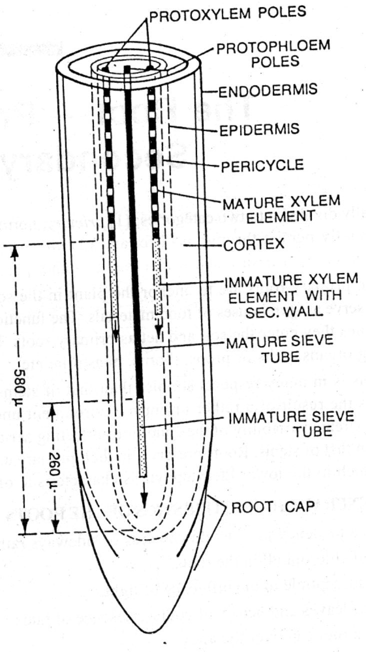


Fig. 9.1. The root. L.S. of a root tip of tobacco. (After Esau).

EPIDERMIS

The epidermis is also known as epiblema or piliferous layer. In most of roots, root hairs develop from some of the epidermal cells at a little distance from the apical meristem. The cells, giving rise to root hairs are known as *trichoblasts*. In the roots of the grass (*Phleum*), trichoblasts are formed by unequal division, of a cell of the immature epidermis, the protoderm. The trichoblast is the distally situated cell of this division. Root hairs are outgrowths of single cells, and function both in the absorption and in anchorage. Root hairs are usually eventually sloughed off, but occasionally they are persistent. Electron microscopy reveals (Leech, Mollenhauer and Whaley, 1963) that the wall of emerging root hair is a continuation of only the inner component of the wall of the epidermal cell which gives rise to it. In some species, root hairs are formed from special cells which are dintinct in size and metabolism from the neighbouring epidermal cells. These cells are known as *trichoblasts*. In other species, root hairs may develop from a whole row of cells, which stain more densely than their neighbours.

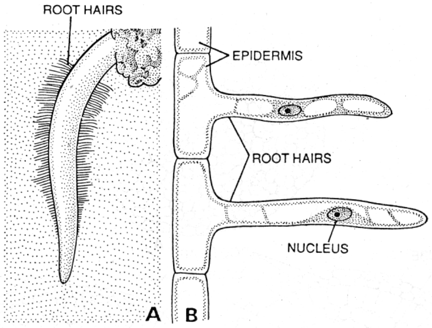


Fig. 9.2. Root hair. A, young seedling of radish with root hairs developing acropetally; B, highly magnified mature root hairs with vacuolated cytoplasm.

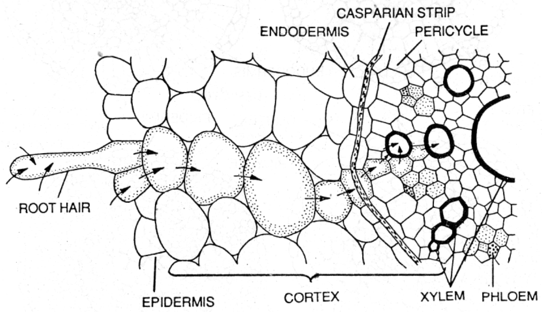


Fig. 9.3. Function of root. In this diagram the arrows indicate the movement of water and salts absorbed from the soil by root hair.

In the aerial roots of certain epiphytic orchids a multiple epidermis, or *velamen* is present. This tissue is derived from the epidermal initials and may be several cells thick. The cells are dead and devoid of contents, the cell walls are strengthened with bands of lignin. On the inner side of the velamen there is a specialized layer of cells which is derived from the periblem and not the dermatogen, and may therefore be considered as the outermost layer of the cortex, the *exodermis*. This layer is composed of alternating long and short cells; the long cells become thick-walled on their radial and outer tangential surface, but the small cells remain thin-walled and are called *passage cells*. The velamen is thought to function as a protective tissue, preventing undue water loss from the delicate cortical cells of the exposed aerial root. Formally this was believed that the cells of the

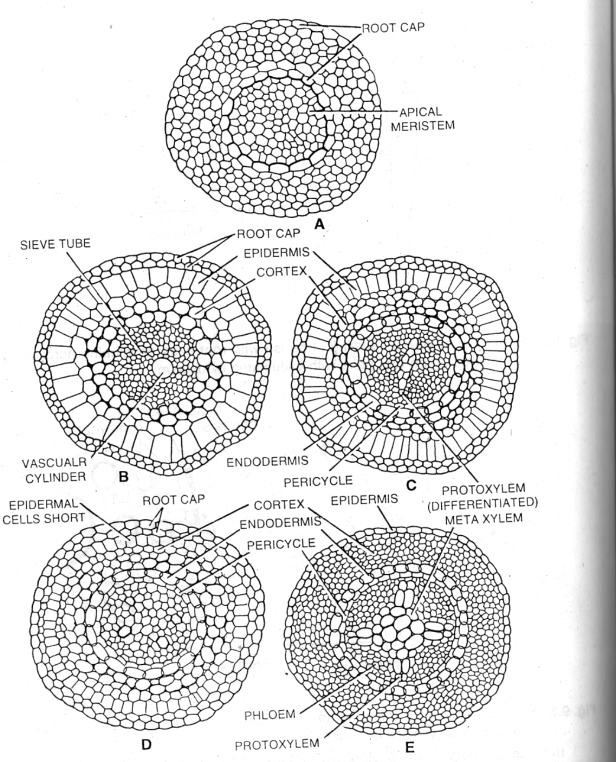


Fig. 9.4. Tissue differentiation in root. Cross sections at various levels of root showing tissue differentiation. A, T.S. root apex showing apical meristem and root tip; B, T.S. showing root cap, epidermis cortex and elements of sieve tubes; C, endodermis, pericycle, sieve elements and xylem elements are seen; D—E, show later stages of development.

velamen also absorbed and conserved water drawn from the atmoshphere, but recent experiments show that the mature velamen and exodermis are nearly impermeable to water and solutes.

CORTEX

In most roots the cortex is parenchymatous. In some roots, the cells of the cortex are very regularly arranged, both radially and in concentric circles. Conspicuous intercellular spaces may be present, and especially evident in aquatic species, where they form a type of aerenchyma. The cortical cells often contain starch, and sometimes crystals. Sclerenchyma is more common in the roots of monocotyledons than those of dicotyledons. The characteristic trichosclereids are found in the roots of *Monstera*. Collenchyma is occasionally present in roots (*e.g.,Monstera*). The outermost layer or layers of the cortex, just beneath the epidermis may be differentiated as an *exodermis*, a kind

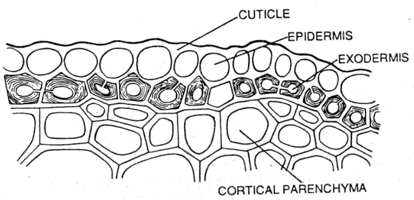


Fig. 9.5. The root. T.S. of the outer part of the *Smilax* root showing a thick-walled exodermis beneath the epidermis. The passage cell of exodermis is thin-walled.

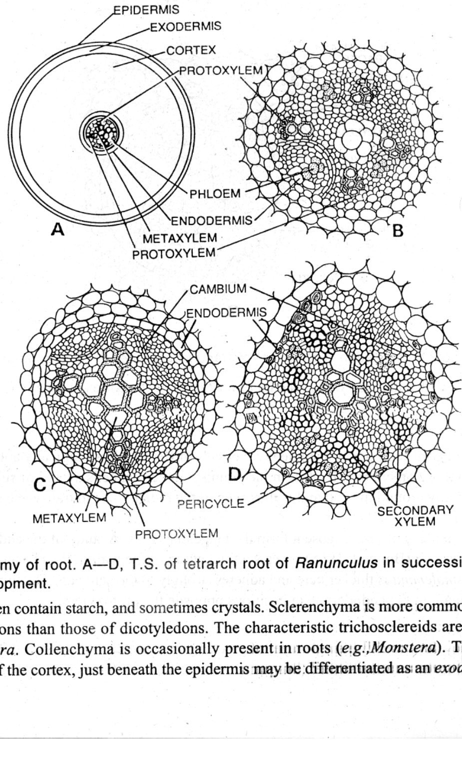


Fig. 9.6. Anatomy of root. A—D, T.S. of tetrarch root of *Ranunculus* in successive stages of development.

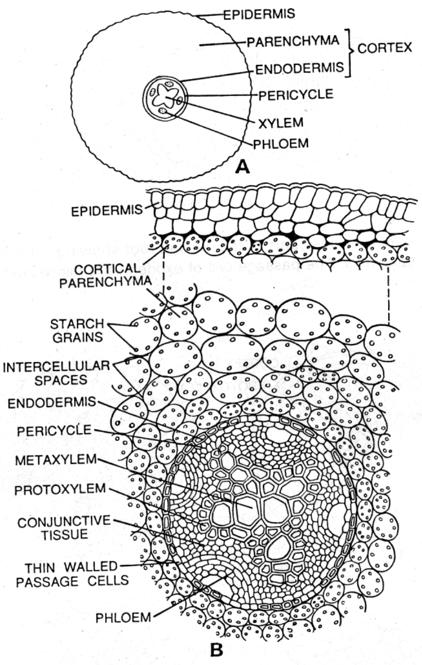


Fig. 9.7. Root of dicotyledon. T.S. of root of *Ranunculus repens*— A, diagrammatic; B, detail.

of *hypodermis*, with suberized walls. The innermost layer of the cortex is usually differentiated as an *endodermis.*

ENDODERMIS

The endodermis comprises a single layer of cells differing physiologically and in structure and function from those on either side of it. In the young endodermal cells a band of suberin, *Casparian strip*, runs radially around the cell and is thus seen in the radial walls in transverse sections of roots. This suberin deposit, to which the protoplast of the cell is attached, is continuous across the middle lamella of the radial walls, but is absent from the tangential walls. A study of the endodermis with the electron microscope (Bonnett, 1968) reveals a thickening of the wall in the region of the Casparian strip. The *plasmalemma* is thicker here and adheres strongly to the cell wall. The thin-walled *passage cells* often remain in the endodermis in positions opposite the protoxylem.

PERICYCLE

The pericycle is usually a single layer of parenchymatous cells lying just within the endodermis and peripheral to the vascular tissues. The pericycle has a capacity for meristematic growth, and gives rise to lateral root primordia, parts of the vascular cambium, and usually the meristem which produces cork, the phellogen. The pericycle is sometimes called pericambium.

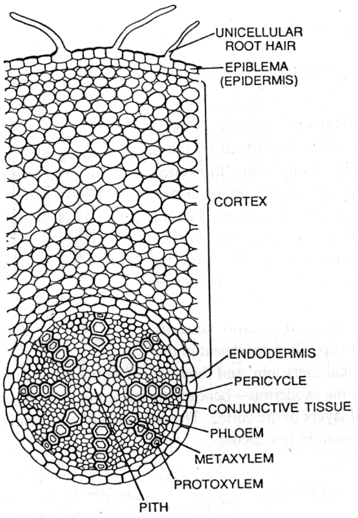


Fig. 9.8. Structure of root. T.S. of a typical monocotyledonous root.

VASCULAR SYSTEM

The vascular system of the root as seen in transverse section consists of a variable number of triangular rays of thick-walled, lignified tracheary elements, alternating with arcs of thin-walled phloem. In the root, the xylem and phloem do not lie on the same radius. The xylem may form a solid central core, or there may be a parenchymatous or sclerenchymatous pith, as in the roots of many monocotyledons. Roots with 1, 2, 3, 4, 5 and many arcs of xylem are respectively called monarch, diarch, triarch, tetrarch, pentarch and polyarch. The xylem is exarch, *i.e.*, protoxylem lies towards periphery and metaxylem towards the centre. The xylem is always centripetal in its development. The phloem bundle consists of sieve tubes, companion cells and phloem parenchyma. The protoxylem consists of annular and spiral vessels and metaxylem of reticulate and pitted vessels.

The parenchyma found in between xylem and phloem bundles is known as *conjunctive tissue*. The pith may be large, small or altogether absent.

ANATOMY OF DICOTYLEDONOUS ROOTS

The important anatomical characteristics of the dicotyledonous roots are as follows:

1. The xylem bundles vary from two to six number, *i.e.*, they may be diarch, triarch, tetrarch, pentarch or hexarch.

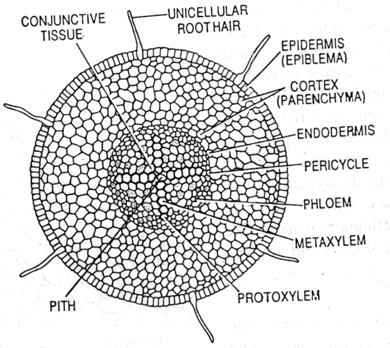


Fig. 9.13. Anatomy of dicot root. T.S. of young root of *Phaseolus radiatus* prior to cambium formation.

firmly attached to the Casparian strip. This firm attachment controls the movement of the materials in the root and their passage into xylem cells. The thin-walled *passage-cells* are also found in the endodermal layer which lie against the protoxylem poles. The passage cells either remain unmodified as long as the root lives or develop thick walls like the rest of the endodermis.

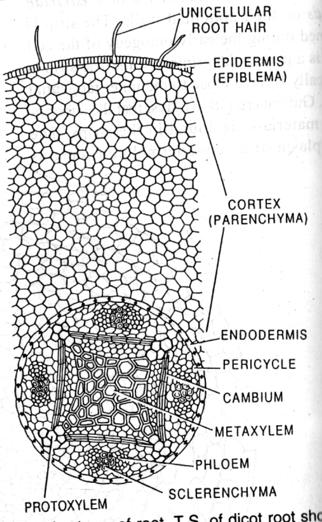


Fig. 9.14. Anatomy of root. T.S. of dicot root showing beginning of secondary growth. Details of a sector and central stele.

PERICYCLE

The layer next to the endodermis is commonly known as *pericycle*. The pericycle of relatively young roots consists of thin-walled parenchyma. It makes the outer boundary of the primary vascular cylinder of the dicotyledonous roots. It may be uniseriate or multiseriate (*e.g.*, *Morus, Salix, Ficus benghalensis,* etc.). The lateral roots in dicots arise in this tissue. The phellogen and part of vascular cambium originate in the pericycle. Roots without pericycle are rare but may be found among water plants and parasites.

THE VASCULAR SYSTEM

The phloem of the root occurs in the form of strands distributed near the periphery of the vascular cylinder, beneath the pericycle. Generally the xylem forms discrete strands, alternating with the phloem strands. Sometimes the xylem occupies the centre, with the strand-like parts projecting from the central core like ridges. If xylem is not differentiated in the centre, the centre is occupied by a pith. The root typically shows an exarch xylem, *i.e.*, the protoxylem is located near the periphery of the vascular cylinder, the metaxylem farther inward. The phloem is also centripetally differentiated, *i.e.*, the protophloem occurring closer to the periphery than the metaphloem. Most dicotyledons have few xylem strands. The taproot is frequently di-, tri-, or tetrarch, but it may have five to six and even more poles, (*e.g.*, many Amentiferae, *Castanea*). Only one xylem strand occurs in the slender root of the hydrophyte *Trapa natans*. In *Raphanus, Daucus, Linum, Lycopersicon* and *Nicotiana* the roots are diarch. In *Pisum* the root is triarch. In *Cicer, Vicia, Helianthus, Gossypium* and *Ranunculus* the roots are tetrarch. In Certain dicots the root of the same plant may show di-, tri-, and tetrarch xylem. For example, tetrarch and polyarch roots have been reported from *Nymphaea chilensis.* (Wardlaw, 1928). Banerji (1932) reported tri-, tetra-, and pentarch roots in *Enhydra fluctuans*. Such roots are known as *heteroarchic roots*. The protoxylem consists of annular and spiral vessels whereas metaxylem of reticulate and pitted vessels. The phloem strand consists of sieve tubes, companion cells and phloem parenchyma. The parenchymatous conjunctive tissue occurs in between xylem and phloem strands. The pith is scanty or altogether absent.

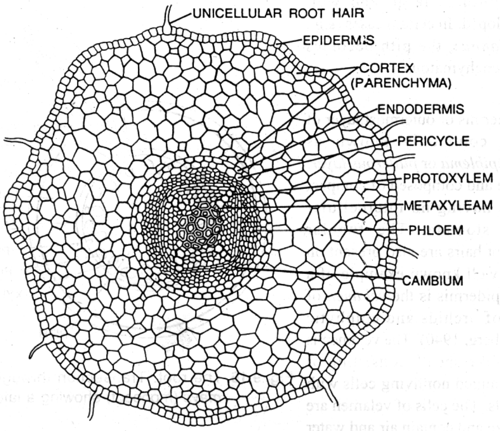


Fig. 9.15. Anatomy of dicot root. T.S. of root of *Phaseolus radiatus* showing beginning of cambium formation.

ANATOMY OF MONOCOTYLEDONOUS ROOTS

The distinctive anatomical characters of the monocotyledonous roots are as follows:

1. The xylem groups are numerous (polyarch condition) and generally vary from twelve to twenty.
2. The pericycle gives rise to lateral roots only.
3. The cambium is altogether absent even in later stages, as there is no secondary thickening in such roots.

2. The pericycle gives rise to lateral roots and secondary meristems (*e.g.*, cambium and phellogen).
3. The cambium appears later as a secondary meristem.
4. The pith is scanty or altogether absent.

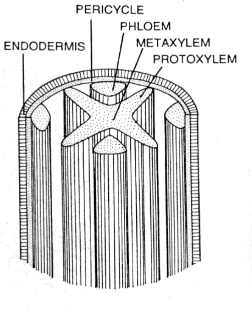


Fig. 9.9. Vascular system—stele of a dicotyledonous root.

EPIDERMIS

The epidermis consists of closely packed elongated cells with thin walls that usually lack a cuticle and stomata. In some dicotyledons thickened outer walls occur in root parts growing in air and also in roots that retain their epidermis for a long time. The root epidermis (also known as *piliferous layer, rhizodermis* or *epiblema*) is typically uniseriate. Most of the epidermal cells extend out in the form of tubular unicellular root hairs. Normally, the root hairs are confined to a region between one and several centimetres in length near the tip. They are absent in the nearest proximity of the apical meristem, and they die off in the older root parts. Some roots also develop a specialized layer—the exodermis—beneath the epidermis. The exodermis arises from one or several of the sub-epidermal layers of the cortex. The cell walls of exodermis become suberized. The exodermis is found to be present in few dicots.

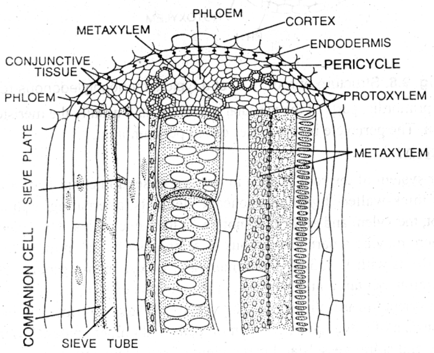


Fig. 9.10. Dicot root—transverse and longitudinal sections of the stele of a typical dicot root.

CORTEX

The cortex is massive and consists of thin-walled rounded or polygonal parenchyma cells having sufficiently developed intercellular spaces among them. The parenchyma cells of the cortex contain abundant starch grains in them. In the roots of dicotyledons which possess secondary growth and shed their cortex early, the cortex consists mainly of parenchyma. As seen in transverse sections, the cortical cells may be arranged in radial rows, or they may alternate with one another in the successive concentric layers. The presence of schizogenous intercellular spaces is typical of the root cortex. In the water plants the intercellular spaces are large and form distinct air spaces. The cortex of roots is usually devoid of chlorophyll. Exceptions are roots of some water plants and aerial roots of many epiphytes (*e.g., Tinospora* spp). Various idioblasts and secretory structures are found in the root cortex. Some dicotyledons (*e.g., Brassica, Pyrus, Prunus, Spiraea,* etc.) may develop prominent reticulate or band-like thickenings in cortical cells outside the endodermis.

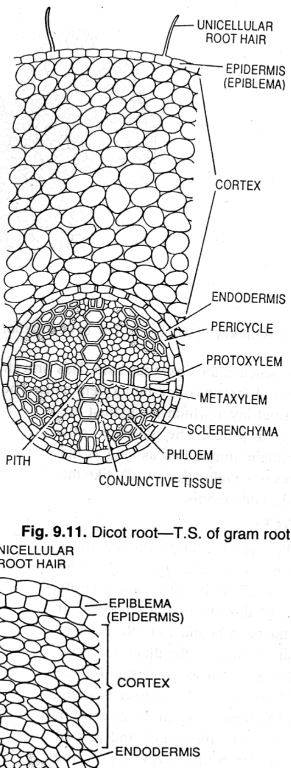


Fig. 9.11. Dicot root—T.S. of gram root.

ENDODERMIS

The innermost distinct layer of the cortex is known as *endodermis*. The endodermis is uniseriate and almost universally present in the roots. The cells of endodermis are living and characterized by the presence of *Casparian strips* or *Casparian bands* on their anticlinal walls. The strip is formed during the early ontogeny of the cell and is a part of the primary wall. The strip is typically located close to the inner tangential wall. Guttenberg (1943) says, that the suberin-like materials are found in the strips. The cytoplasm of an endodermal cell remains

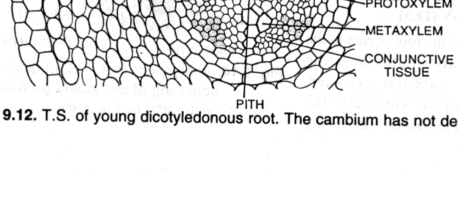


Fig. 9.12. T.S. of young dicotyledonous root. The cambium has not developed.

4. The pith is large and well developed. In certain cases (*e.g.*, in *Canna*), the pith becomes sclerenchymatous.

EPIDERMIS

The epidermis or outermost layer of the root is commonly known as *rhizodermis, epiblema* or *piliferous layer*. It is uniseriate and composed of compact tabular cells having no intercellular spaces and stomata. The tubular unicellular root hairs are also present on this layer. A well known example of a multiseriate epidermis is the *velamen* of aerial roots of orchids and epiphytic aroids (Guttenberg, 1940). The velamen is a parchment-like sheath consisting of compactly arranged nonliving cells with thickened walls. The cells of velamen are quite big in size and contain air and water

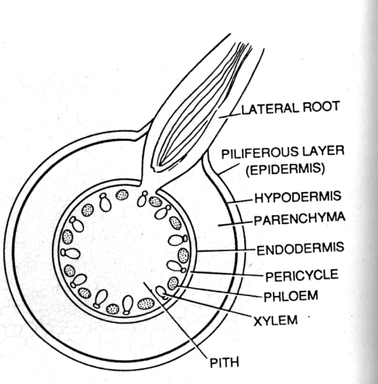


Fig. 9.16. The root. Transection through root of *Zea mays* (monocot) showing a lateral root.

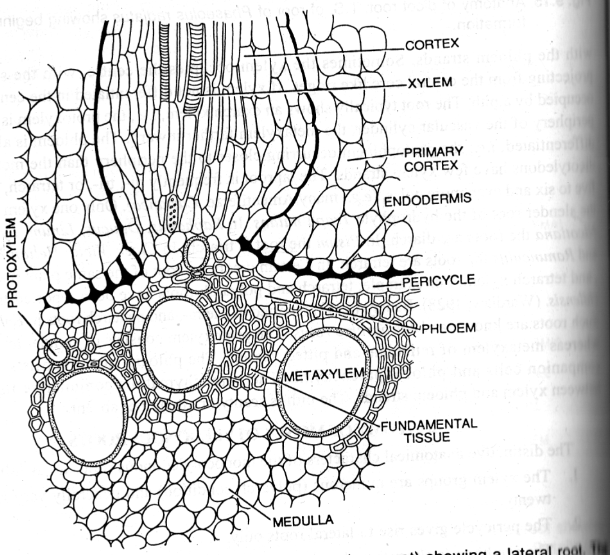


Fig. 9.17. The root. Transection through root of *Zea mays* (monocot) showing a lateral root. Th cortex and xylem are clearly visible in the lateral root.

in them. The cell walls develop fibrous thickenings. Generally, beneath the epidermis there are present one or more layers of *exodermis*. Usually the exodermis consists of a single row of cells with thickened outer and lateral walls except certain passage cells which remain thin-walled.

CORTEX

Immediately beneath the epidermis a massive cortex lies consisting of thin-walled parenchyma cells having sufficiently developed intercellular spaces among them. Usually in an old root of *Zea mays* a few layers of cortex immediately beneath the epidermis undergo suberization and give rise to a simple or multilayered zone—the *exodermis*. This is protective layer which protects internal tissues

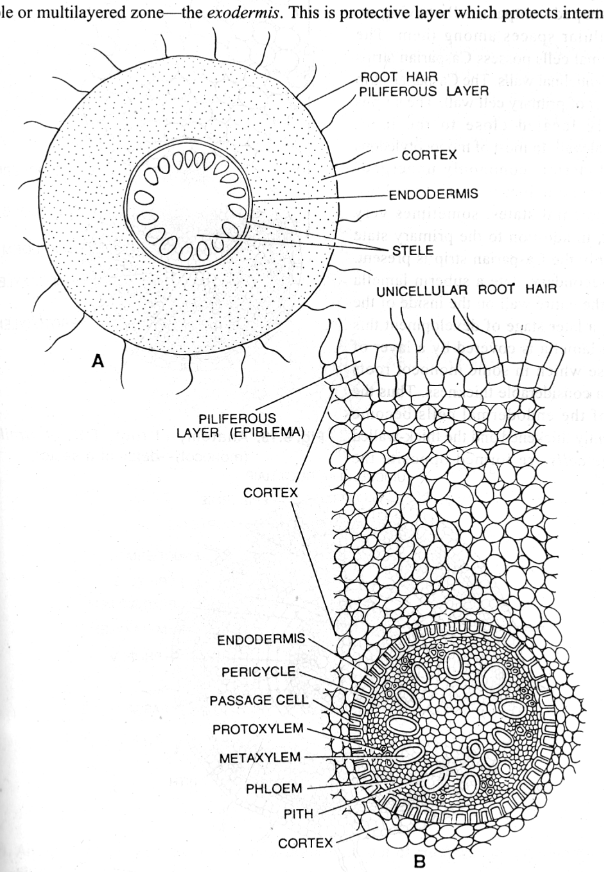


Fig. 9.18. Root. T.S. of monocotyledonous root (*Iris*). A, diagrammatic; B, detailed.

from injurious agencies. The starch grains are abundantly present in the cortical cells. The sclerenchyma cells are commonly found in the cortex of monocotyledons.

ENDODERMIS

The innermost layer of the cortex is called the endodermis. It is composed of barrel-shaped compact cells having no intercellular spaces among them. The endodermal cells possess Casparian strips on their anticlinal walls. The Casparian strip is the part of primary cell wall. The strip is typically located close to the inner tangential wall. In most of monocotyledons the endodermis commonly undergoes certain wall modifications. There are two developmental states, sometimes very distinct, in addition to the primary state when only the Casparian strip is present. In the secondary state a suberin lamella covers the entire wall on the inside of the cell. At a later stage of development this suberin lamella is covered by a layer of cellulose which in some monocot roots attains a considerable thickness. Thus the walls of the endodermal cells become sufficiently thickened and the thick-walled *passage cells* are formed opposite the protoxylem poles. The passage cells are meant for diffusion and are also called the *transfusion cells.*

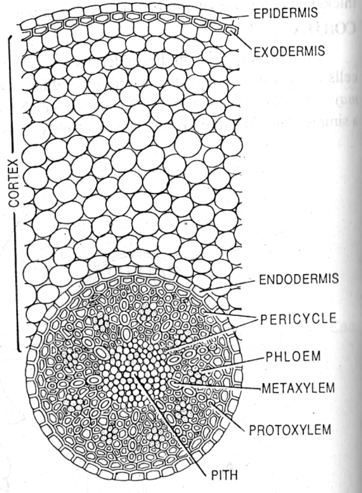


Fig. 9.19. Anatomy of root. T.S. of *Smilax* root (monocot)—detail of a sector.

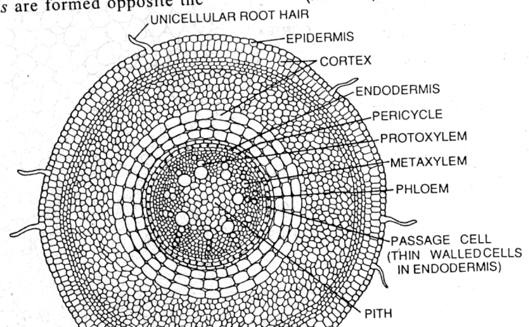


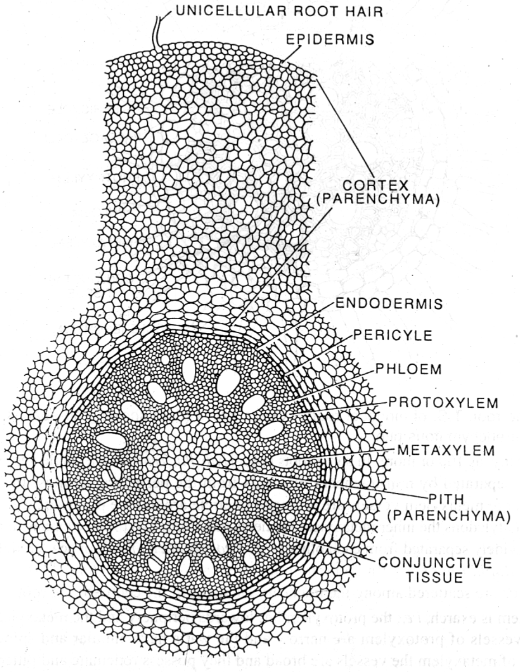
Fig. 9.20. Anatomy of monocot root. Cross section of root of *Commelina.*

PERICYCLE

It is usually uniseriate and composed of thin-walled parenchymatous cells. In the monocotyledons, the pericycle often undergoes sclerification in older roots, partly or entirely. In many monoctyledons (*e.g.*, some Gramineae, *Smilax, Agave, Dracaena,* palms) the pericycle consists of several layers. The pericycle may be interrupted by the differentiation of xylem (many Gramineae and Cyperaceae) or phloem elements (Potamogetonaceae) next to the endodermis (Guttenberg, 1943). Here, the pericycle gives rise to lateral roots only.

VASCULAR TISSUE

The vascular tissue consists of alternating strands of xylem and phloem. The phloem occurs in the form of strands near the periphery of the vascular cylinder, beneath the pericycle. The xylem forms discrete strands, alternating with the phloem strands. The centre is occupied by large pith which may be parenchymatous or sclerenchymatous. Bundles are numerous and referred as *polyarch*. The adventitious roots of Palmae and Pandanaceae have considerably higher number of vascular



9.21. Anatomy of monocot root. T.S. of a portion of root of *Hedychium coronarium,* showing stele and cortex.

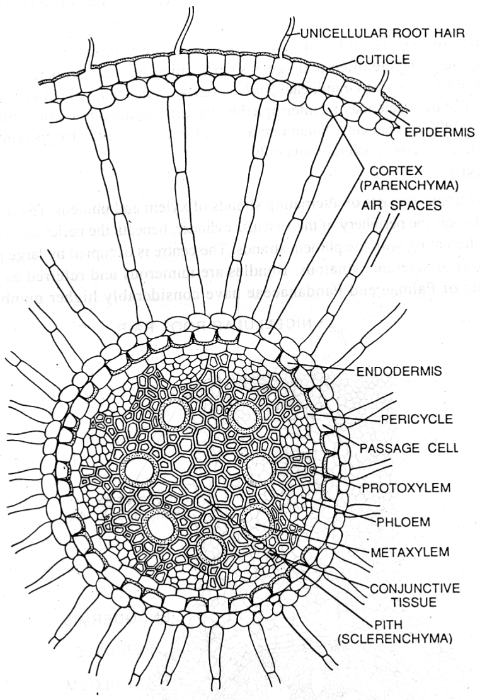


Fig. 9.22. The root. T.S. of monocot root of *Oryza sativa* (rice) showing air-spaces in cortex and sclerenchymatous pith.

bundles, as many as 100 or more. In some roots (*e.g., Hydrilla, Triticum*), a single vessel occupies the centre and is separated by non-tracheary elements from the peripheral strands. In other variable numbers of large metaxylem vessels are arranged in circle around the pith (*e.g., Zea mays*). In the woody monocotyledons the inner metaxylem elements may form two to three circles (*e.g., Latana*), or they may be widely separated from each other (*e.g., Phoenix dactylifera*), or scattered throughout the centre (*e.g., Raphia hookeri*). In some monocotyledons (*e.g., Cordyline, Musa*, Pandanaceae) phloem strands are scattered among the tracheary elements in the centre of the root.

The xylem is exarch, *i.e.*, the protoxylem lies towards periphery and the metaxylem towards the centre. The vessels of protoxylem are narrow and the walls have annular and spiral thickenings whereas that of metaxylem the vessels are broad and they possess reticulate and pitted thickenings.

The phloem strands consist of sieve tubes, companion cells and phloem parenchyma. The phloem strands are also exarch having protophloem towards the periphery and metapholem towards

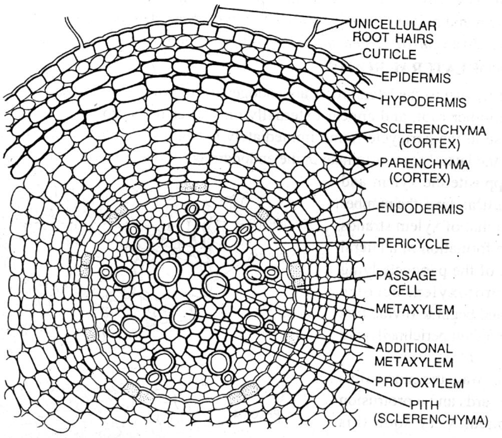


Fig. 9.23. The root. T.S. of monocot root (*Avena sativa*—Oats) showing sclerenchymatous pith and additional metaxylem vessels. The cells of cortical region are being arranged in distinct radial rows.

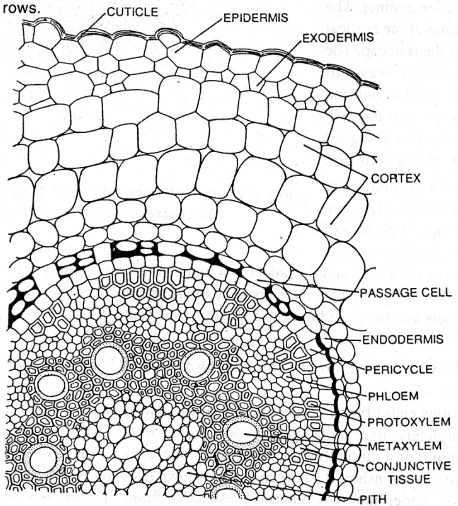


Fig. 9.24. The root. T.S. of monocotyledonous root (grass).

the centre. The parenchymatous or sclerenchymatous conjunctive tissue is found in between and around the xylem and phloem strands. The central part of the stele is occupied by a well developed pith. In *Canna, Oryza sativa, Avena sativa*, the pith is sclerenchymatous.

FORMATION OF LATERAL ROOTS

In flowering plants, the lateral roots are endogenous in origin, that is, they originate in the inner tissue of the mother root, and appear externally only after their growth is well begun. The root meristems arise in the pericycle found immediately beneath the endodermis. (In ferns, and other pteridophytes the lateral roots originate in the endodermis). Usually the lateral roots are restricted to the regions opposite the xylem and come out in vertical rows, the number being equal to that of xylem strands present. In the formation of a lateral root, the cells of the pericycle lying against the protoxylem become meristematic and begin to divide first tangentially and then periclinally and anticlinally, thus a few layers of cells are cut off. This way, the endodermis is pushed outwards and a protrusion is being formed. Very soon this protrusion comes out of the cortex and three regions of root apex, that is, dermatogen, periblem and plerome, become quite distinct. The endodermis and some of the cortical cells form a part of the root cap. The lateral root forces its way out through the cortex, endodermis and epidermis, and passes into the soil. Very soon the root cap is sloughed off and renewed by the calyptrogen.

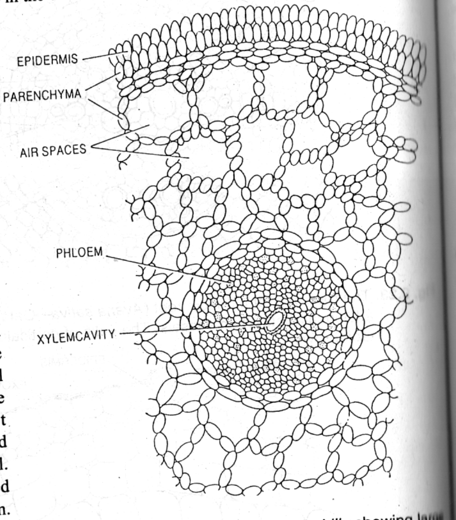


Fig. 9.25. T.S. of monocot root of *Hydrilla* showing larg air spaces in cortex and single xylem cavity

The lateral root primodria are formed in distinctive positions in relation to the xylem and phloem of the parent root. In diarch roots they usually occur between the xylem and the phloem, in triarch and tetrarch roots in positions opposite the protoxylem, and in many polyarch roots opposite to the protophloem. However, in some polyar roots, the lateral roots are developed in sites opposite to the protoxylem.

MYCORRHIZA

This is also known as '*fungus root*'. This is an association of fungus with root of a higher pl Mycorrhizas are of common occurrence. There are two main types —(1) *endo- trophic*, in whi fungus is within cortex cells of root, *e.g.*, orchids, and (2) *ectotrophic*, in which it is external, form a mantle that completely invests the smaller roots, *e.g.*, *Pinus*. The mycorrhizas are believed constitute an example of a mutually beneficial symbiotic association, probably evolved from original host parasite relationship. It has been clearly shown (*a*) that mycorrhizal plants benefit f the association, *e.g.*, under natural conditions presence of fungus partner is vital for establish

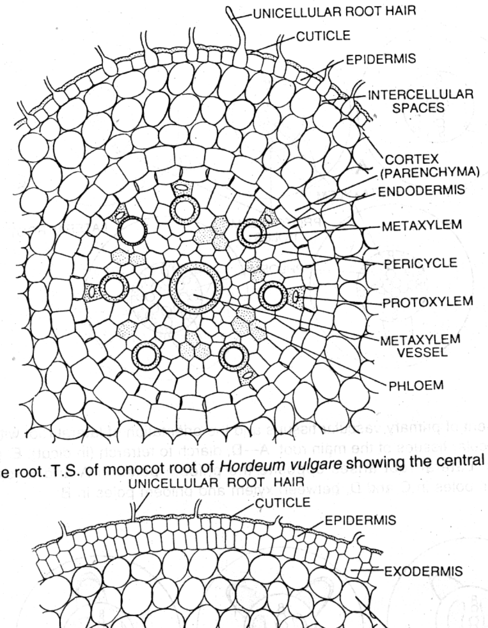


Fig. 9.26. The root. T.S. of monocot root of *Hordeum vulgare* showing the central metaxylem vessel.

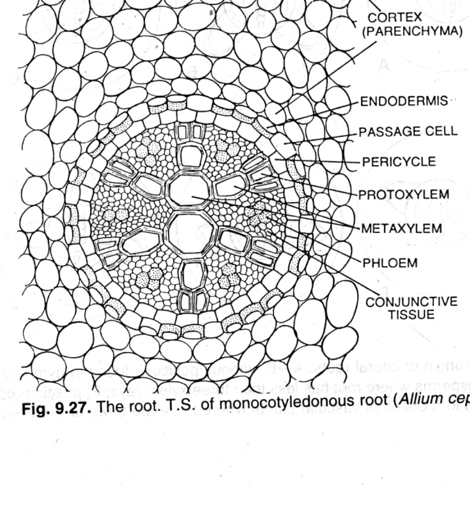


Fig. 9.27. The root. T.S. of monocotyledonous root (*Allium cepa*).

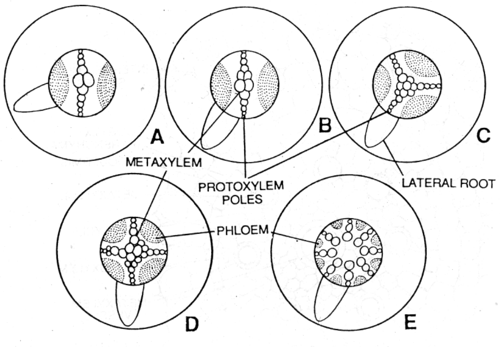


Fig. 9.28. Arrangement of primary vascular tissues and the orientation of lateral root with reference to the vascular tissues of the main root. A—D, diarch to tetrarch (in dicot); E, polyarch (in monocot). Lateral root arises opposite the phloem poles in A and E; opposite the protoxylem poles in C and D; between xylem and phloem poles in B.

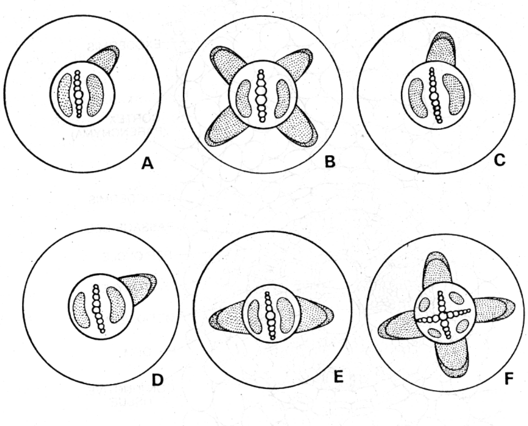


Fig. 9.29. Position of origin of lateral roots. A—E, various positions found in gymnosperms as well as in angiosperms where root has less than three xylem rays; F, position (opposite xylem rays) found in roots of all vascular plants where there are three or more xylem rays.

and growth of seedling trees of a number of different species, *e.g.*, pines, and (*b*) that association of fungus with tree is necessary for development and reproduction by fungus.

FORMATION OF ADVENTITIOUS ROOTS

The adventitious roots may occur on the hypocotyl of a seedling, at nodes and internodes of stems, and in roots. They may be formed in young organs or in older tissues which are still meristematic. Most adventitious roots arise endogenously. Stem-borne adventitious roots make the main vascular system in vascular cryptogms (pteridophytes), in most monocotyledons, in dicotyledons propagating by means of rhizomes or runners, in water plants, in saprophytes and in parasites. The roots which are developed on cuttings, directly from the stem or from the callus tissue, are also adventitious.

Usually the adventitious roots are initiated in the vicinity of differentiating vascular tissues of the organ which gives rise to them (Datta and Majumdar, 1943). In young organ, the adventitious primordium is initiated by a group of cells near the periphery of the vascular system. In older organ, it is located deeper, near the vascular cambium. In young stems, the cells that form the root primordium are derived from the interfascicular parenchyma, while in older stems from a vascular ray. In certain cases the adventitious roots are initiated by divisions in the cambial zone (Smith, 1936). Usually the seat of the root primordium in the case of stems is known as pericycle. The origin of the adventitious roots in the vascular ray, or in the cambium places the young root close to both the xylem and the phloem of the mother axis and makes the vascular connection between the two organs (see fig. 9.30).

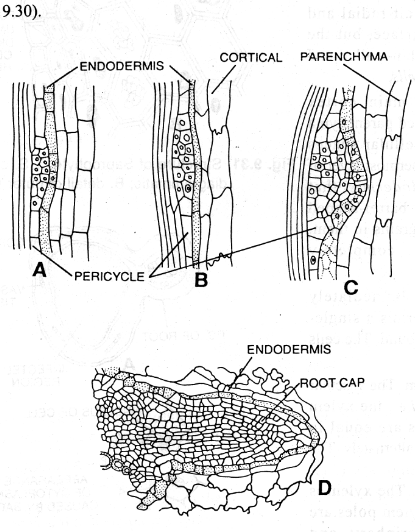


Fig. 9.30. Origin of lateral root. A, initiation of branch of carrot root through formation of meristematic cells in pericycle; B—C, enlargement of meristematic region, D, young root pushing through cortex.

The *pith* consists of thin-walled parenchymatous cells having well-defined intercellular spaces.

ANATOMY OF BANYAN ROOT (*FICUS BENGHALENSIS*-DICOT)

The transverse section of the aerial root of *Ficus benghalensis* reveals the undermentioned structure :

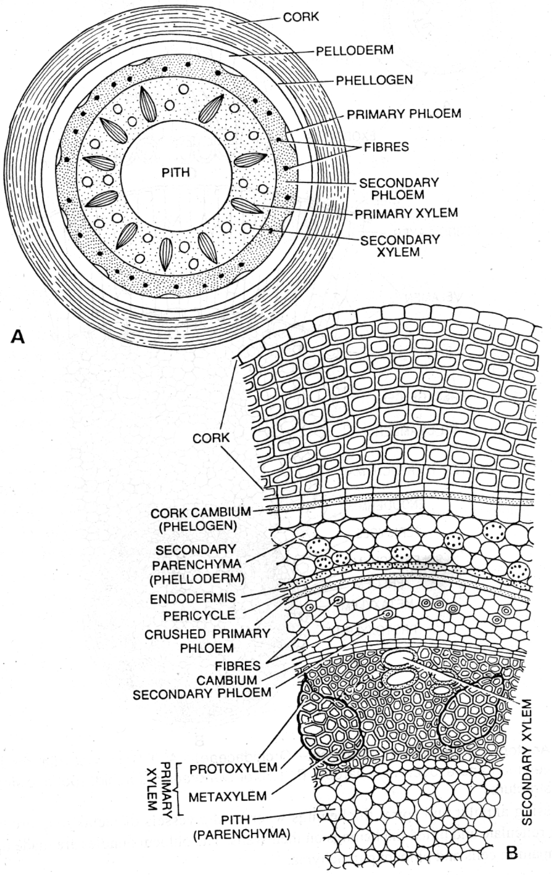


Fig. 9.34. *Ficus benghalensis.* T.S. of dicot aerial root showing periderm, crushed primary phloem, secondary phloem with fibres, cambium, secondary xylem, primary xylem and large pith.

Rhizodermis. The outermost limiting layer of the root is represented by rectangular cells. A thick cuticular layer may also be seen.

Cork. Just beneath the rhizodermis there are several layers of cork cells. These cork cells are somewhat rounded, suberized and having intercellular spaces.

Phellogen. The phellogen or cork cambium is found beneath the cork cells. The rectancular cells of cork cambium divide tangentially forming cork cells towards the outer side and secondary cortex towards the inner side. The secondary cortex is composed of a few layers of parenchyma cells.

Endodermis and pericycle. In young roots, the endodermis and pericycle are distinctly clear, but in older roots they are inconspicuous.

Vascular system. Just beneath the pericycle a crushed layer of primary phloem is visible, which is immediately followed by well developed secondary phloem. The secondary phloem is composed of sieve tubes, companion cells, phloem parenchyma and phloem fibres.

The cambium forms a complete ring in the older roots. Just beneath the cambium there is secondary xylem. The secondary xylem possesses vessels, tracheids and xylem fibres. The primary xylem strands are easily recongnizable having protoxylem poles towards periphery and metaxylem towards centre. The vascular strands are more than six in number.

In the central region there is well developed pith. The pith is composed of thin-walled parenchyma cells having well developed intercellular spaces.

ANATOMY OF THE ROOT OF *TINOSPORA CORDIFOLIA* (DICOT.)

The transverse section of the aerial root of *Tinospora cordifolia* shows the undermentioned structure:

Rhizodermis. The outermost limiting layer of the root is represented by rectangular cells.

Cork. Just beneath the rhizodermis there are few layers of rectangular cork cells. The cork cells are arranged in radial rows.

Phellogen or cork cambium. The phellogen is found beneath the cork. The cells of phellogen divide tangentially forming cork towards the outer side and secondary cortex (of chlorenchyma) towards inner side.

The endodermis and pericycle are inconspicuous.

Vascular system. The crushed primary phloem is found beneath the secondary cortex (chlorenchyma). Next to crushed primary phloem there is secondary phloem. The secondary phloem is composed of sieve tubes, companion cells and phloem parenchyma. In between secondary phloem and secondary xylem there is distinct cambium. Towards the inner side of the cambium there is secondary xylem. The secondary xylem has large vessels. The primary xylem strands are easily recognisable possessing protoxylem poles towards periphery and metaxylem towards centre. There is tetrarch condition. Scanty pith is present in the centre. The meduallary rays of parenchyma are visible. (See figs. 9.36 and 9.37).

ANATOMY OF STORAGE ROOTS

The underground roots may become very much thickened and serve as organs for the storage of food. Such is the case in sweet potatoes, radishes, turnips, carrots and dahlias. In such roots the food may be stored largely in the cortex or xylem region or in both.

In turnips food is stored largely in the xylem, and the phloem and cortex are relatively narrow. In the radish and sweet potato the xylem is also the chief region of food storage, but food is also stored outside the xylem. In the carrot there is a more even distribution between xylem and bark. In beets there are alternate layers of xylem and phloem owing to the formation of successive cambia. The

ANATOMY OF EPIPHYTIC ROOTS

ANATOMY OF ORCHID ROOT (MONOCOT)

The orchids (of family Orchidaceae-monocotyledons) are epiphytes. They possess the aerial roots hanging in the air. The anatomy of the root of *Dendrobium* (an orchid) is given here.

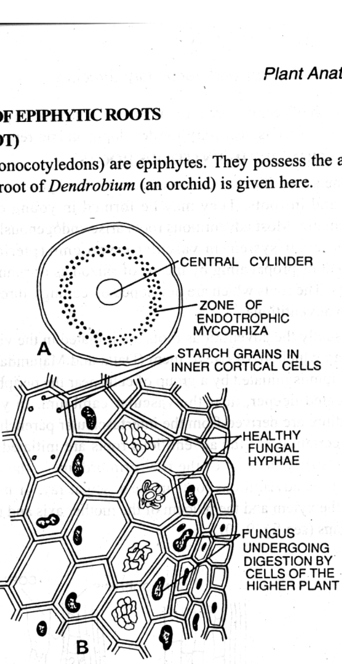


Fig. 9.31. Structure of Saprophyte. T.S. of *Neottia* root; A, diagrammatic; B, detail of outer region.

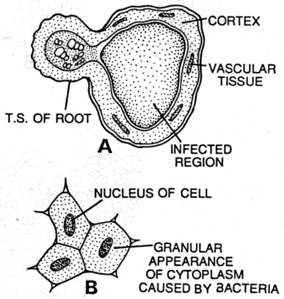


Fig. 9.32. Root. The root nodules. A—B, T.S. of root in region of nodule.

Velamen. The velamen consists of several layers of dead cells often with spirally thickened and perforated walls, which act as sponge, soaking up water that runs over it. The velamen is multiple epidermis. The velamen is thought to function as a protective tissue, preventing undue water loss from the delicate cortical cells of the exposed aerial root.

Exodermis. It is the outermost layer of the cortex. This layer is composed of alternating long and short cells; the long cells become thick-walled on their radial and outer tangential surface, but the small cells remain thin-walled and are called *passage cells.*

Cortex. The main cortex consists of thin-walled parenchyma cells having intercellular spaces among them. The innermost layer of the cortex is *endodermis* that consists of compact barrel-shaped cells having starch grains in them. The endodermis completely encircles the stele.

Pericycle. Immediately beneath the endodermis a single-layered pericycle is found. The cells are thin-walled.

Vascular system. The vascular bundles are radial, *i.e.*, the xylem and phloem strands are equal in number and arranged alternately. The bundles are more than six (*i.e.*, polyarch condition). The xylem is exarch. The protoxylem poles are found towards periphery and metaxylem towards centre. The vessels of the protoxylem are narrow and possessing annular and spiral thickenings whereas the vessels of metaxylem are broad and possessing reticulate and pitted thickenings on their walls. The phloem bundles are made up of sieve tubes, companion cells and phloem parenchyma.

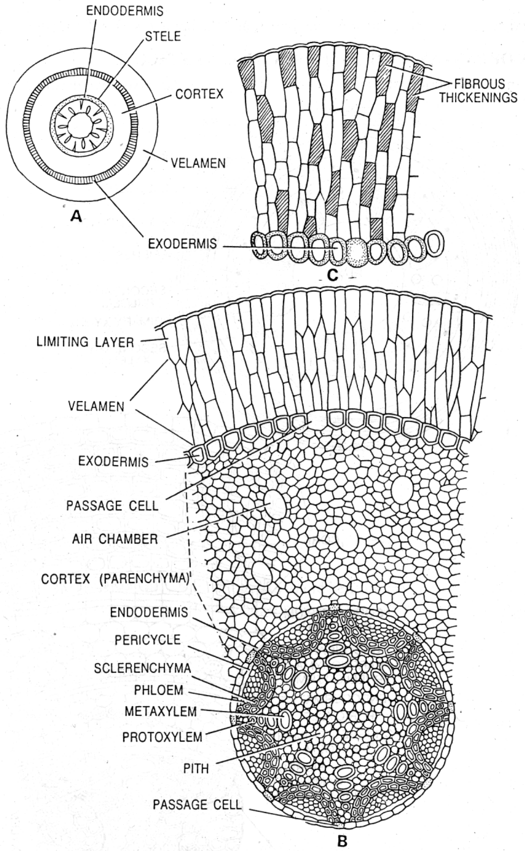


Fig. 9.33. Anatomy of Orchid root (Monocot—Orchidaceae)—A, T.S. of root (diagrammatic); C, velaman and exodermis enlarged; B, T.S. of *Dendrobium* (orchid) root showing detailed structure.

The *conjunctive tissue* is represented by the presence of parenchyma cells in between and around the vascular bundle.

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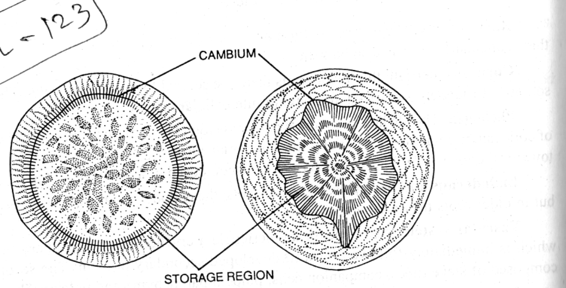


Fig. 9.35. Anatomy of storage roots (dicot). Left—cross section of storage root of *Ipomoea batatas*; right—cross section of root of carrot.

secondary tissues of the root accumulate starch in the same kind of cells as those of the stem, that is various parenchymatous and some sclerenchymatous cells of the xylem and the phloem. In general, roots possess a higher proportion of parenchyma cells than do stems.

***Daucus carota*.** **Carrot (Umbelliferae-Dicot).** In this case, the hypocotyl and base of taproot form jointly one fleshy structure.

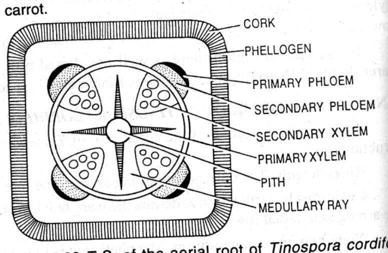


Fig. 9.36. T.S. of the aerial root of *Tinospora cordifolia* (dicot).—diagrammatic.

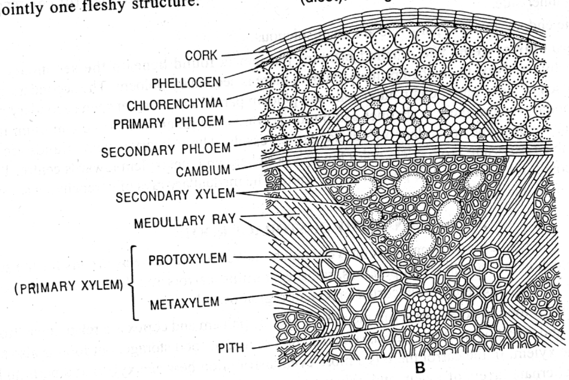


Fig. 9.37. T.S. of the aerial root of *Tinospora cordifolia* (dicot.) showing secondary growth-detail

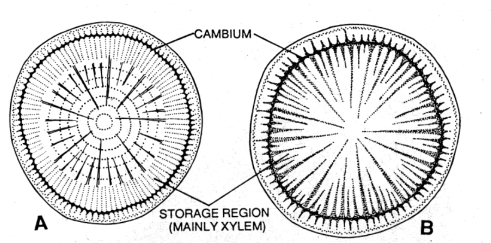


Fig. 9.38. Anatomy of storage root (dicot.) A, cross section of turnip root; B, cross section of radish root.

Here, the fleshy organ has large amount of storage parenchyma associated with ordinary arrangement of tissues. In this type of development, where the hypocotyl and the upper part of the tap root, after sloughing off the cortex, become fleshy through a massive development of parenchyma in the phloem and the xylem. Besides the cambial activity the massive parenchyma, that makes the storage tissue, adds to the thickness of the root.

Raphanus sativus. **Radish (Cruciferae-Dicot)**

The fleshy roots of radish show a proliferation of parenchyma in the pith and in the secondary xylem, and a differentiation of concentric vascular bundles within this parenchyma. Here, the fleshy roots show a diarch primary xylem. The normal cambium cuts off secondary phloem towards periphery and secondary xylem towards the centre. Several concentric vascular bundles are seen in the transverse section of the fleshy root. The concentric bundles are composed of secondary cambial rings with a few vascular elements in the centre.

Ipomoea batatas. **Sweet potato (Convolvulaceae-Dicot.)**

It exhibits a complicated type of anomalous secondary thickening. In primary state the root is pentarch or hexarch. The cortex is delimited by a single-layered distinct endodermis from the stelar region. In the normally developed but highly parenchymatous primary and secondary xylem, anomalous cambia arise around individual vessels or vessel groups and produce phloem rich in parenchyma and with some laticifers away from the vessels, and

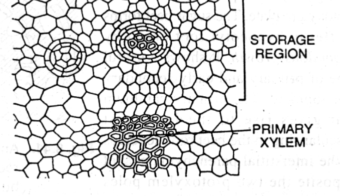


Fig. 9.39. The root. T.S. of a sector of root of *Raphanus sativus* (dicot.)

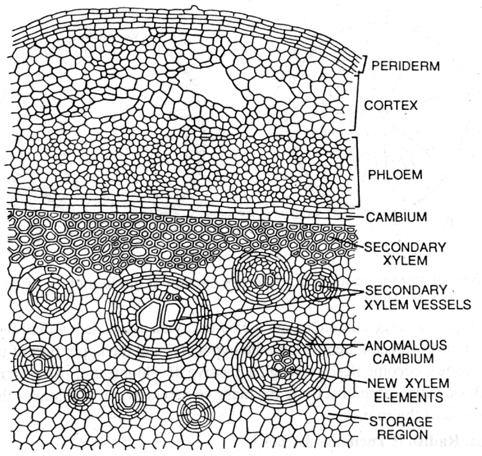


Fig. 9.40. The root. T.S. of storage root of *Ipomoea batatas* a sector.

tracheary elements toward them. Massive amounts of storage parenchyma cells are developed in both the direction, thus forming the tuberous roots.

***Beta vulgaris*. Beet root (Chenopodiaceae-Dicot.)**

The anatomy of beet root has been described in detail by E.F. Artschwager (1924, 1926). The young beet root possesses a diarch protoxylem plate. The sugar beet forms its fleshy hypocotyl root organ by *anomalous growth*. It shows a useful type of primary and early secondary development. The primary cambium that gives rise to the innermost vascular ring in the beet root develops in the interstitial parenchyma except opposite the two protoxylem poles where it is derived from the pericycle. The first secondary cambium in the root and lower part of the hypocotyl arises in the phloem parenchyma, whereas in the upper part of the hypocotyl is derived from the pericycle. Later, however, a series of supernumerary cambia arise outside the normal vascular cylinder and produce several increments of vascular tissue, each consisting of a layer of parenchyma, parenchymatous xylem and parenchymatous phloem. Practically

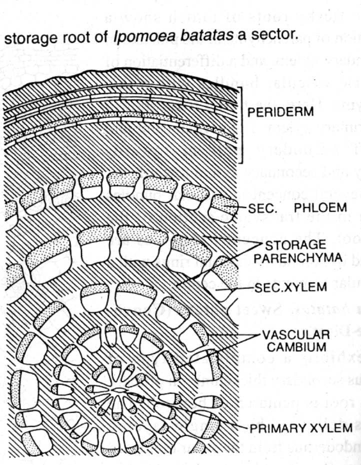


Fig. 9.41. Anomalous secondary growth in *Beta vulgaris* root (T.S.), showing alternate layers of vascular bundles and proliferated pericycle, phloem, lignified xylem cells in radial rows, xylem parenchyma and secondary interfascicular tissue. (After Eames and MacDaniels).

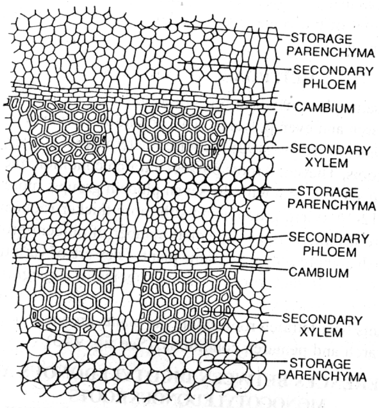


Fig. 9.42. The root. The root of *Beta vulgaris* showing growth layers,

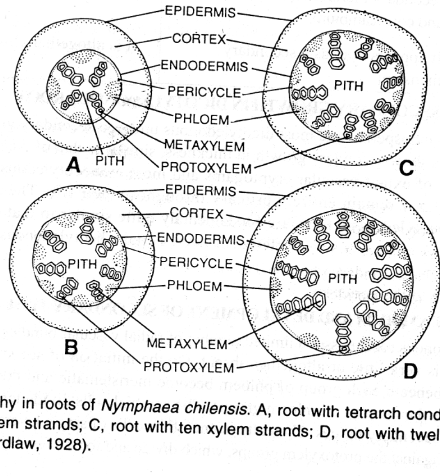


Fig. 9.43. Heteroarchy in roots of *Nymphaea chilensis*. A, root with tetrarch condition; B, root, with seven xylem strands; C, root with ten xylem strands; D, root with twelve xylem strands. (After Wardlaw, 1928).

all the supernumerary cambia that give rise to the vascular rings in the mature root have already been developed when the diameter of the young root is no greater than five millimetres or so. All the cambia are active at the same time.

HETEROARCHY IN ROOTS

In certain cases, the same plant may bear roots of different types. In such plants, the roots may be tetrarch, pentarch, hexarch and even polyarch. This condition is known as *heteroarchy*, and the roots, the *heteroarchic roots*. Wardlaw (1928) reported heteroarchy in *Nymphaea chilensis*. This plant bears four types of roots. The small roots possess tetrarch condition; the slightly thicker roots possess seven xylem groups alternating with the seven phloem groups; more thicker roots possess polyarch condition (*i.e.,* 12-14 xylem groups) and still more thicker roots are also polyarch (*i.e.,* they bear 16-18 xylem groups alternating with equal number of phloem groups). However, these roots lack secondary growth and present on the same plant. They are of various diameters. Wardlaw (1921) reported the presence of such roots in some species of *Eryngium* (of Umbelliferae). Majumdar (1932) reported heteroarchy in the roots of *Enhydra fluctuans* (of Compositae). Here, the normal terrestrial plants bear tetrarch roots while the plants growing in marshy places bear the roots having triarch, tetrarch and pentarch conditions. (See fig. 9.43)

DIFFERENCES BETWEEN DICOTYLEDONOUS AND MONOCOTYLEDONOUS ROOTS

		Dicotyledonous Root	**Monocotyledonous Root**
1.	Xylem bundles	The number varies from two to six (di- to hexarch), rarely more.	Usually they are numerous, rarely a limited number (*e.g.,* in Onion).
2.	Pith	It is small or absent.	It is large and well developed.
3.	Pericycle	It gives rise to lateral roots and secondary meristems, *i.e.,* cambium and cork-cambium.	It gives rise to lateral roots only.
4.	Cambium	It appears later as a secondary meristem.	It is altogether absent.

SECONDARY GROWTH IN DICOTYLEDONOUS ROOT

The roots of gymnosperms and most dicotyledonous undergo secondary growth. Most of the dicotyledonous roots show secondary growth in thickness, similar to that of dicotyledonous stems. However, the roots of extant vascular cryptogams and most monocotyledons do not show any secondary growth; they remain entirely primary throughout their life. The secondary tissues developed in the dicotyledonous roots are fundamentaly 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

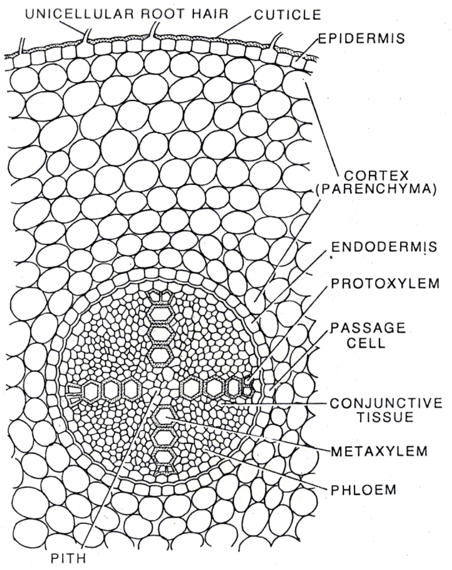


Fig. 9.44. The root. T.S. of a dicotyledonous (gram) root showing tetrarch xylem and small pith.

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.

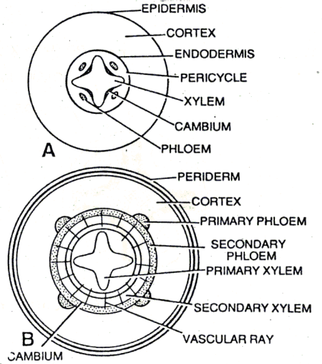


Fig. 9.45. Secondary growth in root A, cross section of a root without secondary growth; B, the same after considerable secondary growth.

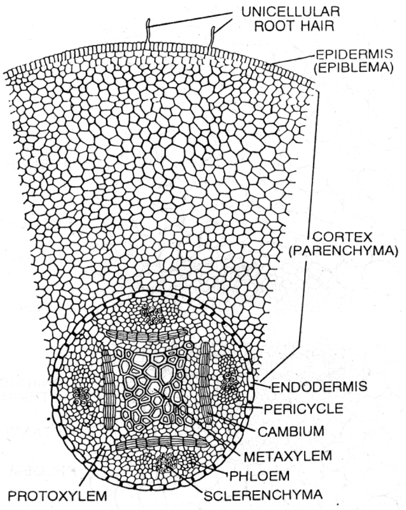


Fig. 9.46. The root. T.S. of gram root (dicot.) showing the beginning of the formation of cambium.

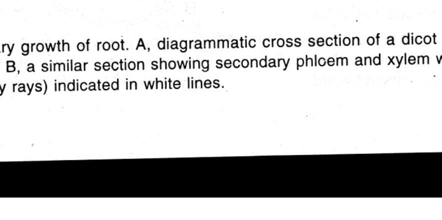


Fig. 9.47. Secondary growth of root. A, diagrammatic cross section of a dicot root showing the cambium; B, a similar section showing secondary phloem and xylem with vascular rays (medullary rays) indicated in white lines.

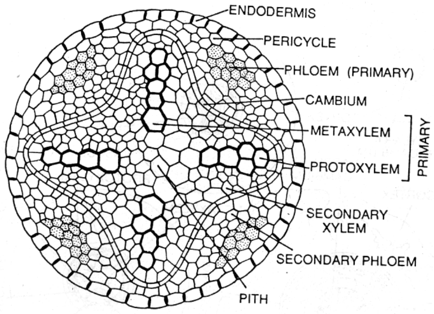


Fig. 9.48. Beginning of secondary growth in dicotyledonous root.

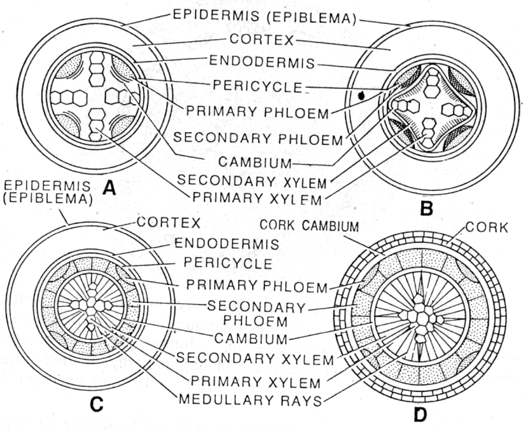


Fig. 9.49. Secondary growth in dicot root. A—D, diagrams showing stages in the secondary growth of a typical dicotyledonous root.

10

The Stem—Primary and Secondary Structure

The part of the axis of the plant which is usually ascending and aerial in nature, and also bears the leaves and reproductive structures is called the *stem*. The stem together with the leaves which it bears constitutes the *shoot*; the relationship between leaves and stem is very close one and a separation of the shoot into its component parts is to some extent artificial. The stem bears conspicuous nodes and internodes and fundamentally differ from roots in their vascular structure. The difference lies chiefly in the arrangement of the xylem and the phloem—in the root the strands of primary xylem and phloem lie in different radii, separated from one another; in the stem the strands lie side by side in the same radius, *i.e.*, they are conjoint, collateral. The xylem of the root is always exarch, whereas that of the stem is exarch, endarch or mesarch, being endarch most commonly in present-day plants.

ORIGIN OF THE STEM

The first stem meristem is organized during the development of the embryo. The fully developed embryo commonly consists of an axis, the *hypocotyl-root axis*. The axis bears at its upper end, one or more cotyledons and the shoot primordium, whereas at its lower end it bears the root primordium covered with a root-cap. The *radicle* (embryonic root) is found at the lower end of the hypocotyl and the embryonic shoot is found above the insertion of the cotyledons. The embryonic shoot is composed of an axis bearing unextended internodes and one or more leaf primordia. This shoot (first bud) is commonly known as *plumule* and its stem part is termed *epicotyl*. The origin of shoot organization is found in the *hypocotyl-cotyledon system* where the hypocotyl is the first stem unit of the plant and the cotyledons are the first leaves. The hypocotyl is located below the cotyledonary node, but not in between nodes. During the germination of the seed, the root meristem forms the first root, whereas the shoot meristem develops the first shoot by adding new leaves, nodes and internodes to the shoot system formed in the embryo. The lateral stems normally arise by the development of new apical meristems laterally in the terminal meristem of the mother axis. The adventitious branches develop on both stem and roots, by the formation of meristems secondarily in the pericyclic, phloic or cambial regions.

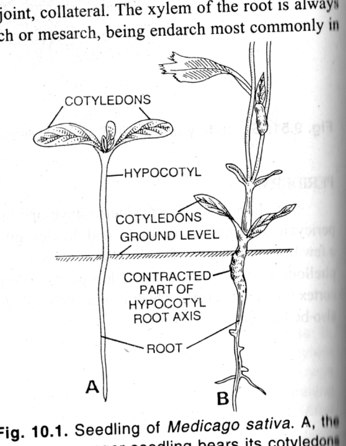
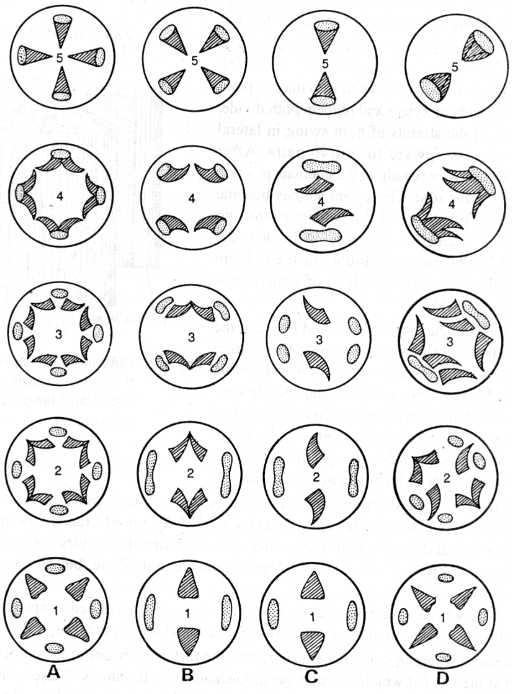


Fig. 10.1. Seedling of *Medicago sativa*. A, the younger seedling bears its cotyledons high above the ground level; B, the older seedling has pulled down the cotyledons close to the ground by contracting the hypocotyl and the upper part of the root.

ROOT-STEM TRANSITION

The root and stem make a continuous structure called the *axis* of the plant. The vascular bundles are continuous from the root to the stem. The epidermis, cortex, endodermis, pericycle and secondary vascular tissues are directly continuous in the two organs, root and stem, but the arrangement of vascular bundles is quite different in the two organs. The stems possess collateral bundles with endarch xylem, whereas the roots possess radial bundles with exarch xylem. Of course,



ig. 10.2. Root-stem transition. Diagrams of four types. A, B, C and D. A, *Fumaria* type; B, *Cucurbtia* type; C, *Lathyrus* type; D, *Anemarrhena* type. (After Fames and MacDaniels).

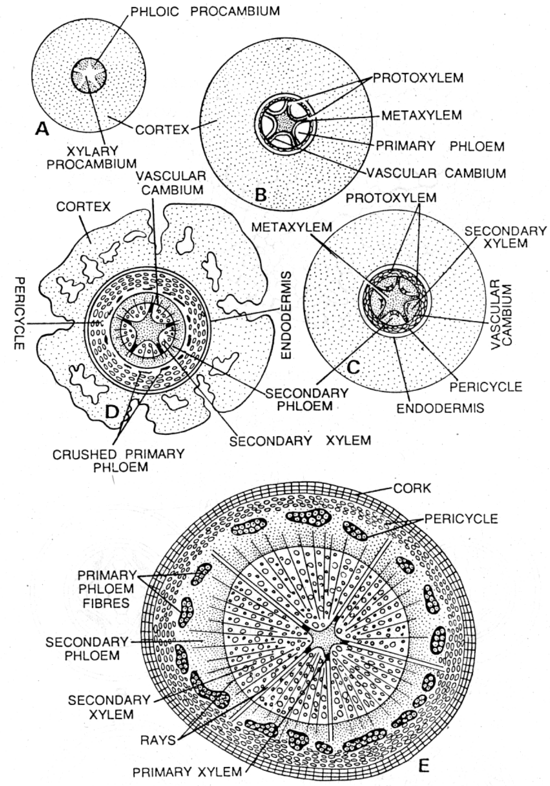


Fig. 9.50. The root. Secondary structure. Development of root in *Pyrus*.A, procambial state; B, primary growth completed; C, vascular cambium in between phloem and xylem produced some secondary vascular tissues; D, further secondary growth, pericycle increased in width by periclinal divisions; endodermis partly crushed cortex breaking down; E, further secondary growth, periderm developed, cortex has been shed. (After Esau.)

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. 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*.

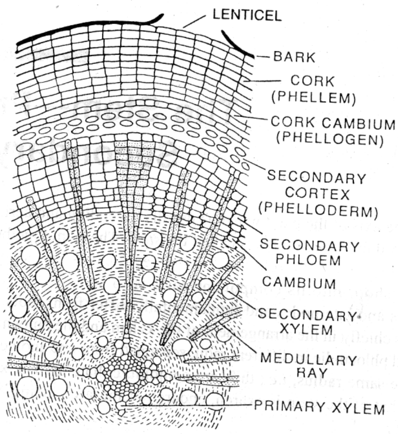


Fig. 9.51. Secondary growth. T.S. of dicotyledonous root showing secondary growth (later stage).

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 *phelloderm* 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.

a region exists where these changes occur and the two different types of vascular tissues maintain their continuity. The change of position involving inversion and twisting of xylem strands from exarch to endarch type is referred to as vascular transition, and the part of the axis where these changes occur is called *transition region*. Commonly this region is quite small and rarely of several centimetres. These changes may be found gradually or abruptly in the top of the radicle or at the base of the hypocotyl, near its middle region, or in the upper part. The phloem bundles remain practically in the same position. The transition may be of four main types which vary from species to species.

Type A. In *Mirabilis*, *Fumaria* and *Dipsacus*, and other plants each xylem strand of the root divides by radial division in the branches. As these branches pass upward, they swing in their lateral direction; one bends towards right and the other goes to the left. Simultaneously these branches join the phloem strands on the inside. The phloem strands, however, do not change their position and also remain unchanged in their orientation. They remain in the form of straight strands continuously from the root into the stem. In this type as many primary bundles are formed in the stem as many phloem strands are formed in the root.

Type B. In *Cucurbita*, *Phaseolus*, *Acer* and *Trapaeolum* and several other plants the xylem and phloem strands fork, the branches. It is to make a point here that the strands of xylem and phloem both divide. The branches of the strands of both swing in lateral direction and pass upward to join in pairs. After joining in the pairs they remain in the alternate position of the strands in the root. The xylem strands become inverted in their position and the phloem strands do not change their orientation. This way, in the stem, the number of bundles becomes double of the phloem strands found in the root. This type of transition is more commonly found.

Type C. In *Medicago*, *Lathyrus* and *Phoenix*, the xylem strands do not fork and continue their direct course into the stem. These strands, however, twist through 180 degrees. The phloem strands divide soon and the resulting halves swing in the lateral direction to the xylem positions. The phloem strands join the xylem strands on the outside. In this type as many bundles are formed as there are phloem strands in the root.

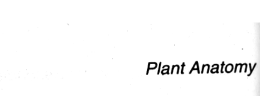


Fig. 10.3. Diagrammatic representation of the stem, showing transverse, radial and tangential planes of the section.

Type D. This type of root-stem transition is rarely found and is known in only a few monocotyledons (*e.g.*, *Anemarrhena*). In this type half of the xylem strands fork and the branches swing in their lateral direction to join the other undivided strands of xylem. Soon after the xylem strands become inverted. However, the phloem strands do not divide, but on the other hand they become united in pairs. Simultaneously these united phloem strands unite with the triple strands of the xylem. This way, a single bundle of the stem consists of five united strands, and thus half as many bundles are formed in the stem as there are phloem strands in the root.

In the stems where internal phloem is present, the forked branches of the phloem strands of the root depart at the level at which the roots begin to change into the stems. These branches of phloem strands pass inward and lie inside the new xylem strands giving rise to bicollateral bundles. In some of the monocotyledonous plants the transitory region is very short and from that too several lateral roots are given out.

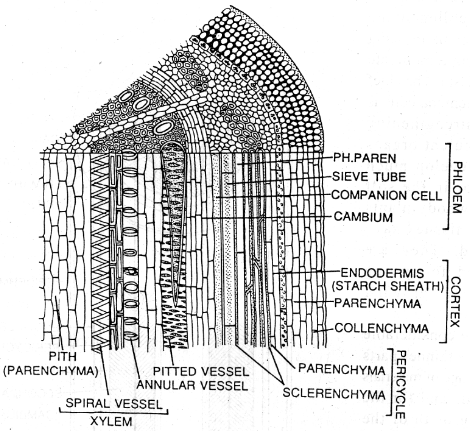


Fig. 10.4. Anatomy of dicot stem. Diagrammatic combined transverse and longitudinal sections of stem.

The seed plants are generally divided into two groups—the *angiosperms* and the *gymnosperms*. The angiosperms are further sub-divided into *dicotyledons* and *monocotyledons*. In a cross section of the stems of dicotyledons and gymnosperms the vascular bundles are found to be arranged in a ring, whereas in most of the monocotyledonous stems the vascular bundles are numerous and scattered.

ANATOMY OF DICOTYLEDONOUS STEMS

In young dicotyledonous stems there are three distinct regions—the epidermis, the cortex and the stele.

Epidermis. The epidermis consists of a single layer of cells and is the outermost layer of the stem. It contains stomata and produces various types of trichomes. The outer cell walls are greatly thickened and heavily cutinized. The cells are compactly arranged and do not possess intercellular spaces. In transverse section the cells appear almost rectangular. It serves mainly for restricting the rate of transpiration and for protecting the underlying tissues from mechanical injury and from disease-producing organisms.

Cortex. The region that lies next to the epidermis is the *cortex*. The innermost layer of the cortex is the *endodermis*, known also as the *starch-sheath*. It consists of a single layer of cells which surrounds the stele and contains numerous starch grains. Frequently it is most easily distinguishable from the surrounding tissue by the presence of these starch grains. The part of the cortex situated between the epidermis and the endodermis is generally divided into two regions, an outer zone of *collenchyma* cells and an inner zone of *parenchyma* cells.

Collenchyma. On the inside of the epidermis there is usually a band of collenchyma. The cells of the collenchyma are modified parenchyma cells with cellulose walls thickened at the angles where three or more cells are in contact. The collenchyma resembles parenchyma in being alive and in having a moderate amount of protoplasm. The chief function of collenchyma cells is to serve as strengthening material in succulent organs which do not develop much woody tissue, or in the soft young parts of woody plants before stronger tissues have been developed. They are especially fitted for giving strength to young, growing organs, since the thickened parts of the walls have considerable rigidity, while the thinner parts allow for an exchange of materials between the cells and for the stretching and growth of the cells. The collenchyma cells of stems sometimes contain chloroplasts and carry on photosynthesis.

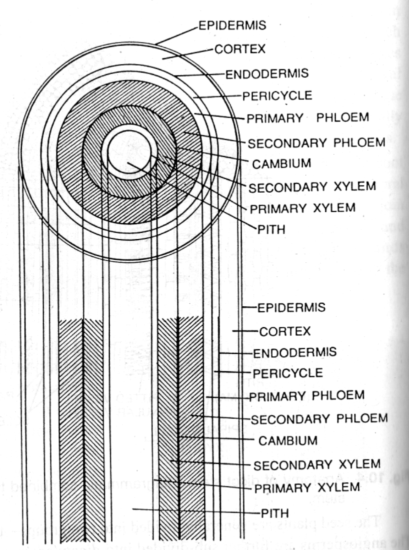


Fig. 10.5. The stem. Diagram showing structure of dicot axis. A, transverse section; B, longitudinal section. (After Eames and MacDaniels).

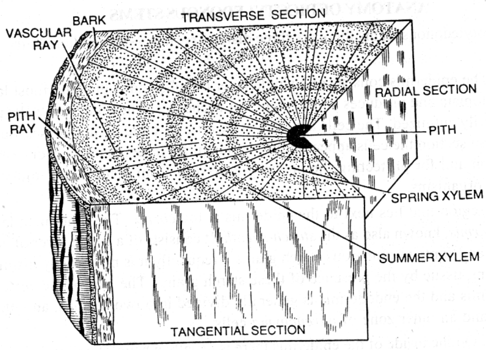


Fig. 10.6. The dicot stem. Three dimensional structure.

Parenchyma. The parenchyma cells are generally regular in shape, have comparatively thin walls, and are not greatly elongated in any direction. They are living cells and contain a moderate amount of protoplasm. When they are exposed to the light they develop chloroplasts and are known as *chlorenchyma cells*. Chlorenchyma cells are thus only a special kind of parenchyma cells. The parenchyma cells in the cortex of a stem are near enough to the light so that some or all of them develop chloroplasts and perform photosynthesis. The turgid parenchyma cells frequently help in giving rigidity to an organ. The function of parenchyma cells is important in succulent stems and in the young parts of the stems and woody plants before strong mechanical tissues have been developed. The parenchyma cells serve for the slow conduction of water and food. In the case of the cortex of stem it becomes evident that the water which is received by the collenchyma and the epidermis must be conducted through the parenchyma. The parenchyma is the special storage tissue of plants.

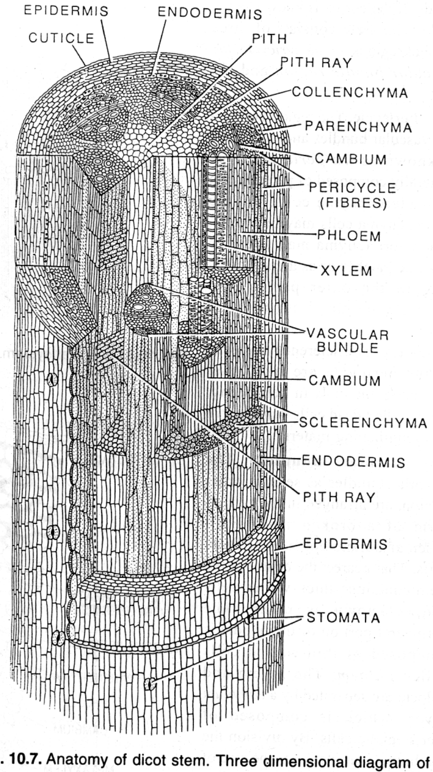


Fig. 10.7. Anatomy of dicot stem. Three dimensional diagram of a portion of an internode of a stem to show transverse, radial and tangential sections.

Sclerenchyma. The sclerenchyma cells are found in the cortex of some stems. There are two varieties of these scelerenchyma cells — short or irregularly shaped cells, known as *stone cells*, and *sclerenchyma fibres*. Sclerenchyma fibres are long, thick-walled dead cells and serve as strengthening material. Stone cells give stiffness to the cortex. The sclereids have been reported from the cortex of many water plants (*e.g.*, *Limnanthemum*, *Nymphaea*, etc.).

Endodermis. The innermost layer of the cortex is the endodermis consisting of barrel-shaped, elongated, compact cells, having no intercellular spaces among them. Usually the cells contain starch grains and thus the endodermis may be termed at starch sheath.

Stele. The part of the stem inside of the cortex is known as the *stele*. The stele consists of three general regions — *the pericycle, the vascular bundle region* and *the pith*.

Pericycle. The region between the vascular bundles and the cortex is known as the *pericycle*. It is generally composed of parenchyma and sclerenchyma cells, but the sclerenchyma cells may be absent. The sclerenchyma may occur as separate patches or as a continuous ring in the outer part of the pericycle, forming a sharp line of demarcation between the stele and the cortex. The sclerenchyma cells in the pericycle are like other sclerenchyma cells in being long, thick-walled dead cells which serve as strengthening material.

Vascular bundles. The vascular bundles as seen in cross section, are arranged in the general form of a broken ring. Each vascular bundle consists of three parts. That nearest the centre of the stem contained thick-walled cells and is known as *xylem*. The peripheral portion of the bundle is composed of thin-walled cells called *phloem*. The xylem and phloem are separated by a *cambium layer*, which is composed of meristematic cells. By division the cambium layer increases the size of vascular bundles by forming xylem cells on the inner side and phloem cells on the outer side. In some stems the bundles are separate and run the length of the internode. In others they are more or less united and form a hollow cylinder in which the medullary rays occur as radiating plates with slight vertical extension.

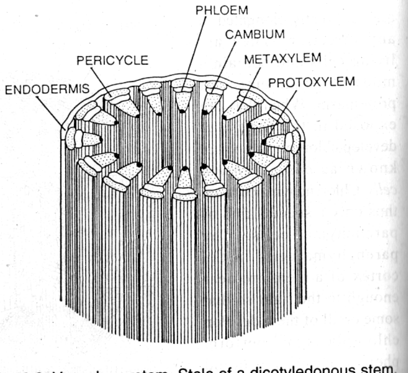


Fig. 10.8. Vascular system. Stele of a dicotyledonous stem.

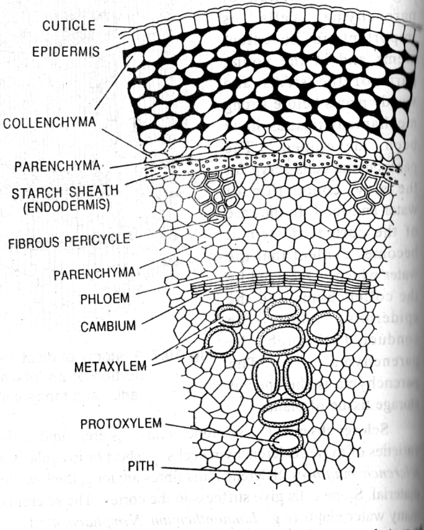


Fig. 10.9. Anatomy of dicot stem. T.S. of a sector of stem of *Ricinus communis*.

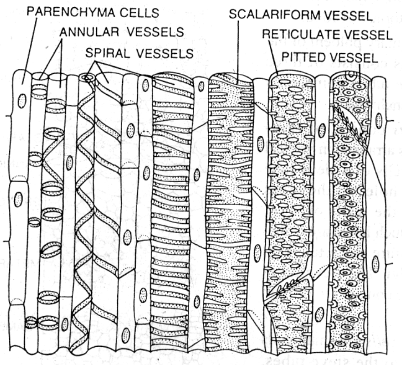


Fig. 10.10. The primary xylem. Types of vessels that occur in primary xylem in an elongating branch. Annular vessels formed first, and are therefore the oldest are more stretched. The pitted vessel formed last is the youngest. Elongation has stopped, so the pitted vessels will not be stretched.

Xylem. The xylem which is formed before the activity of the cambium has begun to produce xylem and phloem cells is called *primary xylem*. It is composed of two parts. The xylem formed first is nearest the centre of the stem and is called *protoxylem*. The more peripheral part of the primary xylem is known as *metaxylem*.

The xylem is composed of three different types of cells— tracheary cells, that include *tracheids* and *vessels*; *wood fibres* and *wood parenchyma*.

The *tracheids* are elongated dead cells, with walls that are thick in some places and thin in others. They serve both as water conducting and as strengthening cells. The walls of the tracheids are heavily impregnated with lignin.

The *vessels* are composed of rows of tracheary cells the cavities of which are connected by the total or partial disappearance of the cross walls. The diameter of vessels is usually much greater than that of tracheids. They form long tubes, and therefore, they constitute the principal water-conducting elements of the dicotyledonous stem.

The tracheary cells may be divided into several types according to the method by which the walls are thickened. *Annular* tracheary cells have thickenings in the form of rings, while *spiral* tracheary cells have spiral thickenings. *Pitted* tracheary cells have walls which are uniformly thickened except for thin places in the form of pits. When ladder-like thickenings are present, the vessel is said to be *scalariform*.

The protoxylem is composed largely of annular and spiral vessels and parenchyma, while the tracheary elements of the secondary xylem are pitted.

The *wood fibres* are long, slender, pointed dead cells with greatly thickened walls and only comparatively few small pits. They serve as strengthening cells. The tracheids that have a structure approaching that of wood fibres are called *fibre tracheids*.

The parenchyma cells in the xylem are known as *wood parenchyma*. They serve mainly for the storage of food.

Phloem. The primary phloem of the dicotyledonous stems consists of three types of cells — sieve tubes, companion cells and phloem parenchyma.

The *sieve tubes* consist of thin-walled, elongated cells arranged in vertical rows. The adjacent cells of a sieve tube are united by small holes in the cross walls. The areas on the walls of sieve tubes which contain such holes are called *sieve plates*. The mature sieve tubes do not contain any nuclei. The sieve tubes serve primarily for the conduction of food material.

The *companion cells* are small cells which are attached to the sieve tubes. Each companion cell is the sister cell of a sieve-tube cell, the two being formed by the division of a mother cell.

The phloem contains parenchyma cells whose structure is very similar to that of other parenchyma cells. These are known as *phloem parenchyma*.

Cambium. There lies a layer of meristematic cells between the xylem and the phloem is known as the *cambium*. The cambium consists of a single layer of cells which, by division gives rise to xylem cells toward the centre of the stem and phloem cells toward the periphery. At first the cambium is confined to the bundles, but later the parenchyma cells of the pith rays which lie between the edges of the cambium in the bundles divide and form a layer of cambium which reaches across the pith rays and connects that in the bundles, so that the cambium becomes a continuous cylinder.

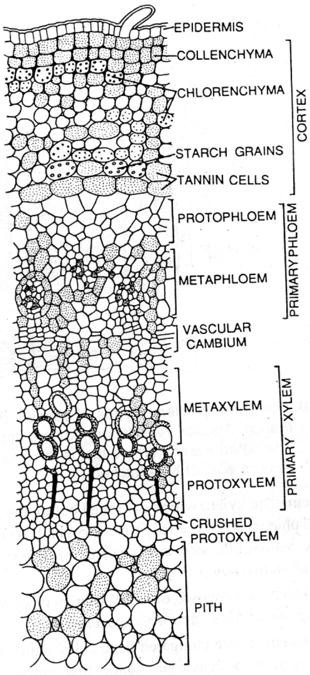


Fig. 10.11. Anatomy of dicotyledonous stem. T.S. of *Prunus* stem showing details.

Pith rays. The vascular bundles are separated from each other by radial rows of parenchyma cells known as pith rays. The pith-ray cells are usually elongated in a radial direction. They serve primarily for the conduction of food and water radially in the stem and for the storage of food.

Pith. In a dicotyledonous plant the centre of the stem is composed of thin-walled parenchyma cells and is known as the *pith*. The cells have distinct intercellular spaces.

VARIATIONS IN STEM STRUCTURE

The above mentioned description of structure of the stems is applicable to the great majority of dicotyledonous plants, but there are a few which show minor variations. The relative development of the various parts, however, varies greatly in different species. In some cases the pith is wide, while in

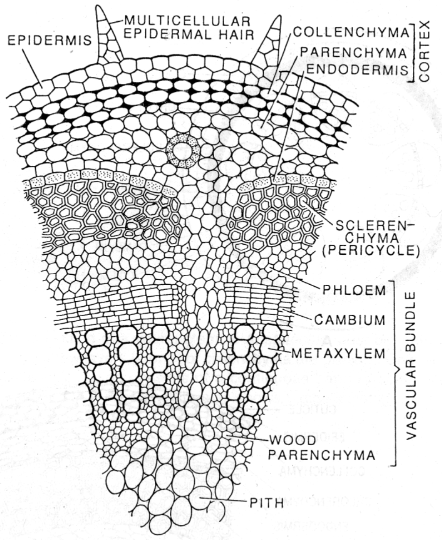


Fig. 10.12. T.S. of a dicotyledonous stem (*Helianthus annuus*).

hers it is narrow. It may be wide and transitory and its early disappearance results in a hollow stem. he vascular bundles vary considerably in number and size, while the pith rays and cortex vary in idth. Bundles which have the phloem only on the outside of the xylem are called *collateral* ndles. The bundles of some plants have phloem on both the outside and the inside of the xylem g., in the members of Cucurbitaceae) and known as *bicollateral* bundles.

NATOMY OF *CUCURBITA* STEM

Epidermis. This single outermost layer consists of compact barrel shaped cells having no ercellular spaces. The epidermis remains covered with a thin cuticle. Some of the epidermal cells ssess multicellular epidermal hairs.

Cortex. This region consists of external collenchyma, chlorenchyma (photosynthetic tissue) d endodermis.

(*a*) Collenchyma. This lies immediately beneath the epidermis consisting of many layers of e cells in the ridges, whereas in furrows it is only two or three layered or sometimes altogether sent.

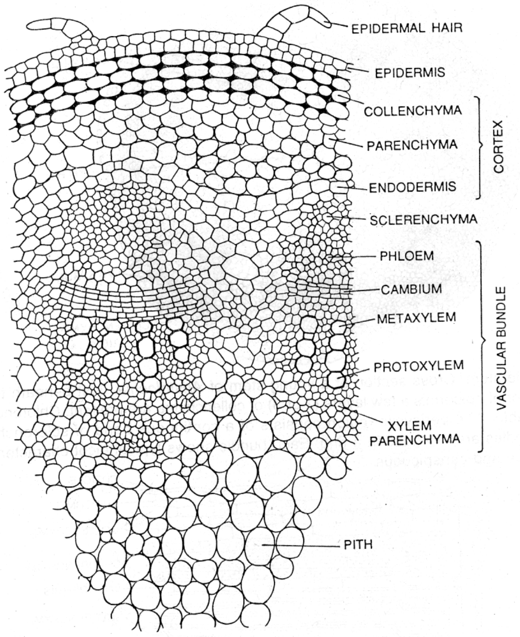


Fig. 10.16. T.S. of dicotyledonous stem (*Xanthium*).

(*c*) **Endodermis.** It is innermost layer of the cortex, lying immediately outside the sclerenchymatous zone of pericycle. This layer is wavy and contains many starch grains.

Pericycle. Just beneath the endodermis there is a multilayered zone of sclerenchymatous pericycle. The cells are lignified and appear polygonal in cross section.

Ground tissue. The vascular bundles are found lying embedded in the thin walled parenchyma cells of

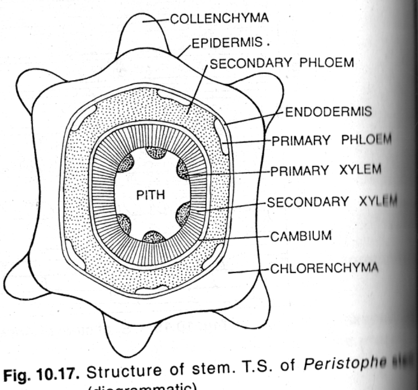


Fig. 10.17. Structure of stem. T.S. of *Peristophe* (diagrammatic).

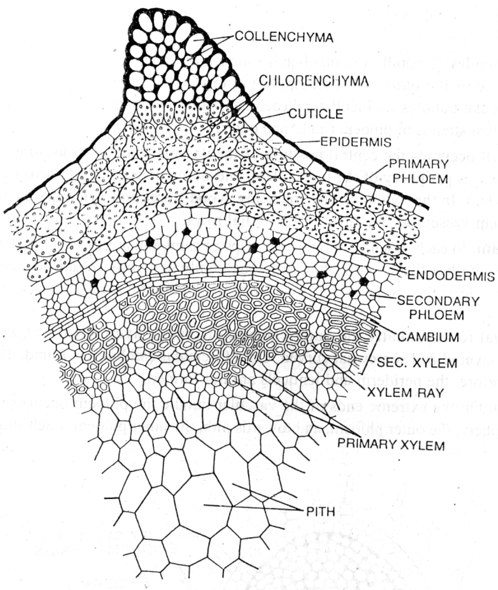
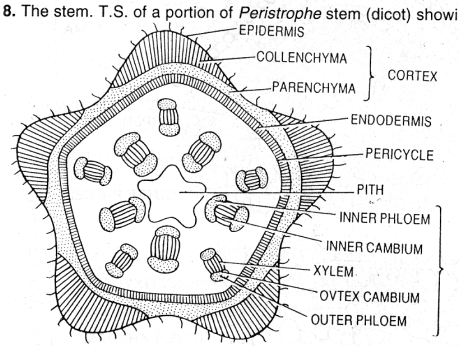


Fig. 10.18. The stem. T.S. of a portion of *Peristrophe* stem (dicot) showing detailed structure.



10.19. T.S. of *Cucurbita* stem (diagrammatic representation). Each vascular bundle possesses external and internal phloem (bicollateral bundles). Small strands of sieve tubes and companion cells traverse the parenchyma of the vascular region and the tissues of the cortex. (After K. Esau).

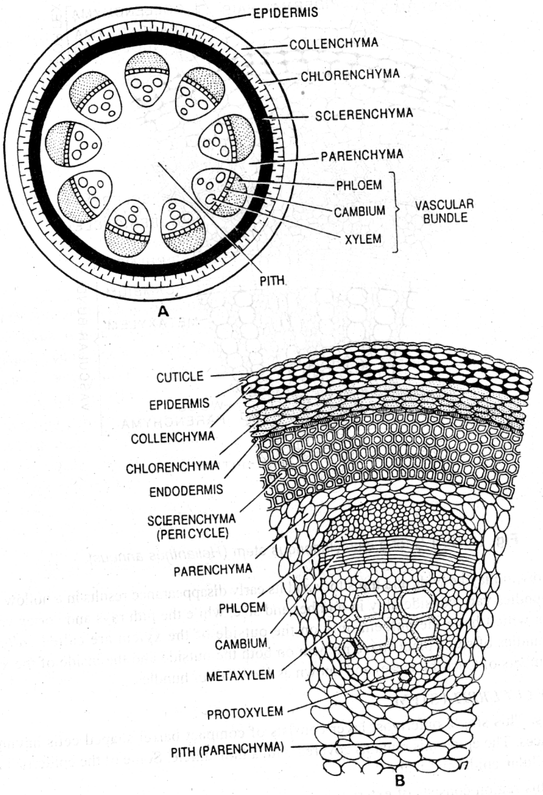
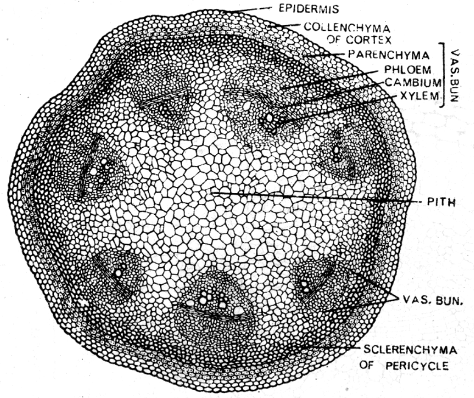


Fig. 10.13. Anatomy of dicot stem. T.S. of young stem of *Aristolochia*. A, diagramm
B, detail of a sector.

(*b*) **Chlorenchyma.** Just below the collenchyma two or three layers of parenchyma cont chloroplasts (chlorenchyma—photosynthetic tissue) present which help in the proce assimilation.



10.14.The stem. Cross section of a young stem of *Aristolochia*. Just beneath the uniseriate layer of epidermis a few layers (2 or 3) of collenchyma are present. Chlorenchyma is also visible. The pericyclic region consists of a continuous band of sclerenchyma. Seven bundles are arranged in a ring. Each bundle shows typical dicot characteristics. Pith is large and conspicuous.

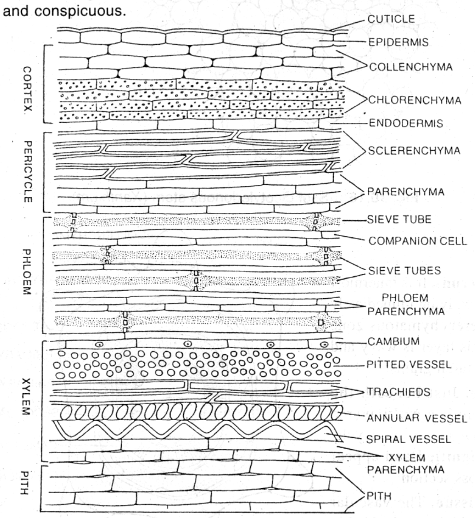


Fig. 10.15. L.S. of stem of *Aristolochia*

ground tissue. The ground tissue extends from just below the sclerenchymatous pericycle to the central medullary cavity.

Vascular bundles. Generally vascular bundles are ten in number which are found to be arranged in two rows, those of the outer row corresponding to the ridges and those of the inner to the furrows. The vascular bundles are bicollateral each consisting of xylem, two strips (inner and outer) of cambium and two strands of phloem (inner and outer).

***(a)* Xylem.** It occupies the central position of the vascular bundle, consisting of very wide, pitted vessels towards periphery of the metaxylem, and on the inner side of narrow vessels which form the protoxylem. In the xylem certain tracheids, wood fibres and xylem parenchyma are also present. The xylem vessels are not arranged in radial rows.

***(b)* Cambium.** In each vascular bundle two strips of cambium are found. The cambial activity remains confined within the vascular bundles. The cambial strip is found between xylem and phloem on either side of the bundle. Of the two strips of cambium it is only the external one which divides and causes growth in thickness. The cells of cambium are thin walled, rectangular and arranged in radial rows. Usually the outer cambium is many layered and flat while the inner cambium is few layered and somewhat curved. Only fascicular cambium is found. The stem is not woody, and therefore, the periderm and lenticels are not formed.

***(c)* Phloem.** On the extreme ends of the vascular bundle the phloem occurs in two patches, towards the periphery, the outer phloem, and towards pith, the inner phloem. Each strand of phloem consists of sieve tubes, companion cells and phloem parenchyma. Sieve tubes are very well developed. The sieve plates with perforations are also visible. Fibres and ray cells are absent.

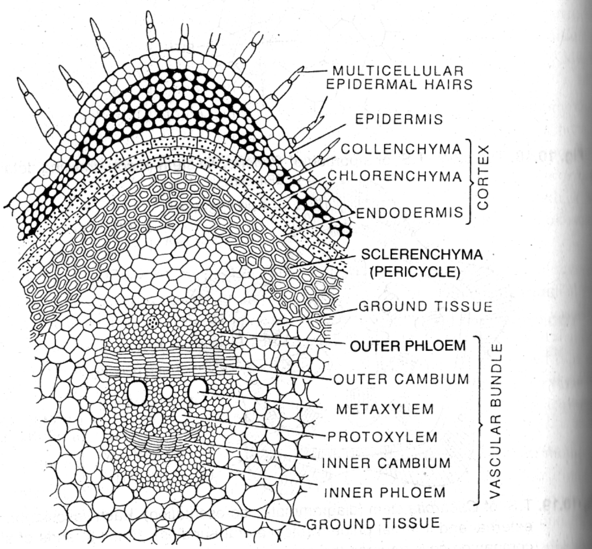


Fig. 10.20. T.S. of young *Cucurbita* stem (dicotyledonous) showing bicollateral vascular bund

SPECIAL STRUCTURE

The bicollateral open vascular bundles are found each consisting of xylem (central position), two strips of cambium (outer and inner) and two patches of phloem (outer and inner). (See figs. 10.19 and 10.20)

ANATOMY OF *BRYONIA* STEM

Epidermis. The single outermost layer consists of compact barrel shaped cells having no intercellular spaces. Usually the epidermis is covered with a thin cuticle. At certain places stomata are also found.

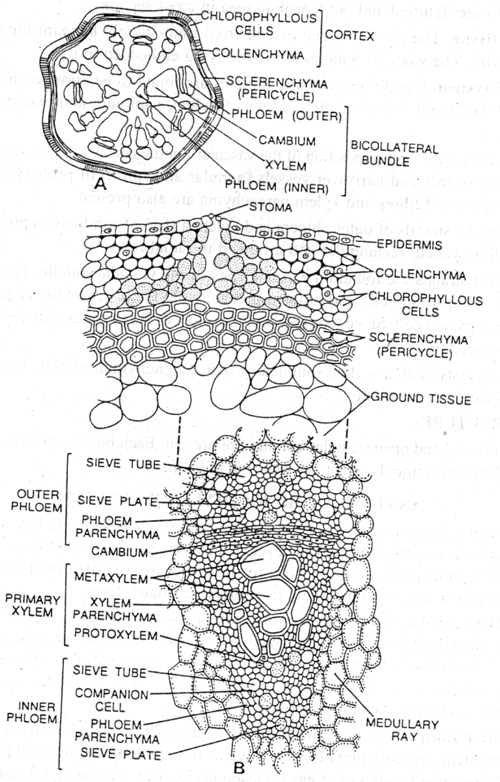


Fig. 10.21. *Bryonia* stem (Cucurbitaceae). Transverse section—A, diagrammatic; B, detailed structure.

Cortex. This consists of collenchyma, loose chlorenchyma and inconspicuous endodermis.

(*a*) **Collenchyma.** This lies immediately beneath the epidermis consisting of rounded or oval cells (in cross section) usually thickened laterally due to the presence of cellulose. The collenchymatous region is multilayered.

(*b*) **Chlorenchyma.** Below the collenchyma few layers of chlorenchyma are found. The cells are thin walled, rounded or oval, with chloroplasts and having intercellular spaces among them.

(*c*) **Endodermis.** The single layered endodermis is inconspicuous. The endodermal cells may contain abundant starch grains in them.

Pericycle. Immediately beneath the endodermis multilayered sclerenchymatous pericycle is found. The cells are lignified and polygonal as seen in cross section.

Ground tissue. The ground tissue extend from immediately beneath the pericycle to the central pith cavity. The vascular bundles are found lying embedded in it.

Vascular system. Usually the vascular bundles are found to be arranged in two rows. They are open and bicollateral. Each bundle consists of xylem, cambium and two strands (inner and outer) of phloem.

Xylem occupies the central position of the vascular bundle consisting of bigger vessels (pitted) of metaxylem outwards and narrower vessels (annular and spiral) of protoxylem towards pith. Certain tracheids, wood fibres and xylem parenchyma are also present.

In between the strands of outer phloem and xylem a strip of cambium is present. The cells of cambium are thin walled, rectangular and arranged in radial rows.

The phloem strands are found on extreme ends of the vascular bundle. Each strand consists of sieve tubes, companion cells and phloem parenchyma. Each sieve tube is accompanied by a conspicuous companion cell. Sieve tubes are well developed. Sieve plates with perforations are also visible in cross section.

Pith. It consists of thin-walled rounded or oval parenchymatous cells having well defined intercellular spaces among them.

SPECIAL STRUCTURE

The bicollateral and open vascular bundles are present. Each bundle consists of central xylem, a cambial strip and two strands (inner and outer) of phloem.

ANATOMY OF MONOCOTYLEDONOUS STEMS

The monocotyledonous stems are similar to dicotyledonous stems in having an *epidermis*, a *cortex* and a *stele*. The cortex may be well developed and sharply marked off from the stele, or it may be quite narrow and inconspicuous. It is in the structure and arrangement of bundles that monocotyledonous stems, differ markedly from dicotyledonous stems.

Stele. The vascular bundles of monocotyledonous stems, instead of being arranged in a cylinder as in dicotyledonous stems, are usually scattered throughout the stele, including the pith, so that there is no distinction between pith and pith rays. Sometimes the centre of the stele is free from vascular bundles and is occupied by parenchyma cells, which dry up and disappear at an early stage, resulting in a hollow stem, as in most grasses.

Vascular bundles. The vascular bundles of monocotyledonous stems are like those of dicotyledonous stems in consisting of xylem towards the centre of the stele and phloem towards the periphery. The vascular bundles of monocotyledonous stems do not possess a cambium layer which is found in dicotyledonous stems. This means that monocotyledonous stems usually do not have secondary thickening. Each bundle remains more or less completely surrounded by a sheath of sclerenchyma cells, the *bundle sheath*, which is particularly well developed on the sides toward the centre and toward the periphery of the stem. The phloem is made up mostly of sieve tubes and companion cells, and the xylem of vessels and wood parenchyma.

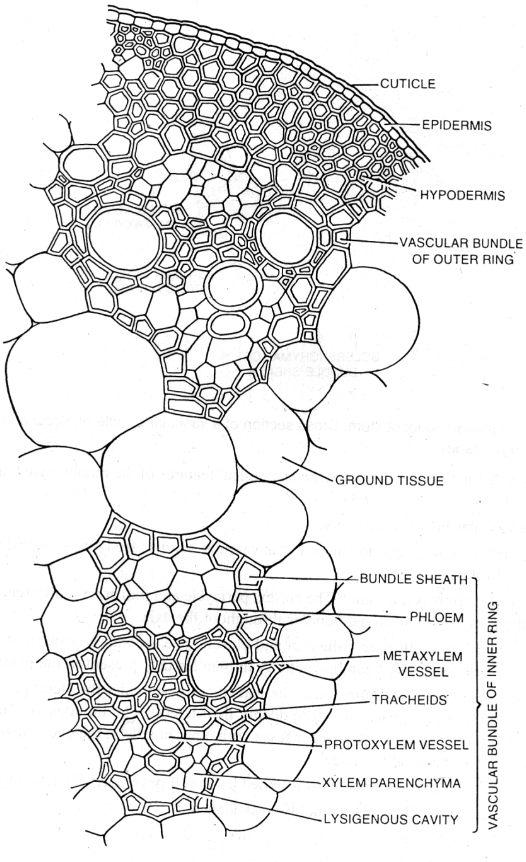


Fig. 10.22. T.S. of a portion of stem of grass (*Cynodon dactylon*) typical monocot stem, showing detailed internal structure.

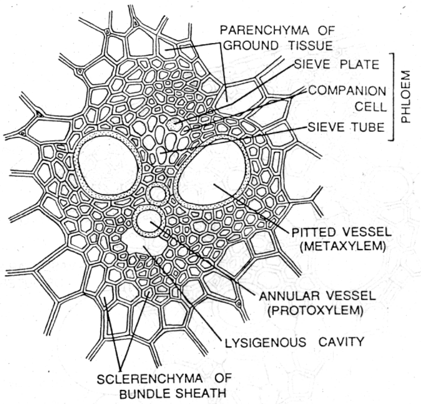


Fig. 10.23. Anatomy of monocot stem. Cross section of a vascular bundle of *Saccharum officinarum* (sugar cane).

The most distinctive and characteristic anatomical features of the monocotyledonous stem are as follows:

1. The vascular bundles are many.
2. The stele is broken up into bundles. The vascular bundles are lying scattered in the ground tissue of the axis.
3. The endodermis is not found. The cortex, pericycle and pith are not differentiated because of the presence of scattered bundles throughout the axis.
4. The vascular bundles are collateral and closed. The secondary growth of usual type is lacking, but vestiges of cambial activity in bundles may present in the plant body.
5. Leaf trace bundles are numerous. The leaf traces when enter the stem, penetrate deeply. The median traces penetrate more deeply than lateral. The bundles are common. Each common bundle somehow or other fuses with other bundle in the due course of time. The anastamoses occur at the nodes.
6. Each vascular bundle remains surrounded by a well developed sclerenchmytous sheath.
7. The vascular bundles are commonly oval shaped.
8. The phloem is represented by sieve tubes and companion cells only. The phloem parenchyma is not found.
9. The pith is not marked out.
10. Usually sclerenchymatous hypodermis is present.
11. Usually epidermal hairs are not present.

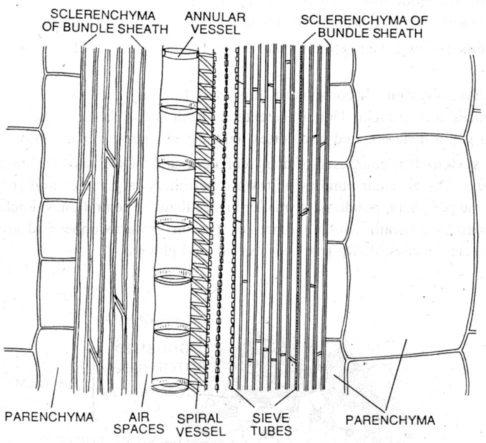


Fig. 10.24. Anatomy of monocot stem. L.S. of a vascular bundle of Saccharum officinarum (sugar cane).

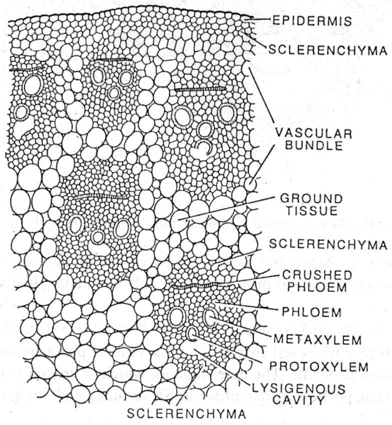


Fig. 10.25. The monocotyledonous stem. T.S. of maize stem showing sclerenchymatous hypodermis, parenchymatous ground tissue and vascular bundles.

form arms of Y and protoxylem, the base. Phloem consists of sieve tubes and companion cells. Bundle sheath is not found.

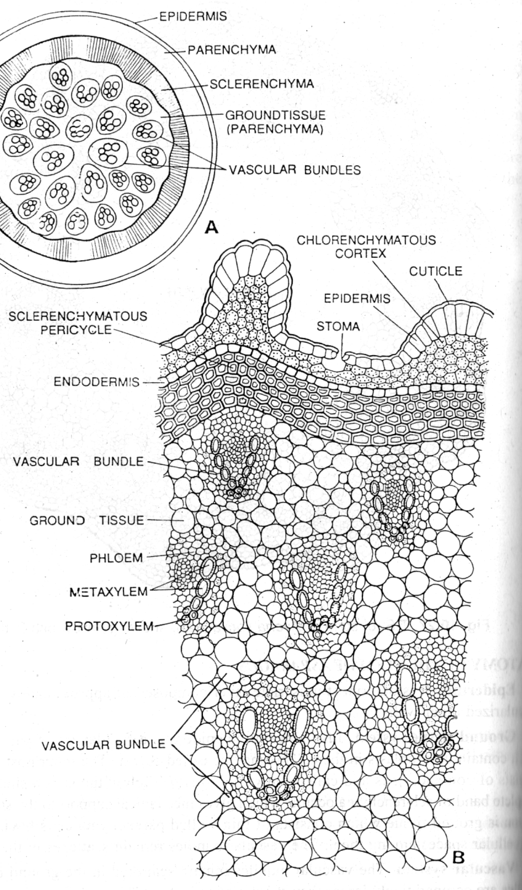


Fig. 10.28. Anatomy of monocotyledonous stem. T.S. of a vascular bundle of *Asparagus* lack secondary growth. Crushed protophloem and protoxylem are also seen.

ANATOMY OF THE SCAPE OF *CANNA*

Epidermis. It is the outermost uniseriate layer consisting of small, polygonal cells with cuticularized outer walls.

Ground tissue system. Just beneath the epidermis a few layers of parenchyma occur forming small cortical region. The cells of cortex are sufficiently large and polygonal. Immediately below the cortex, a single-layered chlorophyllous tissue is found consisting of chloroplast bearing cells. The sclerenchyma patches also remain attached to the chlorophyllous tissue here and there. The rest of the portion consists of a continuous mass of large, thin walled, parenchymatous cells having sufficiently developed intercellular spaces among them. It is called the ground tissue.

Vascular bundles. They are many and of various sizes, lying scattered in the ground tissue. The bundles are closed and collateral. Each bundle is incompletely surrounded by a sheath of sclerenchyma called *bundle sheath*. The outer sclerenchyma patch of the bundle is more distinct and cap like whereas inner patch is not so developed. Each bundle consists of xylem and phloem. The xylem is situated on the inner side and the phloem towards outer side. The xylem consists of a large spiral vessel with one or two smaller vessels of same nature. The phloem consists of sieve tubes and campanion cells.

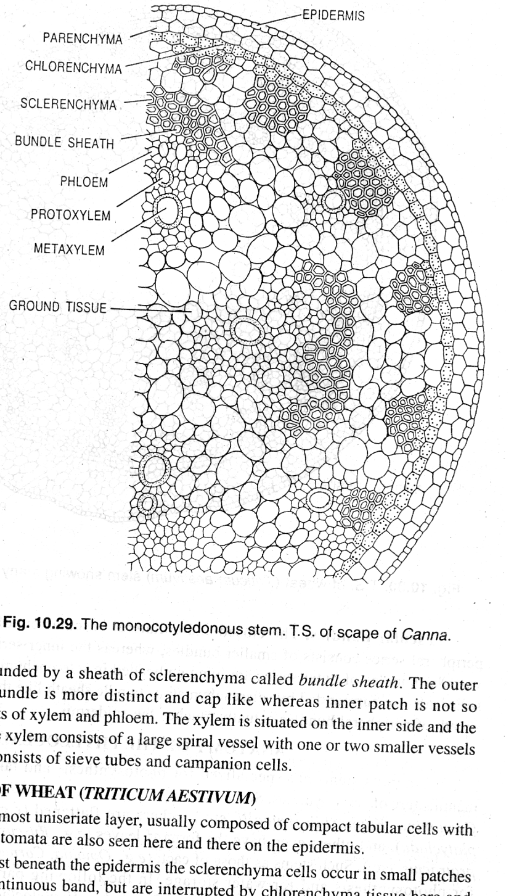


Fig. 10.29. The monocotyledonous stem. T.S. of scape of *Canna*.

ANATOMY OF THE STEM OF WHEAT (*TRITICUM AESTIVUM*)

Epidermis. It is the outermost uniseriate layer, usually composed of compact tabular cells with cuticularized outer walls. The stomata are also seen here and there on the epidermis.

Ground tissue system. Just beneath the epidermis the sclerenchyma cells occur in small patches which are not arranged in a continuous band, but are interrupted by chlorenchyma tissue here and there. The stomata are confined on the epidermis only in chlorenchymatous regions. The rest of the ground tissue consists of thin walled rounded or oval parenchyma cells having sufficiently developed intercellular spaces among them. The central region of the stem is hollow.

ANATOMY OF THE STEM OF *ZEA MAYS*

Epidermis. The epidermis consists of a single layer of compact cells having no intercellular spaces among them. It is covered with thick cuticle. The epidermal hairs are altogether absent.

Hypodermis. Below the epidermis, usually two or three layers of sclerenchyma cells represent hypodermis.

Ground tissue system. It consists of thin walled parenchyma cells having well-defined intercellular spaces among them. This tissue extends from below the sclerenchyma (hypodermis) to the centre. It is not differentiated into cortex, endodermis, pericycle and pith.

Vascular system. It is composed of many collateral and closed vascular bundles scattered in the ground tissue. The vascular bundles lie toward periphery in greater number than the centre. Comparatively the peripheral bundles are smaller in size than the central ones. Each bundle is more or less surrounded by a sheath, which is more conspicuous towards upper and lower sides of the bundle. The bundle consists of two parts, *i.e.*, xylem and phloem.

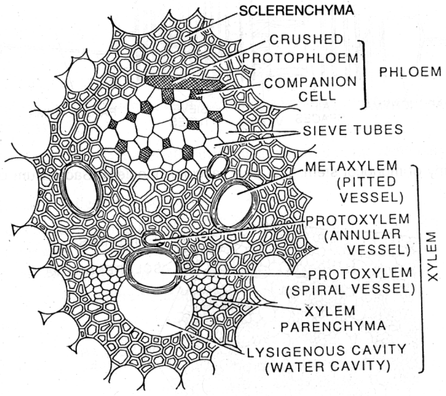


Fig. 10.26. A vascular bundle of maize stem—magnified.

Usually the xylem is Y-shaped and consists of pitted and bigger vessel of metaxylem and smaller vessels (annular and spiral) of protoxylem. In between metaxylem vessels, small pitted tracheids are also found. Around the lysigenous or water cavity wood parenchyma is present. The lysigenous cavity is formed by the breaking down of the inner protoxylem vessel.

Phloem consists of sieve tubes and companion cells. Phloem parenchyma is altogether absent in most of monocotyledonous stems. The outer phloem which is broken mass may be called as protophloem and the inner portion is metaphloem. Sieve tubes and companion cells are quite conspicuous.

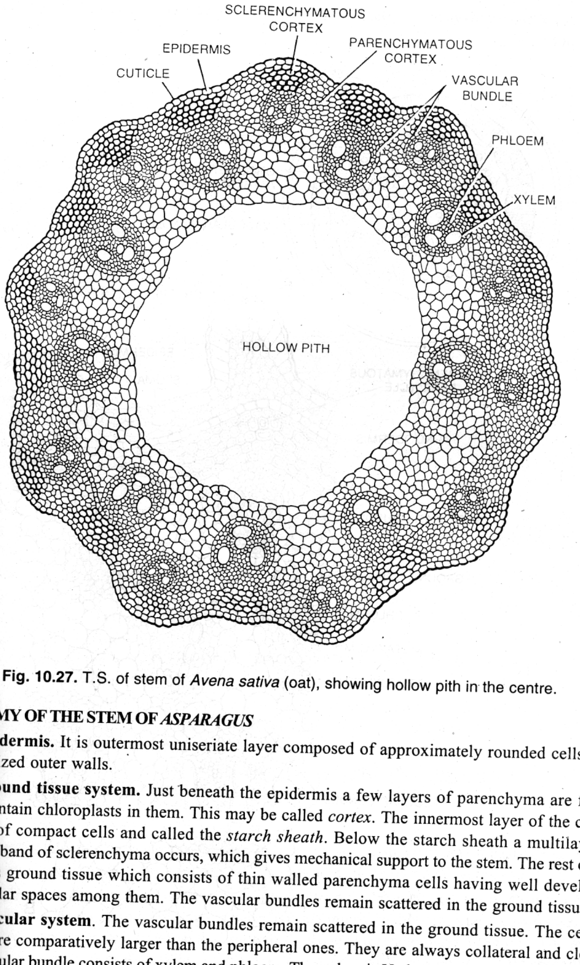


Fig. 10.27. T.S. of stem of *Avena sativa* (oat), showing hollow pith in the centre.

ANATOMY OF THE STEM OF *ASPARAGUS*

Epidermis. It is outermost uniseriate layer composed of approximately rounded cells with cuticularized outer walls.

Ground tissue system. Just beneath the epidermis a few layers of parenchyma are found which contain chloroplasts in them. This may be called *cortex*. The innermost layer of the cortex consists of compact cells and called the *starch sheath*. Below the starch sheath a multilayered complete band of sclerenchyma occurs, which gives mechanical support to the stem. The rest of the portion is ground tissue which consists of thin walled parenchyma cells having well developed intercellular spaces among them. The vascular bundles remain scattered in the ground tissue.

Vascular system. The vascular bundles remain scattered in the ground tissue. The central bundles are comparatively larger than the peripheral ones. They are always collateral and closed. Each vascular bundle consists of xylem and phloem. The xylem is Y-shaped. The metaxylem vessels

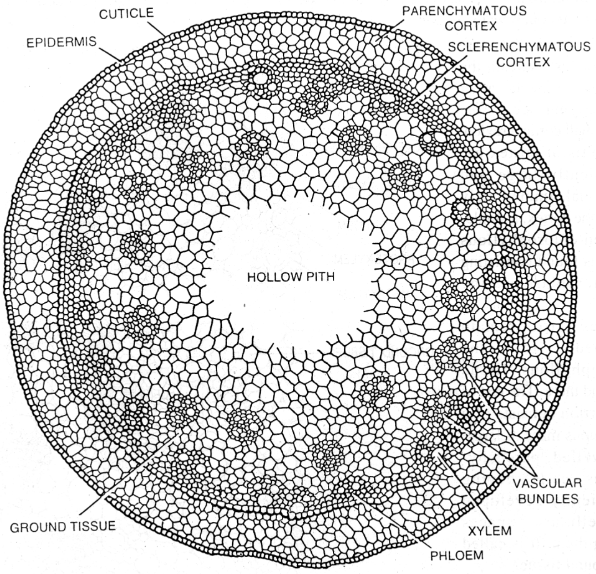


Fig. 10.30. T.S. of wheat (*Triticum aestivum*) stem showing many closed vascular bundles.

Vascular bundles. The closed and collateral vascular bundles occur in two series. The peripheral series consists of smaller bundles, whereas the inner series is of bigger bundles. The vascular bundles of outer series are lying embedded in sclerenchyma band. The bundles of inner series are also surrounded by sclerenchymatous bundle sheath like that of maize stem. The bundle sheath of peripheral bundles actually touches the epidermis.

ANATOMY OF THE PHYLLOCLADE

Numerous stems are specialized for photosynthesis and take the place of leaves in the manufacture of carbohydrates. Some stems which are specialized for photosynthesis are round (*e.g.*, *Casuarina*, *Euphorbia tirucalli,* etc.), others are flattened (*e.g.*, Cocoloba-*Muehlenbeckia platyclada*), and others even have the form of leaves (*e.g.*, *Ruscus*, *Myrsiphyllum*, *Phylloclada protractus,* etc.). Such stems as those of cacti (*e.g.*, *Opuntia*, *Carnegiea,* etc.) are specialized both for photosynthesis and for water storage. In the following paragraphs, the anatomy of the phylloclade of cocoloba—(*Muehlenbeckia platyclada*—*Homalocladium platycladum*) and *Ruscus* has been discussed.

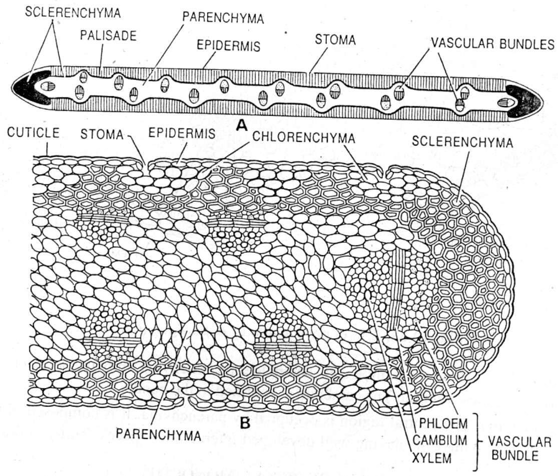


Fig. 10.31. *Homalocladium platycladum* (*Muehlenbeckia platycladus*)—phylloclade (dicot.). A. transection of phylloclade (diagrammatic); B, transaction of phylloclade showing detailed structure. The stomata, the cambium, the vascular bundles, the sclerenchyma and the chlorophyllous cells are clearly visible.

ANATOMY OF THE PHYLLOCLADE OF COCOLOBA (*HOMALOCLADIUM-PLATYCLADUM—MUEHLENBECKIA PLATYCLADA*). DICOT.

Epidermis. The surfaces are bounded on both the sides by upper and lower epidermal layers. A thin cuticle covers the epidermis. The epidermis is interrupted by numerous stomata on both the surfaces. Distinct guard cells of the stomata and sub-stomatal chambers are visible.

Chlorenchyma. Just beneath the epidermis there are few layers of chlorophyllous cells. The chlorophyllous cells are found only underneath the upper and lower epidermal layers. However, the chlorenchyma is not found at the edges of the phylloclade. The stomata are confined to chlorophyllous regions. There are well developed intercellular spaces among these cells. This is assimilatory tissue.

Sclerenchyma. The multilayered sclerenchyma tissue is found at the edges of the phylloclade. This is meant for mechanical strength. Just below the chlorenchyma there is a single layer of sclerenchyma cells, which delimits the central parenchyma and the peripheral chlorenchyma. Usually each vascular bundle is capped by a well developed sclerenchymatous patch.

Vascular bundles. Around the central parenchyma the vascular bundles are found to be arranged in the peripheral region. The vascular bundles of the two corners are bigger in size than the remaining ones. Each vascular bundle is capped by a sclerenchymatous patch, and is composed of xylem, phloem and cambium. The xylem consists of metaxylem and protoxylem groups. The xylem parenchyma is also present. The phloem strand lies towards periphery. The phloem is

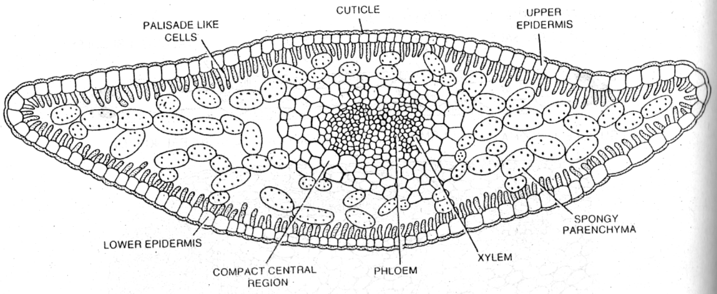


Fig. 10.32. T.S. of phylloclade of *Asparagus* (monocot).

composed of sieve tubes, companion cells and phloem parenchyma. In between xylem and phloem strands there lies the cambium. The cambium is confined to the bundle.

Parenchyma. The central region is occupied by parenchyma. It is composed of thin-walled, rounded or oval, living cells having well developed intercellular spaces. This is storage tissue.

ANATOMY OF THE PHYLLOCLADE OF *RUSCUS* (MONOCOT)

Epidermis. The phylloclade possesses two surfaces (upper and lower). Both the surfaces remain bounded by upper and lower epidermal layers. The upper epidermis consists of a single row of radially elongated epidermal cells. The epidermis is interrupted by stomata at certain places. The sub-stomatal chambers and guard cells with chloroplasts are distinctly seen. The upper surface becomes somewhat bulged in the central region. The lower surface in the central region becomes somewhat angular, otherwise the anatomy of the lower epidermis is quite similar to that of upper epidermis.

Chlorenchyma. Immediately below the upper epidermis few layers of chlorophyllous cells are present. These cells are rounded or oval shaped, containing chloroplasts and having well developed intercellular spaces among them. In between upper and lower epidermis the well developed parenchyma is present.

Vascular system. It is well developed and represented by many amphivasal.(phloem surrounded by xylem) vascular bundles. The phloem bundles remain surrounded by a sclerenchymatous sheath. The phloem consists of sieve tubes and companion cells.

SECONDARY GROWTH IN DICOTYLEDONOUS STEMS

The primary body of the plant is developed from the apical meristem. Sometimes as in monocotyledons and pteridophytes, the primary plant body is complete in itself and does not grow in thickness by cambial activity. However, in dicotyledons, the primary permanent tissues make the fundamental parts of the plant, and the further growth in thick mness is completed by cambial activity, called *secondary growth in thickness*. The tissues, formed during secondary growth are called *secondary tissues*. Secondary tissues may be of two types—the vascular tissues that are

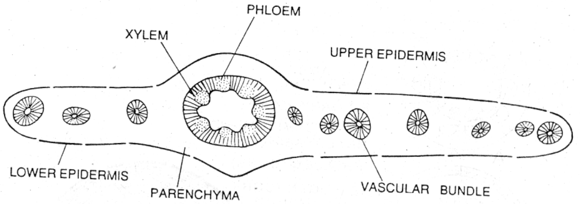


Fig. 10.33. *Ruscus* (monocot). Transection of phylloclade (diagrammatic).

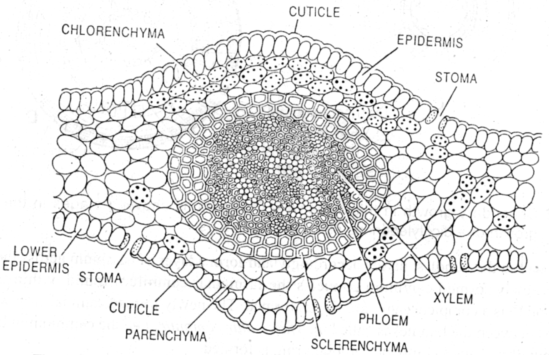


Fig. 10.34. *Ruscus* (monocot). Transection of phylloclade (detail).

called *secondary tissues*. Secondary tissues may be of two types—the vascular tissues that are developed by the true cambium, and cork and phelloderm, which are formed by phellogen or cork-cambium.

In a typical dicotyledonous stem, the secondary growth starts in the intra- and extrastelar regions. The process is as follows.

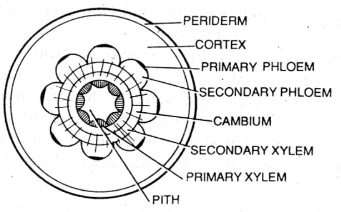


Fig. 10.35. Secondary growth. A herbaceous stem with some secondary growth.

CAMBIUM

The vascular bundles of dicotoledonous stems are collateral and open, and arranged in a ring. They contain a single layer of cambium cells, which separate the xylem from the phloem, called *fascicular cambium*, *i.e.*, the cambium of the vascular bundle, (*fascicle* = bundle). When the primary xylem and primary phloem are first differentiated there is no cambium across the pith rays or medullary rays to connect the edges of the cambium within vascular bundles. As soon as the differentiation of the first xylem and phloem of the bundles takes place, the cells of the pith or medullary rays which lie in between the edges of the

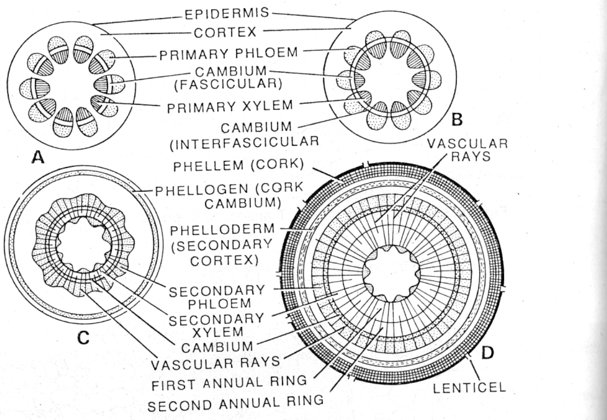


Fig. 10.36. Secondary growth in thickness. A – D, diagrams showing stages in the secondary growth of a dicotyledonous stem upto two years.

cambium within the bundles, divide accordingly and form a layer of cambium across the medullary rays. The newly formed cambium connects the fascicular cambilum found within the vascular bundles, and thus a complete cambium ring is formed. The newly formed cambial strip which occurs in the gaps between the bundles is called *interfascicular cambium*, *i.e.*, the cambium in between two vascular bundles. Thus a complete cambium ring is formed.

The cambium layer consists essentially of a single layer of cells. These cells divide in a direction parallel with the epidermis. Each time a cambial cell divides into two, one of the daughter cells remains meristematic, while the other is differentiated in to a permanent tissue. If the cell that is differentiated is next to the xylem it forms xylem, while if it is next to phloem it becomes phloem towards the outer side of the cambium. The cambium cells divide continuously in this manner producing secondary tissues on both sides of it. In this way, new cells are added to the xylem and the phloem, and the vascular bundles increase in size. While there is more or less alternation in the production of xylem and phloem cells from a cambium cell, more cells are formed on the xylem side than on the phloem side. The cells formed from the cambium in the region of the pith rays become pith-ray cells. The activity of the cambium thus increases the length of the pith rays grow equally. (See Figs. 8.2 and 8.3).

The formation of new cells from the cambium result in an enlargement of the stem that is known as the secondary thickening. The formation of new cells in secondary thickening continues throughout the life of the plant. It is in this way that the trunks of trees continue to grow in diameter. The cambium perpetuates and remains active for a considerable long period of time.

The thin-walled cells of the vascular cambium are highly vacuolate and in this respect are unlike most other meristematic cells. The electron microscopic structure reveals their highly vacuolate nature. Many ribosomes and dictyosomes, and well developed endoplasmic reticulum, are present (Srivastava, L.M., 1966).

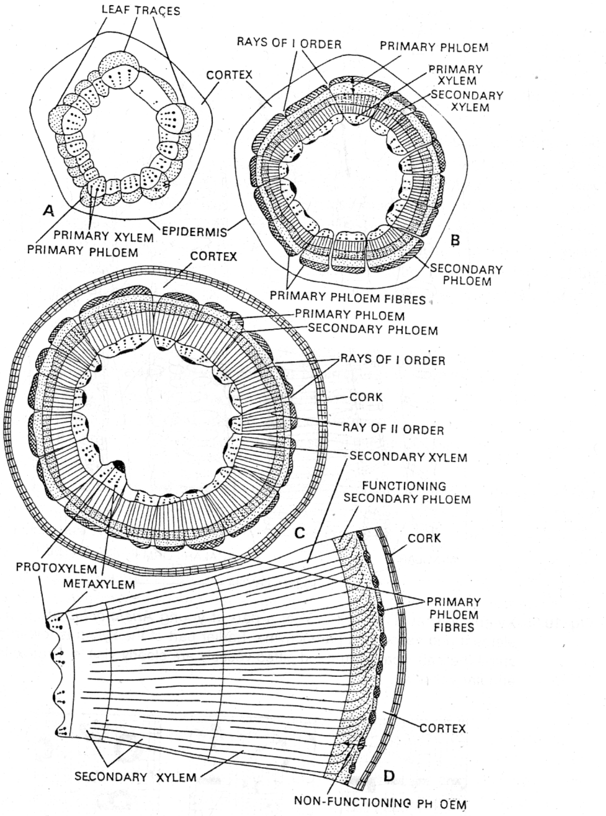


Fig. 10.37. Secondary growth. A – D, primary and secondary structure of *Prunus* stem in transverse sections.

SECONDARY XYLEM

The cambium ring cuts off new cells on its inner side are gradually modified into xylary elements, called the *secondary xylem*. This tissue serves many important functions, such as conduction of water and nutrients, mechanical support, etc. The secondary xylem of tree trunks is of great economic value, since it constitutes the timber and wood of commerce.

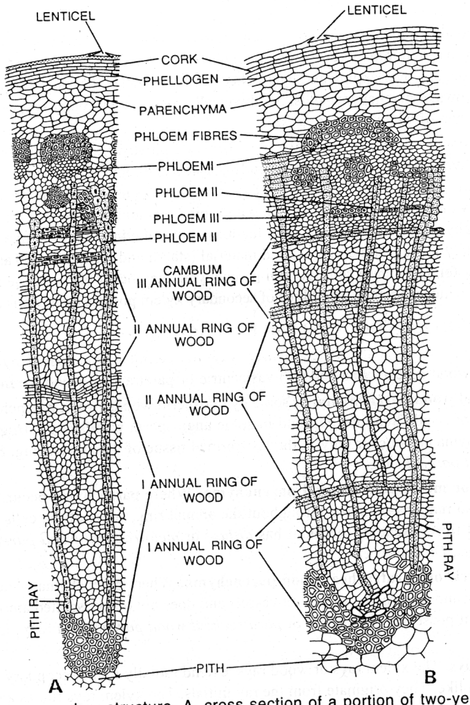


Fig. 10.40. Stem—secondary structure. A, cross section of a portion of two-year old stem of *Liriodendron tulipifera*, B, cross section of a portion of three-year old stem of *Liriodendron tulipifera* (tulip tree) with three annual rings of wood.

ANNUAL RINGS OR GROWTH RINGS.

The secondary xylem in the stems of perennial plants commonly consists of concentric layers, each one of which represents a seasonal increment. In transverse section of the axis, these layers appear as rings, and are called *annual rings* or *growth rings*. They are commonly termed as annual rings because in the woody plants of temperate regions and in those of tropical regions where there is an annual alternation of growing and dormant period, each layer represents the growth of one year. The width of growth rings varies greatly and depends upon the rate of the growth of tree. Unfavourable growing seasons produce narrow rings, and favourable seasons wide ones. Annual or growth rings are characteristic of woody plants of temperate climates. Such rings are weakly developed in tropical forms except where there are marked climate changes such as distinct moist and dry seasons. Annuals and herbaceous stems show, naturally, but one layer.

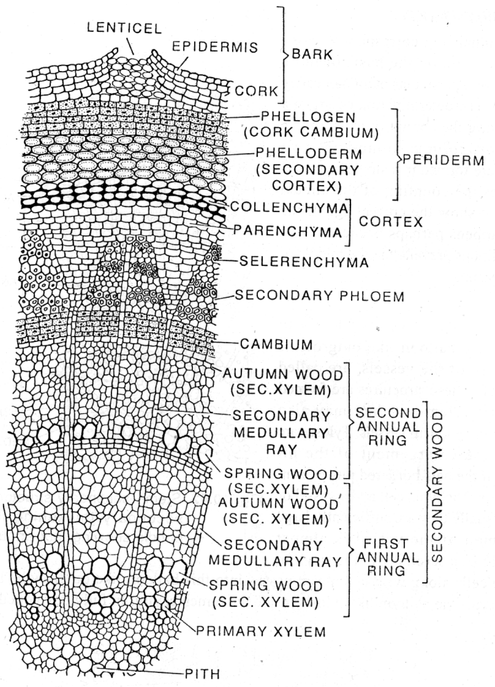


Fig. 10.41. Secondary growth in thickness. T.S. of a two-year old dicotyledonous stem.

In regions with a pronounced cold season, the activity of the cambium takes place only during the spring and summer seasons thus giving rise the growth in diameter of woody plants. The wood of one season is sharply distinct from that of the next season. In spring or summer the cambium is more active and forms a greater number of vessels with wider cavities. As the number of leaves increases in the spring season, additional vessels are needed for the transport of sap at that time to supply the increased leaves. In winter or autumn season, however, there is less need of vessels for sap transport, the cambium is less active and gives rise to narrow pitted vessels, tracheids and wood fibres. The wood developed in the summer or spring season is called *spring wood* or *early wood*, and the wood formed in winter or autumn season is known as *autumn wood* or *late wood*. However, the line of demarcation is quite conspicuous between the late wood of one year and the early wood of next year. An annual ring, therefore, consists of two parts—an inner layer, early wood, and an outer layer late wood.

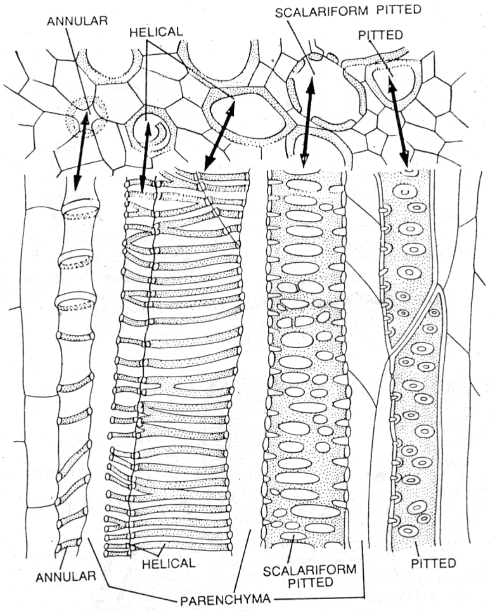


Fig. 10.38. Xylem. vessel. T.S. and L.S. of a part of young *Aristolochia* stem showing vessel element and associated parenchyma. Earlier part of the xylem is towards left. Annular, spiral (helical), scalariform and pitted vessels are clearly visible. Protoxylem consists of annular vessels.

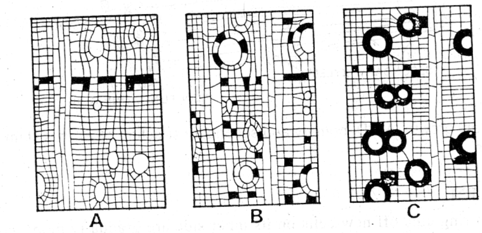


Fig. 10.39. Secondary xylem. Diagrams showing distribution of wood parenchyma, the parenchyma cells are shaded. A, terminal; B, diffuse; C, vasicentric. (After E and M).

The secondary xylem consists of a compact mass of thick-walled cells so arranged as to form two systems—a longitudinal (vertical) and a transverse radiating system. The longitudinal system consists of elongate, overlapping and interlocked cells—tracheids, fibres and vessel elements—and longitudinal rows of parenchyma cells. All these cells possess their long axes parallel with the long axis of the organ of which they are a part.

The secondary xylem consists of scalariform and pitted vessels, tracheids, wood fibres and wood parenchyma. These elements of secondary xylem are more or less similar to those occur in primary xylem. Vessels or tracheae are most abundant and are usually shorter than those of primary xylem. Mostly the vessels are pitted. Annular and spiral tracheids and vessels are altogether absent. Xylem parenchyma cells may be long and fusiform, but sometimes they are short. They are living cells and usually meant for storage of food material (starch and fat) in them. Tannins and crystals are frequently found in these cells. Xylem parenchyma may occur either in the association of the vessels or quite independently. The fibres of secondary xylem possess thick walls and bordered pits.

DISTRIBUTION OF WOOD (XYLEM) PARENCHYMA

Wood parenchyma is distributed in *three* ways: (*i*) Terminal wood parenchyma; (*ii*) diffuse or metatracheal wood parenchyma and (*iii*) vasicentric or paratracheal wood parenchyma.

Terminal wood parenchyma. In some gymnosperm woods, wood parenchyma is absent; in other (*e.g.*, *Larix* and *Pseudotsuga*), and in some angiosperm woods (*e.g.*, *Magnolia* and *Salix*), wood parenchyma cells occur only in the last-formed tissue of the annual ring. Such woods have *terminal wood parenchyma.*

Diffuse or metatracheal wood parenchyma. Where parenchyma occurs not only in this region, but also remains scattered throughout the annual ring, some of the cells lying among the tracheids, and fibre-tracheids the plant has *diffuse* or *metatracheal wood parenchyma* (*e.g.*, in *Malus*, *Quercus*, *Diospyros* etc.).

Vasicentric or paratracheal wood parenchyma. Where parenchyma occurs at the edge of the annual ring and elsewhere only about vessels and does not occur isolated among tracheids and fibres, the plant possesses *vasicentric* or *paratracheal wood parenchyma* (*e.g.*, in *Acer*, *Fraxinus* etc.).

Xylem rays. The xylem rays or wood rays, extend radially in the secondary xylem. They are strap or ribbon like. They originate from the ray initials. The xylem rays run as a continuous band to the secondary phloem through the cambium, thus forming a continuous conducting system. All vascular rays are initiated by the cambium and, once formed, are increased in length indefinitely by the cambium. Commonly these rays are known as medullary rays, or pith rays, on the basis of their similarity and parenchymatous nature with the pith rays of herbaceous dicotyledonous stems. These radial rays may be best called *vascular rays*, as these rays are of vascular tissue partly of xylem and partly of phloem.

The xylem rays traverse in the secondary xylem and establish communication with the living cells of the vascular tissue. In gymnosperm wood where no wood parenchyma is present, every tracheid is in direct contact with at least one ray. Vessels also in their longitudinal extent, come into contact with many rays. In herbaceous stems, such as of *Ranunculus*, where vascular bundles are separated by projecting parenchymatous wedges, and in vines, such as *Clematis*, where the bundles are separated by bands of secondary parenchyma, vascular rays are not found. The xylem rays help in the exchange of gases. They also aid in the conduction of water and food from phloem to the cambium and xylem parenchyma.

DENDROCHRONOLOGY

Each annual ring corresponds to one year's growth, and on the basis of these rings the age of a particular plant can easily be calculated. The determination of age of a tree by counting the annual rings is known as *dendrochronology*. Sometimes two annual rings are formed in a single year, and in such cases the counting of the annual rings does not show the correct age of the tree. This happens perhaps because of the drought conditions prevailed in the middle of a growing season.

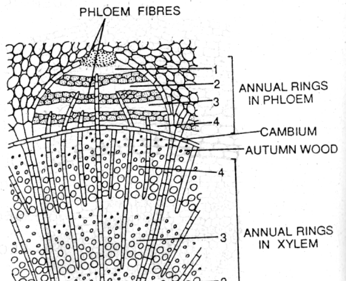


Fig. 10.42. Stem—secondary structure. Diagram of secondary thickening in a vascular bundle showing four annual rings.

TYLOSES

In many plants, the walls of the xylem vessels produce balloon like outgrowths into the lumen of the vessels, are called *tyloses*. Usually these structures are formed in secondary xylem but they may also develop in primary xylem vessels. Tyloses are formed by the enlargement of the pit membranes of the half-bordered pits present in between a parenchyma cell and a vessel or a tracheid. Usually they are sufficiently large and the lumen of the vessel is almost blocked. The nucleus of the xylem parenchyma cells along with cytoplasm passes into this balloon like outgrowth. The delicate pit membrane forms the balloon like tylosis inside the lumen cavity. In fully developed tyloses, starch crystals, resin gums and other substances are found, but they are not found very frequently. The wall of tylosis may remain thin and membranous or very rarely it becomes thick and even lignified. The tylosis may remain very small or sufficiently large in size as the case may be. They may be one

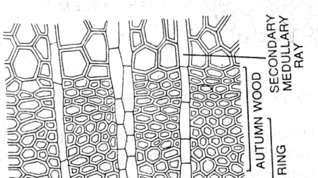


Fig. 10.43. Annual rings. An annual ring in sectional view (magnified).

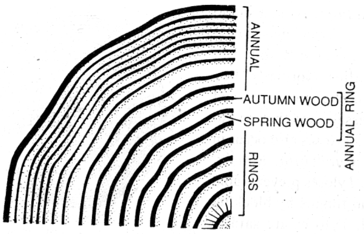


Fig. 10.44. Annual rings (growth rings)—cut surface of a stem showing annual rings.

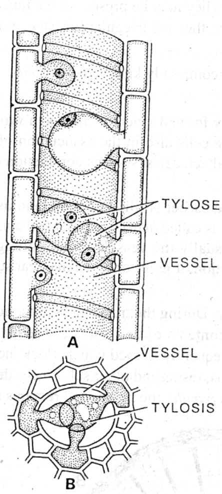


Fig. 10.45. Tyloses. A, L.S. of vessel with tyloses; B, T.S. of vessel with tyloses.

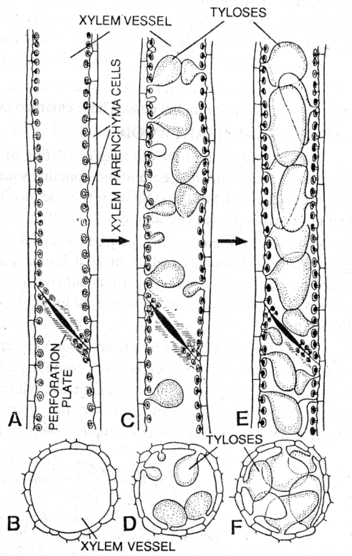


Fig. 10.46. Tyloses. A – F, development of tyloses in xylem vessels depicted in L.S. and T.S.

or few in number (*e.g.*, in *Populus*) in a single cell or many (*e.g.*, in white oak) and may fill the complete cell. They are commonly found in many angiospermic families. Normally they develop in the heart wood of angiosperms and block the lumen of the vessels, and thus add to the durability of the wood. Tyloses also occur in the vessels of *Coleus*, *Cucurbita*, *Rumex*, *Asarum* and *Convolvulus*. Tyloses prevent rapid entrance of water, air and fungus by blocking the lumen of the vessel. Tyloses are said to undergo division in some plants and form *multicellular tissue*, which fills the lumen compactly, as in *Robinia* and *Maclura*. The tyloses are characteristic of certain species, and always absent in others. In many plants the development of tylosis takes place by means of wounding. They may be present in the inner part of leaf traces after the leaf has fallen. Such tyloses occur rarely; they are irregular in shape and size.

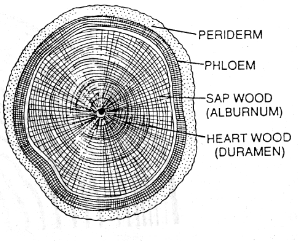


Fig. 10.47. T.S. branch of *Fraxinus*, showing heart and sapwood. (diagrammatic).

In the wood of conifers there is also found a closing of the cavity of resin canals by the enlargement of the epithelial cells. These enlarged cells are commonly known as *tylosoids*.

SAPWOOD AND HEARTWOOD

The outer region of the old trees consisting of recently formed xylem elements in *sapwood* or *alburnum*. This is of light colour and contains some living cells also in the association of vessels and fibres. This part of the stem performs the physiological activities, such as conduction of water and nutrients, storage of food, etc.

The central region of the old trees, which was formed earlier is filled up with tannins, resins, gums and other substances which make it hard and durable, is called *heartwood* or *duramen*. It looks black due to the presence of various substances in it. Usually the vessels remain plugged with tyloses. The function of heartwood is no longer of conduction, it gives only mechanical support to the stem.

The sapwood changes into heart wood very gradually. During the transformation a number of changes occur—all living cells lose protoplasts; water contents of cell walls are reduced; food materials are withdrawn from the living cells; tyloses are frequently formed which block the vessels; the parenchyma walls become liginified; oils, gums, tannins, resins and other substances develop in the cells. In certain plants—for example, *Ulmus* and *Malus pumila*, the heartwood remains saturated with water; in other plants, for example, in *Fraxinus* the heartwood may become very dry. The oils, resins and colouring materials infiltrate the walls, and gums and resins may fill the lumina of the cells. In *Diospyros* and *Swietenia*, the cell cavities are filled with a dark-coloured gummy substance. The colour of heartwood, in general, is the result of the presence of these substances. Generally the heartwood is darker in colour than sapwood. However, in some genera, such as *Betula*, *Populus*, *Picea*, *Agathis* the heartwood is hardly darker in colour than the sapwood.

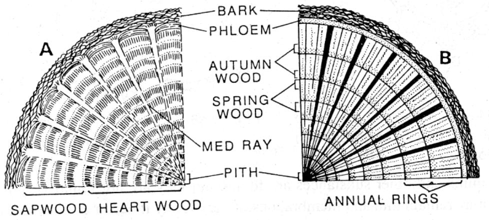


Fig. 10.48. Transections of old dicot stems—left, sector showing heartwood and sapwood; right sector showing annual rings.

The proportion of sapwood and heartwood is highly variable in different species. Some trees do not have clearly differentiated heartwood (*e.g.*, *Populus*, *Salix*, *Picea*, *Abies*), others possess thin sapwood (*e.g.*, *Robinia*, *Morus*, *Taxus*), the still others possess a thick sapwood (*e.g.*, *Acer*, *Fraxinus*, *Fagus*).

From economic point of view, heartwood is more useful than sapwood. Heartwood, as timber, is more durable than sapwood, because the reduction of food materials available for pathogens by the absence of protoplasm and starch. The formation of resins, oils and tannins, and the blocking of the vessels by tyloses and gums, render the wood less susceptible to attack by the organisms of decay. The haemotoxylin is obtained from the heartwood of *Haematoxylon campechianum*. Because of the absence of resin, gums and colouring substances, sapwood is preferred for pulpwood, and for wood to be impregnated with preservatives.

SECONDARY PHLOEM

The cambial cells divide tangentially and produce secondary phloem elements towards outside of it. Normally, the amount of secondary phloem is lesser than the amount of secondary xylem. In most of the dicotyledons; usually the primary phloem becomes crushed and functionless and the secondary phloem performs all physiological activities for sufficiently a long period of time.

This is a complex tissue made up of various types of cells having common origin in the cambium. These cells are quite similar to the cells of primary phloem. However, the secondary phloem

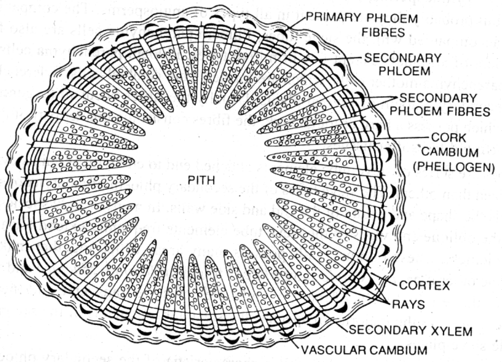


Fig. 10.49. T.S. of grapevine (*Vitis vinifera*) stem, showing arrangement of the vascular tissues. The epidermis, the cortex and the primary phloem were cut off by the activity of the cork cambium which interpolated a layer of cork between primary and secondary phloem. (After K. Esau).

PERIDERM

Due to continued formation of secondary tissues, in the older stem, and roots, however, the epidermis gets stretched and ultimately tends to rupture and followed by the death of epidermal cells and outer tissues, and a new protective layer is developed called *periderm*. The formation of periderm is a common phenomenon in stems and roots of dicotyledons and gymnosperms that increase in thickness by secondary growth. Structurally, the periderm consists of three parts—1. a meristem known as *phellogen* or *cork cambium*, 2. the layer of cells cut off by phellogen on the outer side, the *phellem* or *cork*, and 3. the cells cut off by phellogen towards inner side, the *phelloderm*.

The periderm appears on the surface of those plant parts that possess a continuous increase in thickness by secondary growth. Usually the periderm occurs in the roots and stems and their branches in gymnosperms and woody dicotyledons. It occurs in herbaceous dicotyledons, sometimes limited to the oldest parts of stem or root.

Phellogen. In contrast to the vascular cambium, the phellogen is relatively simple in structure, and composed of one type of cells. The cells of phellogen appear rectangular in cross-section, and somewhat flattened radially. Their protoplasts are vacuolated and may contain tannins and chloroplasts. Except in the lenticels, intercellular spaces lacking.

When we consider the place of origin of the meristem forming the periderm, it becomes necessary to distinguish between the first periderm, and the subsequent periderms, which arise beneath the first and replace it as the axis increases in circumference. In most stems the first phellogen arises in the subepidermal layer. In a few plants the phellogen arises in the epidermal cells (*e.g.*, *Nerium*, *Pyrus*). Sometimes only a part of the phellogen is developed from epidermis while the other part arises in subepidermal cells (*e.g.*, *Pyrus*). In some stems the second or third cortical layer initiates the development of periderm (*e.g.*, *Robinia*, *Aristolochia*, *Pinus*, *Larix*, etc.). In still other plants the phellogen arises near the vascular region or directly in the phloem (*e.g.*, in *Caryophyllaceae*, *Cupressaceae*, *Ericaceae*, *Punica*, *Vitis*, etc.). If the first periderm is followed by the formation of others, these are formed repeatedly, in successively deeper layers of the cortex or phloem.

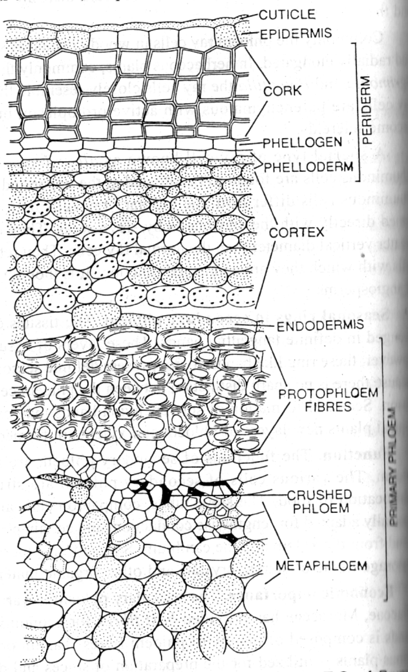


Fig. 10.51. Secondary growth in dicot stem. T.S. of *Prunus* stem showing periderm, cortex and primary phloem details.

At the time of the beginning of the development of a phellogen in epidermal cells, the protoplasts lose their central vacuoles and the cytoplasm increases in amount and becomes more richly granular. As soon as this initial layer develops, it divides tangentially and, to a lesser extent radially, in the similar way as division takes place in true cambium. The derivative cells are normally arranged in radial rows.

Generally, several to many times as many cells are cut off toward the outside (phellem-cork cells) as toward the inside (phelloderm). Phelloderm cells are few or absent; rarely phelloderm is greater in amount than phellem.

Phellem (cork cells). The cells that constitute phellem are commonly known as *cork cells*. They are like the phellogen cells from which they are derived. As seen in tangential section, they are polygonal and uniform in shape, and often radially thin as seen in cross section of the stem. The cells of the commercial cork (*Quercus suber*) are radially elongated as seen in transverse section. In the periderm of *Betula* and *Prunus*, the cork cells are elongated tangentially as seen in cross-section. There are no intercellular spaces among cork cells.

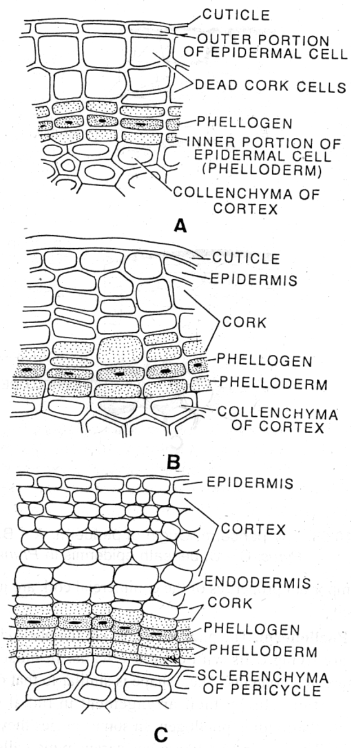


Fig. 10.52. Phellogen. Origin and its development. A, epidermal; B, hypodermal; C, deep-seated.

Commercial cork. The development of the periderm layers in the cork oaks (*Quercus suber*) is of special interest. The ability of the plant produce phellogen in deeper layers when the superficial periderm is removed is utilized in the production of commercial cork from the cork oak (*Quercus suber*). At the age of about twenty years, when the tree is about 40 cm in circumference, this outer layer, known as vi.gin cork is removed by stripping to the phellogen. The exposed tissue dries out to about 1/8 in. in depth. A new phellogen is established beneath the dry layer and rapidly produces a massive cork of a better quality than the first. After nine or ten years the new cork layer has attained sufficient thickness to be commercially valuable and is in turn removed. Of course, this cork is of better quality than the virgin cork, but of inferior quality than the cork obtained at the third and subsequent strippings. These strippings take place at intervals of about nine years until the tree is 150 or more years old. After the successive strippings the new phellogen layers develop at greater depth in the living tissue. The cortex is lost after few strippings and the subsequent cork layers are formed in the secondary phloem.

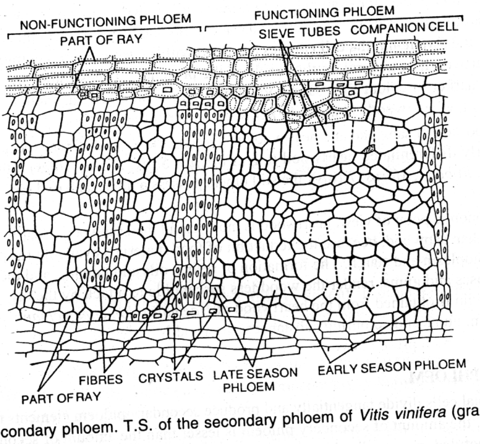


Fig. 10.50. Secondary phloem. T.S. of the secondary phloem of *Vitis vinifera* (grapevine). (After Esau).

possesses a more regular arrangement of the cells in radial rows. The sieve tubes are comparatively larger in number and posses thicker walls. The elements of secondary phloem are sieve tubes, companion cells, phloem parenchyma and phloem ray cells. Sometimes sclerenchyma is also found. Presence of sieve tubes is characteristic of angiosperms, however, they are not found in gymnosperms. In gymnosperms, sieve cells are present. The companion cells are not found in gymnosperms but probably they are present in all types of angiosperms. The companion cells are usually found accompanied with the sieve tubes. Phloem parenchyma cells are also found in the secondary phloem of all plants except few primitive types. Phloem parenchyma cells are formed directly from parenchyma mother cells, which are formed from cambial cells. Sclerenchyma is also found in the secondary phloem of several plants. Usually the fibres occur in tangential bands. In certain plants which possess a hard or tough bark, the fibres consist the greater part of the secondary phloem and surround the softer tissues.

Sieve tubes are series of sieve-tube elements attached end to end with certain sieve areas more highly specialized than others. The sieve tubes of the secondary phloem of dicotyledons are of many types as regards the shape and nature of the end and side walls. In many woody species (*e.g.*, *Carya cordiformis*), the oblique end walls of the sieve tube elements frequently extend for about half the length of the element. These oblique walls possess many areas which together make *compound sieve plates*. The other type, *i.e.*, *simple sieve plate* is found in *Robinia*, *Maclura* and some species of *Ulmus*. Here the terminal walls of the sieve-tube elements are transverse and there is a single specialized sieve area. In the majority of species, the sieve tube elements of the secondary phloem possess simple sieve plates.

Sclerenchyma of one type or another is a characteristic of the secondary phloem of several species. Fibres occur frequently in definite tangential bands (*e.g.*, in *Liriodendron* and *Populus*). In *Cephalanthus*, the fibres are found singly. However, in *Carya cordiformis*, the fibres constit the greater part of the secondary phloem and surround the groups of softer tissues. All conditi

have been reported in gymnosperms. The phloem of *Pinus strobus* lacks sclerenchyma; well developed tangential bands of fibres are found to be present in *Juniperus*, and large masses of sclereids are present in *Tsuga*. In *Thuja occidentalis*, the fibres are arranged in uniseriate tangential rows. These rows of fibres alternate with rows of sieve cells and phloem parenchyma.

In *Platanus* and *Fagus* sclereids are the only type of sclerenchyma present in the phloem. The sclereids are found abundantly in the older, living, but nonconducting phloem of the woody plants.

Phloem rays. The pholem rays are usually present in the vascular tissues developed by the cambium. The vascular rays are formed in the cambium and develop on either side of it with the secondary xylem and secondary phloem of which they are a part. The phloem rays may be one to several cells in width. Normally they are of uniform width throughout their length. They may increase in width outwardly, the increase being due to the multiplication of the cells or to the increase in size of cells toward the outer end of the ray. The phloem rays may be one cell wide (*e.g.*, in *Castanea* and *Salix*), two or three cells wide (*e.g.*, in *Malus pumila*) or many cells wide (*e.g.*, in *Robinia* and *Liriodendron*). However, in oaks there are two types of phloem rays—one very broad and the other uniseriate.

Commonly the phloem ray cells in woody plants, as seen in transverse section, are rectangular and radially elongated. In herbaceous plants, commonly the ray cells are globose. In *Cephalanthus*, *Agrimonia* and *Potentilla* the ray cells closely resemble the phloem parenchyma cells. All phloem ray cells are parenchymatous with active protoplasm, but as they become older many of them become sclereids.

A special type of ray cell known as *albuminous cell* is found in gymnosperms. These albuminous cells are found to be situated at the upper and lower margins of the phloem rays. The albuminous cells differ from the ordinary ray cells both structurally and functionally. They are joined directly with the sieve cells by sieve areas. They do not contain starch, and are of much greater vertical diameter than the normal ray cells. They retain their protoplasts as long as the sieve cells with which they are connected function. It is thought that they function like companion cells of angiosperms.

Seasonal rings in secondary phloem. The tissues of the secondary phloem are generally arranged in definite tangential bands. These layers of tissue have the appearance of annual rings. However, these ring like bands do not possess definite seasonal limits like those of secondary xylem, because there is no sharp distinction between the phloem cells formed in the early and late growing season. Seasonal formation of sclerenchyma bands may exist, but this is not constant feature. In tropical plants new layers of phloem and xylem are formed with each period of new growth.

Function. The functions of secondary phloem are normally the same as that of primary phloem. The various cells of secondary phloem are structurally adapted for the function of translocation of food. The sieve tubes, companion cells and some phloem parenchyma cells are specially adapted for lengthwise conduction, and certain phloem rays help in horizontal conduction to and from the xylem and the cambium. Some of the phloem parenchyma cells in some plants act as storage tissue of starch, crystals and other organic materials.

Economic importance. The secondary phloem of various trees and shrubs of the Malvaceae, Tiliaceae, Moraceae has provided *bast fibres* for economic purposes. The tapa cloth of Pacific islands is composed of mainly of phloem fibres. Tannin obtained from the secondary phloem of various plants is utilized for the preparation of spices and drugs. Secretory canals are abundantly found in the secondary phloem, and the secretions are of much economic value—such as rubber is obtained from the latex of *Hevea brasiliensis*, and resins from various gymnosperms.

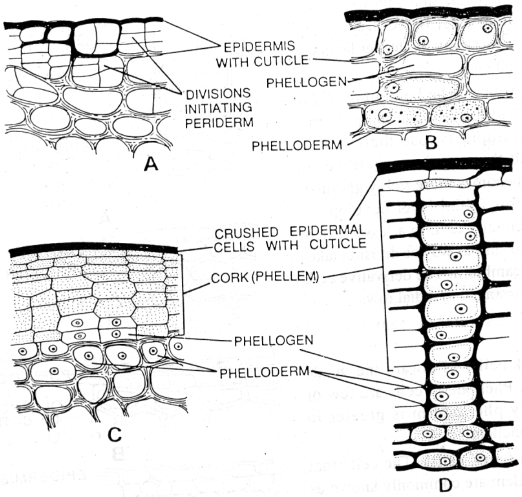


Fig. 10.53. The periderm. Origin of periderm. A – B, partly in epidermis and partly beneath it, in *Pyrus*; C – D, beneath epidermis in *Prunus*.

The important properties of the commercial cork are its imperviousness, its lightness, toughness and elasticity.

Phelloderm. The phellogen cuts off the phelloderm cells towards inner side. The phelloderm cells are living cells with cellulose walls. In most plants, they resemble cortical cells in wall structure and contents. Their shape is similar to that of phellogen cells. They may be distinguished from cortici cells by their arrangement in radial series resulting from their origin from the tangentially dividing phellogen. In some species they act as photosynthetic tissue and aid in starch storage. They are pitted like other parenchyma cells. Occasionally, the sclereids and other such specialized cells occur in phelloderm. The term *secondary cortex* is sometimes applied to phelloderm, which does not seem to be appropriate.

BARK

The term *bark* is commonly applied to all tissues outside the vascular cambium of the stem in either primary or secondary state of growth. In this way, bark includes primary phloem and cortex in stem with primary tissues only, and primary and secondary phloem, cortex and periderm in stem with secondary tissues. This term is also used to denote the tissue that is accumulated on the surface of the stem as a result of the activity of cork cambium. As the periderm develops, it becomes separated, by a non-living layer of cork cells from the living tissues. The tissue layers thus separated become dead. The term bark in restricted sense is applied to these dead tissues together with the cork layers. In wider sense the term is applied to denote the tissues outside the vascular cambium. However, the term bark is loose and non-technical.

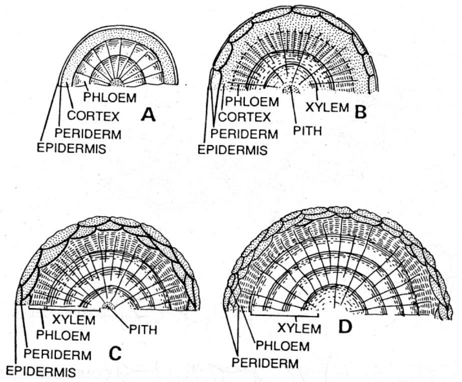


Fig. 10.54. *The periderm. Diagrams showing the position and extent of successively formed periderm layers. A, a one-year-old twig, the first periderm layer, a complete cylinder formed beneath the epidermis; B, a two-year-old twig, the epidermis and first periderm ruptured; C, a three-year-old stem, the outer tissues weathered away and more periderm layer formed deeper in the stem; D, a four-year-old stem, the cortex and outer secondary phloem with their periderm layers largely weathered away.*

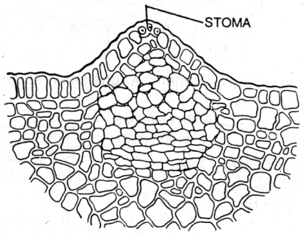


Fig. 10.55. The lenticel. Beginning of lenticel formation under a stoma of *Morus alba* (mulberry).

RHYTIDOME

In most of plants, as soon as the first phellogen ceases to function, second phellogen develops in the tissue below the first one. In this way additional layers of periderm are formed in the progressively deeper regions of the stem, thus new phellogen layers arise in deeper regions of the cortex which may exceed even upto phloem. As the phellogen arises in deeper region and cuts cork cells or phellem towards outside, all the living cells outside the phellogen do not get water supply and nutrients, and become dead. These dead tissues formed outside the phellogen constitute the *rhytidome*.

In some rhytidomes parenchyma and soft cork cells predominate whereas others contain large amounts of fibres usually derived from the phloem. The manners in which the successive layers of

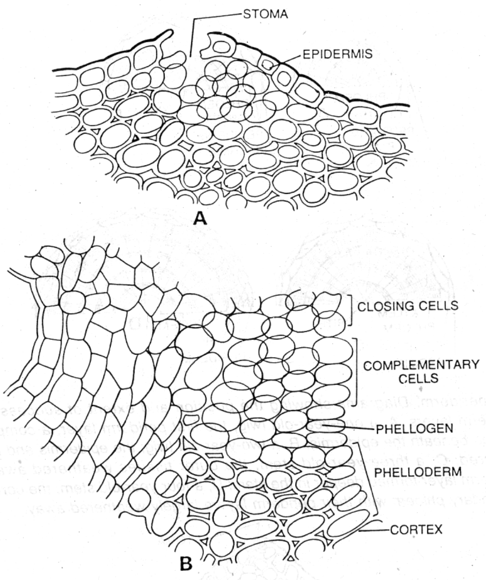


Fig. 10.56. The lenticel. Stages of development. A, phellogen arises just beneath stoma; B, well developed lenticel (half shown).

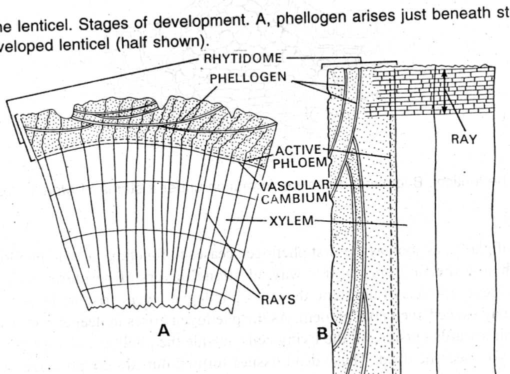


Fig. 10.57. The Periderm. A and B, Transverse and longitudinal sections of part of stem showing rhytidome and its location with reference to vascular tissues; here the rhytidome is composed of periderm and non-living secondary phloem.

periderm originate possesses a characteristic effect upon the appearance of the rhytidome. When the sequent periderms develop as overlapping scale-like layers, the outer tissue breaks up into units related to the layers of periderm, and thus formed outer bark is termed scale-bark. On the other hand, if the phellogen arises around the whole circumference of the stem, a ring bark is formed, which shows the separation of hollow cylinders or rings from the stem.

LENTICELS

Usually in the periderm of most plants, certain areas with loosely arranged cells have been found, which possess more or less raised and corky spots where the underneath tissues break through the epidermis. Such areas are universally found on the stems of woody plants. These broken areas are called the *lenticels*. Wutz (1955) defined a *lenticel as a small portion of the periderm where the activity of the phellogen is more than elsewhere, and the cork cells produced by it are loosely arranged and possess numerous intercellular spaces*. These areas are thicker radially than rest of the periderm because of the presence of loose complementary cells. The lenticels perform the function of exchange of gases during night or when the stomata are closed.

Lenticels are first formed immediately beneath the stomata or group of stomata and the number of lenticels, therefore, depends upon the number of stomata or groups of stomata. The lenticels may be scattered on the stems or they may be arranged in vertical or horizontal rows. The lenticels also occur on the roots.

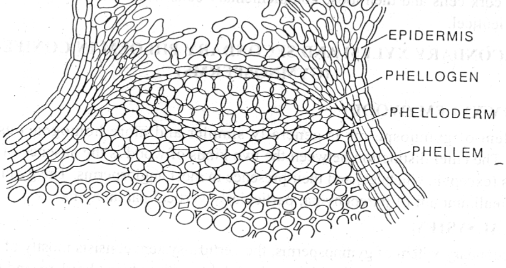


Fig. 10.58. The lenticel. A portion of T.S. of stem of *Prunus* showing lenticel. Successive layers of complementary and closing cells are visible.

The lenticels originate beneath the stomata, either just before, or simultaneously with the initiation of the first layer of the periderm. In most of plants, lenticel formation takes place in the first growing season and sometimes previous to the growth in length has stopped. As the lenticel formation begins, the parenchyma cells found nearabout the sub-stomatal cavity lose their chlorophyll and divide irregularly in different planes giving rise to a mass of colourless, rounded, thin walled, loose cells called *complementary cells*. Such cells are also produced by phellogen towards outside instead of cork cells. As the complementary cells increase in number, pressure is pressed against the epidermis and it ruptures. Very often, the outer most cells die due to exposure to outer atmosphere and are replaced by the cells cut off by cork cambium or phellogen. The thin walled loose complementary cells may alternate with masses of more dense and compact cells called

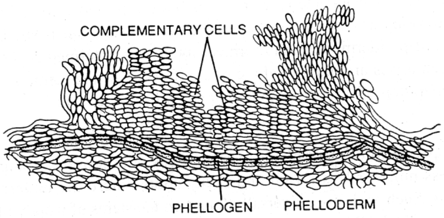


Fig. 10.59. The lenticel of *Mangifera indica* (mango).

the *closing cells*. These cells together form a layer called *closing layer*. With the continuous formation of new loose complementary cells, the closing layers are ruptured. The lenticels are filled up with complementary cells completely in the spring season whereas in the end of the spring season the lenticel becomes closed by the formation of closing layer.

The complementary cells are thin-walled, rounded and loose with sufficiently developed intercellular spaces among them. Their cell walls are not suberized. Due to the presence of profuse intercellular spaces, the lenticels perform the function of exchange of gases between the atmosphere and internal tissues of the plant.

Sometimes, lenticels develop independent of the stomata. In such cases the phellogen cuts for sometime the cork cells and then loose complementary cells which ultimately break the cork and rise to a new lenticel.

SECONDARY XYLEM AND SECONDARY PHLOEM IN CONIFERS (GYMNOSPERMS)

SECONDARY XYLEM (WOOD)

The xylem of gymnosperms is generally simpler and more homogeneous than that of angiosperms. The chief distinction between the two kinds of wood is the absence of vessels in the gymnosperms (except in Gnetales) and their presence in most angiosperms. The gymnosperm wood possesses a small amount of parenchyma, particularly vertical parenchyma.

THE VERTICAL SYSTEM

In the secondary xylem of gymnosperms, the vertical system consists mostly of tracheids. The late wood tracheids possess relatively thick walls and pits with reduced borders, and therefore, they are known as *fibre-tracheids*, but libriform fibres do not occur. The tracheids are long cells (0.5 to 1 mm) with their ends overlapping those of other tracheids. The tracheids of existing gymnosperms are interconnected by circular or oval bordered pit-pairs in single, opposite or alternate arrangement. The number of pits on each tracheid may vary from 50 to 300 (Stamm, 1946). The pit-pairs are abundantly present on the ends where the tracheids overlap each other. Generally the pits are confined to the radial facets of the cells. Tori are present on the pit membranes in *Ginkgo*, Gnetales and most Coniferales. The tracheids possess thickenings of intercellular material and primary walls along the upper and lower margins of the pit-pairs. These thickenings are called *crassulae*. Another wall sculpture is represented by the *trabeculae*. They are found in the form of small bars extending across the lumina of the tracheids from one tangential wall to the other. Helical thickenings on pitted walls have been recorded in the tracheids of some conifers. Wherever present, the vertical xylem parenchyma of the Coniferales is found to be distributed throughout the growth ring and occurs in long strands derived from transverse divisions on the mostly long fusiform cambial cells. Some conifers (*Taxus*, *Torreya* and *Araucaria*) do not have parenchyma in the vertical system.

STRUCTURE OF RAYS

The rays of gymnosperms are composed either of parenchyma cells alone, or of parenchyma cells and tracheids. Ray tracheids are distinguished from ray parenchyma cells chiefly by their bordered pits and lack of protoplasts. The ray tracheids possess lignified secondary walls. In some conifers these walls are thick and sculptured, with projections in the form of bands extending across the lumen of the cell. The ray parenchyma cells possess living protoplasts in the sap wood and often dark coloured resinous deposits in the heartwood. The rays of conifers are for the most part only one cell wide and from 1 to 20 or sometimes upto 50 cells high. Ray tracheids may occur singly or in series, at the margins of a ray. The rays serve to transport the assimilation products formed in the leaves and flowing downwards in the phloem in a radial direction into the wood of the stem and roots.

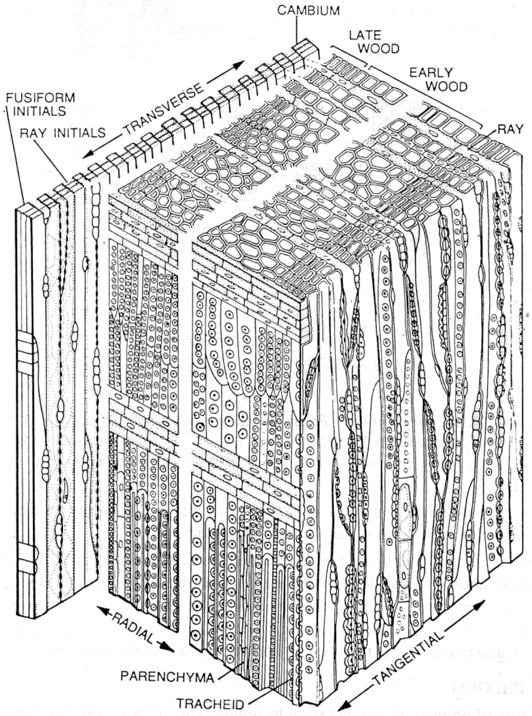


Fig. 10.60. Xylem—wood of conifers. Three-dimensional diagram of the cambium and secondary xylem of *Thuja occidentalis* Linn. (After Bailey).

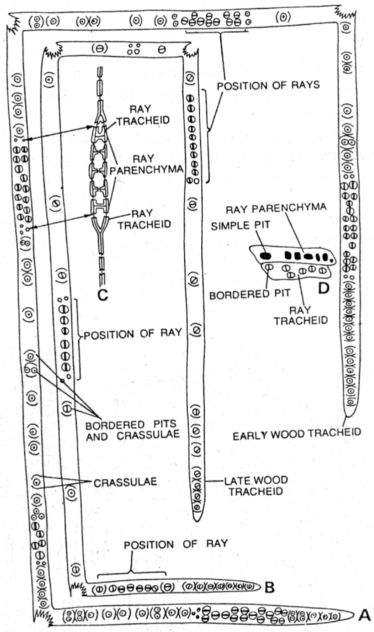


Fig. 10.61. Xylem—secondary xylem of *Pinus*. A, early-wood tracheid; B, late-wood tracheid; C, T.S. of ray as seen in T.L.S. of wood; D, two ray cells as seen in R.L.S. of wood. Tracheids show pits with full borders and are associated with crassulae. (After Forsaith).

They conduct water away from the wood in the opposite direction. The rays penetrate equally into the xylem and the phloem and thus suited for these functions.

Resin ducts. In certain gymmosperms the resin ducts are developed in the vertical system or in both the vertical and horizontal systems. The resin ducts arise as schizogenous intercellular spaces by separation of resin producing parenchyma cells from each other. These cells make the lining, the *epithelium*, of the resin duct and excrete the resin. A resin duct may become closed by the enlarging epithelial cells. These tylosis like extensions are known as *tylosoids* (Record, 1947).

SECONDARY PHLOEM

The structure of phloem of conifers is quite simple. The vertical system contains sieve cells, parenchyma cells and frequently fibres. Companion cells are absent. The sieve plates are present on the lateral walls. The rays are mostly uniseriate and contain parenchyma only or parenchyma and albuminous cells.

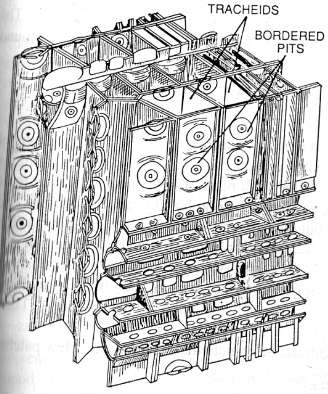


Fig. 10.62. Secondary xylem. Three-dimensional structure of wood of *Pinus strobus*. Tracheids are shown in the figure.

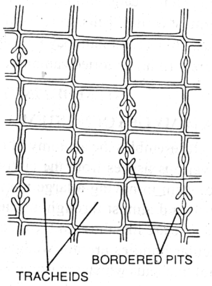


Fig. 10.63. Tracheids with bordered pits of pine stem in T.S.

The sieve cells are slender, elongated elements appear like the fusiform initials from which they are derived. They overlap each other at their ends and each sieve cell remains in contact with several rays. The sieve areas are abundantly found on the ends which overlap those of other sieve cells. The connecting strands in the sieve-areas are aggregated into the groups, and the callose associated with the strands in one group fuses into one structure. The phloem parenchyma cells occur in longitudinal strands. They store reserve food material and also contain resins, crystals and tannins. The phloem rays of the trees of advanced age are characteristic in having albuminous cells. The albuminous cells may also occur among the phloem parenchyma cells (in the vertical system) and in still other plants only among the phloem parenchyma cells. The albuminous cells contain dense cytoplasm and distinct nuclei. They are irregular in shape and store food materials. The secondary phloem also contains resin canals. In *Picea canadensis*, they occur in rays and possess cyst-like bulbous expansions.

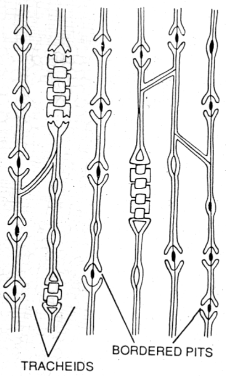


Fig. 10.64. Tracheids with bordered pits of pine stem in T.L.S.

SECONDARY GROWTH IN THE MONOCOTYLEDONS

Commonly, the vascular bundles of monocotyledons do not possess cambium, and therefore, there is no secondary growth. However, it occurs in some monocotyledons (*e.g.*, *Dracaena*, *Yucca*, *Veratrum*, *Aloe*, *Sansevieria*, *Xanthorrhoea*, *Kingia,* etc.). In these plants the secondary growth occurs by the formation of the cylinder of new bundles embedded in a tissue of less specialized

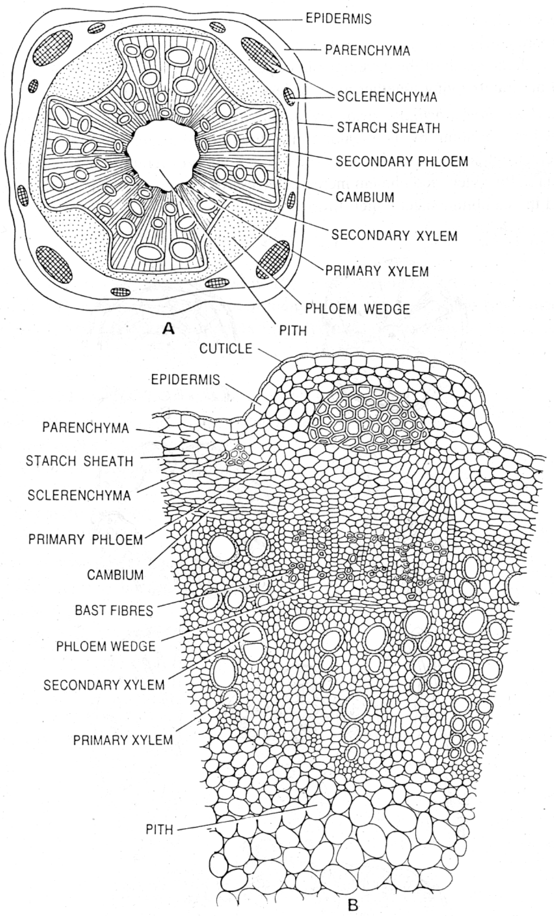


Fig. 11.2. The stem—anomalous structure. T.S. of stem of *Bignonia* (dicot)— A, diagrammatic, B, detailed structure.

ABNORMAL BEHAVIOUR OF NORMAL CAMBIUM

Sometimes when the normal cambium starts cutting cells at several places irregularly, and forms at certain places much larger portions of xylem than of phloem, and at other places more phloem than xylem, and a ridged and furrowed xylem cylinder is produced. This may be of simple structure (*e.g.*, in some Bignoniaceous genus) or very complex (*e.g.*, in *Bignonia* sp.).

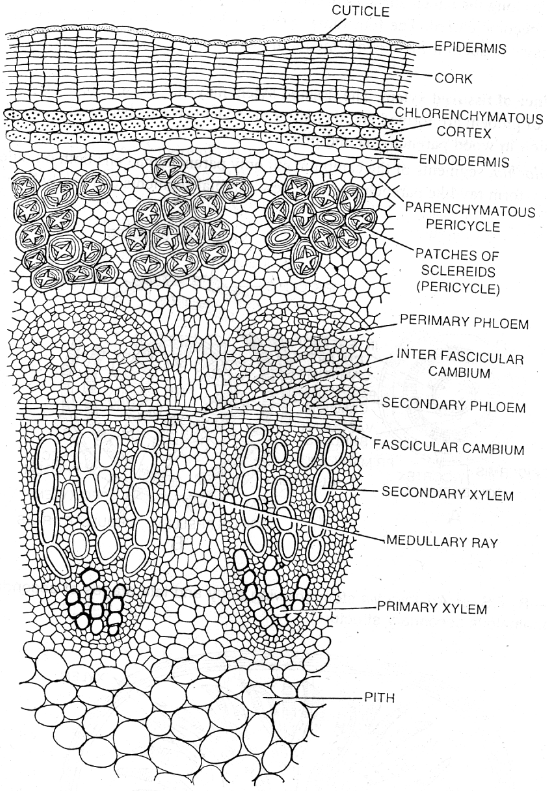


Fig. 11.3. *Aristolochia* (dicot). T.S. of stem showing secondary growth. Beneath the epidermis the cork layers are present; the pericycle splits into groups of sclereids and the inter-fascicular cambium does not produce secondary vascular tissue.

ANATOMY OF *BIGNONIA* STEM

The most interesting anatomical feature in *Bignonia* of Bignoniceae is the occurrence of anomalous secondary structure. (See fig. 11.2) This is as follows:

A. Presence of phloem wedges in the xylem. The young stems which exhibit this type of structure when mature are provided with a normal ring of vascular bundles. The vessels of the young stem are narrow in diameter. The wood formed in later stages contains wider vessels. As soon as this stage is reached four furrows at four equidistant points appear in the xylem, extending almost nature. Here a cambium layer is formed from the meristematic parenchyma of the pericycle or of the innermost cortical cells. In roots of some plants, a cambium of this type forms in the endodermis. The initials of this cambium may be polygonal, rectangular or fusiform in different species. They are found in tiers forming a storied cambium.

STEM OF *PINUS*—PRIMARY AND SECONDARY STRUCTURE

ANATOMY OF YOUNG STEM

It resembles the anatomy of dicotyledonous stem in many respects. The general arrangement of the various tissues from the circumference to the centre is the same. However, it differs, from the dicot stem in having a large number of resin ducts filled with resin. These ducts are found to be distributed almost throughout the stem. The epidermis has an irregular outline. Endodermis and pericycle are like those of the dicotyledonous stem, but the pericycle contains no sclerenchyma. The vascular bundles are not wedge-shaped, as in the dicotyledons. Phloem consists of annular and spiral tracheids which are irregularly disposed towards the centre. Metaxylem consists of exclusively tracheids with bordered pits. The tracheids are arranged in radial rows as seen in the transverse section of the stem. The pits of the pine wood are large and mostly restricted to the radial walls. There are no true vessels. The details of the anatomy of young stem of pine are as follows:—Epidermis—It consists of a single layer of cells with a very thick cuticle. Sclerenchyma—Sometimes a few patches of sclerenchyma occur here and there below the epidermis. Cortex—Many layers of more or less rounded parenchyma cells, with conspicuous resin ducts lying embedded in the cortex. Endodermis—A single layer lying internal to the cortex; the innermost layer of the cortex is treated as endodermis. Pericycle—It consists of parenchyma cells, there is no sclerenchyma in it. Medullary rays—They run from the pith outwards between the vascular bundles. Pith—There is a well defined pith, consisting of a mass of parenchyma cells. A few resin-ducts are also present in the pith. Vascular bundles—These are collateral and open, and arranged in a ring, as in dicot stem. Each bundle consists of phloem, cambium and xylem. Phloem—The phloem consists of sieve tubes and phloem parenchyma, but no companion cells. It lies on the outer side of the bundle. Cambium—A few layers of thin walled, rectangular cells in between xylem and phloem. Xylem—It consists exclusively of tracheids; there are no true vessels. Resin ducts are also present here. Protoxylem lies towards the centre and consists of a few annular and spiral tracheids which are not disposed in any regular order. Metaxylem lies towards the cambium and consists of tracheids with bordered pits which develop on the radial walls. These tracheids are four sided and are arranged in definite rows.

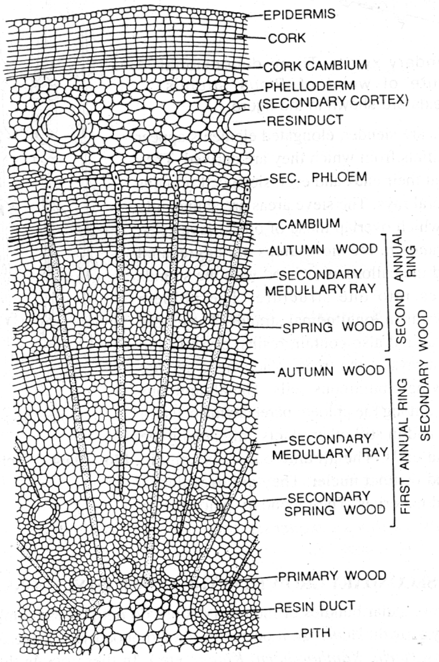


Fig. 10.65. Secondary growth in thickness of the pine stem. T.S. of a two-yearold pine stem.

SECONDARY GROWTH IN THICKNESS OF STEM

The secondary growth in pine stem takes place in exactly the same way as in a dicotyledonous stem. However, the points of differentiation are as follows: The pine stem is characterized by the presence of conspicuous resin-ducts which are distributed throughout the stem. The secondary wood consists exclusively of tracheids with numerous bordered pits on their radial walls. As in the dicotyledonous stem, there are distinct annual rings, consisting of the autumn wood and spring wood. The autumn wood consists of narrow and thick-walled tracheids, and the spring wood of wider and thinner-walled tracheids. The secondary medullary rays are usually one layer of cells in thickness and a few in height. The phloem portion of the medullary ray consists of middle layers of starch—containing cells, called starch cells, and upper and lower layers of protein containing cells, called albuminous cells. The xylem portion of the medullary ray consists of similar starch cells in the middle, and empty cells with bordered pits, called tracheidal cells, in the upper and lower layers. Vessels are absent.

ANATOMICAL DIFFERENCES BETWEEN DICOTYLEDONOUS AND MONOCOTYLEDONOUS STEMS

	Dicotyledonous Stem	Monocotyledonous Stem
1. Hypodermis	It is collenchymatous.	It is sclerenchymatous.
2. Cortex	It consists of a few layers of parenchyma.	There is a continuous mass of parenchyma up to the centre. It is commonly known as ground tissue.
3. Endodermis	It is a wavy layer of compact cells.	
4. Pericycle	Usually it consists of parenchyma and sclerenchyma.	It is not differentiated into distinct tissues.
5. Medullary ray	There lies a strip of parenchyma in between vascular bundles.	
6. Pith	The central cylinder consists of parenchyma.	It is not marked out.
7. Vascular bundles	(*a*) They are collateral and open. (*b*) They are arranged in a ring. (*c*) They are of uniform size. (*d*) Phloem parenchyma present. (*e*) They are wedgeshaped. (*f*) Bundle sheath absent.	They are collateral and closed. They are scattered. They are larger towards the centre. Phloem parenchyma absent. They are usually oval. Bundle sheath strongly developed.

to the pith. The cambium is situated on the inside of the furrows. The phloem increases in bulk, and the tissues slide along the lateral surfaces of the furrows. Later on, because of the development the furrows again become closed. The four radial groups of the phloem are united by medullary ray tissue. In transverse section the narrow medullary rays may be seen traversing the phloem of furrows.

B. Presence of fissured xylem. The fissured xylem may only be seen in fairly old stems. First of all wedges of phloem are formed and thereafter the xylem strands becomes fissured by dilation and cell division in wood parenchyma and pith.

In *Aristolochia*, segments of the cambium cut only parenchyma cells both on outer and inner sides, thus they form ray like parenchyma. The new cambial segments constantly form the rays of parenchyma thus increasing in diameter. As the vascular cylinder, broken by wide rays, increases in circumference the cylinder of sclerenchyma that encircled the bundles become ruptured and adjacent parenchyma grows intrusively into the gaps. Eventually a very fluted vascular cylinder is formed. Species of *Aristolochia* are woody climbers or *lianes,* which have diverse taxonomic affinities and often show anomalous structural features. Among other characteristics, the vessels are often of unusually wide diameter. (See figs. 11.4 and 11.5).

In *Bauhinia rubiginosa*, there is restriction of the activity of the cambium to certain regions which results in the formation of ridged stems. In other species of *Bauhinia*, the strap like stems are formed because of restricted activity of the cambium in certain regions. In this case the cambium is more active at two opposite sides. (Fig 11.1 E.).

In some climbing plants (*e.g., Vitis, Clematis*), the interfascicular cambium forms only parenchyma, so that the original vascular bundles remain discrete throughout secondary growth.

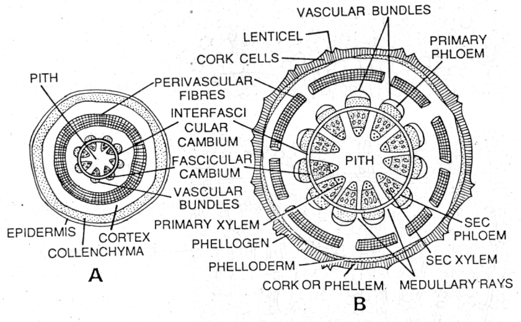


Fig. 11.4. A—B, T.S. of *Aristolochia* stem showing early and late stages of secondary growth—(anomalous secondary structure).

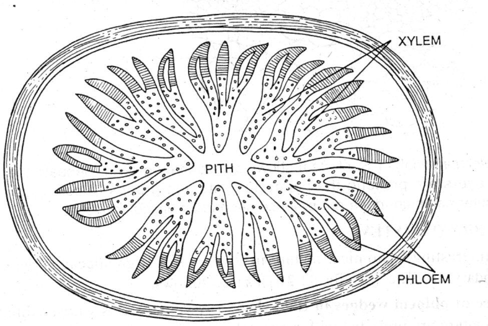
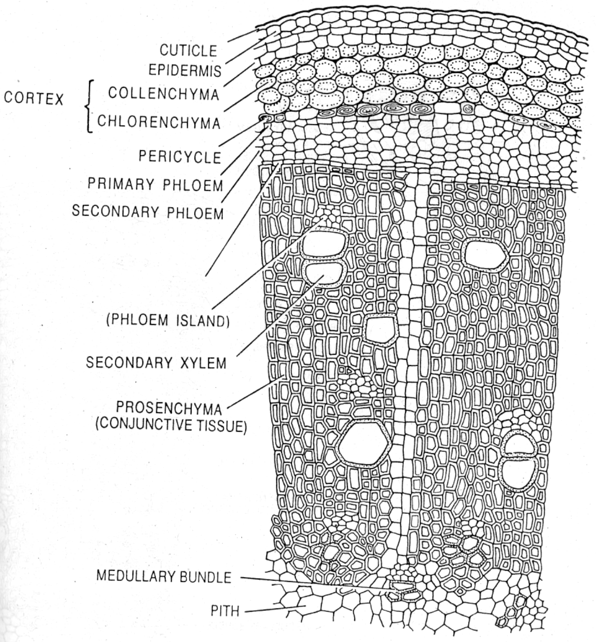


Fig. 11.5. The stem—anomalous structure. T.S. of old *Aristolochia* stem showing anomalous secondary growth.



11.6. Stem-anomalous structure. T.S. of a portion of stem *Bougainvillaea* (dicot.) showing anomalous secondary growth, periderm, thick-walled conjunctive tissue and medullary bundles.

Vascular system. It consists of well developed, collateral and open vascular bundles arranged in a ring. Both primary and secondary tissues are found. Secondary phloem consists of sieve tubes, companion cells and phloem parenchyma and found in the form of continuous cylinder. Xylem is also found in the form of a continuous cylinder traversed by narrow medullary rays. Vessels of primary xylem are comparatively smaller and arranged in radial rows towards pith. Later developed vessels are comparatively larger and confined to certain regions of xylem cylinder.

Laticiferous canals. Commonly the laticiferous canals are found in the cortical region of *Convolvulus*.

Pith— The central region of the axis is occupied by pith, consisting of thin-walled parenchyma cells with intercellular spaces.

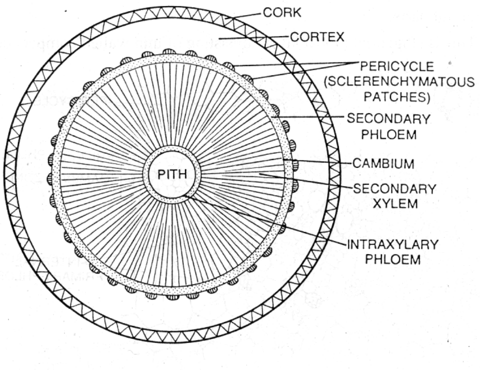


Fig. 11.31. The stem—anomalous structure. T.S. of *Asclepias* stem (dicot-Asclepiadaceae) showing a complete band of intraxylary phloem around the pith.

Special anatomical features. Intraxylary or internal phloem is found in continuous band around the pith.

Anatomy of the stem of *Asclepias*

As seen in cross section, the stem shows the following parts.—**Epidermis**— The outermost layer, the epidermis is normal and ramains covered with a thick cuticle.

Cork and cortex— The cork arises superficially usually in the epidermis or sub-epidermis. The cells of cork are rectangular and thick-walled. The greater portion of the cortex is represented by thin walled parenchymatous cells having well defined intercellular spaces among them. The innermost layer of the cortex is endodermis.

Pericycle— It consists of grouped fibres with intervening parenchyma. The fibres possess usually unlignified walls.

Vascular system. It is well developed and consists of phloem and xylem. Phloem is found in the form of continuous cylinder. It consists of sieve tubes, companion cells and phloem parenchyma. Primary xylem is represented by wide metaxylem vessels and narrow protoxylem vessels. The secondary xylem is found in the form of protoxylem vessels. The secondary xylem is found in the form of continuous cylinder traversed by narrow medullary rays.

Special anatomical features. The intraxylary or internal phloem is found in the form of a continuous band around the pith. Laticiferous canals are present among the parenchyma cells.

VASCULAR BUNDLES ARRANGED IN A RING IN MONOCOTS

Normally, the cross section of monocot stem exhibits many scattered bundles. However, in *Tamus communis* of Dioscoreaceae, the vascular bundles are arranged in a ring around large pith. The vascular bundles are also arranged in a ring in several hollow monocots (*e.g., Triticum, Avena, Hordeum, Oryza* and several other members of Gramineae.)

Anatomy of the stem of *Tamus communis*—Epidermis— It consists of a single layer of compact, barrel shaped cells having no intercellular spaces. A thin cuticle covers the epidermis.

Cortex. The presence of cortex is an anomalous feature in monocot stem. The cortex is well developed and consists of thin walled, rounded or oval parenchyma cells having well defined intercellular spaces among them. The innermost layer of the cortex is endodermis. It is conspicuous, consisting of barrel-shaped cells, having no intercellular spaces.

Pericycle. Immediately beneath the epidermis, multilayered sclerenchymatous pericycle is present. This makes a complete cylinder of sclerenchyma.

Ground tissue. It is represented by large, thin walled, rounded or oval parenchyma cells having intercellular spaces.

Vascular system. It consists of many vascular bundles arranged in a ring (anomalous feature). Usually they are arranged in two rings (outer and inner). Each vascular bundle consists of xylem and phloem. The bigger vessels (pitted) towards outside constitute metaxylem, whereas narrower vessels (annular and spiral) towards centre form protoxylem. Phloem consists of sieve tubes and companion cells. Phloem parenchyma is absent. There is no secondary growth or cambium formation.

Pith. The central region of the stem is occupied by pith. It consists of thin walled, rounded parenchyma cells having well developed intercellular spaces among them.

Anomalous features. The vascular bundles are arranged in a ring; well developed cortex is present; endodermis is conspicuous; the sclerenchymatous pericycle is present; the central region of the stem is represented by pith.

SECONDARY GROWTH IN MONOCOTS

The secondary growth accurs in herbaceous and woody Liliflorae (*Aloe, Sansevieria, Yucca, Agave, Dracaena*) and other groups of monocots (Cheadle, 1937). The meristem concerned with this growth is called cambium. The cambium appears to be a direct continuation of a primary thickening meristem (Eckardt, 1941). However, the cambium functions in the part of the axis, that has completed its elongation. The cambium originates in the parenchyma outside the vascular bundles. This part of the axis is sometimes identified as cortex, and sometimes as pericycle. Here, the anatomy of the stem of *Dracaena* has been discussed.

Anatomy of *Dracaena* stem. The cross section of *Dracaena* stem exhibits the following structure: The single layered epidermis remains covered with thick cuticle. The lenticles are also seen on the epidermis. Beneath the epidermis and hypodermis, the cork cambium arises which gives rise to the cork towards outside. Below the cork cambium, well developed parenchyma is present.

Anomalous structure. *Dracaena* shows anomalous secondary growth. The cambium appears in the parenchyma outside the outermost vascular bundles. This region in which the cambium appears, is sometimes identified as cortex, and sometimes as pericycle. The newly formed cambium cuts cells towards outside and inside both. The tissue developed on the inner side of the cambium is usually differentiated into vascular bundles remain separated from each other by lignified tissue, sometimes this tissue remains unlignified and thinwalled. The cells formed on the outer side of the cambium make parenchyma.

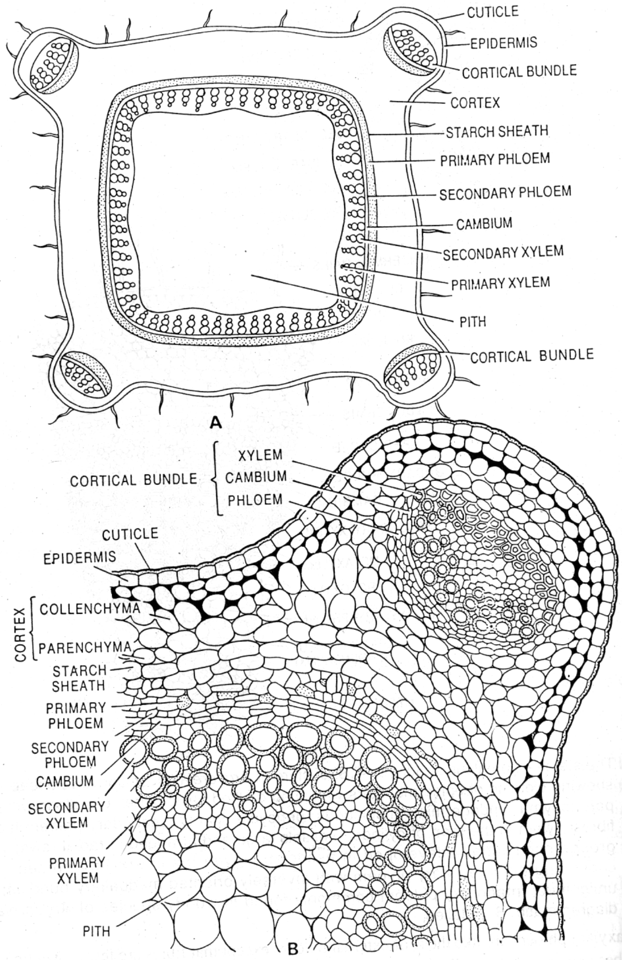


Fig. 11.28. *Nyctanthes arbortristis* (dicot). T.S. of stem showing inversely oriented cortical vascular bundles. A, diagrammatic; B, detailed.

Convolvulaceae; Punicaceae; Loganiaceae; Solanaceae, Apocynaceae; Cucurbitaceae; Lythraceae and several others).

Anatomy of *Punica* stem. As seen in cross section, the stem is provided with appendages. Epidermis is single layered. Usually cork arises in the inner part of the pericycle. The pericycle is represented by a ring of fibres along the outer periphery. Phloem and xylem are found in continuous cylinders. Xylem forms a closed cylinder, traversed by narrow medullary rays. The vessels are provided with simple perforations. The pith consists of parenchyma cells. Usually rosette crystals are abundant in the phloem. Secretory cells are also found in cortex and pith.

Special anatomical feature. The most interesting anatomical feature is the occurrence of intraxylary phloem in a continuous strand around the periphery of pith.

Anatomy of the stem of *Convolvulus floridus*. As seen in transverse section, the stem exhibits the following important parts:

Epidermis. This is single outermost layer consisting of thin walled compact cells covered with a thin cuticle.

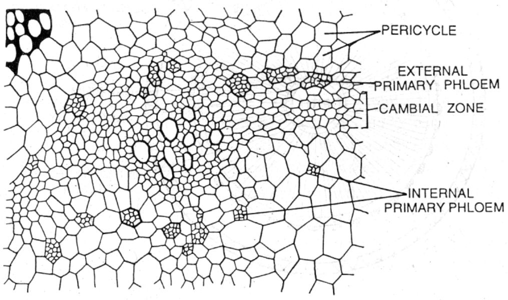


Fig. 11.29. Internal (intraxylary) phloem in T.S. of young stem of *Solanum tuberosum*. Primary phloem cells are seen in small groups external and internal to the cambial zone. (After Artschwager).

Cork and cortex— The cork is usually superficial in origin and consists of thin-walled rectangular cells. Commonly the primary cortex consists of collenchyma. The innermost layer of the cortex is endodermis.

Pericycle—It consists of a thin walled grouped fibres arranged in discontinuous ring. The intervening gaps are filled up with parenchyma cells.

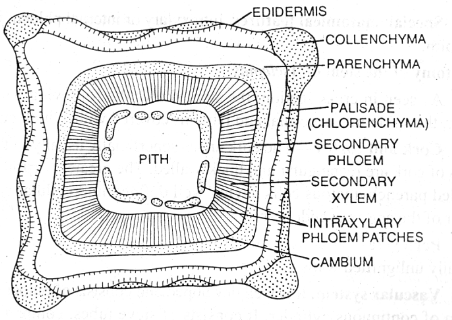


Fig. 11.30. The stem—anomalous structure. T.S. of the stem of *Capsicum* spp. showing intraxylary phloem patches around the pith.

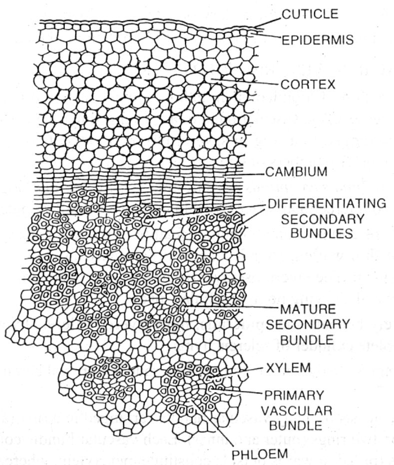


Fig. 11.32. Anomalous secondary growth in *Aloe arborescens* (monocot) stem; T.S. of the stem showing secondary growth.

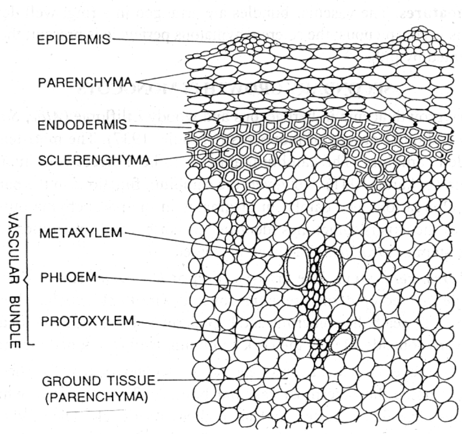


Fig. 11.33. *Tamus communis* (monocot). T.S. of stem (detailed structure) showing vascular bundles in a ring.

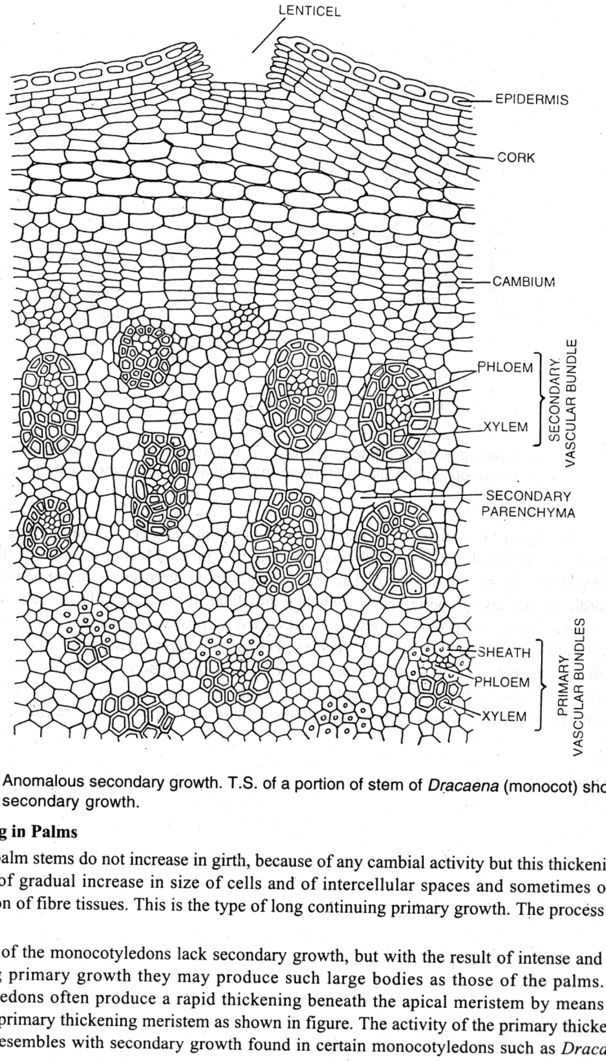


Fig. 11.34. Anomalous secondary growth. T.S. of a portion of stem of *Dracaena* (monocot) showing secondary growth.

Thickening in Palms

The palm stems do not increase in girth, because of any cambial activity but this thickening is the result of gradual increase in size of cells and of intercellular spaces and sometimes of the proliferation of fibre tissues. This is the type of long continuing primary growth. The process is as follows:

Most of the monocotyledons lack secondary growth, but with the result of intense and long continuing primary growth they may produce such large bodies as those of the palms. The monocotyledons often produce a rapid thickening beneath the apical meristem by means of a peripheral primary thickening meristem as shown in figure. The activity of the primary thickening meristem resembles with secondary growth found in certain monocotyledons such as *Dracaena,*

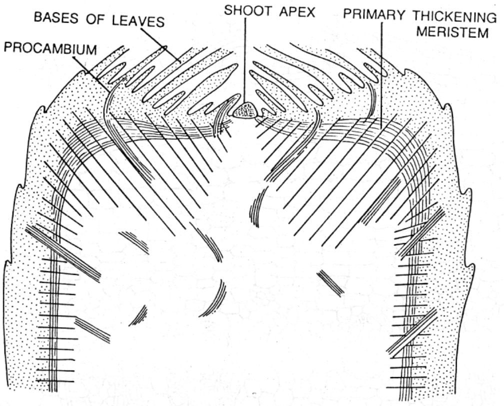


Fig. 11.35. Secondary growth in monocotyledons. The diagrams of the upper part of shoot of a monocotyledon (palm plant) showing the meristems concerned with its growth. (After Eckardt).

Yucca, etc. The apical meristem also known as shoot apex produces only small part of the primary body, *i.e.*, a central column of parenchyma and vascular strands. Most of the plant body is formed by the primary thickening meristem. The primary thickening meristem is found beneath the leaf-primordia, which divides periclinally producing anticlinal rows of cells. These cells differentiate into a tissue formed of ground parenchyma traversed by procambial strands. These procambial strands later on develop into vascular bundles. The ground parenchyma cells enlarge and divide repeatedly, causing increase in thickness. This way, both apical meristem and primary thickening meristem give rise to the main bulk of the stem tissues of monocotyledons. The thickening takes place in monocotyledons, such as palms, due to the activities of the two meristems mentioned above.

12

Anatomy of the Leaf and the Petiole

Commonly there are two types of leaves—1. *dorsiventral leaves* (dicotyledonous) and 2. *isobilateral leaves* (monocotyledonous). The dorsiventral leaves usually grow in a horizontal direction with distinct upper and lower surfaces, the upper being more strongly illuminated than

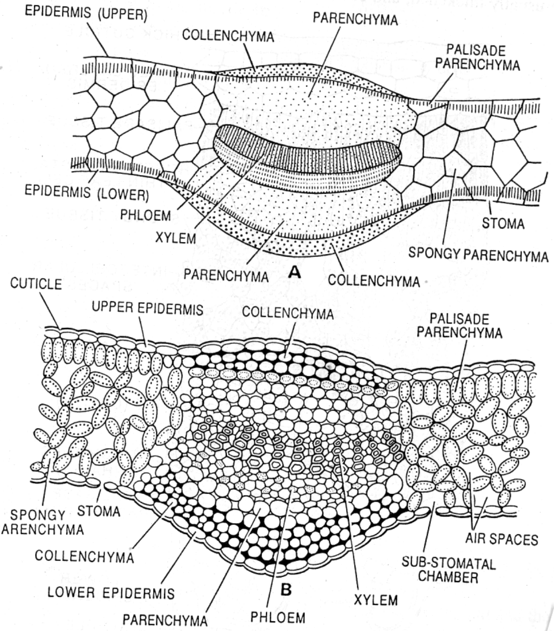


Fig. 12.1. Anatomy of bifacial dicot leaf. A, T.S. of leaf (diagrammatic); B, T.S. of le

the lower. There exists a difference in the internal structure between the upper and lower surfaces of the dorsiventral leaf due to its unequal illumination. Most of the dicotyledonous leaves are dorsiventral. The isobilateral leaves hang vertically so that both surfaces of the leaf receive direct and equal amount of sunlight. The isobilateral leaves possess a uniform structure on both upper and lower surfaces. A very few dicotyledons and most monocotyledons have isobilateral leaves.

Usually the leaf is composed of various tissues, which furnish various functions. In discussions of the form and anatomy of the leaf, it is customary to designate the leaf surface that is continuous with the surface of the part of the stem located above the leaf insertion as *upper, ventral*, or *adaxial* side, the opposite side as the *lower, dorsal* or *abaxial.*

ANATOMY OF DICOTYLEDONOUS LEAF

To study the anatomy of leaf, several vertical sections passing through the mid-rib are required. The internal structure of the dicotyledonous leaf is as follows:

EPIDERMIS

The leaf is covered on both surfaces by a single-layered epidermis. The outer walls of the epidermis are usually thickened, and covered over with a waxy substance called *cutin*. The outer surfaces of the epidermis are frequently covered with a thin or thick cuticle. This cuticular layer is formed of cutin. As the outer walls of the epidermis are thick and cutinized, water does not pass through them rapidly and the transpiration from the surface of the epidermis is greatly reduced, only small quantity of water is evaporated by transpiration. The epidermis checks the transpiration to a great extent. The epidermis also prevents the entrance of pathogens into the interior of the leaf. Another function of the epidermis is the protection of the soft internal tissue of the leaf from the mechanical injuries. Sometimes in the xerophytic leaves the epidermis cells become radially elongated and somewhat lignified. In *Nerium* leaf, the epidermis is multilayerd.

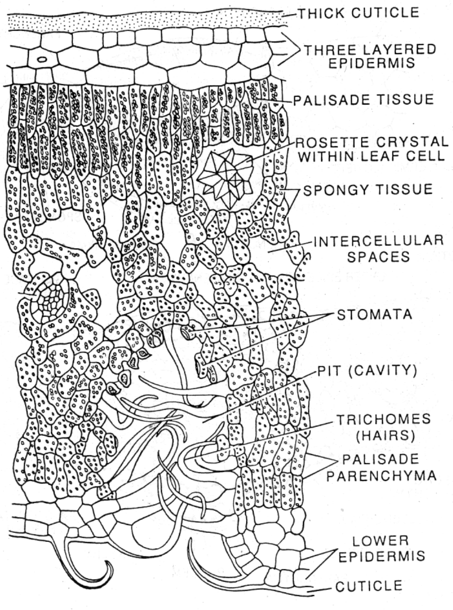


Fig. 12.2. Anatomy of xerophytic leaf. Cross section of a leaf of *Nerium* with upper and lower palisade, three-layered upper epidermis, and stomata in a pit protected by trichomes

Numerous small openings called stomata, are found in the epidermal layers of the leaves. Stomata are found in most abundance in the lower epidermis of the dorsiventral leaf. They are very few in the upper epidermis and sometimes altogether absent. In the floating leaves, stomata remain confined to the upper epidermis; in the submerged leaves the stomata are absent. In xerophytic leaves either stomata are sunken or situated inside the depressions.

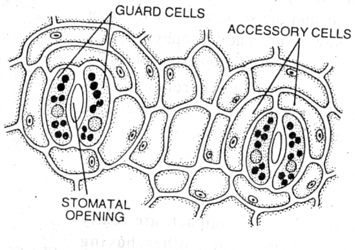


Fig. 12.3. Stomata in epidermal layer—surface view.

Each stoma remains surrounded by two semilunar guard cells. The guard cells are living and contain chloroplasts, they regulate opening and closing of stomata. The guard cells may remain surrounded by two or more *accessory cells* in addition to epidermal cells. The stomata are found in scattered condition.

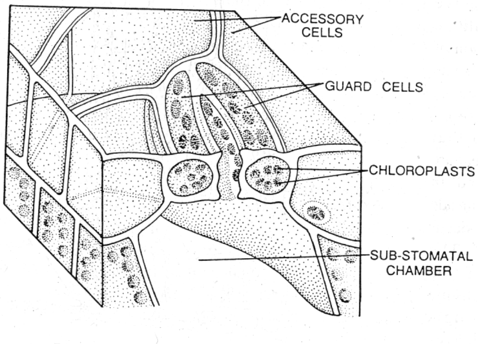


Fig. 12.4. Stomata. Diagrammatic representation of a stoma—surface and sectional views.

Usually the stomata are meant for exchange of gases in between the plant and the atmosphere. To facilitate the diffusion of gases properly, each stoma opens internally into a respiratory cavity or substomatal chamber. The transpiration takes place through the stomata, and the surplus water is being evaporated.

MESOPHYLL TISSUE

The tissue of the leaf that lies between the upper and lower epidermis and between the veins consists of typically thin walled parenchyma is known as *mesophyll.* This tissue forms the major portion of the inner of leaf. Commonly the cells of mesophyll are of two types—the *palisade parenchyma* or *palisade tissue,* and the *spongy parenchyma* or *spongy tissue*. The mesophyll tissues always contain chloroplasts in them.

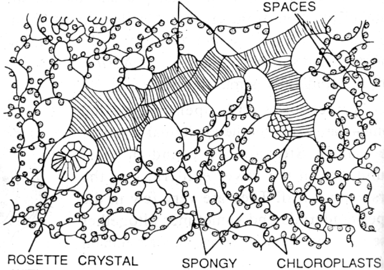


Fig. 12.5. The leaf. Termination of veins in a leaf, as seen in a section cut parallel with the epidermis.

The palisade parenchyma is generally composed of elongated and more or less cylindrical cells which are close together with long axes of the cells perpendicular to the epidermis. In transverse section the cells appear to be arranged quite compact, are really separate from each other having intercellular spaces among them. The palisade tissue may consist of a single or more layers. These cells are arranged near to the upper surface of the leaf, where they receive sunlight and facilitate to carry the function of photosynthesis. Sometimes the leaves hang vertically (*e.g., Eucalyptus*), so that both surfaces of leaf are equally illuminated. In such leaves the palisade parenchyma may occur on both sides. The compactness of the palisade parenchyma depends upon light intensity. The leaves which receive direct sunlight develop more compact parenchyma in comparison to the leaves which develop in shady places.

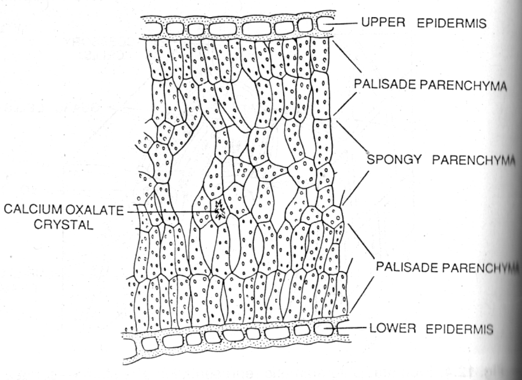


Fig. 12.6. Anatomy of leaf. Cross section of a vertical leaf of *Eucalyptus* showing a palisade layer on each side.

The lower portion of the mesophyll in the leaf is known as spongy parenchyma or spon tissue. The spongy tissue is usually composed of loose, irregular, thin walled cells having intercellular spaces (air spaces) among them. The cells of spongy parenchyma also contain chloroplasts and carry on photosynthesis, but in comparison of palisade parenchyma less chloroplasts are developed. Due to the presence of a large air space in the spongy tissue they are more adaptable to the exchange of gases between the cells and the atmosphere.

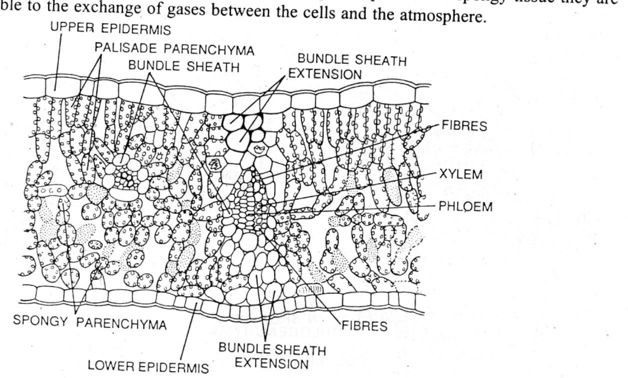


Fig. 12.7. Anatomy of leaf. T.S. of pear leaf. Palisade parenchyma towards upper side consists of 2 or 3 layers. Bundles are enclosed in bundle sheaths. The large vascular bundle has bundle sheath extensions reaching to the epidermis on both sides of the leaf.

The large air spaces that surround the spongy parenchyma cells are near the stomata and directly connected with them. There is therefore a much more free circulation of gases around these cells than around the palisade parenchyma cells, with the result that they are better suited to the exchange of gases between the cells and the surrounding atmosphere. The air spaces of the spongy chlorenchyma are not isolated chambers but a series of intercommunicating passages.

Both spongy and palisade parenchyma contain discoid chloroplasts arranged in parallel rows in the cells. As the chloroplasts are more dense in the palisade tissue than the spongy tissue the upper surface of the leaf appears to be deeper green than the lower surface.

MECHANICAL SUPPORT IN THE LEAF

The functions of the midrib and the lateral veins are to strengthen the leaf. The important tissue giving mechanical strength to leaf are—collenchyma, sclerenchyma, turgid parenchyma and woody xylem.

Collenchyma. In the centre of the upper portion of the midrib, just below the epidermis, there is usually a group of cells which give strength by having thickened walls and by being turgid. A group of the same kind of cells usually occurs also just above the lower epidermis. These cells constitute the *collenchyma*. Collenchyma is composed of living cells with walls which are thickened at the angles where three or more cells come in contact with one another. The thick places in the walls increase the strength of the cells, while the thin places allow for a more rapid transfer of materials from cell to cell than would take place if the cell walls were thickened throughout. These cells are more or less turgid, and so give strength to the leaf in the way also. The weight of the leaf causes it to tend to bend downward, with the result that there is a tendency for the upper portion to be stretched and the lower portion compressed. The collenchyma occurs, therefore, in those parts of the midrib in which there is the greatest need for strengthening material.

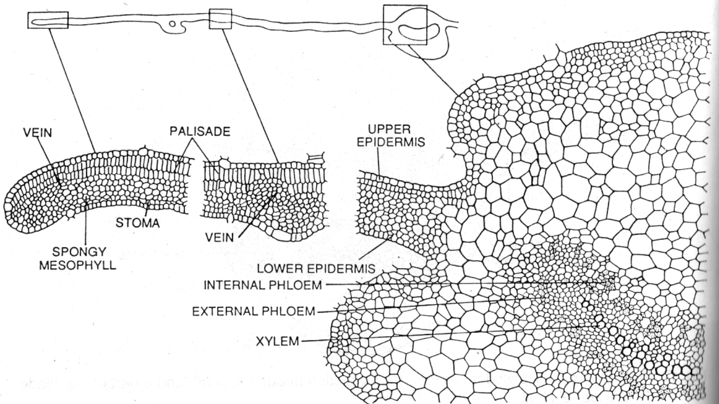


Fig. 12.11. Anatomy of dicotyledonous leaf of *Nicotiana tabacum*. T.S. through a part of leaf. Diagrammatic detail. (After Avery).

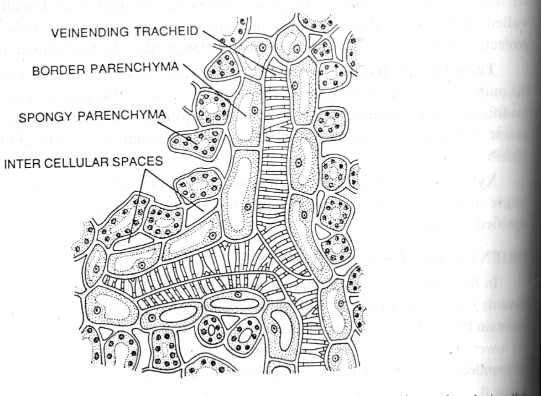


Fig. 12.12. Veins of the leaf. Diagram of vein ending in a leaf. The parenchyma tissue bordering the vein is conspicuous.

Xylem is composed of various kinds of vessels, trachieds wood fibres and wood parenchyma. Specially the vessels are annular and spiral. Xylem conducts water, raw food material and also gives mechanical support to the leaf. The phloem consists of sieve tubes, companion cells and phloem parenchyma. The phloem serves for the translocation of prepared food material from the mesophyll of the leaf.

Veins. The structure of large veins is more or less similar to that of a midrib. As they pass from the base of a leaf blade towards the apex or margin of the leaf, they get reduced in size, and simple in structure. The small veins consist of only of few conducting cells. The xylem is always found towards the upper surface and phloem towards lower even in very small veins. The cells of the mesophyll (chlorenchyma) are usually arranged so that the conduction of materials to and from the veins is facilitated.

The bundle sheath. The larger vascular bundles of dicotyledonous leaves remain surrounded by parenchyma with small number of chloroplasts, whereas the small bundles occur in the mesophyll. However, these small bundles do not remain in contact with intercellular spaces but are commonly enclosed with a layer of compactly arranged parenchyma, the *bundle sheath*. In dicotyledons the bundle-sheath parenhyma is also called *border parenchyma*. The bundle sheaths of dicotyledonous leaves usually consist of cells elongated parallel with the course of the bundle and having walls as thin as those of adjacent mesophyll. In some plants these cells have chloroplasts similar to those the mesophyll (*e.g.*, in *Humulus, Nicotiana tabacum*); in others they have few or no chloroplasts. The bundle sheath cells are in direct contact with the conducting cells of the vascular bundle of parenchyma and on the outer face with the mesophyll tissue. Individual sheath cells may contain crystals.

The parenchymatous bundle sheaths are more common, but in certain dicotyledons bundles of various sizes are enclosed in sclerenchyma, *e.g.*, Winteraceae, Melastomaceae; (Bailey and Nast, 1944; Foster, 1947).

Vertical leaves. The leaves of many species of *Eucalyptus* do not spread out horizontally but hang vertically, so that both surfaces of the leaf receive direct sunlight. In keeping with this fact, palisade chlorenchyma is developed on both sides.

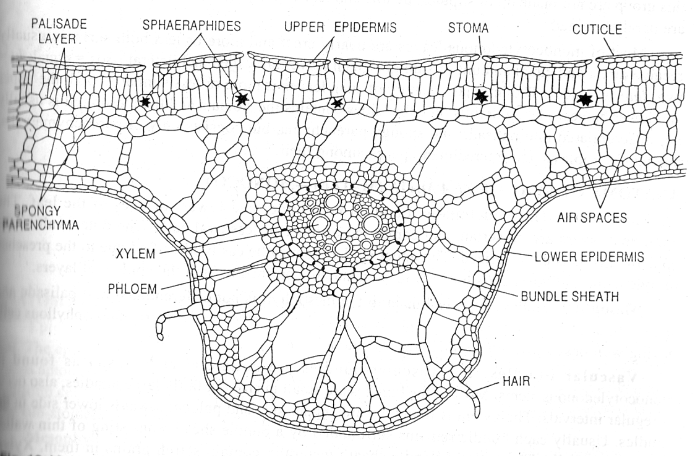


Fig. 12.13. Hydrophytic leaf. T.S. of floating leaf of *Trapa bispinosa*, showing big air spaces, the stomata confined to upper epidermis only.

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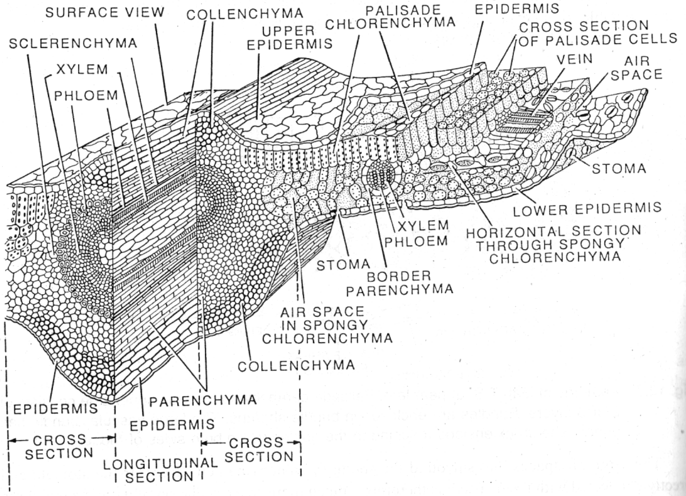


Fig. 12.8. The leaf. A three dimensional view of a section of a midrib and a small part of the leaf blade. On the left side is a cross section of half of the midrib followed by a longitudinal section, and this by a cross section of the remainder of the midrib and a portion of the blade. The leaf on the right side is dissected in various ways to show the arrangement of the tissues. (After Brown).

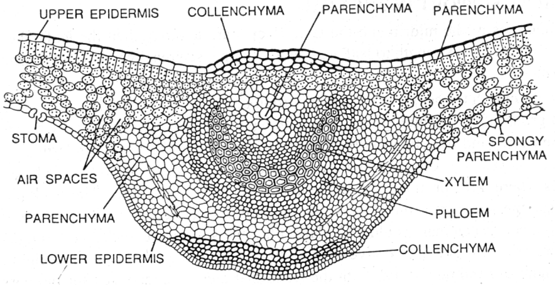


Fig. 12.9. Anatomy of dicotyledonous leaf. Cross section of midrib and leaf blade of leaf of *Erythroxylon*.

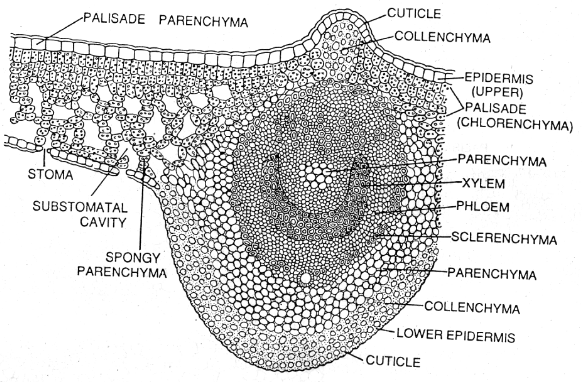


Fig. 12.10. Anatomy of dicotyledonous leaf. Cross section through a midrib and a part of leaf blade of a leaf of *Ixora*.

Sclerenchyma. Usually the sclerenchyma cells or the fibres are associated with the vascular tissues of the leaves. They occur usually as bundle caps adjacent to the phloem. Sometimes the fibres are found on both the sides of large vascular bundle of the leaves. Usually these cells are thick walled, dead and lignified. Their position just exterior to thin-walled phloem affords mechanical protection to the latter. The fibres are greatly elongated in the longitudinal direction of the midrib.

Turgid parenchyma. The regions between the collenchyma cells and the central portion of the midrib are occupied by parenchyma cells. In structure the parenchyma cells are not specially modified for any particular function, but they perform all the general functions of cells to a limited extent. Parenchyma cells have thin walls, but on account of their turgidity they strengthen the midrib.

Xylem. Usually the vessels and tracheids of xylem conduct water, but due to their thick walled nature they also give mechanical support to the leaves. The xylem elements are composed of lignified and dead cells.

ORIENTATION OF VASCULAR TISSUE

In the leaf traces of flowering plants, before they have the stele, the phloem is always found towards the outside of the stem. The leaf traces after their entrance in the petiole and lamina, also maintain the relative position of the xylem and the phloem, *i.e.*, the phloem is always found towards the lower side and the xylem towards the upper side in the leaf. Sometimes the xylem ring remains surrounded by a ring of phloem. The phloem occurs only below the xylem or rarely both above and below it.

Conducting system. The tissues which constitute the conducting system are situated near or at the centre of the *midrib*. This system may have various shapes, *e.g.*, the form of a ring, a crescent shaped ring, a crescent or scattered patches. In the ring shaped conducting system parenchyma cells are usually found in the centre of the ring. The inner part of the ring is composed of xylem (towards upper surface), and phloem (towards lower surface).

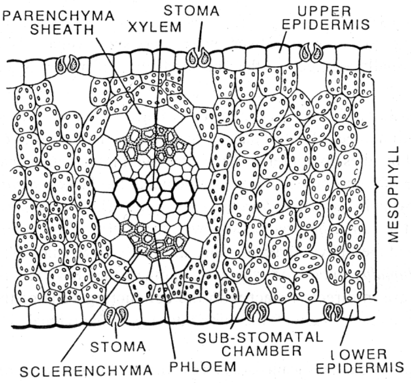


Fig. 12.14. An isobilateral leaf. T.S. of lily leaf.

ANATOMY OF MONOCOTYLEDONOUS LEAF

The monocotyledons as a group show greater diversity of specialized leaf types. The leaves of this group are not made up of stipules, petiole and leaf blade. In general monocotyledonous leaves are parallel-veined.

Most of monocotyledonous leaves are nearly erect and more or less both surfaces usually receive direct and equal amount of sunlight. Such leaves are called isobilateral (*isos* = equal; *bi* = two; *lateris* = side). The internal structure of such leaves is more or less similar in both the upper and lower halves. The epidermis on either sides contains the stomata and the mesophyll is usually not differentiated into palisade and spongy parenchyma, but consists only of parenchyma cells, having chloroplasts and intercellular spaces among them.

ANATOMY OF LEAF OF *ZEA MAYS* (MAIZE)—MONOCOT

Epidermis. The epidermis is found on both upper and lower surfaces of the leaf. The epidermal layers are uniseriate and composed of more or less oval cells. The outer wall of the epidermal cells is cuticularized. The upper epidermis may be easily identified due to the presence of xylem and *bulliform cells* towards it. Stomata are confined to both the epidermal layers.

Mesophyll. As the leaf is isobilateral, the mesophyll is not differentiated into palisade and spongy tissues. It is composed of compactly arranged thin walled, isodiametric chlorophyllous cells having well developed intercellular spaces among them.

Vascular bundles. The vascular bundles are collateral and closed as found in monocotyledonous stems. Most of the bundles are small in size but fairly large bundles, also occur at regular intervals. The xylem is found towards upper side and phloem towards lower side in the bundles. Usually each bundle remains surrounded by a bundle sheath consisting of thin walled parenchyma cells. The cells of bundle sheath generally contain starch grains in them. Xylem consists of vessels and phloem of sieve tubes and companion cells. Sclerenchyma cells occur in patches on both ends of the large vascular bundles which give mechanical support to the leaf.

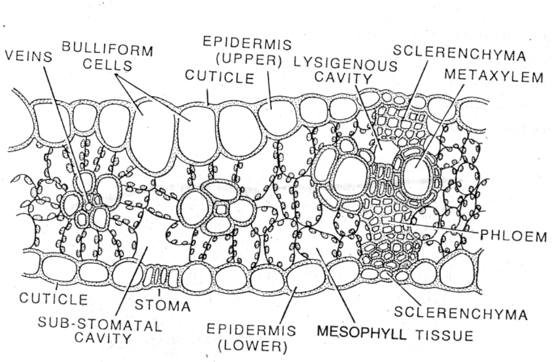


Fig. 12.15. Anatomy of monocotyledonous leaf of *Zea mays* similar structure of the two sides of vertical leaf.

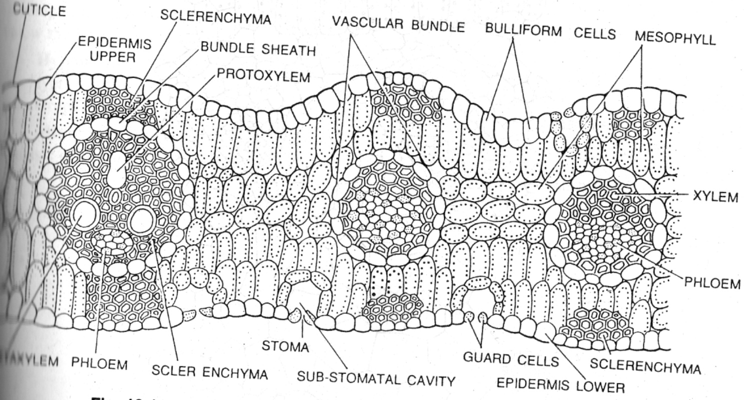


Fig. 12.16. Anatomy of isobilateral leaf. T.S. *Triticum aestivum* (monocot).

ANATOMY OF THE LEAF OF *TRITICUM AESTIVUM* (WHEAT)—MONOCOT

Epidermis. As usual the epidermis layers are found on both upper and lower surfaces of the leaf. The epidermises are uniseriate and composed of more or less oval cells having no intercellular spaces among them. The outer walls of epidermal cells are cuticularized. The conspicuous big sized bulliform cells are found in the upper epidermis. The stomata are confined to both epidermis layers. The sub-stomatal chambers are also seen in vertical section.

Mesophyll. It is composed of more or less oval chlorenchyma cells having intercellular spaces among them. The mesophyll tissue is not clearly differentiated into palisade and spongy parenchyma; however, the cells towards epidermal layers are somewhat elongated and palisade-like. Substomatal chambers are seen beneath the stomata.

Vascular bundles. The vascular bundles are collateral and closed as found in monocotyledonous stems. The bundles are arranged in parallel series. Xylem occurs towards upper surface and phloem towards lower surface. Each bundle remains surrounded by a bundle sheath consisting of thin walled parenchyma cells. The sclerenchyma strands are found on both the ends of each big vascular bundle.

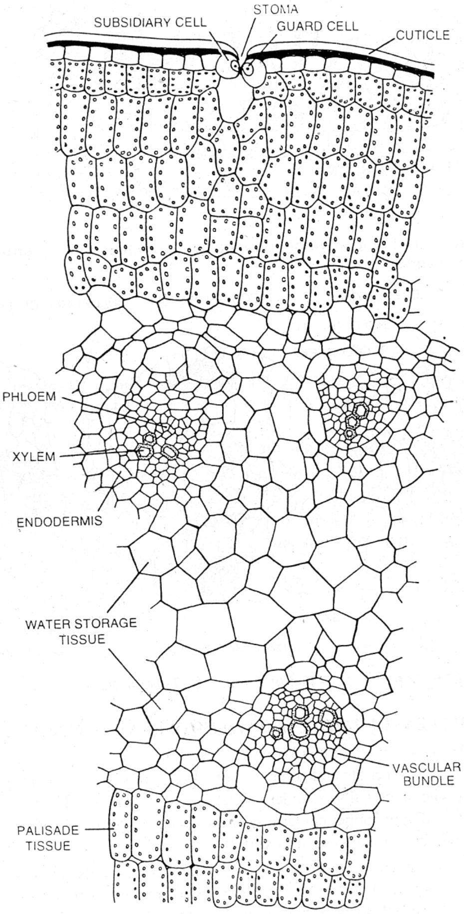


Fig. 12.17. Anatomy of *Aloe* (monocot) leaf. T.S. of a portion of leaf showing detailed internal structure.

ANATOMY OF GYMNOSPERM LEAF

The anatomy of the conifer leaf is described here with reference to the needle of *Pinus* because the leaf of this genus has been investigated in most detail.

The leaf of *Pinus* is xeromorphic. The whole anatomy of the leaf makes it adaptable to withstand the low temperature and the scarcity of water supply.

The outline of the needle (foliage leaf) in a transverse section depends on the number of needles in the dwarf shoot (spur). In *P. monopylla* the spur bears a single needle and therefore, the outline of the needle is circular. In *P. sylvestris* each spur consists of two needles and the outline of each needle is semi-circular. In *Pinus roxburghii* and *P. wallichiana* each spur consists of three needles and therefore, the two flat faces of each needle are towards the inner side and the curved face towards the outside. Here the outline of the needle appears somewhat triangular. The centre of the needle is traversed by one or two vascular bundles surrounded by a peculiar vascular tissue, called *transfusion tissue,* and a thick walled layer the endodermis. Outside the endodermis is the mesophyll. The peripheral layers are the epidermis and the morphologically differentiated hypodermis.

Epidermis. The outermost layer is the epidermis which consists of extremely thick-walled and cuticularized cells. A number of depressions are found over the epidermis. The stomata are developed all over the epidermis in these depressions. The guard cells are sunken in depression below the level of the epidermis.

Hypodermis. Just beneath the epidermis there is a hypodermis which is composed of one or two layers of sclerenchyma cells. The hypodermis is several layered at the corners. The hypodermis is interrupted by air-spaces beneath each stoma.

Mesophyll. The mesophyll is not differentiated into palisade and spongy parenchyma. It consists of thin-walled cells containing a large number of chloroplasts and starch grains. These

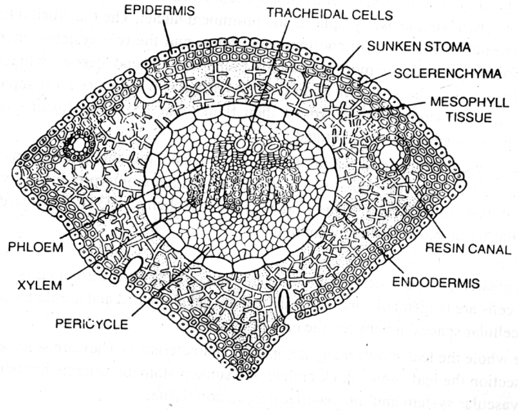


Fig. 12.18. Leaf. T.S. of pine leaf.

change takes place in the number of chromosomes and the resultant daughter cells remain similar to parent cells. In the last stage of metaphase, the chromatids are separated from each other in the divided parts of centromeres. This separation takes place because of repulsion.	the opposite poles themselves. The number of chromosomes travelling towards one of the poles remain half to the normal number. The resultant daughter cells are dissimilar to parent cell. The maternal and paternal chromosomes are separated because of repulsion of homologous chromosomes.
6. In anaphase the chromosomes travel upto poles.	6. As in mitosis.
7. As the result of telophase the two nuclei bear diploid (2n) number of chromosomes.	7. Two haploid (n) nuclei are formed during first telophase stages.
8. There is no second division in mitosis.	8. The second division occurs in meiosis. The reduction division takes place during the first telophase, whereas during second telophase ordinary mitotic division takes place.
9. As the result of mitosis, the number of chromosomes, their characters and constitution do not change.	9. As the result of meiosis, four daughter cells are formed. Each daughter cell or nucleus is haploid (n), *i.e.*, it contains half number of the chromosomes, thus the characters and the constitution of the chromosomes also change.
10. Cytokinesis always takes place after each division.	10. Cytokinesis does not necessarily occur in telophase one, normally it occurs in second telophase.

5

The Tissue

Groups or masses of the cells that are alike in origin, structure, and function form tissue. The plant body consists of *vegetative tissue* and *reproductive tissue*. In the higher plants the plant body is somewhat more complex in its cellular structure. The cells differ very much in their kind, form and origin in higher plants. Morphologically, a tissue is a group or a mass of cells or vessels, alike in form, origin and function. From the study point of view, the tissues may be grouped into three principal groups — 1. *Meristems* or *meristematic tissue*; 2. *Permanent tissue*, and 3. *Secretory tissue*.

1. MERISTEMS OR MERISTEMATIC TISSUE

A meristematic tissue consists of a group of cells which remain in a continuous state of division or they retain their power of division. The characteristic features of meristematic tissue are as follows:

1. They are composed of immature cells which are in a state of division and growth.
2. Usually the intercellular spaces are not found among these cells.
3. The cells may be rounded, oval or polygonal in shape; they are always living and thin-walled.
4. Each cell of meristematic tissue possesses abundant cytoplasm and one or more nuclei in it.
5. The vacuoles in the cells may be quite small or altogether absent.

MERISTEMS AND GROWTH OF PLANT BODY

Beginning with the division of the oospore, the vascular plant generally produces new cells and forms new organs until it dies. In the beginning of the development of the plant embryo cell division occurs throughout the young organism. But as soon as the embryo develops and converts into an independent plant the addition of new cells is gradually restricted to certain parts of the plant body, while the other parts of the remain concerned with activities other than growth. This shows that the portions of embryonic tissue persists in the plant throughout its life, and the mature plant is a composite of adult and juvenile tissues. These juvenile tissues are known as the *meristems*. The presence of meristems remarkably differentiates the plant, from the animal. In the growth resulting from meristematic activity is possible throughout the life of the organism, whereas in animal body the multiplication of the cells mostly ceases when the organism attains adult size and the number of organs is fixed.

The term meristem (Greek *meristos*, meaning divisible) emphasizes the cell-division activity characteristic of the tissue which bears this name. It is obvious that the synthesis of new living substance is a fundamental part of the process of the formation of new cells by division. The living tissues other than the meristems may also produce new cells, but the meristems carry on such activity indefinitely, because they not only add cells to the plant body, but also perpetuate themselves, that is, some of the products of division in the meristems do not develop into adult cells but remain meristematic.

The meristems usually occur at the apices of all main and lateral shoots and roots and thus their number in a single plant becomes quite large. In addition, plants bearing secondary increase in thickness possess extensive meristems, the vascular and cork cambia, responsible for the secondary growth. The combined activities of all these meristems give rise to a complex and large plant body. The primary growth, initiated in the apical meristems expands the plant body and produces the reproductive parts. On the other hand, the cambia, aid in maintenance of the expanding body by increasing the volume of the conducting system and forming supporting and protecting cells.

CLASSIFICATION OF MERISTEMS

Various systems of classifying meristems have been proposed by many eminent workers which are based on the characteristics such as stage of development, position in plant body, origin, function and topography. No system is exclusive and rigid. A few important types have been discussed here:

1. Meristems Based on Stage of Development

Promeristem or primordial meristem. Promeristem is the region of new growth in a plant body where the foundation of new organs or parts of organs is initiated. Sometimes, it is also called *primordial meristem*, *urmeristem* and *embryonic meristem*. From the view point of its structure, this region consists of the initials and their immediate derivatives. The cells of this region are isodiametric, thinwalled, vacuolate, with active cytoplasm and early stages of pits. Prominent nuclei and inconspicuous intercellular spaces may be seen. As soon as the cells of this region begin to change in size, shape, and character of wall and cytoplasm, setting off the beginning of tissue differentiation, they are no longer a part of typical meristem; they have passed beyond that earliest stage.

2. Meristems Based on Origin of Initiating Cells

Primary and secondary meristems. The meristems are classified as *primary* and *secondary*, on the basis of type of tissue in which origin occurs.

The primary meristems are those that build up the primary part of the plant and consist in part of promeristem. In primary meristems, promeristem is always the earliest stage. The possession of promeristem continuously from a early embryonic origin is characteristic of primary meristems. The main primary stems are the apices of roots, stems, leaves and similar appendages.

The secondary meristem appears later at a stage of development of an organ of a plant body. Secondary meristems always arise in permanent tissues and they are always found lying lateral along the side of the stem and root. Sometimes,.some of the primary permanent tissues acquire the power of division and become meristematic. These tissues build up the secondary meristem which is not Secondary meristems are so called because they arise as new meristems in tissue which is not meristematic. The most striking example of secondary meristem is phellogen or cork cambium. It is formed from mature cells — cortical, epidermal or phloem cells.

The primary meristems build up the early and structurally and functionally complete plant body. The secondary meristems later add to that body forming supplementary tissues that functionally replace the early formed tissues or serve in protection and repair of wounded regions.

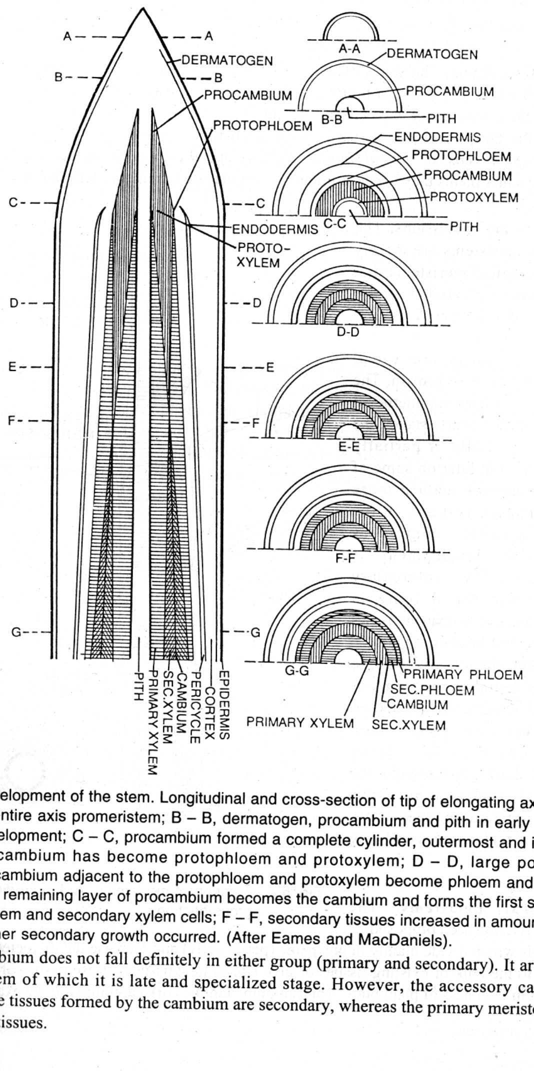


Fig. 5.1. Development of the stem. Longitudinal and cross-section of tip of elongating axis. At A – A, entire axis promeristem; B – B, dermatogen, procambium and pith in early stages of development; C – C, procambium formed a complete cylinder, outermost and innermost procambium has become protophloem and protoxylem; D – D, large portions of procambium adjacent to the protophloem and protoxylem become phloem and xylem; E – E, remaining layer of procambium becomes the cambium and forms the first secondary phloem and secondary xylem cells; F – F, secondary tissues increased in amount; G – G, further secondary growth occurred. (After Eames and MacDaniels).

The cambium does not fall definitely in either group (primary and secondary). It arises from apical meristem of which it is late and specialized stage. However, the accessory cambia are secondary. The tissues formed by the cambium are secondary, whereas the primary meristems form only primary tissues.

3. Meristems Based on Position in Plant Body

As regards their position in plant body, the meristems may be classified into three groups — *apical meristem, intercalary meristem* and *lateral meristem.*

Apical meristem. The apical meristem lies at the apex of the stem and the root of vascular plants. Very often they are also found at the apices of the leaves. Due to the activity of these meristems, the organs increase in length. The initiation of growth takes place by one or more cells situated at the tip of the organ. These cells always maintain their individuality and position and are called '*apical cells*' or '*apical initials*'. Solitary apical cells occur in pteridophytes, whereas in higher vascular plants they occur in groups which may be terminal or terminal and sub-terminal in position.

Intercalary meristems. The intercalary meristems are merely portions of apical meristems that have become separated from the apex during development by layers of more mature or permanent tissues and left behind as the apical meristem moves on in growth. The intercalary meristems are internodal in their position. In early stages, the internode is wholly or partially meristematic, but later on some of its part, becomes mature more rapidly than the rest and in the internode a definite continuous sequence of development is maintained. The intercalary meristems are found lying in between masses of permanent tissues either at the leaf base or at the base of internode. Such meristems are commonly found in the stems of grasses and other monocotyledonous plants and horsetails, where they are basal. Leaves of many monocotyledons (grasses) and some other plants, such as *Pinus*, have basal meristematic regions. These meristematic regions are short living and ultimately disappear, ultimately, they become permanent tissues.

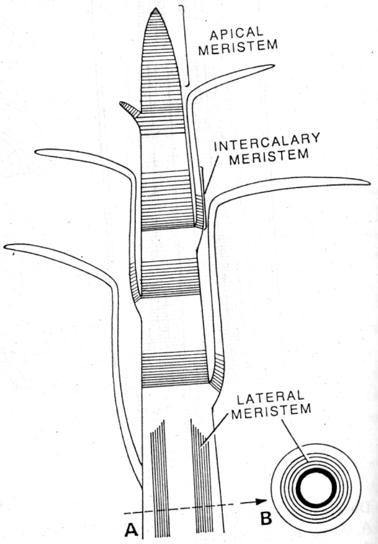


Fig. 5.2. Position of meristems. A, longitudinal view, cross-section.

Lateral meristems. The lateral meristems are composed of such initials which divide mainly in one plane (periclinally) and increase the diameter of an org They add to the bulk of existing tissues or give rise to new tissues. These tissues are respon for growth in thickness of plant body. The cambium and the cork cambium are the examples of th type.

4. Meristems Based on Function

As regards their function a system of classification of meristems was proposed by Haberlandt in the end of nineteenth century. He suggested that the primary meristem at the apex of the stem and root is distinguished into three tissues — *protoderm*, *procambium* and *ground* or *fundamental meristem*. The protoderm is the outermost tissue which develops into epidermis. The procambium develops into primary vascular tissue. It forms isolated strands of elongated cells very near to the central region; in cross-section each procambium appears as a small group of cells in the ground or fundamental meristem, but in longitudinal section the cells appear to be long and pointed. The ground or fundamental meristem develops into ground tissue and pith; the cells of this region are large, thin walled, living and isodiametric. In later stages, they become differentiated into hypodermis, cortex, endodermis, pericycle, pith rays and pith.

Meristem and meristematic. The terms meristem and meristematic, as applied to developing cells and tissues, are somewhat loose. According to Eames and MacDaniels, the term '*meristem*' is applied to regions of more or less continuous cell and tissue initiation; the adjective '*meristematic*' is used to indicate resemblance in an important way to a meristem, but not necessarily as consisting of or constituting meristem, *i.e.*, it is applied to those cells, tissues and regions that have characteristics of developing structures — especially cell division — but do not themselves strictly constitute meristems. For example, the apices of the stems and the cambium are regions of tissue initiation, developing xylem and phloem are meristematic tissues, because they form some new cells and are immature but they are not permanent or semipermanent initiating regions (meristems). On the other hand, cells in mature tissue, such as the primary cortex of stems, may divide. Such cells are meristematic, but neither they nor the tissues of which they are a part constitute a meristem.

MERISTEMS AND PERMANENT TISSUES

In active meristems there occurs a continuous separation between cells that remain meristematic — the *initiating cells* — and those that develop into the various tissue elements — the *derivatives* of the initiating cells. During this process of developing the derivatives gradually change, physiologically and morphologically, and assume more or less specialized characteristics. In other words, the derivatives differentiate into the specific elements of the various tissue-systems. As the cells of vascular plants vary in their physiologic and morphologic characteristics, they also vary in details of differentiation. Different types of cells attain different degrees of differentiation as compared with their common meristematic precursors. For example, various parenchyma cells diverge relatively little from their meristematic precursors and retain the power of division to a high degree. On the other hand, such as sieve elements, fibres, tracheary elements are more thoroughly modified and lose most, or all of their former meristematic potentialities. These variously differentiated cells are known as *mature* or *permanent* in the sense that they have reached the degree of specialization and physiological stability that normally characterizes them as components of certain tissues of an adult plant part. During the differentiation of tissues from meristems the derivatives of meristematic cells synthesize protoplasm, enlarge and divide. It is difficult to delimit the meristem proper from its recent derivatives. The development of meristematic derivatives into mature cells also is gradual. In other words, the differentiation is a continuous process.

2. PERMANENT TISSUES

The permanent tissues are those in which growth has stopped either completely or for the time being. Sometimes, they again become meristematic partially or wholly. The cells of these tissues may be living or dead and thin-walled or thick-walled. The thin-walled permanent tissues are generally living whereas the thick-walled tissues may be living or dead. The permanent tissues may be *simple* or *complex*. A simplè tissue is made up of one type of cells forming a uniform of homogeneous system of cells. The common simple tissues are — *parenchyma*, *collenchyma* and *sclerenchyma*. A complex tissue is made up of more than one type of cells working together as a unit. The complex tissues consist of parenchymatous and sclerenchymatous cells; collenchymatous cells are not present in such tissues. The common examples are — the *xylem* and the *phloem*.

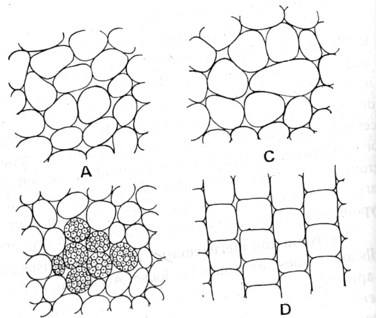


Fig. 5.3. Parenchyma. A, from pith of rhizome of *Polypodium*; B, from cortex of root of *Asclepias*, the cells containing starch grains; C and D, from pith of *Zea* in transverse and longitudinal sections.

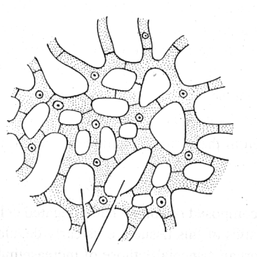
SIMPLE TISSUES

1. Parenchyma. *The parenchyma tissue is composed of living cells which are variable in their morphology and physiology, but generally having thin walls and a polyhedral shape, and concerned with vegetative activities of the plant*. The individual cells are known as *parenchyma cells*. The word parenchyma is derived from the Greek *para*, beside and en*chein*, to pour. This combination of words expresses the ancient concept of parenchyma as a semi liquid substance *poured beside* other tissues which are formed earlier and are more solid. Phylogenetically the parenchyma is a primitive tissue since the lower plants have given rise to the higher plants through specialization and since the single type or the few types of cells found in the lower plants have become by specialization the many and elaborate types of the higher plants. The unspecialized meristematic tissue is parenchyma and is often called parenchyma thus it can be said that, ontogentically parenchyma is a primitive tissue.

The parenchyma consists of isodiametric, thin-walled and equally expanded cells. The parenchyma cells are oval, rounded or polygonal in shape having well developed spaces among them. The cells are not greatly elongated in any direction. The cells of this tissue are living and contain sufficient amount of cytoplasm in them. Usually each cell possesses one or more nuclei.

Parenchyma makes up large parts of various organs in many plants. Pith, mesophyll of leaves, the pulp of fruits, endosperm of seeds, cortex of stems and roots, and other organs of plants cons mainly of parenchyma. The parenchyma cells also occur in xylem and phloem.

In the aquatic plants, the parenchyma cells in the cortex possess well developed air spa (intercellular spaces) and such tissue is known as *aerenchyma*. Parenchyma may be specialized water storage tissue in many succulent and xerophytic plants. In *Aloe*, *Agave*, *Mesembryanthe* *Hakea* and many other plants chlorophyll-free, thin-walled and water-turgid cells are found w represent water storage tissue. When the parenchyma cells are exposed to light they dev chloroplasts in them, and such tissue is known as *chlorenchyma*. The chlorenchyma posses developed aerating system. Intercellular spaces are abundant in the photosynthetic paren (chlorenchyma) of stems too.



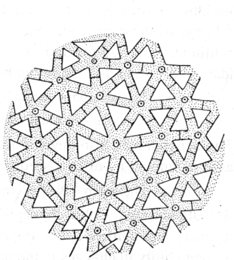


Fig. 5.4. Aerenchyma—in the petiole of *Canna*. **Fig. 5.5.** Aerenchyma—in the petiole of *banana*.

Commonly the parenchyma cells have thin primary walls. Some such cells may have also thick primary walls. Some storage parenchyma develop remarkably thick walls and the carbohydrates deposited in these walls, the hemicellulose, are regarded by some workers as reserve materials. Thick walls occur, in the endosperm of *Phoenix dactylifera*, *Diospyros*, *Asparagus* and *Coffea arabica*. The walls of such endosperm become thinner during germination.

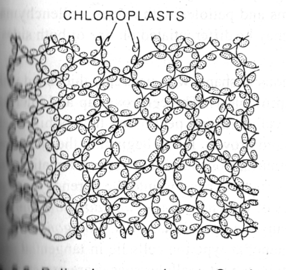


Fig. 5.6. Palisade parenchyma. Section cut parallel with the epidermis. Each cell contains many chloroplasts.

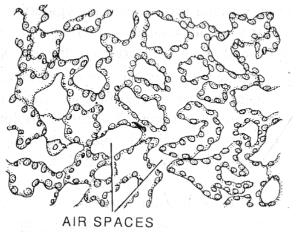


Fig. 5.7. Spongy chlorenchyma. Section cut parallel with the epidermis showing irregular cells with chloroplasts and well developed intercellular spaces.

The turgid parenchyma cells help in giving rigidity to the plant body. Partial conductioen of water is also maintained through parenchymatous cells. The parenchyma acts as special storage tissue to store food material in the form of starch grains, proteins, fats and oils. The parenchyma that contain chloroplasts in them make chlorenchyma which are responsible for photosynthesis in green plants. In water plants the aerenchyma keep up the buoyancy of the plants. Such air spaces facilitate exchange of gases. In many succulent and xerophytic plants such tissues store water known as water storage tissue. Vegetative propagation by cuttings takes place because of meristematic potentialities of the parenchyma cells which divide and develop into buds and adventitious roots.

result from stretching and bending of plant organs without any damage to the thin-walled softer cells. The individual cells of sclerenchyma are termed *sclerenchyma cells*. Collectively sclerenchyma cells make sclerenchyma tissue. Sclerenchyma cells do not possess living protoplasts at maturity. The walls of these cells are uniformly and strongly thickened. Most commonly, the sclerenchyma cells are grouped into *fibres* and *sclereids*.

Fibres. The fibres are elongate sclerenchyma cells, usually with pointed ends. The walls of fibres are usually lignified. Sometimes, their walls are so much thickened that the lumen or cell cavity is reduced very much or altogether obliterated. The pits of fibres are always small, round or slit-like and often oblique. The pits on the walls may be numerous or few in number. The middle lamella is conspicuous in the fibres. In most kinds of fibres, however, on maturation of cells the protoplast disappears and the permanent cell becomes dead and empty. Very rarely the fibres retain protoplasts in them.

The fibres are abundantly found in many plants. They may occur in patches, in continuous bands and sometimes singly among other cells. As already mentioned, they are dead and purely mechanical in function. They provide strength and rigidity to the various organs of the plants to enable them to withstand various strains caused by outer agencies. The average length of fibres is 1 to 3 mm. in angiosperms, but exceptions are there. In *Linum usitatissimum* (flax), *Cannabis sativa* (hemp), *Corchorus capsularis* (jute), and *Boehmeria nivea* (ramie), the fibres are of excessive lengths ranging from 20 mm. to 550 mm. Such long, thick-walled and rigid cells constitute exceptionally good fibres of commercial importance. In addition to these plants common long fibre yielding plants are *Hibiscus cannabinus* (Madras hemp), *Agave sisalana* (sisal hemp), *Sansevieria* and many others.

The fibres are divided into two large groups — *xylem fibres* and *extraxylary fibres*. The xylem fibres develop from the same meristematic tissues as the other xylem cells and constitute an integral part of xylem. On the other hand, some of the extraxylary fibres are related to the phloem. The fibres that form continuous cylinders in monocotyledonous stems arise in the ground tissue under the

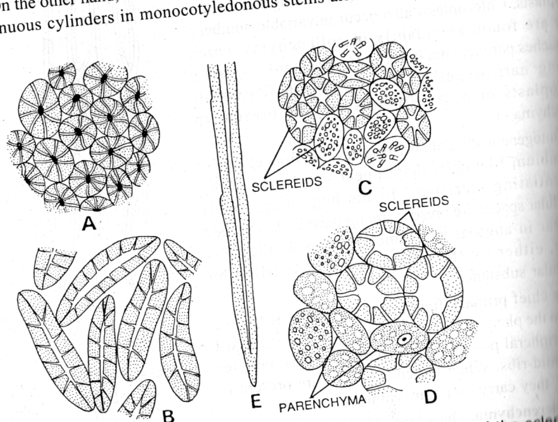


Fig. 5.11. Sclerenchyma. A and B, transverse and longitudinal sections of the sclereids endocarp of *Cocos nucifera*; C, sclereids from the pericarp of *Pyrus commu* sclereids and parenchyma cells from stem cortex of *Dracaena fragrans*; E.L.S. sclereids and parenchyma cells from stem cortex of *Dracaena fragrans*; (After Eames and MacDaniels).

epidermis at variable distances. They are known as *cortical fibres*. The fibres forming sheaths around the vascular bundles in the monocotyledonous stems arise partly from the same procambium as the vascular cells, partly from the ground tissue. The fibres present in the peripheral region of the vascular cylinder, often close to the phloem are known as *pericyclic fibres*. The extraxylary fibres are sometimes combined into a group termed *bast fibres*. Generally the term extraxylary fibres is used for bast fibres, which are classified as follows — *phloem fibres*, fibres originating in primary or secondary phloem; *cortical fibres*, fibres originating in the cortex; *perivascular fibres* (Van Fleet, 1948), fibres found in the peripheral region of the vascular cylinder inside the innermost cortical layer but not originating in the phloem. The extraxylary fibres may vary in length, and their ends are sometimes blunt, rather than tapering, and may be branched. The longest fibres (primary phloem fibres) measured *Boehmeria nivea* (ramie). The cell walls of extraxylary fibres are very thick. The pits are simple or slightly bordered. Some possess lignified walls, others non-lignified. The fibres of *Linum usitatissimum* are non-lignified, and their secondary walls consist of pure cellulose. On the other hand, the extraxylary fibres of the monocotyledons, are strongly lignified. Concentric lamellations are found in extraxylary fibres. In the fibres of *Linum usitatissimum* the individual lamellae vary in thickness from 0.1μ to 0.2μ.

Xylem fibres typically possess lignified secondary walls. They vary in size, shape, thickness of wall, and structure and abundance of pits.

Sclereids. The sclereids are widely distributed in the plant body. They are usually not much longer than they are broad, occurring singly or in groups. Usually these cells are isodiametric but some are elongated too. They are commonly found in the cortex and pith of gymnosperms and dicotyledons, arranged singly or in groups. In many species of plants, the sclereids occur in the leaves. The leaf sclereids may be few to abundant. In some leaves the mesophyll is completely permeated by sclereids. Sclereids are also common in fruits and seeds. In fruits they are disposed in the pulp singly or in groups (*e.g.*, *Pyrus*). The hardness and strength of the seed coat is due to the presence of abundant sclereids.

The secondary walls of the sclereids are typically lignified and vary in thickness. In many sclereids the lumina are almost filled with massive wall deposits and the secondary wall shows prominent pits. Commonly the pits are simple and rarely bordered pits may also occur.

The sclereids are grouped into four categories (Foster, 1949). They are as follows — *brachysclereids*, *macrosclereids*, *osteosclereids* and *astrosclereids*.

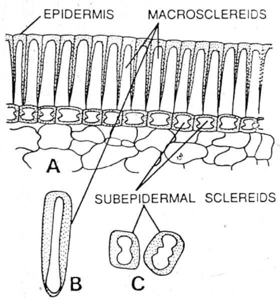


Fig. 5.12. Sclereids of leguminous seed coats. A, the epidermis of a solid layer of macrosclereids; B, single epidermal macro-sclereid; C, sub-epidermal sclereids. (After K. Esau).

Brachysclereids. These stone cells or sclereids are short and more or less isodiametric. They are commonly distributed in cortex, phloem and pith of stem and in the pulp of fruits.

Macrosclereids. They are more or less rod-like cells forming palisade-like epidermal layer of the seeds (of Leguminosae) and fruits and frequently found in xerophytic leaves and stem cortices.

Origin. As regards their origin, the parenchyma tissue of the primary plant body, that is, the parenchyma of the cortex and the pith, of the mesophyll of leaves, and of the flower parts, differentiates from the ground meristem. The parenchyma associated with the primary and secondary vascular tissues is formed by the procambium and the vascular cambium respectively.

Procambium—parenchyma associated with the primary vascular tissues.

Vascular cambium—parenchyma associated with the secondary vascular tissues.

Parenchyma may also develop from the phellogen in the form of phelloderm, and it may be increased in amount by diffuse secondary growth.

Phellogen—Phelloderm (parenchyma).

2. Collenchyma. Collenchyma is a living tissue composed of somewhat elongated cells with thick primary nonlignified walls. Important characteristics of this tissue are its early development and its adaptability to changes in the rapidly growing organ, especially those of increase in length. When the collenchyma becomes functional, no other strongly supporting tissues have appeared. It gives support to the growing organs which do not develop much woody tissue. Morphologically, collenchyma is a simple tissue, for it consists of one type of cells.

Collenchyma is a typical supporting tissue of growing organs and of those mature herbaceous organs which are only slightly modified by secondary growth or lack such growth completely. It is the first supporting tissue in stems, leaves and floral parts. It is the main supporting tissue in many dicotyledonous leaves and some green stems. Collenchyma may occur in the root cortex, particularly, if the root is exposed to light. It is not found in the leaves and stems of monocotyledons. Collenchyma chiefly occurs in the peripheral regions of stems and leaves. It is commonly found just beneath the epidermis. In stems and petioles with ridges, collenchyma is particularly well developed in the ridges. In leaves it may be differentiated on one or both sides of the veins and along the margins of the leaf blade.

The collenchyma consists of elongated cells, various in shape, with unevenly thickened walls, rectangular, oblique or tapering ends, and persistent protoplasts. The cells overlap and interlock, forming fibre-like strands. The cell walls consist of cellulose and pectin and have a high water content. They are extensible, plastic and adapted to rapid growth. In the beginning the strands are of small diameter but they are added to, as growth continues, from surrounding meristematic tissue. The border cells of the strands may be transitional in structure, passing into the parenchyma type. As regards the cell arrangement there are three types of collenchyma — *angular*, *lamellar* and *tubular*. In angular type the cells are irregularly arranged (*e.g.*, *Ficus*, *Vitis*, *Polygonum*, *Beta*, *Rumex*, *Boehmeria*, *Morus*, *Cannabis*, *Begonia*); in lamellar type the cells lie in tangential rows (*e.g.*, *Sambucus*, *Rheum*, *Eupatorium*) and in tubular type the intercellular spaces are present (*e.g.* Compositae, *Salvia*, *Malva*, *Althaea*). The common typical condition, is that with thickenings the corners. The three forms of collenchyma have been named by Muller (1890) angular (Eckencollenchym), lamellar (Plattencolenchym), and tubular or lacunate (Luchencollenchym) respectively. The word lamellar has reference to the plate like arrangement of the thickenings, lacunate (tubular) to the presence of intercellular spaces.

The walls of collenchyma are chiefly composed of cellulose and pectic compounds and con much water (Majumdar and Preston, 1941). In some species collenchyma walls possess alternation of layers rich in cellulose and poor in pectic compounds with layers that are rich pectic compounds and poor in cellulose. In many plants collenchyma is a compact tissue lacking intercellular spaces. Instead, the potential spaces are filled with intercellular material (Majumdar 1941).

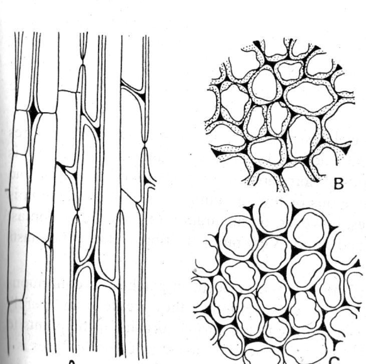


Fig. 5.8. Collenchyma. A and B, longitudinal and transverse sections from stem of *Solanum tuberosum*; C, transverse section from stem of *Abutilon*.

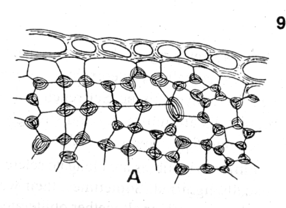


Fig. 5.9. Collenchyma. A, angular collenchyma of *Cucurbita* stem (thickenings in the angles); B, lacunar collenchyma of *Lactuca* stem where intercellular spaces are present and the thickenings are located next to these spaces.

The mature collenchyma cells are living and contain protoplasts. Chloroplasts also occur in variable numbers. They are found abundantly in collenchyma which approaches parenchyma in form. Collenchyma consisting of long narrow cells contains only a few small chloroplasts or none. Tannins may be present in collenchyma cells.

Ontogenetically collenchyma develop from elongate, procambium like cells that appear very early in the differentiating meristem. In the beginning, small intercellular spaces are present among these cells, but they disappear in angular and lamellar types as the cells enlarge, either by the enlarging cells or filled by intercellular substance.

The chief primary function of the tissue is to give support to the plant body. Its supporting value is increased by its peripheral position in the parts of stems, petioles and leaf mid-ribs. When the chloroplasts are present in the tissue, they carry on photosynthesis.

3. Sclerenchyma. The sclerenchyma (Greek, *sclerous*, *enchyma*, an infusion) consists of thick walled cells, lignified, whose main function is mechanical. This is supporting tissue that withstands various strains which

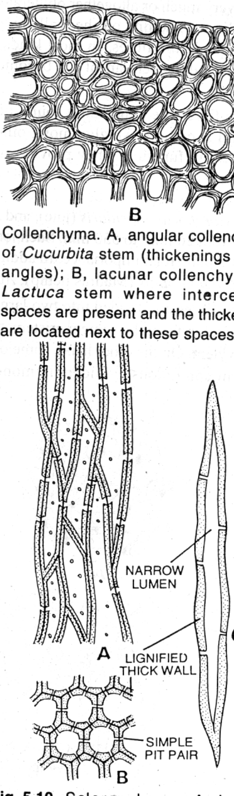


Fig. 5.10. Sclerenchyma. A, L.S. of fibres; B, T.S. of fibres; C, a single fibre as seen in longitudinal section.

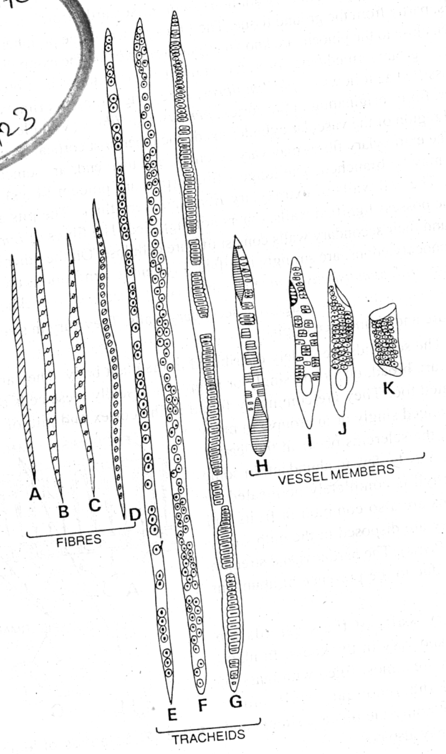


Fig. 5.13. Xylem. A – D, fibres; E – G, tracheids and H – K, vessel members. (After Bailey & Tupper).

Osteosclereids. They are bone-shaped sclereids, *i.e.*, columnar cells are enlarged at their They are Such sclereids are commonly found in the hypodermal layers of many seeds and fruits. found in xerophytic leaves.

Astrosclereids. They are star-shaped sclereids; such sclereids with lobes projecting, like are commonly found in the intercellular spaces of the leaves and stems of hydrophytes.

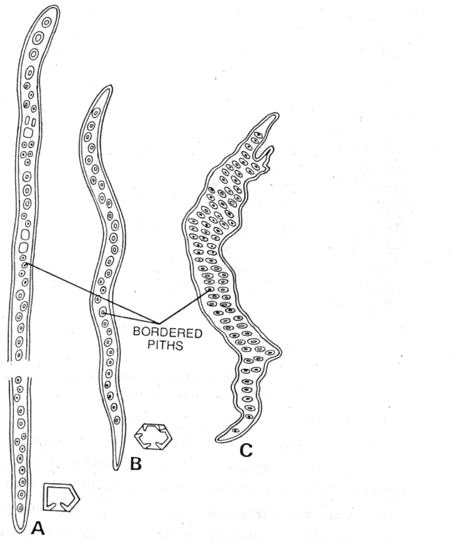


Fig. 5.14. Tracheids. A, L.S. and T.S. of tracheid from *Pinus strobus*; B, L.S. and T.S. of normal tracheid from *Quercus alba*; C, flattened and distorted tracheid from the spring wood of *Quercus alba*. (After E & M).

COMPLEX TISSUES

Here the vascular tissues have been treated as *complex tissues*. The most important complex tissues are — *xylem* and *phloem*.

XYLEM

Xylem is a conducting tissue, which conducts water and mineral nutrients upward from the root to the leaves. The xylem is composed of different kinds of elements. They are: (*a*) tracheids, (*b*) fibres and fibre-tracheids, (*c*) vessels or tracheae, (*d*) wood fibres and (*e*) wood parenchyma. The xylem is also meant for mechanical support to the plant body.

(*a*) **Tracheids.** The tracheid is a fundamental cell type in xylem. It is an elongate tube like cell having tapering, rounded or oval ends and hard and lignified walls. The walls are not much thickened. It is without protoplast and non-living on maturity. In transverse section the tracheid is typically angular, though more or less rounded forms occur. The tracheids of secondary xylem have fewer pits and are more sharply angular than the tracheids of primary xylem. The end of a tracheid of secondary xylem is somewhat chisel-like. They are dead empty cells. Their walls are provided with circular, bordered pits arranged in rows or in other patterns. The cell cavity or lumen of a tracheid is large and without any contents. The tracheids possess various kinds of thickenings in them and may be distinguished as annular, spiral, scalariform, reticulate or pitted tracheids. Tracheids alone form the xylem of ferns and gymnosperms, while in the xylem of angiosperms they occur associated

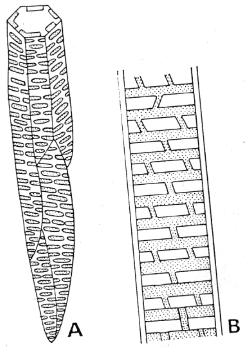


Fig. 5.15. Tracheids. A, a scalariform tracheid of fern; B, a portion of the wall of the same magnified.

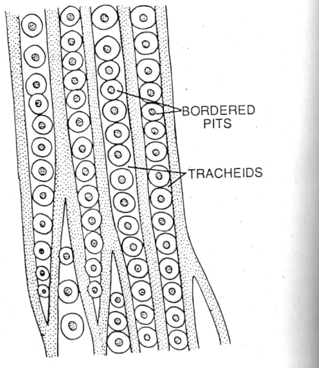


Fig. 5.16. Tracheids. Tracheids of pine stem in R.L.S. with bordered pits.

with the vessels and other xylary elements. The tracheids are specially adapted to function of conduction. The thick and rigid walls of tracheids also aid in support and where there are no fibres or other supporting cells, the tracheids play a prominent part in the support of an organ.

(b) Fibres and fibre-tracheids. In the phylogenetic development of the fibre, the thickness of the wall increases while the diameter of the lumen decreases. In most types the length of the cell also decreases and the number and size of the pits found on the walls also decrease. Sometimes the lumen of the cell becomes too much narrow or altogether obliterated and simultaneously pits become quite small in size. At this stage it is assumed that either there is very little conduction of water or no conduction through such type of cells, typical *fibres* are formed. Between such cells (*i.e.*, fibres) and normal tracheids there are many transitional forms which are neither typical fibres nor typical tracheids. These transitional types are designated as *fibre-tracheids*. The pits of fibre-tracheids are smaller than those of vessels and typical tracheids. However, a line of demarcation cannot be drawn in between tracheids and fibre-tracheids and between fibre-tracheids and fibres. When the fibres possess very thick walls and reduced simple pits, they are known as libriform wood fibres because of their similarity to phloem fibres (liber phloem fibres). The libriform wood fibres chiefly occur in woody dicotyledons (*e.g.*, in Leguminosae). The walls of fibre tracheids and fibres of many genera of different families possess gelatinous layers. The cells possessing such layers are known as *gelatinous tracheids*, *fibre-tracheids* and *fibres*. In certain fibre-tracheids the protoplast persists after the secondary wall is mature and may divide to produce two or more protoplasts. These protoplasts are separated by thin transverse partition walls and remain enclosed within the original wall. Such fibre tracheids are called *septate fibre-tracheids*. In fact, they are not individual cells but rows of cells. Here, the transverse partitions are true walls, and each chamber has a protoplast with nucleus.

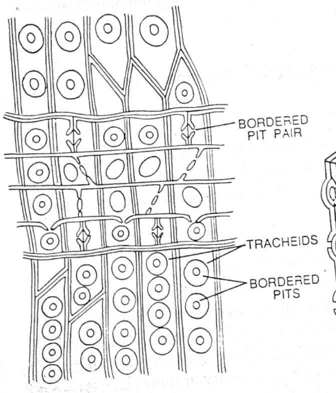


Fig. 5.17. Tracheids with bordered pits of pine stem in R.L.S.

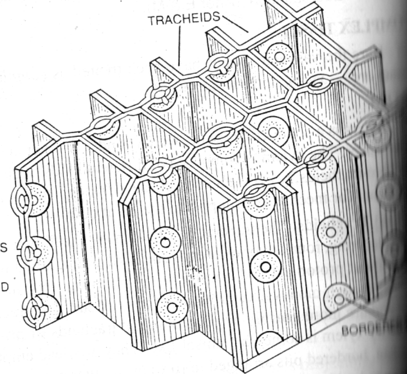


Fig. 5.18. Tracheids with bordered pits of pine stem (diagrammatic).

(c) Vessels. In the phylogenetic development of the tracheid the diameter of the cell has increased and the wall has become perforated by large openings. Due to these adaptations and specializations water can move from cell to cell without any resistance. In the more primitive types of vessels the general form of the tracheid is retained and increase in diameter is not much. In the most advanced types, increase in diameter is much and the cell becomes drum-shaped (*e.g.*, *Quercus alba*). The tracheid is sufficiently longer than the cambium cell from which it is derived. The primitive vessel is slightly longer than the cambium cell. The most advanced type of vessel retains the length of cambium cell or is somewhat shorter, with a diameter greater than its length (drum-shaped vessel). The ends of the cells change in shape in the vessels from least to highest specialization. The angle formed by the tapering end wall becomes greater and greater until the end wall is at right angles to the side walls (as in drum-shaped vessel in *Quercus*

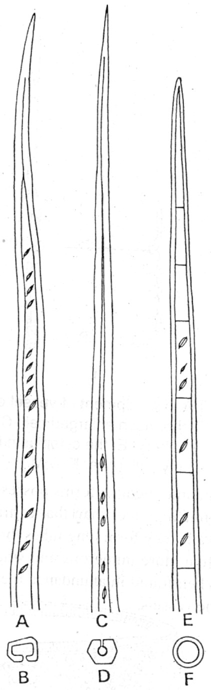


Fig. 5.19. Wood fibres and fibre-tracheids. A and B, L.S. and T.S. of fibre-tracheid from *Malus pumila*; C and D, L.S. and T.S. of libriform fibre from *Quercus alba*; E and F, L.S. and T.S. of septate fibre-tracheid from *Swietenia mahagoni*. (After E. and M.)

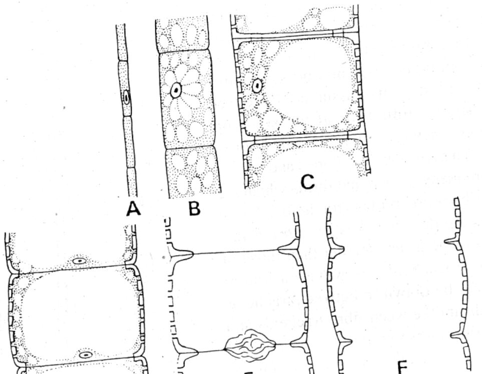


Fig. 5.20. The development of vessel element. (Ontogeny of the vessel) — A, the cambium initi B, the much enlarged cell; C, the cell further enlarged; D, the cytoplasm restricted to th periphery; E, the cytoplasm lost, thin end walls disintegrating; F, the mature, perfora empty cell. (After E. & M.)

alba). Some intermediate forms possess tail-like lips beyond the end wall. Usually the diamete vessels is much greater than that of tracheids and because of the presence of perforations in partition walls they form long tubes through which water is being conducted from root to leaf. pits are often more numerous and smaller in size than are those of tracheids and cover the closely. When found in abundance they are either scattered or arranged in definite patterns on walls of the vessels.

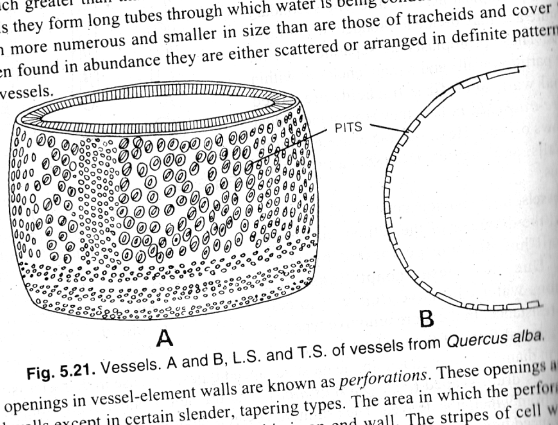


Fig. 5.21. Vessels. A and B, L.S. and T.S. of vessels from *Quercus alba.*

The openings in vessel-element walls are known as *perforations*. These openings are to the end walls except in certain slender, tapering types. The area in which the perfora is known as *perforation plate*. Commonly this is an end wall. The stripes of cell wall scalariform perforations are the *perforation bars*. The perforation plate when bears single is described as having *simple perforation*. If there are two or more openings, they are *multiple perforations*.

The secondary walls of vessel-elements develop in a wide variety of patterns. Generally, in the first-formed part of the primary xylem a more limited area of the primary wall is covered by secondary wall layers than in the later-formed primary xylem and in the secondary xylem. The secondary thickenings are deposited in the vessels as rings, continuous spirals or helices, with the individual coils of a helix here and there interconnected with each other, giving the wall a ladder-like appearance. Such secondary thickenings are called — *annular*, *spiral* or *helical* and *scalariform* respectively. In a still later ontogenetic type of vessel elements, the *reticulate* vessel elements, the secondary wall appears like a reticulum. When the meshes of the reticulum are transversely elongated, the thickening is called *scalariform-reticulate*. The *pitted* elements are characteristic of the latest primary xylem and of the secondary xylem.

Vessels are characteristic of the angiosperms. However, certain angiospermic families lack the vessels — the Winteraceae, Trochodendraceae and Tetracentraceae. In many monocotyledons (*e.g.*, *Yucca*, *Dracaena*) they are absent from the stems and leaves. They are found in some species of *Selaginella*, in two

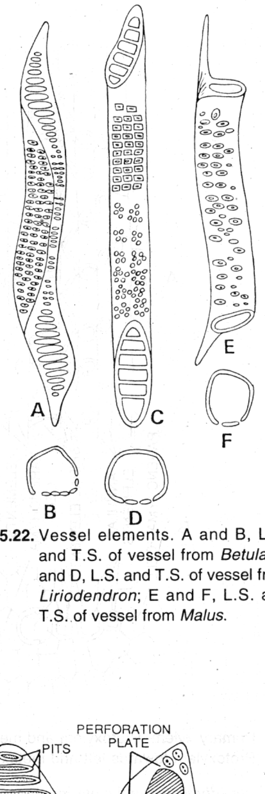


Fig. 5.22. Vessel elements. A and B, L.S. and T.S. of vessel from *Betula*; C and D, L.S. and T.S. of vessel from *Liriodendron*; E and F, L.S. and T.S. of vessel from *Malus*.

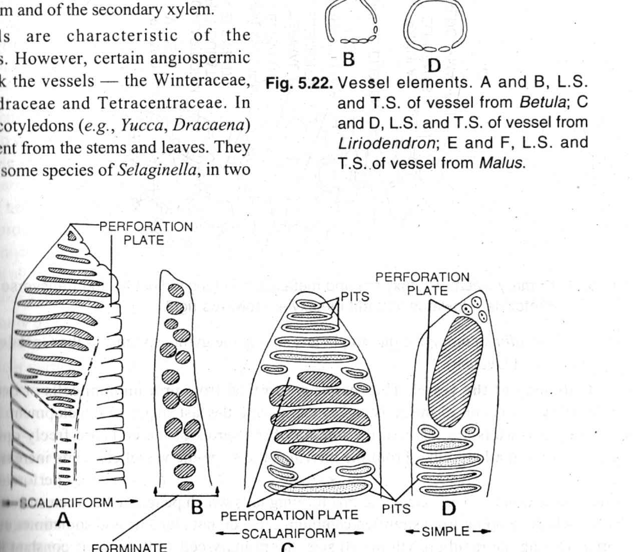


Fig. 5.23. End walls of vessels with perforation plates. A scalariform vessel of *Pteridium*; B, foraminate type of *Ephedra*; C, scalariform vessel of *Vitis* and D, simple type of *Vitis*.

starch or fat. Tannins, crystals and various other substances also occur in xylem parenchyma cells. These cells assist directly or indirectly in the conduction of water upward through the vessels and tracheids.

2. PHLOEM

The xylem and phloem have evolved along more or less on similar lines. In xylem a series of tracheids, structurally and functionally united, has become a vessel whereas in phloem a series of cells similarly united, forms a sieve tube. The fundamental cell type of xylem is tracheid, whereas in phloem the basic cell type is the sieve element. There are two forms of sieve element — the more primitive form is the *sieve cell* of gymnosperms and lower forms where series of united cells do not exist, the unit of a series, the sieve tube element. Phloem like xylem, is a complex tissue, and consists of the following elements — (*a*) sieve elements, (*b*) companion cells, (*c*) phloem fibres and (*d*) phloem parenchyma. In the pteridophytes and gymnosperms only sieve cells and phloem parenchyma are present. In some gymnosperms, sieve cells, phloem parenchyma and phloem fibres are present. In angiosperms, sieve tubes, companion cells, phloem parenchyma, phloem fibres, sclereids and secretory cells are present.

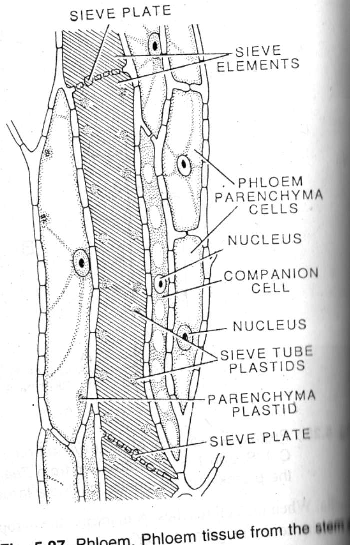


Fig. 5.27. Phloem. Phloem tissue from the stem of *Nicotiana*.

(*a*) **Sieve elements.** The conducting elements of the phloem are collectively known as the sieve elements. They may be segregated into the less specialized *sieve cells* and the more specialized sieve

COMPARISON OF TRACHEID AND VESSEL

Tracheid	Vessel
1. The tracheids are short and are generally upto 1 mm. in length. In rare cases their length becomes upto 1.2 cm. or so.	1. They are comparatively longer and reach upto 10 cm. in length. In rare they attain the length upto 2–6 (*e.g.*, in *Eucalytus*, *Quercus*, etc.)
2. It consists of a single elongated cell which possesses tapering end walls.	2. The vessel consists of a row of placed one above the other. The intervening walls are absent.
3. The tracheids are not tubular. The tracheids found one above the other are separated by cross walls which bear bordered pits. They are not perforated	3. The vessels are tubular and have walls. They are well adapted for conduction of water. They perforated by small or large pores

tubes or *sieve tube elements*. The morphologic specialization of sieve elements is expressed in the development of sieve areas on their walls and in the peculiar modifications of their protoplasts. The *sieve areas* are depressed wall areas with clusters of perforations, through which the protoplasts of the adjacent sieve elements are interconnected by *connecting strands*. In a sieve area each connecting strand remains encased in a cylinder of substance called *callose*. The wall in a sieve area is a double structure consisting of two layers of primary wall, one belonging to one cell and the other to another, cemented together by intercellular substance. Like the pits in the tracheary elements, the sieve areas occur in various numbers and are variously distributed in sieve elements of different plants. The wall parts bearing the highly specialized sieve areas are called *sieve plates* (Esau, [illegible]). If a sieve plate consists of a single sieve area, it is a *simple sieve plate*. Many sieve areas, arranged in scalariform, reticulate, or any other manner, constitute a *compound sieve plate*. However,

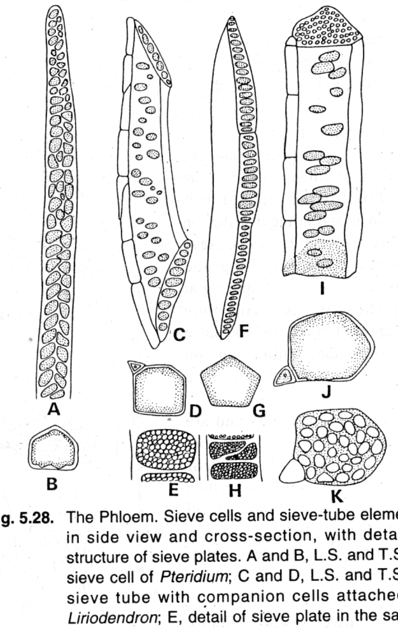


Fig. 5.28. The Phloem. Sieve cells and sieve-tube elements in side view and cross-section, with detailed structure of sieve plates. A and B, L.S. and T.S. of sieve cell of *Pteridium*; C and D, L.S. and T.S. of sieve tube with companion cells attached in *Liriodendron*; E, detail of sieve plate in the same; F and G, sieve tube from *Malus pumila* in L.S. and T.S.; H, detail of sieve plate in same; I and J sieve tube from *Robinia* in L.S. and T.S. with companion cells attached; K, detail of sieve plate in same.

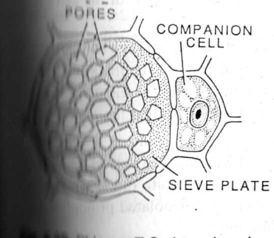


Fig. 5.29. Phloem. T.S. through a sieve plate and companion cell.

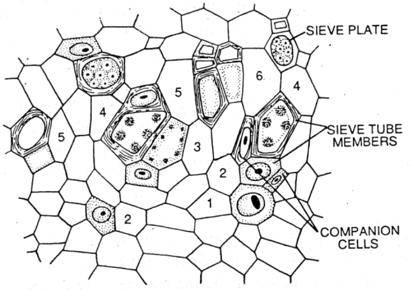


Fig. 5.30. Phloem. Differentiation of sieve tube members in *Cucurbita*.

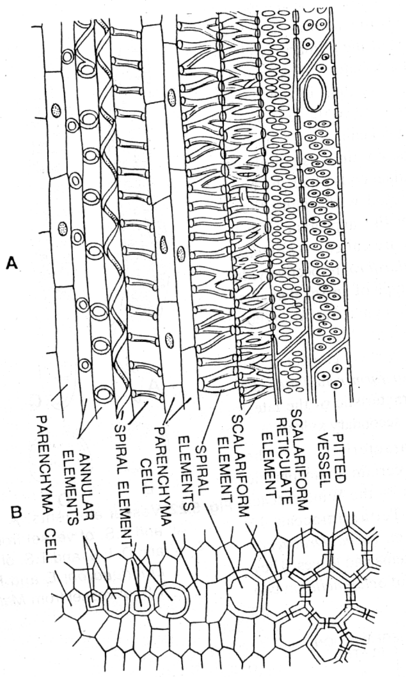


Fig. 5.24. Primary xylem. Protoxylem and metaxylem in longitudinal A, and transverse section Protoxylem towards left and metaxylem towards right.

species of *Pteridium* among the pteridophytes; among the gymnosperms, in the Gnetales (*Eph* *Welwitschia* and *Gnetum*).

Ontogeny of the vessel. The vessels are formed from procambium cells or derivat cambium by the fusion of the cells end to end during the last stages of development. Durin fusion the end walls are lost and the lumina of the series of the cells are freely open int another, forming a long tube. From the meristematic stage the vessel elements increase grea diameter. The vessels with scalariform perforations and the elongate, simply perforate type increase in length to some extent, the tips forming tails which penetrate between surroundin The vessels developing from stratified cambium cells, do not elongate and sometimes even be shorter. During the rapid growth in cell size, the primary cell wall, remains constant in thi except in those areas which later disintegrate to form the perforations. These areas become th and limited in their margins. In the sectional view they are lens-shaped or plate like and seen to be three layered, composing of the primary walls of the two adjacent cells and the

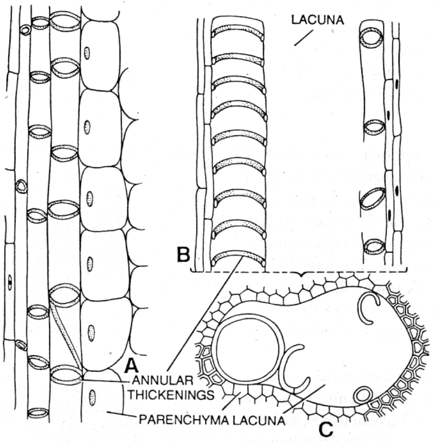


Fig. 5.25. Protoxylem. A, L.S. of protoxylem from *Arisaema* fruit, the elements are all annular; B – C, L.S. and T.S. of protoxylem from *Zea*, the surrounding parenchyma pulled away from the protoxylem elements, leaving a large lacuna.

mella. When the cell reaches its maturity, the cytoplasm of the ll begins to disintegrate. In certain woody plants the nucleus comes quite small and flat and lies in scant cytoplasm against wall where perforation is about to occur. As soon as the mary wall becomes mature, the perforation of the end wall and of the protoplast begin. The wall in the perforation area comes thinner and thinner and ultimately disintegrates. The foration in all members of a vessel series takes place from one to the other and not simultaneously (see Fig. 5.22).

(*d*) **Wood parenchyma.** The parenchyma cells which ently occur in the xylem of most plants. In secondary xylem cells occur vertically more or less elongated and placed end nd, known as *wood* or *xylem parenchyma*. The radial verse series of the cells form the wood rays and are known d or *xylem ray parenchyma*. The xylem parenchyma cells be as long as the fusiform initials, or they may be several shorter, if a fusiform derivative divides transversely before ntiation into parenchyma (wood parenchyma). The shorter xylem parenchyma cells is the more common. The ray and lem parenchyma cells of the secondary xylem may or may secondary walls. If a secondary wall is present, the pit pairs between the parenchyma cells tracheary elements may be simple, half-bordered or bordered. In between, parenchyma cells mple pit pairs occur. The xylem parenchyma cells are noted for storage of food in the form of

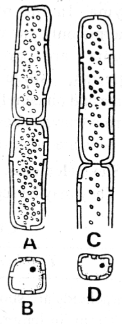


Fig. 5.26. Wood parenchyma. A and B, L.S. and T.S. of wood parenchyma from *Quercus alba*; C and D, L.S. and T.S. of wood parenchyma from *Carya ovata*.

just as vessels may have perforation plates in their side walls, sieve tube elements may have sieve plates in their lateral walls.

The two types of sieve elements, the sieve cells and the sieve-tube elements differ in the degree of differentiation of their sieve areas and in the distribution of these areas on the walls. Sieve cells are commonly long and slender, and they are tapering at their ends. In the tissue they overlap each other, and the sieve areas are usually numerous on these ends. In sieve-tube elements, the sieve areas are more highly specialized than others and are localized in the form of sieve plates. The sieve plates occur mainly on end walls. Sieve-tube elements are usually disposed end to end in long series, the common wall parts bearing the sieve plates. These series of sieve-tube elements are *sieve-tubes*.

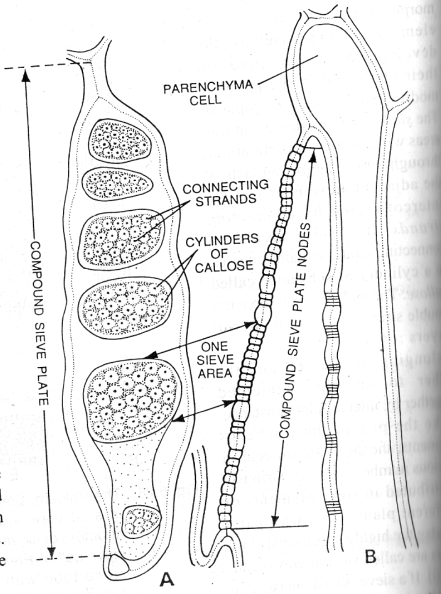


Fig. 5.31. Phloem. Structure of sieve areas. A, compound sieve plate of *Nicotiana* in surface view; B, parts of sieve tube members and a phloem parenchyma cell.

The lower vascular plants and the gymnosperms generally have sieve cells, whereas most angiosperms have sieve-tube elements. The sieve-tube elements show a progressive localization of highly specialized sieve areas on the end walls; a gradual change from in the orientation of these end walls from very oblique to transverse; a gradual change from compound to simple sieve plates; and a progressive decrease in conspicuousness of the sieve areas on the side walls.

The sieve elements generally possess primary walls, chiefly of cellulose. The characteristic of the primary walls of sieve elements is their relative thickness (Esau, 1950). The thickening of the wall generally becomes evident during the late stages of differentiation of the element. In some plants this wall is exceptionally thick. The thick sieve element is usually called the *nacre wall*.

The most important characteristic feature of the sieve-element protoplast is that it lacks a nucleus when the cell completes its development and becomes functional. The loss of the nucleus occurs during the differentiation of the element. In the meristematic state the sieve element resembles other procambial or cambial cells in having a more or less vacuolated protoplast with a conspicuous nucleus. Later the nucleus disorganizes and disappears.

The important property of the sieve-element protoplast of dicotyledons is the presence of variable amounts of a relatively viscous substance, the *slime*. The slime is proteinaceous in nature.

The slime appears to be located mainly in the cell-sap together with various organic and inorganic ingredients. The slime originates in the cytoplasm in the form of discrete bodies, the *slime-bodies*. They may be spherical, or spindle shaped, or variously twisted and coiled. They occur singly or in multiples in one element.

(*b*) **Companion cells.** The *companion cell* is a specialized type of parenchyma cell which is closely associated in origin, position and function with sieve-tube elements. When seen in transverse section the companion cell is usually a small, triangular, rounded or rectangular cell beside a sieve-tube element. These cells are living having abundant granular cytoplasm and a prominent elongated nucleus which is retained throughout the life of the cell. Usually the nuclei of the companion cells serve for the nuclei of sieve tubes as they lack them. The companion cells do not contain starch. They live only so long as the sieve-tube element with which they are associated and they are crushed with those cells. The companion cells are formed by longitudinal division of the mother cell of the sieve tube element before specialization of this cell begins. One daughter cell becomes a companion cell and other a sieve tube element. The companion cell initial may divide transversely several times producing a row of companion cells so that one to several companion cells may accompany each sieve-tube element. A companion cell or a row of companion cells formed by the transverse division of a single companion-cell initial may extend the full length of the sieve-tube element. The number of companion cells accompanying a sieve-tube element is fairly constant for a particular species. The solitary and long companion cells occur in primary phloem of herbaceous plants whereas numerous companion cells occur in the secondary phloem of woody [illegible]

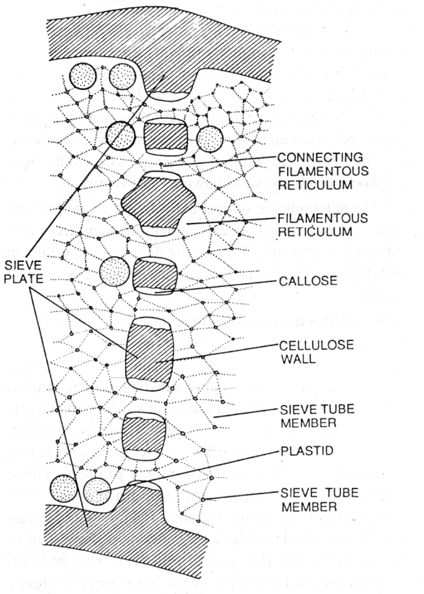


Fig. 5.32. Phloem. Diagrammatic representation of the ultrastructure of a sieve plate.

The companion cells occur only in angiosperms where they accompany most sieve-tube elements. In the phloem of many monocotyledons, they are abundant, together with sieve tubes making up the entire tissue. The sieve cells of the gymnosperms and vascular cryptogams have no companion cells.

(*c*) **Phloem fibres.** In many flowering plants, fibres form a prominent part of both primary and secondary phloem. The phloem fibres are rarely found or absent in phloem of living

Digestive glands. In certain insectivorous plants there are special glands which secrete protein-digesting enzymes. These enzymes act upon insects so that the products of digestion can be absorbed by the plant. In *Drosera*, the secretory tissue is at the tips of the leaf tentacles. Here in addition to the digestive enzymes, there are secreted viscid substances which hold the insects. These are internal glands.

Hydathodes (water secreting glands). Many plants possess special structures which exudate water under conditions of low transpiration and abundant soil moisture. These modified special structures are known as *hydathodes* or *water stomata*. The water stoma resembles an ordinary stoma, and morphologically it is considered to be enlarged stoma which has lost the power of movement and serves for water secretion. Commonly, the hydathodes occur at the tips of the leaves of *Pistia* and other aroids, water hyacinth, grasses, garden nasturtium and many other plants of humid climate. The hydathodes are internal glands.

Nectaries. Many insect-pollinated plants produce *nectar* which attracts insects. This substance is secreted by special cellular structures, the nectaries. Definite and elaborate nectaries occur in certain families (*e.g.*, Euphorbiaceae). In the less specialized nectaries the secreting cells are superficial upon the floral parts. Here, the epidermal cells do not possess cuticle. The nectar is exuded through the wall and exposed upon the outer surface. The *septal nectaries* are commonly found in many monocotyledonous flowers where they make pockets in the septal walls of syncarpous ovaries where the carpel walls are fused incompletely and the epidermal cells are glandular. These glands are external in nature.

6

Apical Meristems

The apical meristem includes the meristematic initials and their immediate derivatives at the apex of a shoot or root. The apical meristem, thus delimited corresponds approximately to the promeristem, and to contrast with the partly developed derivatives of the promeristem, *i.e.*, the protoderm, the ground meristem, and the procambium. This seems quite impracticable, to think of the apical meristem as consisting of the initiating cells only because cells may be poorly differentiated from their most recent derivatives.

The terms *shoot apex* and *root apex* are more convenient to use instead of apical meristem of the shoot and apical meristem of the root, respectively. In the similar way, the terms shoot apex and root apex are more conveniently used as the substitutes of growing points. Growth in the sense of cell division, which is characteristic of the meristematic state, is not restricted to the so-called growing point but occurs abundantly — and may be even more intense — at some distance from the apical meristem (Wardlaw, 1945; Goodwin and Stepka, 1945). On the other hand, growth in the sense of increase in size of cells, tissues, and organs is most pronounced, not in the apical meristem, but in its derivatives.

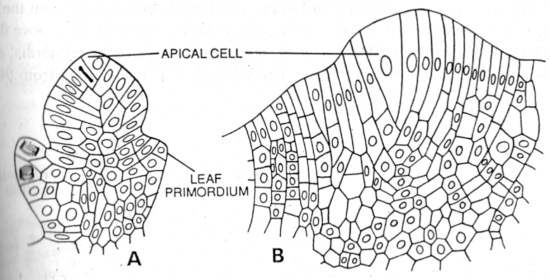


Fig. 6.1. Apical meristems. A, shoot apex with apical cell of *Equisetum* shoot; B, shoot apex of *Pteridium*.

INITIALS AND DERIVATIVES

An *initial* or initiating cell, is a cell that remains within the meristem indefinitely with the addition of cells to the plant body by combining self-perpetuation. The concept regarding meristematic initials, implies that a cell is an initial, not because of its inherent characteristics, but only because of its particular position in the meristem, a position that cannot be treated as permanent.

pteridophytes. They are also not found in some gymnosperms and angiosperms. Only simple pits are found on the walls of phloem fibres. The walls may be lignified or non-lignified. The *Cannabis* (hemp) fibres are lignifed, whereas fibres of *Linum* (flax) are of cellulose and without lignin. Because of the strength of strands of phloem fibres, they have been used for along time in the manufacture of cords, ropes, mats and cloth. The fibre used in this way has been known since early times as *bast* or *bass*, and this way the phloem fibres are also known as bast fibres.

The sclereids are occasionally found in the primary phloem. The older secondary phloem of many trees also contains the sclereids. These cells develop from phloem parenchyma as the tissue ages and the sieve tubes cease to function.

(*d*) Phloem parenchyma. The phloem contains parenchyma cells that are concerned with many activities characteristic of living parenchyma cells, such as storage of starch, fat and other organic substances. The tannins and resins are also found in these cells. The parenchyma cells of primary phloem are elongated and are oriented, like the sieve elements. There are two systems of parenchyma found in the secondary phloem. These systems are — vertical and the horizontal. The parenchyma of the vertical system is known as *phloem parenchyma*. The horizontal parenchyma is composed of *phloem rays*. In the active phloem, the phloem parenchyma and the ray cells have only primary unlignified walls. The walls of both kinds of parenchyma cells have numerous primary pit fields. The phloem parenchyma is not found in many or most of monocotyledons.

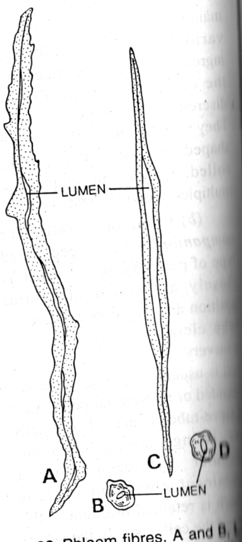


Fig. 5.33. Phloem fibres. A and B, L and T.S. of phloem fi from *Malus pumila*; C a L.S. and T.S. of phloem fi from *Robinia*. (After E. &

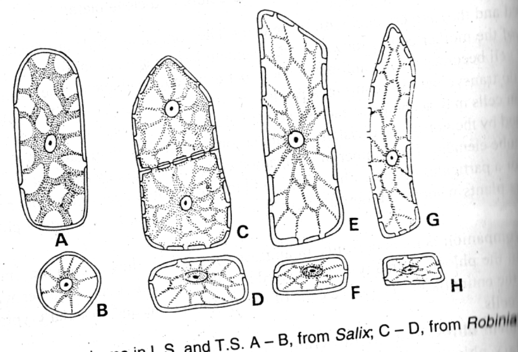


Fig. 5.34. Phloem parenchyma in L.S. and T.S. A – B, from *Salix*; C – D, from *Robinia*; E *Liriodendron*; G – H, from *Malus*.

3. SECRETORY TISSUE

The tissues that are concerned with the secretion of gums, resins, volatile oils, nectar, latex and other substances are called *secretory tissues*. These are further subdivided into two groups — (*a*) laticiferous tissue and (*b*) glandular tissue.

(*a*) **Laticiferous tissue.** Usually latex is present in the families of many flowering plants. This substance may be white, yellow or pinkish in colour. This is a viscous fluid and established to be colloidal in nature. Many substances like sugars, proteins, gums, alkaloids, enzymes, rubber, etc., remain suspended in a matrix of watery fluid. Starch grains may be abundantly present. The latex of some plants is of great importance, especially as a source of rubber (*e.g.*, *Haevea*, *Ficus*, etc.), chicle (*Achras*), and papain (*Carica*). The laticiferous ducts, in which latex is found may be of two types — *latex cells* or *non-articulate latex ducts* and *latex vessels* or *articulate latex ducts*. The functions and the contents of the two are same but they differ in their nature and morphology. They contain numerous nuclei in the thin layer of cytoplasm along the cell wall. The function of these tissues is not yet clearly understood. They may act as food storage organs or as reservoirs of waste products.

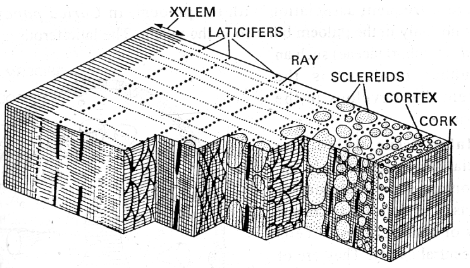


Fig. 5.35. Laticiferous tissue. Three dimensional diagram of bark of *Haevea brasiliensis* showing arrangement of articulated laticifer in secondary phloem. In tangential sections, laticifers form a reticulum.

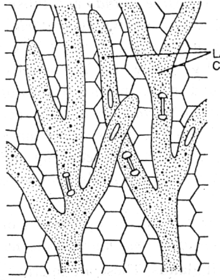


Fig. 5.36. Laticiferous tissue. Latex cells.

Nonarticulate latex ducts or latex cells. These ducts [illegible] independent units which extend as branched [illegible] for long distances in the plant body. They [illegible] as minute structures, elongate quickly and [illegible] in all directions of the plant body by repeated branching, but they do not fuse together, thus no netted [illegible] are formed as they are formed in articulate [illegible]. The walls of the ducts are soft and very often thick. [illegible] ducts are commonly found in *Calotropis*, [illegible], *Nerium*, *Vinca*, etc.

Branched nonarticulated laticifers commonly occur [illegible]. Here they travel through the vascular bundles, [illegible] the mesophyll, and often reach the epidermis.

The number of initials in root and shoot apices is variable. In most of pteridophytes a single initial cell occurs at the apex. In the lower vascular plants, as well as in the higher, several initials are present. The single initial in its morphology is quite distinct from its derivatives and is commonly known as the *apical cell*. If the initials are numerous, they are called apical initials.

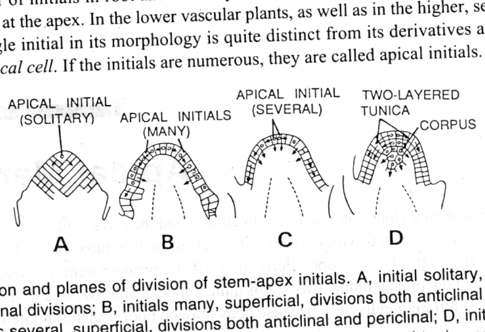


Fig. 6.2. Position and planes of division of stem-apex initials. A, initial solitary, with oblique an anticlinal divisions; B, initials many, superficial, divisions both anticlinal and periclinal; C initials several, superficial, divisions both anticlinal and periclinal; D, initials in three tie the two outer, with anticlinal divisions, forming a two-layered tunica and the innermo with divisions in all planes, forming a corpus. (After Eames and MacDaniels).

Usually the apical initials occur in one or more tiers. If there is only one tier, all cells of a pl body are ultimately derived from it. On the other hand, different parts of a plant body are deriv from different groups of initials.

VEGETATIVE SHOOT APEX

The vegetative shoot apices vary in shape, size and cytohistologic structure, and in th relation to the lateral organs. The shoot apex of *Pinus* and other conifers are commonly narrow a conical in form. In *Cycas* (cycads) and *Ginkgo* they are usually broad and flat on the other h the apical meristem of a grass and some other monocotyledons remains elevated above the youn leaf primordium. In many dicotyledons the apical meristem rises above the primordia, and in o cases it appears to be sunken beneath them. The diameters of apices range from 90μ in s

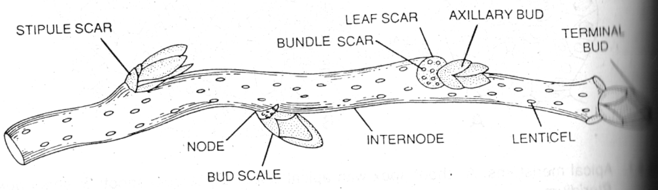


Fig. 6.3. Apical Meristem. Stem of *Aesculus hippocastanum* in winter condition showing *axillary* and *adventitious* buds. Axillary buds may be classified according to the at a node into (1) alternate with a single bud at a none, (2) opposite, with two node on opposite sides of the stem, and (3) whorled with more than two buds node. Buds which arise anywhere on the plant except at the tips of stems or in of leaves are called *adventitious buds*. In this figure, terminal bud is located at the leaf scars are left by the breaking away of the leaf stalks. Leaf trace scars are the ends of leaf traces. When the scales of terminal bud are shed a *ring* or *girdle* is

angiosperms to 3.5 mm in *Cycas revoluta* (Foster, 1949). The size and shape of the apex marked by change during the plant development.

Pteridophytes (vascular cryptogams). In the vascular cryptogams (lower tracheophyta) growth at the apex proceeds either from one or few initial cells, which are usually distinctive in their morphology (Bower, 1889; Hartel, 1938; Wardlaw, 1945). Most commonly the single apical cell is tetrahedral (pyramid like) in shape (*e.g.*, in Psilotales, Equisetaceae, and ferns). The base of this pyramid is turned towards the free surface, and the new cells are formed at the other three sides. The *Salvinia* and *Azolla* (water ferns) have three sided apical cells with two sides from which new cells are cut off. In *Selaginella* apical growth occurs from a single three or four-sided apical cell or from a group of initials, and the two situations may be found in the same plant. The eusporangiate ferns have two or four initials, the leptosporangiate ferns have one, but there is no sharp line of division between the two groups with reference to this character. As regards their

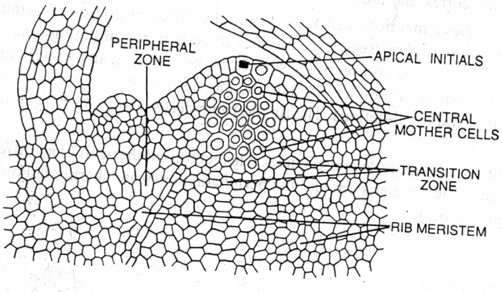


Fig. 6.4. The shoot apex. L.S. of shoot apex of *Pinus strobus*. Apical initials divide anticlinally contributing the cells to the surface layer, also divide periclinally adding the cells to central mother cell zone. The central mother cells divide actively and contribute to the transition zone. The products of these divisions form the rib meristem. (After K. Esau).

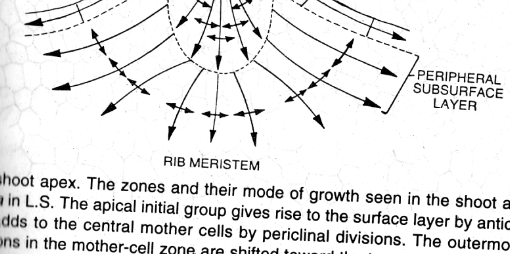


Fig. 6.5. The shoot apex. The zones and their mode of growth seen in the shoot apex of *Ginkgo biloba* in L.S. The apical initial group gives rise to the surface layer by anticlinal divisions, and adds to the central mother cells by periclinal divisions. The outermost products of divisions in the mother-cell zone are shifted toward the transition zone where they divide periclinally. (After Foster).

ontogeny much information supports the view that in the ferns the types of apex with several initials is more primitive that the one with a single apical cell (Bower, 1890, 1935; Wardlaw, 1945).

Gymnosperms. They commonly show several interrelated growth zones which are derived from a group of surface initials. These initials divide periclinally resulting in the formation of a subsurface group of cells, known as *mother cells*. The cell division is quite slow in the interior of this group but is active on its periphery. The derivatives of the divisions along the flanks of mother-cell group combine with products resulting from anticlinal divisions of the apical initials. All together these lateral derivatives form a mantle-like peripheral zone of deeply stainable small cells which are less differentiated (eumeristem) than the mother cells and the cells or initiating zone. The derivatives produced at the base of the mother-cell zone become pith cells, and usually they pass through a rib-meristem form of growth. The part of the pith may arise from the peripheral zone. The peripheral mantle of cells, rich in cytoplasm, is the seat of origin of leaf primordia and of the epidermis, the cortex and the vascular tissues of the axis.

The details of above mentioned pattern vary in the different groups of gymnosperms. The cycads have wide apices and possess large number of cells in the initiating zone. This way the initiating zone occupies a large portion of the surface of the meristem and its periclinal derivatives converge toward the centre of the meristematic mound. This is characteristic of the cycads. The mother-cell zone in cycads is ill-defined. The rib meristem derived from the base of the central zone is conspicuous.

In *Ginkgo* the zones are quite conspicuous. The central mother-cell zone differentiates close to the apical initials. The rib meristem and the peripheral zones are sharply deliminated from the central zone. (see Fig. 6.5).

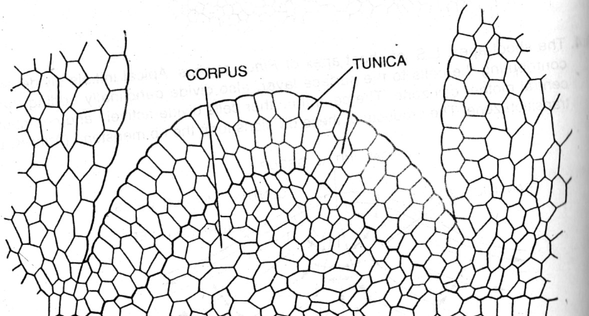


Fig. 6.6. Tunica and Corpus organization.

The apical zonation in *Pinus* and other Coniferales is less diversified than in the cycads and less well defined than in *Ginkgo*.

In Gnetales, there is a definite separation into a surface layer and an inner core derived from its own initials. The shoot apices of *Ephedra* and *Gnetum* (Johnson, 1950) have been described as having a tunica-corpus pattern of growth.

Angiosperms. There is *tunica-corpus organization* in the shoot apex of angiosperms. One to five layers tunica have been observed in the dicotyledons, and one to three-layered in the monocotyledons. However, tunica-corpus organization is not found in *Saccharum officinarum*. To draw a clear cut demarcation line in between tunica and corpus is not simple matter. In angiosperms, the number of parallel periclinal layers in the shoot apex may vary during the ontogeny of the plant body and under the influence of seasonal growth changes.

In the angiosperms the segregation of apical-meristem zones is more definite than in lower groups. There are two sets of initials, one above the other, which give rise to tunica and *corpus*. The tunica has no or only rare periclinal divisions and varies in thickness from several to one with two or three layers probably most frequent. The number of layers in the tunica may vary even in individual plant.

OTHER THEORIES OF SHOOT APEX ORGANIZATION

In support of shoot apex organization other theories have also been proposed. Dermen (1947) put forth *histogenic layer concent*. According to him there is no distinct of apical meristems. He named

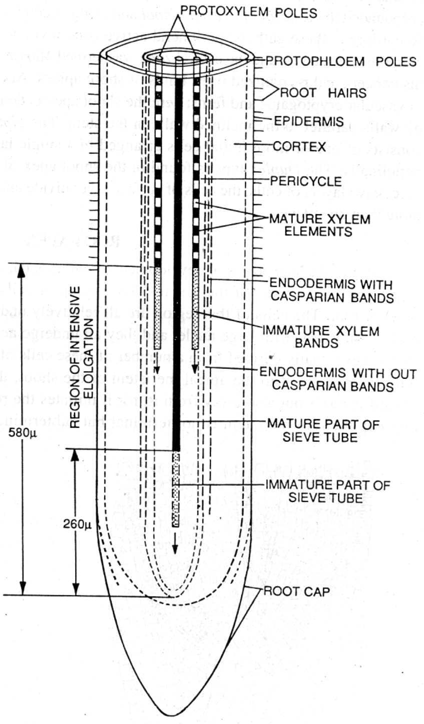


Fig. 6.7. L.S. of root tip of tobacco. The epidermis and the root cap show common origin. The cortex and the vascular cylinder have separate initials in the apical meristem. The pericycle is delimited close to the apical meristem. The sieve tubes mature first within the vascular cylinder. The root hairs develop beyond this region. The Casparian strips develop in the endodermis close to the position of first mature xylem elements. (After K. Esau).

the different layers of apical meristem as L_1, L_2, L_3, etc. He recognized these layers on the basis of their origin. However, this concept did not get any support. Popham and Chan (1950) put forth Mantle Core Concept. This concept is comparable to tunicacorpus theory. They used the term mantle instead of tunica and core in place of corpus. Plantefol (1947, 1950), Buvat (1955) and Amefort (1956) propounded the *concept of French school* and recognized three distinct regions in the apical meristem. According to these authors, peripheral active zone was known as *Anneu initial*, the zone next to it *Meristem medullaire*. Newman (1961) put forth *Meristeme de attente* and the central zone was termed *Meristem medullaire*. Newman (1961) put forth his concept and recognized three kinds of shoot apices. According to him, *Monoplex* type is found in vascular cryptogams and ferns; here the shoot apex is denoted by one or more cells which divide by walls parallel to the inclined walls in the stem. The *Simplex* type is found in gymnosperms; it consists of one or more initial cells arranged in a single layer; these cells divide anticlinally and periclinally. The *Duplex* type is found in the shoot apex of angiosperms; it consists of atleast two successive layers of cells; the cells of surface layer divide anticlinally and that of inner layer divide in more than one plane.

ROOT APEX

During the later stages of development of embryo, the cells at the root pole become arranged in a pattern characteristic of the species. This group of cells comprises the *apical meristem* of the primary root. The cells of this region are all relatively undifferentiated and meristematic, densely protoplasmic and with large nuclei and they all undergo active division. The tissues of the mature root are eventually derived from a number of these cells of the apical meristem, which are termed *initials*. In contrast to the apical meristem of the shoot, that of the root produces cells not only toward the axis but also away from it, for it initiates the root cap and because of the presence of root cap the root meristem is not terminal but subterminal in its position, in the sense that it is located beneath the root cap. The root apex also differs from the shoot meristem in that it forms no lateral appendages comparable to the leaves, and no branches. The root branches are usually initiated beyond the region of most active growth, and they arise endogenously. It also produces no nodes, and internodes, and therefore, the root grows more uniformly in length than the shoot, in which the internodes elongate much more than the nodes.

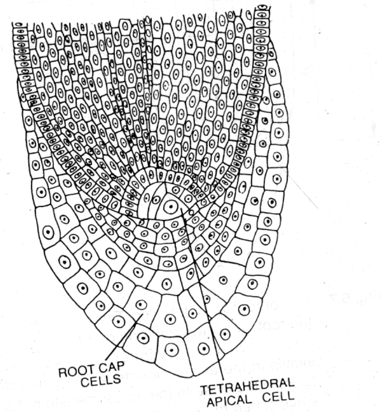


Fig. 6.8. Root apex of *Pteris* (fern) in longitudinal section showing tetrahedral apical cell.

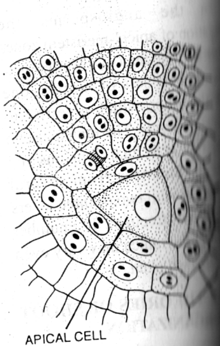


Fig. 6.9. Root apex of *Pteris* (
cross section showing
sided apical cell, one s
in contact with the root

APICAL CELL THEORY

This theory was put forth by Nageli. In the roots of vascular cryptogams (pteridophytes), *e.g.*, *Dryopteris*, a single tetrahedral apical cell is present, it is generally thought that by its division this gives rise to all the tissues of the root. However, the apical cell theory was superceded by the histogen theory.

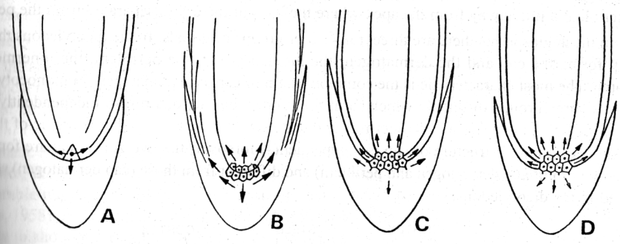


Fig. 6.10. The root apex. Diagrams showing different root apex types, A, initial solitary, cap distinct; B, initials in two groups, cap not distinct structurally; C, initials in three groups, cap not distinct; D, initials in three groups, cap distinct, and independent in origin. (After E. & M.)

In number, the initials range from one to many. Where the initials are more than one, they are arranged in one to four fairly distinct, uniseriate groups. In each group there are one to several initials. Where there is more than one group, the groups lie adjacent to one another on the longitudinal axis of the root. Each of these groups quickly develops one or more growth zones. In many plants these zones appear to represent 'the histogens'. The terms dermatogen, periblem and

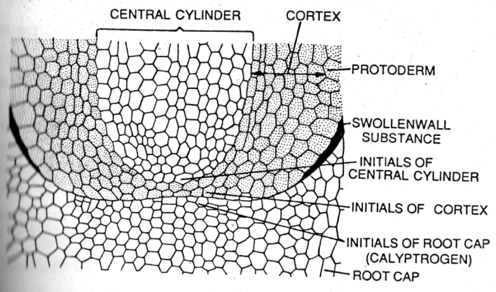


Fig. 6.11. The root apex. Root tip of *Zea mays* in L.S. The swollen wall substance originates through the gelatinization of the wall between the root cap and the protoderm.

plerome are no longer in general use in descriptions of stem ontogeny but they have been continued to indicate general zones in studies of root development. A fourth histogen, the *calyptrogen*, is added where the cap has an independent origin. There are basic patterns for the major plant groups. The pattern is determined by the number of initials, the number of groups of these initials, the zones formed by each group, the morphological nature of the cap, and the degree of independence of the cap.

The vascular cryptogams such as horsetails, most of the ferns, some species of *Selaginella* have a solitary apical cell in the root. This one cell forms the entire root and the cap.

In many gymnosperms there are two groups of initials. The inner forms the plerome; the outer forms the periblem and the cap. The cap appears as a distal proliferation of the periblem. A dermatogen is not set off at the very apex, as in all other groups, but is formed from the layers of the periblem a little away from the apex where the base of the cap is separated from the periblem.

In the angiosperms there are three, rarely four groups of initials. In the dicotyledons the distal group forms the cap and the dermatogen; the median group, the periblem; the innermost, the plerome. The most characteristic is the common origin of cap and dermatogen. In monocotyledons there are three groups of initials which form four zones, but the outermost, independently, forms the cap, and that next beneath, the dermatogen and periblem. The most characteristic of this type is that the origin and structure of cap is independent. Moreover, the two zones that are formed by one group of initials (dermatogen and periblem) and different from those (cap dermatogen) similarly formed in the dicotyledons.

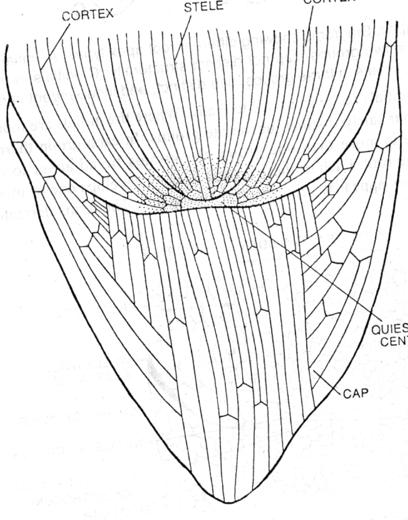


Fig. 6.12. Root apex. Pattern of cell lineages in the root apex of Zea mays. The cortex, the cylinder or stele, root cap and quiescent centre are indicated. (After Clowes)

Korper-kappe theory

This theory was put forth by Schuepp in 1917. Since the root changes in diameter during growth, there are various points at which a single longitudinal file of cells has become a double file as a result of cell division. At these points a cell first divides transversely and thereafter one of its daughter cells divides longitudinally. This was known as T division, because the cell walls form a T-shaped structure. In some zones of the root, mainly in the centre, the bar of the T faces the root apex, in other it faces away from the apex (⊥). These zones of the root, delimited by the planes of cell division, were called *Korper* (body) and *Kappe* (cap) respectively. This theory may be compared with the tunica-corpus theory in the shoot apex.

Mainly in roots with a very regular arrangement of cells in the apical meristem, such as of *Zea mays*, it is possible to conclude from the study of cell lineages that there is a central region of cells which divide rarely or not at all. The cells on the periphery of this hemispherical or cup-shaped region are meristematic. This inactive or passive region of cells is known as '*quiescent centre*'.

The Quiescent Centre

In the apical meristem of root of *Zea mays*, and other plants with a regular arrangement of cells in the apical meristem, it is possible to conclude from the study of cell lineages that there is a central region of cells which divide, rarely or not at all. These inactive or passive cells constitute the *quiescent centre*. The cells on the periphery of this hemispherical or cupshaped region are meristematic and may be regarded as the constituents of the promeristem (Clowes, 1958). By various techniques, the existence of quiescent centre, has now been demonstrated in the root apices of a considerable number of species. The quiescent centre develops during the ontogeny of the root (Clowes, 1958). A quiescent centre is not found in the roots with a single apical cell. In 1956, Clowes was able to show that there was a central region (quiescent centre) in the roots of *Zea* where the cytoplasm had the lower content of RNA and where the cells had smaller nucleoli. He was also able to demonstrate that the cells in the quiescent centre did not actively synthesize DNA.

The physiological and cytological properties of the cells in the quiescent centre have now been studied in a number of species. The cells in the region have a lower concentration of DNA, RNA and protein than any other cells in the root apex (Clowes, 1958; Jensen, 1958). The cells of quiescent centre also have fewer mitochondria, little endoplasmic reticulum, and the smallest dictyosomes, nuclei and nucleoli (Clowes, 1964). They are less sensitive to radiation damage than other cells of the meristem (Clowes, 1959, 1964).

The function of the quiescent centre may be to provide a reserve block of diploid cells within the root. The quiescent centre may be the site of hormone synthesis.

THE PROMERISTEM

Clowes (1961) has defined the promeristem as that part of the root apex which is capable of giving rise to all the tissues of the root. In the roots of vascular cryptogams, for example, the promeristem would consist of apical cell only, and in angiosperms it would comprise the initials of the histogens. This way there is a tendency to regard the promeristem as a rather small region, located terminally in the root apical meristem, below the root cap. On the basis of modern work it has been suggested that in many roots the promeristem is broad and consists of a somewhat cup-shaped group of cells on the periphery of a central inactive region. This grouping of the initial cells of the promeristem was suggested by Clowes (1950) on the basis of an anatomical study of the root apex of *Fagus sylvatica*.

THEORIES OF STRUCTURAL DEVELOPMENT AND DIFFERENTIATION

It has been discussed by several workers (Foster, 1939, 1941; Sifton, 1944; Wardlaw, 1945), the views regarding the number, the arrangement, and the activity of the initial cells and their

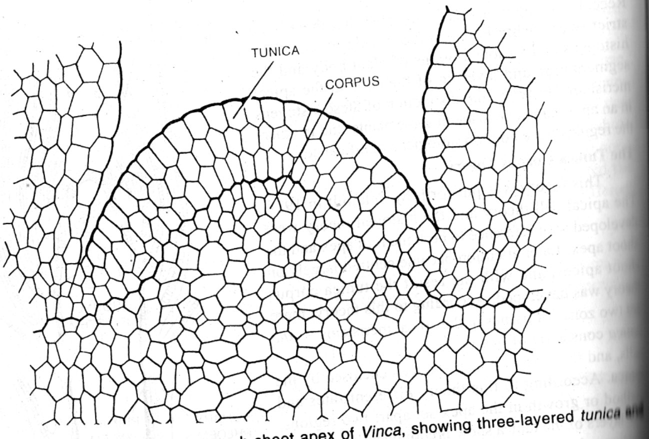


Fig. 6.16. Apical meristem. L.S. through shoot apex of *Vinca*, showing three-layered *tunica* and *corpus* beneath it.

group of separate initials, and the corpus has one layer of such initials. In the tunica the number of layers of initials is equal to the number of layers of tunica, that is, each layer of tunica has its own layer of initials. The corpus arises from a single tier of initials which divide first periclinally to give the

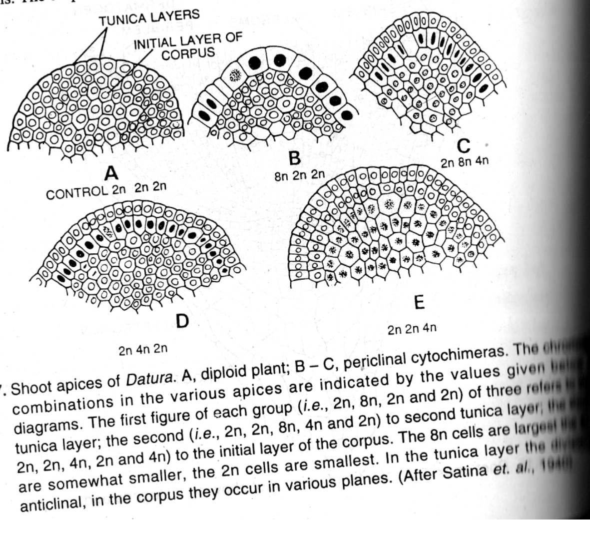


Fig. 6.17. Shoot apices of *Datura*. A, diploid plant; B – C, periclinal cytochimeras. The chr combinations in the various apices are indicated by the values given be diagrams. The first figure of each group (*i.e.*, 2n, 8n, 2n and 2n) of three refers t tunica layer; the second (*i.e.*, 2n, 2n, 8n, 4n and 2n) to second tunica layer; the 2n, 2n, 4n, 2n and 4n) to the initial layer of the corpus. The 8n cells are largest th are somewhat smaller, the 2n cells are smallest. In the tunica layer the div anticlinal, in the corpus they occur in various planes. (After Satina *et. al.*, 1940)

to group of derivatives, which divide in various planes resulting in the formation of the inner mass of cells.

The number of initials varies from few to many. For example, in small very slender apices, such as those of grass seedlings, there may be only one or two in the tunica and about two in the corpus.

In vascular plants, the differentiation of the zones of stem-apex follows more or less definite patterns that seem to be characteristic of the major groups. These patterns show increasing complexity from the lower to the higher groups and appear to represent a series in specialization from simplicity to complexity.

As regards the concept of tunica and corpus, there may be several types which are found in the stem apices of several vascular plants. The types may be as follows.

The primitive type of stem apex having no distinction of tunica and corpus. *Lycopodium*, *Isoetes*, *Selaginella* (pteridophytes) and *cycads* (gymnosperms) belong to this group. They have simple apices with surface initials and no distinction of tunica and corpus. In *Lycopodium*, the initiating layer is weakly defined, having uniseriate surface area which divides freely both anticlinally and periclinally. Here all the cells of the layer are morphologically alike. The anticlinal divisions increase the area of the surface layer, whereas the periclinal divisions form the inner core.

The stem apices with weak tunica-corpus demarcation. The demarcation of tunica and corpus layers begins in some of the lower conifers. In *Abies* and *Pinus* (Coniferales), the initials make an apical uniseriate group. These initials further give rise to a central core and an enveloping uniseriate layer by both periclinal and anticlinal divisions. The uniseriate layer that envelops the central core suggests a tunica in appearance, but there is no clearcut demarcation between the tissues of two regions. However, in the apices of *Sequoia sempervirens*, the initials are a small group of surface cells in one tier, with both anticlinal and periclinal divisions. These divisions result in the formation of a dermatogen like layer and a central mass. The outer layer suggests a tunica and the central mass, the corpus. The species of *Cryptomeria* and *Taxodium* (Coniferales) have a dermatogen, in which there are no periclinal divisions. There appears to be structural segregation of tunica and corpus in the apices of many Coniferales, but there is only one tier of initials and no independent meristematic regions are recognized.

The stem apices with distinct tunica and corpus. In angiosperms the demarcation of meristematic zones of apical region is usually more distinct and definite than in lower groups. There are two sets of initials, one above the other, which give rise to tunica and corpus which seem to be completely independent. The tunica has no or only rare periclinal divisions. It ranges in thickness from one to several layers. Usually there occurs two or three layers. The larger numbers of tunica layers occur more frequently in the dicotyledons. A single-layered tunica occurs in the grasses. However, in monocotyledons the number of tunica layers is one to three. In *Zea*, tunica divides periclinally, which shows an exceptional condition. The number of the layers in tunica may vary even in an individual plant. The corpus varies from a large complex type to a slender, simple type.

Significance of the tunica corpus theory. The tunica-corpus theory served well in the establishment of meristematic patterns of the shoot apices of seed plants. The position, number and behaviour of the initiating cells in seed-plant stems, and early stages in the development of primary tissues of the shoot are now much better understood. The tunica-corpus theory is of topographical value in studies of detailed development. The lateral organs of the stem, *i.e.*, leaves, branches and floral organs, arise near the apex and studies of tunica and corpus have added greatly to a knowledge of origin and early development of these organs.

derivatives in the apical meristems has undergone many changes since the shoot apex was first recognized by Wolff in 1759 as an undeveloped region from which the growth of the plant proceeded.

The Apical Cell Theory

This theory was put forth by Nageli in 1858. Solitary apical cells occur in many of algae, bryophytes and vascular cryptogams (pteridophytes). The discovery of the apical cell in cryptogams led to the concept that such cells exist in phanerogams (seed plants) as well. The apical cell was interpreted as a constant structural and functional unit of apical meristems governing the whole process of growth. However, this was confirmed by later researches that this theory may hold good for cryptogams but is not applicable to the phanerogams. Further researches have refuted the universal occurrence of apical cells and replaced it by a concept of independent origin of different parts of plant body. The apical cell theory was superceded by the *histogen theory*.

The Histogen Theory

This was introduced in 1870 by Hanstein who considered that the primordial meristem was sharply separable into three distinct zones or *histogens*. According to this theory the apical meristem or growing region of the stem and root are composed of small mass of cells which are all alike and are in a state of division. These meristematic cells constitute promeristem. The cells of the promeristem soon differentiate into three regions — *dermatogen*, *periblem* and *plerome*. Every zone consists of a group of initials and is called a *histogen* or a *tissue builder*. *Dermatogen* — This is the single outermost layer of the cells which later gives rise to the epidermis of the stem. In the root it is also single layered, but at the apex it merges into the periblem and just outside the periblem the dermatogen cuts off many new cells resulting into a small celled tissue, the *calyptrogen*, which is also meristematic and gives rise to the *root cap*. *Periblem* — This region is found internal to the dermatogen, and is the middle region of the apical meristem. It is single layered at the apex but in central part it becomes multilayered. It develops into the cortex of the stem. In the roots it is also single layered at the apex and many layered in the central portion. In the case of root, it also develops into the cortex. *Plerome* — It is the central meristematic region of stem apex and lies internal to the periblem. It is also composed of thin walled isodiametric cells. Ultimately it develops and differentiates into the central stele consisting of primary vascular tissues and ground tissues, such as, pericycle, medullary rays, and medulla. In the roots the function of plerome is practically same as in stem. At a little distance behind the apex certain strands of cells show a tendency to elongate. These strands of elongated cells make the *procambium*. The procambial strands ultimately become differentiated, into vascular bundles. A portion, however, remains undifferentiated, and it forms the cambium of the vascular bundle.

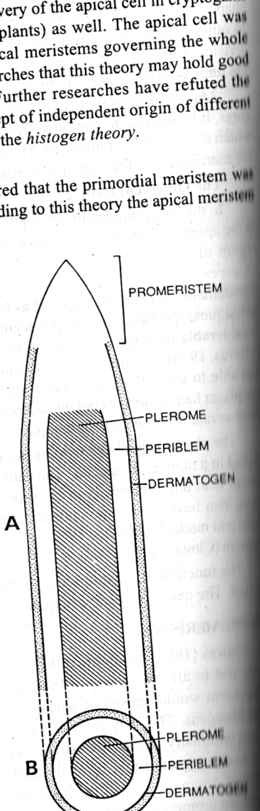


Fig. 6.13. The shoot apex—diag showing histogen regi longitudinal section; B, trans section. (After E. & M.).

Recent investigations have revealed that there is no strict relationship between the development of the histogens and various regions of plant body and the segmentation and layering of the cells in the apical meristem. However, the distinction of these histogens in an apex cannot be made in some plants, and in others the regions have no morphological significance.

The Tunica-Corpus Theory.

This theory was put forth by Schmidt in 1924. The apical cell theory and the histogen theory were developed with reference to both the root apex and the shoot apex. Later attention became centred largely on shoot apices, and with the result the tunica corpus theory was developed. According to this theory, there are two zones of tissues in the apical meristems — *the tunica* consisting of one or more peripheral layers of cells, and the *corpus*, a mass of cells enclosed by the tunica. According to this theory different rates and method or growth in the apex set apart two regions. The layers of the tunica show predominantly anticlinal divisions, that is, they are undergoing surface growth. In the corpus the cells are large, with arrangement and planes of cell division irregular, and the whole mass grows in volume. Each layer of the tunica arises from a

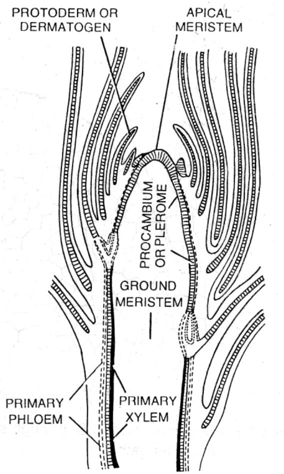


Fig. 6.14. Apical meristems. L.S. of stem tip (diagrammatic) showing the histogens.

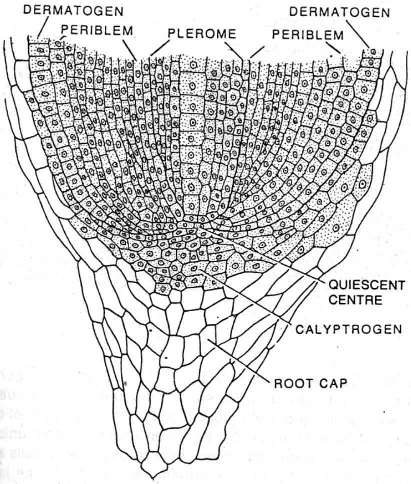


Fig. 6.15. Root apex. L.S. of a tip of onion root showing histogens and root cap.

(*Ficus elastica*), banyan tree (*Ficus bengalensis*), oleander (*Nerium* spp.), etc. It becomes two to multilayered. The epidermal cells may be somewhat irregular in outline, usually varying in shape and size and arranged very close to each other having no intercellular spaces among them. The cells possess a large central vacuole and thin peripheral cytoplasm. The cells may contain leucoplasts, anthocyanins and chromoplasts, but no chloroplasts except in guard cells. In the epidermal cells of certain aquatic (*e.g., Hydrilla*) and shade loving plants the chloroplasts are also found. Sometimes, the substances like mucilage, tannin and calcium carbonate crystals (cystoliths) are also found in these cells. The walls of epidermal cells are unevenly thickened. The inner and radial walls are comparatively thicker. This additional thickness is due to the impregnation of suberin or cutin. The suberization and cutinization of the walls protect the epidermis from mechanical injuries and prevent from loss of water.

In the case of roots the outermost layer is known as the *epiblema, piliferous layer* or *rhizodermis*. Usually its cells extend outwards in the form of tubular unicellular root hairs, which help in the absorption of water and mineral nutrients from the soil.

Functions of the Epidermis

1. The epidermis is primarily a covering layer which helps in the protection of the internal soft tissues against mechanical injury.

2. It prevents excessive evaporation of water from the internal tissues, for this, several adaptations like development of thick cuticle, wax, hairs, etc., take place.

3. It also serves in photosynthesis and secretion.

4. The epidermis acts as store house of water in many xerophytic plants.

5. Some of the epidermal cells develop into the secretory tissues of nectaries, the stom leaves and stems, and the absorbing hairs of roots.

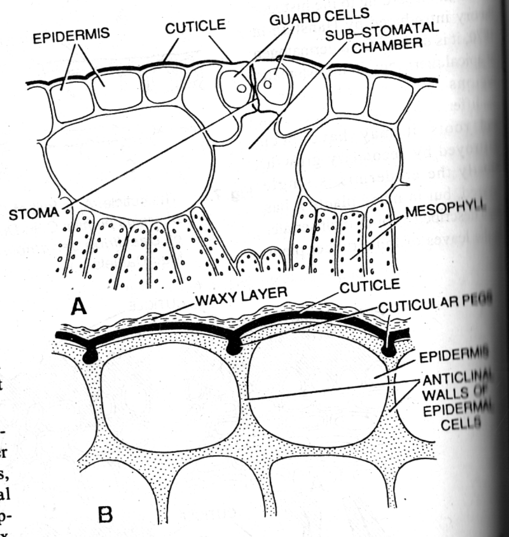


Fig. 7.4. The cuticle. A, a section of upper epidermis of *Musa* through stomatal region, showing extent of cuticle guard cells; B, section of the banana (*Musa*) leaf thr pulvinar band showing *pegs* of cuticle over epide cells.

STOMATA

The stomata are minute pores which occur in the epidermis of the plants. Each stoma surrounded by two kidney or bean shaped epidermal cells the *guard cells*. The stomata may

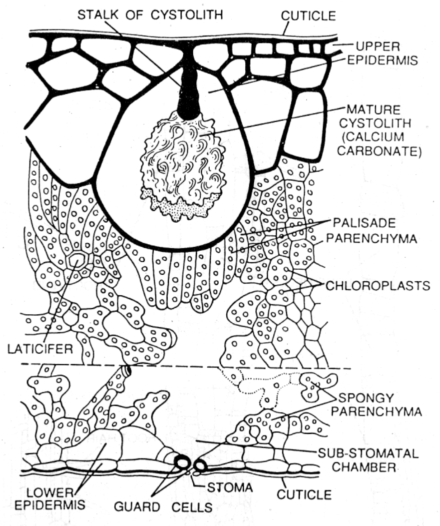
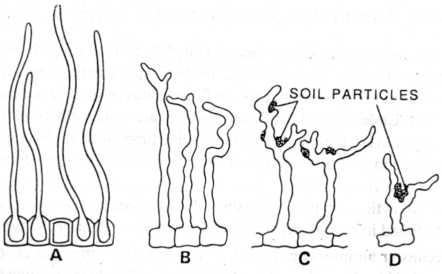


Fig. 7.5. Epidermis. Multiple epidermis in T.S. of *Ficus elastica leaf.* A mature cystolith with calcium carbonate deposited on its stalk in the epidermal cell.

part of a plant except the roots. The epidermal cells bordering the guard cells are called *accessory* or *subsidiary cells*. Generally the term stoma is applied to the stomatal opening and the guard cells. The guard cells are living and contain chloroplasts in them. They also contain a larger portion of protoplasm than other epidermal cells. Usually in the leaves of dicotyledons the stomata scattered whereas in the leaves of monocotyldons they are arranged in parallel rows. The



Root hairs, A, grown in water; B, grown in moist soil; C and D, grown in dry soil. (After Schwarz).

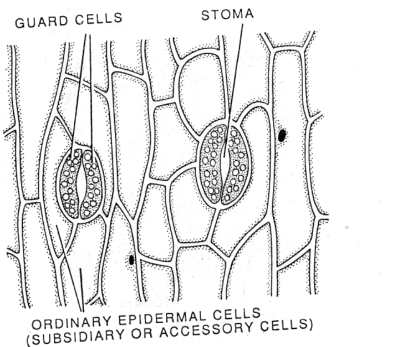


Fig. 7.10. Epidermis. Lower surface of leaf showing stomata.

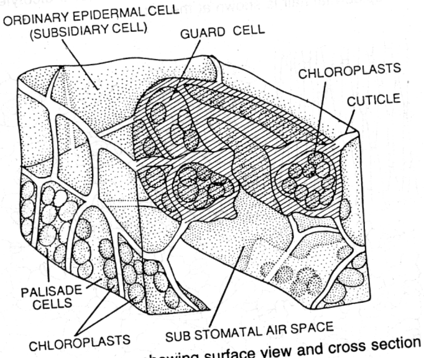


Fig. 7.11. Stomata. Diagram showing surface view and cross section of stoma

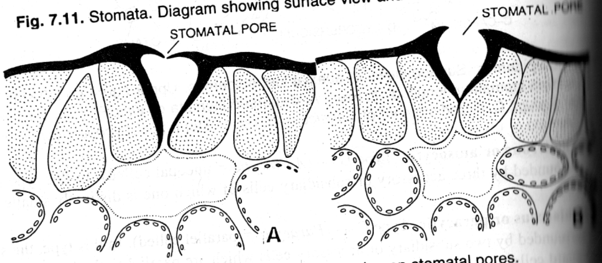


Fig. 7.12. Stomata. A—B, closed and open stomatal pores.

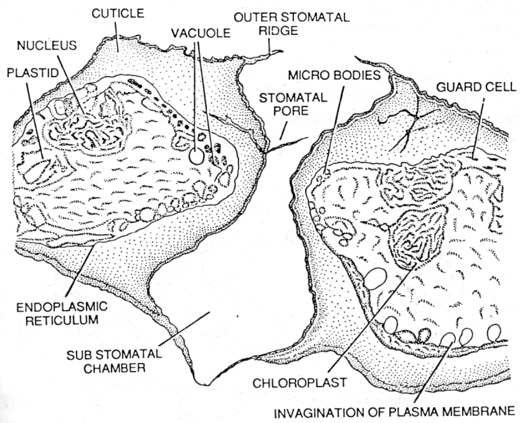


Fig. 7.13. Guard cells of *Vicia faba* as seen in electron microscope.

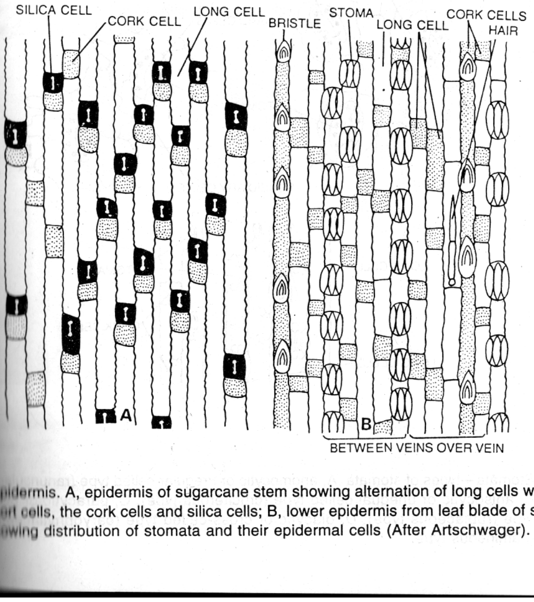


Fig. 7.14. Epidermis. A, epidermis of sugarcane stem showing alternation of long cells with pairs of short cells, the cork cells and silica cells; B, lower epidermis from leaf blade of sugarcane, showing distribution of stomata and their epidermal cells (After Artschwager).

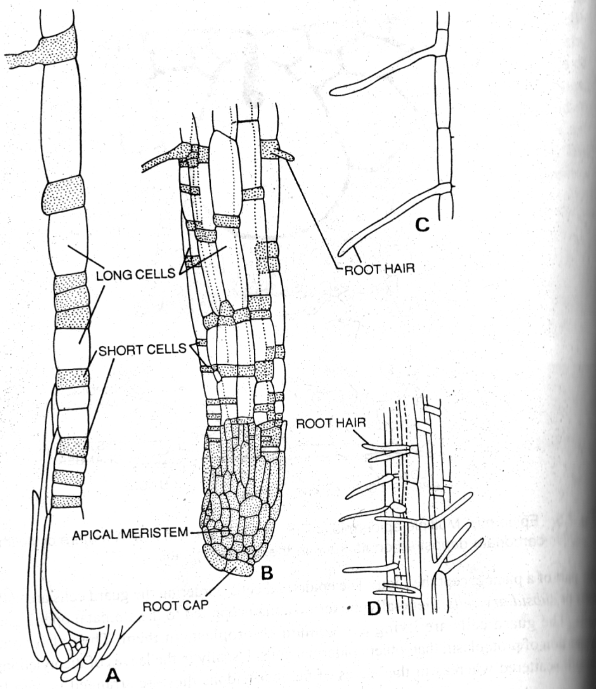


Fig. 7.7. Development of root hair from protruded cells. A,C, in *Cyperus*. B,D, in *Anigozanth*

number of stomata may also range on the surface of a single leaf from a few thousand to hundreds of thousands per square centimetre. Stomata occur on both upper and lower surfaces of leaf, especially they are confined to the lower surface. In floating leaves stomata are confined only on upper surface of the leaf. Under normal conditions the stomata remain closed in the absence of or in night or remain open in the presence of light or in day time. Structurally the stomata may different types. The four main types of stomata which occur in dicotyledons are known as Ranunculaceous or anomocytic type — type A; 2. Cruciferous or anisocytic — type B; Caryophyllaceous or diacytic — type C; 4. Rubiaceous or paracytic— type D. the fifth type stomata is commonly found in monocotytledons are known as —gramineous type.

1. Ranunculaceous or anomocytic. Type A — (*Anomocytic* = irregular celled). In this type stoma remains surrounded by a limited number of subsidiary cells which are quite alike the rem epidermal cells. The accessory or subsidiary cells are five in number.

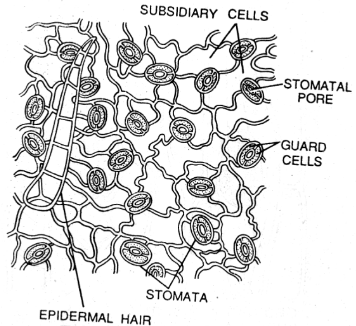
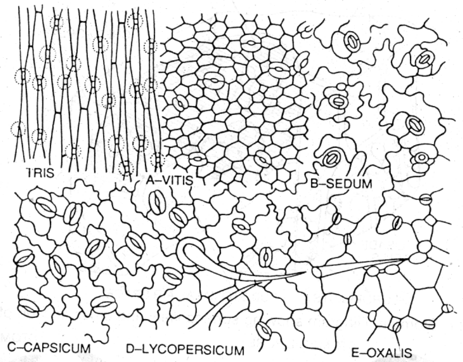


Fig. 7.8. The epidermis—stomata. Surface view of epidermis of a dicotyledonous leaf showing stomata. An epidermal hair is shown at the left.



The Epidermis. Surface views of abaxial leaf epidermis. Upper figure on left side of *Iris*, sunken stomata in longitudinal rows. A, dispersed stomata of *Vitis*; B, anisocytic stomata of *Sedum*; C, raised stomata of *Capsicum;* D, raised stomata of *Lycopersicon;* E, sunken stomata of *Oxalis.*

Cruciferous or anisocytic. Type B — (*Anisocytic* = unequal celled). In this type stoma surrounded by three accessory or subsidiary cells of which one is distinctly smaller than other two.

Rubiaceous or paracytic. Type C — (*Paracytic* = parallel celled). In this type, the stoma surrounded by two subsidiary or accessory cells which are parallel to the long axis of the guard cells.

4. Caryophyllaceous or diacytic. Type D—(*Diacytic* = cross celled)—In this type the stoma remains surrounded by a pair of subsidiary or accessory cells and whose common wall is at right angles to the guard cells.

Gramineous. The gramineous stoma possesses guard cells of which the middle portions are much narrower than the ends so that the cells appear in surface view like dump-bells. They are commonly found in Gramineae and Cyperaceae of monocotyledons.

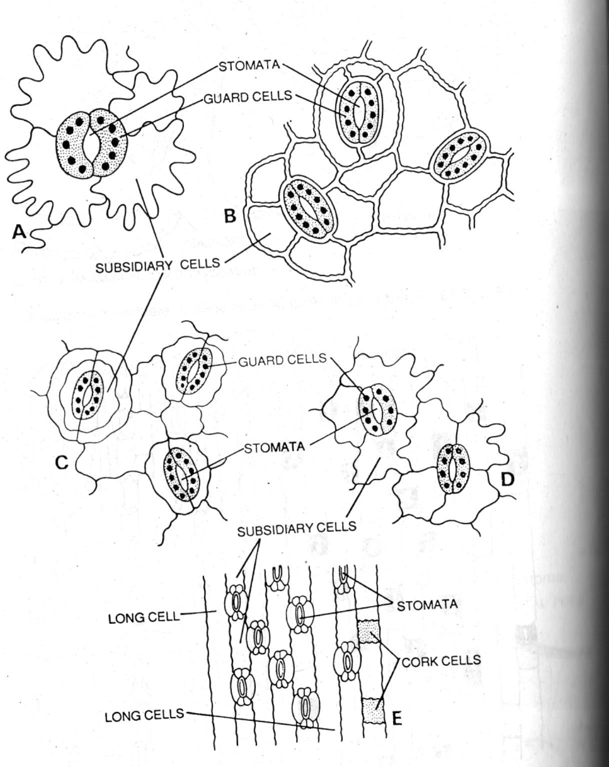


Fig. 7.15. Stomata—types of stomata. A, anomocytic or irregular celled type (ranunculaceous ty B, anisocytic or unequal celled type (cruciferous type); C, paracytic or parallel type (rubiaceous type); D, diacytic or cross-celled type (caryophyllaceous type gramineous type.

Coniferous Stomata

They are sunken and appear as though suspended from the subsidiary cells arching over them. In their median parts the guard cells are elliptical in section and have narrow lumina. At their ends they have wider lumina and are triangular in section. The characteristic of these guard cells is that their walls and those of the subsidiary cells are partly lignified and partly non-lignified.

Function of Stomata

They are used for the exchange of gases in between the plant and atmosphere. To facilitate this function, each stoma opens in a sub-stomatal chamber or respiratory cavity. Evaporation of water also takes place through stomata.

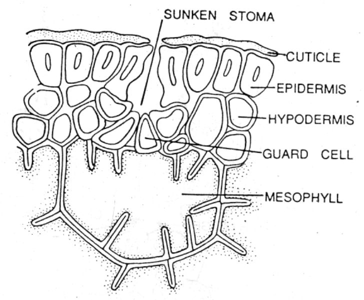


Fig. 7.16. Sunken stoma. Sectional view of a sunken stoma of pine leaf.

HAIRS OR TRICHOMES

Some of the epidermal cells of most plants, grow out in the form of hairs or trichomes. They may be found singly or less frequently in groups. They may be unicellular or multicellular and occur in various forms. They vary from small protuberances of the epidermal cells to complex branched or stellate multicellular structures. The cells of the hairs may be dead or living. Very frequently the hairs lose their protoplasm in their cells.

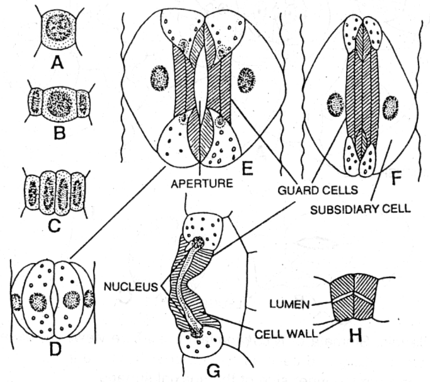


Fig. 7.17. Development (A—D) and structure of stomata (E—H) in sugarcane (a monocot). A, stoma mother cell; B, stoma mother cell with two subsidiary cells derived from two adjoining cells; C, early stage of guard-cell development; D, young stoma with two guard cells; E and F, mature stomata seen from the outer surface in open (E) and closed (F) states; G, L.S. of one guard cell; H, transection through the central portion of two guard cells from a closed stoma

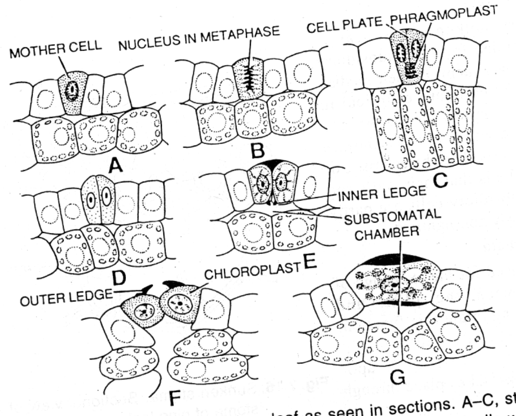


Fig. 7.18. Development of stoma in *Nicotiana* leaf as seen in sections. A–C, stoma mother before and during division in two guard cells; D, young guard cells with thin walls; thickening of the walls of guard cells begun; F, mature guard cells with uneven thickened walls; G, one mature guard cell.

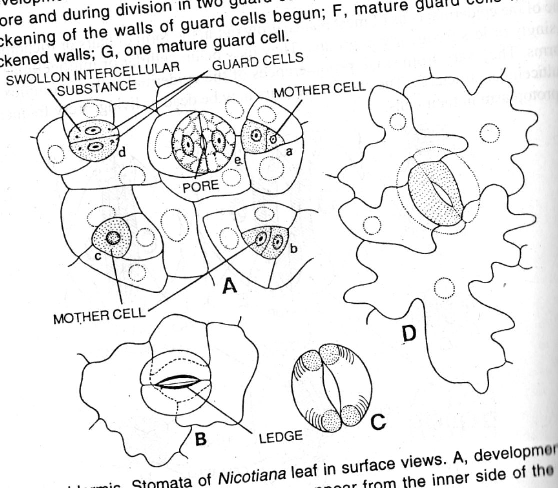


Fig. 7.19. The epidermis. Stomata of *Nicotiana* leaf in surface views. A, developmental mature stoma; C, guard cells as they appear from the inner side of the epid stoma seen from the inner side of the abaxial surface.

The hairs may be of several types, as—*stinging hairs; laticiferous hairs, bladder mucilage hairs, arachnoid hairs, calcified or silicified hairs, non-glandular shaggy glandular shaggy hairs, non-glandular tufted hairs, two-armed non-glandular hairs glandular hairs, branched non-glandular hairs, branched glandular hairs, capitate*

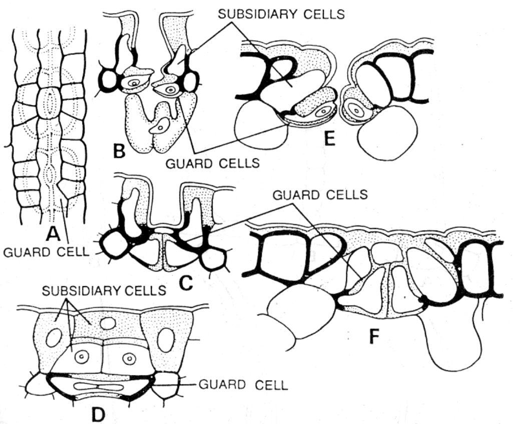


Fig. 7.20. Stomata of conifer leaves. A, surface view of the epidermis of *Pinus merkusii* showing two deepely sunken stomata, guard cells are overarched by subsidiary and other epidermal cells; B—D, stoma and other cells from *Pinus* spp; E and F, stomata and other cells from *Sequoia*.

glandular capitate stalked hairs, non-glandular peltate hairs, glandular peltate hairs and *stellate hairs.*

Trichomes may be classified into different morphological categories. One common type is referred to as *hair.* The hairs may be subdivided into (i) *unicellular*; and (ii) *multicellular.* The unicellular hairs may be unbranched or branched. Multicellular hairs may consist of a single row of cells or several layers. Some multicellular hairs are branched in dendroid (tree-like) manner, others have branches oriented largely in one plane (stellate hairs.)

Some important types have been described here.

Stinging hairs. They are one of the most interesting types of the trichomes. it contains a [illegible] liquid and consists of a basal bulb like portion from which a stiff, slender and tapering [illegible] is given out. This tapering structure ends in a small knob like or a sharp point. The tip is [illegible] somewhat oblique, and as the body of an animal or human being comes in its contact with [illegible], the tip is broken off, and the sharp pointed end readily penetrates the skin of the animal, [illegible] is being transferred from the basal knob of the hair to the body of the animal.

Glandular hairs. Many plants possess glandular hairs. These hairs may secrete oil, resin or [illegible]. A typical glandular hair possesses a stalk and an enlarged terminal portion, which may be [illegible] as gland. The glandular hairs may be uni- or multicellular. Active secretory cells of [illegible] trichomes have dense protoplasts and elaborate various substances, such as volatile oils, [illegible] mucilages, and gums. These substances are excreted and accumulate between the walls [illegible]. Their final removal from the hair occurs by rupture of the cuticle.

Scale or peltate hair. A common type of trichome is the *scale,* also called *peltate hair* (from the [illegible], target-shaped or shield like, and attached by its lower surface). A scale consists of a [illegible] plate of cells, often borne on a stalk or attached directly to the foot.

[illegible]

[illegible] walls of trichomes are commonly of cellulose and are covered with a cuticle. They may [illegible]. Plant hairs often produce thick secondary walls as, for instance, the cotton seed hairs or

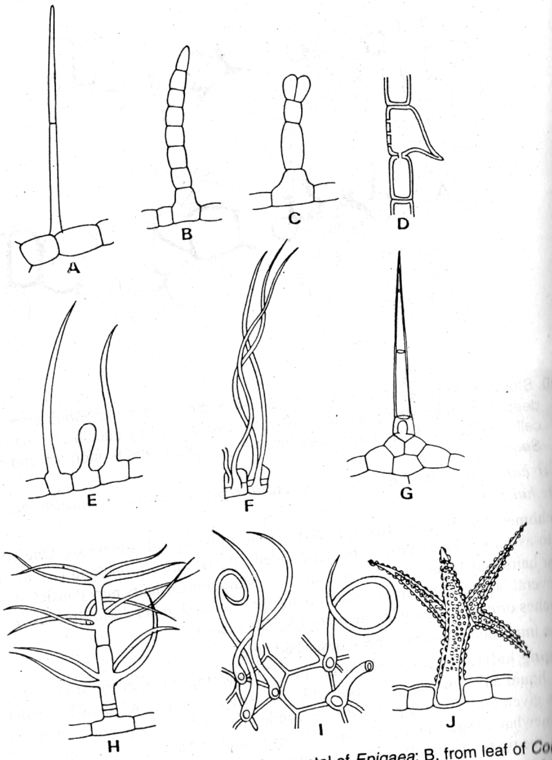


Fig. 7.21. Various types of trichomes (hairs). A, from petal of *Epigaea*; B, from leaf of *Core* from petal of *Phryma*; D, from leaf of *Avena*; E, from sepal of *Heliotropium*; F, from *Onopordum*; G, from *Cucumis* leaf; H, from *Platanus* leaf; I, from *Rubus* fruit; *Aubrietia* stem. (After E. & M).

the climber hairs of *Humulus*. The walls or trichomes are sometimes impregnated with silica carbonate. Their contents are varied in relation to function. Cystoliths and other cryst develop in hairs.

Development

A trichome is initiated as a protuberance from an epidermal cell. The protuberance and if it develops into a multicellular structure various divisions may follow the initial elong

Trichomes and Taxonomy

The trichome types have been successfully used in the classification of genera and species in certain families and in the recognition of interspecific hybrids (Metcalfe and Ch

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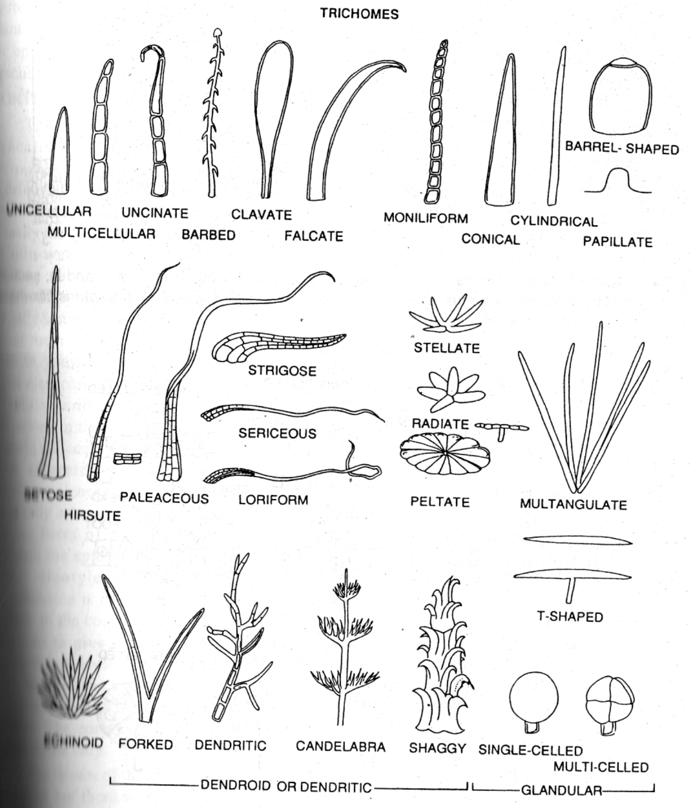


Fig. 7.22. Trichomes of different types.

1930, Sporne, 1956; King and Robinson, 1969, 1970; Ramayya, 1972). King and Robinson (1969, and trichome types to determine genetic limits among Compositae. Ramayya (1972), used the types to establish genetic limits among Magnoliales.

of Trichomes

nerally a dense covering of wooly trichomes controls the rate of transpiration. They also the heating effect of sunlight. They aid in the protection of plant body from outer injurious

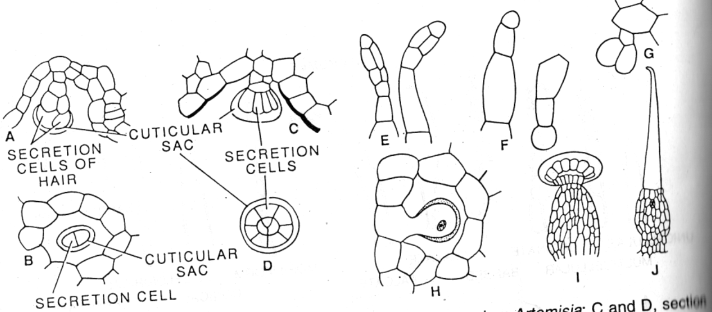


Fig. 7.23. Types of glandular hairs. A and B, section and surface view *Artemisia*; C and D, section and surface view, *Thymus*; E, *Hyascyamus*; F, *Atropa*; G, *Digitalis*; H, *Dryopteris filix-mass* (rhizomes); I, *Cannabis*; J, *Urtica dioica*.

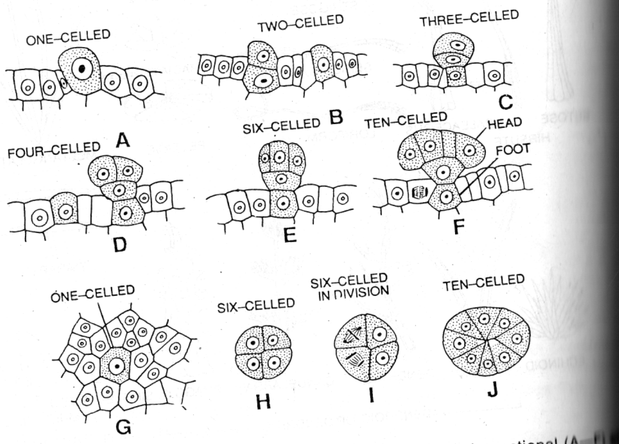


Fig. 7.24. Development of glandular trichomes in *Lingustrum* as seen in sectional (A—F) and surface (G—J) views.

2. THE FUNDAMENTAL OR GROUND TISSUE SYSTEM

Usually in stems which possess the vascular system in the form of solid cylinder, the ground tissue found in between epidermis and vascular cylinder is called *cortex*. In such vascular system the central tissue may be called medulla or pith and the rays of parenchyma cells arising from medulla pith are termed *medullarry* or *pith rays*. If the vascular bundles are found in dispersed condition throughout in the axis (as in monocotyledonous stems) then there is no delimitation of the ground tissue into pith and cortex. The ground or fundamental tissue system consists of main bulk of plant body and extends from below the epidermis to the centre, leaving vascular bundles apart.

CORTEX

The ground tissue found beneath the epidermis which surrounds the central cylinder and is delimited from the cylinder by the endodermis is called the *cortex*. Usually the cortex of stems consists of thin-walled parenchyma cells having sufficiently developed intercellular spaces among them. Usually some of the cortical cells or all of them contain chloroplasts at least in young stems. The cortical cells also contain starch, tannins, crystals and other common secretions in them. The cortex may contain collenchyma, sclerenchyma and sclereids in addition to ordinary parenchyma. Collenchyma is usually arranged as a cylinder or in the form of strands near or beneath the epidermis. In most of the dicotyledonous stems collenchyma is often found in the ridges, in the corners and in other portions to give temporary support to the plant body. Sometimes a few layers of fibres of sclerenchyma develop just beneath the epidermis forming an outer protective layer called *hypodermis*. Just beneath the hypodermis a few layers of parenchyma and chlorenchyma are found. The innermost layer of the cortex is endodermis which is single-layered and sometimes known as *starch sheath*. The cortex of roots is more homogeneous than that of stems and usually consists of parenchyma only.

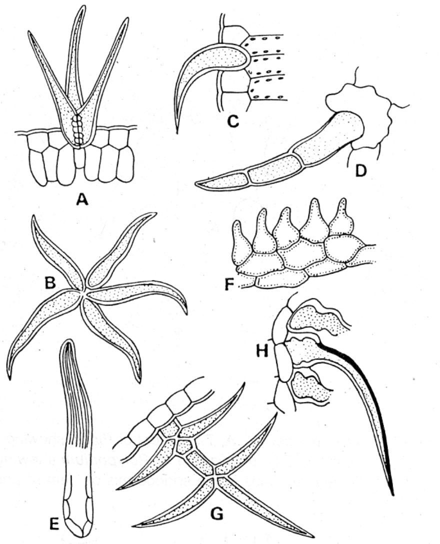


Fig. 7.25. Various kinds of trichomes. A and B, leaf of *Hamamelis*; C, leaf of *Cassia*; D, leaf of *Datura*; E, testa of *Strychnos nuxvomica*; F, petal of *Arnica*; G, leaf of *Verbascum*; H, testa of *Strophanthus*.

The tissues of the cortex are strictly primary and as a whole, mature with the primary tissues of the stele, but there is considerable overlapping of development with secondary-tissue formation within the stele. Collenchyma develops early, but sclerenchymatous cells are usually late in reaching maturity. The cortex of an axis in which marked secondary growth has occurred has tissues crowded and even more or less crushed radially.

Functions of the Cortex

In stems it acts as a protective tissue, but secondarily carbon assimilation, storage of water, storage of food and other functions are also carried on. Collenchyma of the cortical region aids in the primary mechanical support of plant cody. In roots it is a storage tissue and helps in pumping water from hairs to the xylem.

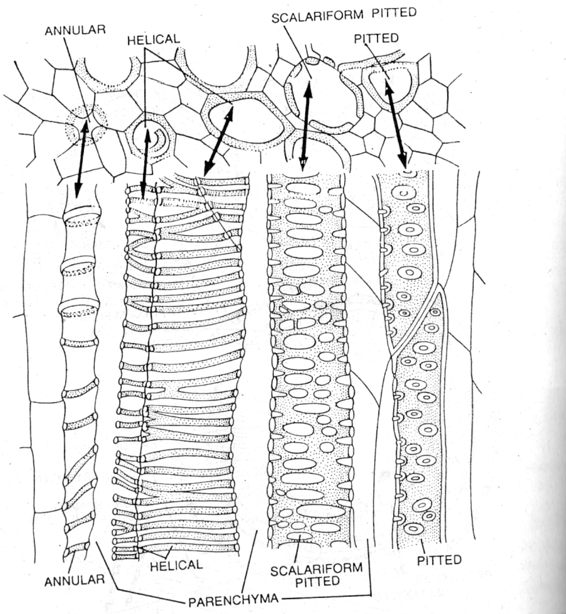


Fig. 10.38. Xylem. vessel. T.S. and L.S. of a part of young *Aristolochia* stem showing vess element and associated parenchyma. Earlier part of the xylem is towards left. Annul spiral (helical), scalariform and pitted vessels are clearly visible. Protoxylem consis annular vessels.

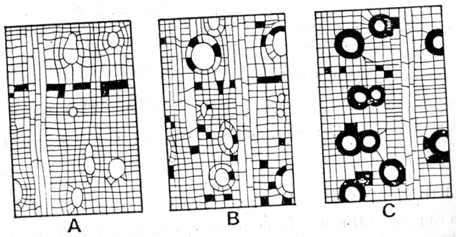


Fig. 10.39. Secondary xylem. Diagrams showing distribution of wood parenchyma. parenchyma cells are shaded. A, terminal; B, diffuse; C, vasicentric. (After E and M

The secondary xylem consists of a compact mass of thick-walled cells so arranged as to form two systems—a longitudinal (vertical) and a transverse radiating system. The longitudinal system consists of elongate, overlapping and interlocked cells—tracheids, fibres and vessel elements—and longitudinal rows of parenchyma cells. All these cells possess their long axes parallel with the long axis of the organ of which they are a part.

The secondary xylem consists of scalariform and pitted vessels, tracheids, wood fibres and wood parenchyma. These elements of secondary xylem are more or less similar to those occur in primary xylem. Vessels or tracheae are most abundant and are usually shorter than those of primary xylem. Mostly the vessels are pitted. Annular and spiral tracheids and vessels are altogether absent. Xylem parenchyma cells may be long and fusiform, but sometimes they are short. They are living cells and usually meant for storage of food material (starch and fat) in them. Tannins and crystals are frequently found in these cells. Xylem parenchyma may occur either in the association of the vessels or quite independently. The fibres of secondary xylem possess thick walls and bordered pits.

DISTRIBUTION OF WOOD (XYLEM) PARENCHYMA

Wood parenchyma is distributed in *three* ways: (*i*) Terminal wood parenchyma; (*ii*) diffuse or metatracheal wood parenchyma and (*iii*) vasicentric or paratracheal wood parenchyma.

Terminal wood parenchyma. In some gymnosperm woods, wood parenchyma is absent; in other (*e.g.*, *Larix* and *Pseudotsuga*), and in some angiosperm woods (*e.g.*, *Magnolia* and *Salix*), wood parenchyma cells occur only in the last-formed tissue of the annual ring. Such woods have *terminal wood parenchyma*.

Diffuse or metatracheal wood parenchyma. Where parenchyma occurs not only in this region, but also remains scattered throughout the annual ring, some of the cells lying among the tracheids, and fibre-tracheids the plant has *diffuse* or *metatracheal wood parenchyma* (*e.g.*, in *Malus*, *Quercus*, *Diospyros* etc.).

Vasicentric or paratracheal wood parenchyma. Where parenchyma occurs at the edge of the annual ring and elsewhere only about vessels and does not occur isolated among tracheids and fibres, the plant possesses *vasicentric* or *paratracheal wood parenchyma* (*e.g.*, in *Acer*, *Fraxinus* etc.).

Xylem rays. The xylem rays or wood rays, extend radially in the secondary xylem. They are strap or ribbon like. They originate from the ray initials. The xylem rays run as a continuous band in the secondary phloem through the cambium, thus forming a continuous conducting system. All vascular rays are initiated by the cambium and, once formed, are increased in length indefinitely by the cambium. Commonly these rays are known as medullary rays, or pith rays, on the basis of their similarity and parenchymatous nature with the pith rays of herbaceous dicotyledonous stems. These radial rays may be best called *vascular rays*, as these rays are of vascular tissue partly of xylem and partly of phloem.

The xylem rays traverse in the secondary xylem and establish communication with the living cells of the vascular tissue. In gymnosperm wood where no wood parenchyma is present, every tracheid is in direct contact with at least one ray. Vessels also in their longitudinal extent, come into contact with many rays. In herbaceous stems, such as of *Ranunculus*, where vascular bundles are separated by projecting parenchymatous wedges, and in vines, such as *Clematis*, where the bundles are separated by bands of secondary parenchyma, vascular rays are not found. The xylem rays help in exchange of gases. They also aid in the conduction of water and food from phloem to the cambium and xylem parenchyma.

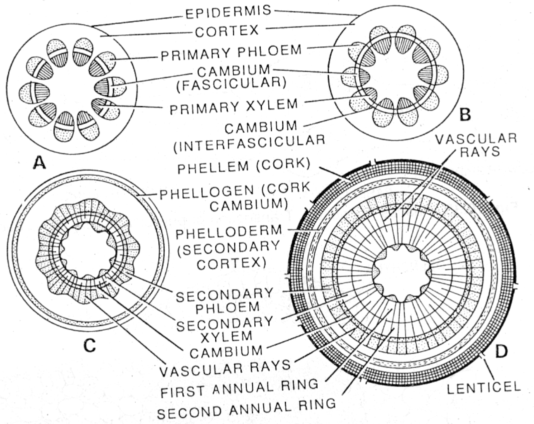


Fig. 10.36. Secondary growth in thickness. A – D, diagrams showing stages in the secondary growth of a dicotyledonous stem upto two years.

cambium within the bundles, divide accordingly and form a layer of cambium across the medullary rays. The newly formed cambium connects the fascicular cambilum found within the vascular bundles, and thus a complete cambium ring is formed. The newly formed cambial strip which occurs in the gaps between the bundles is called *interfascicular cambium*, *i.e.*, the cambium in between the vascular bundles. Thus a complete cambium ring is formed.

The cambium layer consists essentially of a single layer of cells. These cells divide in a direction parallel with the epidermis. Each time a cambial cell divides into two, one of the daughter cells remains meristematic, while the other is differentiated in to a permanent tissue. If the cell that is differentiated is next to the xylem it forms xylem, while if it is next to phloem it becomes phloem towards the outer side of the cambium. The cambium cells divide continuously in this manner producing secondary tissues on both sides of it. In this way, new cells are added to the xylem and the phloem, and the vascular bundles increase in size. While there is more or less alternation in the production of xylem and phloem cells from a cambium cell, more cells are formed on the xylem side than on the phloem side. The cells formed from the cambium in the region of the pith rays become pith-ray cells. The activity of the cambium thus increases the length of the pith rays grow equally. (See Figs. 8.2 and 8.3).

The formation of new cells from the cambium result in an enlargement of the stem that is known as the secondary thickening. The formation of new cells in secondary thickening continues throughout the life of the plant. It is in this way that the trunks of trees continue to grow in diameter. The cambium perpetuates and remains active for a considerable long period of time.

The thin-walled cells of the vascular cambium are highly vacuolate and in this respect unlike most other meristematic cells. The electron microscopic structure reveals their highly vacuolate nature. Many ribosomes and dictyosomes, and well developed endoplasmic reticulum are present (Srivastava, L.M., 1966).

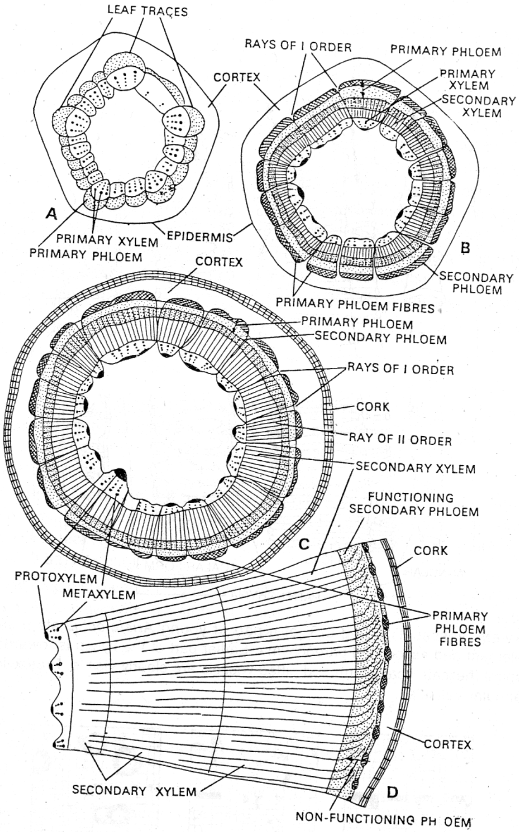


Fig. 10.37. Secondary growth. A – D, primary and secondary structure of *Prunus* stem in transverse sections.

SECONDARY XYLEM

The cambium ring cuts off new cells on its inner side are gradually modified into xylary elements, called the *secondary xylem*. This tissue serves many important functions, such as conduction of water and nutrients, mechanical support, etc. The secondary xylem of tree trunks is of great economic value, since it constitutes the timber and wood of commerce.

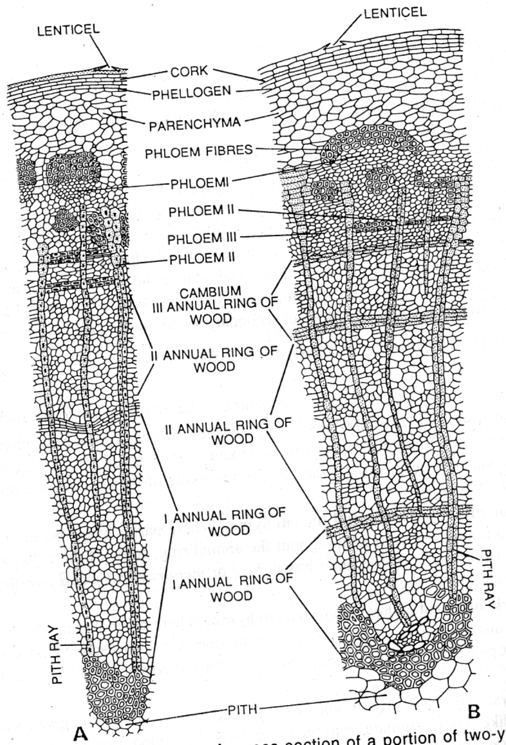


Fig. 10.40. Stem—secondary structure. A, cross section of a portion of two-year old stem *Liriodendron tulipifera*, B, cross section of a portion of three-year old stem *Liriodendron tulipifera* (tulip tree) with three annual rings of wood.

ANNUAL RINGS OR GROWTH RINGS.

The secondary xylem in the stems of perennial plants commonly consists of concentric each one of which represents a seasonal increment. In transverse section of the axis, these appear as rings, and are called *annual rings* or *growth rings*. They are commonly termed as rings because in the woody plants of temperate regions and in those of tropical regions where is an annual alternation of growing and dormant period, each layer represents the growth of The width of growth rings varies greatly and depends upon the rate of the growth Unfavourable growing seasons produce narrow rings, and favourable seasons wide ones. A growth rings are characteristic of woody plants of temperate climates. Such rings are developed in tropical forms except where there are marked climate changes such as distinct dry seasons. Annuals and herbaceous stems show, naturally, but one layer.

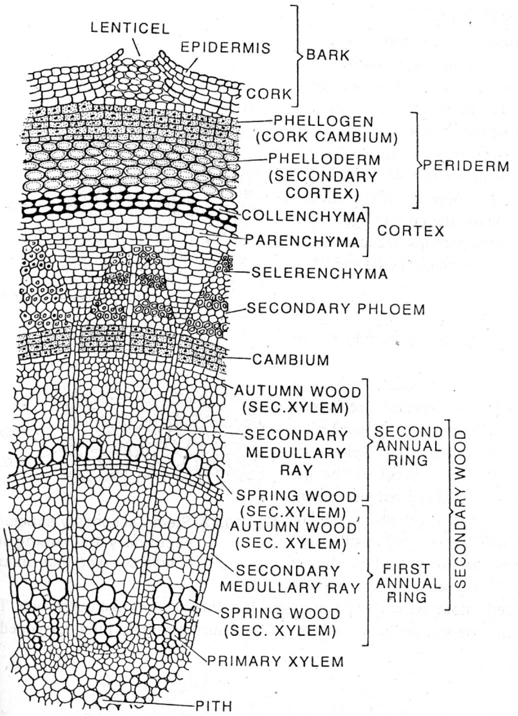


Fig. 10.41. Secondary growth in thickness. T.S. of a two-year old dicotyledonous stem.

regions with a pronounced cold season, the activity of the cambium takes place only during and summer seasons thus giving rise the growth in diameter of woody plants. The wood season is sharply distinct from that of the next season. In spring or summer the cambium active and forms a greater number of vessels with wider cavities. As the number of leaves in the spring season, additional vessels are needed for the transport of sap at that time the increased leaves. In winter or autumn season, however, there is less need of vessels transport, the cambium is less active and gives rise to narrow pitted vessels, tracheids and The wood developed in the summer or spring season is called *spring wood* or *early* the wood formed in winter or autumn season is known as *autumn wood* or *late wood*. the line of demarcation is quite conspicuous between the late wood of one year and the of next year. An annual ring, therefore, consists of two parts—an inner layer, early an outer layer late wood.

DENDROCHRONOLOGY

Each annual ring corresponds to one year's growth, and on the basis of these rings the age of a particular plant can easily be calculated. The determination of age of a tree by counting the annual rings is known as *dendrochronology*. Sometimes two annual rings are formed in a single year, and in such cases the counting of the annual rings does not show the correct age of the tree. This happens perhaps because of the drought conditions prevailed in the middle of a growing season.

TYLOSES

In many plants, the walls of the xylem vessels produce balloon like outgrowths into the lumen of the vessels, are called *tyloses*. Usually these structures are formed in secondary xylem but they may also develop in primary xylem vessels. Tyloses are formed by the enlargement of the pit membranes of the half-bordered pits present in between a parenchyma cell and a vessel or a tracheid. Usually they are sufficiently large and the lumen of the vessel is almost blocked. The nucleus of the xylem parenchyma cells along with cytoplasm passes into this balloon like outgrowth. The deli membrane forms the balloon like tylosis inside the lumen cavity. In fully developed tyloses,

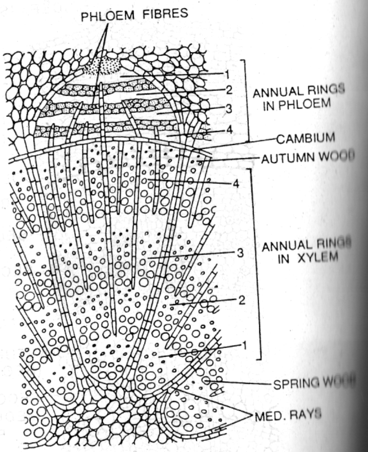


Fig. 10.42. Stem—secondary structure. Diag secondary thickening in a vas bundle showing four annual rings

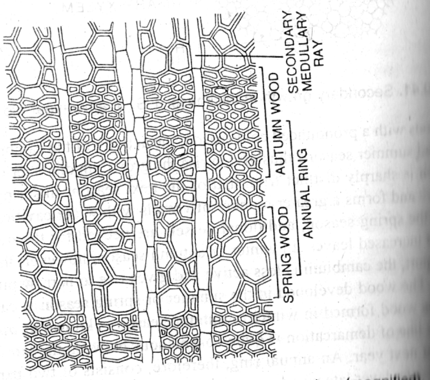


Fig. 10.43. Annual rings. An annual ring in sectional view (magnified)

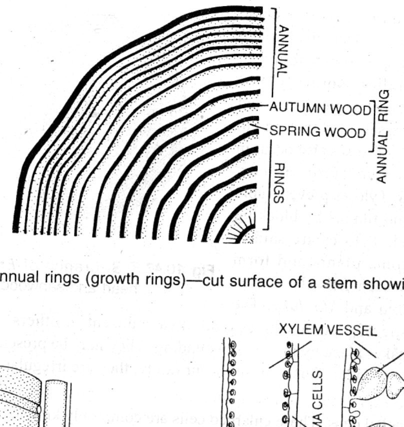
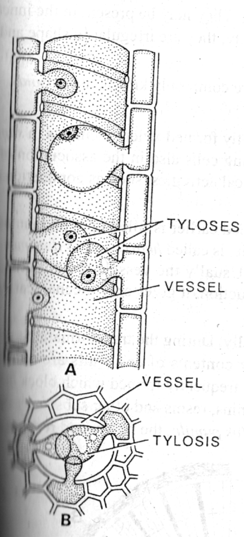


Fig. 10.44. Annual rings (growth rings)—cut surface of a stem showing annual rings.



Tyloses. A, L.S. of vessel with tyloses; B, T.S. of vessel with tyloses.

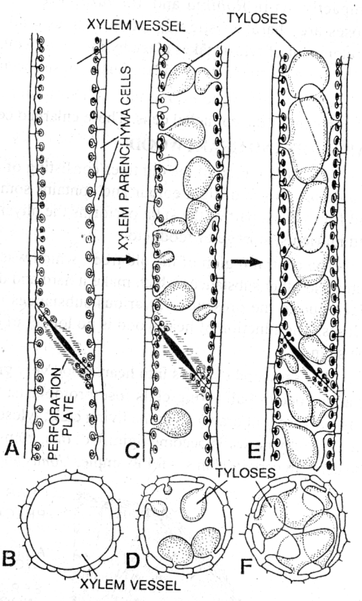


Fig. 10.46. Tyloses. A – F, development of tyloses in xylem vessels depicted in L.S. and T.S.

tain gums and other substances are found, but they are not found very frequently. The ls may remain thin and membranous or very rarely it becomes thick and even lignified. may remain very small or sufficiently large in size as the case may be. They may be one

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Populus) in a single oak) and may fill the e commonly found in families. Normally they t wood of angiosperms and of the vessels, and thus add to of the wood. Tyloses also occur in of *Coleus*, *Cucurbita*, *Rumex*, nd *Convolvulus*. Tyloses prevent rapid e of water, air and fungus by blocking umen of the vessel. Tyloses are said to dergo division in some plants and form *multicellular tissue*, which fills the lumen compactly, as in *Robinia* and *Maclura*. The tyloses are characteristic of certain species, and always absent in others. In many plants development of tylosis takes place by means of wounding. They may be present in the inner par leaf traces after the leaf has fallen. Such tyloses occur rarely; they are irregular in shape and siz

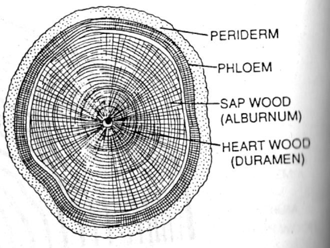


Fig. 10.47. T.S. branch of *Fraxinus*, showin heart and sapwood. (diagrammati

In the wood of conifers there is also found a closing of the cavity of resin canals by enlargement of the epithelial cells. These enlarged cells are commonly known as *tylosoids*.

SAPWOOD AND HEARTWOOD

The outer region of the old trees consisting of recently formed xylem elements in *sapw* *alburnum*. This is of light colour and contains some living cells also in the association of and fibres. This part of the stem performs the physiological activities, such as conduction of and nutrients, storage of food, etc.

The central region of the old trees, which was formed earlier is filled up with tannins, gums and other substances which make it hard and durable, is called *heartwood* or *duramen*. black due to the presence of various substances in it. Usually the vessels remain plugged tyloses. The function of heartwood is no longer of conduction, it gives only mechanical supp the stem.

The sapwood changes into heart wood very gradually. During the transformation changes occur—all living cells lose protoplasts; water contents of cell walls are reduced materials are withdrawn from the living cells; tyloses are frequently formed which block the the parenchyma walls become liginified; oils, gums, tannins, resins and other substances the cells. In certain plants—for example, *Ulmus* and *Malus pumila*, the heartwood remains

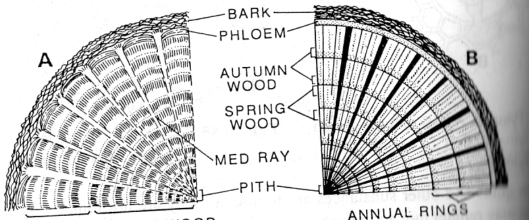


Fig. 10.48. Transections of old dicot stems—left, sector showing heartwood and sap sector showing annual rings.

ith water; in other plants, for example, in *Fraxinus* the heartwood may become very dry. The oils, ins and colouring materials infiltrate the walls, and gums and resins may fill the lumina of the cells. *Diospyros* and *Swietenia*, the cell cavities are filled with a dark-coloured gummy substance. The lour of heartwood, in general, is the result of the presence of these substances. Generally the rtwood is darker in colour than sapwood. However, in some genera, such as *Betula*, *Populus*, *ea*, *Agathis* the heartwood is hardly darker in colour than the sapwood.

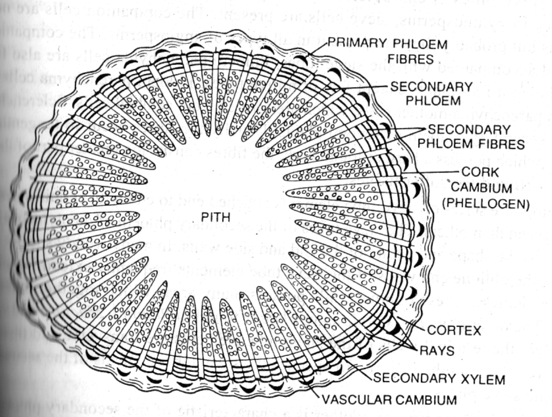
The proportion of sapwood and heartwood is highly variable in different species. Some trees do have clearly differentiated heartwood (*e.g.*, *Populus*, *Salix*, *Picea*, *Abies*), others possess thin wood (*e.g.*, *Robinia*, *Morus*, *Taxus*), the still others possess a thick sapwood (*e.g.*, *Acer*, *Fraxinus*, *gus*).

From economic point of view, heartwood is more useful than sapwood. Heartwood, as timber, is durable than sapwood, because the reduction of food materials available for pathogens by the nce of protoplasm and starch. The formation of resins, oils and tannins, and the blocking of the els by tyloses and gums, render the wood less susceptible to attack by the organisms of decay. haemotoxylin is obtained from the heartwood of *Haematoxylon campechianum*. Because of the nce of resin, gums and colouring substances, sapwood is preferred for pulpwood, and for wood impregnated with preservatives.

NDARY PHLOEM

The cambial cells divide tangentially and produce secondary phloem elements towards outside Normally, the amount of secondary phloem is lesser than the amount of secondary xylem. In of the dicotyledons; usually the primary phloem becomes crushed and functionless and the dary phloem performs all physiological activities for sufficiently a long period of time.

This is a complex tissue made up of various types of cells having common origin in the ium. These cells are quite similar to the cells of primary phloem. However, the secondary phloem



of grapevine (*Vitis vinifera*) stem, showing arrangement of the vascular tissues. The dermis, the cortex and the primary phloem were cut off by the activity of the cork mbium which interpolated a layer of cork between primary and secondary phloem. ter K. Esau).

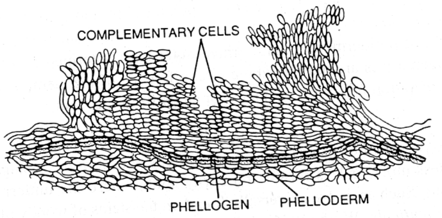


Fig. 10.59. The lenticel of *Mangifera indica* (mango).

the *closing cells*. These cells together form a layer called *closing layer*. With the continu formation of new loose complementary cells, the closing layers are ruptured. The lenticels are fill up with complementary cells completely in the spring season whereas in the end of the spri season the lenticel becomes closed by the formation of closing layer.

The complementary cells are thin-walled, rounded and loose with sufficiently devel intercellular spaces among them. Their cell walls are not suberized. Due to the presence of pro intercellular spaces, the lenticels perform the function of exchange of gases between the atmosp and internal tissues of the plant.

Sometimes, lenticels develop independent of the stomata. In such cases the phellogen cu sometime the cork cells and then loose complementary cells which ultimately break the cork rise to a new lenticel.

SECONDARY XYLEM AND SECONDARY PHLOEM IN CONIFERS (GYMNOSPERMS)

SECONDARY XYLEM (WOOD)

The xylem of gymnosperms is generally simpler and more homogeneous than th angiosperms. The chief distinction between the two kinds of wood is the absence of vessels gymnosperms (except in Gnetales) and their presence in most angiosperms. The gymnosperm possesses a small amount of parenchyma, particularly vertical parenchyma.

THE VERTICAL SYSTEM

In the secondary xylem of gymnosperms, the vertical system consists mostly of trachei late wood tracheids possess relatively thick walls and pits with reduced borders, and therefo are known as *fibre-tracheids*, but libriform fibres do not occur. The tracheids are long cells (mm) with their ends overlapping those of other tracheids. The tracheids of existing gymnosp interconnected by circular or oval bordered pit-pairs in single, opposite or alternate arrange number of pits on each tracheid may vary from 50 to 300 (Stamm, 1946). The pit-pairs are present on the ends where the tracheids overlap each other. Generally the pits are confin radial facets of the cells. Tori are present on the pit membranes in *Ginkgo*, Gnetales Coniferales. The tracheids possess thickenings of intercellular material and primary walls upper and lower margins of the pit-pairs. These thickenings are called *crassulae*. An sculpture is represented by the *trabeculae*. They are found in the form of small bars extend the lumina of the tracheids from one tangential wall to the other. Helical thickenings on have been recorded in the tracheids of some conifers. Wherever present, the verti parenchyma of the Coniferales is found to be distributed throughout the growth ring and

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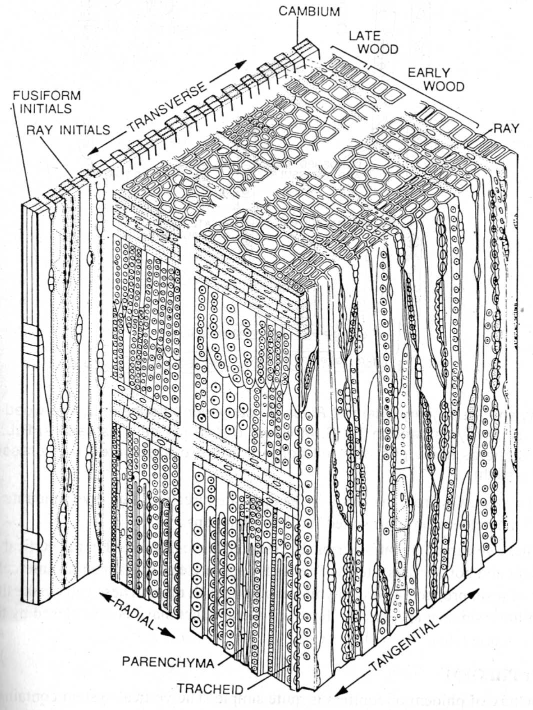
long strands derived from transverse divisions on the mostly long fusiform cambial cells. Some conifers (*Taxus*, *Torreya* and *Araucaria*) do not have parenchyma in the vertical system.

STRUCTURE OF RAYS

The rays of gymnosperms are composed either of parenchyma cells alone, or of parenchyma cells and tracheids. Ray tracheids are distinguished from ray parenchyma cells chiefly by their bordered pits and lack of protoplasts. The ray tracheids possess lignified secondary walls. In some conifers these walls are thick and sculptured, with projections in the form of bands extending across the lumen of the cell. The ray parenchyma cells possess living protoplasts in the sap wood and often dark coloured resinous deposits in the heartwood. The rays of conifers are for the most part only one cell wide and from 1 to 20 or sometimes upto 50 cells high. Ray tracheids may occur singly or in series, at the margins of a ray. The rays serve to transport the assimilation products formed in the leaves and flowing downwards in the phloem in a radial direction into the wood of the stem and roots.



0.60. Xylem—wood of conifers. Three-dimensional diagram of the cambium and secondary xylem of *Thuja occidentalis* Linn. (After Bailey).

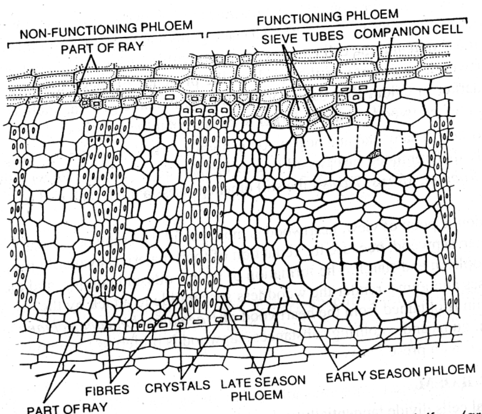


Fig. 10.50. Secondary phloem. T.S. of the secondary phloem of *Vitis vinifera* (grapevine). (Af Esau).

possesses a more regular arrangement of the cells in radial rows. The sieve tubes are compar larger in number and posses thicker walls. The elements of secondary phloem are sieve companion cells, phloem parenchyma and phloem ray cells. Sometimes sclerenchyma is also Presence of sieve tubes is characteristic of angiosperms, however, they are not fou gymnosperms. In gymnosperms, sieve cells are present. The companion cells are not fou gymnosperms but probably they are present in all types of angiosperms. The companion usually found accompanied with the sieve tubes. Phloem parenchyma cells are also found secondary phloem of all plants except few primitive types. Phloem parenchyma cells are directly from parenchyma mother cells, which are formed from cambial cells. Sclerenchyma found in the secondary phloem of several plants. Usually the fibres occur in tangential certain plants which possess a hard or tough bark, the fibres consist the greater part of the phloem and surround the softer tissues.

Sieve tubes are series of sieve-tube elements attached end to end with certain sieve highly specialized than others. The sieve tubes of the secondary phloem of dicotyledons are types as regards the shape and nature of the end and side walls. In many woody species *cordiformis*), the oblique end walls of the sieve tube elements frequently extend for abou length of the element. These oblique walls possess many areas which together make *sieve plates*. The other type, *i.e.*, *simple sieve plate* is found in *Robinia*, *Maclura* and som of *Ulmus*. Here the terminal walls of the sieve-tube elements are transverse and there specialized sieve area. In the majority of species, the sieve tube elements of the second possess simple sieve plates.

Sclerenchyma of one type or another is a characteristic of the secondary phloem species. Fibres occur frequently in definite tangential bands (*e.g.*, in *Liriodendron* and In *Cephalanthus*, the fibres are found singly. However, in *Carya cordiformis*, the fibres the greater part of the secondary phloem and surround the groups of softer tissues. All

ve been reported in gymnosperms. The phloem of *Pinus strobus* lacks sclerenchyma; well veloped tangential bands of fibres are found to be present in *Juniperus*, and large masses of lereids are present in *Tsuga*. In *Thuja occidentalis*, the fibres are arranged in uniseriate tangential ws. These rows of fibres alternate with rows of sieve cells and phloem parenchyma.

In *Platanus* and *Fagus* sclereids are the only type of sclerenchyma present in the phloem. The lereids are found abundantly in the older, living, but nonconducting phloem of the woody plants.

Phloem rays. The pholem rays are usually present in the vascular tissues developed by the bium. The vascular rays are formed in the cambium and develop on either side of it with the ndary xylem and secondary phloem of which they are a part. The phloem rays may be one to eral cells in width. Normally they are of uniform width throughout their length. They may ease in width outwardly, the increase being due to the multiplication of the cells or to the ease in size of cells toward the outer end of the ray. The phloem rays may be one cell wide (*e.g.*, *stanea* and *Salix*), two or three cells wide (*e.g.*, in *Malus pumila*) or many cells wide (*e.g.*, *binia* and *Liriodendron*). However, in oaks there are two types of phloem rays—one very broad the other uniseriate.

Commonly the phloem ray cells in woody plants, as seen in transverse section, are rectangular adially elongated. In herbaceous plants, commonly the ray cells are globose. In *Cephalanthus*, *monia* and *Potentilla* the ray cells closely resemble the phloem parenchyma cells. All phloem ells are parenchymatous with active protoplasm, but as they become older many of them me sclereids.

A special type of ray cell known as *albuminous cell* is found in gymnosperms. These minous cells are found to be situated at the upper and lower margins of the phloem rays. The minous cells differ from the ordinary ray cells both structurally and functionally. They are directly with the sieve cells by sieve areas. They do not contain starch, and are of much vertical diameter than the normal ray cells. They retain their protoplasts as long as the sieve with which they are connected function. It is thought that they function like companion cells sperms.

sonal rings in secondary phloem. The tissues of the secondary phloem are generally in definite tangential bands. These layers of tissue have the appearance of annual rings. these ring like bands do not possess definite seasonal limits like those of secondary xylem, there is no sharp distinction between the phloem cells formed in the early and late growing easonal formation of sclerenchyma bands may exist, but this is not constant feature. In plants new layers of phloem and xylem are formed with each period of new growth.

tion. The functions of secondary phloem are normally the same as that of primary The various cells of secondary phloem are structurally adapted for the function of tion of food. The sieve tubes, companion cells and some phloem parenchyma cells are dapted for lengthwise conduction, and certain phloem rays help in horizontal conduction m the xylem and the cambium. Some of the phloem parenchyma cells in some plants act ssue of starch, crystals and other organic materials.

mic importance. The secondary phloem of various trees and shrubs of the Malvaceae, Moraceae has provided *bast fibres* for economic purposes. The tapa cloth of Pacific mposed of mainly of phloem fibres. Tannin obtained from the secondary phloem of ts is utilized for the preparation of spices and drugs. Secretory canals are abundantly secondary phloem, and the secretions are of much economic value—such as rubber from the latex of *Hevea brasiliensis*, and resins from various gymnosperms.

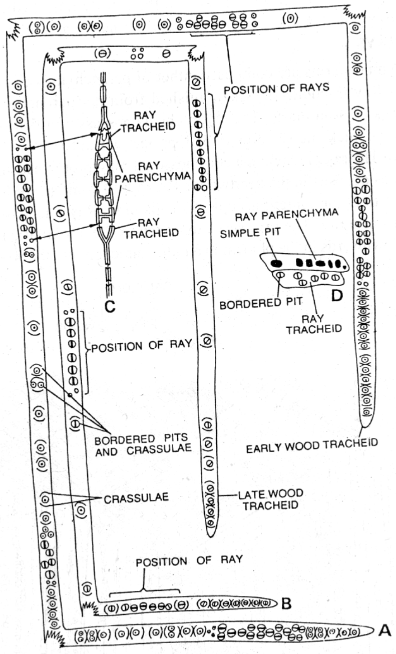


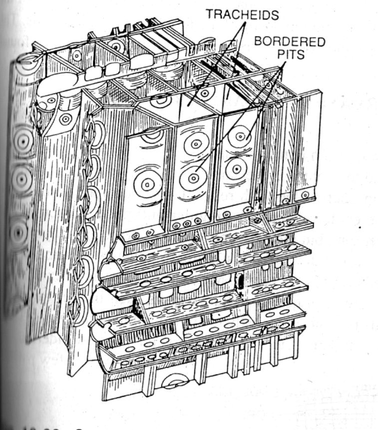
Fig. 10.61. Xylem—secondary xylem of *Pinus*. A, early-wood tracheid; B, late-wood tracheid; T.S. of ray as seen in T.L.S. of wood; D, two ray cells as seen in R.L.S. of w Tracheids show pits with full borders and are associated with crassulae. (A Forsaith).

They conduct water away from the wood in the opposite direction. The rays penetrate equally the xylem and the phloem and thus suited for these functions.

Resin ducts. In certain gymmosperms the resin ducts are developed in the vertical system both the vertical and horizontal systems. The resin ducts arise as schizogenous intercellular by separation of resin producing parenchyma cells from each other. These cells make the lining *epithelium*, of the resin duct and excrete the resin. A resin duct may become closed by the enl epithelial cells. These tylosis like extensions are known as *tylosoids* (Record, 1947).

SECONDARY PHLOEM

The structure of phloem of conifers is quite simple. The vertical system contains sieve parenchyma cells and frequently fibres. Companion cells are absent. The sieve plates are on the lateral walls. The rays are mostly uniseriate and contain parenchyma only or parench albuminous cells.



10.62. Secondary xylem. Three-dimensional structure of wood of *Pinus strobus*. Tracheids are shown in the figure.

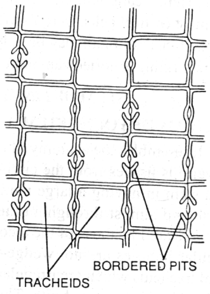


Fig. 10.63. Tracheids with bordered pits of pine stem in T.S.

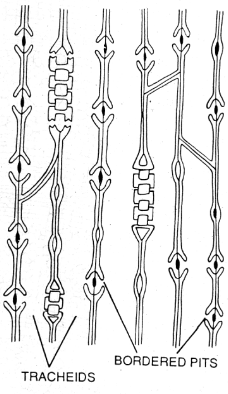


Fig. 10.64. Tracheids with bordered pits of pine stem in T.L.S.

The sieve cells are slender, elongated elements appear the fusiform initials from which they are derived. They lap each other at their ends and each sieve cell remains ntact with several rays. The sieve areas are abundantly on the ends which overlap those of other sieve cells. nnecting strands in the sieve-areas are aggregated the groups, and the callose associated with the strands the group fuses into one structure. The phloem hyma cells occur in longitudinal strands. They store food material and also contain resins, crystals and The phloem rays of the trees of advanced age are eristic in having albuminous cells. The albuminous y also occur among the phloem parenchyma cells (in tical system) and in still other plants only among the parenchyma cells. The albuminous cells contain ytoplasm and distinct nuclei. They are irregular in and store food materials. The secondary phloem also resin canals. In *Picea canadensis*, they occur in rays and possess cyst-like bulbous ions.

SECONDARY GROWTH IN THE MONOCOTYLEDONS

mmonly, the vascular bundles of monocotyledons do not possess cambium, and therefore, secondary growth. However, it occurs in some monocotyledons (*e.g.*, *Dracaena*, *Yucca*, Aloe, *Sansevieria*, *Xanthorrhoea*, *Kingia*, etc.). In these plants the secondary growth the formation of the cylinder of new bundles embedded in a tissue of less specialized phloem and the cortex. During the healing process of a wound the callus is formed. In this there is at first abundant proliferation of the cambium cells, with the production of massive parenchyma. The outer cells of this tissue become suberized, or periderm develops within them, with the result a bark is formed. However, just beneath this bark the cambium remains active and forms new vascular tissue in the normal way. The new tissue formed in the normal way extends the growing layer over the wound until the two opposite sides meet. The cambium layers then unite and the wound becomes completely covered.

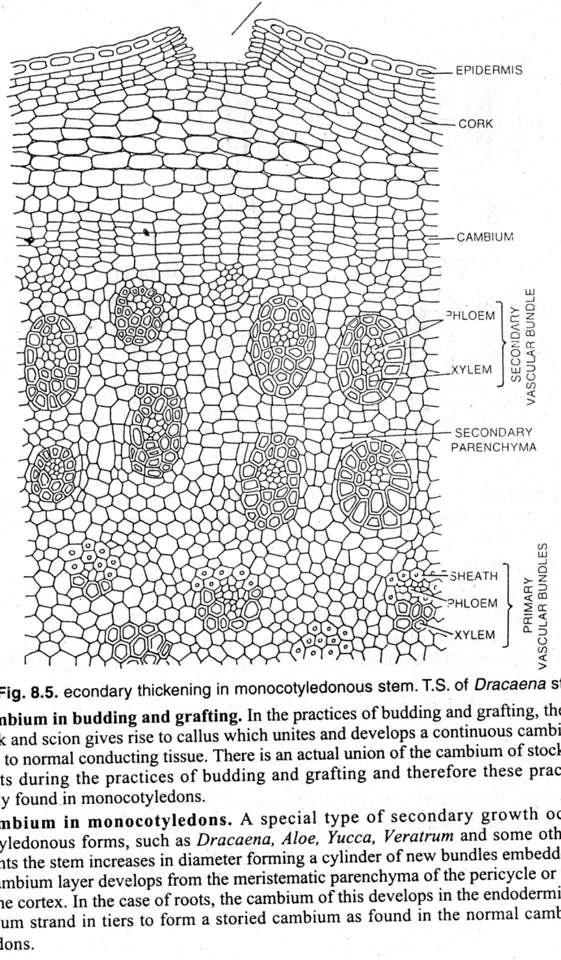


Fig. 8.5. econdary thickening in monocotyledonous stem. T.S. of *Dracaena* stem.

Cambium in budding and grafting. In the practices of budding and grafting, the cambium of both stock and scion gives rise to callus which unites and develops a continuous cambium layer that gives rise to normal conducting tissue. There is an actual union of the cambium of stock and scion of two plants during the practices of budding and grafting and therefore these practices are not commonly found in monocotyledons.

Cambium in monocotyledons. A special type of secondary growth occurs in few monocotyledonous forms, such as *Dracaena, Aloe, Yucca, Veratrum* and some other genera. In these plants the stem increases in diameter forming a cylinder of new bundles embedded in a tissue. Here a cambium layer develops from the meristematic parenchyma of the pericycle or the innermost cells of the cortex. In the case of roots, the cambium of this develops in the endodermis. The initials of cambium strand in tiers to form a storied cambium as found in the normal cambium of some dicotyledons.

9

The Root — Primary and Secondary Structure

The roots are generally divided into two categories: (1) *primary*, normal roots, which originate from the embryo and usually persist throughout life, and (2) *adventitious* roots, which arise secondarily from stem, leaf or other tissues and which may be either permanent or temporary.

The functions of the primary roots are to anchor the plant in the soil, to absorb water and soluble substances and to serve as storehouses of food materials. The functions of adventitious roots are very various. Sometimes they enter the soil and act as primary roots. In other cases they may be modified into climbing organs, stilts or props, thorns, haustoria, etc.

The anatomy of roots is in many respects simpler than that of stems and it is considerably more uniform, perhaps as the result of a rather uniform environment underground, which is in marked contrast with the extreme variability of the conditions affecting aerial shoots. Root anatomy is more ancient in type than that of stems. Roots preserve, in their primary condition, the actinostely of the vascular tissues, which in the lower Pteridophyta is characteristic of both stems and roots.

GENERAL CHARACTERISTICS OF THE ROOTS

1. The roots possess a tendency to grow downwards or sideways rather than upwards.
2. There is absence of chlorophyll in the roots.
3. The roots are not susceptible to the influence of light.
4. There is absence of leaves and hence, of course, absence of buds.
5. The roots possess a root cap over the apex.
6. They possess endogenous origin and branching.
7. In roots, the phloem and xylem are situated on different radii in the primary structure.
8. There is a relatively short zone of growth at the apex.
9. They possess root hairs near the apex.

ANATOMICAL CHARACTERISTICS OF THE ROOT

ROOT CAP

The root cap consists of parenchymatous cells in various stages of differentiation. It is protective in function. Recent experiments have indicated that the root cap has another function that is physiologically of great importance. The root cap is apparently the site of the perception of gravity; thus it appears to be capable of controlling the production in the meristem of the growth-regulating substances involved in *geotropism* or their movement. However, the root cap itself is not the site of synthesis of growth substances. The experiments show that the root cap can control the movement, if not also the synthesis of endogenous auxin in the root apex.