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PAPER – V - ANATOMY AND EMBRYOLOGY

Unit - 1

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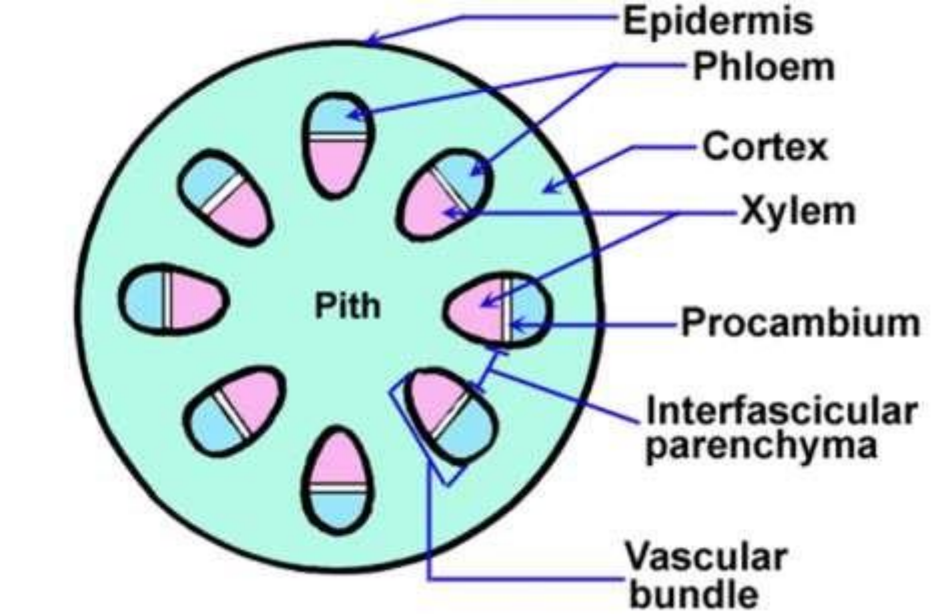
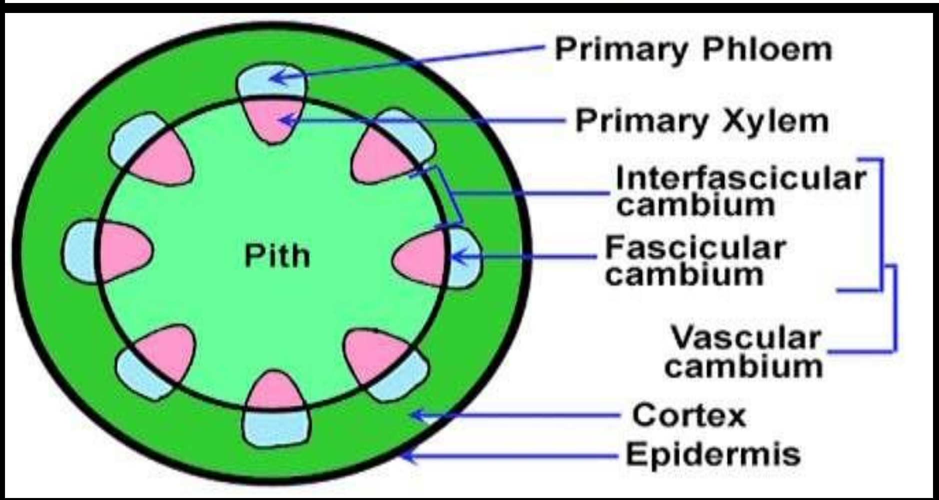
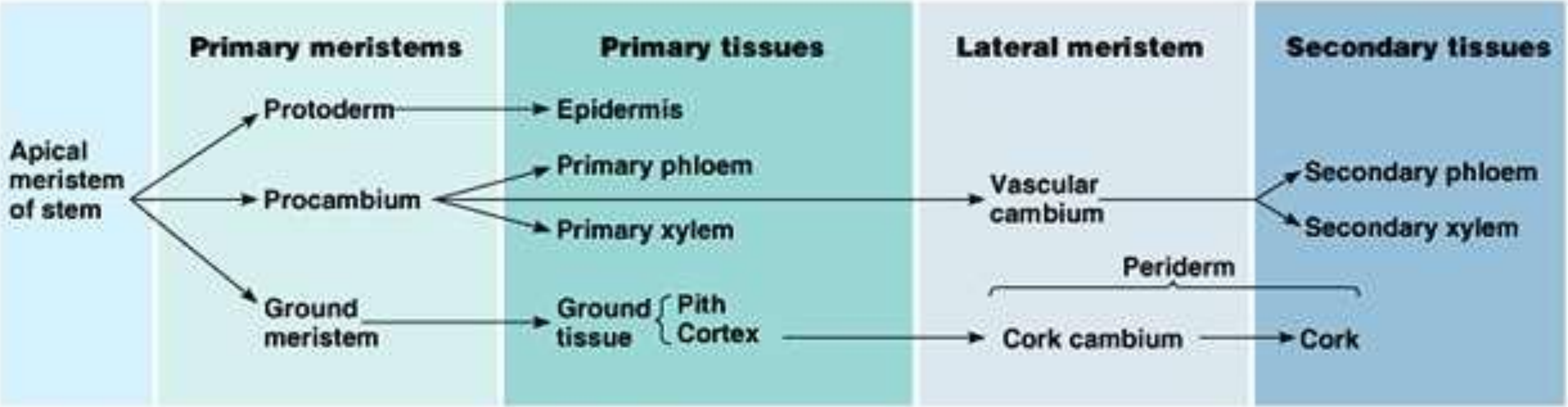
vascular cambium

Introduction

- The vascular cambium is a lateral meristem.
- In dicots, it lies in between the xylem and phloem elements.
- In the woody dicotyledons and gymnosperms, the primary vascular tissues (primary xylem and phloem) of the stem and root exists for only short period, and their function is taken over by the secondary vascular tissues (secondary xylem and phloem).
- Secondary vascular tissues are produced by the cambium.
- In many herbaceous angiosperms and in most of the lower vascular plants, cambium is absent.

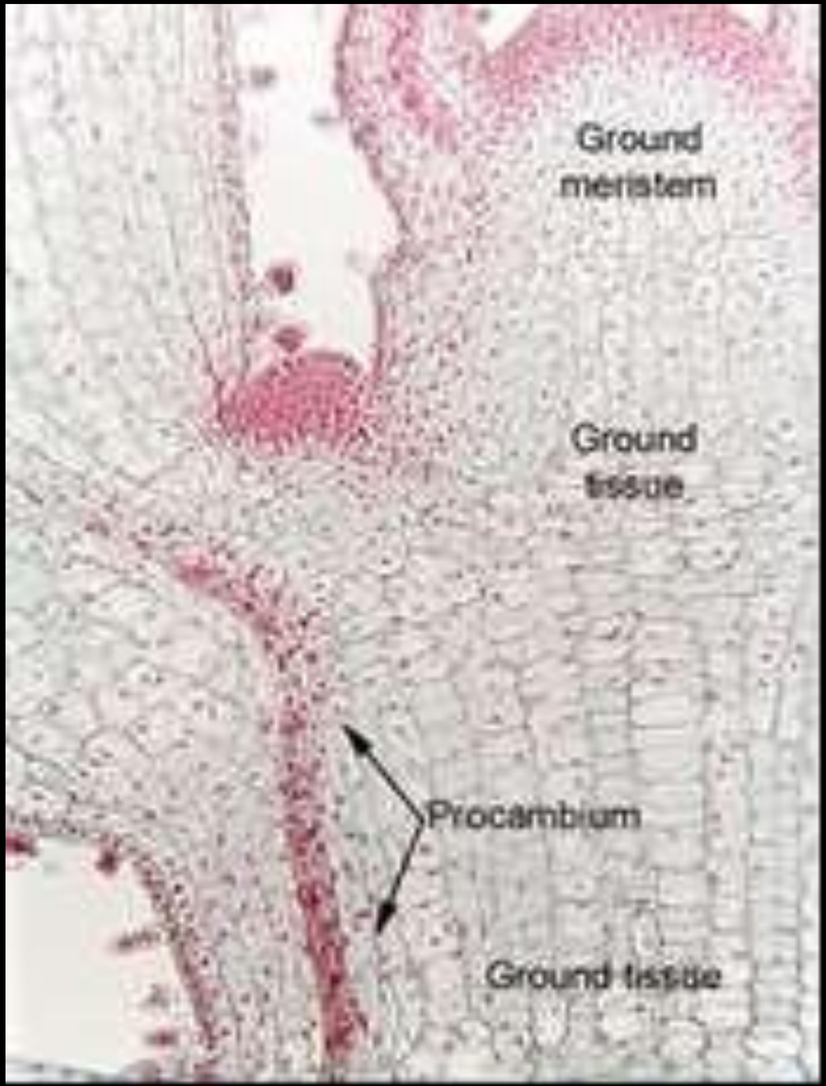





Primary meristems
Primary tissues
Lateral meristem
Secondary tissues
Apical meristem of stem
Protoderm
Epidermis
Procambium
Primary phloem
Primary xylem
Vascular cambium
Secondary phloem
Secondary xylem
Periderm
Ground meristem
Ground tissue
Pith
Cortex
Cork cambium
Cork

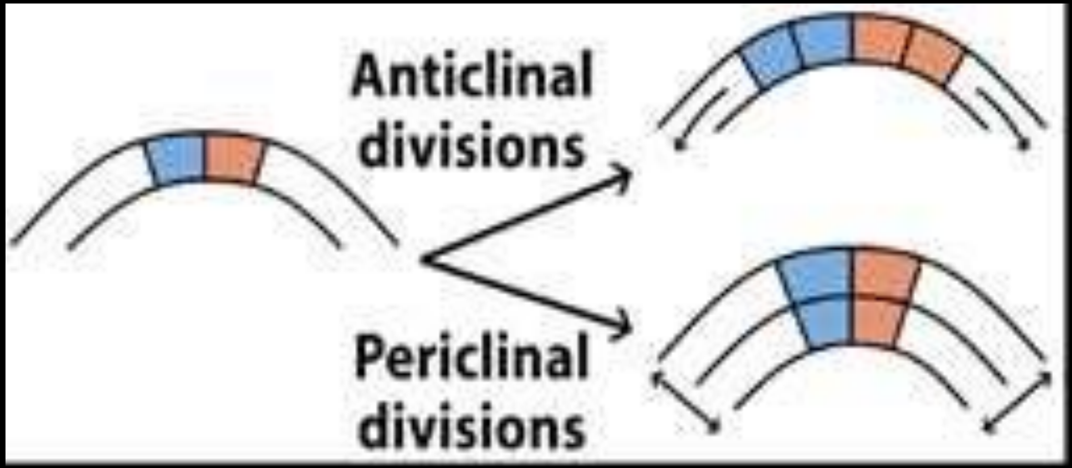
Procambium

- Procambium lies just inside of the protoderm.
- Procambium produce primary xylem and phloem.
- In woody dicots and gymnosperms, the procambium becomes the vascular cambium (secondary meristem).
- Procambium is not originate from the shoot apical meristem (SAM).
- Procambial cells arise from ground cells (parenchyma) during growth and development of lateral organs



Cell division in Procambium

- Procambial cells get their narrow shape through periclinal division.

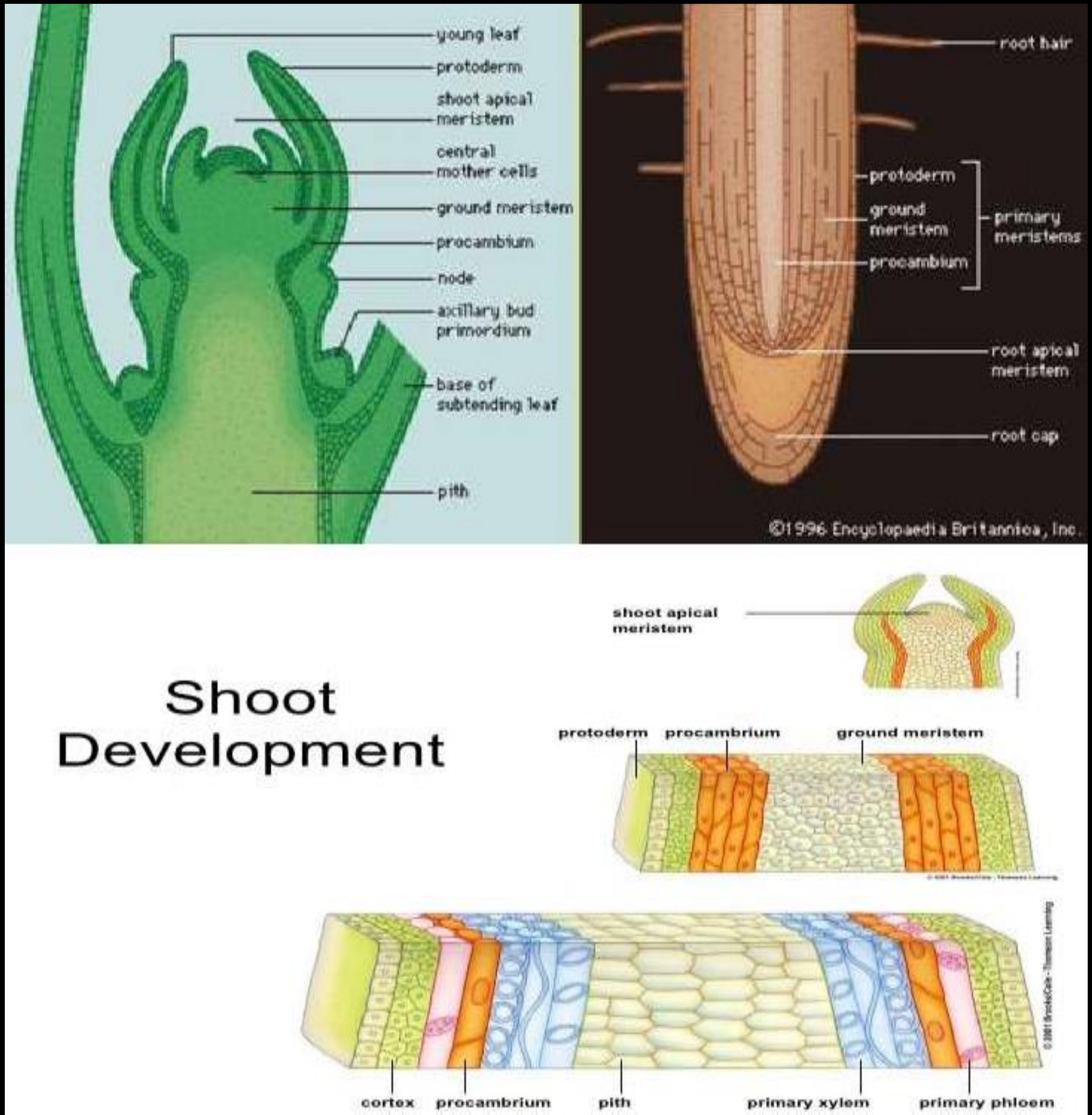


Difference between Procambium and Cambium cells [Fahn et al.,1972]

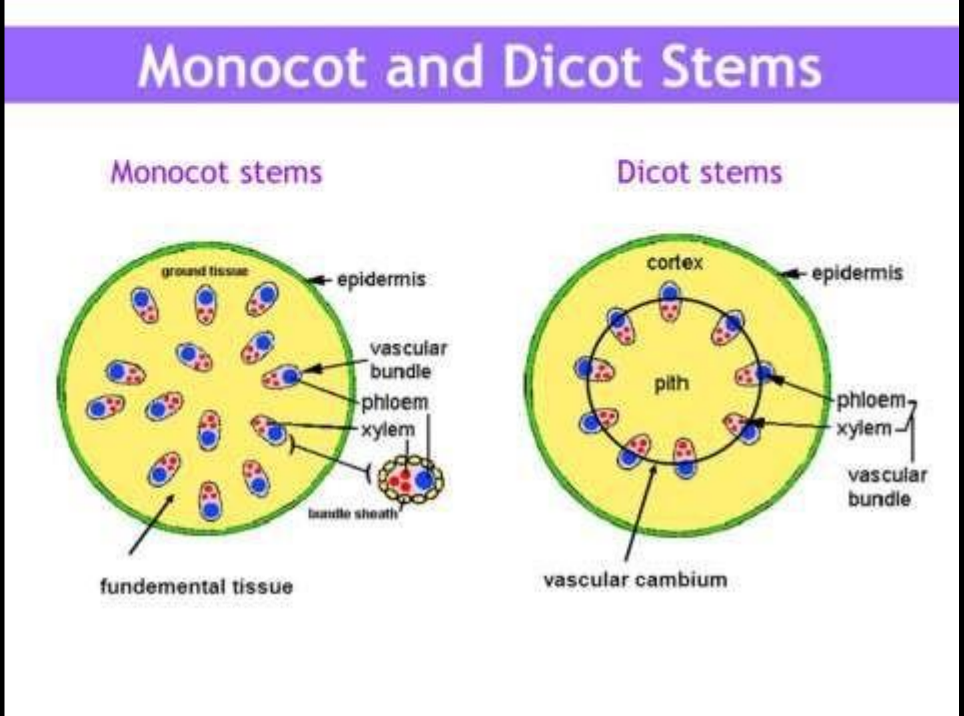
Procambium	Cambium
Posses globosed cell ends	Flat cell ends
Shorter cells	Elongated cells
Cell - storied one	Both storied & non-storied cells present
Protoplast - non-vacuolated	Protoplast - vacuolated
Protoplast take stain deeply	Protoplast not take stain
Cells homogenous	Cells heterogenous (fusiform and ray initials)

Origin of Vascular Cambium

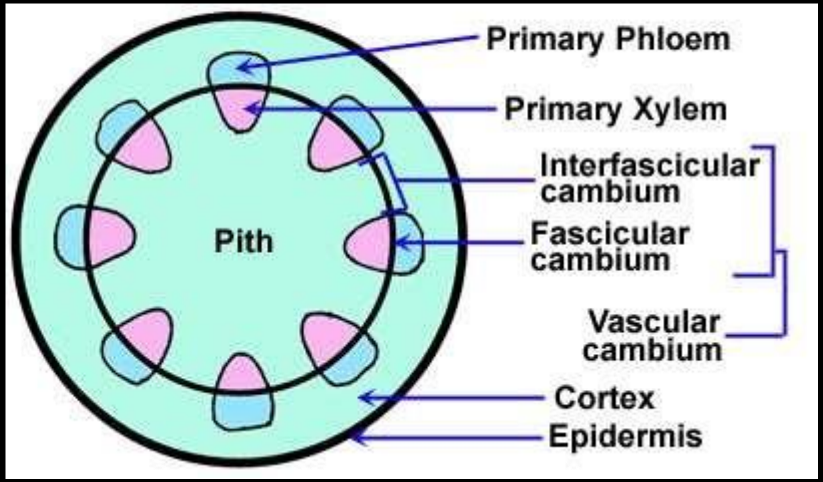
- The meristem present in apical regions of stem and root is called promeristem.
- In stems, beneath the insertion of the leaf primordia, the promeristem cells undergo periclinal divisions without a considerable increase in width of cells produce somewhat elongated cells.
- After cell divisions in the promeristematic cells, the resulting daughter cells undergo differentiation leads to form three meristems namely, protoderm, ground meristem and procambium.



- The primary vascular tissue is built up by the maturing cells of procambium.
- In plants that have no secondary growth (most of the monocots), all cells of the procambium (i.e., initials as well as derivatives) undergo differentiation and form primary vascular tissues (primary xylem and phloem).
- In plants in which secondary growth later appears (almost all the dicots and gymnosperms), a part of the procambium cells remain meristematic even after the completion of primary growth gives rise to the cambium proper.
- Cambium by division produces the secondary vascular tissues (secondary xylem and phloem) or wood.



- In stems, cambia have a double origin.
- One part is initiated within the provascular strands (procambium) and is called fasicular cambium or intrafasicular cambium.
- Second part is originates in the ground tissue between the vascular strands and forms the interfasicular cambium.



- Procambial strands exhibit two waves of differentiation.
- One wave is differentiation of protophloem on the peripheral side
- Second wave is differentiation of protoxylem towards the inner edges in normal angiosperm.

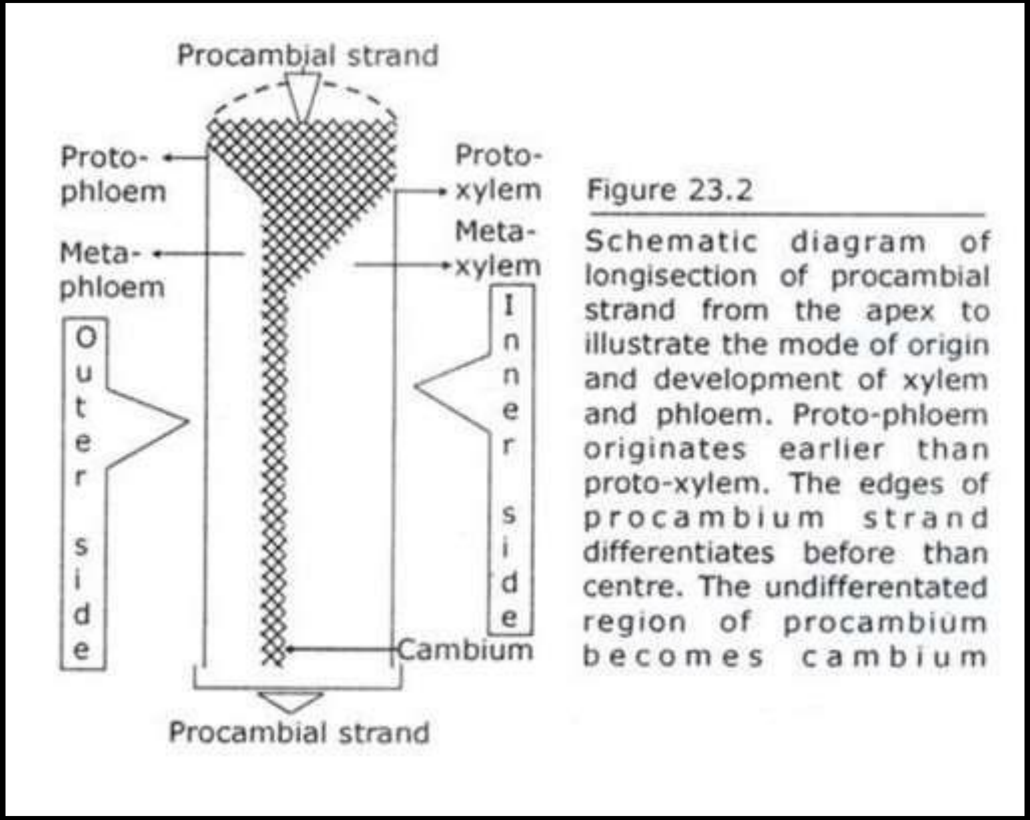


Figure 23.2
Schematic diagram of longisection of procambial strand from the apex to illustrate the mode of origin and development of xylem and phloem. Proto-phloem originates earlier than proto-xylem. The edges of procambium strand differentiates before than centre. The undifferentated region of procambium becomes cambium

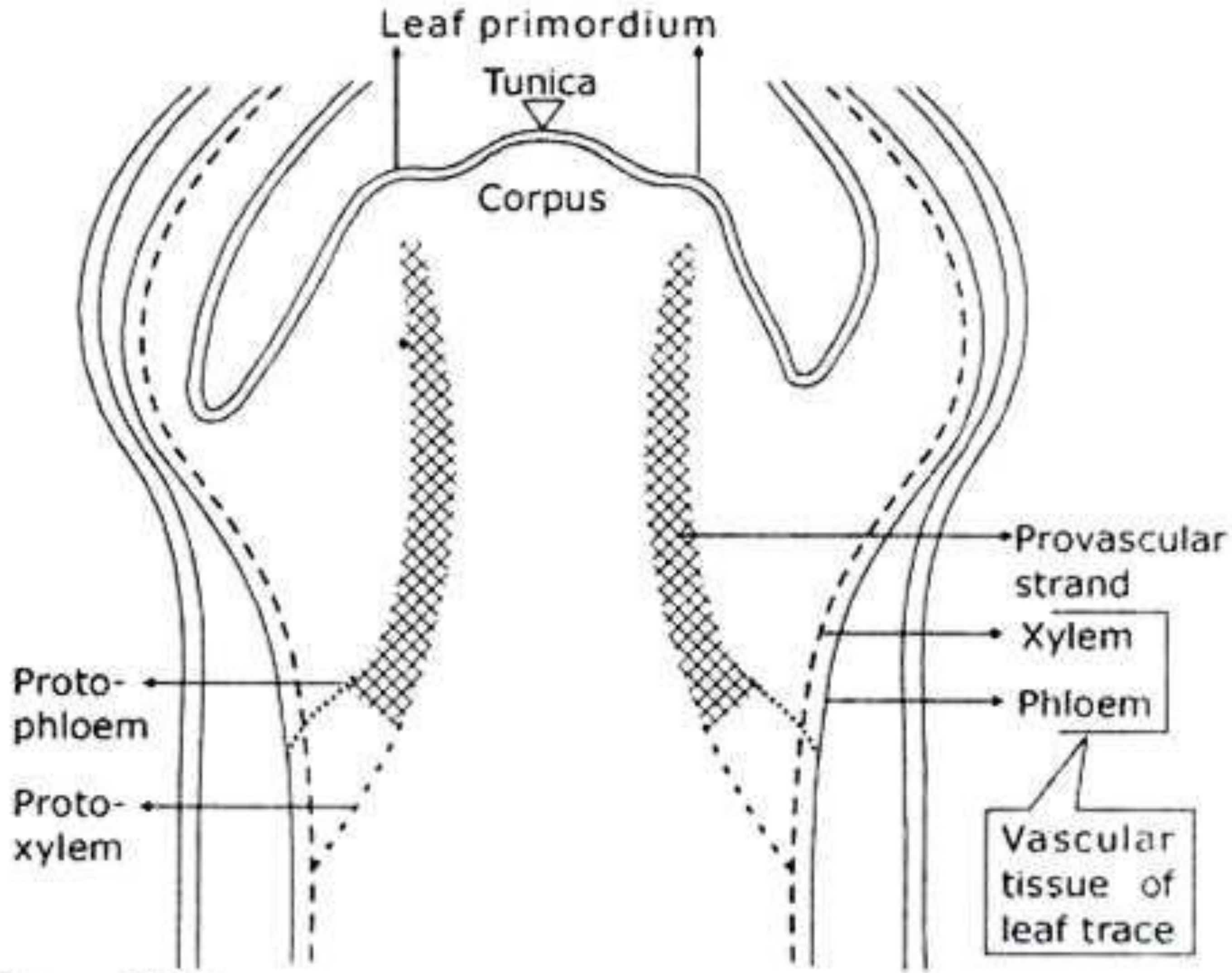
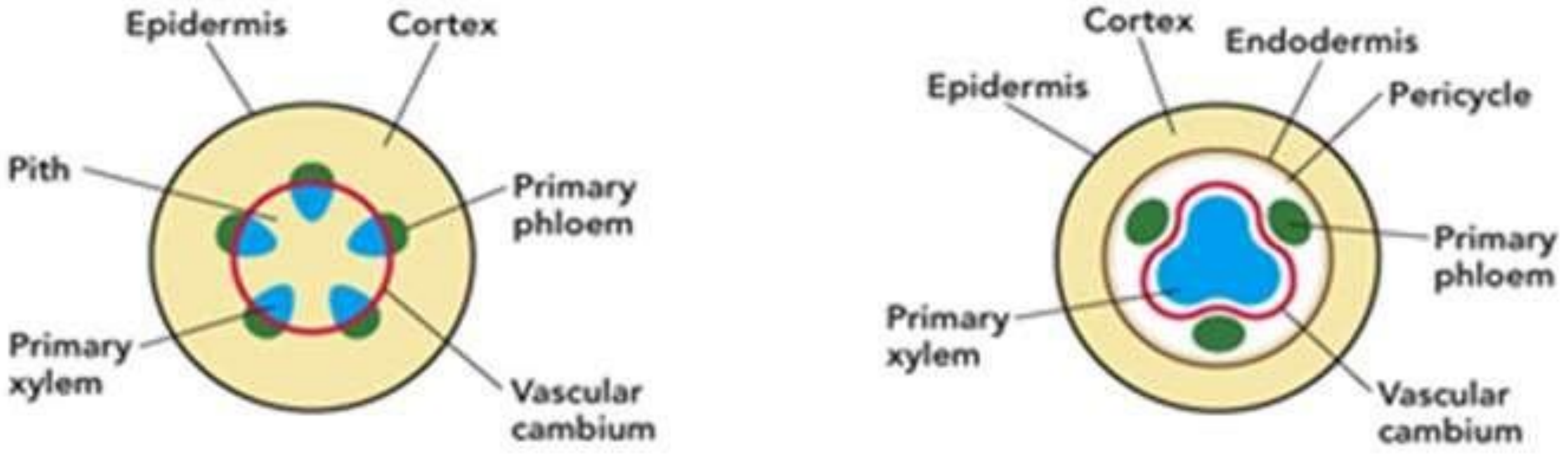


Figure 23.3

Diagram of longisection of angiosperm shoot apex illustrating the topographical relationship between leaf primordium and provascular strand, and representing the linkage of differentiating provascular strand and existing leaf trace.

- In monocotyledons the two waves of differentiation meet and the whole procambial strand form the primary vascular tissue.
- In most dicotyledons these waves do not meet.
- A zone of procambial meristematic cells remains.
- This zone that occurs between primary xylem and phloem is the vascular cambium.
- If it is not in the form of a continuous ring, a continuous ring of cambium is formed by dedifferentiation of interfascicular parenchyma into interfascicular cambium and their subsequent lateral union with fascicular cambium.

- Procambium gives rise to permanent tissues and is designated as primary.
- The derivative cells of cambium are designated as secondary.
- In normal dicotyledonous stem the ring of vascular cambium is composed of fascicular and interfascicular cambium.
- In the normal dicotyledonous root the vascular cambium is wavy.
- In dicot root, there is no distinction between fascicular and interfascicular cambium.
- The ridges of the wavy cambium occur overarching the protoxylem while the furrows lie below the primary phloem.

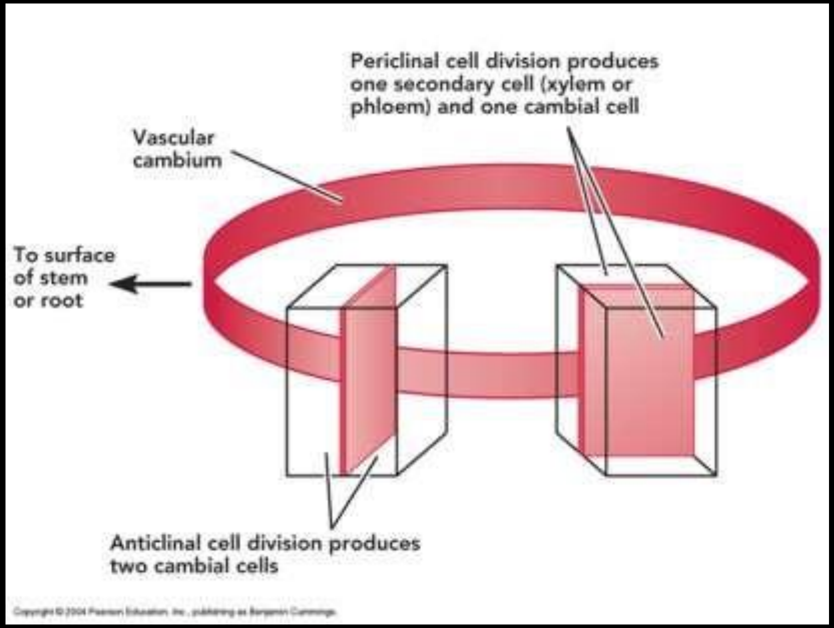


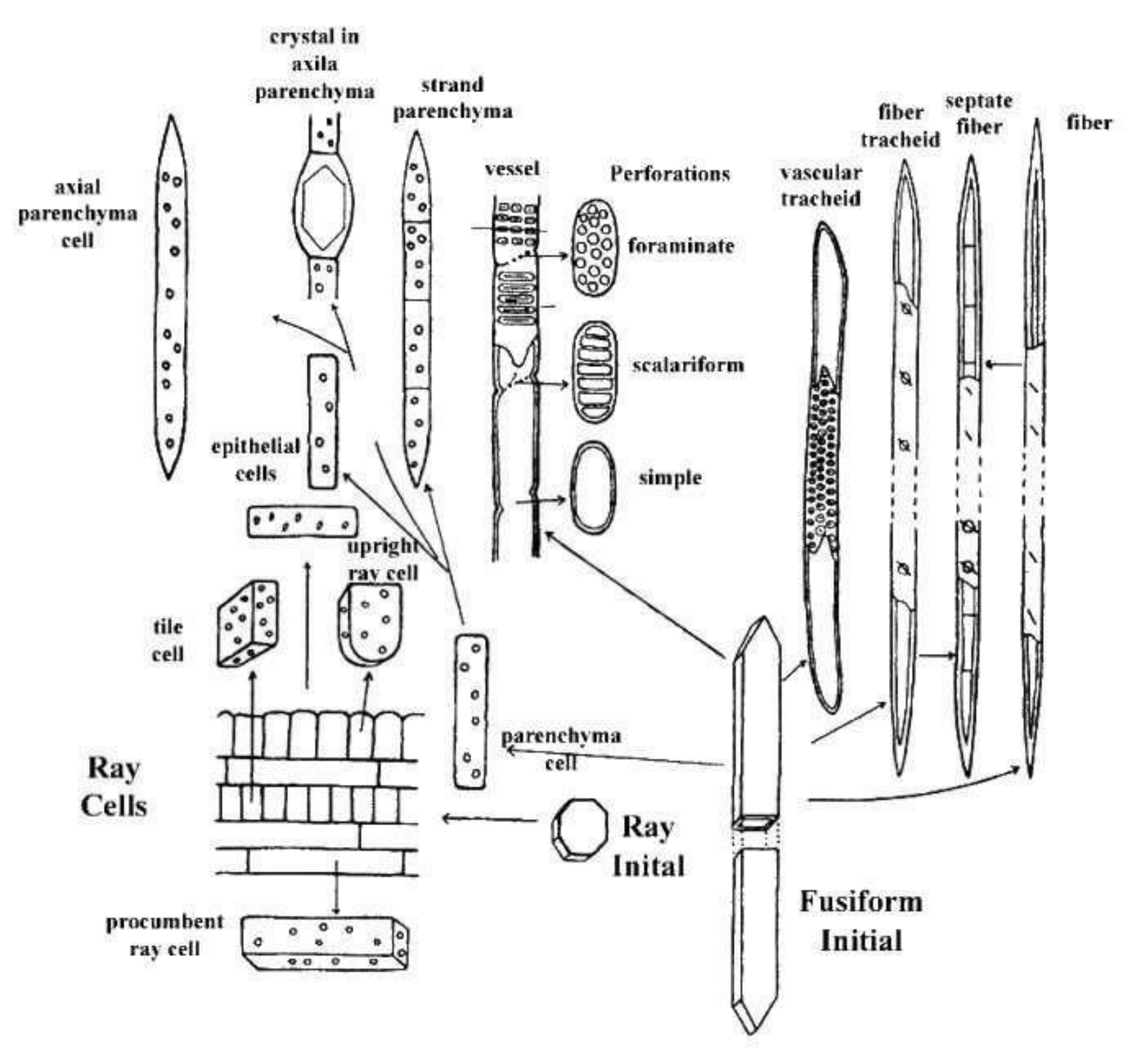
(a) Initial formation of vascular cambium in stem

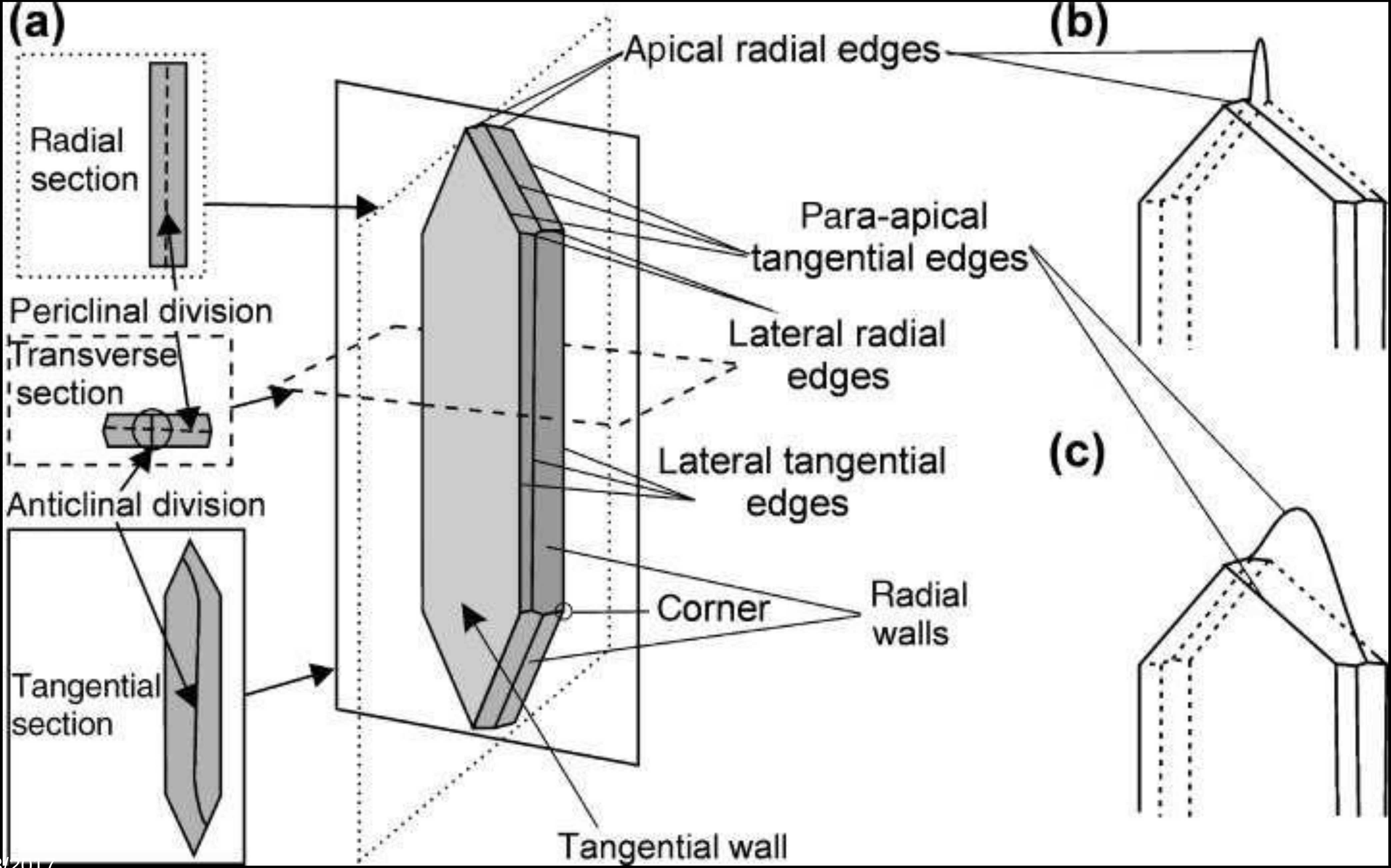
(b) Initial formation of vascular cambium in root

Activity of Vascular Cambium

- The vascular cambium is one cell thick and the cells of cambium are compactly set without having any intercellular spaces.
- Cambium and its immature derivatives form a cambial zone where it is difficult to differentiate the cambial initial.
- Two types of mitotic divisions characterize an active cambium periclinal and anticlinal.
- As a result of periclinal divisions new cells of secondary xylem and phloem are produced.
- Anticlinal divisions give rise to new cambial initials.




crystal in
axila
parenchyma
strand
parenchyma
axial
parenchyma
cell
vessel
Perforations
foraminate
scalariform
simple
vascular
tracheid
fiber
tracheid
septate
fiber
fiber
epithelial
cells
upright
ray cell
tile
cell
parenchyma
cell
Ray
Cells
Ray
Inital
Fusiform
Initial
procumbent
ray cell


(a)
(b)
(c)
Radial section
Periclinal division
Transverse section
Anticlinal division
Tangential section
Apical radial edges
Para-apical tangential edges
Lateral radial edges
Lateral tangential edges
Corner
Radial walls
Tangential wall

- At the time of secondary growth the fusiform initial divides periclinally.
- One of the two cells thus formed remains as fusiform cambial initial whereas the other is an immature cambial derivative that is added to the cambial zone.
- The fusiform cambial initial continually cuts of new cambial derivatives to the exterior and to the interior.

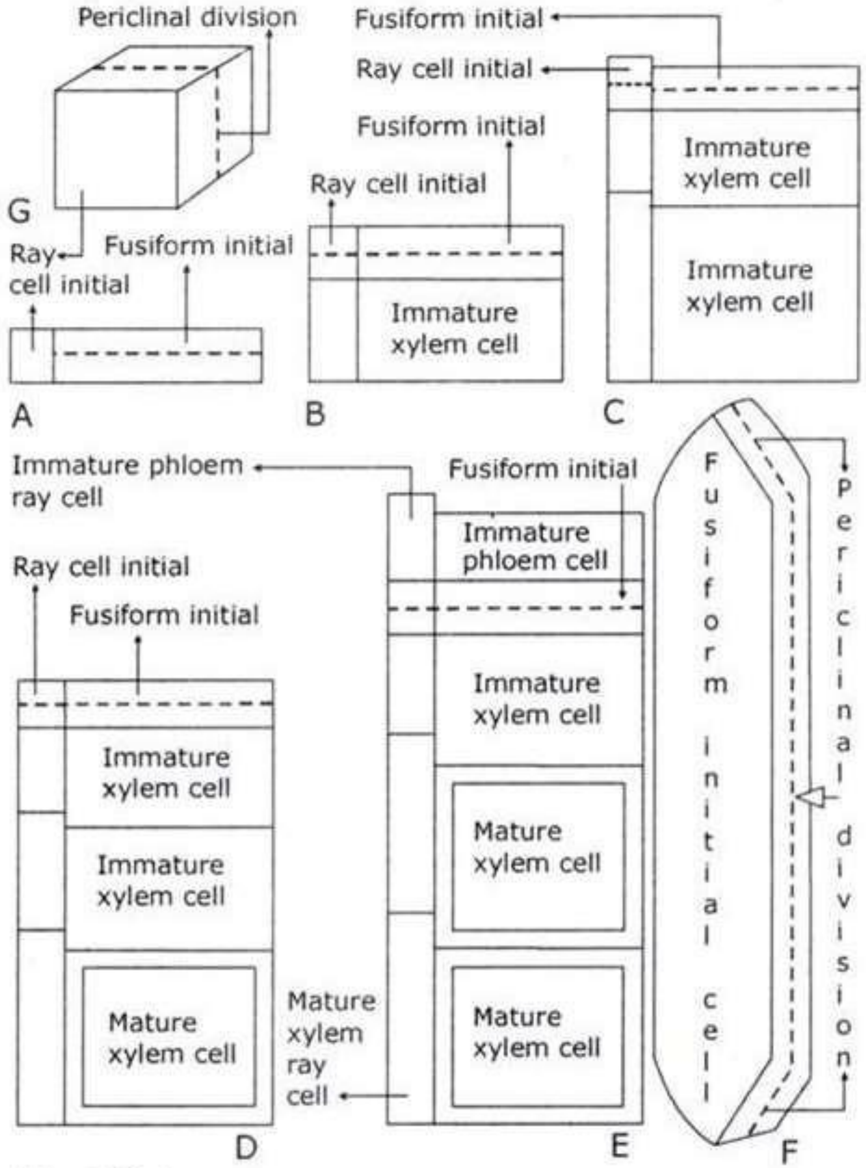
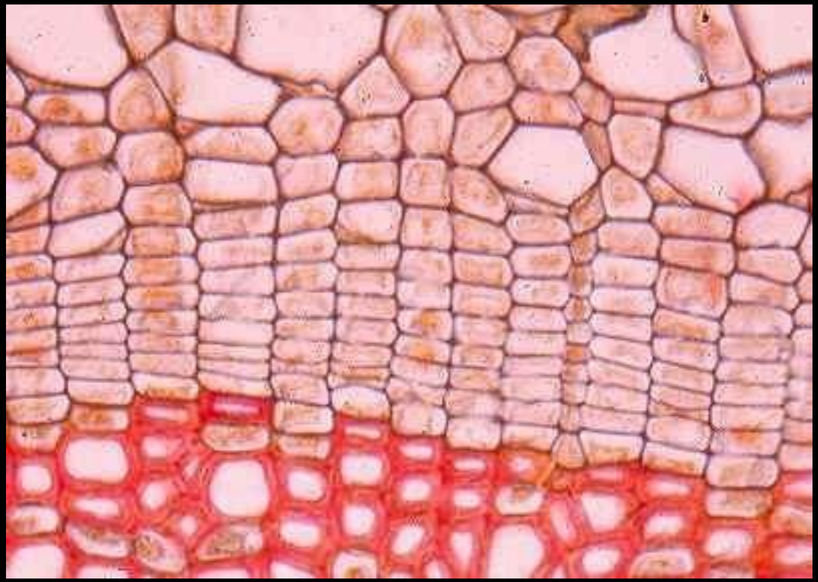


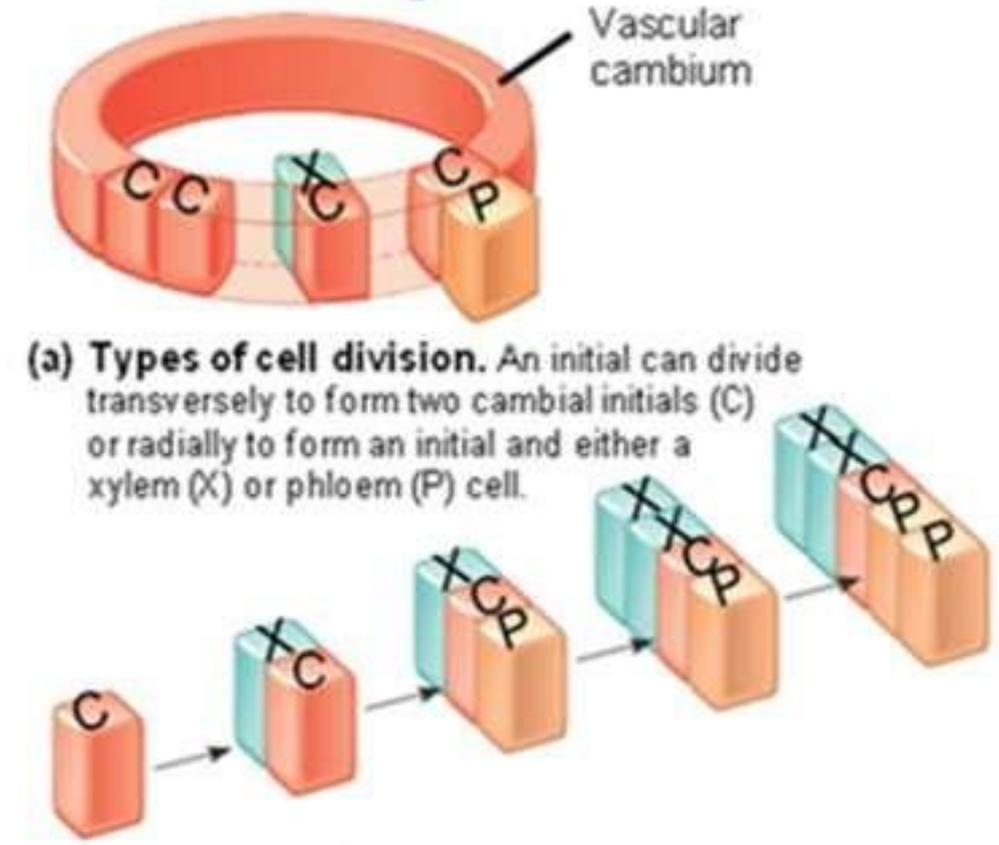
Figure 23.4

Schematic drawings of the production of secondary xylem and secondary phloem by cambial initial cells (A-E).
Broken lines indicate periclinal division.
F. & G. are fusiform initial and ray cell initial in three dimensional view respectively

- The derivative cells may differentiate directly into new secondary phloem to the exterior and new secondary xylem to the interior.
- In this case the cambial zone is narrow.
- But more commonly the cambial initial and its derivative cells divide further.
- As a result a wide cambial zone is formed.

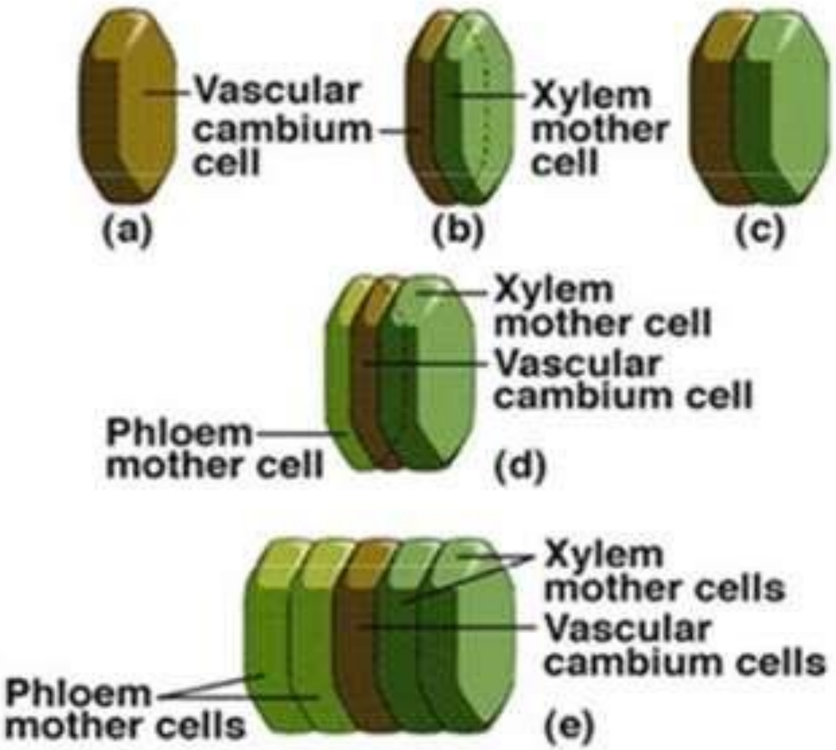


- Continued periclinal divisions in fusiform cambial initials and in their derivative cells result in radially oriented files of cells of similar shape that mature to secondary vascular tissues.
- Such radial oriented files of cells are conspicuous (detectable) in the secondary xylem of conifers where the secondary xylem is largely composed of tracheids.
- In angiosperms such radial files of cells are less conspicuous due the formation of vessels.
- Vessels often increase greatly in diameter and as a result distortion [to change something from its usual condition or shape] of files occurs.



(a) Types of cell division. An initial can divide transversely to form two cambial initials (C) or radially to form an initial and either a xylem (X) or phloem (P) cell.

(b) Accumulation of secondary growth. Although shown here as alternately adding xylem and phloem, a cambial initial usually produces much more xylem.



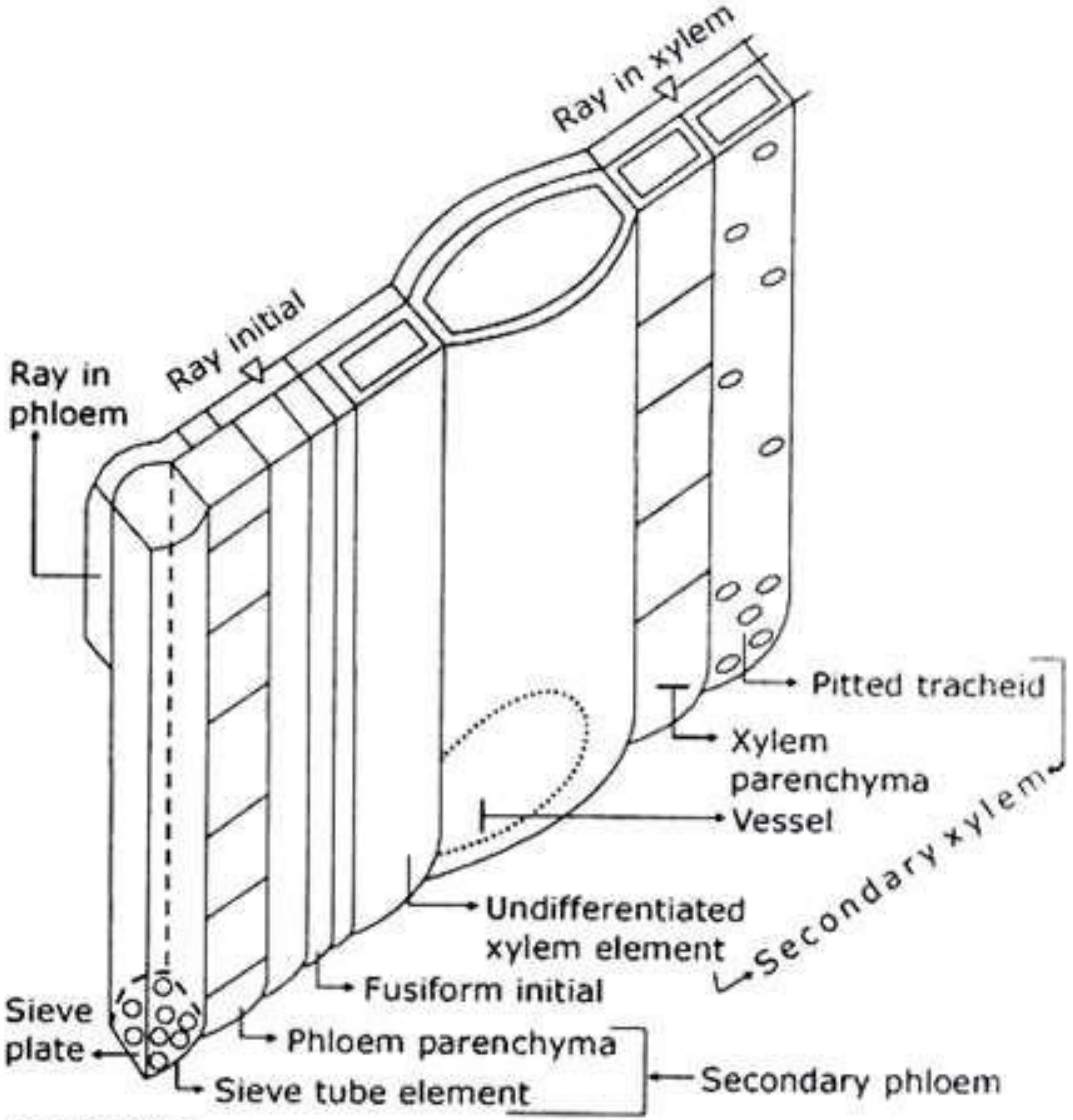


Figure 23.5

A diagrammatic interpretation of the production of secondary vascular tissues by cambium

- As the fusiform initials compose the axial system of vascular cambium, their derivatives mature into the elements of vascular tissues that compose the axial system.
- The derivative cells mature into tracheids, vessel and xylem fibre of xylem and sieve tube, companion cell and phloem fibre of phloem as they compose the axial system of plants.

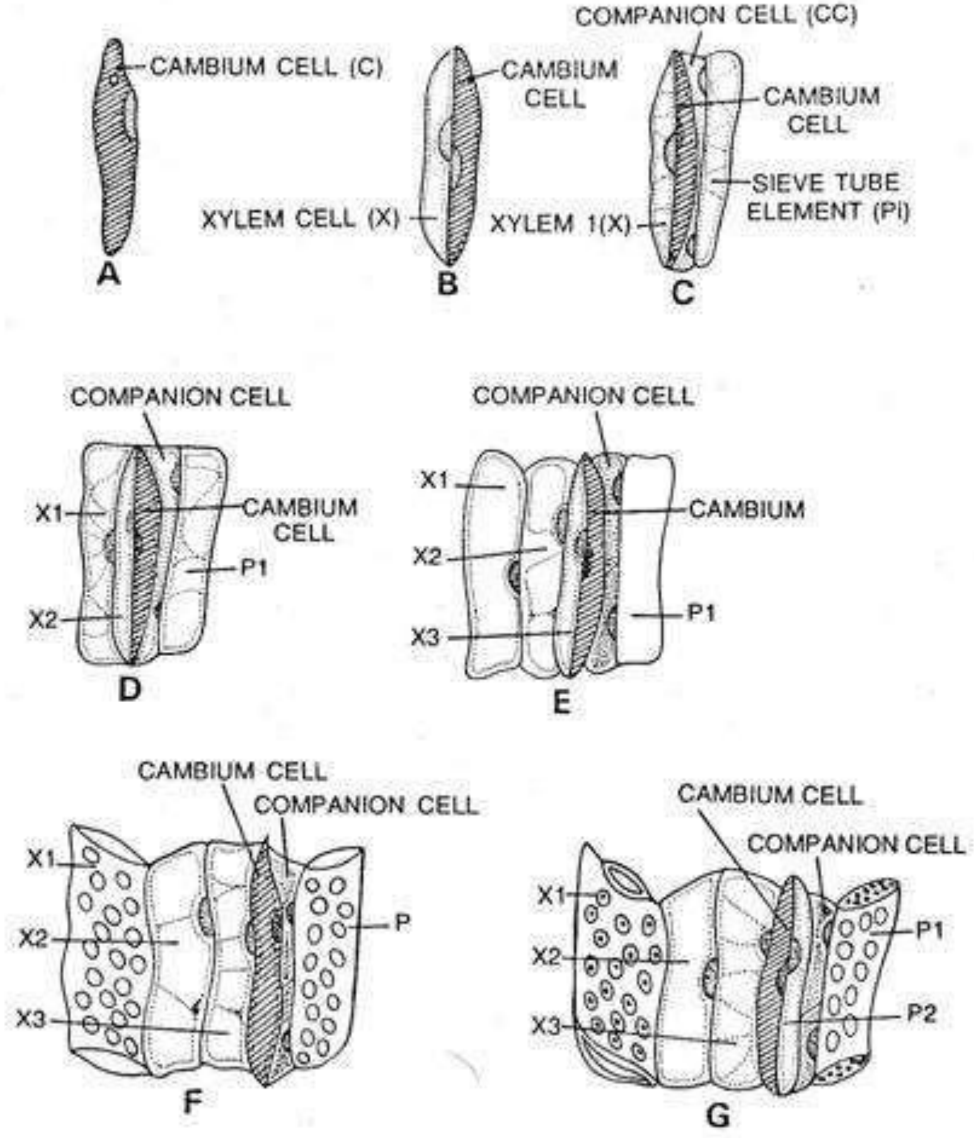


Fig. 39.4. The cambium. Differentiation of phloem and xylem from vascular cambium. A—G, diagrams as seen in radial section, showing stages in differentiation of vascular cambium cells.

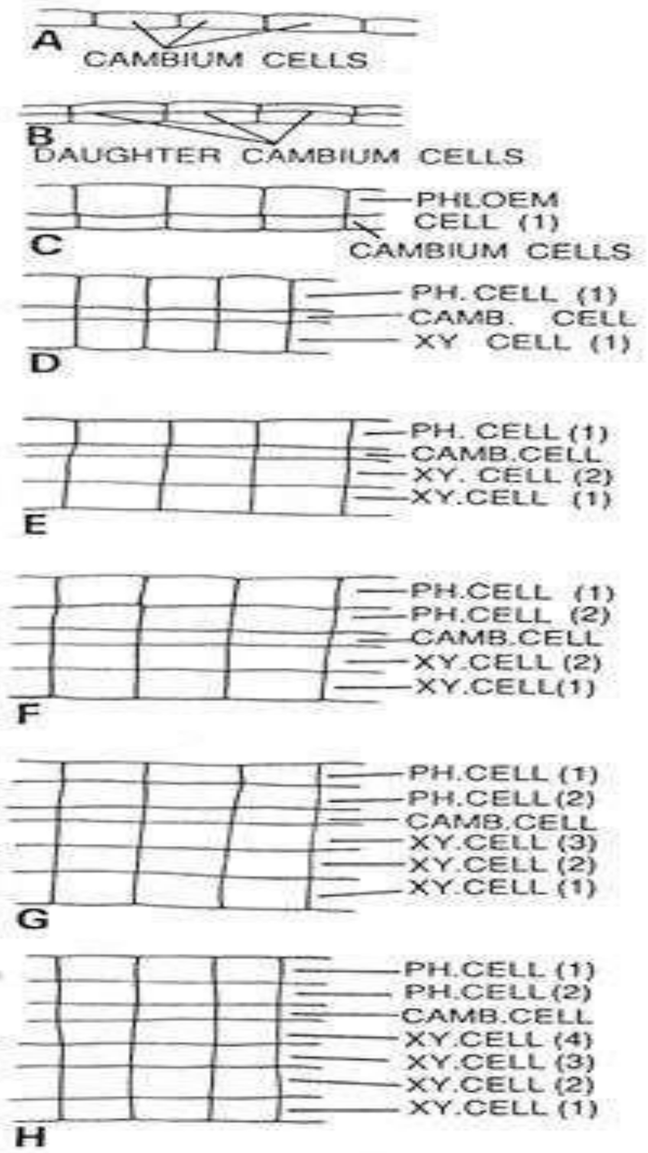
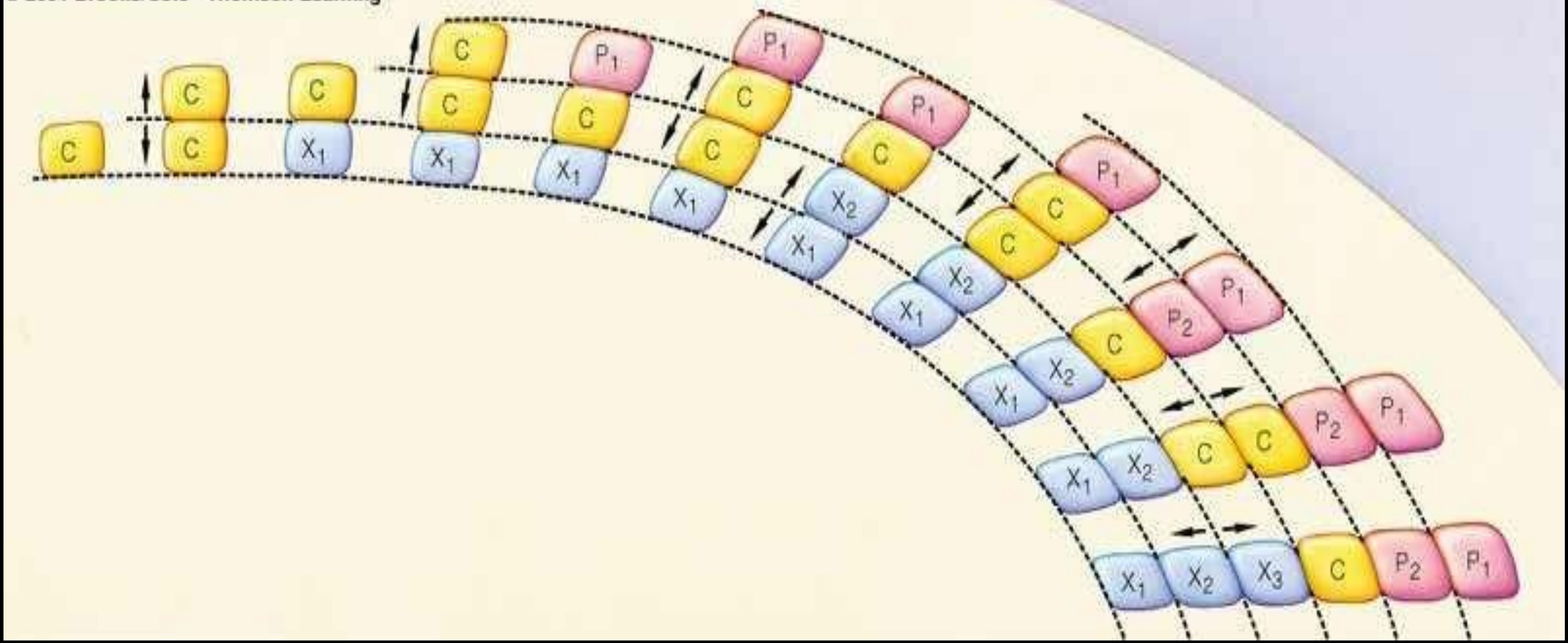


Fig. 39.3. The cambium. A—H, diagrams showing the formation of xylem and phloem by the cambium, and changes in position of phloem and cambium by this activity.


C
C
C
C
X1
C
C
X1
P1
C
X1
P1
C
C
X1
P1
C
X2
X1
P1
C
C
X2
X1
P1
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X1
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C
X3
X2
X1

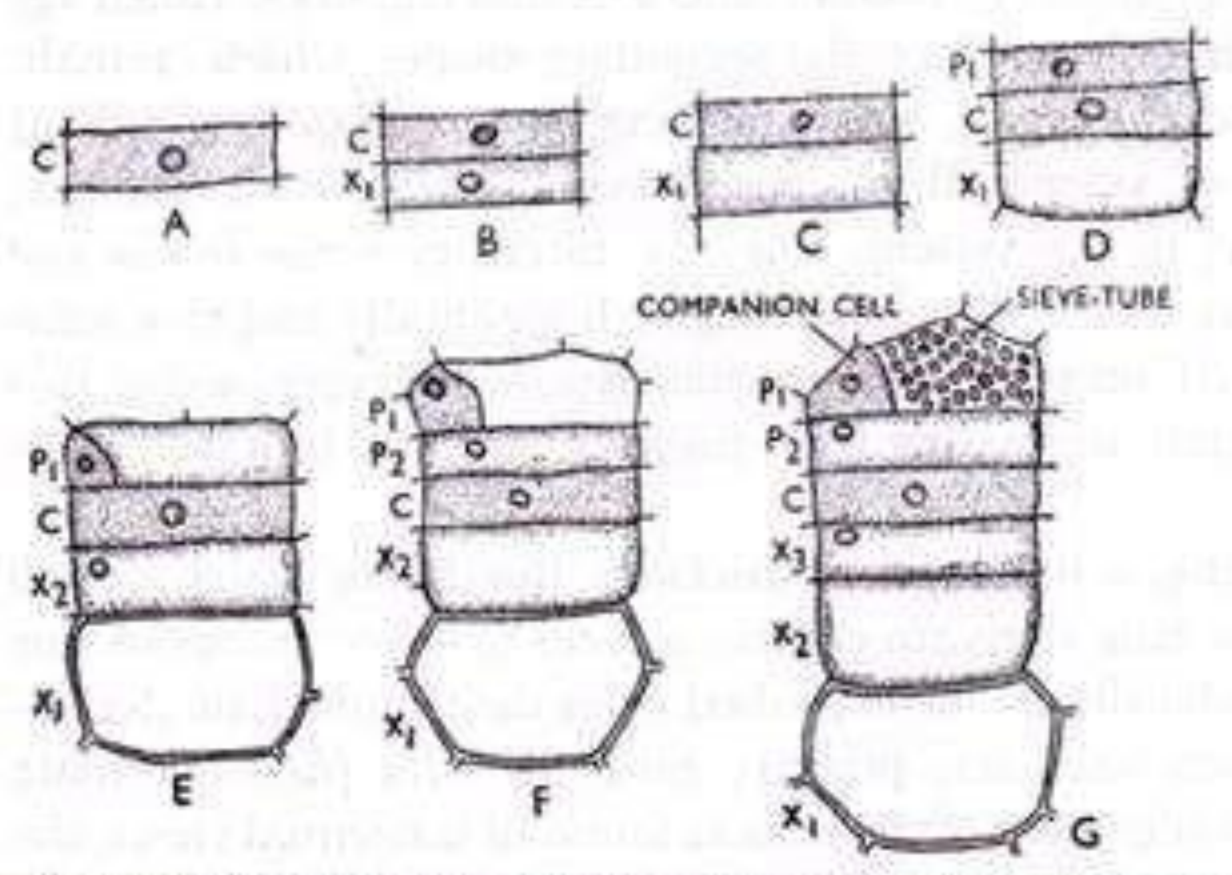


FIG. 629. Formation of secondary xylem and secondary phloem by the cambium—stages.

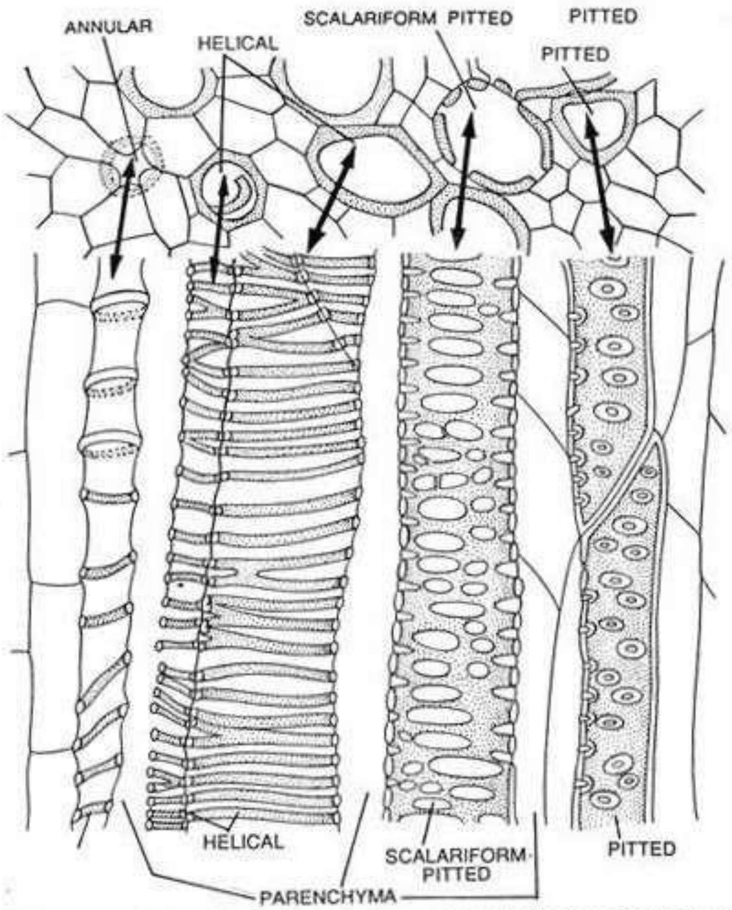


Fig. 40.38. Xylem. vessel. T.S. and L.S. of a part of young *Aristolochia* stem showing vessel element and associated parenchyma. Earlier part of the xylem is towards left. Annular, spiral (helical), scalariform and pitted vessels are clearly visible. Protoxylem consists of annular vessels.

- The ray cell initial divides periclinally to form two cells.
- One of the daughter cells remains as cambial ray initial.
- The other cell differentiates into either xylem parenchyma if it is the inner cell or phloem parenchyma if it is the outer cell.
- Ray initials produce mostly xylem and phloem parenchyma.
- In gymnosperm ray initials form albuminous cell.
- The ray initial and its derivatives compose the radial system of plants.

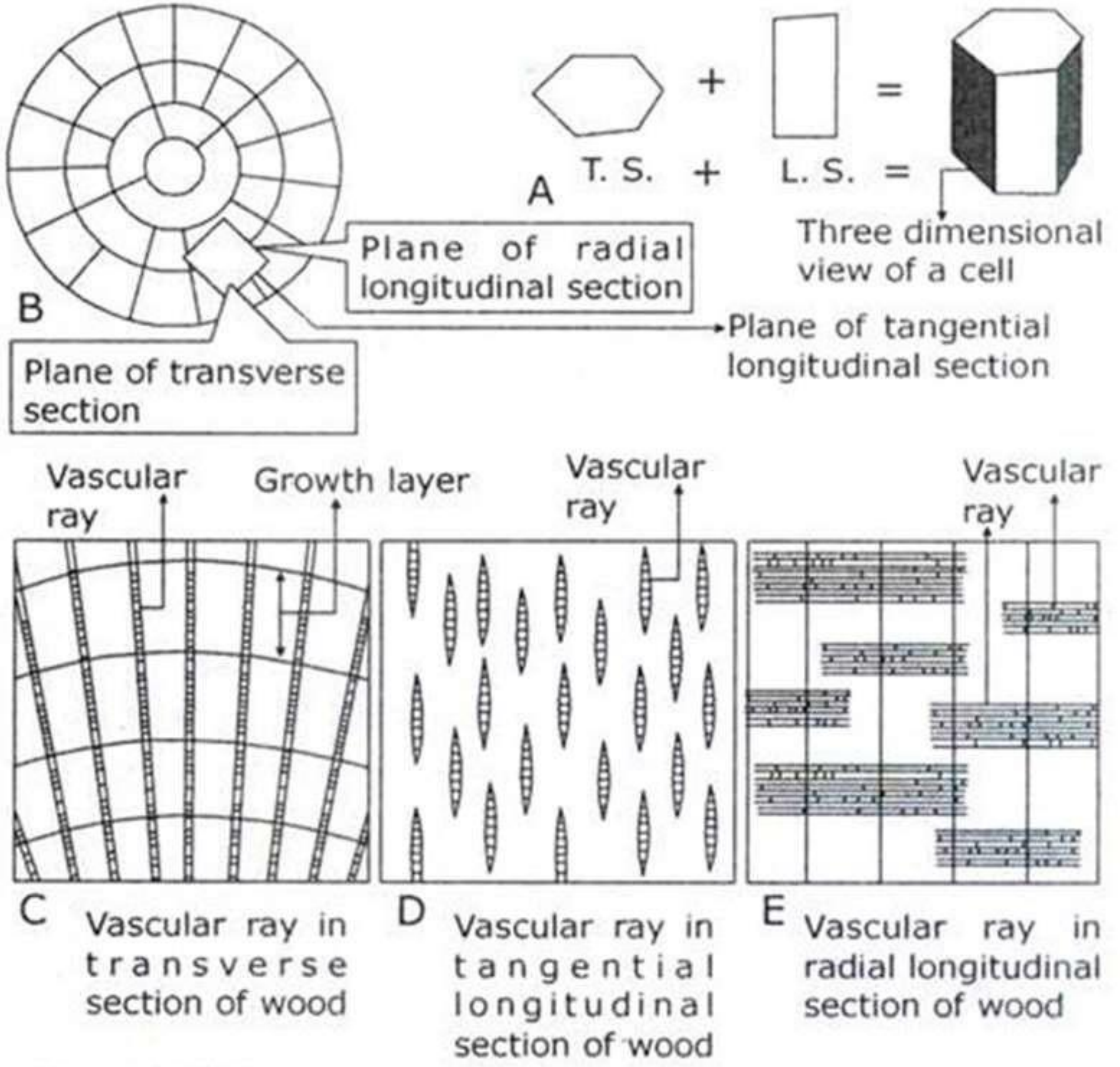
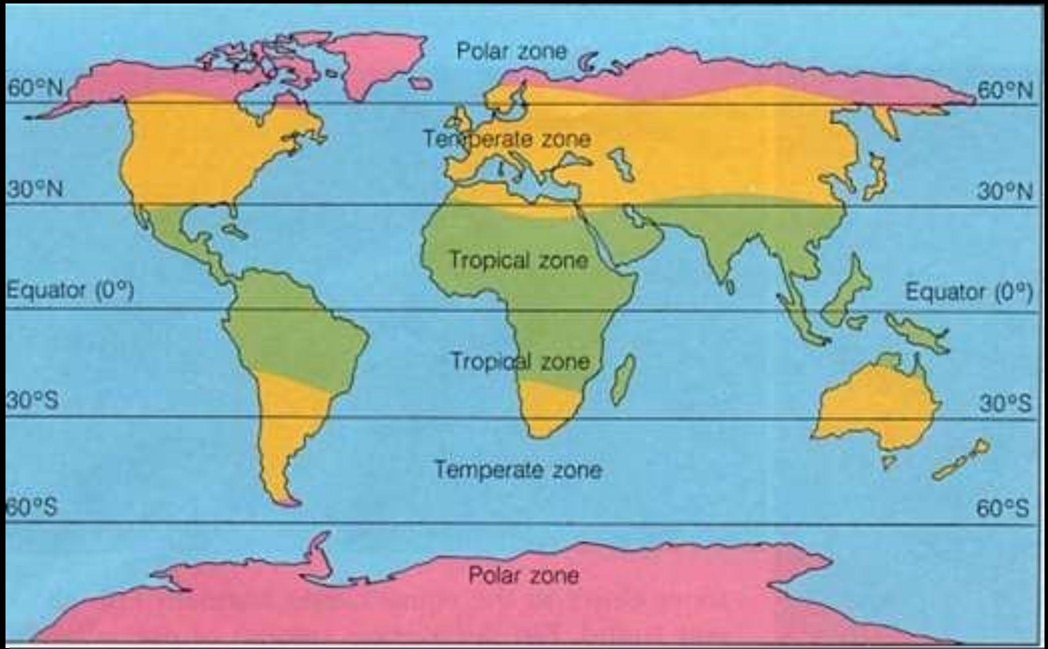


Figure 20.10

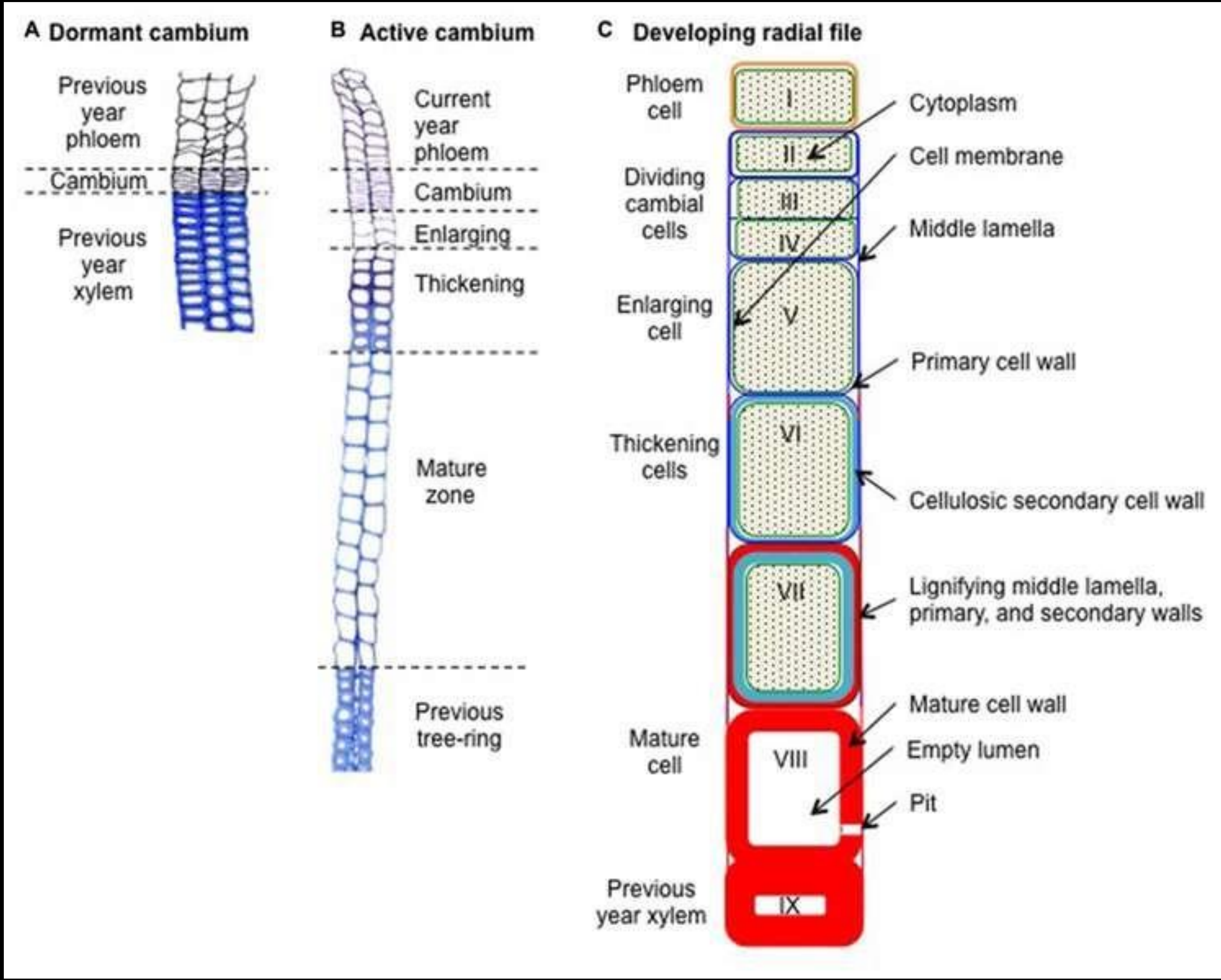
A. With the images of l. s. & t. s. the three dimensional view of a cell can be obtained. B. Diagram pointing the planes of section of wood. C., D. & E. The appearance of ray parenchyma in different planes.

- Normally the amount of secondary xylem formed is in excess in comparison to secondary phloem.
- The ratio of differentiation between secondary xylem and secondary phloem is 3 to 1 in conifers.
- In dicotyledons the ratio is variable and may be as great as 10 to 1.
- In an experiment *Eucalyptus camaldulensis* was exposed to labeled $^{14}CO_2$ that was incorporated in secondary vascular tissues.
- The incorporation of $^{14}CO_2$ indicates that the ratio of layers of secondary xylem and — phloem produced by the cambium is 4 to 1.

- The cambial activity is related to rainfall and temperature in tropical and temperate zone respectively.
- In tropical zones the vascular cambium of some species is continually active throughout the entire life.
- In temperate zones the vascular cambium remains dormant in winter. It activates in spring and produces secondary vascular tissue.
- Activation and cessation of cambial activity occur at an earlier age in ring porous trees (e.g. *Quercus*) than in diffuse porous trees (e.g. *Fagus*).
- There is experimental evidence that day-length affects the duration of cambial activity.



- In short-day condition the cambium remains dormant in *Robinia pseudacacia*.
- Activation / reactivation of cambial activity followed by a period of dormancy occur over the entire life of a plant.
- It leads to the formation of growth rings that reveal approximate age of plant.
- Thus the age of *Pinus aristata* and *Sequoiadendron* was estimated to be more than three thousand years.
- The cambial activity causes the increase in girth of axis.
- The circumference of vascular cambium also increases to cope up with the increase in girth of axis.
- This is accomplished by the formation of new fusiform- and ray initials.


A Dormant cambium
Previous year phloem
Cambium
Previous year xylem
B Active cambium
Current year phloem
Cambium
Enlarging
Thickening
Mature zone
Previous tree-ring
C Developing radial file
Phloem cell
Dividing cambial cells
Enlarging cell
Thickening cells
Mature cell
Previous year xylem
I
II
III
IV
V
VI
VII
VIII
IX
Cytoplasm
Cell membrane
Middle lamella
Primary cell wall
Cellulosic secondary cell wall
Lignifying middle lamella, primary, and secondary walls
Mature cell wall
Empty lumen
Pit

Formation of the fusiform cambial initial occurs in the following ways

- Fusiform initials in a storied cambium divide by anticlinal divisions and thus new initials are added to cambium.
- Short fusiform initials divide by radial anticlinal divisions where the partition walls occur parallel to long axes (Fig. 23.6A-C).
- The production of new initials from long non-storied fusiform initials occurs by oblique anticlinal divisions with walls of various degrees of inclination (pseudo-transverse).
- The daughter cells thus formed elongates by apical intrusive growth of overlapping ends (Fig. 23.6 D – E).

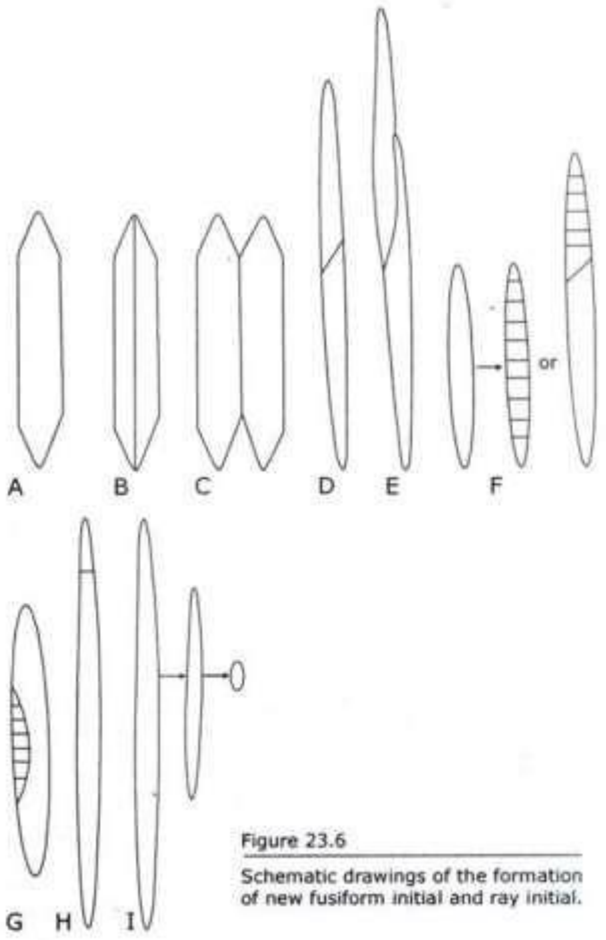


Figure 23.6

Schematic drawings of the formation of new fusiform initial and ray initial.

Fusiform initials give rise to ray initials in the following ways

- An entire or part of short fusiform initial divides by a series of transverse anticlinal divisions thus forming a tier of ray cell initials (Fig. 23.6F).
- Fusiform initial cuts off a single cell on its lateral side by an arcuate wall.
- In the small lateral daughter cell series of transverse anticlinal division occur and as a result a new ray initial is formed (Fig. 23.6G).
- Fusiform initial cuts off a single cell at its end (Fig. 23.6H).
- A fusiform initial is reduced to a ray cell initial (Fig. 23.6 I).

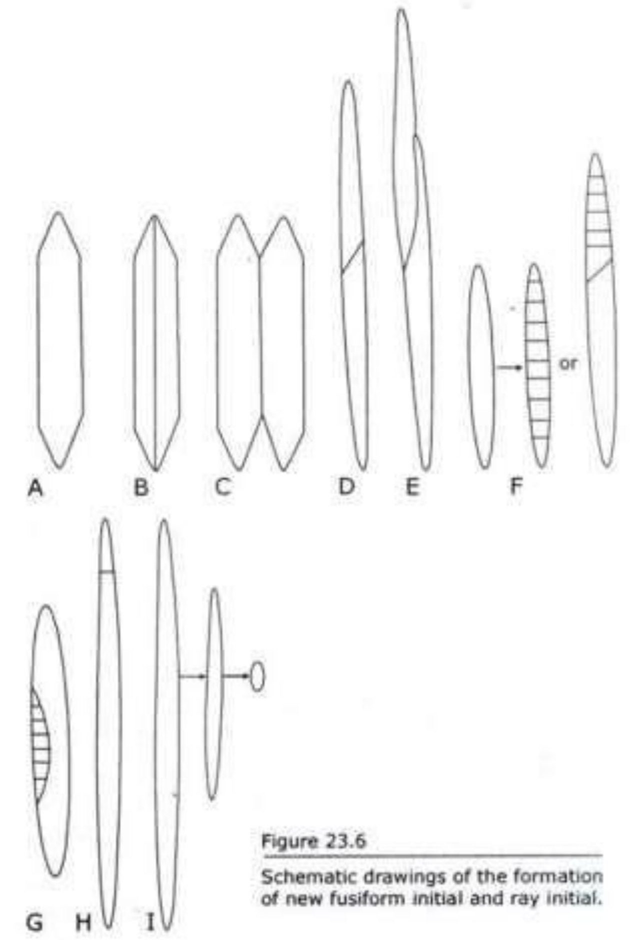


Figure 23.6

Schematic drawings of the formation of new fusiform initial and ray initial.

- In the above cases a uniseriate ray initial is formed.
- The ray initials may divide by a series of longitudinal anticlinal divisions to form biseriate or multiseriate rays.
- During secondary growth as the cambium increases in circumference a balance between the number and distribution of fusiform and ray initial is always maintained, because rays are the passageways for the transport of nutrients to cambium and its immediate incipient derivatives.
- In case of dicotyledons the wavy cambium of root donates secondary xylem towards interior and secondary phloem towards exterior.
- The portion of the wavy cambium ring that occurs at the furrow forms more secondary xylem.
- As a result at later stage of development the wavy ring becomes more or less circular.

- In dicotyledonous stem the fascicular cambium becomes active before the differentiation of interfascicular cambium (Fig. 23.7A-D).
- In many plants at the interfascicular region there originate provascular strands.
- The strands arise close to the initial vascular bundles (Fig. 23.7B).
- At later stage differentiating provascular strands and initial vascular bundles may contact to each other laterally thus forming vascular cambium continuous across the vascular bundles (Fig. 23.7C & D).

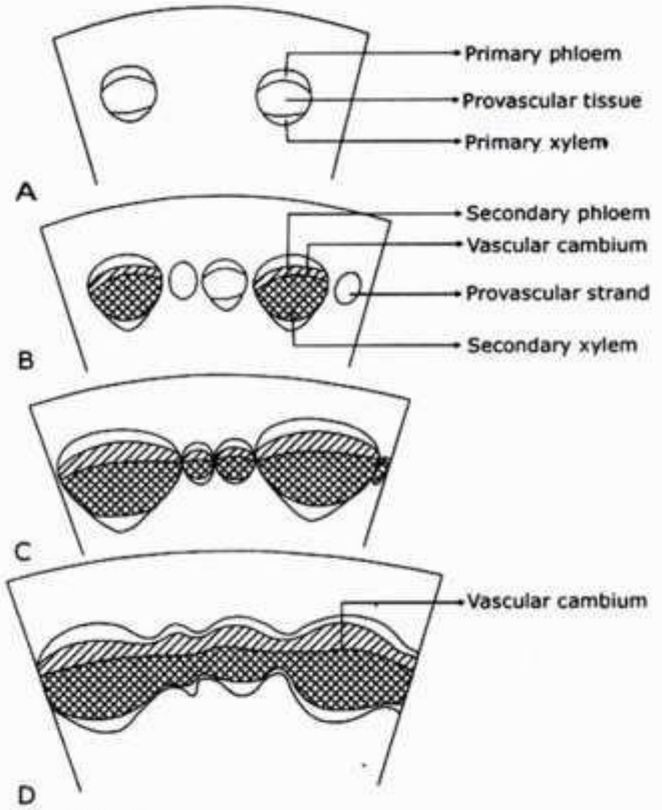


Figure 23.7
Diagram illustrating stages of formation of provascular strand, vascular cambium and secondary vascular tissues. Secondary xylem = crosshatched. Secondary phloem = obliquely hatched.

- In many woody herbs (Fig. 23.8A & B) interfascicular cambium originates from ground meristem when it differentiates early.
- In later stages mature interfascicular parenchyma by dedifferentiation forms interfascicular cambium.
- The fascicular cambium becomes active initially in the vascular bundles.
- When the vascular cambium becomes continuous and complete, the derivative cells of cambium cause the increments of secondary vascular tissues in normal secondary growth.

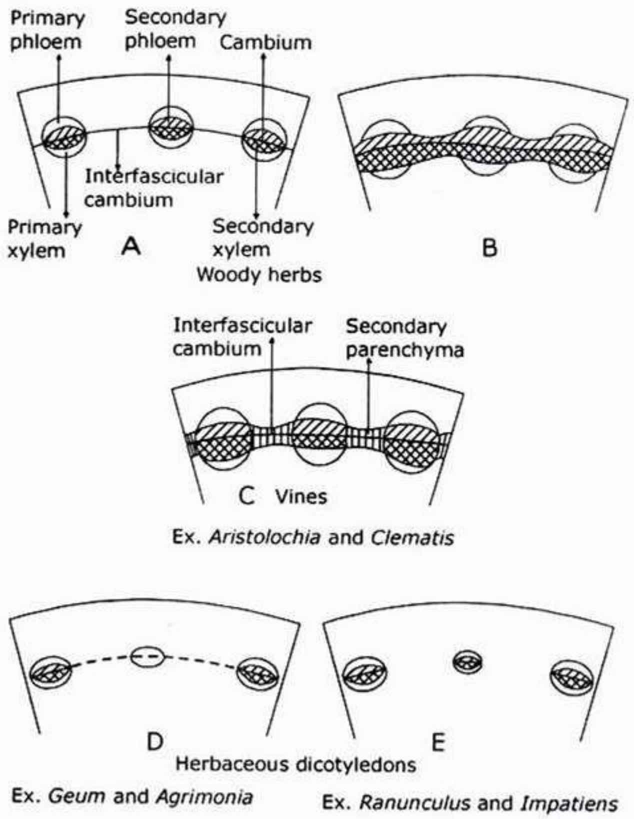


Figure 23.8
Diagram showing fascicular cambium, formation of interfascicular cambium, formation of secondary xylem (= crosshatched) and secondary phloem (= obliquely hatched).

- In herbaceous dicotyledons, e.g. *Geum*, Agrimonia etc. (Fig. 23.8D) the fascicular cambium is active only.
- In *Ranunculus*, *Impatiens* etc. (Fig. 23.8E) cambium does not develop usually or if it develops it remains inactive.
- In annuals the vascular cambium remains active only during the growth of the plant and ceases its activity before the plant dies.
- The vascular cambium functions throughout the life of woody perennials.

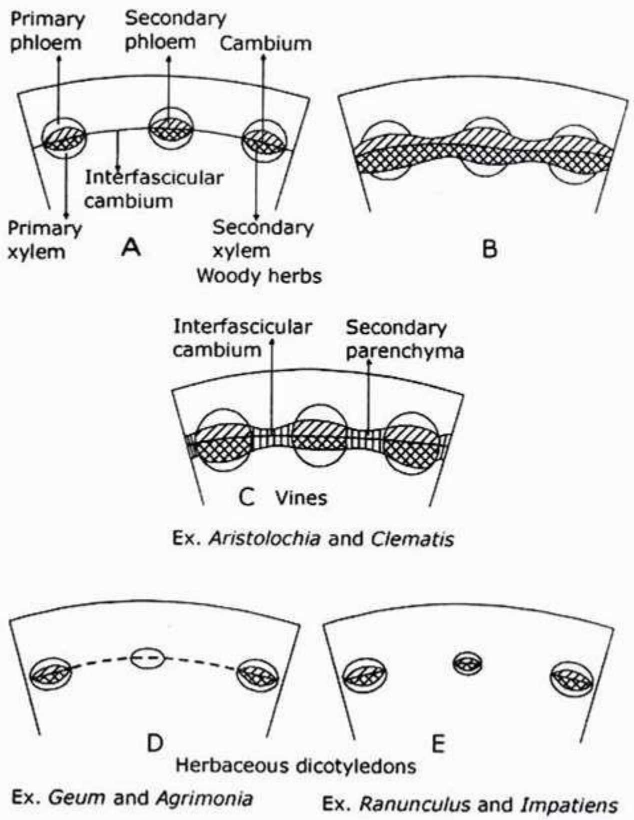


Figure 23.8
Diagram showing fascicular cambium, formation of interfascicular cambium, formation of secondary xylem (= crosshatched) and secondary phloem (= obliquely hatched).

- It is to note that vascular cambium is absent from most monocotyledons, pteridophytes and some herbaceous dicotyledons.
- In woody lianas, e.g. Aristolochia, Clematis etc. (Fig. 23.8C) the derivatives of fascicular cambium differentiates into characteristic secondary xylem and phloem.
- But the derivative cells of interfascicular cambium differentiate into parenchyma cells only.
- This type of cambial activity is regarded as abnormal.

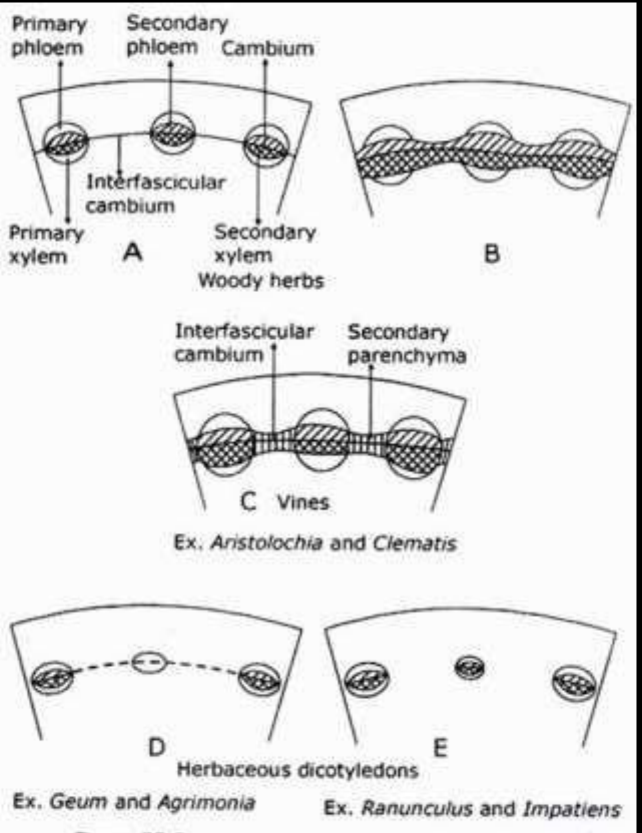


Figure 23.8
Diagram showing fascicular cambium, formation of interfascicular cambium, formation of secondary xylem (= crosshatched) and secondary phloem (= obliquely hatched).

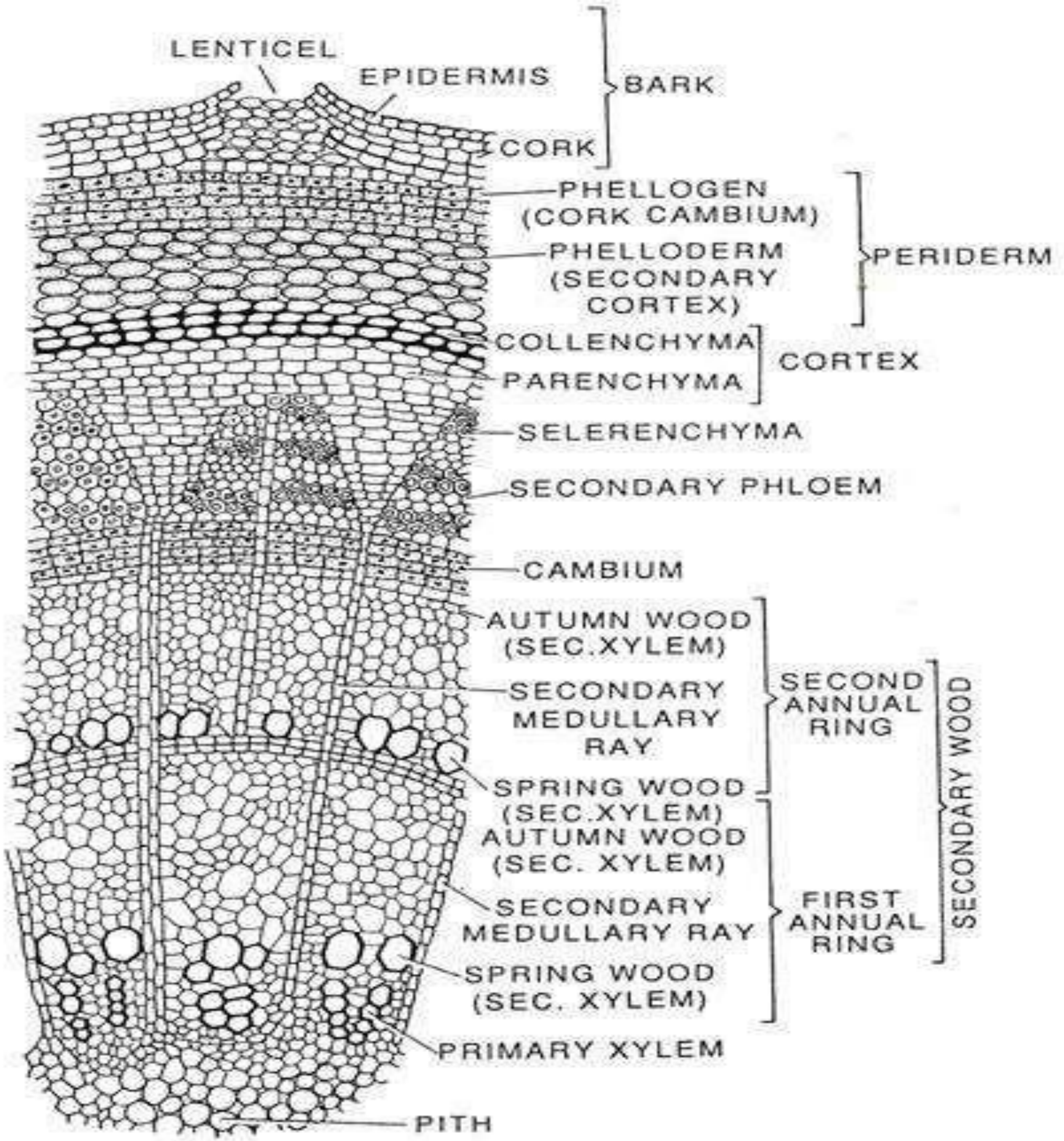


Fig. 40.41. Secondary growth in thickness. T.S. of a two-year old dicotyledonous stem.