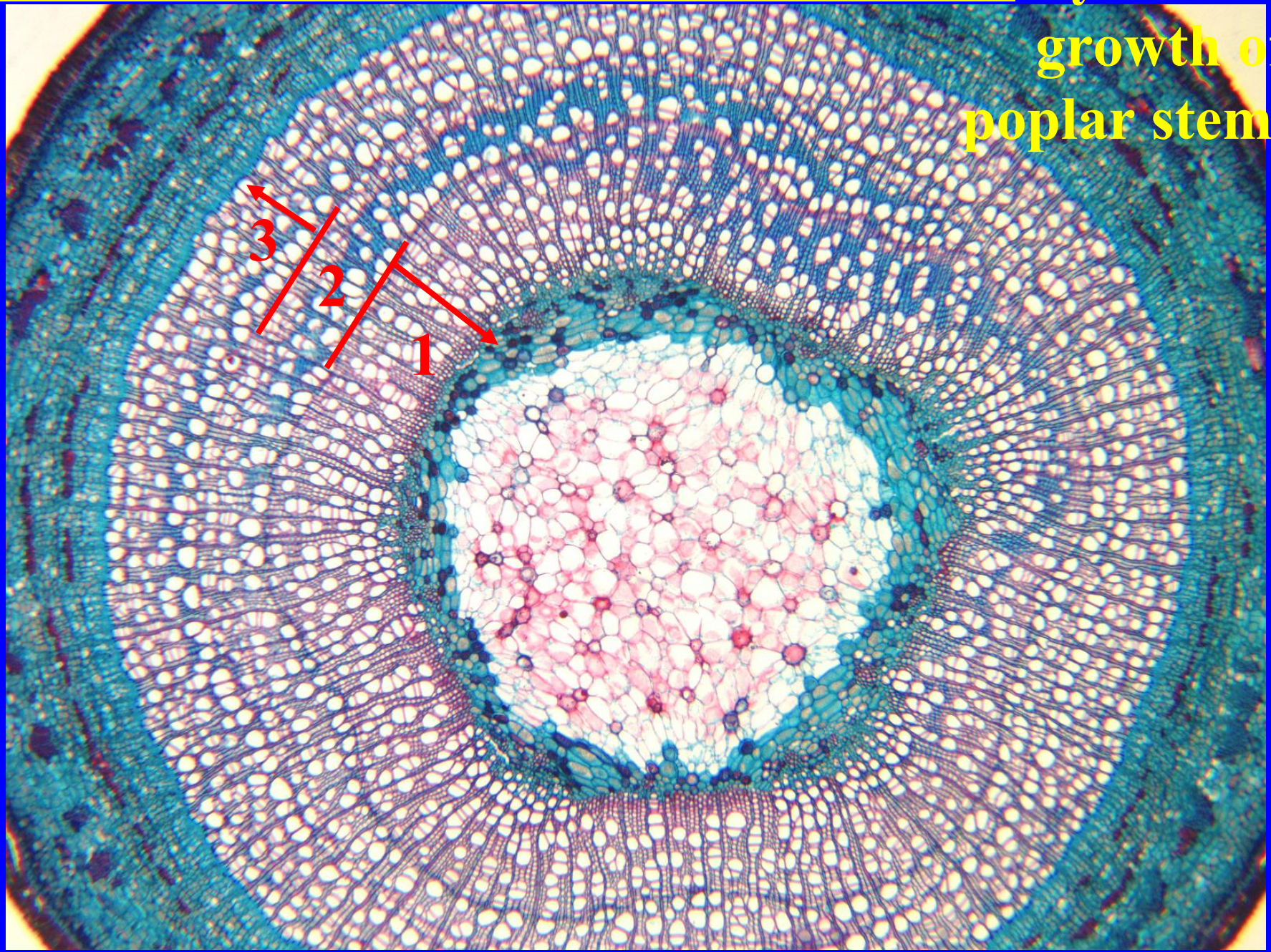
Activities of the cambium are varied accentually as the alternation of seasons:

① Early wood: During the Spring in the temperate zone or wet seasons in the tropical zone, the cambial activities are vigorous due to high temperature and abundant moisture, and cells of the formed secondary xylem have large radius and thin wall, which is so called the early wood. It has loose texture and light color.

② Late wood: During the late Summer or early Autumn in the temperate zone or dry seasons in the tropical zone, the cambial activities are gradually attenuated, the formed cells have thick wall, and usually the tracheid number is increased, which is so called the late wood. It has dense texture and deep color.

③ Growth ring: In regions having remarkable seasonal climate, as for the secondary xylem of plant, there is a very clear demarcation between the late wood of previous year and the early wood of current year in normal cases. A ring of early wood and late wood are indicated for per year, which is customarily called the growth ring.

3-year-old growth of poplar stem.



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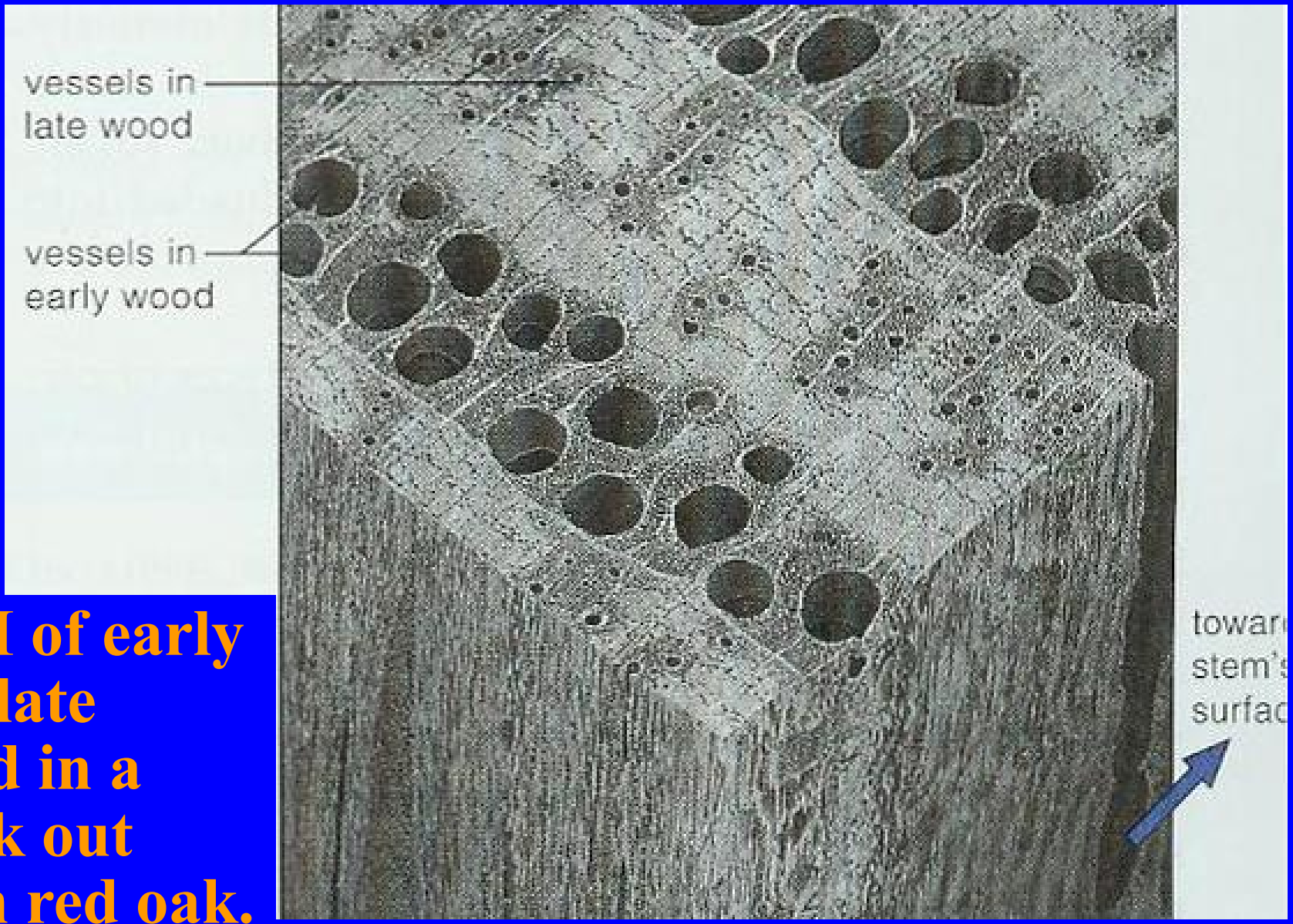

SEM of early and late wood in a block out from red oak.

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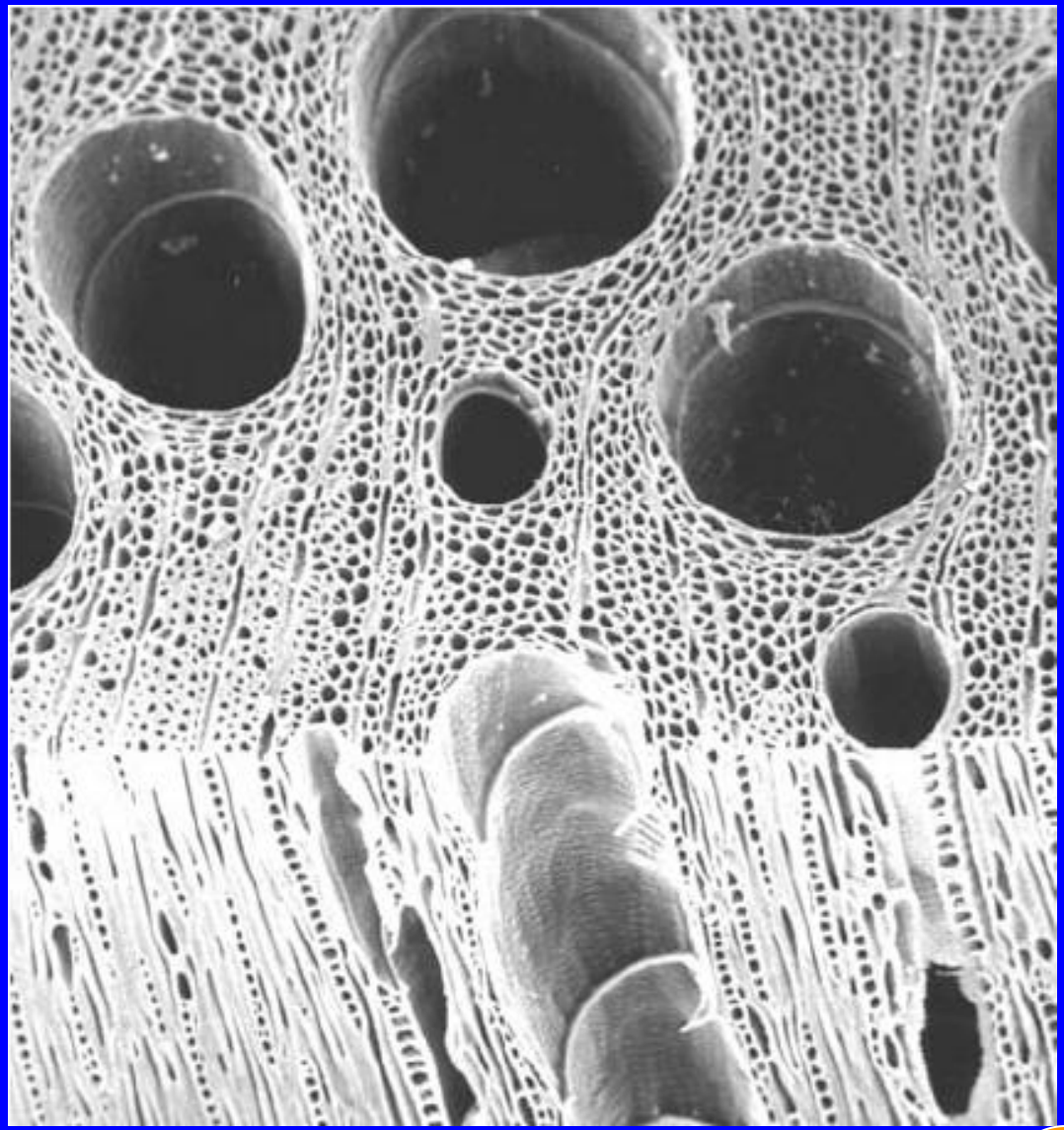

Secondary xylem: *Quercus robur* (Fagaceae), block of wood at edge of transverse and tangential longitudinal surfaces, showing large early (spring) wood vessels.

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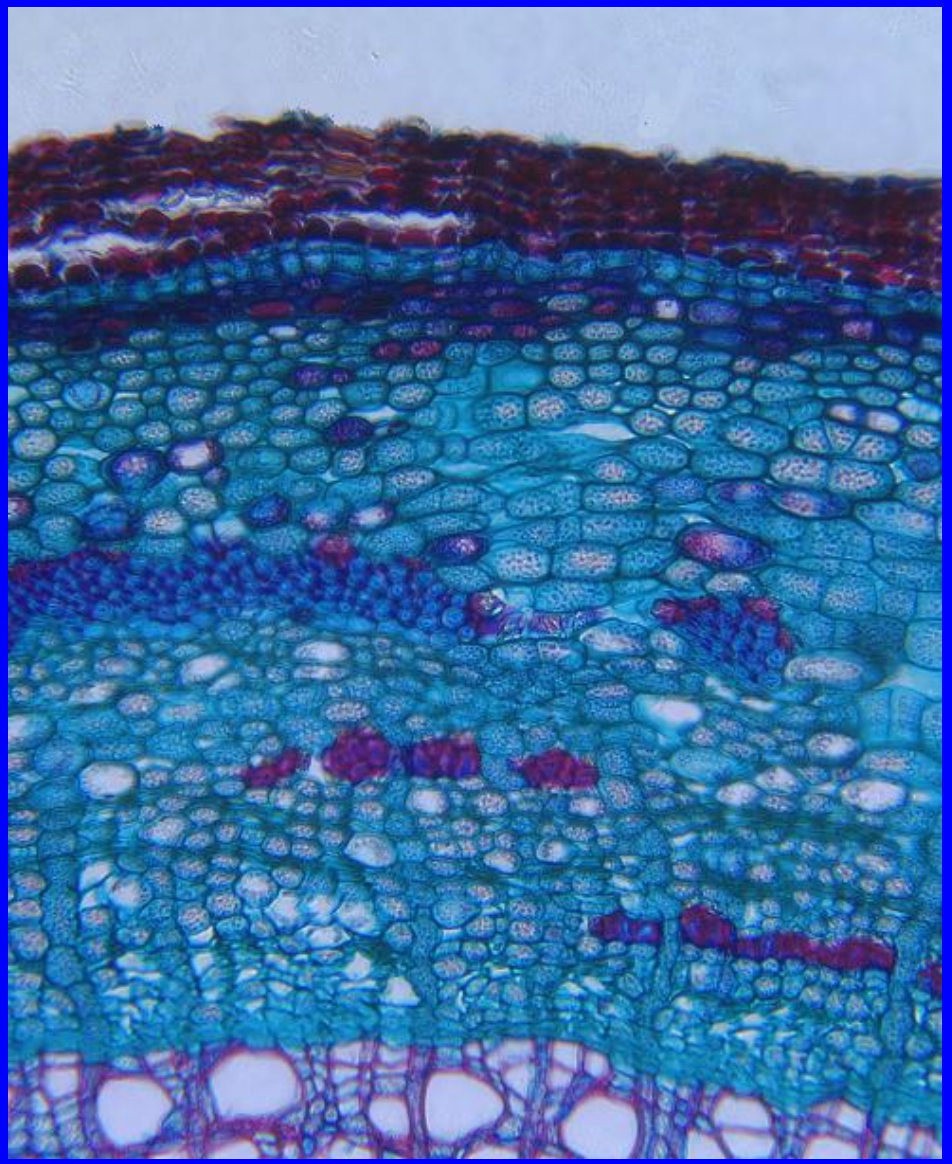
2. Origins and activities of cork cambium

The cork cambium has a simple structure, containing only one type of initial cell, indicated as a narrow rectangular on the cross section, which is a lateral meristem. The active period of most cork cambium is limited.



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(1) Origin: Different

① Usually referring to cortical cell close to the epidermis (poplar, walnut and elm).

② Some transformed from the second and third layers of cortical cells (black locust, birthwort).

③ Some transformed from parenchyma inside the near phloem (grape, pomegranate).

④ Some also transformed from the epidermis (willow, quercus suber and pear)

When the first cork cambium stops activities, new cork cambium will be generated inside it, which can be as deep as the secondary phloem inside the old trunk.

(2) Periderm

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(3)Bark

In terms of the plant anatomy, all tissues outside the vascular cambium or xylem can be called “bark”. In the secondary state, it contains secondary phloem, primary tissue possibly existing outside it, periderm and all dead tissues external to the periderm; in the primary state, it only contains primary phloem, cortex and epidermis.

(4) Type of lenticel

Having closing stratum: The structure has obvious stratification, having a closing stratum formed by suberized cells densely arranged with thickness of one to multiple cells, which encircles complementary tissues and cells not suberized inside.

Having no closing stratum: The structure is relatively simple without stratification, but the cells have distinction between the loose and dense arrangement, or suberization and non-suberization.

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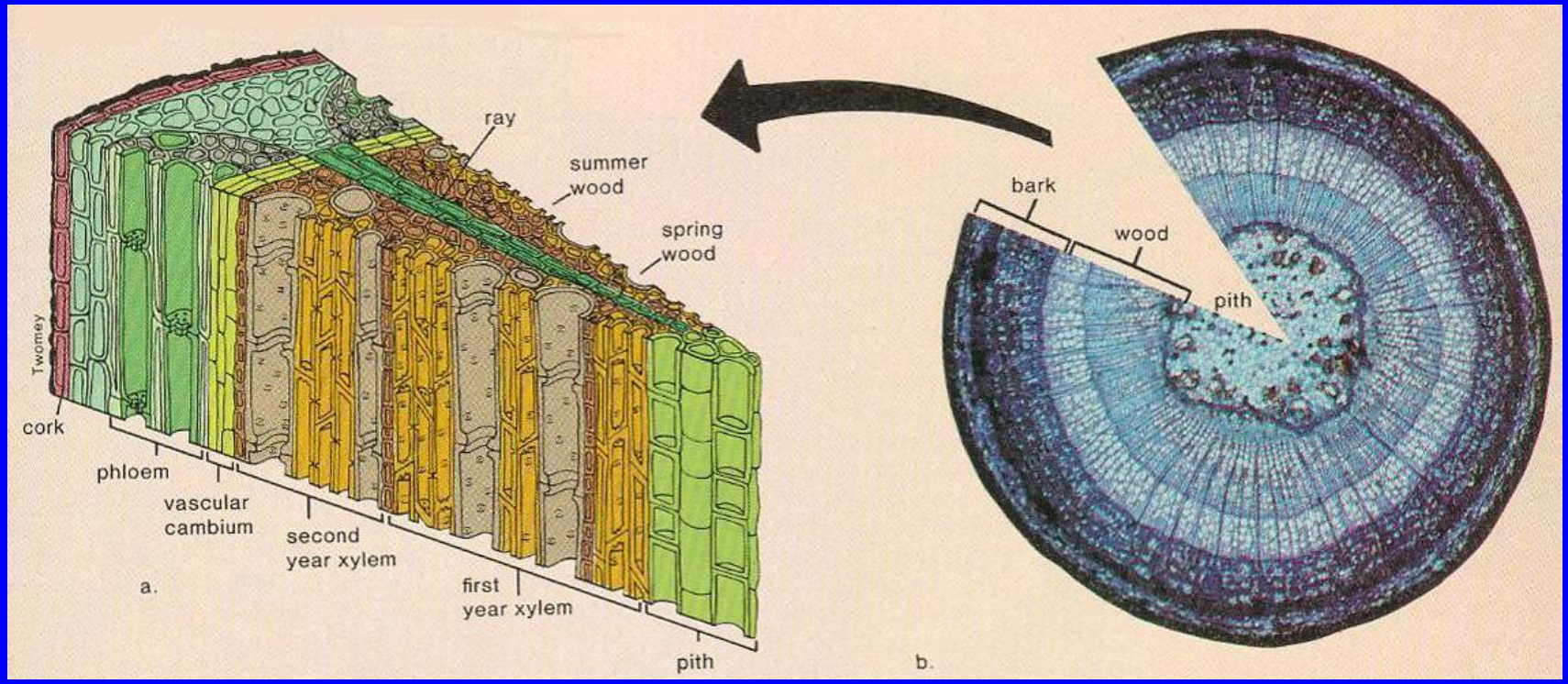

Woody stem. *a*. A drawing indicating the location of cork, phloem, vascular cambium, and xylem that accumulates to give annual rings. *b*. A photomicrograph of a cross section shows the three parts of woody stem: bark, wood, pith.

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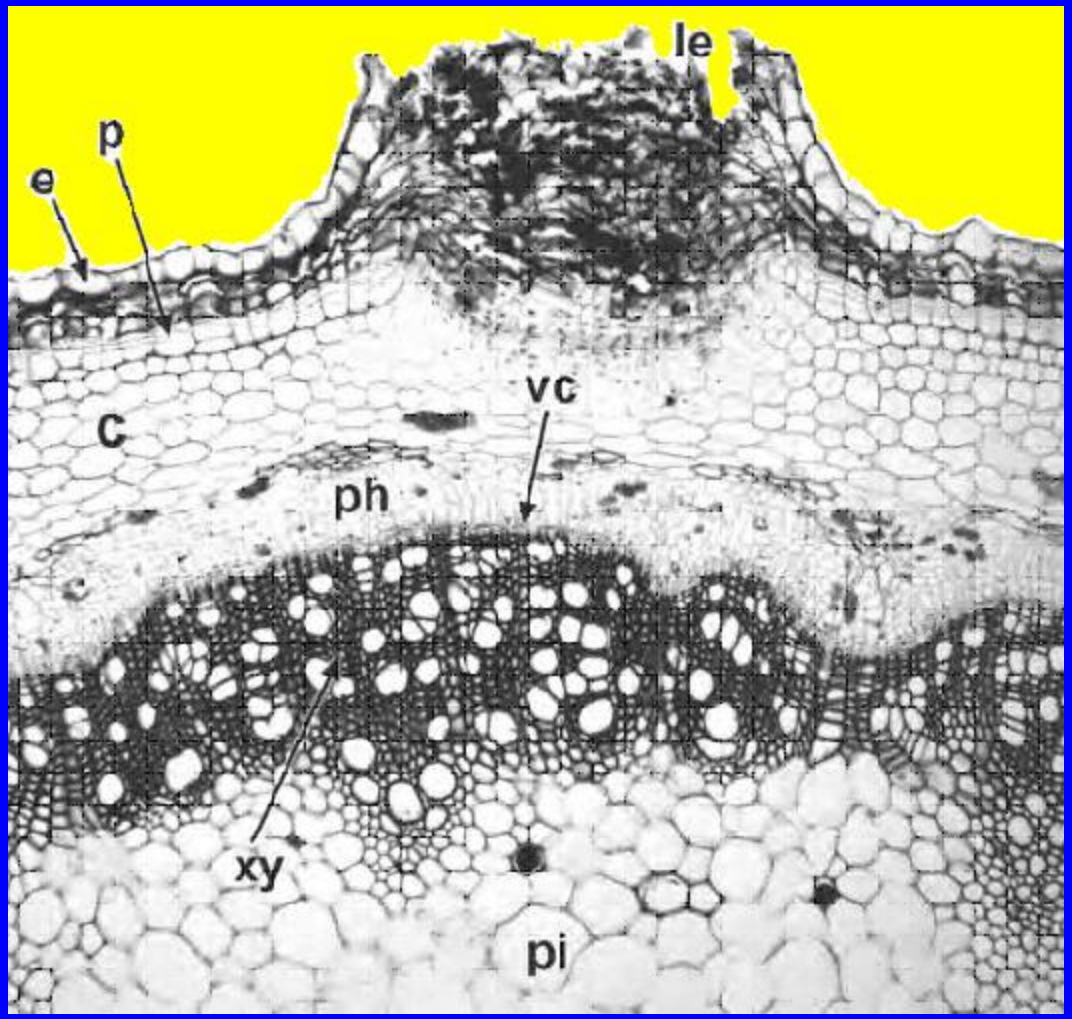
Sambucus nigra **(Caprifoliaceae). Transverse section of stem surface, showing periderm forming in outer cortical layers. c=cortex, e=epidermis, le=lenticel, p=periderm, ph=secondary phloem, pi=pith, vc=vascular cambium, xy=secondary xylem. Scale=100 μm.**



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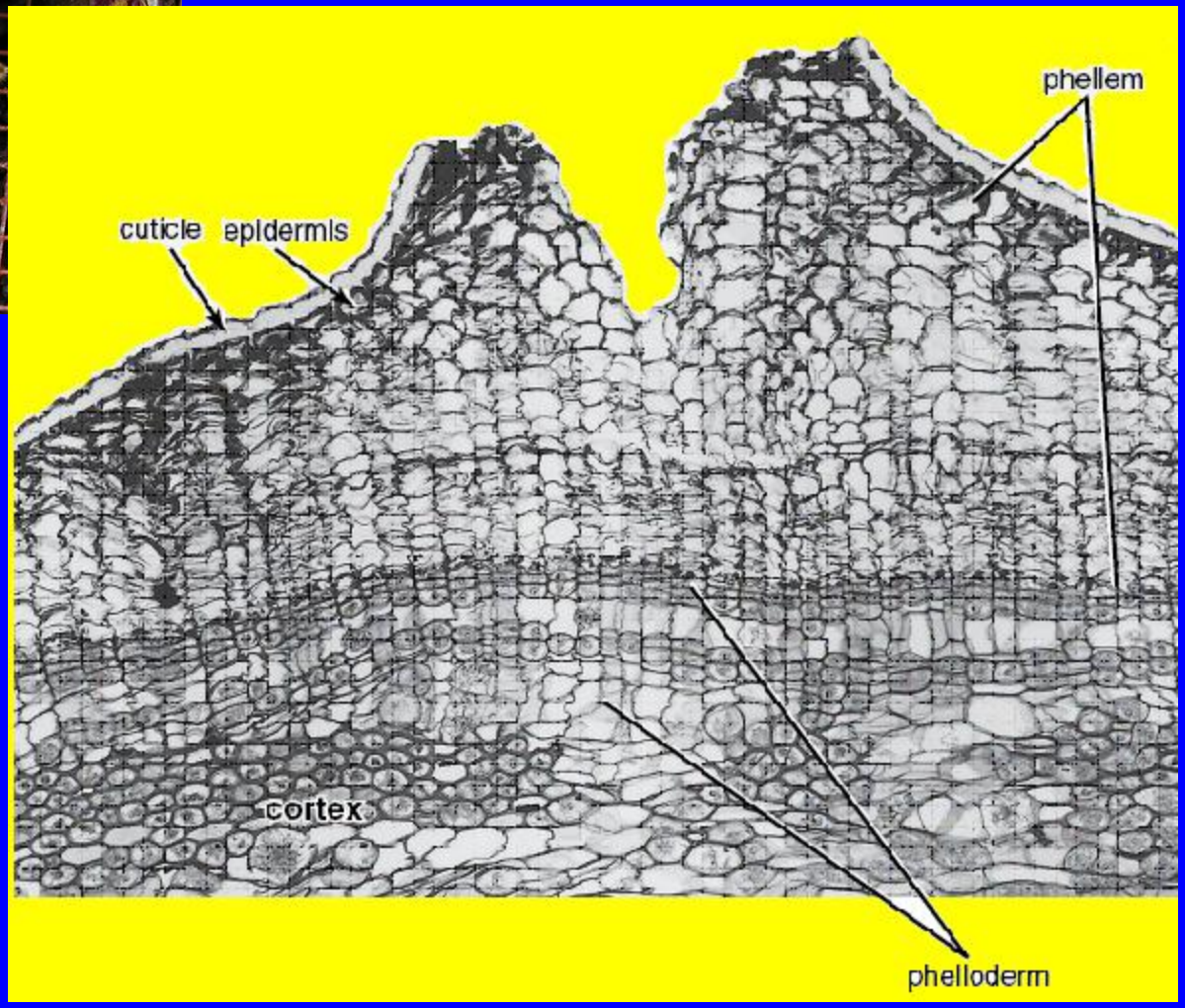

Transverse section through the stem of *Aristolochia* (Dutchman's pipe), showing the periderm, the phelloderm of which consists of several layers of cells. (×140)

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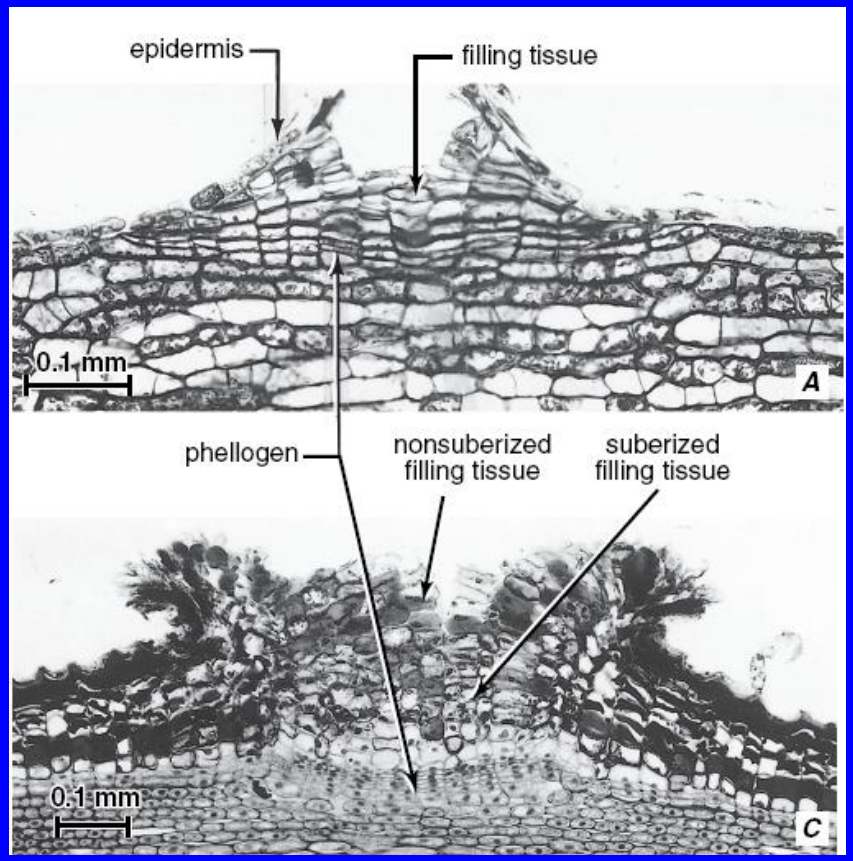

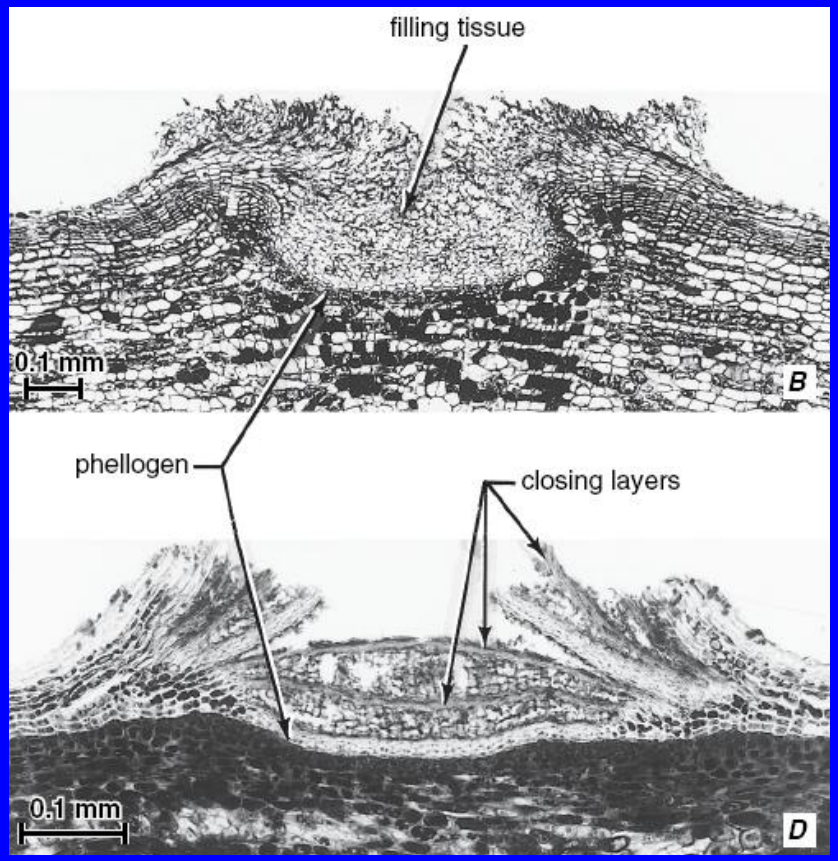

Lenticels in transverse sections of stems. A, B, avocado (*Persea americana*). Young lenticel in A, older in B. No closing layers present. C, elderberry (*Sambucus canadensis*). Lenticel with compact layer of suberized cells interior to loosely structured nonsuberized filling tissue. D, beech (*Fagus grandifolia*). Lenticel with closing layers. (A, B, D, from Esau, 1977)

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(II) Characteristics of secondary structure of the gymnosperm stems

1. The secondary xylem of most gymnosperm stems mainly comprises tracheid, xylem parenchyma and ray, without vessel and typical xylogen, which is evenly spaced on the cross section.
2. The secondary phloem has a simple structure, comprising sieve cells, phloem parenchyma and ray, without companion cell and phloem fiber.
3. Normally many tubular resin canals are distributed in the cortex and vascular cylinder of some gymnosperm stems.

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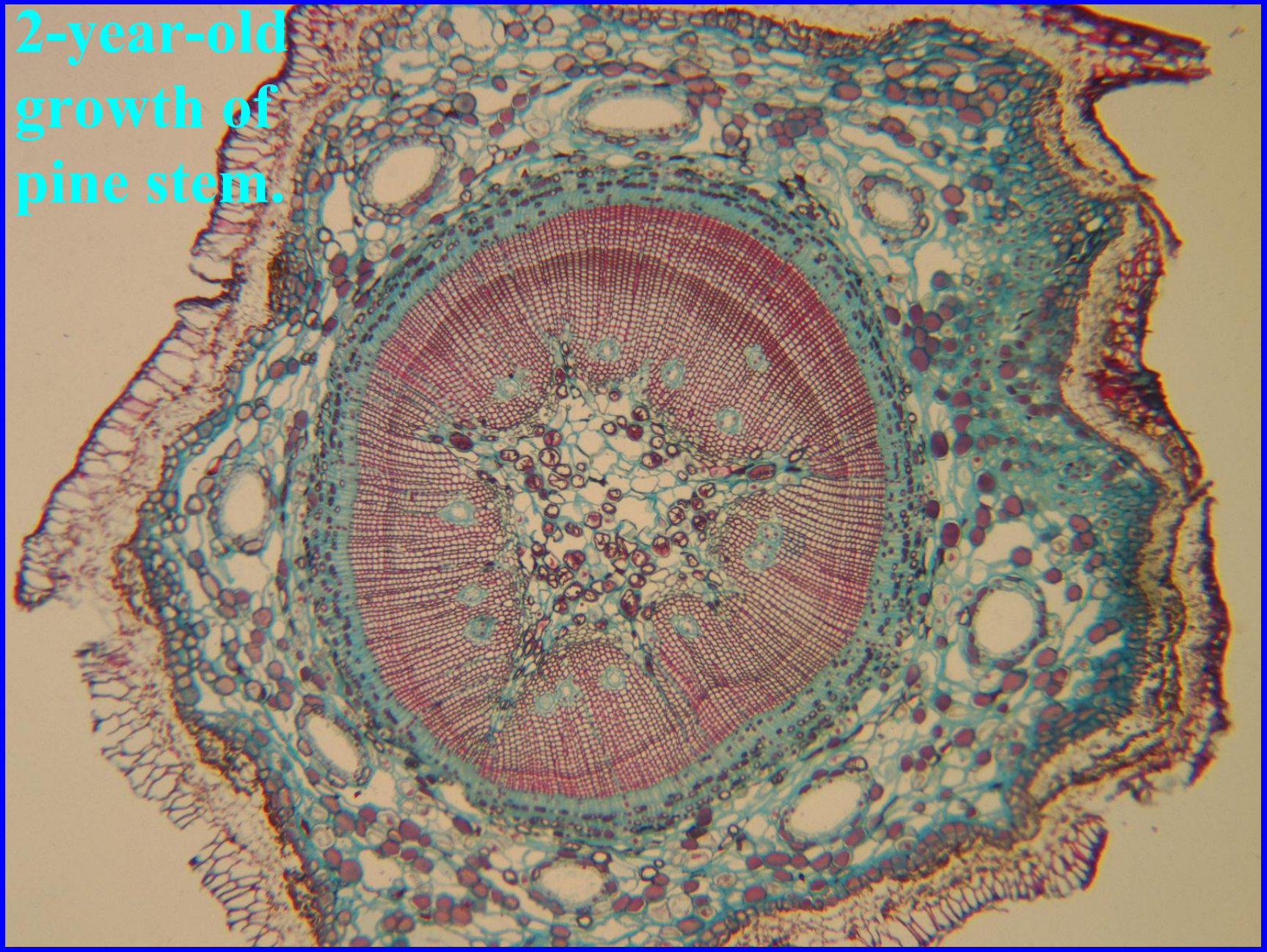
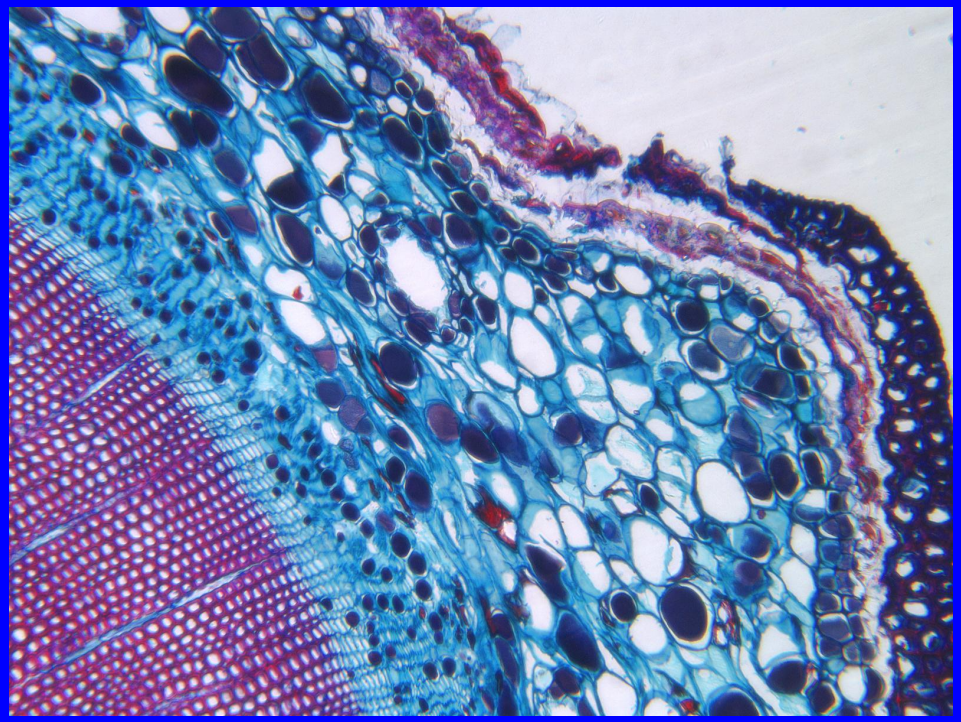
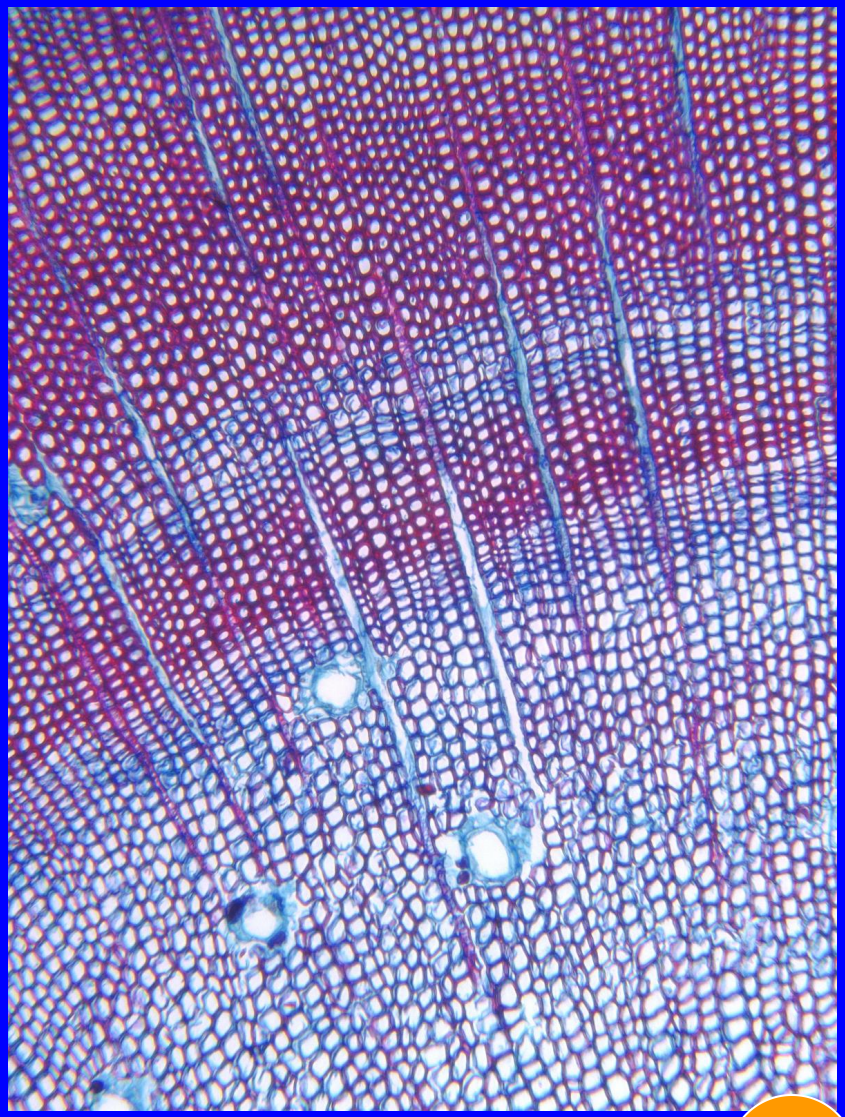


Secondary structure of pine stem.





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(III) Characteristics of secondary structure of the monocot stems

1. Parenchyma cells outside the vascular bundle are transformed to the cambium, generating little parenchyma outwards by tangential division and producing fundamental tissue inwards. In which parts of cells are relatively long with small diameter and grow in fascicles, split into secondary vascular bundle in the future. It is scattered and denser.
2. There is little phloem. The xylem is composed of tracheids and wraps periphery of the phloem, forming the amphivasal vascular bundle. The primary one is the collateral vascular bundle, formed by vessels.

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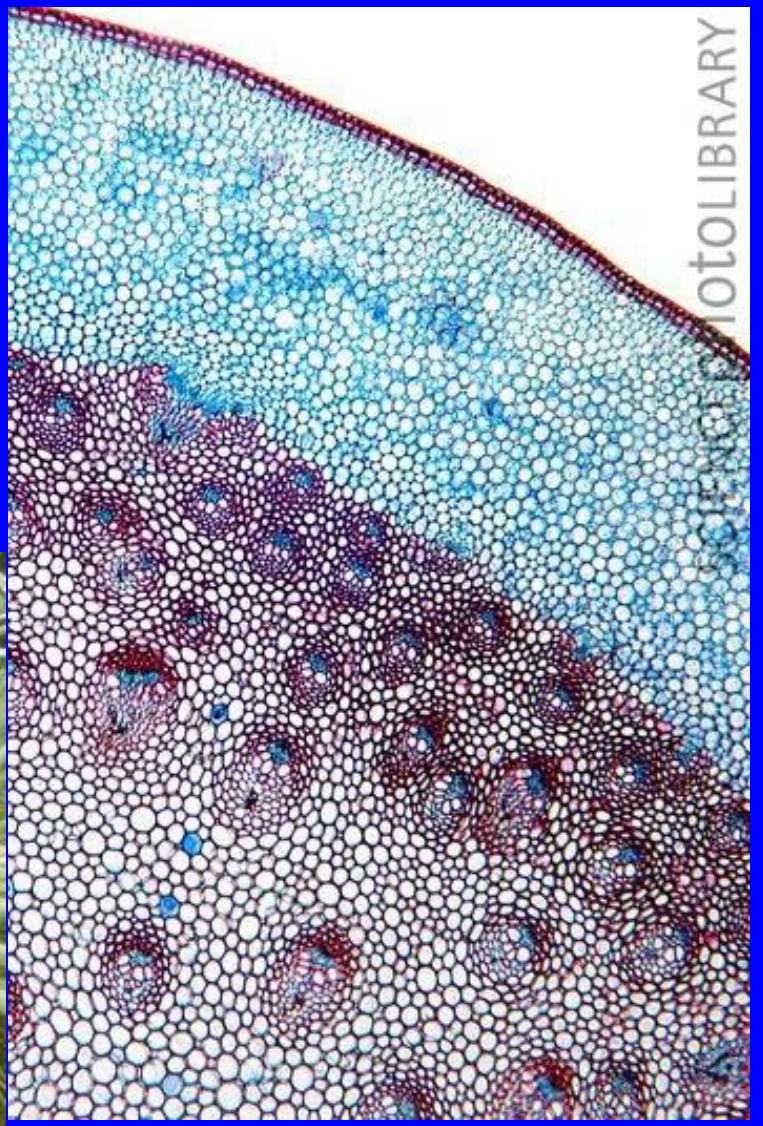
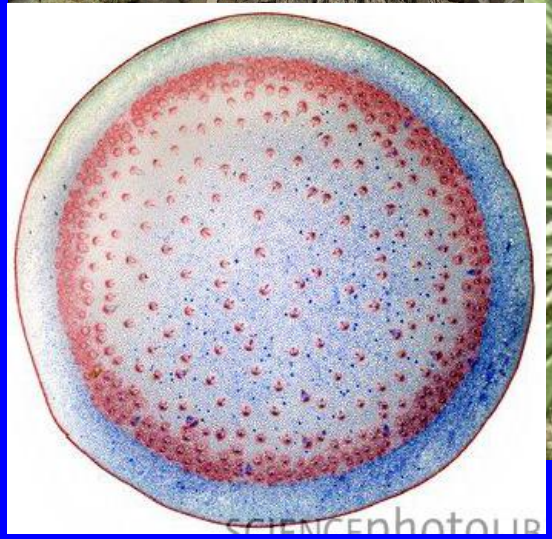
Dracaena draco





Assignments

- The circular cutting board commonly used is the cross section of stem. It's easy to split from the center when used. Why it happens?