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PLANT ANATOMY,EMBRYOLOGY,TISSUE CULTURE AND BASIC MOLECULAR BIOLOGY

1. Plant Anatomy:
Structure of epidermal cells; Structure, function and types of Stomata.
Structure, distribution, types and function of Laticifers.
Structure, distribution, functions and ecology of Nectaries.
Structure and activity of Vascular Cambium.
Structure and function of Periderm.
Secondary growth of stem of *Leptadenia* and *Boerhaavia.*

Structure of epidermal cells;

The outermost layer or layers of cell covering all plant organs are the **epidermis**. It is in direct contact with the environment and so it modifies itself to cope up with the natural surroundings.

It thus protects the inner tissues from any adverse natural calamities like high temperature, desiccation, mechanical injury, external infection etc. In some plants the epidermis may persist throughout the life, while in others it is replaced by periderm when the epidermis is sloughed off along with underlying tissues.

Origin : The epidermis of all organs originates from the outermost layer of apical meristem. Haberlandt, Hanstein and Schmidt called this surface layer of meristem as protoderm, dermatogen and tunica respectively.

Structure : Usually the epidermis consists of one layer of cells. Several-layered epidermis, termed multiple epidermis, is found in the leaves of Ficus, Nerium and in the aerial roots of orchid. The initials of epidermis divide periclinally to form multiple epidermis. The multiple epidermis of orchid root has the special name - velamen.
Contents : The epidermis of aerial parts of a plant consists of living parenchyma cells whose shape, size and arrangement may differ. The epidermal cells are more or less tabular (=horizontally flattened) in cross sectional view. In leaves, the epidermal cell walls appear as sinuous in dicots and in monocots they appear as straight or sinuous in surface view. Usually the cells of epidermis are compactly set with none or few intercellular spaces (e.g. flower petals).

The epidermal cells are devoid of chloroplasts. The guard cells of stomata that are specialized epidermal cells contain chloroplastids. Other pigment like anthocyanin may occur in epidermal cells. In some plants silicon may be deposited in the epidermal cells cither in the lumen or wall. The wall of trichome may be silicified.

Silicon containing cell can be differentiated from the adjacent epidermal cells by its shape and size. This cell is solitary and may be either scattered over the leaf surface or situated over the veins in longitudinal rows. Silicon is deposited in the bracts of rice, in the marginal trichomes of oat, in the leaves of Cyperus, Avena etc.

In the internode of Avena sativa, the epidermal cells at the intercostal position form cork-silica cell pairs, i.e. cork and silica containing cells are in close contact with each other. In the leaf of Ficus, some of the epidermal cells contain crystals of calcium carbonate, known as cystolith. These cells are easily distinguishable from the other epidermal cells by their large size and these specialized epidermal cells containing cystolith are called lithocyst.

Usually the walls of epidermal cells are thin. Thick walled lignified epidermal cells occur in some gymnosperms. Cutin, a fatty substance, is very often deposited on the outer surface of the epidermal cell wall to form cuticle over which wax may also be deposited. The cuticle is resistant to decay and is well preserved in fossils.

The cuticle often preserves the characteristic features of the epidermal surfaces such as the types and distribution of hairs and stomata. Thus the fossil plants may be identified by cuticular studies. Palmer (1976) used the fossil grass cuticle instead of grass pollen,as a new palaeoecological tool to reconstruct the nature of past vegetation of East African lake sediments.

Now a days cuticular pattern is used in recognizing small fragments of plants, which are necessary in forensic medicine, animal nutrition, pharmacognosy etc. Cuticular pattern is also taxonomically useful to characterize genus and species. The cuticle is impervious to water but in grapes water diffuses out when it is transformed to sultana. It has protective function. Cutin is resistance to microorganisms and prevents the entry of the pathogen.

In many plants wax is deposited on the surface of the cuticle. This forms a powdery coating on various fruits, e.g. plum, grapes etc. and on leaves. This gives a glossy appearance to the surface of leaves and fruits (e.g. grapes). Wax is deposited either in the form of granules, rods or tubes, which form various specific patterns on the surface.

The deposition may also be in the form of projections and folds. Wax is also deposited on the inside of the pitcher of Nepenthes in the form of overlapping scales. The scales adhere to the feet of insects, which fall inside the pitcher. So the insects cannot climb out of the pitcher. The morphological form of the deposition of wax is typical for the species.

With the aid of scanning electron microscope the wax and cuticular pattern can be observed directly. The study of wax pattern on the epidermal surface is extremely useful in agricultural practices. Waxy epidermis is not wetted. So the effectiveness of fungicide and herbicide can be obtained by studying the extent of wax deposition. Wax obtained from the wax palm Coperniciacerifera is commercially used in making polishes and phonographs records.

Hairs : Hairs are present all over the surfaces of plant organs namely - roots, stems, leaves, floral parts, seeds (e.g. Gossypium) and stamens (ex. Tradescantia).

Root hair : They are present at a short distance behind the root tip of most monocots and dicots. Root hairs in some species are formed from distinct epidermal cells termed trichoblast.
Trichoblasts may be morphologically similar to other epidermal cells or they are distinguishable by their smaller size with dense cytoplasm. Trichoblast prolongs to form unicellular root hairs. The cell wall is generally thin and is covered by a thin layer of cuticle; mucilage may also occur on the surface (Fig. 12.1)

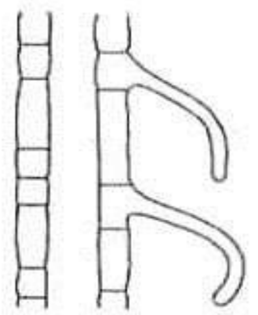

Figure 12.1

Root-hairs from short cells in *Cyperus*.

Apart from anchorage the other main function of root hairs is absorption. It has been found that the rate of absorption in the epidermal surface with and without root hairs is same. Moreover the short root hairs are more efficient in absorption than longer ones. So it appears that the longer hairs absorb the distantly situated water. The root hairs synthesize cellulose at their tips.

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Hairs other than root hairs : Hairs or trichomes are the outgrowths of epidermal cells. They are either unicellular or multicellular. Multicellular hairs may be composed of a single linear row of cells or several rows. Trichomes, either unicellular or multicellular, are classified into glandular and non-glandular hairs. The former is secretory in function and the latter is the covering hair and does not secrete. It is believed that non-glandular trichomes are protective in function and may prevent undue water loss (Fig. 12.2).

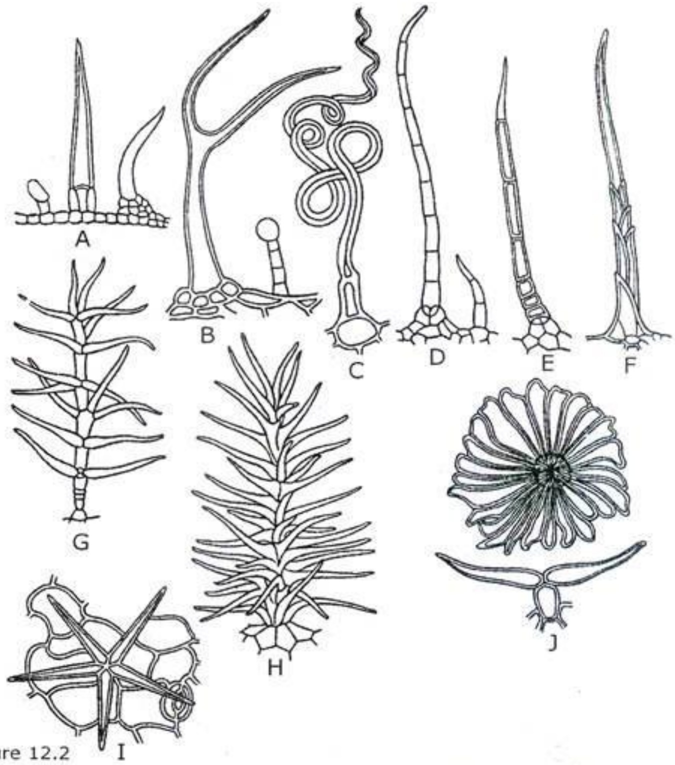

Figure 12.2

Epidermal hairs - different types. A. Sharp hairs of *Lantana*. B. Lobed hair of *Amaranthus*. C. Wooly hair of *Banksia*. D. *Lycopersicum*. E. *Helianthus*. F. *Mimosa*. G. Dendroid hair of *Platanus*. H. Dendroid hair of *Mimosa*. I. Stellate hair of *Althaea*. J. Peltate hair in surface and side view of *Olea*.

The covering trichomes may have a star like appearance (stellate hair) or a miniature tree (dendroid hair, e.g. Verbascum). In Hamamelis the covering hairs occur in tufts. Hair like projections are present in may flower petals termed papillae. The glandular hairs consist of a stalk and a head that may be unicellular or multicellular. A cuticle like structure covers the head.

The secretory substances accumulate in the sac formed between the cuticle and the cell of head. Example: Oils, resins, camphor, peppermint (e.g. Mentha) etc. The leaves of Olea have scales, which are composed of a short stalk and head, consisting of discoid plate of cells.

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Some of the epidermal cells of Mesembryanthemnm may enlarge where water accumulates. These specialized epidermal cells are termed as vesicles or bladders. Most trichomes have thin and cellulosic cell wall; lignified cell walls also occur (ex. seed coat of Strychnos nuxvoniica).

Trichomes with their different types may be of taxonomic significance. The types of trichome can identify the several species of Oleaceae and Rhododendron to some extent.

Bulliform cell : It is a group of outer epidermal cells that can be easily distinguished from the typical epidermal cells by their fan like appearance in cross section and larger sizes. The median cell of bulliform cell is the tallest and the size of the other cells, present on the two sides, diminishes gradually. The cells are thin walled, hyaline and have large vacuole.
The cells contain much water and are devoid of chloroplastids. The cell walls are composed of cellulose and pectic substances; cutin occurs on the outermost wall that is covered by cuticle. They usually form isolated strips that are situated on parallel between the veins. They are present on the outer epidermis of the leaves of Poaceae and other monocotyledons except Helobiae (Fig. 12.3).

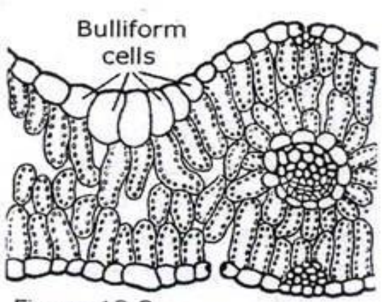

Figure 12.3

Bulliform cells in the section of *Triticum* leaf.

Opinion varies regarding the functions of bulliform cell, which are:

(i) The rolled leaf in bud unrolls with the help of bulliform cell.

(ii) The turgidity and flaccidity of bulliform cell due to water uptake and loss respectively cause the closing and opening of mature leaves.

(iii) These cells act as water reservoir.

(iv) These cells are often filled with silica and their outer walls become thick and cuticularized thus providing mechanical rigidity to leaves.

Stomata : Stoma (pl. stomata, physiologists usually call stomate) that occurs predominantly on leaves and young stems can be defined as a pore enclosed by two specialized cells - the guard cells that move to open and close the pore, and thus control gaseous exchange during transpiration, respiration and photosynthesis.

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In Greek the word stoma means mouth. 'Link and de Candole in 1827 jointly claimed to be the first to have called the pores by that name'. Stoma is reported as early as lower Devonian period (about 390 million years ago) from the extinct genera Rlnjnia, Asteroxylon, Zosterophyllum and Drepattophycus.

Structure, function and types of Stomata.

Stomata was discovered by Pfeffer& name 'stomata' was given by Malphigii. Stomata cover 1-2% of leaf area. It is minute pore present in soft aerial parts of the plant. Algae, fungi and submerged plants do not possess stomata.

Structure

(a) Stomata are minute pores of eliptical shape, consists of two specialized epidermal cell called guard cells.

(b) The guard cells are **kidney shape** in dicotyledon and **dumbell** shape in monocotyledon.

(c) The wall of the guard cell surrounding the pore is thicken and inelastic due to rest of the walls are thin, elastic and semi-permeable.

(d) Each guard cell has a cytoplasmic lining, central vacuole.It cytoplasm contains single nucleus and number of chloroplast. The chloroplast of guard cell are capable of very poor photosynthesis, because the absence of RUBISCO enzyme.

(e) Guard cells are surrounded by modified epidermal cells, known as **subsidiary** or accessory cells, which supports in the movement of guard cells.

(f) The Size and shape of stoma and guard cell vary from plant to plant. When fully open, the stomatal pore measures 3-12 in width and 10-40 in length.

(g) In many gymnosperms and xerophytic plants (plants growing in desert), the stomata are present embedded deeply in the leaves, so that they are not exposed to sunlight directly. Such deeply embedded stomata are called sunken stomata. This is an adaptation to check excessive transpiration in these plants.

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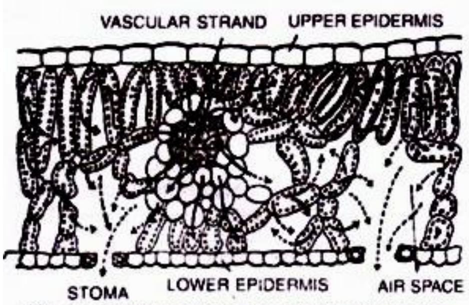

Fig. 4.2. Vertical section of leaf blade showing the passage of water vapours during transpiration

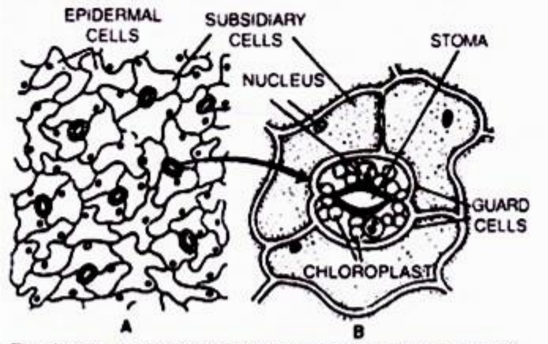

Fig. 4.3 (A). A portion of lower epidermis of leaf magnified to show stomata : (B). A stoma magnified.

Number of Stomata (Stomatal Frequency) : The number of stomata in a definite area of leaf varies from plant to plant. Xerophytes possess larger number of stomata than mesophytes. Number of stomata/sq cm. is 1000 —60,000 in different plant species. The number of stomta per unit area of leaf is called Stomatal Frequency.
Stomata frequency of trees and shrubs is higher than herbs. Stomata nearly occupy one to two percent of total leaf area when fully open. In isobilateral leaves (in monocots).approximately the same number of stomata are found on upper surface (adaxial) and lower (abaxial) surface. But in dorsiventral leaves (indicots) the number of stomata on the upper surface is much less in comparison to those found on the lower surface.

Types of Stomata : Metacalf and Chalk recognized four types of stomata on the basis of their structure-

a. Anomocytic type: In these stomata, accessory cells are absent. The guard cells are surrounded by ordinary epidermal cells, e.g., families Ranunculaceae, Cucurbitaceae, Papaveraceae and Malvaceae.

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b. Anisocytic type: In these stomata the guard cells are surrounded by three accessory cells. Of these two are larger whereas one is smaller in size.g., family Brassicaceae.

c. Diacytic type: In these stomata the guard cells are surrounded by two accessory cells. Their common walls are at right angle to the walls of guard cells, families Caryophyllaceae, Acanthaceae.

d. Paracytic type: In these stomata the guard cells are also surrounded by two accessory cells, but their common walls are parallel to guard cells, e.g., families Rubiaceae, Fabaceae etc.

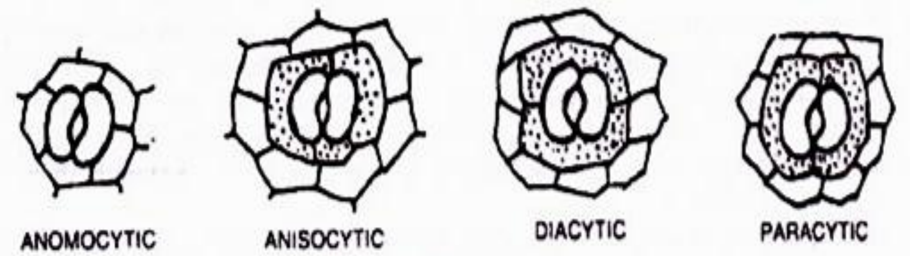

Fig. 4.4 Types of stomata.

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Structure of Stomata

The stomata consist of minute pores called stoma surrounded by a pair of guard cells. This stoma functions as a turgor, an operated valve which functions by opening and closing according to the turgidity of guard cells. The cell wall surrounding the stoma is tough, flexible and thinner. The shape of guard cells usually differs in both monocots and dicots, though the mechanism continues to be the same.

The Guard cells are specialized, bean-shaped cells, which are found surrounding the stoma and are connected at both ends. These cells enlarge and contract to open and close the stomata pores. Guard cells also contain **chloroplasts**, the light-capturing organelles in plants.

The subsidiary cells also called accessory cells. They are the accessory cells to guard cells and are found in the epidermis of plants. These cells are surrounded and supported by the guard cells and act as a buffer between guard cells and epidermal cells, which function by protecting epidermal cells against the expansions of the guard cells.

The average number of stomata is about 300 per square mm of the leaf surface.

The table given below explains the total number of stomata present on the upper and lower surfaces of leaves of different plants.

Total Number of Stomata / mm^2		
	Upper Surface	**Lower surface**
Monocotyledon		
Wheat	50	40
Barley	70	85
Onion	175	175
Dicotyledon		
Sunflower	120	175
Alfalfa	169	188
Geranium	29	179

Functions of Stomata

The main functions of stomata are:

1. Helps in the exchange of gases by opening and closing the pores in the leaves.
2. It helps to expel the excess water out from the leaves in the form of water vapour.
3. Based on the weather conditions, it closes or opens its pores to maintain the moisture balance.
4. Allows the uptake of carbon dioxide and to give out oxygen during the process of photosynthesis.
5. Stomata remain open during the day and closed at night. This closure prevents water from escaping through open pores.

Opening and Closing of Stomata

What is Stomata ?

When a leaf is examined under the microscope, we observe many tiny pores, which are collectively called stomata.

Stomata are the minute openings, generally found in the epidermis of leaves. They are typically found in plant leaves and can also be found in stems and other parts of plants. Stomata play an important role by permitting the movement of gases such as oxygen, carbon dioxide, and water vapour to diffuse between the interior and outer surface of the plant tissues.

Structure, distribution, types and function of Laticifers.

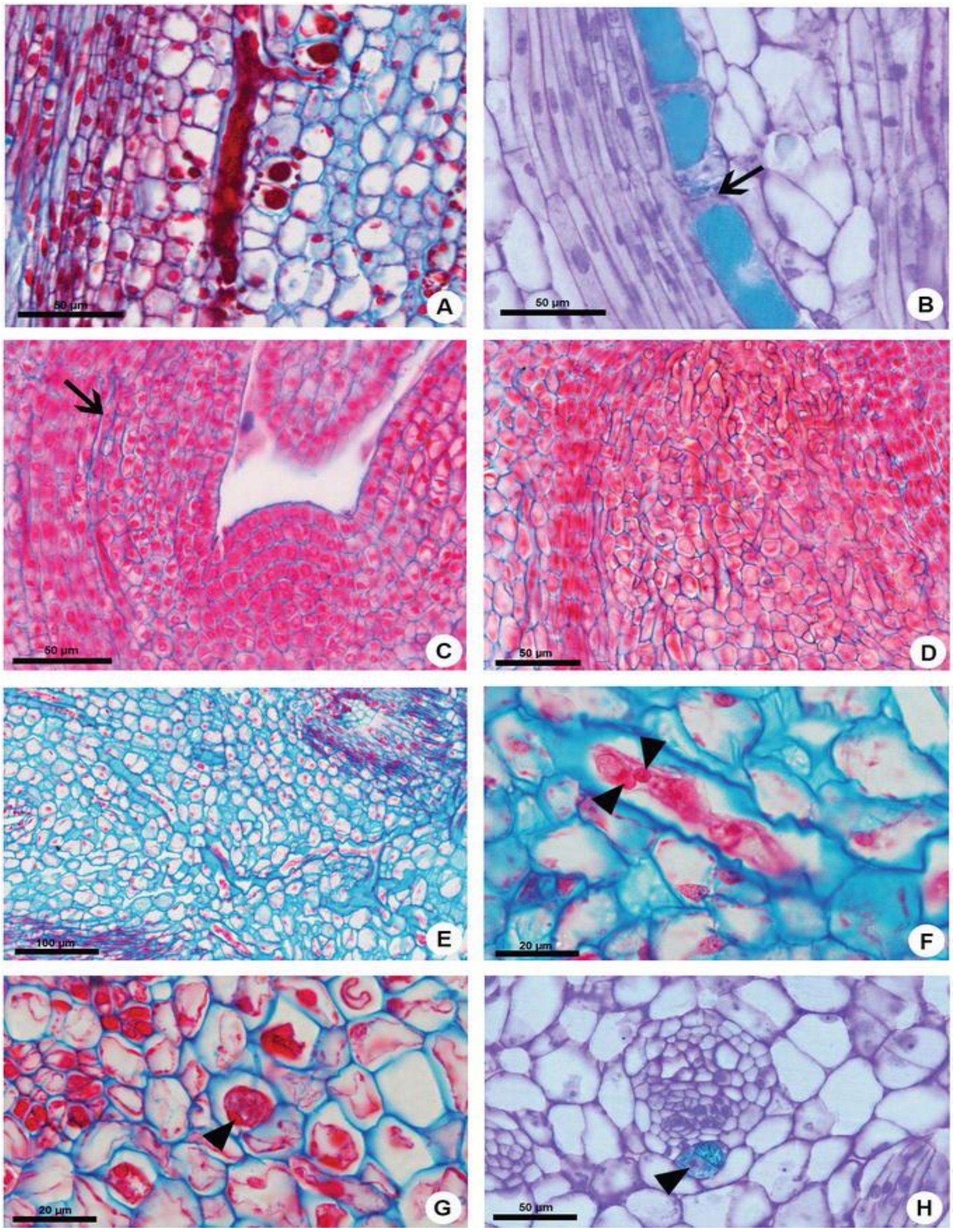
Laticifers : Laticifers are the specialised cell or row of cells that secrete the milky or watery fluid termed latex. The term encompasses the various structures like latex cell, latex vessel, latex duct, latex tube and laticiferous duct. The laticiferous duct is a tubular cavity into which latex is secreted and remains stored.

A **laticifer** is a type of elongated secretory cell found in the leaves and/or stems of plants that produce latex and rubber as secondary metabolites. **Articulated laticifers**, i.e. composed of a series of cells joined together, or. **Non-articulated laticifers**, consisting of one long coenocytic cell.

A single vegetative cell may be converted into a simple or branched latex cell. The latex ducts are also modifications of the vegetative cells into aseptated, elongated and branched structures. The latex vessel is usually an anastomosing tubular structure. It may also be simple or unbranched.

The latex vessel is formed as a result of enlargement and fusion of a group of cells. Based on origin the laticifers may be simple or compound. The simple laticifer is derived from a single cell whereas the compound laticifer originates from a longitudinal pile of cells.

The cell wall of the laticifer is non-lignified but thicker than the adjacent cells.of course, the latex cell tip is thin-walled. The cell walls of laticifersgrow in apposition and are composed of cellulose, hemicellulose and pectin.



Latex is produced within the latex vessels or cells. It is usually white and milky (e.g., Euphorbia, Asclepias, Lactuca etc.), yellow and brown (e.g.Cannabis), orange and sometimes colourless and clear (e.g. Morus, Nerium etc.). It contains many substances like sugars, proteins, alkaloids, oils, mineral salts, organic acids, terpenes, resins, rubber etc.

The latex of Euphorbia milii contains dumb-bell shaped starch grains. The latex of Carica papaya contains the proteolytic enzyme papain. The latex of Asclepiassyriaca contains the enzyme pectinase.The latex of some Euphorbia species is rich in vitamin B_1.
The laticifers, where present, may remain distributed throughout the plant body or may be confined to certain tissues. Laticifers may be non-articulated and articulated. The former, which is derived from the enlargement of a single cell, has the potentiality of unlimited and rapid growth, and elongates to form a long unbranched latex tube (e.g., Vinca, Cannabis, Urtica etc.).

In some plants (e.g.Euphorbia, Nerium etc.) the non-articulated latex tubes may be branched. The non-articulated laticifers are coenocytic and multinucleate, and also termed as laticiferous cell. There is continuity of laticifers between the shoots and branches. The laticifers grow through the intercellular spaces with the help of the enzyme pectinase secreted by the growing tips of the laticifers.

The articulate laticifers or the laticiferous vessels, consist of longitudinal pile of cells. The transverse end walls of the individual cells may remain intact or partly or totally obliterated to form a continuous tube called the latex vessel. Therefore, they are of compound origin. They occur in primary or secondary phloem and in cortex.

The articulated laticifers may remain as a single chain of cells without anastomosis -articulated non-anastomosing laticifer (e.g.Convolvulus, Allium, Musa etc.). They may also form a complex anastomosing system called articulated anastomosing laticifers (e.g., Lactuca, Papaver, Carica papaya etc.). The enzyme cellulase is found in the latex of articulated laticifers suggesting that it may be involved in the lysis of common transverse walls during development.

Latex occurs in 900 genera distributed in 20 families, mostly in dicotyledons (e.g.Apocynaceae, Asclepiadaceae, Compositae, Euphorbiaceae, Papavaraceae etc.) and in a few families of monocotyledons (e.g.Araceae, Musaceae and Liliaceae).The different types of latex are of great economic value.

The opium, a medicinally important alkaloid, is obtained from Papaver somniferum. The most important latex is rubber whose principal source is Heveabrasiliensis.The species of Palaquium yields gutta-percha. The latex of Achras sapota yields chicle, from which chewing gum is made.

Structure, distribution, functions and ecology of Nectaries.

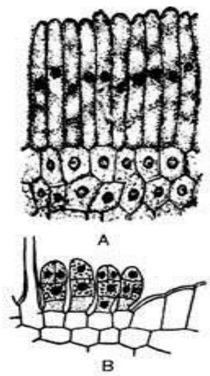


Fig. 5.63 : Nectary in sectional view. A. Nectary of *Euphorbia pulcherima*. B. Extrafloral nectary on the stipule of *Vicia* sp.

Structure : External surfaces of the plant bear several secretory structures of epidermal origin or epidermal derivatives or emergences from deeper tissues. These include glands, glandular trichomes, nectaries, osmophores, hydathodes and salt glands.

Nectary : Nectary is defined as a gland or any floral part that secretes nectar to attract the pollinators. Sometimes, it may occur on the vegetative organs and is not directly concerned with pollination. These structures are epidermal outgrowths or deeply sunken or at the level of the epidermis of the organ.
The nectariferous tissues may not form any anatomically differentiated structure known as non-structural nectaries (e.g., Dracaena reflexa leaves, bracts of Sansevieriazeylanica, tepals of Cattleyapercivaliana etc.). Histochemically, the cells of the non-structural nectaries can be distinguished. These cells show high acid phosphatase activity like the structural ones.

Anatomically and morphologically, differentiated nectariferous tissues are called structural nectaries. These structures have stalks and spe-cialisedparenchymatous secretory cells with cuticle.

The nectary cells are small, thin-walled with dense protoplasts containing dictyosomes, endoplasmic reticulum, small vacuoles and large nuclei. The structures have vascular supplies through which nectar is supplied and accumulated between the cuticle and secretory cells.

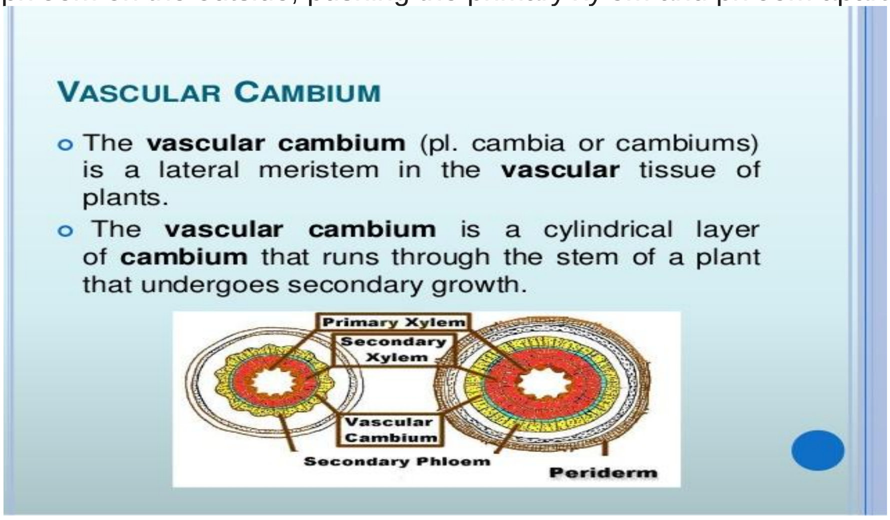
Exudation of nectar from non-structural nectaries takes place through stomata whereas in structural nectaries it takes place trough epidermal cells or trichomes directly to the outside.

Functions : The nectar contains glucose, sucrose and fructose as major components. In addition maltose, melobiose, mucilage, proteins, phosphates, mineral ions, organic acids, oxidases, sucrose, vitamins, essential amino acids, etc. are also found to be present in the nectar. The essential amino acids attract the insects for pollination.

Distribution : The extra floral nectaries are very common in dicots and much less in monocots. It rarely occurs in Poaceae (e.g., Andropogon and Eragrostis). In dicots it is present on all the organs.

Structure and activity of Vascular Cambium.

Structure and function. The **cambium** present between primary xylem and primary phloem is called the
intrafascicular **cambium** (within **vascular** bundles)The **vascular cambium** produces secondary xylem on the inside of the ring, and secondary phloem on the outside, pushing the primary xylem and phloem apart.



Vascular Cambium : Origin and Activities

Origin of Vascular Cambium :

In stems the vascular cambium and the primary vascular tissues differentiate from procambium. Procambium develops from the derivative cells of apical meristem. Transverse sections of a growing vegetative shoot apex reveal the presence of a cylinder of cells that are highly cytoplasmic and more densely staining.

This ring of cells is regarded as a residuum of the meristematic tissue of apical meristem and so termed as residual meristem. Within the residua] meristem more densely staining regions are present and these regions have a topographic relationship with leaf primordia. This region constitutes procambium that develops as leaf trace.

The remainder of residual meristem forms the interfascicular parenchyma. In longitudinal section of vegetative apical shoot of angiosperm and gymnosperm it is observed that the procambial ring or strand is continuous and develops acropetally (Figs. 23.2 & 23.3).

Procambial strands exhibit two waves of differentiation, that is, differentiation of protophloem on the peripheral side and differentiation of protoxylem towards the inner edges in normal angiosperm.

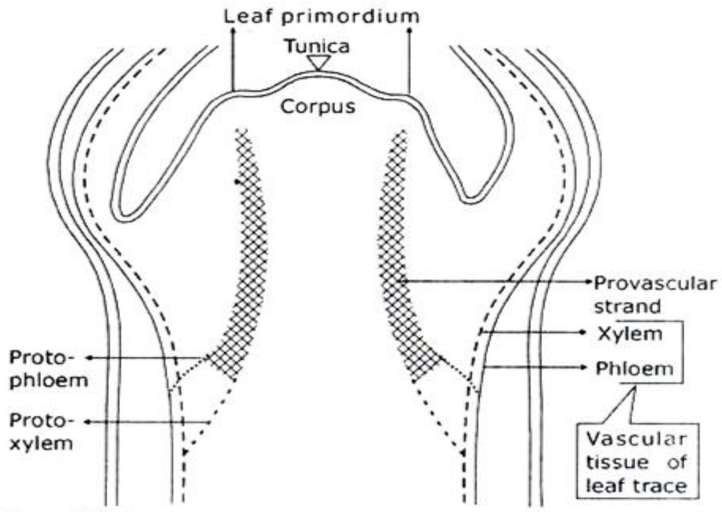


Figure 23.3

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 procambialmeristematic 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 it is customary to designate the tissues 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.

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In the normal dicotyledonous root the vascular cambium is wavy.There is no distinction between fascicular and interfascicularcambium.The ridges of the wavy cambium occur overarching the protoxylem while the furrows lie below the primary phloem.

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.

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 (Fig. 23.4).The fusiform cambial initial continually cuts of new cambial derivatives to the exterior and to the interior.

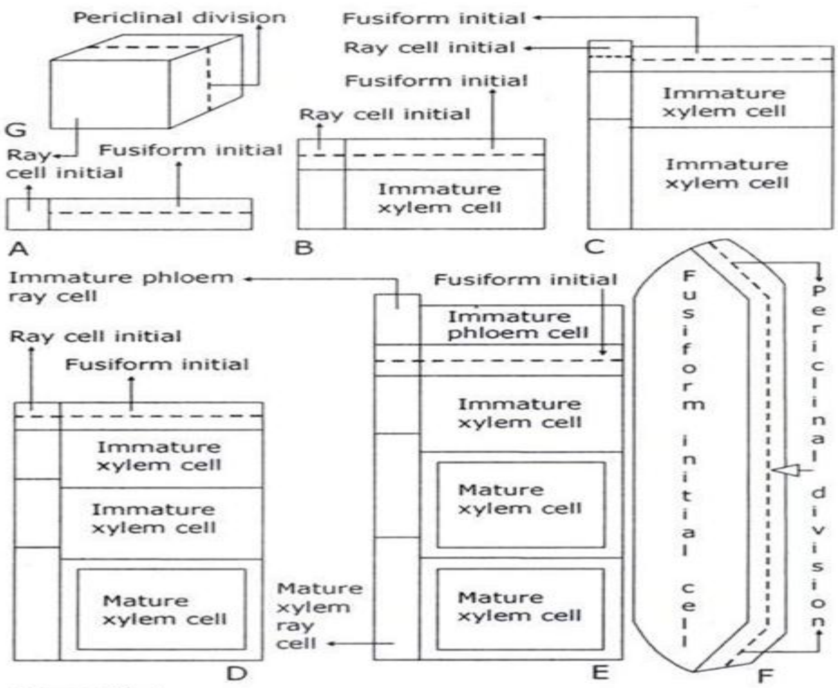

Figure 23.4

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

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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 in the secondary xylem of conifers where the secondary xylem is largely composed of tracheids. In angiosperms (Fig. 23.5) such radial files of cells are less conspicuous due the formation of vessels. Vessels often increase greatly in diameter and as a result distortion of files occurs.

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, trachea and xylem fibre of xylem and sieve tube, companion cell and phloem fibre of phloem as they compose the axial system of plants.

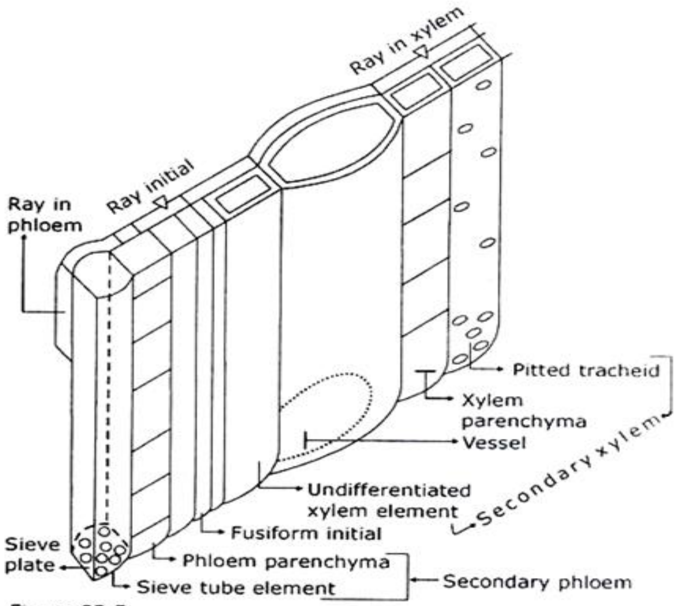

Figure 23.5
A diagrammatic interpretation of the production of secondary vascular tissues by cambium

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.

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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.

In a cambial zone only one layer of true cambial initials is present. Periclinal division in a cambial cell forms two cells. One of the daughter cells differentiates into secondary xylem or —phloem.

The other cell retains its meristematic properties. This process continues throughout the life of a plant and therefore the division of cambium is limitless. This virtual immortality of cambial cells ideally displays the 'continuing meristematic residue' of Newman (1965).

The derivatives of cambial initials are incipient vascular tissues. They differentiate into secondary xylem cells and secondary phloem cells. 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 Robiniapseudacacia.

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 Pinusaristata 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.

Formation of the fusiform cambial initial occurs in the following ways:
i. Fusiform initials in a storied cambium divide by anticlinal divisions and thus new initials are added to cambium.

ii. Short fusiform initials divide by radial anticlinal divisions where the partition walls occur parallel to long axes (Fig. 23.6A-C).

iii. 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.

iv. The elongation and intrusive growth of ray cell initials may form new fusiform initials. The elongation of ray cell initials occur parallel to the long axis of plants (Fig. 23.6D-E).

Fusiform initials give rise to ray initials in the following ways:
i. 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).

ii. 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).

iii. Fusiform initial cuts off a single cell at its end (Fig. 23.6H).

iv. A fusiform initial is reduced to a ray cell initial (Fig. 23.6I).

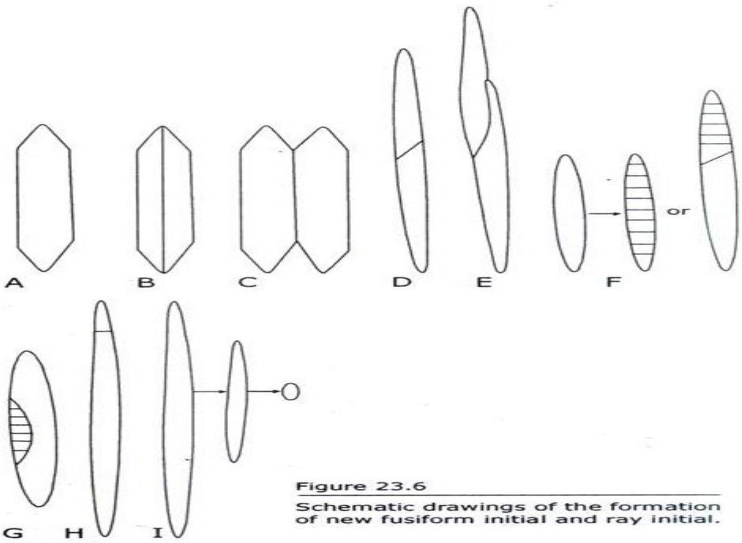

Figure 23.6
Schematic drawings of the formation of new fusiform initial and ray initial.

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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).

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.

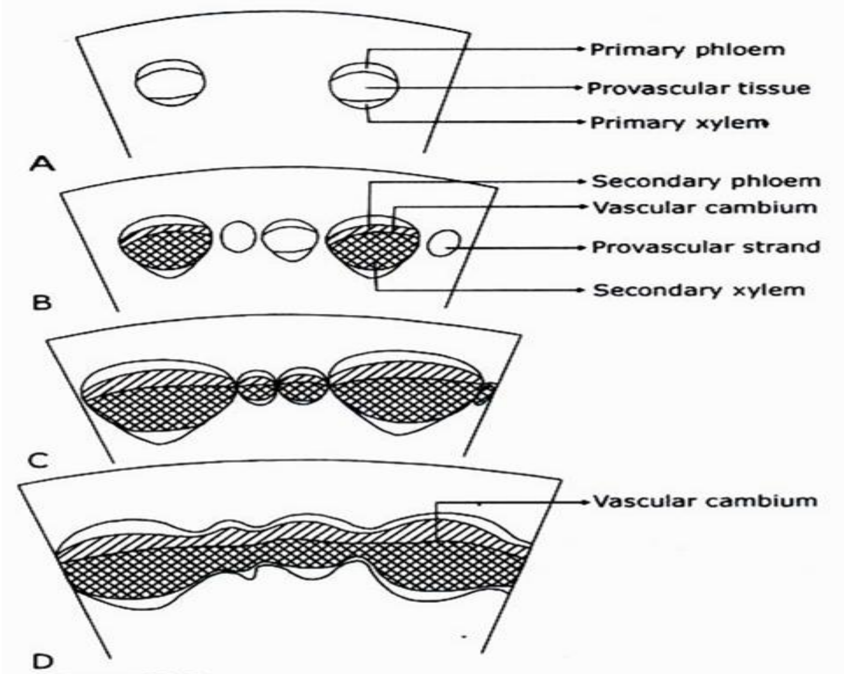

Figure 23.7

Diagram illustrating stages of formation of provascular strand, vascular cambium and secondary vascular tissues. Secondary xylem = crosshatched. 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.

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 interfascicularcambium differentiate into parenchyma cells only.This type of cambial activity is regarded as abnormal.

Anomaly in the activity of cambium is also observed in Serjania, Paullinia. Thinouia etc. where in stems the cambium ring is split into several isolated segments that form separate vascular strands,often in a regular pattern.

In Bauhinia stem different sectors of cambium donate unequal amount of secondary xylem and as a result the stem becomes lobed. In Bignonia stem symmetrically located segments of cambium cease to form xylem inwards and

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form phloem in excess outwards. As a result xylem becomes separated by radial slits.

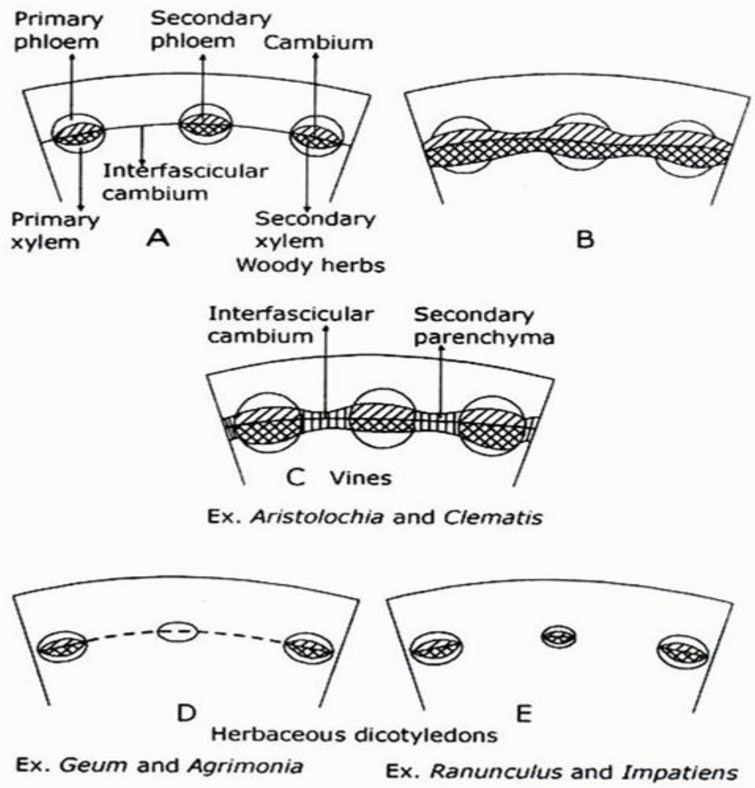

Figure 23.8
Diagram showing fascicular cambium, formation of interfascicular cambium, formation of secondary xylem (= crosshatched) and secondary phloem (= obliquely hatched).

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Accessory cambium : Accessory cambium develops both in stems and root. In the stem of Amaranthus, Boerhaavia, Mirabilis etc. this secondary cambium originates on the peripheral side surrounding vascular bundles. Accessory cambium divides and the derivative cells differentiate into conjunctive tissue and secondary vascular bundles. In Tecoma stem two arcs of accessory cambium develop at the peripheral margins of pith.

The cambium produces vascular tissues that have inverse orientation, i.e. secondary xylem on the peripheral side and secondary phloem (intraxylary phloem) on the inside. Accessory cambia also develop in monocotyledon (ex. Dracaena). In Dracaena accessory cambium forms thin-walled conjunctive tissue and leptocentric vascular bundles towards the inner side.

In the root of Beta vulgaris concentric rings of accessory cambia originate in succession outwards. Most of the derivative cells store nutrients and as a result Beta root swells.

Cheadle (1937) reported the existence of vascular cambium in monocotyledon. The cambium occurs at the peripheral region of the stem. The peripheral parenchyma divides to form the vascular cambium. The cambial cells are narrow and elongated, ex. Agave.

The cells may be fusiform, polygonal or rectangular in shape. The cambium divides and the inner derivatives differentiate into vascular bundles, consisting of both xylem and phloem. The peripheral derivatives form parenchyma only. The vascular bundles, thus formed, remain embedded in the ground parenchyma.

Cork Cambium : Cork cambium, also known as phellogen, is a secondary lateral meristem. It originates from the permanent cells of epidermis, hypodermis, cortex and phloem by dedifferentiation.
The cells of phellogen are compactly set without any intercellular spaces and rectangular or radially flattened in cross- sectional view.In longitudinal section they are rectangular or polygonal and sometimes irregular in outline. Each cell of phellogen is highly vacuolate and may contain chloroplast and tannins.

The phellogen divides periclinally and the derivative cells differentiate into peripheral phellem (also called cork) and inner phelloderm. Cork cells have suberized cell walls that are impervious to air and water,and have protective properties. Phellem, phellogen and phelloderm are collectively called periderm.Periderm forms a protective layer in stems and roots.

The following factors influence the cambial activity:
I. Hormone : It was first shown by Jost, 1893 that the activity of stem-cambium is greatest just below the growing leaves. In later years after the discovery and identification of indole-3-acetic acid (IAA) and after various experiments it was definitely concluded that the stimulus that activates the cambium is hormonal in nature.
Hormone is produced in young buds and leaves and it is translocated downwards thus stimulating the cambium to divide. It was previously mentioned that the activity of cambium is highest in spring in the trees of temperate regions. It gradually declines as summer advances. In spring new buds develop where hormones are produced.

Hormones move basipetally and then the growth activity of cambium is initiated and promoted. Later researches reveal that the interactions among IAA, gibberellic acid (GA) and 6-furfurylaminopurine (Kinetin) stimulate the division of cambium. In an experiment the shoots of Acer pseudoplatanus were completely disbudded. It was treated with IAA only and the formation of xylem was observed.

II. Gravity: In the branches of gymnosperm and angiosperm a special type of wood is formed termed reaction wood. In gymnosperm branches the reaction wood is formed on the lower side and is specially called compression wood. In the branches of angiosperm the reaction wood is formed on the upper side and is specially termed as tension wood.The reaction wood is the collective term of tension wood and compression wood.
Various experiments reveal that these unequal proportions of wood are formed with respect to gravity. Gravity is the stimulus that causes the formation of reaction wood and there are ample evidences that auxin is present behind the process. In an experiment plants were grown in klinostat and it was noted that no reaction wood is formed. This proves that reaction wood is formed in response to gravity.

III. Day length:
In short days late wood is formed only, e.g. Robinia. In this wood no vessels are formed. The vessels, if formed, are few in number and with small diameter. In long days early wood is formed. In this wood many vessels are developed and they have large diameter. In long days tracheids with large diameter are formed in conifers in contrast to short days where tracheids with narrow diameter are formed.
In long days the needles of conifers elongate and there is no doubt that this is associated with auxin production. The production of auxin promotes to form tracheids with large diameter. In an experiment short day (i.e. long night) plants were given a low intensity of light for a short time during the long night period. It was observed that tracheids of wide diameter were formed.

It indicates that the cambial activity is influenced by day length and it is a true photoperiodic phenomenon.Temperature influences the activity of cambium.

IV. Pressure:
The vascular cambium always remains compressed by the tissues present on internal and peripheral side of it. It is needed for the normal functioning of cambium. In an experiment with Pinus strobus and Populustrichocarpa the pressure was released on the peripheral side. Releasing a strip of bark from the tree by incisions while the apical end is still attached with the tree did this.

Structure and function of Periderm.

The **origin** of the cork cambium is variable depending on the species and plant part. In stems of most dicots and gymnosperms, the first **periderm** originates in a layer of cortical cells immediately below the epidermis. In many species it originates in the epidermis.The walls of the cork cells may also become lignified.

Definition of Periderm : In roots and stems having secondary growth, the epidermis is replaced by a protective layer of secondary origin known as **periderm**. It generally develops in gymnosperms and dicotyledonous axis and is rarely produced in leaves or monocotyledons. The periderm is also formed along surfaces exposed after abscission of plant parts, such as leaves or branches. It also evolves as protective layer near injured parts (wound periderm).
The term periderm is more distinct than bark. The latter designates all tissues outside the vascular cambium. In secondary state, it consists of secondary phloem and all tissues outside it. It can be distinguished into outer non-living and inner living parts. The functional phloem is the innermost part of the living bark

Structure of Periderm : The periderm consists of the phellogen or cork cambium, the meristem that produces the periderm; the cork or phellem, the protective tissue produced outside by the phellogen, and the inner cortex or phelloderm, the living parenchyma, formed inside by the phellogen. Because of the formation of cork, the tissues outside it usually die out.
The phellogen is simple in structure and it has only one kind cells.They appear as continuous tangential layer (lateral meristem) of rectangular, radially flattened cells in cross section. In longitudinal section they are rectangular or polygonal in outline.

The phellem or cork cells are often prismatic in shape and can be elongated vertically, radially or tangentially to form irregularly shaped structures. These are compactly arranged and absent inter-cellular spaces.These are dead cells at maturity.The cell walls are suberized.

The suberin, a fatty substance, generally occurs as a distinct lamella that covers the original primary cellulose wall. The thickness of cells walls of cork is variable. In thick-walled cells lignified cellulose layer exists on the inner side of suberin lamella. The walls of cork cells are brow or yellow in colour, while coloured resinous or tanniferous material can be filled in the lumina.

The commercial cork generally has thin walls and air-filled lumina.It is highly impervious to water and resistant to oil. It has thermal insulating quality and is light in weight. The mature cork of type is also a resilient and compressible tissue. These properties also make it useful to protect the plant parts.

In many species viz., Rhododendron maximum, the phellem includes non-suberized cells, called phelloid cells together with cork. These may also be thin or thick walled. When thick walled these are known as sclereids.

The phelloderm is a typical parenchyma which may be distinguished from other parenchyma by being present in the same radial files as the phellem cells.

Polyderm : It is a special kind of protective tissue developed from phellogen in the same way as the cork. It is observed in roots and underground stems of certain families like Myrtacea, and Rosaceae etc. It includes alternating layers of one cell deep of partly suberized cells and layers many cells deep of non-suberized cells. Its outermost layer is the only dead layer and it can attain a thickness of up to 20 or more cell layers.

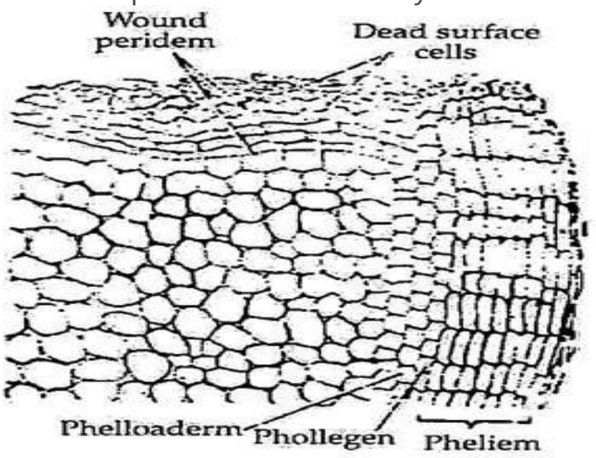

Fig. 7.1. Periderm of root of sweet potato.

Periderm:The first periderm commonly appears during the first year of growth of stem and root. In stem most usually it originates in the sub-pepidermal layer. In some species, the first periderm appears rather deep in the stem, usually in the primary phloem viz., Berberis, and Vitis etc. In roots, in other word, the first periderm originates in the pericycle. In some cases, where the root cortex serves for food storage, it can originate near the surface also. The subsequent periderms may appear the same year or later in the successively deeper layers beneath the first, i.e., from the parenchyma of the phloem, including ray cells.

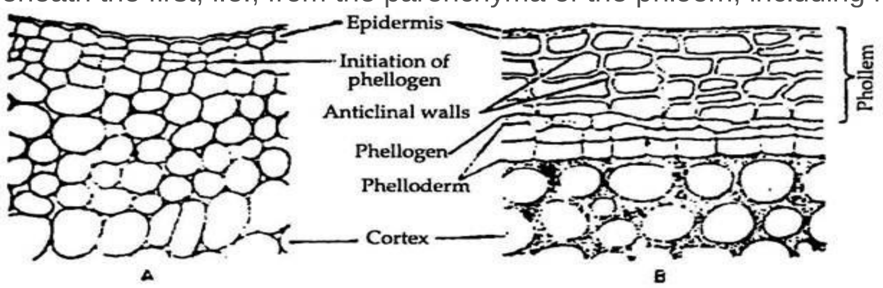

Fig. 7.2. Origin of periderm is *Pelargonium* stem as seen in cross section.

The first phellogen is generally initiated uniformly around the circumference of the axis. Sometimes, e.g., roots in localized area which becomes continued afterwards. The subsequent periderms appear as discontinuous but overlapping layers. These can finally appear as continuous, or partly so, layers, around the axis.

The phellogen arises from living cells which are potentially meristematic. In these cells, the initiating divisions can start in presence of chloroplast and orgastic substances, viz., starch, tannins. But gradually these structures disappear. The phellogen is initiated by periclinal divisions and it forms the phellem and phelloderm by the same type of divisions.

The exact sequence of divisions in the initiating periderms can be different even in the plants of same species growing under various conditions. Some preparatory divisions take place before the phellogen is defined. The phellogen is usually the outer layer of the two produced by periclinal division.

The activity of the phellogen is more on the outside and thus, the amount of phelloderm formed is generally very small, sometimes restricted only few layer of cells. A given phellogen cell usually produces a few cork cells every year. There may or may not be certain difference in the size of cells formed during earlier part of the season or later part of the year.

On the basis of manner of function, two kinds of barks are distinguished—scale bark and ring bark. The former occurs when subsequent periderms exist in restricted overlapping strata, each cutting out scale of tissue, e.g., Finns and Pyrus etc. Ring bark results from the formation of successive periderms approximately concentrically around axis, in the produce of sheets e.g.Vitis, and Lonicera, etc.

Parts of Periderm:

I. Wound Periderm : The wound periderm is similar to normal periderm in origin and cellular structure. They vary only in time and place of origin, the wound periderm being restricted only to the injured areas. Its formation is preceded by a sealing of the newly exposed surface by scar (Cicatrice) tissue. This tissue consists of dead (necrossed) cells on the surface and living cells beneath, which become suberized and lignified to form the Closing layer. Wound phellogen arises beneath the closing layer and produces the cork cells on the outside and the parenchyma on the inner side.

At the injured parts the periderm is peeled off to the living cells underneath. The cells so exposed die and a new periderm arises below them. Such reaction is made use in commercial cork production of oak, where the first periderm is of inferior quality, the latter formed cork is of superior quality.

Protective Tissue in Monocotyledons:

A periderm similar to that of dicotyledons is rarely formed in the monocotyledons. In most of these plants the epidermis is permanent and thus, the surface layers are not replaced. In some monocotyledons e.g., Aloe, coconut, periderm similar to that of dicotyledons is produced.

The process of formation, however, is different. The parenchyma cells in successively deeper layers divide several times periclinally and their products get suberized. This tissue is known as storied bark, due to its storied appearance as in transactions.

II. Lenticels: The limited part of the periderm with more active phellogen producing a tissue with intercellular spaces can be called a lenticel. The phellogen in this part itself also has intercellular spaces. Due to this special structure the lenticels are used for entry of air through the periderm. The lenticels are commonly produced in stems and roots.
The protrude out of the surface of axis. Their size is also variable, becoming even up to 1 centimeter. Generally they are irregularly distributed but sometimes they exist in vertical rows opposite the rays.

The phellogen in the lenticels is a continuation of the rest but is bent inwards in this area. The loose tissue produced outside is called filling tissue or complementary tissue. On the inner side the phelloderm is produced in the normal fashion (Fig. 7.3.).

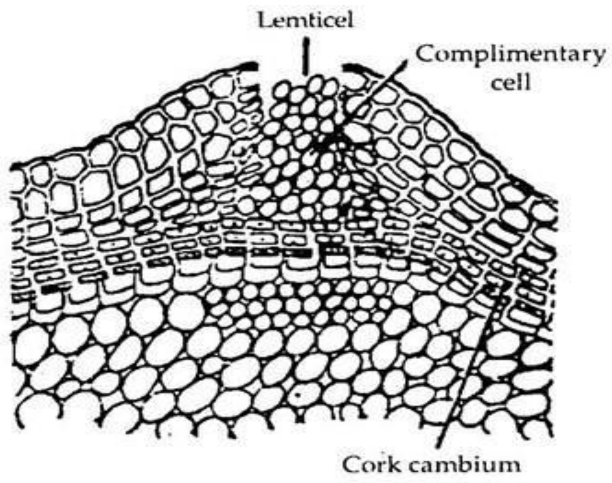

Fig. 7.3. Lenticel.

Function : (1) Its main function is to protect the underlying tissues from • Desiccation • Freezing • Heat injury • Mechanical destruction • Disease
(2) Loss of epidermis. Bounding tissue restricting the pathogen & insects.
(3) Allowing gaseous exchange through lenticels.

Secondary growth of stem of *Leptadenia*and

Anatomy of Leptadenia – Stem (Family – Asclepiadaceae)
Epidermis:
1. Outermost, single-layered epidermis consists of many barrel-shaped cells arranged compactly.

2. The cells are covered externally by thick cuticle.

Cortex:
3. It consists of hypodermis, chlorenchyma and endodermis.

4. Hypodermis follows epidermis and consists of thin walled, parenchymatous cells arranged in one to three layers.

5. Chlorenchymatous layers (3 to 6 or more) are present inner to the hypodermis. The cells are filled with chloroplasts and show many intercellular spaces.

6. Endodermis is the innermost layer of cortex consisting of barrel shaped cells, filled with starch grains. The cells lack characteristic casparian strips.

Pericycle:
7. A big zone of pericycle is present below the endodermis consisting of parenchymatous cells.

8. It is interrupted by the sclerenchymatous patches at certain intervals.
Vascular System:
9. It consists of primary phloem, secondary phloem, cambium, secondary xylem, interxylary phloem, primary xylem and intraxylary phloem.

10. A ring of vascular bundles is present in the primary state which are conjoint, bicollateral, open and endarch.

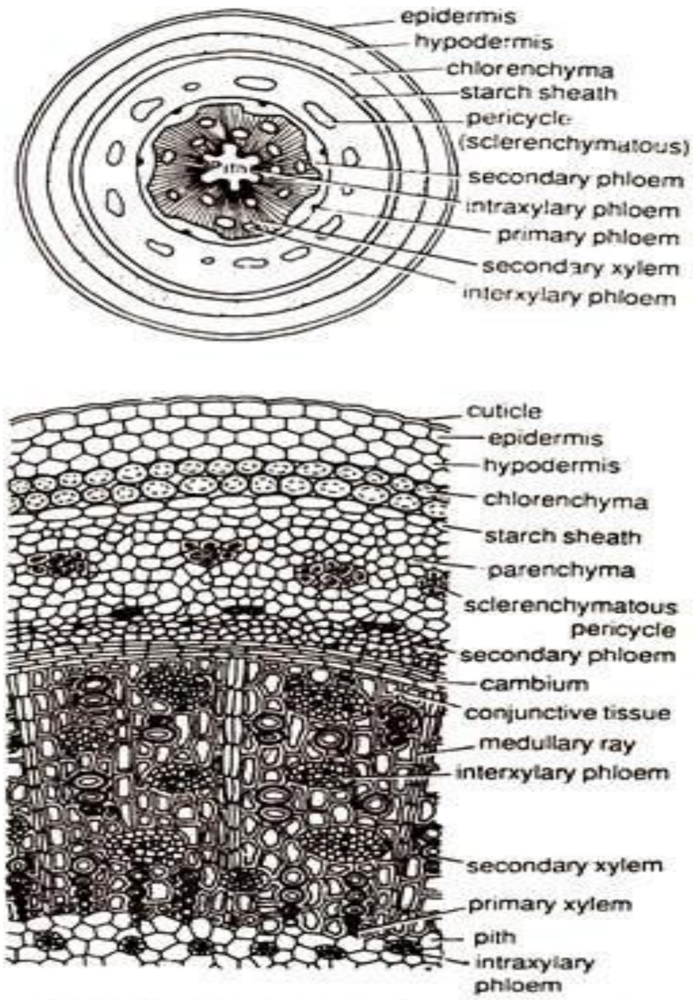

Fig. 120. *Leptadenia* : **Upper – T. S. stem (diagrammatic);**
Lower – T. S. stem (A part cellular).

11. Primary phloem is present in patches at certain places.
12. Secondary phloem ring is present inner to pericycle and consists of sieve tubes, companion cells and phloem parenchyma with no phloem fibre.

13. Cambium consists of thin-walled, brick shaped, actively dividing cells arranged in one layer but later on new cells are cut off and it becomes multilayered.

14. Secondary xylem zone consists of xylem vessels, tracheids and xylem parenchyma. The zone is traversed by many secondary medullary rays.

15. Many patches of interxylary phloem or included phloem are present in the secondary xylem cylinder. Their development is centripetal.

16. Primary xylem consists of protoxylem and metaxylem. The protoxylem is endarch and present near the pith.

17. Intraxylary phloem is present in the form of patches at the periphery of the pith.

Pith: It is thin walled and parenchymatous.
Abnormal Secondary Growth:
Due to the irregular activity of the cambium at certain places, the secondary phloem is formed towards inner side instead of secondary xylem. Other adjacent cambium cells are normally producing secondary xylem towards inner side.

After some time the cambium resumes its normal activity and thus forms many patches of secondary phloem in the secondary xylem. These are called interxylary phloem or included phloem patches Internal or intraxylary phloem is the primary structure of the primary bicollateral bundles.

Identification:
(a) 1. Presence of vessels in the xylem.

2. Vessels have perforated end walls with scalariform and regularly arranged holes. (Angiosperms)

(b) Conjoint, collateral, open and endarch vascular bundles. (Stem)

(c) Vascular bundles in a ring.

2. Presence of cambium. (Dicotyledones)

Boerhaavia

Anatomy of Boerhaavia – Stem (Family – Nyctaginaceae):
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 : Inner to the endodermis is present parenchymatouspericycle but at some places it is represented by isolated patches of sclerenchyma.

Vascular System: 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.

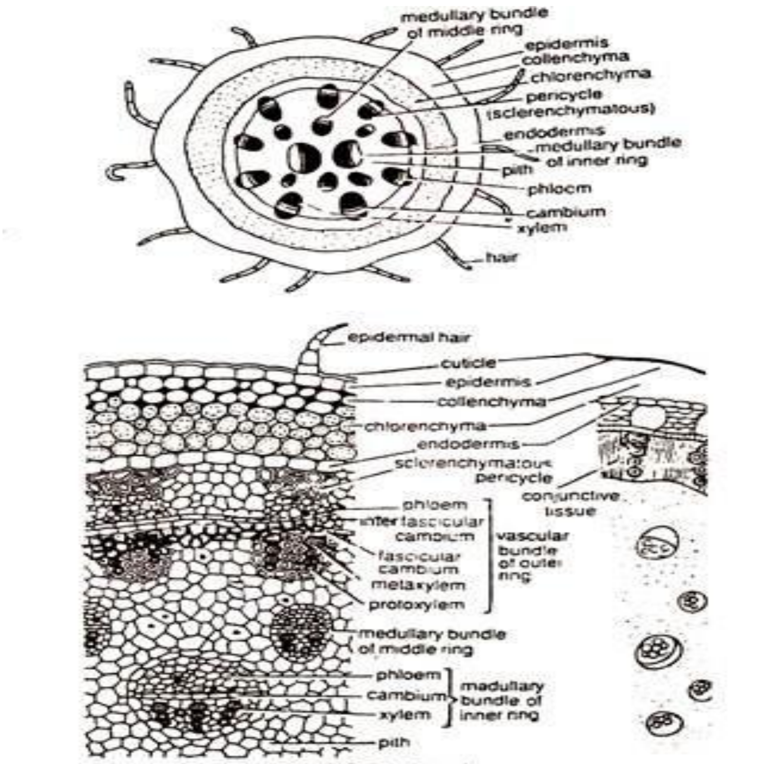

Fig. 119. *Boerhaavia*
Upper – T. S. stem (Diagrammatic); Lower Left – A part of young stem (magnified); Lower Right – A magnified part of old stem.

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: It is well developed, parenchymatous and present in the centre.
Identification:
(a) Presence of vessel in the xylem. (Angiosperms)

(b) 1. Cortex is well-differentiated.

2. Vascular bundles are conjoint, collateral,open and endarch.(Stem)

(c) 1. Vascular bundles are present in ring.

2. Well-developed secondary growth.

3. Well-defined pith. (Dicotyledones)