Secondary growth in Plants

Normal Secondary Growth in Dicot Stem

Secondary growth is the formation of secondary tissues from lateral meristems.

It increases the diameter of the stem. In woody plants, secondary tissues constitute the bulk of the plant.

They take part in providing protection, support and conduction of water and nutrients.

Secondary tissues are formed by two types of lateral meristems, vascular cambium and cork cambium or phellogen.

Vascular cambium produces secondary vascular tissues while phellogen forms periderm.

Secondary growth occurs in perennial gymnosperms and dicots such as trees and shrubs. It is also found in the woody stems of some herbs. In such cases, the secondary growth is equivalent to one annual ring, e.g., Sunflower.

Formation of Secondary Vascular Tissues

- They are formed by the vascular cambium. Vascular cambium is produced by two types of meristems, fascicular or intra-fascicular and inter-fascicular cambium.
- Intra-fascicular cambium is a primary meristem which occurs as strips in vascular bundles.
- Inter-fascicular cambium arises secondarily from the cells of medullary rays which occur at the level of intra-fascicular strips.
- These two types of meristematic tissues get connected to form a ring of vascular cambium.
- Vascular cambium is truly single layered but appears to be a few layers (2-5) in thickness due to presence of its immediate derivatives.
- Cells of vascular cambium divide periclinally both on the outer and inner sides (bipolar divisions) to form secondary permanent tissues.

Vascular Rays:

- The vascular rays or secondary medullary rays are rows of radially arranged cells which are formed in the secondary vascular tissues. They are a few cells in height.

- Depending upon their breadth, the vascular rays are uniseriate (one cell in breadth) or multiseriate (two or more cells in breadth). Vascular rays may be homo-cellular (having one type of cells) or hetero-cellular (with more than one type of cells). The cells of the vascular rays enclose intercellular spaces.

- The part of the vascular ray present in the secondary xylem is called wood or xylem ray while the part present in the secondary phloem is known as phloem ray. The vascular rays conduct water and organic food and permit diffusion of gases in the radial direction. Besides, their cells store food.

Secondary Phloem (Bast):

- It forms a narrow circle on the outer side of vascular cambium. Secondary phloem does not grow in thickness because the primary and the older secondary phloem present on the outer side gets crushed with the development of new functional phloem (Fig. 6.28 D). Therefore, rings (annual rings) are not produced in secondary phloem. The crushed or non-functioning phloem may, however, have fibres and sclereids.

- Secondary phloem is made up of the same type of cells as are found in the primary phloem (metaphloem)— sieve tubes, companion cells, phloem fibres and phloem parenchyma.

- Phloem pairenchyma is of two types— axial phloem parenchyma made up of longitudinally arranged cells and phloem ray parenchyma formed of radially arranged parenchyma cells that constitute the part of the vascular ray present in the phloem.

- Elements of secondary phloem show a more regular arrangement. Sieve tubes are comparatively more numerous but are shorter and broader. Sclerenchyma fibres occur either in patches or bands. Sclereids are found in many cases. In such cases secondary phloem is differentiated into soft bast (secondary phloem without fibres) and hard bast (part of phloem with abundant fibres).

Secondary Xylem:

- It forms the bulk of the stem and is commonly called wood. The secondary xylem consists of vessels, tracheids (both tracheary elements), wood fibres and wood parenchyma.
- Wood parenchyma may contain tannins and crystals besides storing food. It is of two types— axial parenchyma cells arranged longitudinally and radial ray parenchyma cells arranged in radial or horizontal fashion. The latter is part of vascular ray present in secondary xylem.
- Secondary xylem does not show distinction into protoxylem and meta-xylem elements. Therefore, vessels and tracheids with annular and spiral thickenings are absent. The tracheary elements of secondary xylem are similar to those of meta-xylem of the primary xylem with minor differences. They are comparatively shorter and more thick-walled. Pitted thickenings are more common. Fibres are abundant.
- Width of secondary xylem grows with the age of the plant. The primary xylem persists as conical projection on its inner side. Pith may become narrow and ultimately get crushed. The yearly growth of secondary xylem is distinct in the areas which experience two seasons, one favourable spring or rainy season) and the other un-favourable (autumn, winter or dry summer).
- In favourable season the temperature is optimum. There is a good sunshine and humidity. At this time the newly formed leaves produce hormones which stimulate cambial activity. The activity decreases and stops towards the approach of un-favourable season. Hence the annual or yearly growth appears in the form of distinct rings which are called annual rings

- Annual rings are formed due to sequence of rapid growth (favourable season, e.g., spring), slow growth (before the onset of un-favourable period, e.g., autumn) and no growth (un-favourable season, e.g., winter). Annual rings are not distinct in tropical areas which do not have long dry periods.
- It is the wood formed in a single year. It consists of two types of wood, spring wood and autumn wood (Fig. 6.31). The spring or early wood is much wider than the autumn or late wood. It is lighter in colour and of lower density. Spring wood consists of larger and wider xylem elements.
- The autumn or late wood is dark coloured and of higher density. It contains compactly arranged smaller and narrower elements which have comparatively thicker walls. In autumn wood, tracheids and fibres are more abundant than those found in the spring wood.

Fig. 6.30. Part of T.S. old stem showing annual rings.

- The transition from spring to autumn wood in an annual ring is gradual but the transition from autumn wood to the spring wood of the next year is sudden. Therefore, each year’s growth is quite distinct. The number of annual rings corresponds to the age of that part of the stem. (They can be counted by increment borer).
- Besides giving the age of the plant, the annual rings also give some clue about the climatic conditions of the past through which the plant has passed. Dendrochronology is the science of counting and analysing annual growth rings of trees.
- **Softwood and Hardwood:**
- Softwood is the technical name of gymnosperm wood because it is devoid of vessels. Several of the softwoods are very easy to work with (e.g., Cedrus, Pinus species). However, all of them are not ‘soft’. The softness depends upon the content of fibres and vascular rays. 90-95% of wood is made of tracheids and fibres. Vascular rays constitute 5-10% of the wood.
- Hardwood is the name of dicot wood which possesses abundant vessels. Due to the presence of vessels, the hardwoods are also called porous woods. In Cassia fistula and Dalbergia sisso the vessels are comparatively very broad in the spring wood while they are quite narrow in the autumn wood. Such a secondary xylem or wood is called ring porous.
- In others (e.g., Syzygium cumini) larger sized vessels are distributed throughout spring wood and autumn wood. This type of secondary xylem or wood is known as diffuse porous. Ring porous wood is more advanced than diffuse porous wood as it provides for better translocation when the requirement of the plant is high.

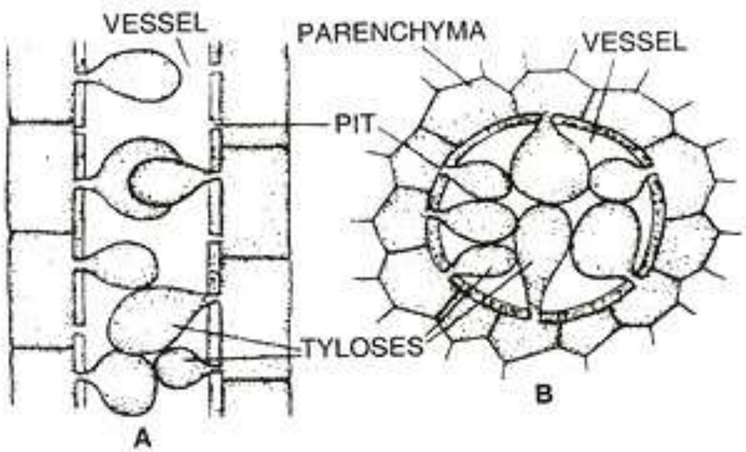


Fig. 6.32. Formation of tyloses in heartwood.
A, L.S. vessel showing tyloses.
B, T.S. vessel showing tyloses.

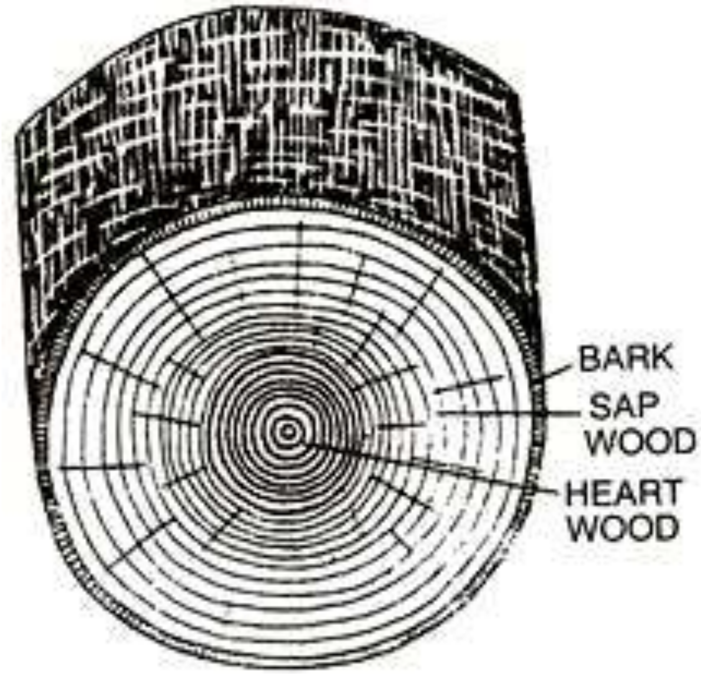


Fig. 6.33. Sapwood and heartwood in T.S. of trunk.

- **Sapwood and Heartwood:**
- The wood of the older stems (dalbergia, Acacia) gets differentiated into two zones, the outer light coloured and functional sapwood or alburnum and the inner darker and nonfunctional heartwood or duramen.
- The tracheids and vessels of the heart wood get plugged by the in growth of the adjacent parenchyma cells into their cavities through the pits. These ingrowths are called tyloses.
- Ultimately, the parenchyma cells become lignified and dead. Various types of plant products like oils, resins, gums, aromatic substances, essential oils and tannins are deposited in the cells of the heartwood.
- These substances are collectively called extractives. They provide colour to the heartwood. They are also antiseptic. The heartwood is, therefore, stronger and more durable than the sapwood.
- It is resistant to attack of insects and microbes. Heart wood is commercial source of Cutch (Acacia catechu), Haematoxylin (Haematoxylon campechianum), Brasilin (Caesalpinia sappan) and Santalin (Pterocarpus santalinus). Heartwood is, however, liable to be attacked by wood rotting fungi. Hollow tree trunks are due to their activity.

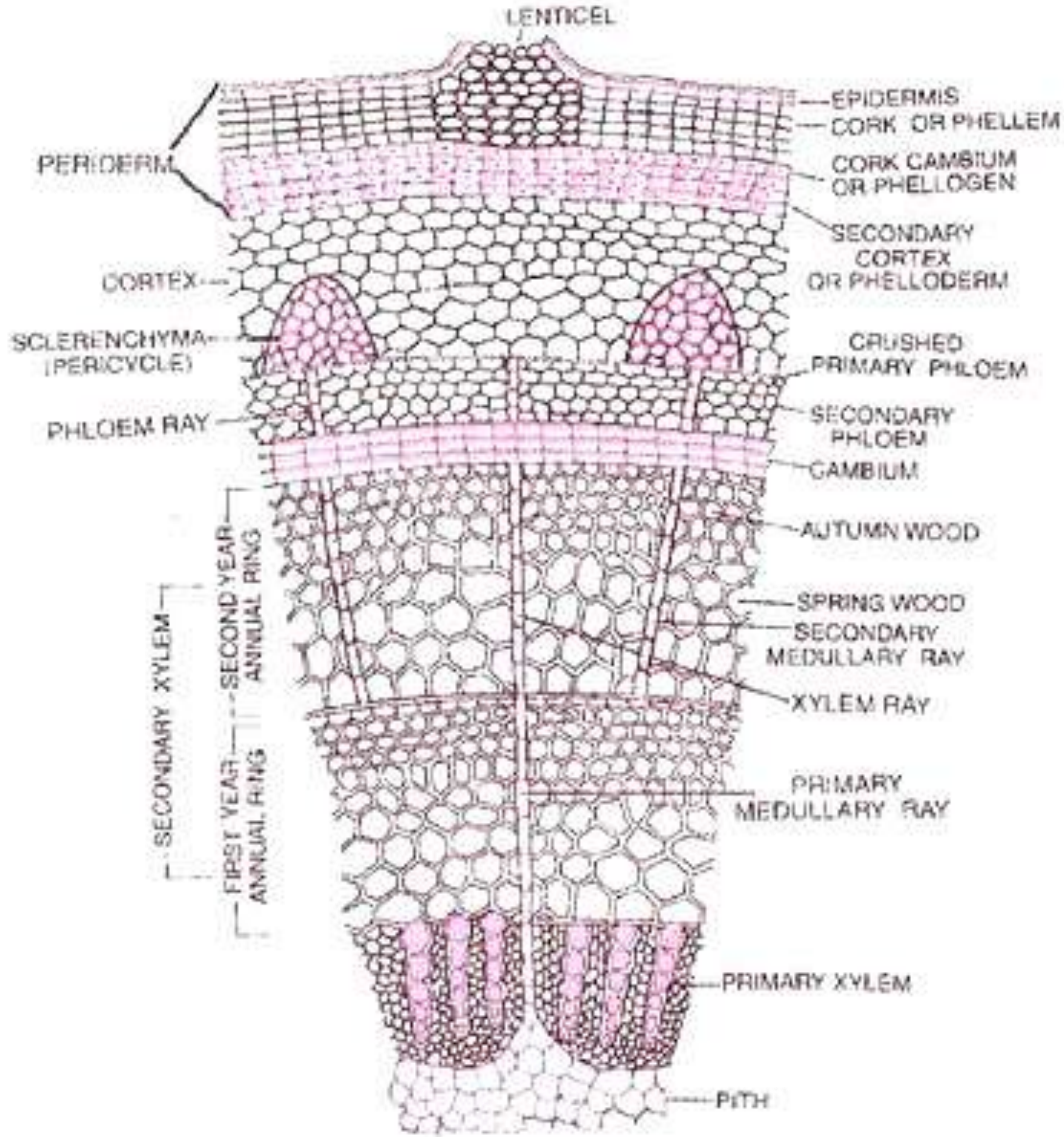


Fig. 6.31. Part of detailed structure of transverse section of two year old dicot stem showing secondary growth.

- **Formation of Periderm:**
- In order to provide for increase in girth and prevent harm on the rupturing of the outer ground tissues due to the formation of secondary vascular tissues, dicot stems produce a cork cambium or phellogen in the outer cortical cells. Rarely it may arise from the epidermis (e.g., Teak, Oleander), hypodermis (e.g., Pear) or phloem parenchyma.
- Phellogen cells divide on both the outer side as well as the inner side (bipolar) to form secondary tissues. The secondary tissue produced on the inner side of the phellogen is parenchymatous or collenchymatous. It is called secondary cortex or phelloderm. Its cells show radial arrangement.
- Phellogen produces cork or phellem on the outer side. It consists of dead and compactly arranged rectangular cells that possess suberised cell walls. The cork cells contain tannins. Hence, they appear brown or dark brown in colour. The cork cells of some plants are filled with air e.g., Quercus suber (Cork Oak or Bottle Cork). The phelloderm, phellogen and phellem together constitute the periderm (Fig. 6.34).
- Cork prevents the loss of water by evaporation. It also protects the interior against entry of harmful micro-organisms, mechanical injury and extremes of temperature. Cork is light, compressible, nonreactive and sufficiently resistant to fire.
- It is used as stopper for bottles, shock absorption and insulation. At places phellogen produces aerating pores instead of cork. These pores are called lenticels. Each lenticel is filled by a mass of somewhat loosely arranged suberised cells called complementary cells.

Lenticels:

- Lenticels are aerating pores in the bark of plants. They appear on the surface of the bark as raised scars containing oval, rounded or oblong depressions (Fig. 6.34 A). They occur in woody trees but not in climbers. Normally they are formed in areas with underlying rays for facilitating gas exchange. Lenticels may occur scattered or form longitudinal rows.
- A lenticel is commonly produced beneath a former stomate or stoma of the epidermis. Its margin is raised and is formed by surrounding cork cells. The lenticel is filled up by loosely arranged thin walled rounded and suberised (e.g., Prunus) or un-suberised cells called complementary cells (Fig. 6.34 B).
- They enclose intercellular spaces for gaseous exchange. The complementary cells are formed from loosely arranged phellogen cells and division of sub-stomatal parenchyma cells. The suberised nature of complementary cells checks excessive evaporation of water.
- In temperate plants the lenticels get closed during the winter by the formation of compactly arranged closing cells over the complementary cells.

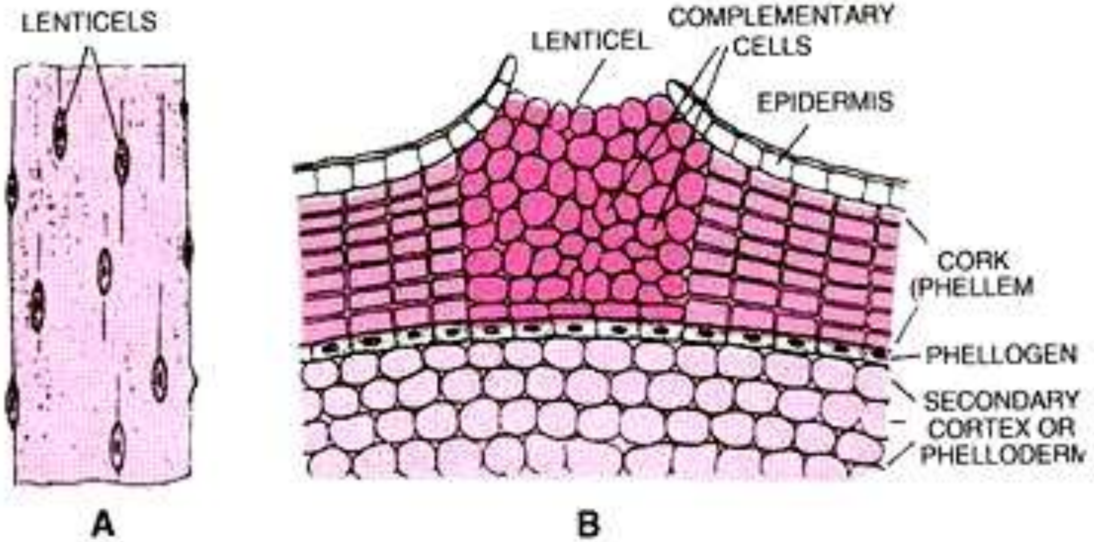


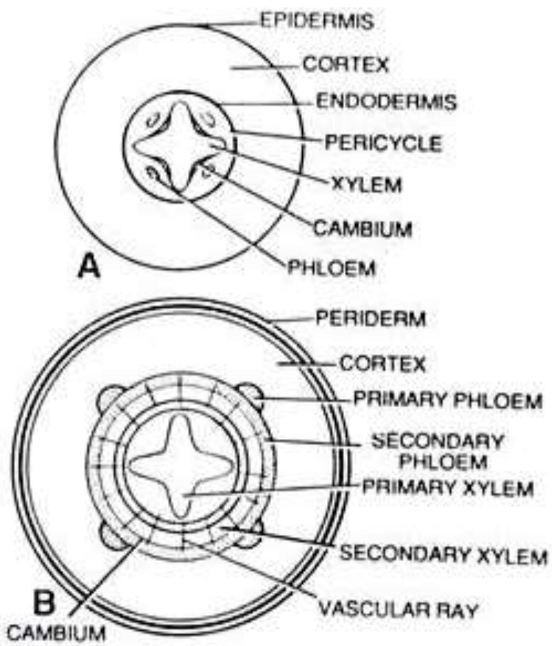
Fig. 6.34. Lenticels. A, external view of lenticels; B, T.S. lenticel.

- **Bark:**
- In common language and economic botany, all the dead cells lying outside phellogen are collectively called bark. The outer layers of the bark are being constantly peeled off on account of the formation of new secondary vascular tissues in the interior. The peeling of the bark may occur in sheets (sheets or ring bark, e.g., Eucalyptus) or in irregular strips (scaly bark).
- The scaly bark is formed when the phellogen arises in strips instead of rings, e.g., Acacia (vem. Kikar). Bark formed in early growing season is early or soft bark. The one formed towards end of growing season is late or hard bark.
- Bark is insect repellent, decay proof, fire-proof and acts as a heat screen. Commercially it is employed in tanning (e.g., Acacia), drugs (e.g., Cinchona— quinine) or as spice (e.g., Cannamon, vem. Dalchini). The cork of Quercus suber is employed in the manufacture of bottle stoppers, insulators, floats, sound proofing and linoleum.

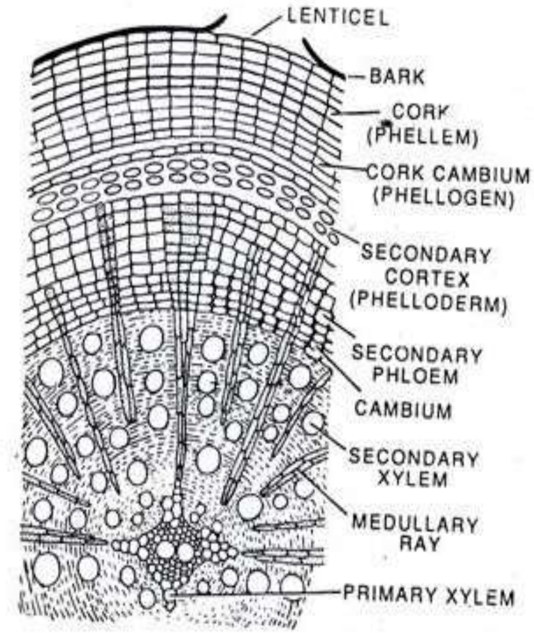
Secondary growth in Dicot Root

- The secondary tissues developed in the dicotyledonous roots are fundamentally quite similar to that of dicotyledonous stems, but the process initiates in some different manner. Certain dicotyledonous roots do not show secondary growth. The secondary vascular tissues originate as a result of the cambial activity. The phellogen gives rise to the periderm.
- **Formation of Cambium and Development of Secondary Tissues:**
- The dicotyledonous roots posses a limited number of radial vascular bundles with exarch xylem. Normally the pith is very little or altogether absent. On the initiation of secondary growth, a few parenchyma cells beneath each group of phloem become meristematic and thus as many cambial strips are formed as the number of phloem groups.

- The cambial cells divide tangentially again and again and produce secondary tissues. Thereafter some of the cells of single layered pericycle become meristematic lying against the protoxylem groups, which divide and form a few layers of cells.
- The first formed cambium now extends towards both of its edges and reaches the inner most derivatives of the pericycle, thus giving rise to a complete ring of cambium.
- The cambium ring is wavy in outline, as it passes internal to phloem and external to xylem groups. The cambial cells produce more xylem elements than phloem.
- The first formed cambium produces secondary xylem much earlier, and the wavy cambium ring ultimately becomes circular.
- Now whole of the cambium ring becomes actively meristematic, and behaves in the similar way as in the stem, giving rise to secondary xylem on its inner side and secondary phloem towards outside.
- The secondary vascular tissues form a continuous cylinder and usually the primary xylem gets embedded in it. At this stage distinction can be made only by exarch primary xylem located in the centre. The primary phloem elements are generally seen in crushed condition.



Secondary growth in root A, cross section of a root without secondary growth; B, the same after considerable secondary growth.



Secondary growth. T.S. of dicotyledonous root showing secondary growth (later stage).

- The cambial cells that originate from the pericycle lying against the groups of protoxylem function as ray initials and produce broad vascular rays. These rays are traversed in the xylem and phloem through cambium; this is characteristic feature of the roots. Normally, such rays are called medullary rays.
- **Periderm:**
- Simultaneously the periderm develops in the outer region of the root. The single layered pericycle becomes meristematic and divides, giving rise to cork cambium or phellogen. It produces a few brownish layers of cork cells or phellem towards outside, and the pheliodorm on the inside.
- The phelloderm does not contain chloroplasts. The pressure caused by secondary tissues ruptures the cortex with endodermis, which is ultimately sloughed off. The epiblema dies out earlier. Lenticels may also be formed.

Anomalous Secondary Growth in Dicot Stems

Anatomy of Nyctanthes – Stem

The outline of T.S. appears quadrangular and reveals the following tissues from outside with-in:

Epidermis:

1. Single-layered epidermis consists of rectangular cells.
2. A thick uninterrupted cuticle is present on the epidermis.
3. Many multicellular hairs are present.

Cortex:

4. It is differentiated into collenchyma and parenchyma.
5. Collenchyma is several cells deep below the four protruded comers while only few layers deep at the other places just beneath the epidermis.
6. Parenchyma is present below the collenchyma. Many intercellular spaces are present. The region extends upto the vascular tissue.

Cortical bundles:

7. Four vascular bundles are present in the cortex, situated one each in each protruded bulge.
8. Each conical bundle faces its pointed xylem end towards outer side, i.e., epidermis, and is conjoint, collateral, open and exarch.
9. These bundles may show secondary growth at maturity.

Endodermis:

10. Not well-developed.

Pericycle:

11. It is in the form of sclerenchymatous patches.

Vascular System:

12. It consists of primary phloem, secondary phloem, cambium, secondary xylem and primary xylem.
13. Primary phloem is crushed and irregularly present in patches below pericycle.
14. Secondary phloem is present in the form of a continuous ring and consists of sieve tubes, companion cells and phloem parenchyma
15. Cambium is one to three cells thick continuous layer present in between phloem and xylem.
16. Secondary xylem is present just inner to the cambial ring and consists mainly of thick walled wood parenchyma and fibres. Tracheids and vessels are also present
17. Primary xylem is situated just near the pith facing its protoxylem towards the centre.

Pith:

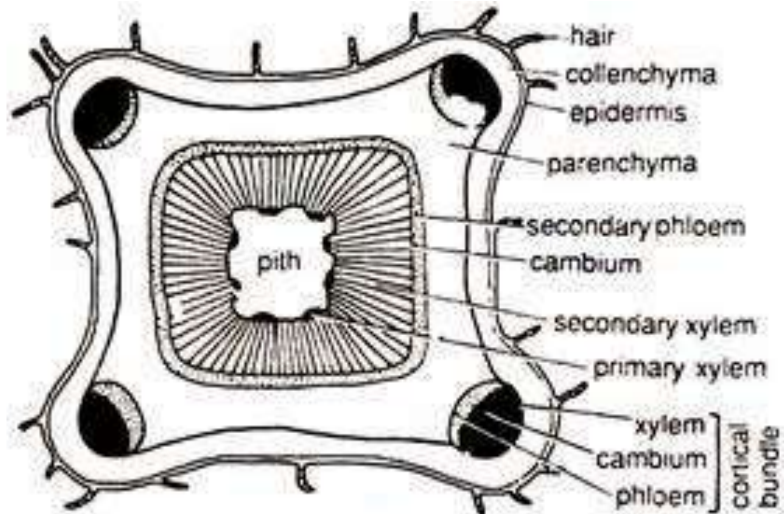
18. It is thin walled and parenchymatous.

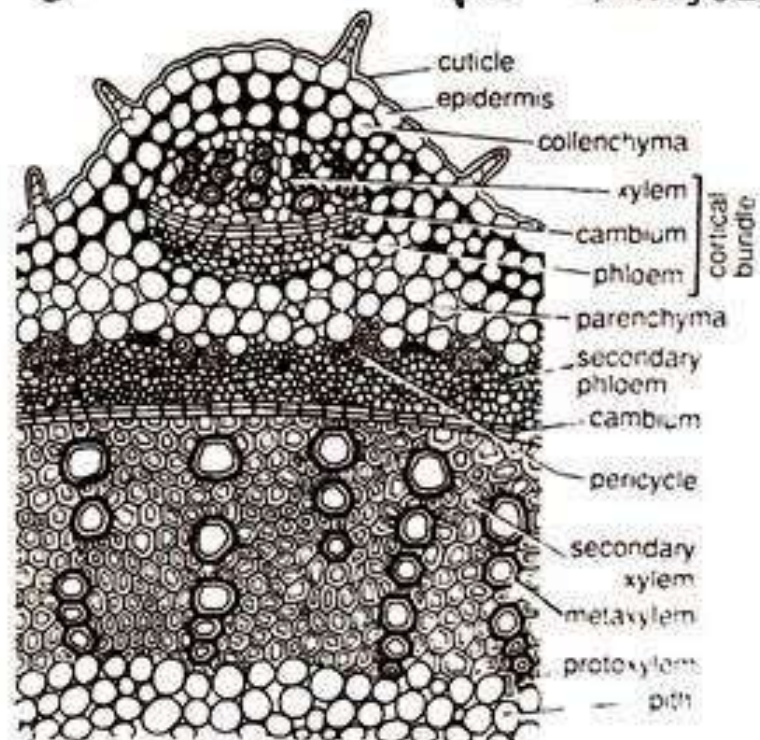
Abnormality:

Abnormality in Nyctanthes ii the presence of cortical bundles, which are inversely oriented, 4 in number and never directly connected with the main axial ring of the vascular cylinder. These are leaf trace bundles.

Cortical bundles have also been reported in some other families such as Casuarinaceae (Casuarina), Umbelliferae (Eryngium), Papilionaccae (Latkyrus marytimus). Mclastomaccac, Rutaccae, etc.

T.S. of Nyctanthes stem





Anatomy of Boerhaavia – Stem

Epidermis:

1. Single layered epidermis consists of small, radially elongated cells.
2. Multicellular epidermal hairs arise from some cells.
3. A thick cuticle is present on the epidermis.
4. Some stomata are also present.

Cortex:

5. It is well differentiated and consists of few layered collenchymatous hypodermis followed by chlorenchyma.
6. Collenchyma is 3 to 4 cells deep, but generally near stomata it is only one layered.
7. Chlorenchyma is present inner to collenchyma in the form of 3 to 7 layers.
8. Chlorenchymatous cells are thin walled, oval, full of chloroplasts and enclose many intercellular spaces.
9. Endodermis is clearly developed and made up of many, tubular, thick-walled cells.

Pericycle:

10. Inner to the endodermis is present parenchymatous pericycle but at some places it is represented by isolated patches of sclerenchyma.

Vascular System:

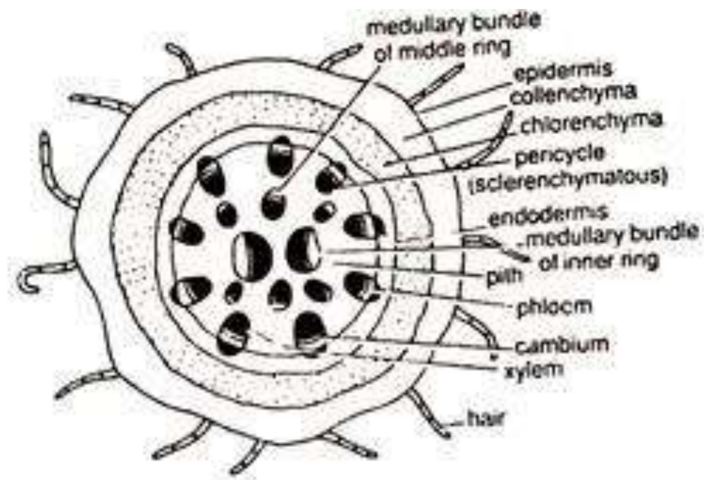
11. Vascular bundles are present in three rings. In the innermost ring are present two large bundles; in the middle ring the number ranges from 6 to 14 while the outermost ring consists of 15 to 20 vascular bundles.

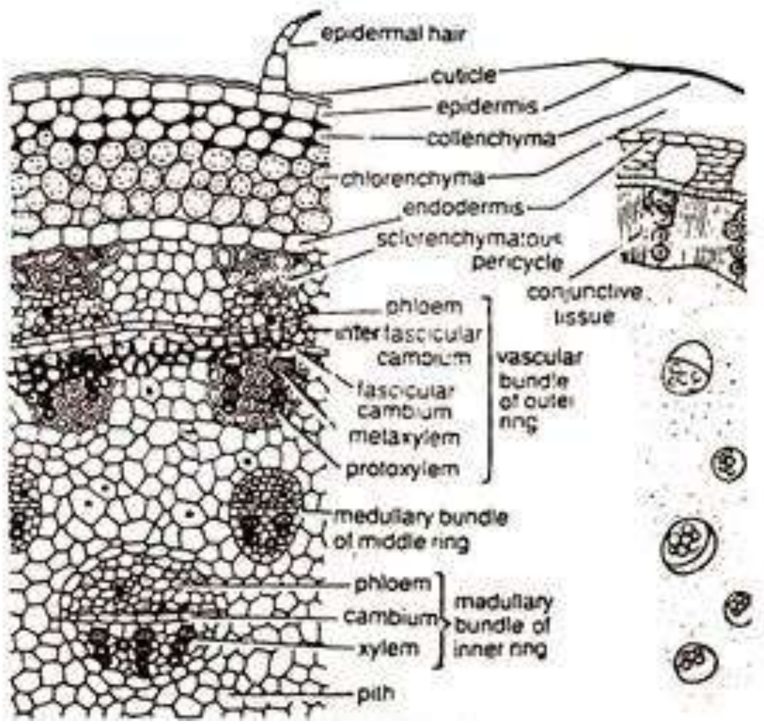
12. Vascular bundles of innermost and middle rings are medullary bundles.
13. Vascular bundles are conjoint, collateral and endarch.
14. Two vascular bundles of the innermost ring arc large, oval and lie opposite to each other with their xylem facing towards centre and phloem outwards.
15. Middle ring consists of 6-14 small vascular bundles.
16. Vascular bundles of inner and middle rings may show a little secondary growth.
17. Phloem consists of sieve tubes, companion cells and phloem parenchyma while the xylem consists of vessels, tracheids and xylem parenchyma.
18. Outermost ring of the vascular bundles contain inter-fascicular cambium which is absent in other two rings.
19. Cambium develops secondarily from the pericycle and becomes active. It cuts secondary phloem towards outer side and secondary xylem towards inner side. Due to these changes the primary phloem becomes crushed and present next to pericycle. Primary xylem is situated near the pith.
20. Interfascicular cambium also soon becomes active and cuts internally the row of cells which become thick walled and lignified and are known as conjunctive tissue.

Pith:

21. It is well developed, parenchymatous and present in the centre.

T. S. of Boerhaavia stem





Anomalous secondary growth in Monocot stem

Some monocotyledons belonging to the family Liliaceae, mainly the arborescent ones like Dracaena, Yucca, Cordyline, Agave, Aloe and others exhibit a peculiar type of secondary increase in thickness.

In the regions which have ceased to elongate some cells occurring outside the vascular bundles become meristematic and form the cambium. The secondary meristem originates in the cortex, in fact, deep layers of cortex or pericycle, though it is difficult to locate those zones in many stems.

The cambial cells are fusiform or rectangular in shape. Instead of forming phloem and xylem on the outer and inner sides, as in normal condition, the cambial cells go on dividing and producing secondary tissues on the inner side first, and later small amount of new tissues are cut off on the outer side as well.

Those formed on the inner side differentiate into oval-shaped vascular bundles and radially arranged parenchyma cells. These parenchyma cells in which the vascular bundles remain embedded are said to constitute the conjunctive tissue.

The radial arrangement of the parenchyma cells of conjunctive tissue is due to their origin by tangential divisions of the cambial cells. So they may be easily distinguished from the irregularly arranged parenchyma of the primary ground tissues. They may be thin-walled or thick- walled.

A few derivatives of the cambium divide longitudinally, initially anticlinally, then periclinally and even haphazardly to form xylem and phloem elements of the secondary vascular bundles. These differ from the primary ones in presence of small amount of phloem and in absence of annular and spiral protoxylem elements.

The secondary bundles are mostly amphivasal, some of them may be collateral as well. The small amount of phloem consists of short sieve tubes, companion cells and parenchyma. The xylem is made of only tracheids, usually with scalariform thickening and small amount of xylem parenchyma which have lignified walls.

The tissues cut off by the cambial cells on the outer side are scanty in amount and are parenchymatous in nature. The primary bundles are comparatively larger. They are also mostly amphivasal or rather rarely collateral ones.

In Aloe, coconut and royal palm periderm is formed in the same manner as in the dicotyledons. A special type of protective tissue is produced in the majority of the monocotyledons with secondary increase in thickness.

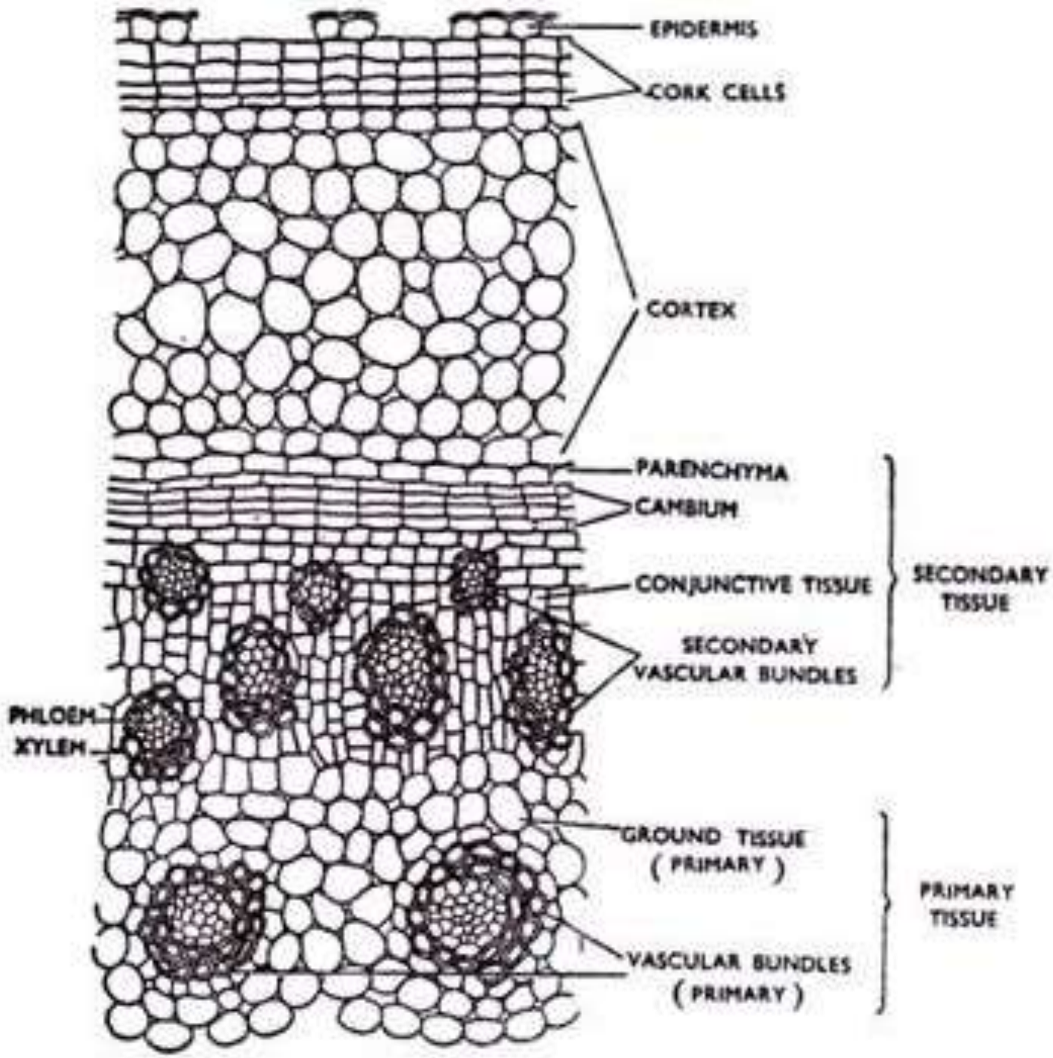
Parenchyma cells in the deeper layers of cortex divide periclinally several times and produce radially arranged layers of cells, suggesting something like a storied meristem. The series of cells thus formed undergo suberisation and differentiate into cork cells. This tissue is called storied cork, mainly' because of its storied appearance.

Considerable thickening which is often noticed at the bases of many palms (Fig. 644) is not due to the activity of a cambial layer, but it is really a case of protracted or long-continuing primary growth.

The apical meristem or shoot apex produces only a part of the primary body —-a central column of parenchyma and vascular strands. Another meristem occurs just beneath the leaf primordia forming a mantle-like tissue region. This is known as primary thickening meristem.

The cells of the same divide periclinally and form rows of cells which differentiate into ground parenchyma traversed by procambial strands. The latter, ultimately develop into vascular bundles. There are further enlargement and divisions of the ground parenchyma, causing increase in thickness.

Thus the primary thickening meristem produces the main bulk of stem tissues, viz., ground parenchyma and most of the vascular bundles. The thickening is due to the activities of the two meristems stated above.



A portion of *Dracaena* stem in t.s. showing special type of secondary growth.

Nodal Anatomy

In dicotyledons, the vascular bundles are usually more or less in a ring and show different arrangements at the nodes and internodes. The vascular cylinders are generally continuous at the internode and their continuity is interrupted at the nodal region due to the emergence of bundles that terminate either at the leaf bases, axillary buds or stipules etc.

At the node three types of bundles are recognized:

(i) Leaf trace bundle:

The single vascular bundle that connects the leaf base with the main vascular cylinder of stem is designated as leaf trace bundle. In a leaf there may be several leaf trace bundles that collectively are termed as leaf traces.

(ii) Cauline bundle:

The vascular bundles that entirely form the vascular system of stems are known as cauline bundles. Sometimes these bundles anastomose with each other and extend from stem to leaf as leaf traces.

(iii) Common bundle:

The vascular bundles, which run unbranched through a few successive nodes and internodes and ultimately terminate as leaf traces are called common bundles.

The arrangement of vascular tissues at the nodes is more complex than the internodes due to emergence of vascular traces to the leaves, buds, stipules etc., present at the node.

A cross-section through node reveals that, there is a break in the vascular cylinder of stem, that is, the vascular cylinder is not in the form of a continuous ring. In this region the vascular tissue is interrupted and .parenchyma cells fill the gap. Pith and cortex are continuous through this gap.

The following types of anatomy at nodes in dicots are recognized:

(a) Unilacunar single-trace node:

This type of node exhibits one leaf trace to a leaf and the leaf trace is associated with one lacuna. Ex. Spiraea. Unilacunar nodes are exstipulate.

(b) Unilacunar two-trace node:

This type of node has two leaf traces to a single leaf and one lacuna. The two leaf traces are associated with the single lacuna. Ex. Clerodendron.

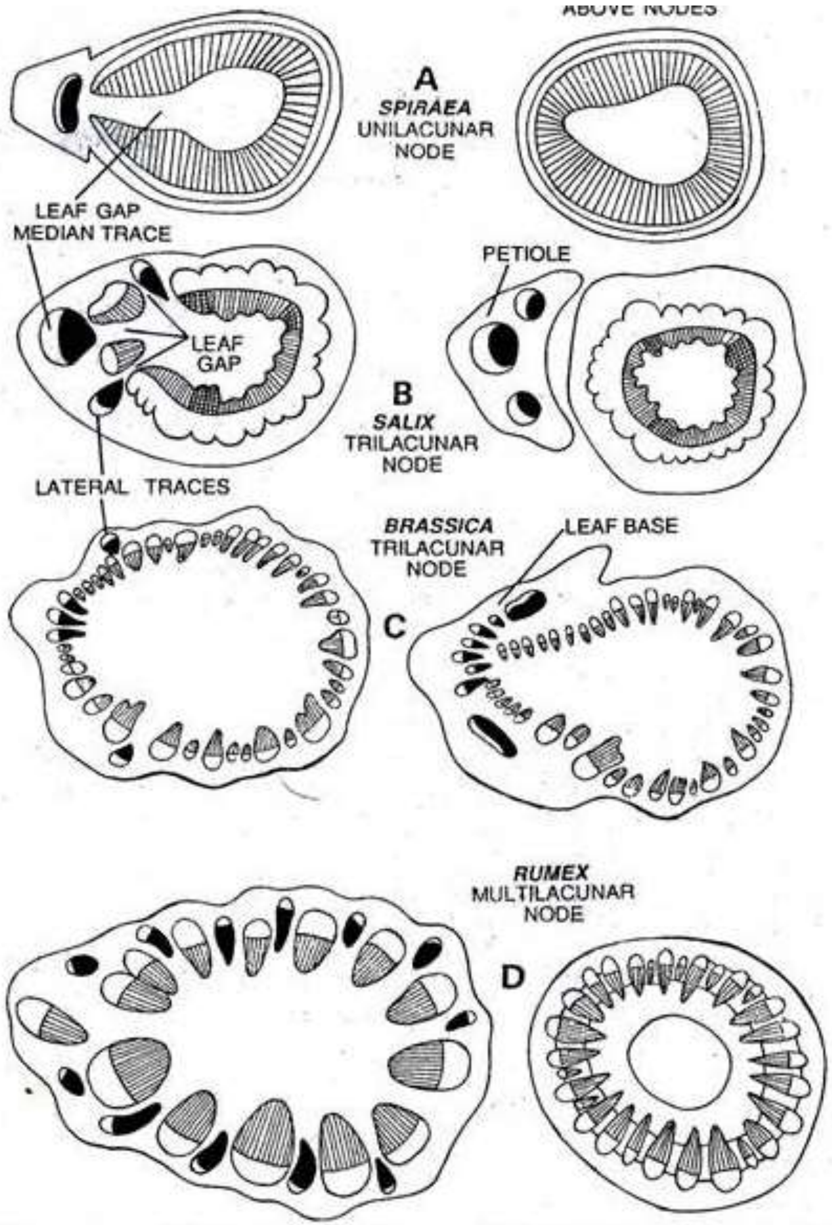
(c) Trilacunar node:

This type of node has three leaf traces to a leaf and three lacunae. Each trace is associated with single lacuna (Fig. 17.4B). Ex. Salix. Among the three traces, the trace that occurs in the median position with reference to leaf is referred to as median trace. The others are called lateral traces. This type of node has stipules.

(d) Multilacunar node:

This type of node has more than three traces to a leaf and more than three lacunas. Each trace is confronted with single lacuna. Ex. Rumex. Multilacunar node is exhibited in the plants that have sheathing leaf bases.

It is to note that the terms unilacunar-, trilacunar- and multilacunar node are applied with reference to a single leaf. In this sense in unilacunar node each leaf is associated with one lacuna. A node may consist more than one leaf. A cross-section of such node reveals the presence of more than one lacuna and more than one leaf trace.



. Nodal anatomy of dicotyledons. A. *Spiraea*— each leaf has one leaf trace and one leaf gap (unilacunar node); B, *Salix*— each leaf has three leaf traces and three leaf gaps (trilacunar node); C, *Brassica*— three leaf traces and three leaf gaps per leaf (trilacunar node); D, *Rumex*— many leaf traces and many leaf gaps per leaf (multilacunar node).