10

Epidermal Tissue System

Epidermis is made up of two Greek words-- Epi = *upon* and derma =*skin.*

It is a system of cells, constituting the outer covering of the primary plant body and is variable in structure and function. Epidermis is the tissue, originated from the protoderm. The epidermis of roots, according to some workers differs from that of the shoot in origin, structure and function. It has, therefore, been given a separate name *epiblema, rhizodermis* or *piliferous layer*. In broader sense, however, the term epidermis is used to represent the superficial layer of cells of the primary plant body—root, stems, leaf, flower, fruit and seed etc. Due to the presence of many types of hairs, stomatal guard cells and several other specialized cells, the epidermal cells are not uniform in morphology and function.

UNI- AND MULTISERIATE EPIDERMIS

In most of the spermatophytes the epidermis consists of a single layer of cells (uniseriate epidermis) but in certain plants e.g., members of Moraceae, certain species of Bignoniaceae, Piperaceae and some of the species of Chenopodiaceae, several celled layers (multiseriate), are present, which are morphologically and physiologically distinct from the inner ground tissue. In the former case (uniseriate epidermis) the layers present inside this layer, termed as *Hypodermis*

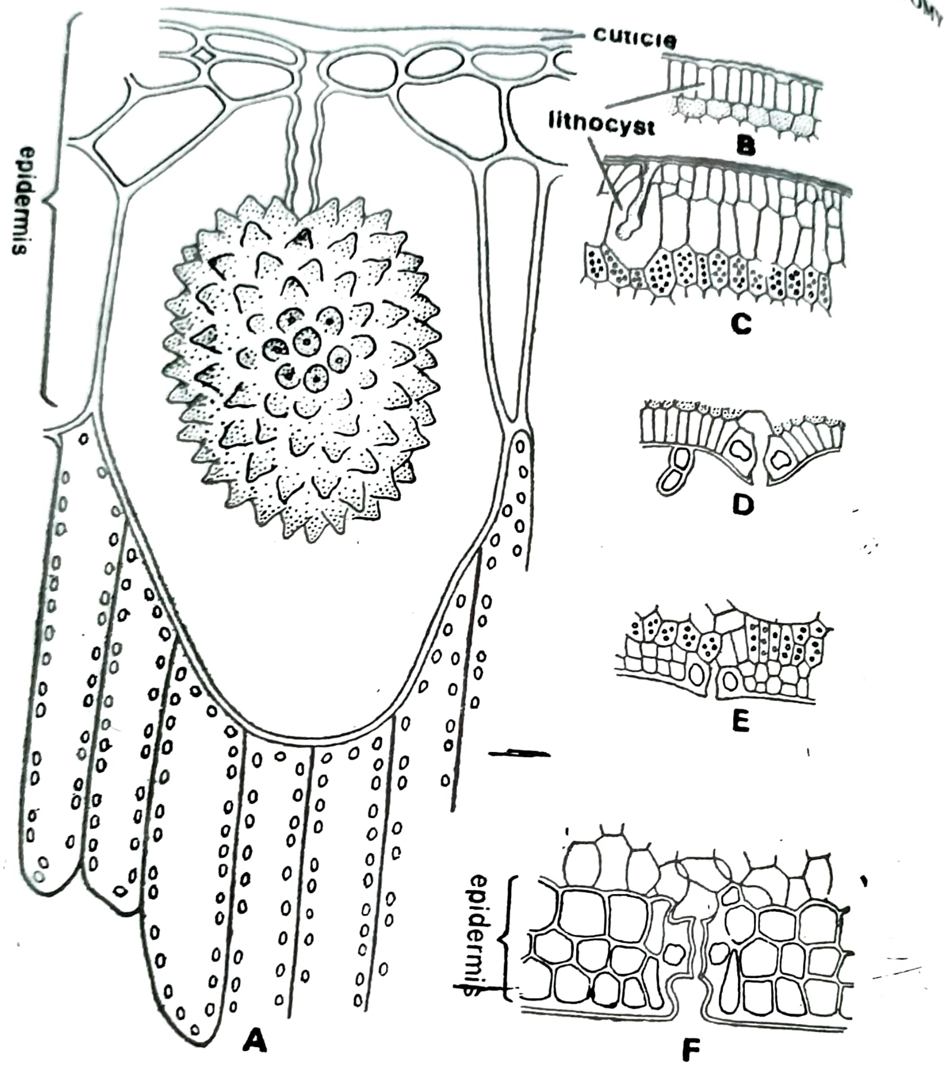
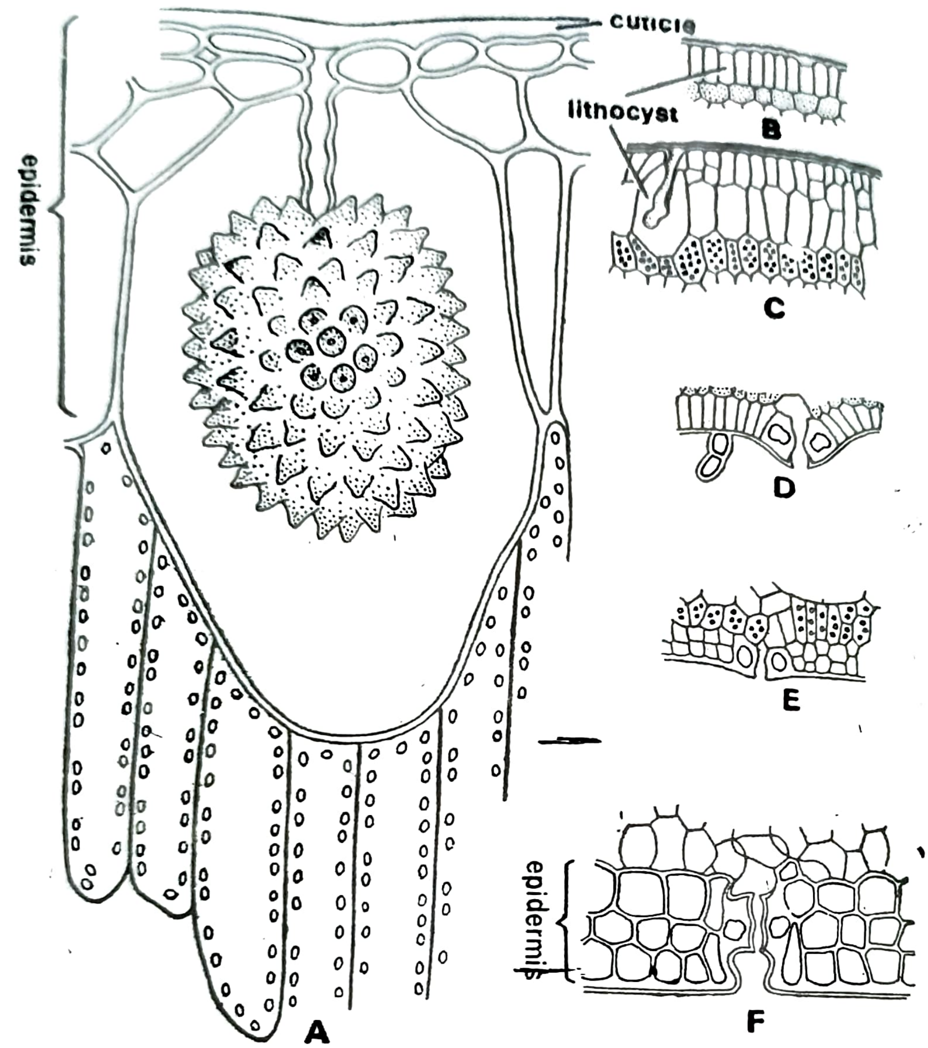


Fig. 10-1. A—Portion of cross-section of the leaf blade of *Ficus elastica* showing multiple epidermis and cystolith. B—F stages in the formation of cystolith.

(Hypo=*Below* Derma=*Skin*), while in the later case (multiseriate epidermis) this tissue is regarded as multiseriate epidermis. It develops due to periclinal divisions of protoderm. The derivatives may divide again to form a tissue of several ontogenetically similar layers. The outermost layer in such cases assumes epidermal characteristics and develops cuticle (Fig. 10-1). *Velamen*, the special absorbing tissue of orchid roots; is also a *multiseriate epidermis.*

COMPONENTS OF EPIDERMIS

The epidermis is a complex tissue system, therefore, there are present several distinct types of cells, which are more or less similar in their function. These cell types are—



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COMPONENTS OF EPIDERMIS

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1. **The ordinary cells.** These may be studied under the following heads—(i) Wall structure, (ii) Protoplast, (iii) Epidermal cells with special structure and contents.

2. **Stomata.** These can be studied under five heads—(i) What is stomata ? (ii) distribution of stomata on leaf surface, (iii) stomatal index, (iv) structure of the stomata, and (v) and (vi) types of stomata.

3. **Epidermal appendages.** Hairs or trichomes are of two types—(i) Non-glandular trichomes and (ii) glandular trichomes.

THE ORDINARY CELL OF EPIDERMIS

The ordinary cells of the epidermis are parenchymatous. These vary in shape, size and arrangement but are always closely attached, without intercellular spaces. In the petal epidermis, sometimes, air spaces covered by cuticle are present (Eames and Mac Danniels, 1947). The epidermal cells may be *sinuous, elongated or polyhedral.*

[I] Wall structure

The epidermal cell walls differ in thickness—some cells are thin walled while in the other, the outer wall is thicker than the other walls. e.g., in the *leaves of conifers.*

In the walls of many leaves, primary pits and plasmodesmata are also present. These are present in the anticlinal and the inner periclinal walls. Regions with wide interfibrillar spaces, the ***trichodes*** (ectodesmata) are also sometimes seen in the outer walls of epidermis. *Cutin* is a fatty substance synthesized in living protoplast and migrate to the surface through the cell wall. It is usually present in the outer wall of the epidermal cells, and constitute a layer called *cuticle.* The process of impregnation with cutin is called ***cutinization*** (cutin formation =cuticularization). Cutin stains red with Sudan IV. Cuticle is absent from the actively growing parts of roots. It is of

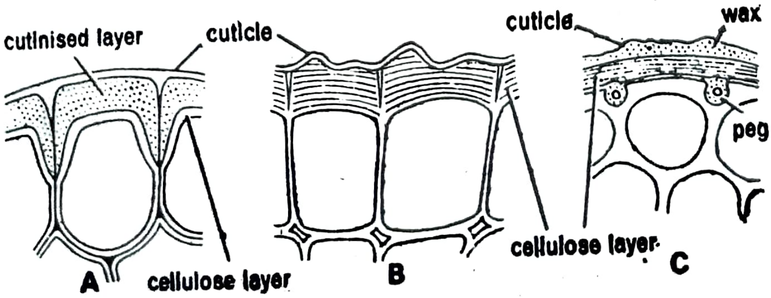

Fig. 10-2. Epidermal cells showing cuticle. A—*Aloe sps.*, B—***Allium cepa***, C—*Musa sps.* (Diagrammatic).

varying thickness in different plants, and is thicker normally in those plants growing in dry habitats. The surface of cuticle may be smooth, rough, ridged or furrowed. Deposits of wax in the form of granules e.g. in *Brassica, Dianthus* or in shape of *rods* as in *Saccharum* or may be in the form of a continuous layer e.g. in *Thuja*, may be present outside the cuticle. In *Agave* a *wax layer* is found below the cuticle.

Silicon salts. Silicon salts are also present in the epidermal cell walls e.g. *Equisetum*, members of the families Cyperaceae, Palmae, and Magnoliaceae, etc. (Metcalfe and Chalk, 1950).

Lignin. It is rarely found in the walls. e.g., *Nerium*, grasses, *Quercus*, rhizomes of Gramineae, etc.

Pectin. Pectin layer is present below the cuticle. It explains as to why fungi grows between the epidermal wall and cuticle layer.

[II] Protoplast

The protoplast of the epidermal cells of most plants contains minute leucoplasts and is devoid of chloroplasts (sometimes present in hydrophytes, pteridophytes and shade loving plants). Anthocyanin pigments are also found in vacuoles of epidermal cells in some cases. Tannin, mucilage and crystals also present in the protoplast in some cases. As is known that the *epidermal cells are the living* cells, *a well developed nucleus* also is present.

[III] Epidermal cells with special structure or contents

1. In Gramineae, between the elongated epidermal cells i.e. *long cells*, above the veins, there are present *short cells* which are of two types—(i) silicon and (ii) cork cells.

These cells occur in pairs. Silica cells contain silica and their walls become thick and cutinised, while the cork cells have suberized walls.

2. **Bulliform cells.** These cells are larger than the typical cells. These are thin walled and having larger vacuoles. Such cells are found in the members of families Gramineae and other monocotyledons except Helobiales. Their function in the rolling and unrolling of leaves has been questioned by Shields (1951).

3. **Cystoliths and Myrosin cells.** Cystolith present in the members of Acanthaceae, Moraceae, Urticaceae, Cucurbitaceae, etc. In Cruciferae, *myrosin*—sac like secretory cells containing the nzyme, are present. They stain red in Millon's test.

STOMATA

(Stoma = *singular*; stomata = *plural.*)

Stomata are the minute units of the epidermal tissue system. These are the openings (stomatal pores or apertures) in the epidermis, limited by two specialized cells termed the *guard cells*. The guard cells together with the opening form *stoma.*

Position of the stomata

Stomata are usually found on the green aerial stems and universally on leaves. They are also present on the petals (although these are functionless), stamens and gynoecium of flowers. In some submerged plants stomata are absent from roots and the entire plant body of certain parasitic plants that lack chlorophyll e.g., *Monotropa, Neottia.* In *Xerophytes* the stomata are *sunken.*

Distribution of stomata on leaves

The leaves may have stomata on both their surfaces or only on their under surfaces. Their distribution is found to be different in different plants.

(1) In *Polygonum amphibium* stomata are present on the upper surface of floating leaves—In *Nymphea* also these are present only on the upper surface. This position is true for most of the floating leaves.

(2) In most of the *mesophytic leaves* (dicot) stomata are found on the lower surface. In some cases they may be present on the upper surface also e.g., potato.

(3) In the *monocot leaves,* the stomata are present equally on both the surfaces.

(4) In *xerophytes,* the stomata are deeply sunken below the level of the other epidermal cells.

(5) In the *submerged plants,* the stomata are totally absent or are vestigial organs.

Arrangement of the stomata on leaves

Two types of arrangement of the stomata is found on leaves—

1. In **monocotyledons** stomata are arranged in parallel rows, the sub-stomatal cavities in each row fused together.

2. In **dicotyledons** stomata are irregulary arranged. In Aroids (monocots) with netted veins also the arrangement of stomata is irregular.

Stomatal index

$$\text{Stomatal index} = \frac{\text{No. of stomata}}{\text{No. of stomata} + \text{No. of epidermal cells}} \times 100$$

The number of stomata and of ordinary epidermal cells are measured with in a unit area This number per square millimeter is different in different plants, e.g.

i. In *Pistacia palaestina* there are 176 stomata/sq. mm.
ii. In *Pistacia lentiscus* there are 255 stomata/sq. mm.
iii. In *Quercus calliprines* there are 402 stomata/sq. mm.
iv. In *Olea europaca* there are 545 stomata/sq. mm.

Structure of the stomata

A stoma consists of a pore surrounded by two guard cells. The epidermal cells adjoining the guard cells often differ in size or arrangement from the rest of the epidermal cells and are called the *subsidiary cells*. The stomata together with the subsidiary cells, is sometimes termed as *stomatal complex*. Below the stomata and directed inwards to the mesophyll are larger intercellular spaces, which are termed as substomatal chambers (Figs. 10-3, 10-4, 10-5).

Guard cells. Structurally these are different in the dicotyledons and monocotyledons. In the former these are somewhat kidney-shaped have unevenly thickened walls (inner wall is thinner while outer thick). The guard cells usually contain chloroplasts. In the latter the guard cells of the *Gramineae* and *Cyperaceae* constitute a rather special type. As seen from the surface, these are *domb-bell* shaped, narrow in middle and enlarged at both ends. The central narrow part has a very thick wall, the bulbous ends have thinner walls (Fig. 10-6). The chemical composition of the guard cell is the same as of the ordinary epidermal cell of the same plant.

Functions of guard cells. Due to the unevenly thick walls, the guard cells are helpful in the opening and closing of the stomata

Types of stomata

On the basis of number and arrangement of the subsidiary cells, Metcalfe and Chalk (1951) found the following types of stomata—

1. Anomocytic. (*Irregular celled* or Ranunculaceous according to Solereder), The surrounding cells or subsidary cells are *indefinite in number* and do not differ from the other epidermal cells. e.g., Ranunculaceae, Malvaceae and Papaveraceae, etc.

2. Anisocytic. (*Unequal celled* or Cruciferous type according to Solereder). Usually 3 subsidiary cells surround the stoma, one cell being considerably smaller or larger than the other two e.g. Cruciferae, *Solanum* and *Nicotiana*, etc.

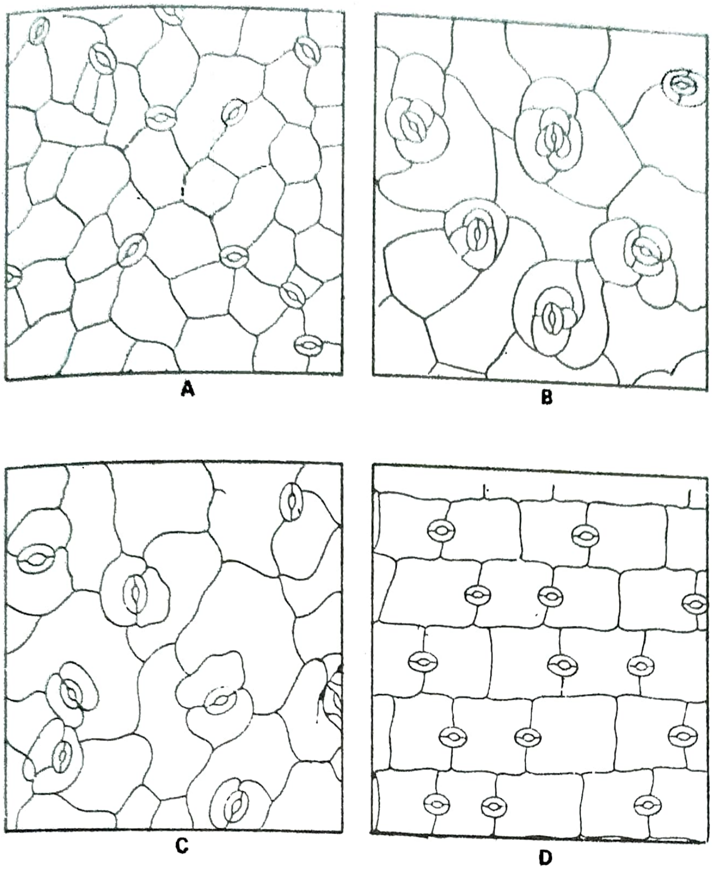

Fig. 10-7. Epidermis in surface views illustrating patterns formed by guard cells around neighbouring cells. A–*Citrullus*. anomocytic B—*Sedum*, anisocytic; C—*Vigna*, paracytic; D—*Dianthus*, diacytic.

3. **Diacytic.** (*Cross celled* or Caryophyllaceous type according to Solereder). Two subsidiary cells surround the stoma with their common walls at right angels to the guard cells. e.g. Caryophyllaceae, Acanthaceae.

4. **Paracytic.** (*Parallel celled* or Rubiaceous type-according to Solereder). One or more (often 2) subsidiary cells are present with their longitudinal axis parallel to the guard cells. e.g., Rubiaceae, Magnoleaceae.

5. **Antinocytic.** Four or more subsidiary cells, elongated radially to the stoma, e.g., in Araceae, Commelinaceae, Musaceae.

6. **Cyclocytic.** Four or more subsidiary cells, arranged in a narrow ring around the stoma e.g., Palmae, Pandanaceae Cyclanthaceae (Fig. 10-7).

Development of stomata

A protodermal cell usually divides by an unequal division to form a smaller *precursor of stomata* which divides into two guard

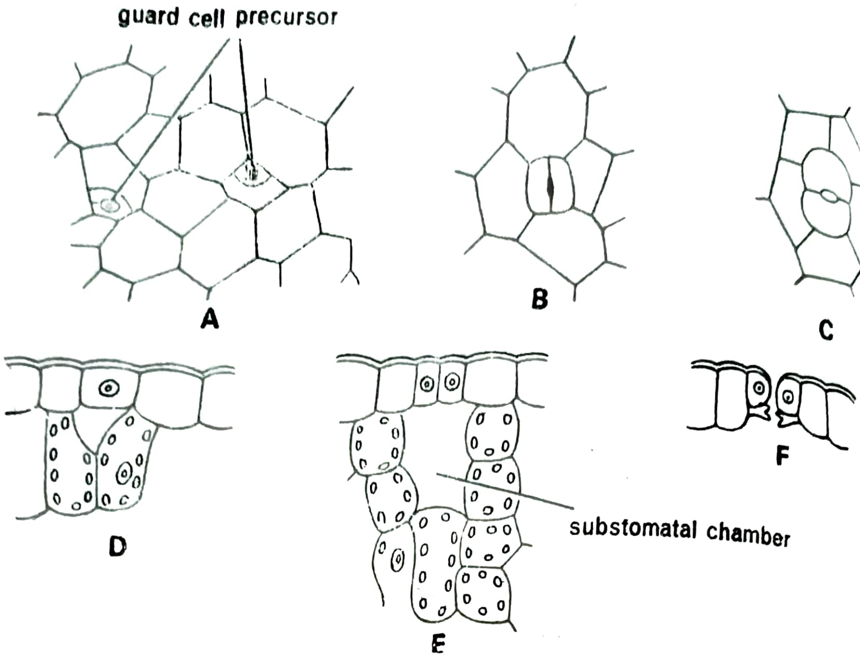

Fig. 10-8. Development of stomata in *Beta vulgaris* leaf.

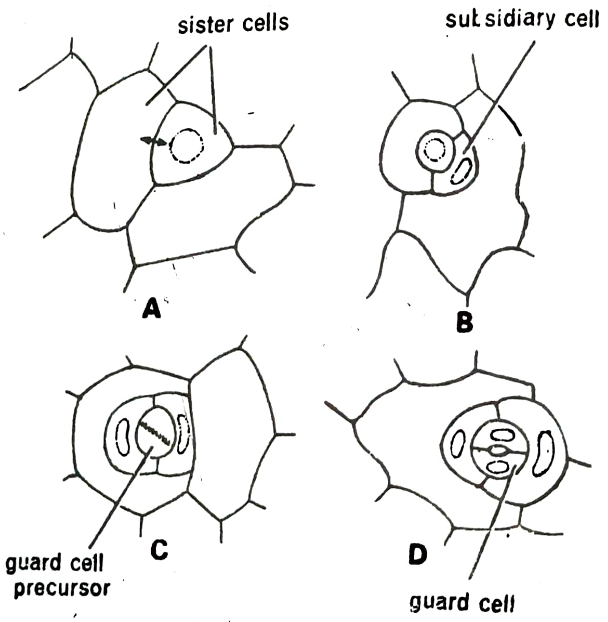

Fig. 10-9. Development of stomata with mesogenous subsidiary cells in a leaf of *Thunbergia erecta*.

cells. These cells through their differentiation and expansion acquire their characteristic shape. The septum between these two cells swell, become weak and finally separates to form the opening of stoma. By readjustments between guard cells and other cells

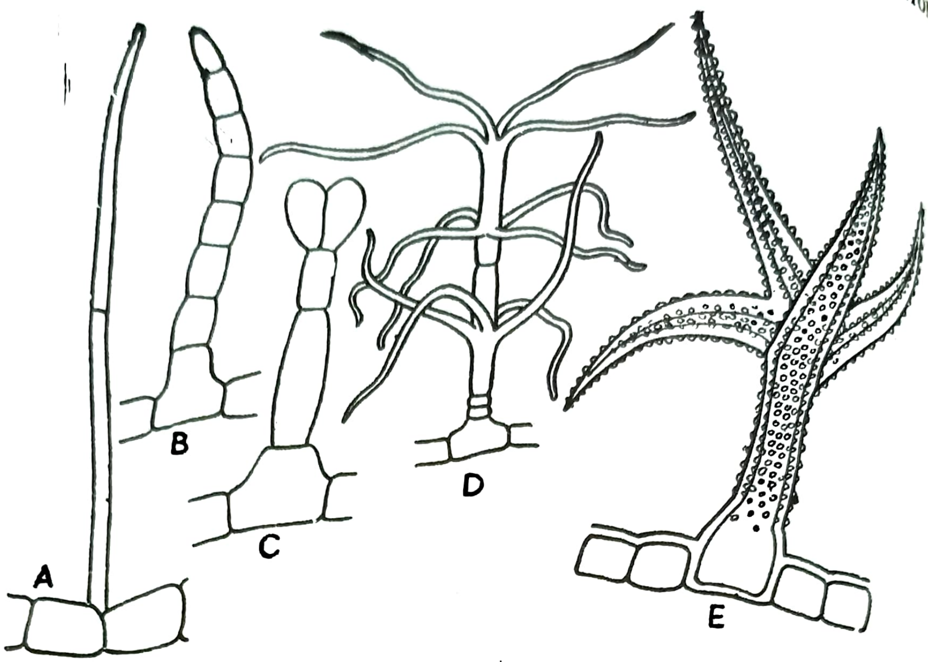

Fig. 10-11. Hairs from. A—Corolla, B—Leaf, C—Corolla D—Young leaf, and E—stem.

Haplocheilic type. The subsidiary cells are not related to the guard cells. (This type corresponds to perigenous type but this m now-a-days is not used) e.g., *Cycads, Conifers, Ginkgo.*

Syndetocheilic type. The subsidiary cells have a common gin with guard cells. A protodermal cell divides into a guard other cell and two lateral cells, each of which either becomes a subsidiary or cell gives rise to subsidiary cell by divisions e.g., *Gnetum, Welwitschia.*

Functions of stomata. (1) Interchange of gases between atmosphere and the plant body.

(2) These are meant for transpiration.

EPIDERMAL APPENDAGES

The outgrowths are present on the epidermis, termed as *Epidermal appendages.* These are of two types—

1. **Trichomes.** All unicellular and multicellular appendages of the epidermis are designated by the term *Trichomes.*
2. **Emergences.** More massive structure, such as warts and spines. e.g,, thorn of rose consisting of epidermal as well as subepidermal tissues are called *emergences.*

Trichomes

The four more common types of trichomes are—*hairs, colletors, water vesicles* or *bladders* and *root hairs.*

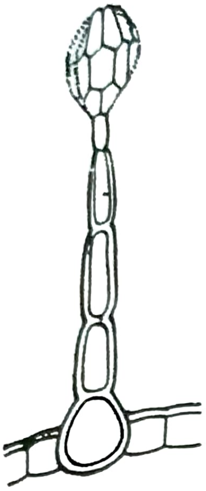

Fig. 10-12. Colleters of *Ononis matrix*.

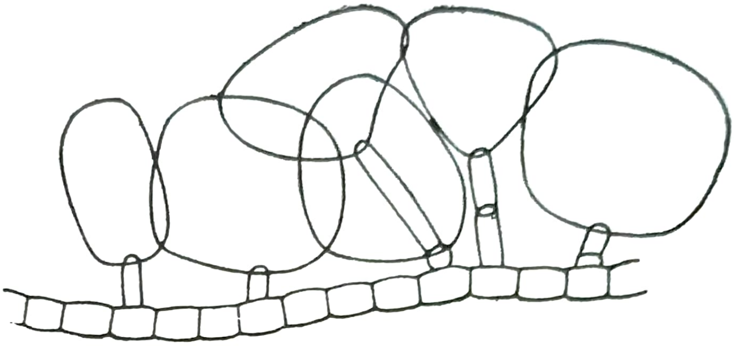

Fig. 10-13. Vesiculate hairs of *Atriplex sps.*

1. Shoot hairs. Hairs form the chief appendages of the epidermis. These may be unicellular or multicellular. A unicellular hair may be unbranched e.g., *Salvia plebia* or branched e.g. *Aerua sps.* or stellate e.g. *Sida sps.* A multicellular hair commonly have foot embedded in the epidermis and a body projecting out. Hairs are present on stem, root, leaves, gynaecium and androecium, etc. The wall of the hairs is made up of cellulose. Hairs are of great use in Taxonomy. On the basis of the hair structure several plants may be classified. The hairs may be glandular or non-glandular. The *glandular hairs* consist of a *head* and a *stalk* and secreting a sticky substance. Such types are mainly present on the insectivorous plants. Shoot hairs may be either branched or unbranched.

2. Colleters. Glandular trichomes which secrete a sticky substance and which usually consist of a multicellular stalk and head, are termed as colleters. Such trichomes are mainly found on budscales and stipules, e.g., *Rosa* and on the calyx e.g., *Plumbago*.

3. Water vesicle or bladder. The epidermal cell becomes much enlarged to reserve the water (Fig. 10-13). These are also known as *vesiculate hairs* e.g., *Atriplex*. When the vesicle dries out during maturation, the salt content remains on the leaf surface as a white, powdery layer.

4. Root hairs. Root hairs are developed from any cell of the epidermis or a particular group of cells. The root hairs are thin walled, short lived, unicellular, meant for absorption of water from soil.

Functions of trichomes. (1) Hairs on leaves are helpful in reducing the transpiration and the intensity of illumination.

(2) Hairs present on stigma are helpful in pollination.

(3) When present on seeds these are helpful in dispersal.

(4) Glandular hairs give secretory or excretory products which protect them from enemies.

(4) Hairs present on insectivorous plants give enzymes.

Emergence

Spines, scales and warts are the epidermal emergences.

Scales. These are made up of discoid plate of cells which are usually situated on a short stalk, e.g, *Salvia*.

Suggested reading

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6. Tomilson, P.B. (1974). Development of the stomatal complex as a taxonomic character in monocotyledons. *Taxon 23* : 109–128.

7. Uphof, J.C T. (1962). *Plant hairs, Handbuchder Pflavangenatomic.* Band 4. Teil. 5.

Selected questions

1. Write in details the structure of epidermis in Angiosperms
2. Describe the structure, development and classification of stomata.
3. Write short notes on:—

(i) Trichomes, (ii) Stomata, (iii) Cystolith, (iv) Multiple epidermis.

11

Ground and Vascular Tissue System

GROUND TISSUE SYSTEM

This system extends from below the epidermis to the centre (except for vascular bundles), and forms the main bulk of the plant body. It can be divided into the following parts—(1) Cortex, (2) Pericycle, (3) Primary medullary rays, and (4) Pith.

[I] Cortex

The zone of tiseue between the epidermis and pericycle is known as cortex. It is variable in thickness, and consists of mainly parenchyma. The cells may be rounded, polygonal, cylindrical or even stellate in some cases. The cells have large intercellular spaces which in some cases become very large and are called air spaces. Chloroplasts may be present in all or some of the cortex cells. Resin ducts, oil ducts, laticiferous cells, laticiferous ducts, etc., may be present in the cortex. Sometimes, sclerenchyma may also be present. In dicotyledonous stems the outer few layers become transformed into strengthening tissue and are called as *hypodermis*.The remaining tissue is now known as *general cortex*. The innermost layer is the *endodermis*. In monocotyledonous stems cortex is not distinct, there being present a general ground tissue.

The cortex primarily is a protective tissue—but it also serves for storage and sometimes for photosynthesis.

Endodermis. The innermost layer of cortex has barrel-shaped cells (in cross section) with intercellular spaces and is known as the

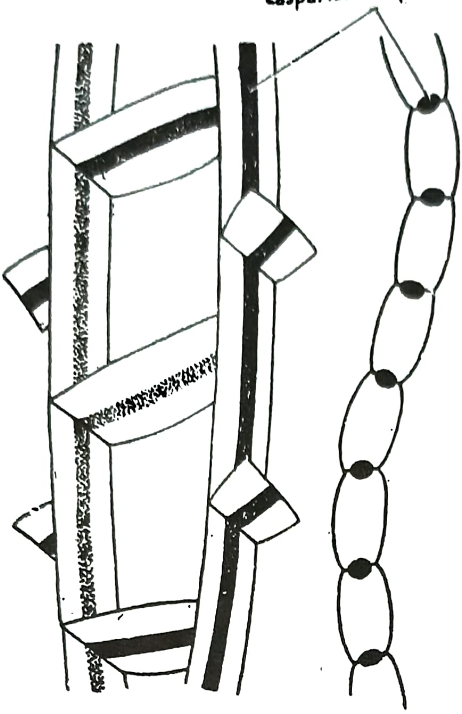

Fig. 11-1. Endodermis.

endodermis. Usually endodermis is a single layer of compactly arranged cells. These are vertically elongated living cells containing starch, because of which it is also called as *starch sheath.* Some endodermis cells may also contain mucilage, tannin or gum etc. The radial and inner walls of endodermal cell are thick (may be suberized or cutinized) and the outer walls are thin. Sometimes, the thickening of the radial walls is in the form of a strip, called *casparian strip* (after Caspary, 1865, who recognised it first of all). The wall material of casparian strips is different from other walls. It is believed to show lignin reaction and is also believed to be made up of suberin. In transverse section it lookslike a large dot and is of variable thickness.

The endodermis is present in most of the roots, while in stems it is present in all pteridophytes and in a number of herbaceous angiosperms. It is more clearly represented in rhizomes than in aerial stems.

The thickening of endodermis is more pronounced in the roots. In some cases e.g., *Smilax rotundifolia* roots, all the walls of endodermis are thickened so much so that even the lumen may be closed. In the latter stages the thickening material may be cellulose. In roots, when the endodermal cells become lignified or suberized, outside the protoxylem, some cells become thin-walled and, called as the *passage cells.* As the name indicates, they serve as the passage for the water, conducted by root hairs to move to xylem. In woody plants, generally the endodermis is not distinct.

Various persons have assigned different functions to the endodermis. By some, it is regarded as a water-tight jacket between the xylem and the surrounding tissue, because of (i) the intercellular spaces are absent, and (ii) the cell walls are thickened. Some gave it purely protective function, while others take it to be helpful in maintaining root pressure. The idea of its being a storage tissue has also been proposed by some and some took it to be a sort of airdom, which checks the air-clogging of the water-conducting tissue.

[II] Pericycle

The strip of tissue, present between the endodermis and vascular bundles is known as the *pericycle.* It may be one or few layered and is generally parenchyma, but in some cases it is partially (e.g., sunflower) or wholly (e.g., *Cucurbita*) sclerenchyma. In roots, it is generally one-layered parenchyma and gives rise to the cork cambium. In aquatics and parasites it is not distinct. When endodermis is absent it lies between the cortex and vascular cylinder. In partially sclerenchymatous pericycle e.g., sunflower, the thick walled portion lies just above the phloem of the vascular bundles. Some workers now believe that these fibrous layers of pericycle are a part of phloem. The sieve elements of protophloem get obliterated and its outer cells differentiate into fibres. The term 'perivascular fibres' is used in such cases to designate the so-called pericycle.

It is mainly mechanical in function but when parenchymatous, it also serves for storage. In dicotyledonous roots it becomes meristematic' and forms the cambium and cork cambium.

[III] Primary medullary rays

The tissue lying between the vascular bundles is known as the primary medullary rays and are the extensions of the pith. These are made up of parenchyma cells, that are slightly elongated in cross section. Its main function is the storage of water and reserve food.

[IV] Pith or medulla

The central, solid, cylindrical tissue, surrounded by the vascular bundles and pith rays, is called as *pith.* It is made up of large living parenchyma, having intercellular spaces. The cells are generally round and have thin cellulose walls. Sometimes, the pith is torn due to rapid elongation and radial expansion of the stem and the stem becomes hollow e.g., *Cucurbita.* In some cases, there may develop some lignified or stone cells in the pith. Ontogenetically pith develops from ground meristem and is the inner portion of fundamental tissue system. In most of the dicotyledonous roots the pith is very small and is almost completely obliterated after secondary growth. In its earlier stages of development the pith cells are smaller and have even chloroplasts. With its maturation the cells enlarge and loose some of their contents. Its main function is the storage of reserve

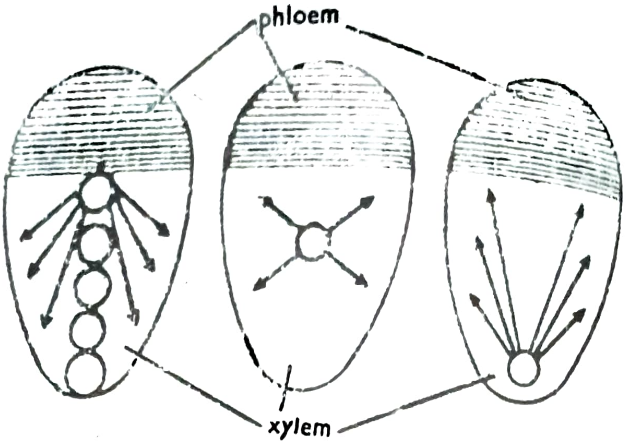

Fig. 11-2. Centripetal and centrifugal development of xylem.
A—Exarch. B—Mesarch. C—Endarch.

food materials. When sclerenchymatous cells develop, it gives mechanical support.

VASCULAR TISSUE SYSTEM

The tissue derived from the procambium is called as vascular tissue system. It consists of varying number of strands or bundles called the 'vascular bundles', that are embedded in the ground tissue to form the central cylinder. The vascular bundles are made up of xylem and phloem. A strip of meristem, the cambium, may or may not be present between the two tissues. In former case the vascular bundle is called *open* as is found in dicotyledonous stem and *closed* in the second case e.g., monocotyledonous stem. The arrangement of bundles is variable in different parts. They may be arranged regularly in a ring as in dicotyledonous stem, root and monocotyledonous root, or may be irregularly distributed e.g., monocotyledonous stem.

With reference to the centre of the axis, the xylem groups are either produced *centripetally* or *centrifugally*. These are called *exarch* and *endarch* respectively However, in some cases, the formation of xylem is both centripetal and centrifugal e.g., *Ferns* and *Cycads*. It is called as *mesarch* condition. The development of phloem is always centripetal. The first differentiated xylem and phloem are known as *protoxylem* and *protophloem* and those differentiated afterwards are called as *metaxylem* and *metaphloem*. The vessels of protoxylem have annular and spiral thickening and those of meta-xylem have reticulate and pitted thickenings. In primary xylem both meta-and protoxylem are present. Protophloem sometimes consists of only phloem parenchyma.

According to relative positions of the xylem and phloem, the bundles are classified variously.

Radial and conjoint. The bundles are called as radial, when the xylem and phloem are arranged on different radii alternating with each other e.g., roots. When xylem and phloem combine in the same bundle and are present on the same radius, it is called as *conjoint bundle*. The conjoint bundles are known as *collateral*, when xylem is situated on the inner side of phloem (e.g., sunflower stem); when both cambium and phloem are present on both the sides of xylem, these are called *bicollateral bundles* (e.g., *Cucurbita* stem).

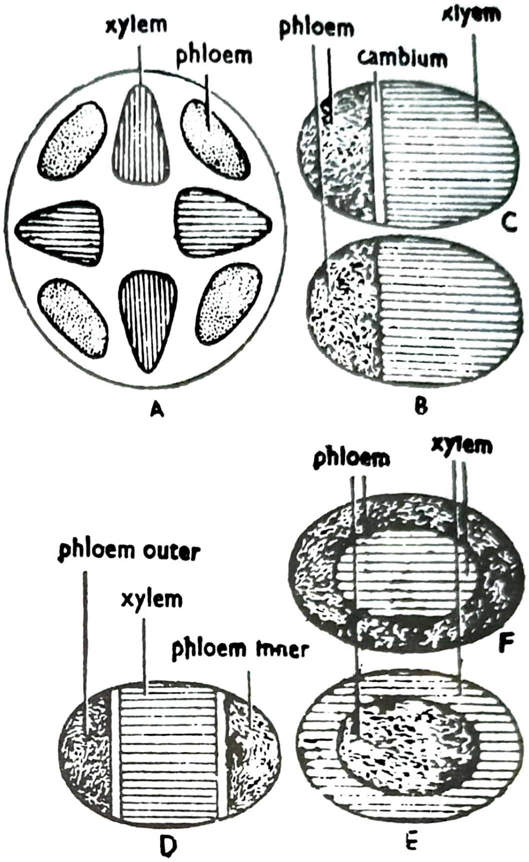

Fig. 11-3. Vascular bundles. A—Radial B—Conjoint closed C—Conjoint open. D—Bicollateral, E—Leptocentric and F—Hederocentric.

Concentric bundles. When out of the xylem and phloem, one surrounds the other; the bundle is called as concentric bundle. It may be *hederocentric* or *amphicribral* i.e., xylem is surrounded by phloem as in ferns, or *leptocentric* or *amphivasal* i.e., phloem surrounded by xylem e.g., *Dracaena* stem.

The tissues enclosed within the endodermis but excluding it are also called as *stele*. It usually consists of *pericycle*, vascular bundles, pith and medullary rays. Mitra (1972) reported the absence of endodermis and pericycle in the young and old stem of *Eupatorium ayapna*. In this case pith also originates from procambial strands that fail to differentiate into vascular tissue. He feels that the absence of these two layers in this and many other plants falsifies the concept of stele which takes pericycle (or endodermis) as its outer-most layer. Esau (1948) felt that the term vascular region be used in place of stele.

The typical steles are found in the case of *Pteridophytes*, which show, protostele, siphonosteles, solenostelic or dictyostelic condition.

The pith in these cases have been shown to be intrastelar in origin arising by the metamorphosis of inner vascular tissue into parenchyma (Bower 1911, Fahn 1960). The seed plants where *Eustele* (dicotyledons) or *atactostele* (monocotyledons) is described, the term stele in its original sense cannot be applied as in many plants e.g., sunflower, the pericycle is taken to be part of protoplasm and is absent in others. Esau, therefore, suggested to call it as *vascular cylinder*.

Suggested reading

1. Esau, K. (1953). *Plant Anatomy*, 2nd ed., Wiley, N.Y.
2. Fahn, A. (1967). *Plant Anatomy*, Oxford Pergamon Press

Selected questions

1. Give in deteails the vascular tissue system met within Angiosperms.
2. What do you understand by ground tissue system ? Describe the various elements of this system.
2. Write notes on:—
   (i) Cortex (ii) Endodermis, (iii) Medullary rays,
   (iv) Pericycle.

12

Vascular Cambium

Vascular cambium is the meristem that produces *secondary xylem* and phloem. It is a lateral meristem, which develops either as longitudinal strands or as a hollow cylinder. In three dimensional aspects it is a continuous sheath about the xylem of stem and root. Their branches may also exist in leaf. In the woody *Angiosperms* and *Gymnosperms* the primary vascular tissues of the stem and root exist for relatively shorter period. The vascular cambium develops from the procambium.

ORIGIN OF PROCAMBIUM

There is a sequence of differentiation of procambium from the '*apical meristem*' of the axis to a single cylinder of vascular bundles.

The vascular differentiation is detectable above the level of leaf or leaf initiation. This is called "*Promeristem*". Beneath the insertion of leaf primordia, longitudinal divisions without a considerable increase in width of cells, produce somewhat elongated cells. Later or further below, the distinction occurs as the procambial cells become relatively *narrower* after additional longitudinal divisions. In this way with the progressive differentiation of the promeristematic cells, three meristems the *Protoderm*, *Ground Meristem* and *Procambium* are recognized.

The procambium may be in the form of a *solid* or *hollow cylinder* or *strips*. Develoment of procambium is acropetal. The differen-

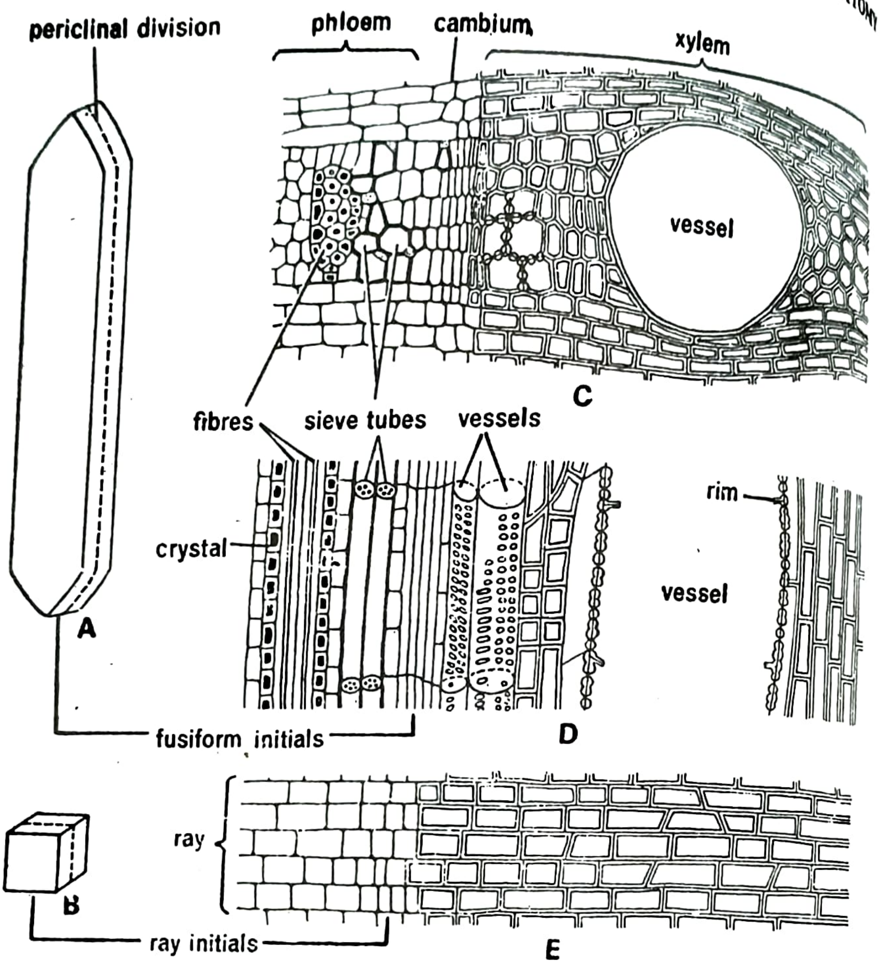

Fig. 12-1. Vascular cambium in relation to derivative tissues. A—fusiform initial; B—ray initial; C, D, E, sections of stem; C—transverse; D—radial (only axial) and E—radial (only ray). (After, Esau, 1977),

tiation of procambial cells into the cells of vascular tissue take place in different plants at different stages of procambial development.

ORGANIZATION OF CAMBIUM

The cells of vascular cambium are different from the usual meristematic cells that have dense cytoplasm, large nucleus and are isodiametric. The cambial cells are vacuolated. The resting cells have less of vacuoles while the active cambial cells are highly vacuolated. The cambial cells are of 2 types—*fusiform initial* and *ray initial*.

[I] Fusiform initials

The term fusiform implies that the cell is shaped like a spindle. A fusiform initial, however, is a prismatic cell in its middle and wedge shaped at the ends. These cells are several to many times longer than wide. These are very long in *Sequoia sempervirens* where they reach a maximum length of 8-7 mm. The pointed ends of wedge is seen in tangential sections and the truncated end in radial sections (Fig 12-1).

The fusiform initials and their derivatives constitute the axial system of cambial zone.

[II] Ray initials

These are much smaller than fusiform intials, slightly elongated and nearly isodiametric in shape. They form the *radial system* of the cambial zone.

TYPES OF CAMBIUM

The cambium cells can be classified in different ways.

[I] According to their origin or position

1. **Intra fascicular cambium.** The cambium that arises within the bundles of primary vascular tissue of the stem is called intrafascicular cambium.

2. **Interfascicular cambium.** The strip of intrafascicular cambium usually become jointed by additional strips of cambium which are called *Interfascicular cambium*. This develops from the interfascicular parenchyma. As it is not in continuation with the intrafascicular cambium and secondary in origin, it is a *secondary meristem.*

[II] According to the arrangement of the fusiform cells (as seen in tangential section)

1. **Storied or stratified cambium.** In this case the fusiform initials are shorter and are arranged in horizontal rows so that their ends are approximately at the same level. This type of cambium is found in *Tamarix* and *Robinia* etc.

According to *Bailey* the storied cambium have developed by gradual reduction of the size of the cells and by longitudinal sliding growth. (Fig. 12-2A).

2. **Non-storied or non-stratified cambium.** In this case the fusiform initials are longer, partially overlap one another and are not arranged in horizontal rows. This type of cambium occurs more commonly in plants (Fig. 12-2B).

CELL DIVISION IN CAMBIUM

When the cambial initials produce secondary xylem and phloem, they divide periclinally. At one time a derivative cell is produced towards the xylem, at another time towards the phloem although not necessarily in alternation. Thus each cambial initial produces radial files of cells one towards the outside and the other towards inside and the two files meet at the cambial initial.

When the cambium is active, addition of cells occur so radialy that older cells are still meristematic when new cells are added to them. Thus a wide zone of more or less undifferentiated cells accumulates and is called *cambial zone*. In this zone only one cell in a radial file is initial cell. These initials are difficult to distinguish from their recent derivatives especially because the derivatives divided by periclinal division one or more times before they begin to differentiate into xylem and phloem cells. Due to this Bannan (1955, 1957) use the term '*Cambium*' to include the *cambial initial*, as well as undifferentiated periclinally dividing derivatives and to these derivative cells as '*Phloem mother cells*' and '*Xylem mother cells*'. Bannan (1968) has shown that the initial of a given radial file of cells in the cambial zone does not necessarily have an accurate tangential allignment with the initials in the neighbouring radial files. It may be located closer to the xylem or the phloem in one than the other file. Any initial may cease dividing and may be replaced by one of its derivatives.

Developmental changes in the initial layers

With the increase in thickness of core of secondary xylem, the cambium is displaced outwardly and its circumference increases. This increase is acccomplished by divisions of cells. The division increasing the number of initial cells are called '*Multiplication divisions*' by Bannan (1956). In cambium with short fusiform initials, the divisions are mostly radial *anticlinal* (Fig. 12-3A). Thus, two cells appear side by side and enlarge tangentially. In herbaceous dicotyledons the anticlinal divisions are lateral. They intersect twice, the same mother cell wall. Long fusiform initial divide by anticlinal walls of various degrees of inclination (Fig. 12-3, CE). Now each of the new cells elongates at its end till it is as long as or even longer than the cell from which it was derived. They come to lie side by side in the tangential plane and form non-storied or stratified cambium.

Thus, they increase the circumference of the cambium. This increase also involves complex phenomenon of *intrusive growth elimination of initials* and formation of new ray initials (Fig. 12-3, F & G). Formation of cell plate during the process of longitudinal division of fusiform initials is peculiar. The cell plate begins to form between the two new nuclei and it spreads slowly on both the sides so it takes much time to reach the end walls. While the cell plate is not complete, its free margins are surrounded