

The latter two zones are transitional zone can be distinguished. This is a cup between the central mother cells and the rib and peripheral meristems. According to Phillipson (1954) this zone is only a temporary feature in many of the plants in which it occurs, as it disappears towards the end of the plastochron. The time gap between the successive initiations of two leaves or pair of leaves is termed as Plastochron. The opuntia type apex is found in *Phoenix*, *Chrysanthemum*, *Xanthium*, *Bougainvillea* etc.

Johnson and Tolbert (1960) used the term **metameristem** to include the initials of the tunica and corpus. The epidermis and its derivatives originate from the outermost layer of the tunica. The peripheral meristem contributes to the development of the leaf primordia, the cortex, all or part of the procambium and some times the outer region of the pith.

1-6 THEORIES OF SHOOT APEX ORGANIZATION

Several theories have been put forward from time to time to explain the organization of the shoot apices. Some important ones are discussed here :

1. Apical cell theory :

This theory was put forward by *Nageli* in 1858. According to this theory, a solitary apical cell is the structural and functional unit of apical meristem. It was assumed that the plant body arises from this single cell and its derivatives. Such a single cell occurs only in higher algae, bryophytes and some pteridophytes, but not in higher plants. Recent investigations also showed that different parts of the plant body in higher plants originate independently. So this theory is not applicable to the shoot apices of seed plants. The apical cell of pteridophytes is usually four sided with three cutting faces. But in some taxa (*Salvia*, *Azolla*) the apical cell is three sided with two cutting faces only.

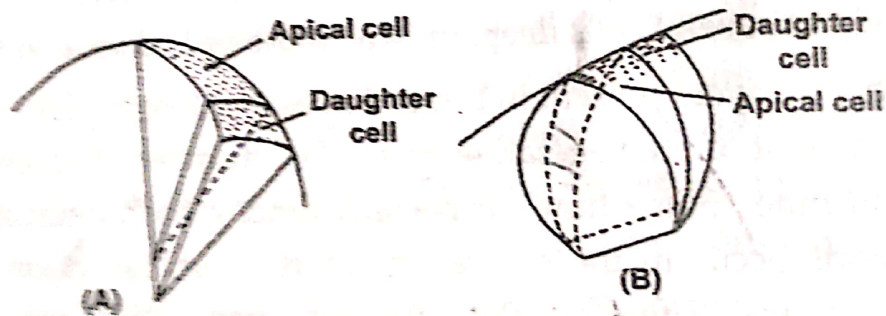


Fig. 1-7 : Two forms of an apical cell – (A) pyramidal ; (B) lenticular

2. Histogen Theory :

This theory was proposed by *Hanstein* in 1870. He distinguished three distinct meristematic zones in the shoot apex. Each zone consisting of a group of initials was called a **histogen** (or) **tissue builder**. The histogens arise from separate sets of

Fig. 1-8 : SH

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initials and have different courses of development. The major histogens found at the root and stem apices are - **dermatogen** (outermost uniseriate layer), **periblem** (the middle layer) and **plerome** (central massive core). The dermatogen (skin) cells divide anticlinally and give rise to the epidermis. The periblem (clothing) forms the cortex and the plerome (to fill) gives rise to the primary vascular tissues and pith.

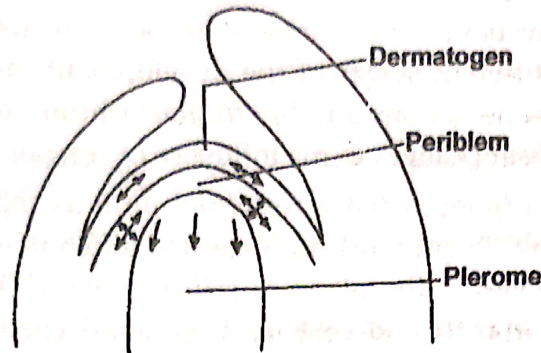


Fig. 1-8 : Shoot apex of a dicot : Histogen theory (Arrows indicate direction of growth)

Histogen theory is inadequate to explain the shoot apex of seed plants because --

(i) In many gymnosperms and angiosperms, distinction between periblem and plerome is absent.

(ii) There is no sharp distinction between dermatogen and periblem and

(iii) the origin of different regions from the histogens can not be demonstrated.

Haberlandt (1914) proposed the terms protoderm, ground meristem and procambium for dermatogen, periblem and plerome respectively.

3. Tunica - Corpus Theory :

This theory was proposed by Schmidt (1924) to explain the organization of the shoot apex. According to this theory, two distinct zones of tissues occur at the extreme tip of the stem. The peripheral zone, **tunica**, consists of one or more layers of regularly arranged cells. The central core of cells covered by the tunica is termed the **corpus**. These two zones can be distinguished on the basis of plane of cell division. The cells present in tunica are smaller and show predominantly anticlinal divisions. The cells present in the corpus are larger and show irregular divisions.

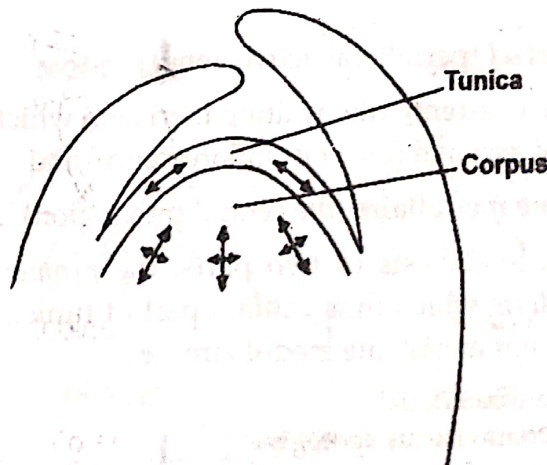


Fig. 1-9 : Shoot apex of dicot : Tunica-corpus theory

This theory does not imply any relationship between the apical zones and subsequent formation of tissues. In this point, the theory sharply differs from the histogen theory. The outermost layers of tunica commonly gives rise to the epidermis. Other tissues like cortex, endodermis and vascular tissues may have their origin in the inner layer of tunica and corpus.

The number of layers in tunica varies from species to species and even in the same species during different stages of the development. According to Schmidt (1924) and others, these variations are due to plastochron periodicity. However, Hara (1962) attribute these changes to the influence of seasons.

The term tunica is some what a restricted term as regard to cell division which is always *anticlinal*. Some workers suggested different terms to make it more flexible without emphasising the plane of cell division. POPHAM and CHAI (1950) used the terms **mantle** and **core** for tunica and corpus respectively. The mantle includes all the outer layers of the apex. Tunica is confined only to those layers of mantle which divide anticlinally. The mass of cells surrounded by mantle was termed as **core**.

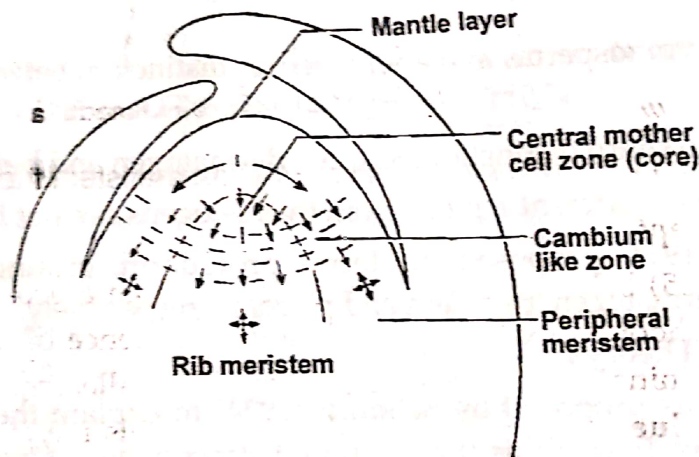


Fig. 1-10 : Shoot apex of a dicot : Mantle - core concept

4. Theory of Waiting meristem :

This theory was developed by the French School (Plantefol, 1947; Buval, 1952). They recognized three zones in the apical meristems, based on the rate of mitotic activity.

- (i) the **anneau initial** (peripheral active zone),
- (ii) the **meristem 'd' attente** (the waiting meristem which becomes active only during the formation of terminal flower or inflorescence) and
- (iii) the **meristeme medullaire** (the central pith region).

Meristem d'attente consists of two parts, the *promeristeme sporogene* and *promeristeme receptaculaire* which thus contain part of tunica (except annue initial) and part of corpus (except meristeme medullaire, i.e.,

Tunica	{	anneau initial	
		Promeristeme sporogene	
Corpus	{	Promeristeme receptaculaire	} meristeme d' attente.
		Promeristeme medullaire	

They believe that the meristem is inert and does not wait for a productive stage before building the shoot. Schmidt considers meristem as apical initial.

5. Newmar

Newmar's theory of the shoot apex. Newmar (1952) proposed a new initial cell which functions as a meristem shoot apical.

They believed that the distal group of cells at the shoot apex, are relatively inert and do not divide during the vegetative growth. This inert zone is termed as waiting meristem (*meristeme d'attente*); because it becomes active only during reproductive stage. The peripheral meristem (*anneau initial*) alone play main role in building the shoot. This theory was challenged by many workers, because it considers *meristeme d'attente* as waiting meristem which was previously regarded as apical initials.

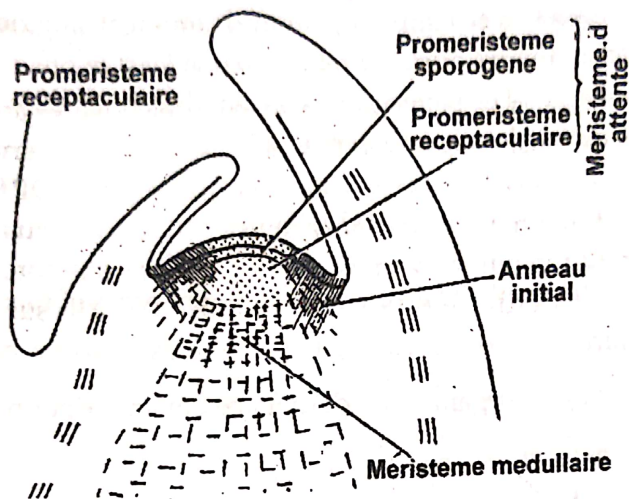


Fig. 1-11 : Shoot apex of dicot : Waiting meristem theory

5. Newman's Concept :

Newman (1965) believed that there is nothing like a group of permanent initial cells in the shoot apex. Instead, there is a sequence of meristematic cells which function as initials over a period of time. He called them as **continuing meristematic residue**. On the basis of the form of this meristem, he classified shoot apices into three main types.

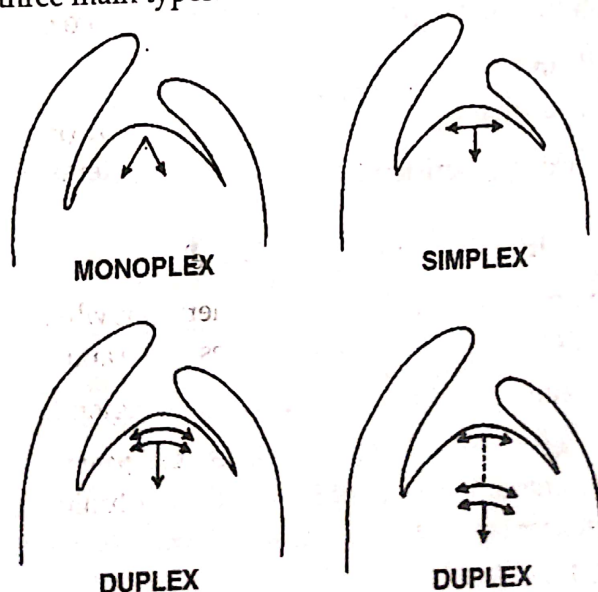


Fig. 1-12 : Types of shoot apices

1. **Monoplex type** : This type is found in ferns and their related genera. The meristem is represented by the superficial layer which is pointed inwardly. Only single division is needed for growth, both in length and breadth.

2. **Simplex type** : It is commonly found in gymnosperms. This type is characterized by a parallel - sided meristematic residue which is limited to the superficial layer. These cells divide both by anticlinal and periclinal walls, but their divisions are restricted to a single layer.

3. **Duplex type** : It is commonly found amongst angiosperms. Here the continuing meristematic residue is parallel sided at least in one superficial layer and in one successive layer. The superficial layer divides anticlinally and the inner layers of cells divide both anticlinally and periclinally.

Questions

1. Define meristems. Write an essay on different types of meristems.
2. Describe various theories relating to the organisation of root tips.
3. Give the details of organisation of root apex in angiosperms.
4. Write short notes on :
 - (i) Apical Cell Theory.
 - (ii) Korper - Kappe Theory.
5. Explain different types of meristematic tissues of root apex.
6. Give a detailed account of organisation of Shoot apex in Angiosperms.
7. Describe various theories proposed relating to the shoot apex.
8. Write short notes on :
 - (a) Apical cell theory.
 - (b) Histogen theory.
 - (c) Tunica-Corpus theory.
 - (d) Theory of waiting meristem.

(v) **Trichosclereids** : These are found in the intercellular spaces in the leaves of hydrophytes, and in the aerial roots of *Monstera* and in the leaves of *Onice* (Cela sp.).

[B] Complex Tissues :

Tissues in which different kinds of cells perform a common function are called **complex tissues**. They are composed of two or more cell types (heterogenous). **Xylem** and **Phloem**, which together form the vascular tissue, are the two principal types of complex tissues.

[I] Xylem (Xylos = wood) :

Xylem is the principal water conducting tissue in all vascular plants. It is closely associated with phloem both structurally and functionally and together form the vascular system throughout the plant body. Further, xylem also provides mechanical support to the plant organs.

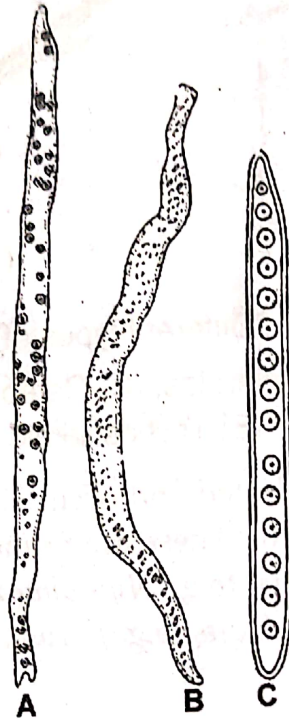


Fig. 2:12 : Tracheids from Xylem (A) *Aristolochia*, (b) *Ephedra*, (C) *Pinus*

Xylem originates from two sources :

1. *Procambium* of apical meristem, which gives rise to the *primary xylem* (Present in vascular bundles) and
2. *Vascular cambium*, which gives rise to the *secondary xylem* during secondary growth. Most of the wood in a stem is composed of secondary xylem.

The first formed primary xylem elements are called **protoxylem** and the latter found elements are called **metaxylem** elements. Protoxylem elements usually have tracheary elements embedded in wood parenchyma. These elements are subjected to stress and disorganise during secondary growth. The metaxylem possesses fibres

in addition to tracheary elements and wood parenchyma. It becomes non-functional after secondary growth and is usually not destroyed. In those plants, where secondary growth does not take place, metaxylem continues to function.

Structure :

Xylem is composed of three principal types of cells. They are - (1) Tracheary elements (tracheids and vessels) (2) Xylem fibres and (3) Xylem parenchyma. Among these, except parenchyma, all other elements are thick-walled and dead.

1. Tracheary elements :

These are the chief conducting elements of water and mineral salts in the plant body. Besides, they also give mechanical support.

Tracheary elements can be recognised into two types : *Tracheids* and *Vessels*.

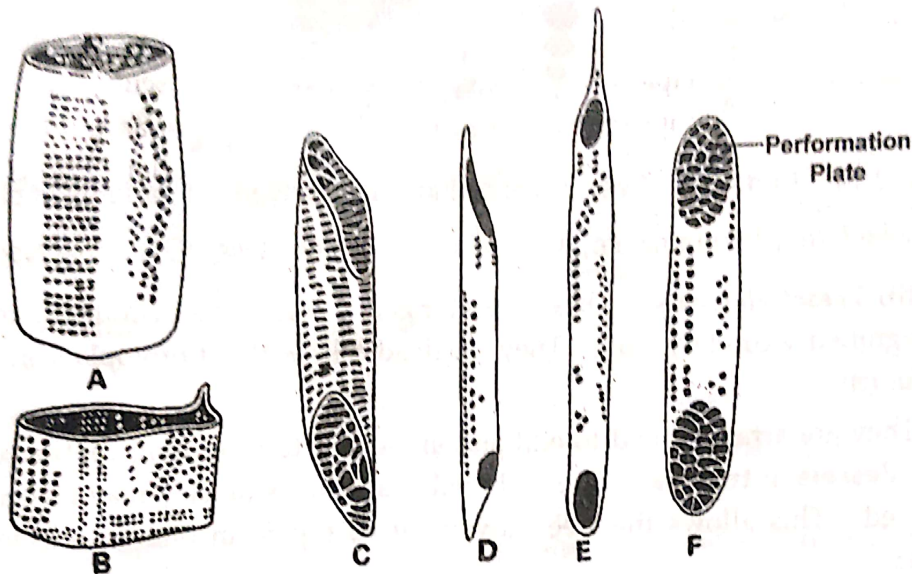


Fig. 2-13 : Different types of Vessels

(A-B) Wide vessels with simple perforation plate.

(C) Vessel with scalariform perforation

(D-E) Narrow Vessels with simple perforation plate

(F) Narrow vessel with reticulate perforation plate.

(i) **Tracheids** : These are elongated tube-like cells with broad middle part and sharp tapering ends. The cell wall is thick, lignified and consists of bordered pits in pairs on their common walls. They are dead cells and have no protoplasm. The inner space (lumen) is narrow and empty. In a transverse section, the tracheid may appear angular, circular or polyhedral in shape. The secondary wall material is deposited in various ways viz., annular, spiral, scalariform, reticulate and pitted.

In vascular bundles, the tracheids are arranged in parallel rows with partial overlapping and are intertwined to form continuous strands. The continuity between the overlapping tracheids is maintained through pit pairs present on their common walls. The conduction of water and dissolved mineral salts occurs through the cell lumen and through bordered pits. The perforations at the end of tracheid cells are absent.

Phylogenetically, tracheids are primitive to xylem vessels, because they are found in lower vascular plants like pteridophytes and gymnosperms. They are found in angiosperms also, associated with vessel members.

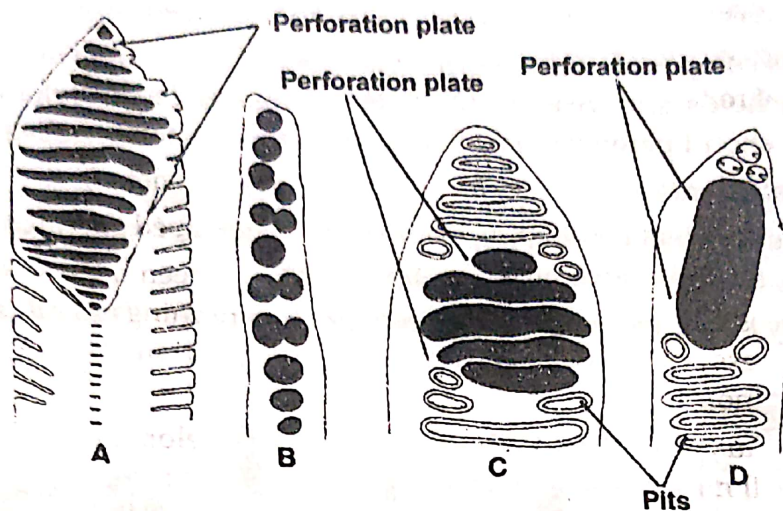


Fig. 2-14 : End walls of vessels showing various types of perforation plates.

(A) Scalariform, (B) Foraminate, (C) Scalariform type of *Vitis*, (D) Simple type of *Vitis*

(ii) **Vessel elements** : These are elongated, wide and cylindrical cells with thick lignified secondary walls. They are dead cells without protoplasts and show a wide lumen.

They are arranged end-to-end and are joined to form long continuous tubes called **Vessels** or **tracheae**. The end walls have holes or they may be completely dissolved. This allows the free movement of sap from one vessel element to another.

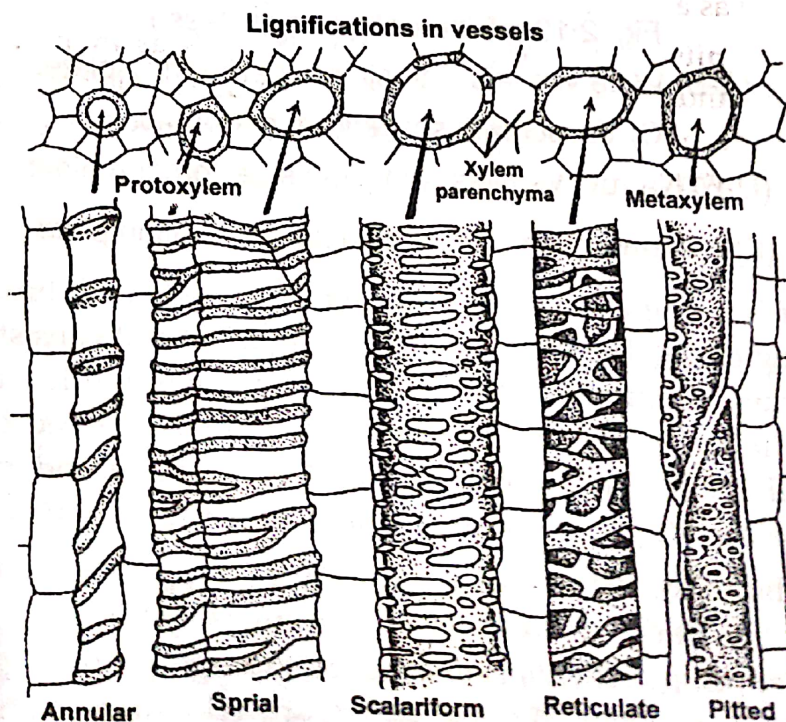


Fig. 2-15 : Wall thickening of vessel elements

TISSUES AND TISSUE SYSTEMS

The end wall has perforation (pore) perforation plate and

There are several plates. They are :

(a) Scalariform

(b) Reticulate

(c) Foraminate

Simple perforation plate frame work. V. phylogenetically

The second patterns. The w.

(i) Annular

(ii) Spiral

(iii) Reticulate

(iv) Scalariform

(v) Pitted

the primary wall

(iii) Ty

Bordered pits.

(a) Simple

secondary cell

(b) Bordered

over the pit

bordered pits

thickened and

The end wall bearing holes is called **perforation plate**. It may have a single perforation (pore) or several perforations (pores). They are known as *simple perforation plate* and *multiple perforation plate* respectively.

There are several ways in which pores are arranged in multiple perforation plates. They are :

(a) **Scalariform** : Pores are elongated and arranged in parallel rows. e.g. *Liriodendron*.

(b) **Reticulate** : Pores are arranged in the form of a network.

(c) **Foraminate** : Pores are almost circular and grouped together. e.g. *Ephedra*.

Simple perforation plates are considered to have been derived from multiple perforation plates by the loss of secondary wall thickenings from the secondary frame work. Vessels with transverse end walls and simple perforations are phylogenetically more advanced.

The secondary walls of tracheary elements develop in a wide variety of patterns. The wall material is deposited in various ways :

- (i) Annular thickenings - ring like thickenings
- (ii) Spiral thickenings - continuous helicals (springs)
- (iii) Reticulate thickenings - net-work like thickenings
- (iv) Scalariform thickenings - Ladder like deposition
- (v) Pitted thickenings - secondary wall material is deposited completely on the primary wall except for certain unthickened circular areas known as pits.

(iii) **Types of pits** : Pits are of two types. They are (a) Simple pits and (b) Bordered pits.

(a) **Simple pits** : The pit cavities are uniformly wide and are not enclosed by secondary cell wall as an arch - like structure.

(b) **Bordered pits** : The secondary cell wall bends as an arch - like structure over the pit cavity and gives a border - like appearance. Hence, these are called **bordered pits**. The portion of the middle lamellum crossing the pits becomes thickened and is known as **torus**.

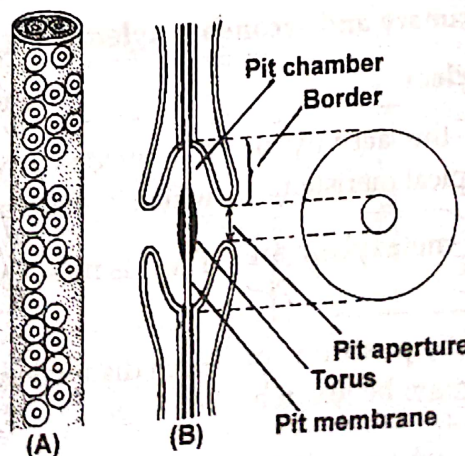


Fig. 2-16 : Bordered Pits

(A) Surface view, (B) Sectional View

Pits generally develop in pairs, i.e., when a pit is present on the secondary wall of one cell, a similar or dissimilar pit will be present on the opposite side of the adjacent cell. Such type of pits form a morphological and functional unit called *pit pair*.

(iv) **Distribution** : Vessels are the main elements of conduction in angiosperms and are phylogenetically more evolved than tracheids. However, vessels are absent in some primitive angiosperms like *Drimys* and *Trochodendron* (Ranales). These are called **vesselless angiosperms**. The vessels are normally absent in lower vascular plants. However, they can be seen in pteridophytes like *Selaginella*, and *Equisetum* and gymnosperms like *Gnetum*.

2. Xylem fibers :

Fibres present in the xylem are called xylem fibres. They are found both in primary and secondary xylem. They have thick lignified walls and reduced pit borders in comparison to tracheids. Xylem fibres give mechanical strength to the vascular bundles.

Xylem fibres are of two main types : (1) **Libriform fibres** and (2) **Fibre tracheids**. *Libriform fibres* are true fibres belonging to the sclerenchyma and possess simple pits on their walls. The *fibre tracheids* originate from non functional tracheids by reduction and show bordered pits on their walls.

3. Xylem parenchyma :

Parenchymatous cells are present both in primary and secondary xylem. They form a major part of primary xylem. The cells are arranged in longitudinal rows (axial parenchyma). In secondary xylem, the xylem parenchyma is of two types : (i) axial or wood parenchyma and (ii) Ray parenchyma.

Axial parenchyma develops from *fusiform cambial initials* along with other tracheary elements. These cells are characteristically arranged in vertical rows and are placed end to end.

Ray parenchyma is arranged in radial transverse series and develops from the *ray initials* of the cambium. The xylem parenchyma cells are useful in storage of food materials such as starch, oils and fats. The ray parenchyma is concerned with radial conduction of water.

Differences between primary and secondary xylem :

Primary Xylem	Secondary Xylem
1. It is formed by the activity of procambium of apical meristem.	It develops from vascular cambium, which is a lateral meristem.
2. Protoxylem and metaxylem are distinct.	There is no such distinction.
3. Depending upon position of protoxylem, it may be exarch, endarch or mesarch.	Such distinction is not observed.
4. Tracheids and vessels are relatively narrow and longer.	Both are normally wide and short.

Primary Xylem	Secondary Xylem
5. Parenchyma is not differentiated into axial and ray parenchyma.	The two systems are clearly distinct and well marked.
6. Vessels lack tyloses.	Old vessels show tyloses.
7. Xylem fibres are either absent and if present, these are very few in number.	Xylem fibres are found abundantly.
8. Madullary rays of this region are derived from apical meristem.	Secondary medullary rays arise by the activity of ray initials of cambial ring.

II Phloem :

Like xylem, phloem is also a complex tissue that conducts organic solutes from the leaves to the other parts of the plant body. It is also known as **leptoma** or **bast**. The term '**Phloem**' was coined by Harting in 1837.

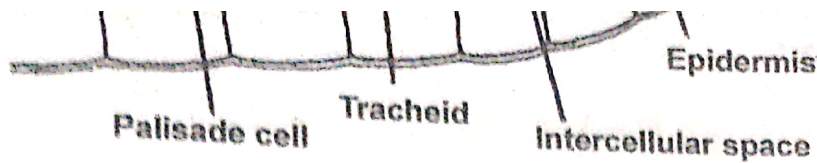


Fig. 2-26 : Hydathode in T.S.

6. Laticiferous tissue :

Laticifers are specialized parenchyma cells which secrete a viscous fluid, known as *latex*. Latex is mostly white in colour, but may be yellow (e.g. Pappaveraceae, Cannabinaceae) or colourless (e.g. Moraceae). It is stored in the vacuoles and is released into the cytoplasm when the tonoplast is ruptured. The latex is an emulsion of proteins, carbohydrates, organic acids, salts, sterols, fats, tannins, resins, gums, alkaloids, enzymes and essential oils in colloidal solution.

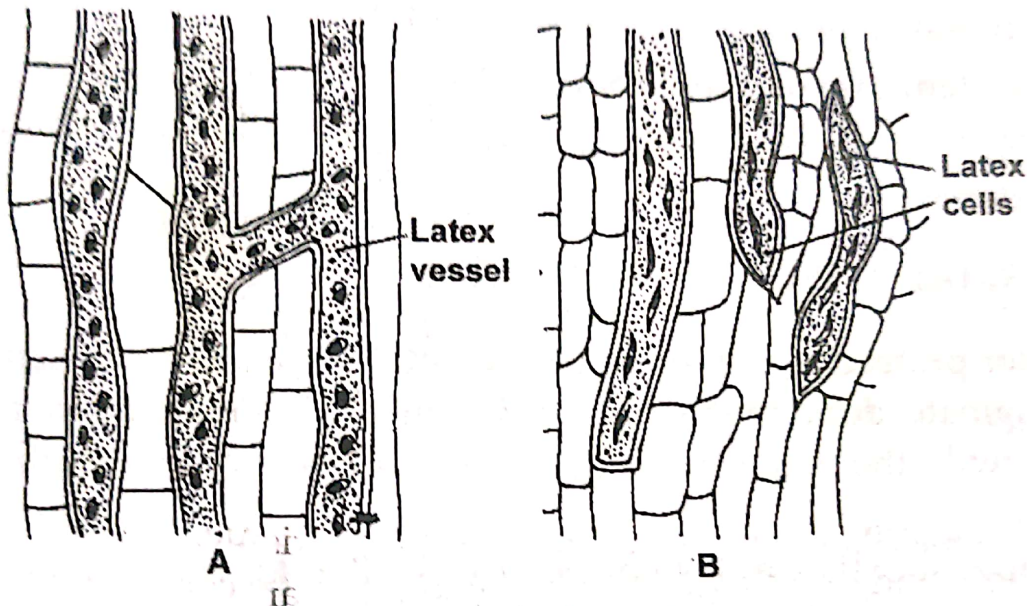


Fig. 2-27 : Laticiferous tissue

(A) Vessels (Carica), (B) Cells (Euphorbia)

Laticiferous tissue is widely distributed in tropical plants. They are living cells and occur almost every where in a plant body. Most commonly they are associated with the phloem. Laticifers are recognized into two types : laticiferous cells and laticiferous vessels.

(a) *Laticiferous cells* : They are isolated cells. They are elongated, slender, branched or unbranched. They are uninucleate in the beginning, but later become coenocytic due to nuclear divisions.

E.g. Apocyanaceae, Asclepiadaceae, Euphorbiaceae and Urticaceae.

(b) *Laticiferous Vessels* : They are formed by a series of cells whose end walls are dissolved to form continuous canals. Apparently, this structure resembles xylem vessels. The latex vessels may be unbranched (e.g. Musaceae, Convolvulaceae, Sapotaceae) or branched (e.g. Caricaceae, Compositae).

The latex is of great economic value. It is a source of enzyme Papain (*Carica papaya*), Opium (*Papaver somniferum*), chewing gum (*Achras sapota*), asafoetida (root stocks of *Ferula asafoetida*) and rubber. Indian rubber is manufactured from the latex of *Ficus elastica*. Whereas para rubber is manufactured from the latex of *Hevea brasiliensis*.

TISSUE SYSTEMS

Introduction :

The vascular plant body consists of different vegetative and reproductive organs. Each organ is made up of different types of tissues, which are organised into definite units, called *tissue systems*. The tissue system can be defined as "A group of tissues which perform similar functions, irrespective of position in the plant body".

According to Sachs (1875), the plant body is made up of three kinds of tissue systems. They are : (1) Epidermal tissue system ; (2) Ground tissue system, and (3) Vascular tissue system.

These systems are derived from three distinct zones of apical meristem. The outer *protodermal* zone gives rise to epidermal tissue system, *ground meristem* gives rise to ground tissue system and *procambium* gives rise to vascular tissue system.

EPIDERMAL TISSUE SYSTEM

Unit-I

3. ANOMALOUS SECONDARY GROWTH

3-1 INTRODUCTION

Anomalous secondary growth is the result of deviation in the cambial activity from the normal type found in most of the dicotyledons. The abnormal secondary growth is commonly seen in tropical plants than in temperate plants.

In some cases, anomaly is related to the growth habit serving its physiological needs. Then it is known as **adaptive anomaly** and is seen in many woody climbers. In other cases, the variation is not of any functional advantage to the plant. In such case, it is called **non-adaptive anomaly**. e.g. Herbaceous plants like *Amaranthus*, *Achyranthes*, *Boerhaavia* etc.

3-2 ANOMALOUS SECONDARY GROWTH IN DICOTYLEDONS

On the basis of cambial activity and distribution of secondary tissues, abnormal secondary growth can be studied under the following heads.

1. Abnormal behaviour of normal cambium
2. Abnormal behaviour of abnormal cambium
3. Formation of accessory cambial rings
4. Formation of interxylary phloem.

I Abnormal behaviour of normal cambium :

In many woody climbers or lianas, the cambium is normal in position, but its activity is abnormal, and with the result anomalous structures are formed.

(1) In the stems of *Vitis* and *Clematis*, the cambium forms vascular tissue in the region of vascular bundles and parenchyma in between the vascular bundles. As a result of this, the original vascular bundles remain discrete throughout the secondary growth.

(2) In *Bauhinia rubiginosa* (Fa. Caesalpinaceae), the secondary vascular cylinder appears in the form of ridges and grooves. This is due to the abnormal activity of the cambium. At certain places, the cambium divides more actively, the result more secondary vascular tissues are produced in these areas. At other places, however, it is inactive or shows limited activity. Such a growth pattern results in the formation of ridged secondary vascular cylinder. In some species of *Bauhinia*, the cambial activity is restricted at the two opposite sides. Consequently the stem becomes flattened strap like structure.

(3) In the woody climbers of Bignoniaceae (e.g. *Adenocalymma*, *Bignonia*, *Doxantha*) furrows of secondary phloem are present in the cylinder of secondary xylem. In these plants, the cambium is normal in position and activity in the beginning. But very soon, the cambium cuts off different proportions of xylem

ANOMALOUS SECONDARY GROWTH
phloem at four points, the
cambium forms little or
As a result, the woody
These furrows are filled

Fig. 3-1: Diagram

phloem at four points, arranged in the form of a cross. At these four points, the cambium forms little or no xylem and on the outside extensive amount phloem. As a result, the woody cylinder appears to be deeply furrowed at these points. These furrows are filled with secondary phloem.

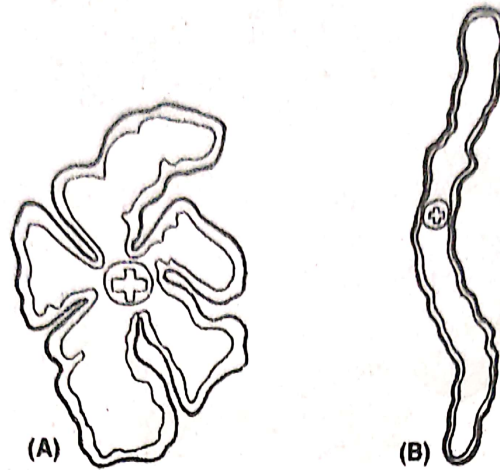


Fig. 3-1: Diagrammatic representation of transverse sections of stem

(A) *Bauhinia rubiginosa*, (B) *Bauhinia* sp

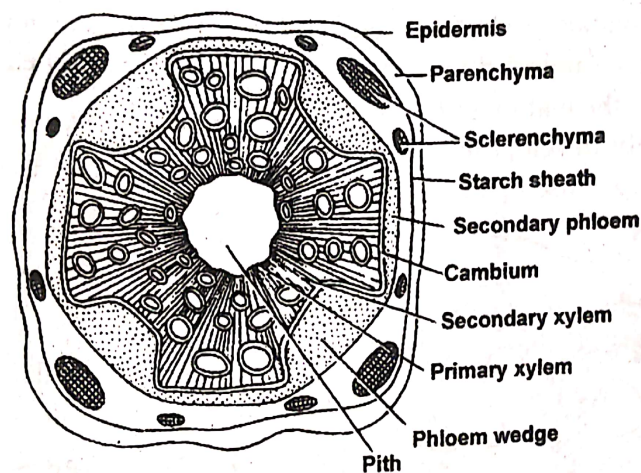


Fig. 3-2 : T.S. of *Bignonia* stem

Initially four furrows of phloem are formed, but in the older stems, additional furrows may be formed. They occur either between the existing furrows as additional sets of four or directly adjacent to the existing furrows. The woody cylinder which is furrowed due to phloem makes the stem stronger and flexible. This is anomaly adapted to the climbing habit.

II Abnormal behaviour of abnormal cambium :

In some plants, an abnormal cambium originates either in the cortex or pericycle and results in the formation of anomalous structures. In these stems either the normal cambial ring does not develop at all or soon loses its activity.

(1) In the young stem of *Thinouia ventricosa* (Sapindaceae), the cambium appears as a folded structure, instead of a circular ring. As the secondary growth proceeds, the cambium at the folds become constricted and gets separated. Each

cambial piece independently forms secondary vascular tissues. Consequently, the secondary growth becomes abnormal with several distinct steles, each with its own secondary xylem and phloem. As a result, the mature stem gets a peculiar shape.

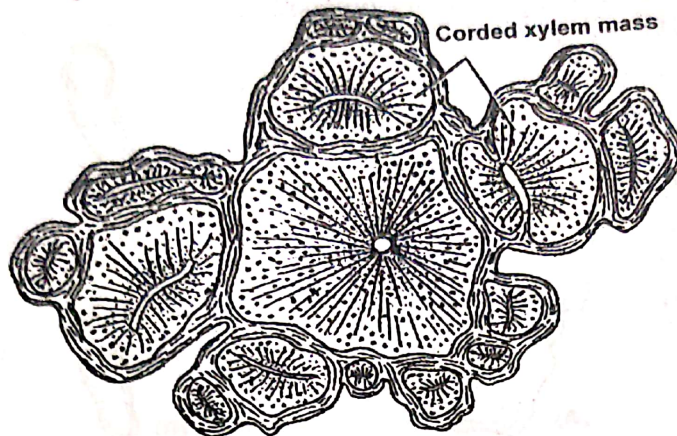


Fig. 3-3 : T.S. of stem of *Thinouia ventricosa*

(2) In some tendril climbers like *Serjania corrugata* and *Paullinia* (Sapindaceae) the primary stem shows individual strands of xylem surrounded by separate strip of cambia. As secondary growth proceeds, each strip of cambium forms almost separate ring. These cambial rings function normally producing secondary xylem and phloem. Thus, the mature stem shows several discrete vascular cylinders each of which ultimately develops its own periderm. This gives the appearance of several separate stems fused together like the strands of a rope.

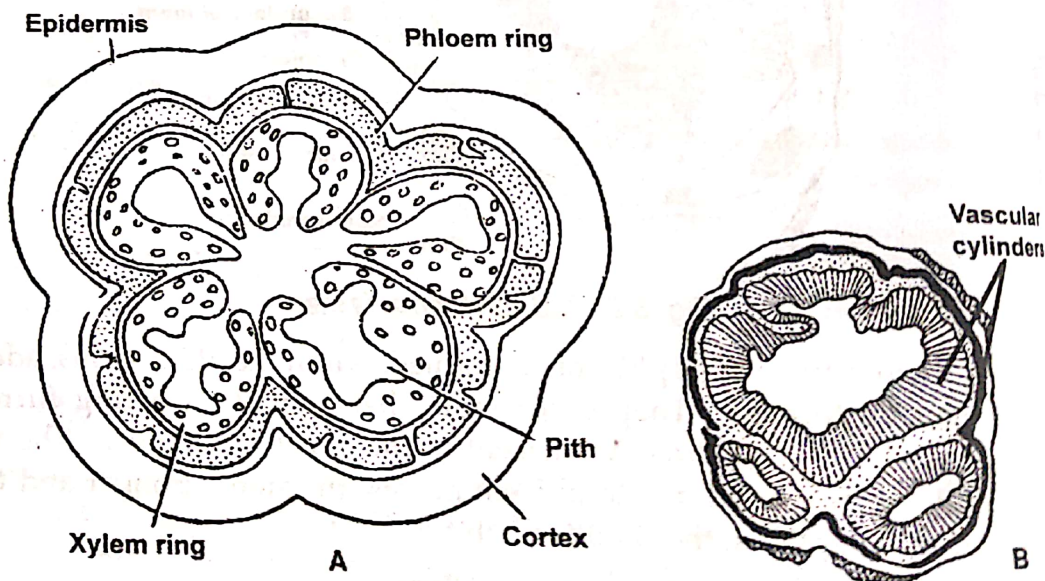


Fig. 3-4 : T.s. of stem - (A) *Serjania corrugata*, (B) *Paullinia*

III Formation of accessory cambial rings :

In many dicotyledons, several rings of cambia arise successively in centrifugal manner. The abnormal cambium develop either in the cortex or pericycle after the primary cambium ceases to function (e.g. *Boerhaavia*) or does not develop at all (e.g. *Amaranthus*).



Fig. 3-5 : T.S.



Fig. 3-6 :

(1) In *Boerhaavia* (e.g. *Mirabilis* etc.) normal secondary growth is limited quantity of secondary growth in central region, either bidirectionally produced. The secondary growth is relatively thin wall of conjunctive tissue fusiform and more cortex in the form of concentric rings of

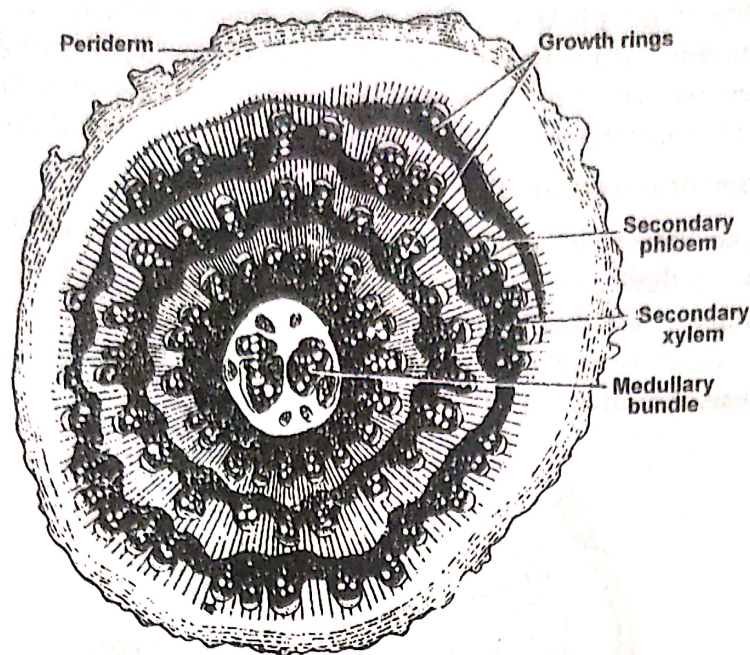


Fig. 3-5 : T.S. of old stem of *Boerhaavia* showing four growth rings

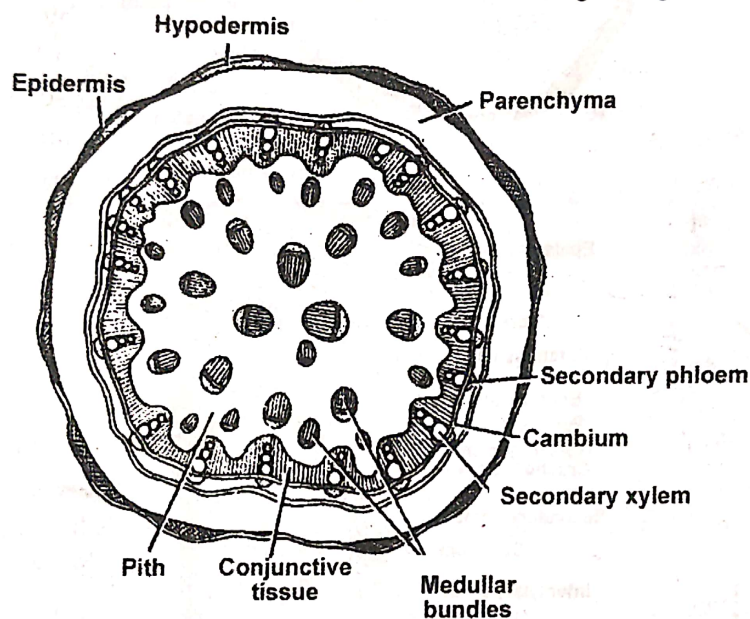


Fig. 3-6 : T.S. of *Mirabilis* stem showing concentric rings of VBs.

(1) In *Boerhaavia* and other members of Nyctaginaceae (e.g. *Bougainvillea*, *Mirabilis* etc.) normal vascular cambium ceases to function after the production of a limited quantity of vascular tissues. New cambial rings are initiated outside the central region, either in the pericycle or cortex. Each cambium ring functions bidirectionally producing thick walled xylem tissue alternating with the bands of relatively thin walled conjunctive tissue towards the innerside, and phloem and conjunctive tissue towards outside. The cells of the conjunctive tissue are fusiform and more or less radially arranged. Thus, they remain distinct from the cortex in the form and arrangement of cells. As a result of secondary growth, concentric rings of vascular bundles are formed embedded in the conjunctive tissue.

(2) In the stems of *Amaranthaceae* (e.g. *Amaranthus*) the normal ring of cambium is absent. At the time of secondary growth, pericycle gets activated and forms the accessory cambium. This cambium shows abnormal activity and forms a ring of conjoint, collateral vascular bundles embedded in the parenchyma.

IV Formation of Interxylary Phloem :

It is also called *included phloem* and is seen in about 25 families of dicotyledons. In these plants, islands of secondary phloem are formed embedded in the secondary xylem due to abnormal activity of cambium. e.g. *Malpighiaceae*, *Oleaceae*, *Combretaceae*, *Gentianaceae*, *Salvadoraceae*, *Loganiaceae*, *Asclepiadaceae*, *Acanthaceae* etc.

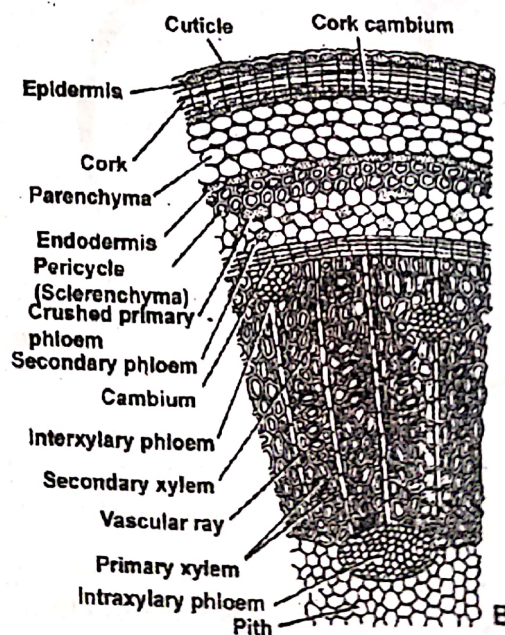
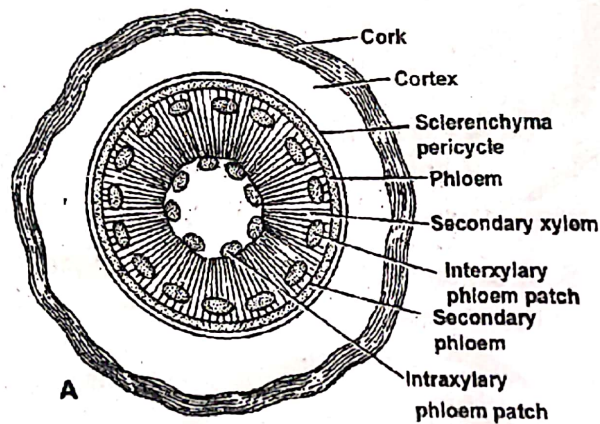


Fig. 3-7 : T.S. of *Strychnos* stem showing inter- and intraxylary phloem patches

(A) Diagrammatic, (B) Sector

(1) In *Strychnos* (*Loganiaceae*), the cambium first functions normally producing secondary vascular tissues. Subsequently, small segments of cambium cease their function and their cells are converted into phloem. The continuity of the main ring of cambium is thus interrupted. Thereafter, complementary segments of cambium then arise as a secondary meristem in the pericycle or in the peripheral region of

ANOMALOUS SECONDARY

phloem above the non-functional strips of cambium join with the formed. Soon this cambium produces secondary xylem towards the inner side. In this process, patches of secondary



Fig. 3-8

(2) In plants like *Achyranthes*, included phloem arises in a different manner. It arises in a different side. Subsequently, at the time of secondary growth, it moves towards the inner side of the secondary xylem and soon the cambium produces secondary xylem elements towards the inner side. Consequently a number of patches of secondary xylem are formed in the secondary xylem.

Included phloem is a secondary meristem. It possesses it. In such plants, the cambium produces long summer dormancy. It is functional to carry food

ANOMALOUS

Achyranthes Ster

A cross section of a single-layered cons... outside. The epidermis, hypodermis, genera

phloem above the non-functional segments of the cambium. These newly formed strips of cambia join with those of the normal cambium. Thus a wavy cambium is formed. Soon this cambial cylinder starts functioning normally i.e., producing secondary xylem towards inner side and secondary phloem to the outer side. In this process, patches of secondary phloem become included in the secondary xylem.

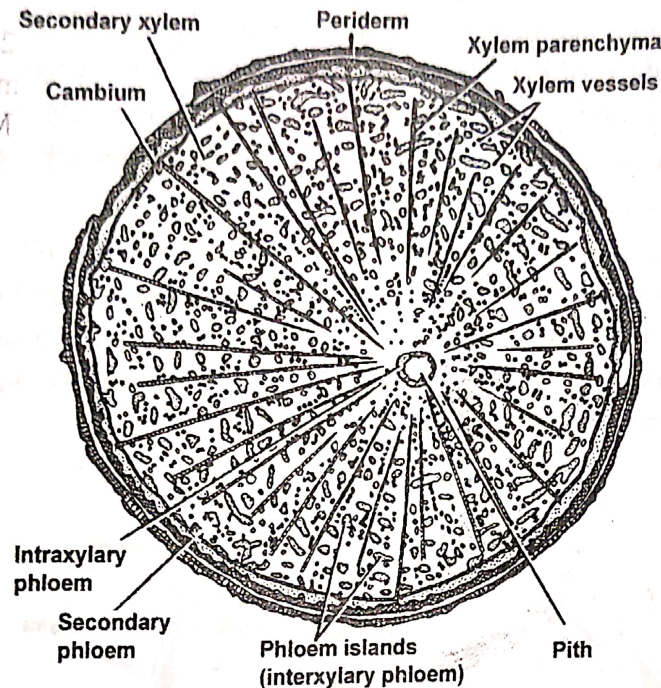


Fig. 3-8 : T.S. of Old stem of *Leptadenia sparatum*

(2) In plants like *Leptadenia*, *Combretum*, *Entada* and *Salvadora*, the included phloem arises in a different manner. The cambium first functions normally giving rise to secondary xylem to the inner side and secondary phloem towards the outer side. Subsequently, at certain points, the cambium begins to cut off phloem cells towards the inner side instead of secondary xylem. This is only a temporary phase and soon the cambium resumes its normal activity i.e., it starts producing secondary xylem elements towards the inner side. This process is repeated several times and consequently a number of islands of phloem are formed in the thick-walled cells of the secondary xylem.

Included phloem is of great significance to some xerophytic plants which possess it. In such plants, the external phloem and other tissues become dry during long summer drought conditions. In such cases, the included phloem remains functional to carry food to buds.

3-3 ANOMALOUS SECONDARY GROWTH IN SOME DICOTS

I Achyranthes Stem (Fam. Amaranthaceae)

A cross section of young stem shows ridges and furrows. The epidermis is single-layered consisting of tabular cells. It is covered by a thick cuticle on the outside. The epidermal hairs are long and multicellular. The cortex shows hypodermis, general cortex and endodermis. Below the epidermis, alternating

groups of collenchymatous and chlorenchymatous cells are present. Collenchyma is well developed inner to the ridges. The general cortex shows colourless parenchyma cells having few intercellular spaces. Endodermis is not very distinct, and is made up of thin walled cells.

Pericycle lies inner to the endodermis. It consists of perivascular fibres (sclerenchyma) and parenchyma. The normal ring of vascular bundles are separated by wide medullary rays of parenchyma. The bundles are conjoint, collateral, endarch and open. The phloem is towards the outer side and xylem towards the inner side. A distinct strip of cambium is present between phloem and xylem.

In addition to normal ring of vascular bundles, two medullary bundles are present. They lie opposite to each other. In *A. aspera*, the two bundles may remain free throughout the length of the plant or may be fused in the lower internode. When there is fusion, the two bundles form a single *amphixylic* vascular bundle (phloem in the centre and xylem on its either side).

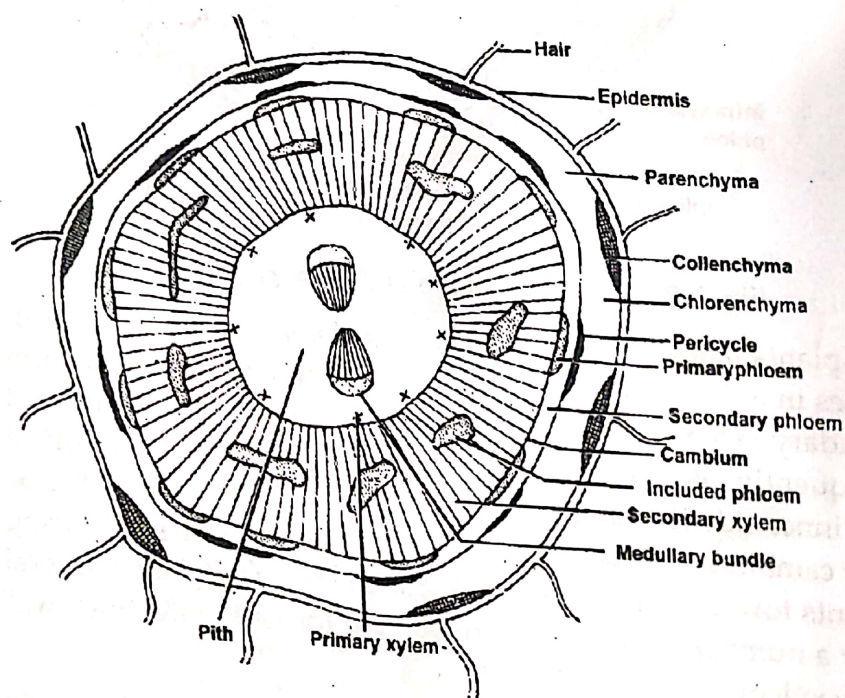


Fig. 3-9 : Diagrammatic representation of transverse section of the stem of *Achyranthes*

Secondary growth :

The primary vascular bundles are in a ring inner to pericycle. Strips of cambium arise between these bundles and join the intrafascicular cambium of adjacent vascular bundles forming a ring. The activity of this cambium is like that of *Boerhaavia* stem. The intrafascicular cambium forms secondary xylem towards the inner side and secondary phloem towards the outside. Its activity is very limited. The interfascicular cambium forms conjunctive tissue between the bundles. The conjunctive tissue between the secondary xylem masses is formed of thick lignified walls.

ANOMALOUS SECONDARY GROWTH

An extra-stelar cambium produces vascular bundles which are produced by the cambium. As a result, bundles appear as distinct. These bundles are mistaken as *interxylary* bundles by the activity of cambium.

Pa
Pericycle sc
Prim
Seco

Sec
Inter

Medullar

II Boerhaavia Stem

A young stem has a ring of vascular bundles.

The primary vascular bundles occur in a ring.

(a) The inner part of the stem is parenchymatous pith.

(b) The middle part of the stem is formed of thick lignified walls.

An extra-stelar cambium appears in the pericycle. It produces secondary vascular bundles which at first remain irregularly scattered. The conjunctive tissue produced by the cambium becomes lignified. So the secondary vascular bundles lose their identity. As a result, the thin walled phloem of the secondary vascular bundles appear as distinct patches in the secondary lignified tissue. Hence it is mistaken as *interxylary* or *included phloem*. The medullary bundles increase in size, by the activity of cambium.

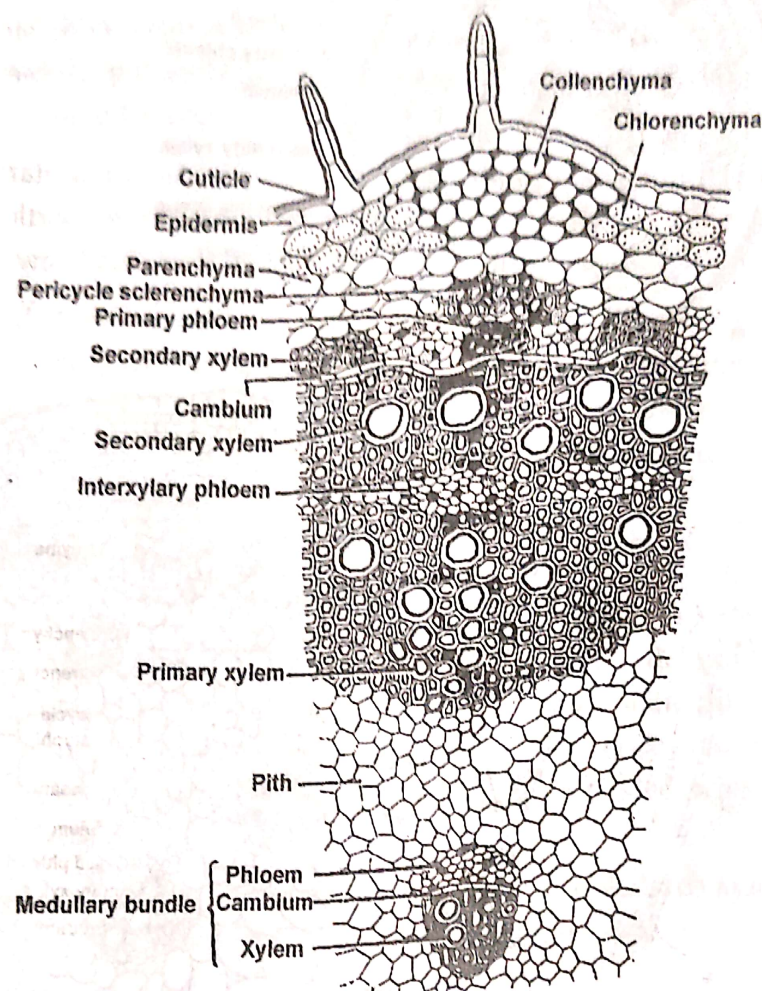


Fig. 3-10 : T.S. of *Achyranthes* stem

II *Boerhaavia* Stem (Fam. Nyctaginaceae)

A young stem of *Boerhaavia* shows abnormality in possessing medullary vascular bundles. A transverse section shows epidermis, collenchymatous hypodermis, parenchymatous cortex, endodermis and single layered pericycle. The pericycle consists of parenchymatous cells with isolated patches of sclerenchyma.

The primary vascular bundles are conjoint, collateral, open and endarch. These bundles occur in three concentric rings.

(a) The inner most ring consists of two large vascular bundles present in the parenchymatous pith. They lie opposite to each other with their protoxylem facing each other.

(b) The middle ring consists of 6 - 14 small vascular bundles.

(c) The outer ring consists of 15 - 20 smaller vascular bundles. These are normal vascular bundles. Whereas the middle and inner rings of bundles are considered as medullary bundles.

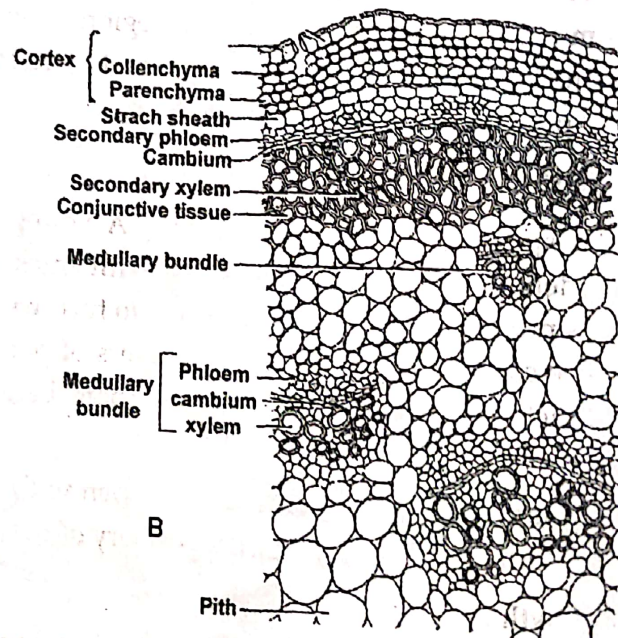
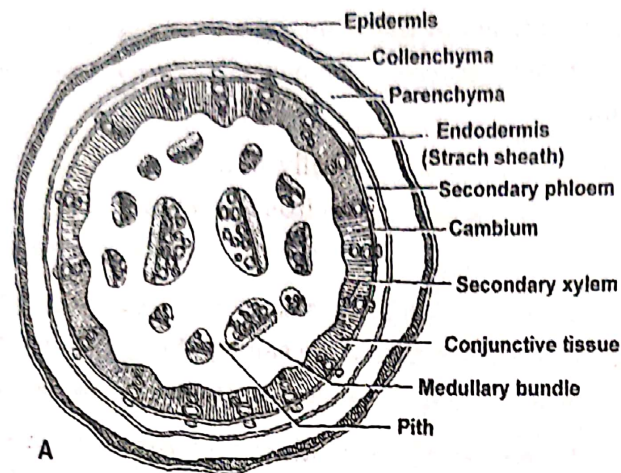


Fig. 3-11 : T.S. of *Boerhaavia* stem - (A) Diagrammatic, (B) Detailed structure

Secondary Growth :

During secondary growth, the two central bundles and the middle ring bundles increase in size to a limited extent by the activity of fascicular cambium. Inter-fascicular cambium do not develop.

The outer ring of vascular bundles is responsible for most of the secondary growth in the stem. The fascicular and interfascicular cambial strips unite to form a complete cambial ring. This cambial ring behaves in an unusual manner.

The cambium produces secondary xylem vessels towards the innerside and secondary phloem towards the outside only in the fascicular region. In between the bundles, the inter fascicular cambium produces thick walled parenchyma cells to

innerside and thin walled parenchyma cells to the outside. The thick walled cells formed inbetween the secondary xylem vessels is called the **conjunctive tissue**. After sometime, this cambium ring stops its activity.

Then, a new cambial ring is formed external to the secondary phloem. The parenchymatous cells and pericycle cells take part in the formation of second cambial ring. This cambial ring is called *accessory cambium*.

The accessory cambium behaves normally and produces secondary xylem towards innerside and secondary phloem towards the outside. In between them conjunctive tissue is formed.

After a period of activity, this cambium also stops its function. Another ring of cambium arises outside which behaves in the same pattern. In this manner, 4 - 5 successive rings of collateral bundles are produced embedded in conjunctive tissue.

As secondary vascular tissues are produced in the stelar region, a new protective covering, the **periderm**, is produced in the cortex region. **Phellogen** or **cork cambium** is initiated in the hypodermal region. It produces *phellem* or *cork* to the outside and *phelloderm* or *secondary cortex* to the innerside. The phellem, phellogen and phelloderm constitute the *periderm*.

III Bignonia stem (Fam. Bignoniaceae).

Bignonia species are woody climbers. A young stem shows ridges and furrows. Epidermis is the outermost layer with thick cuticle on its outside. Collenchyma is prominent below the ridges and in furrows, some chlorenchyma may be present. The cortex is made up of a few layers of parenchyma. Endodermis is not very distinct. The pericycle shows alternate bands of sclerenchyma and parenchyma.

The vascular bundles are collateral, and open with endarch xylem. They are arranged in the form of a ring around the periphery of the pith.

Secondary Growth :

The inter-and intra fascicular cambial strips become active to form the normal ring of cambium. In the initial stages, the cambium behaves normally and produces more secondary xylem and less secondary phloem.

Subsequently, at four points, the cambium begins to produce more of secondary phloem on the outside and relatively small amount of secondary xylem on the innerside. This results in the formation of four deep wedges of phloem projecting into the secondary xylem. So the secondary xylem appears to be ridged and furrowed.

The cambial ring breaks up into a number of strips due to this anomalous behaviour. Some cambial strips occupy the base of the phloem wedges and the remaining strips occur at the projecting edges of the xylem. Each phloem furrow is protected by bars of sclerenchyma which gives mechanical support against the crusting pressure of secondary xylem.

ANOMALOUS SECONDARY GROW	
3-4	ANOMALOUS SECOND

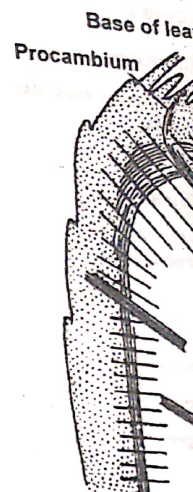
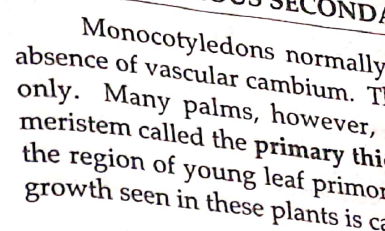


Fig. 3-13 : Diagrammatic showing

Secondary growth b in some woody *Liliflorae* develops in the parench vascular cambium of dico and conjunctive tissue to outside. The newly for *Dracaena*) or collateral (e

Primary structure
Liliaceae. A young stem
number of collateral an-

The cambium forms
in radial rows. The cells
the outside and the
outside are parenchyma

Periderm is produced in the cortex region, due to the activity of phellogen.

3-4 ANOMALOUS SECONDARY GROWTH IN MONOCOTYLEDONS

Monocotyledons normally do not show secondary growth because of the absence of vascular cambium. Therefore, the plant body consists of primary tissues only. Many palms, however, develop thick stems by the activity of a special meristem called the **primary thickening meristem**. This cambium originates below the region of young leaf primordia by periclinal divisions. This type of secondary growth seen in these plants is called **diffuse secondary growth**.

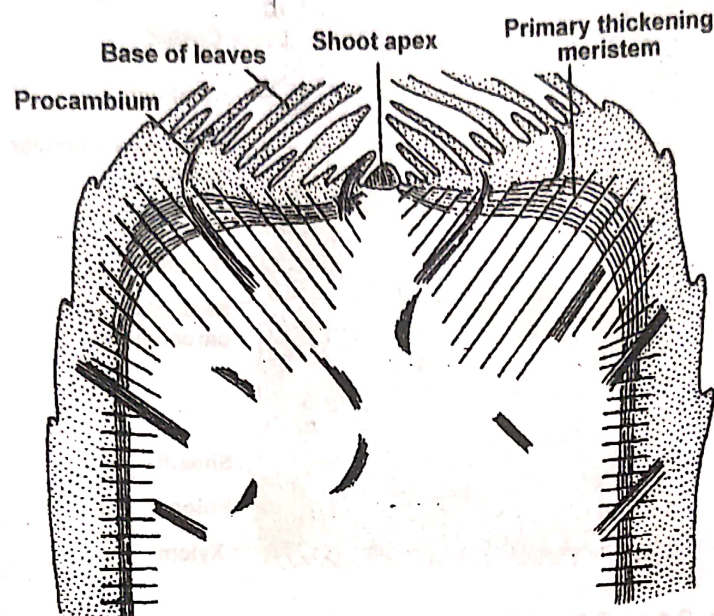


Fig. 3-13 : Diagrammatic representation of the upper part of monocot shoot (Palm) showing the meristems concerned with its growth

Secondary growth by means of special type of vascular cambium takes place in some woody *Liliiflorae* (e.g. *Agave*, *Dracaena*, *Yucca*, *Cordyline*). This cambium develops in the parenchyma outside the primary vascular bundles. Unlike the vascular cambium of dicotyledons, this meristem produces *secondary vascular tissues* and *conjunctive tissue* towards innerside and only a little parenchyma towards the outside. The newly formed secondary vascular bundles may be *amphivasal* (e.g. *Dracaena*) or *collateral* (e.g. *Kingia*).

I Anatomy of *Dracaena* stem :

Primary structure : *Dracaena* is an *arborescent* plant, belonging to the family Liliaceae. A young stem shows typical monocotyledonous structure. It has a number of collateral and closed bundles, scattered in the ground tissue.

Formation of Cambium : During secondary growth, the parenchymatous cells external to the primary vascular bundles become meristematic and function as cambium. The cambium is formed in the region of the stem which has ceased to elongate.

The cambium forms a continuous ring. The cells are rectangular and arranged in radial rows. The activity of this cambium is abnormal as it cuts off a few cells on the outside and more cells on the inner side. The cells produced towards outside are parenchymatous in nature.

The cells produced towards the inside are partly *parenchymatous* and partly *vascular* in nature. These parenchyma cells develop thick walls and transform into *conjunctive tissue*.

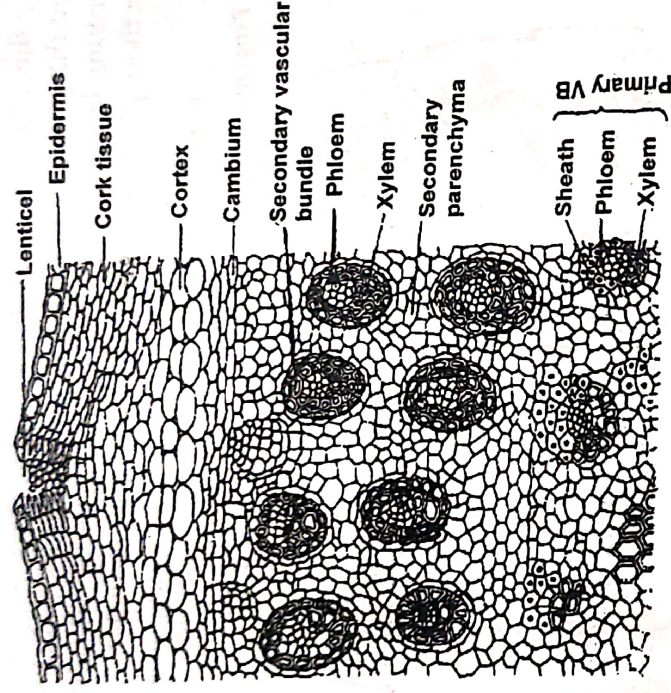


Fig. 3-14 : T.S. of Stem of *Dracaena* showing secondary growth

Formation of Bundles : Each vascular bundle develops from a single *cambium* initial. This initial divides first by anticlinal walls to form a row of 2 - 3 cells. These cells further undergo periclinal divisions to form *peripheral* and *central* cells. Later divisions are irregular and results in the formation of a group of cells.

The centrally placed cells of this group metamorphose into phloem strands whereas the peripheral cells differentiate into *xylem elements*. This leads to the development of a *leptocentric* or *amphivasal* vascular bundle, where the central phloem is surrounded by peripheral xylem vessels. Around each vascular bundle, a sclerenchymatous sheath is formed.

Formation of cork : After some time, the outer protective covering is formed. The cork cambium is initiated below the hypodermis. It forms cork or phellem on the outside and secondary cortex on the inside. In transverse section, the cells of the cork gives storied appearance and hence called *storied cork*.

Questions

1. Give an illustrated account of anomalous secondary growth found in dicotyledonous stems.

2. Describe the process of Boerhaavia.
3. Write an illustrated account of the process.
4. Describe the anatomy of the stem.
5. Write short notes on :
 - (a) Secondary growth
 - (b) Anomalous secondary growth
 - (c) Accessory cambium

- (3) Timbers are used in constructions because of their light weight and low cost values.
- (4) Timbers are used for decorative appearances as well.
- (5) The second grade timber is used for making doors, windows, window frames, grills etc.
- (6) The inferior Quality Timber is used for making Boxes, Poles, Furniture, Sports Goods etc.

4-6	FEW IMPORTANT TIMBER - YIELDING PLANTS OF ECONOMIC IMPORTANCE
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I Teak :

Botanical Name	: <i>Tectona grandis</i>
Family	: Verbenaceae
Vern. Name	: Sagun (Hindi), Segun (Beng), Tekkamaram (Tam), Adaviteeku (Tel), Thekku (Malayalam).

Teak is one of the most important timber plants of the world. It is renowned for its durability and strength. Teak plant is native to India, Java, Sumatra and parts of Indonesian Archipelago.

In India, teak forests are chiefly found in Madhya Pradesh, Maharashtra, Gujarat, and Karnataka. Other teak producing states are Andhra Pradesh, Rajasthan, Uttar Pradesh, Tamil Nadu and Orissa. In Andhra Pradesh, teak forests occur in Adilabad, Karimnagar, Kurnool, Cuddaph and East Godavari districts.

Morphology : Teak plant is a large deciduous tree, reaching a height of 30m. with a girth of 2 to 4 m. The branches are quadrangular and pubescent. The leaves are opposite, simple and elliptical to obovate, 25 - 50 cm long and 20 - 40cm wide. They are rough and densely covered with reddish brown ramenta beneath. The flowers are small and arranged in large terminal panicles. They are bracteate, bisexual, hypogynous and pentamerous. The fruit is a hard, bony, 4 - lobed nut, about 1 cm in diameter. Seeds are usually one or two.

Cultivation : Teak is a fairly quick growing tree. It grows on different types of soils, but requires perfect drainage. It is a light demanding tree and requires free circulation of air. The plant thrives well at a temperature of 26°-30°C and an annual rainfall of 130-300 cm. Frost is harmful to teak. The growth is stunted if there is nitrogen deficiency in the soil.

For plantation, seedlings of teak are raised in the nursery beds in April - May. Teak seedlings do not thrive in shade. When the seedlings are about 30 cm. high, they are transplanted. A good quality of timber is obtained from 50 - 80 years old trees.

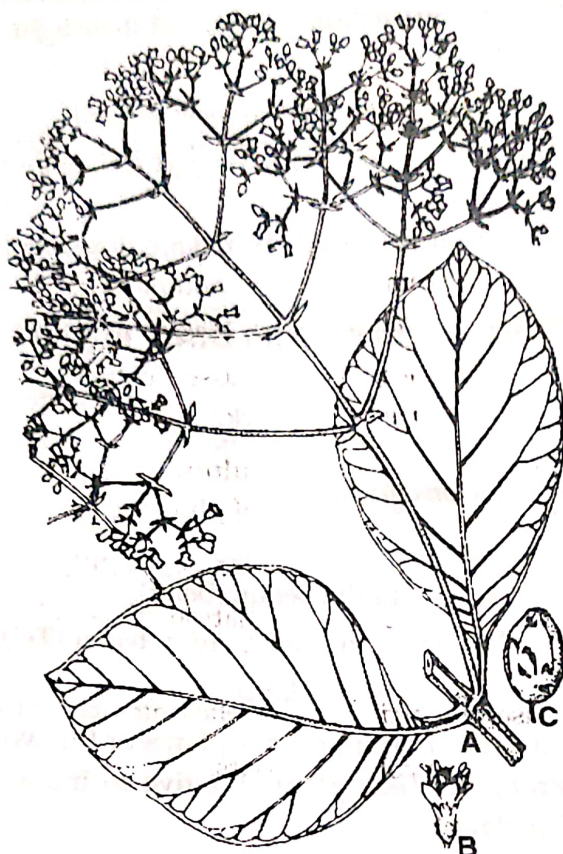


Fig. 4.1 : *Tectona grandis* (Teak) — (A) Twig; (B) Flower; (C) Fruit

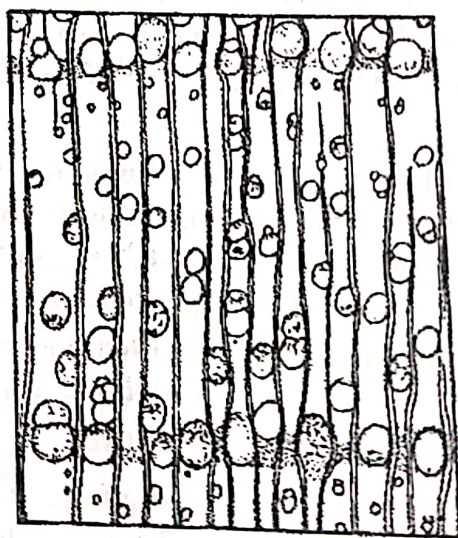


Fig. 4.2 : *Tectona grandis* : Wood

Properties of the wood : The timber is of excellent quality. It is moderately hard and very strong. It contains a characteristically scented oil, which acts as the preservative of the wood. The sapwood is white to pale yellowish and is susceptible to attack by termites and wood rotting fungi. The heartwood is golden-yellow, often with darker streaks. It turns to dark brown to black on exposure to air. The heart wood is relatively resistant to attack by pests.

STUDY OF TIMBER

The grain is normally straight, average weight is about 600 - 700 kg/m³, shows distinct growth rings, quite porous and is marked by the presence of medullary rays. The medullary rays are moderately distinct.

Uses of Teak :

- (1) The teak timber is extremely strong and is one of the best timbers for furniture, shipbuilding, etc.
- (2) It is widely used for posts, frames, planking and other construction work.
- (3) Teak is also used for making musical instruments and for decorative work.
- (4) The wood waste is used for fuel.
- (5) An oily product of the wood is used for the treatment of eczema.
- (6) The flowers are used for medicinal purposes.
- (7) The root bark is used for medicinal purposes.

II Rose Wood :

Botanical name

Family

Vern name

Indian Rose wood is found in the northwards through the Himalayas. The plant is found in deciduous forests of India and England as "Rose wood".

Morphology :

It has a straight trunk. Its leaves are alternate, simple, ovate. Flowers are small, white. The fruit is 1-3 seeds.

Properties :

The sapwood is white. The heart wood is dark brown to black. The heart wood is coarse textured. The weight is about 600 kg/m³.

The grain is normally straight, and the texture is very coarse and uneven. The average weight is about 600 - 700 Kg/m³ at 12% moisture content. The wood shows distinct growth rings, quite visible to the naked eyes. The wood is *ring-porous* and is marked by the presence of large vessels. Tyloses are quite common. The medullary rays are moderately broad and widely spaced.

Uses of Teak :

(1) The teak timber is extremely durable and hard and resists decay. It is one of the best timbers for furniture, cabinet work, wagons and railway carriages.

(2) It is widely used for poles, beams, trusses, columns, roofs, doors, window frames, planking and other constructional work.

(3) Teak is also used for making agricultural implements, sound boards of musical instruments and for different grades of plywood.

(4) The wood waste is the raw material for paper pulp.

(5) An oily product obtained by distillation of wood chips is used in the treatment of eczema.

(6) The flowers are used medicinally, for relieving kidney troubles.

(7) The root bark is used for colouring mats.

II Rose Wood :

Botanical name : *Dalbergia latifolia*

Family : Fabaceae

Vern name : Shisham (Hindi), Cittegi, Yerugudu, Jittegi (Telugu), Iti (Tamil),

Indian Rose wood ranks first amongst the finest woods for furniture and cabinet work. The plant occurs throughout the peninsular India, extending northwards through the Central Province, Chota Nagapore and Bihar to the Sikkim, Himalayas. The plant reaches its largest size on the Western Ghats, where it is found in deciduous forests, associated with Teak and Bamboo. It is known in England as "*Rose wood*" and in India as "*Bombay Black wood*".

Morphology : *Dalbergia* is a large deciduous tree, with cylindrical, fairly straight trunk. It may attain a height of 20 m. or more with a girth of 2 - 4 m. The leaves are alternate, odd-pinnate with 3 - 7 unequal sized orbicular leaflets. Flowers are small, whitish, numerous and are arranged in short, axillary panicles. The fruit is 1-3 seeded, linear - lanceolate pod.

Properties of wood : The wood is differentiated into sapwood and heart wood. The sap wood is narrow, pale yellowish in colour, often with a purple tinge. The heart wood is dark purple with black longitudinal streaks. The wood is medium coarse textured with fairly straight to somewhat interlocked grains. The average weight is about 780 kg/m³ at 12% moisture content.

The wood is diffuse porous with a tendency to semi - ring porous. The annual rings are indistinct to fairly distinct. The pores are moderately large, visible to the naked eye, mostly solitary or in short radial multiples. They are often filled with dark gummy deposits. The medullary rays are fine, numerous, uniform, equidistant and very short.

STUDY OF TIMBER

III Red Sanders :

Botanical name
Family
Vern names

Red sanders is a tree found in the regions around Cuddalore.

Morphology : The tree is branching at some height and crowded towards the top with axillary panicles.



Fig. 4-3 : Leaves, flowers and pods of *Dalbergia latifolia*

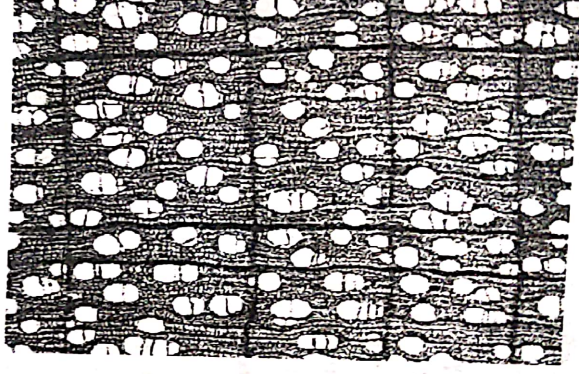


Fig. 4-4 : *Dalbergia latifolia* Wood

Uses :

- (1) Indian rose-wood is a high class furniture and cabinet wood.
- (2) It is also used for railway sleepers, musical instruments, hammer handles, hookah tubes and carving.
- (3) The leaves are used as fodder. It is grown in coffee plantations as a shade tree.
- (4) The bark of the tree contains tannin.

Properties of wood :
The wood is hard, strong and horizontally and differentially. The wood is orange-brown in color and scattered and very hard.

Uses :

- (1) The wood is used for furniture and cabinet wood.
- (2) The wood is also used for railway sleepers, musical instruments, hammer handles, hookah tubes and carving.
- (3) The leaves are used as fodder. It is grown in coffee plantations as a shade tree.
- (4) The bark of the tree contains tannin.

The dye gives a red color.

purposes.

III Red Sanders :

Botanical name :	<i>Pterocarpus santalinus</i>
Family :	Fabaceae
Vern names :	Lal chandan (Hindi), Erra chandanamu (Telugu), Seyapu chandanam (Tamil).

Red sanders is a small sized tree growing in Southern India. It is common in the regions around Cuddapah, North Arcot, Nellore and Southern Kurnool districts.

Morphology : The Red sanders is a pretty tree, having an upright bole, only branching at some height above the ground. The leaves are alternate, odd-pinnate and crowded towards the ends of branches. The flowers arise in April - May, in axillary panicles.



Fig. 4-5 : *Pterocarpus santalinus*

Properties of wood : The bark is blackish - brown, deeply cleft both vertically and horizontally into rectangular plates. Wood is extremely hard, close-grained and differentiated into sap wood and heart wood. Sap wood is white, while heart wood is orange - red to almost black in colour. Pores are moderate - sized, scattered and very scanty. Medullary rays are fine, numerous, and equidistant.

Uses :

- (1) The wood is largely used for house - posts and agricultural implements.
- (2) The wood shavings give a blood red coloured dye (santalin) on distillation. The dye gives a beautiful salmon-pink colour when dissolved in alcohol or ether.
- (3) The wood is extensively used for carvings and statues.
- (4) The wood is also excellent for boxes, picture - frames and other joinery purposes.

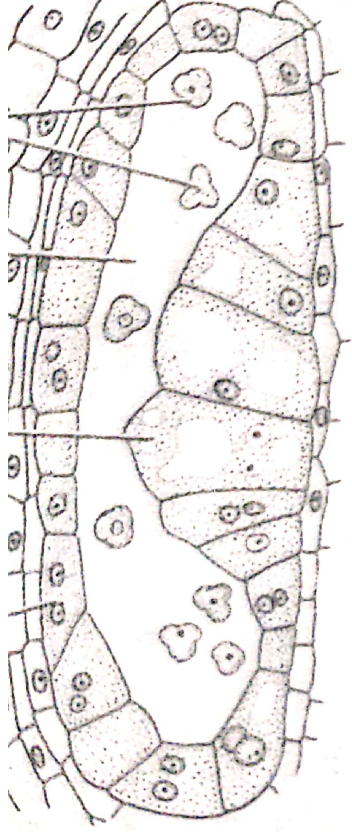


Fig. 2.4 : Dimorphic tapetum in *Alectra thomsonii*
(I) *Types of Tapetum :*

Two types of tapetum are seen in angiosperms -
(a) *Amoeboid Tapetum :*

This is also known as *plasmodial tapetum*. In this type, the inner and radial walls of the tapetal cells breakdown early due to the action of hydrolytic enzymes. The protoplasts of these cells enter into the anther locules and fuse to form a common mass called *periplasmodium*. This mass surrounds the pollen grains till they mature and provides them proper nutrition. The periplasmodium also contributes to their exine by providing sporopollenin precursors.

The amoeboid tapetum is considered to be of primitive type and is found in monocots and in some lower dicots e.g. *Alisma*, *Typha*, *Butomopsis*, *Tradescantia*, *Helianthus*, *Sagittarius*, *Potamogeton*, etc.

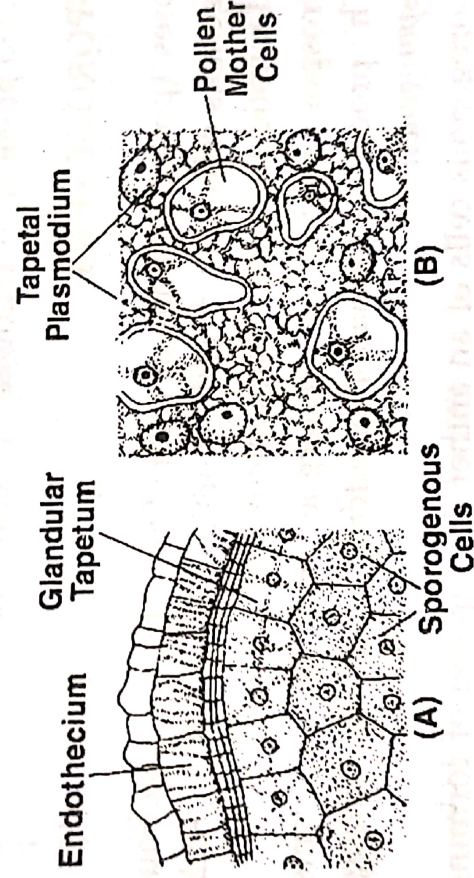


Fig. 2.5 : Tapetum - (A) Glandular (B) Amoeboid

(b) *Secretory Tapetum :* This is also known as *glandular tapetum*. The cells of the secretory tapetum remain in their original position till the development of pollen grains. At the pre - mitotic stage of the pollen mother cells, tapetal cells are very thin and possess almost all cell organelles. Some spherical structures, called *pro - ubisch bodies* (Carotenes, Carotenoid esters) are also present in these cells. Just before the pollen mother cells undergo meiosis, the walls of the tapetal cells become thick and there is considerable increase in the number of ribosomes and *pro - ubisch*

bodies. With the completion of the pollen development, pro-ubisch bodies pass into the anther locule from the tapetal cells. Here, they are coated with sporopollenin and get transformed into *Ubisch bodies*. They perhaps help in the formation of exine of pollen grains. The secretory type of tapetum is found in most of the angiosperms.

(II) Functions of Tapetum :

(1) Tapetum plays an important role in the development of microspores (Pollen grains). This assumption is based on the fact that if in an anther, tapetum degenerates before microsporogenesis, the pollen grains produced are sterile and abortive.

(2) Tapetum also helps in the transport of food material to the inside of the anther. The food material stored in the tapetal cells is not utilized in the early stages of anther development. But, after pollen mother cells have undergone meiosis, the protoplast of the tapetal cells enter into the pollen chamber to form the periplasmodium. This provides nutrition to the developing pollen grains and also helps in the formation of exine.

(3) They secrete the enzyme callose (β - 1, 3 - glucanase) which dissolves the callosic wall of the tetrad and set them free.

(4) Tapetum is involved in the synthesis and release of the materials which take in the deposition of *tryphine* and *pollenkit*. They are deposited on the pollen surface and helps to bind pollen grains together, and for efficient insect pollination. Both these substances are synthesized in the plastids of tapetal cells.

(5) The tapetal proteins present in the pollen - wall are responsible for the common hay fever and pollen allergy.

(6) Tapetum initiates the process of abortion of pollen in cytoplasmic male sterile (CMS) lines. Low levels of DNA synthesis in the tapetum are the first indications of CMS phenotype, followed by disruption of the young microspores.

2-2 MICROSPOROGENESIS

Microspores (pollen grains) develop from the sporogenous tissue. The primary sporogenous cells may directly function as *microspore mother cells* or they undergo several mitotic divisions to form microspore mother cells.

Each microspore mother cell undergoes meiosis and forms four haploid microspores. The process of formation of microspores from sporogenous tissue is known as *microsporogenesis*.

All the sporogenous cells of an anther are capable of forming microspore mother cells. But usually some of these cells disorganise and provide nutrition to the active sporogenous mother cells.

I Cytokinesis :

During meiotic division of microspore mother cell, the wall formation may take place in two ways - *Successive and Simultaneous*.

1. **Successive Type** : In this type of wall formation, a cell plate is laid between two daughter nuclei after *meiosis - I*. This wall gradually extends towards the periphery on both sides dividing the cell into two equal halves. Each cell of the

dyad thus formed, now undergoes *meiosis - II*. The wall formation between the two daughter nuclei occur in the same way as after *meiosis - I*. This results in the formation of isobilateral tetrad. This type is more common in monocotyledons. e.g. *Zea mays*, *Lilium*, *Sansevieria*. and in some plants of the diest families e.g. *Podostema* ceae, *Apocyanaceae*.

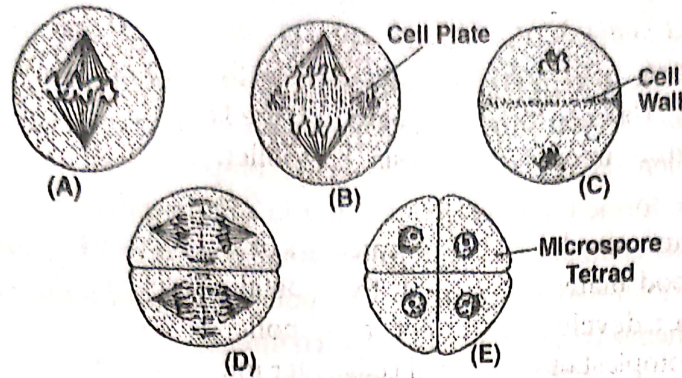


Fig. 2-6 : Successive division of cytoplasm in Microspore Mother Cell

2. Simultaneous Type : This type is common among dicotyledons. Here, there is no wall formation after *meiosis - I*. As such instead of a diad, a binucleate cell is formed after *meiosis - I*. The two daughter nuclei undergo second meiotic division, which is usually synchronous. At this stage, four daughter nuclei lie in the common cytoplasm. The wall formation begins in the form of four peripheral constrictions, which gradually extend from periphery towards the centre. These constrictions eventually meet at the centre of the cell and divide the cytoplasm into four haploid microspores e.g. *Magnolia*, *Nicotiana*, *Helleborus*, *Melothria*.

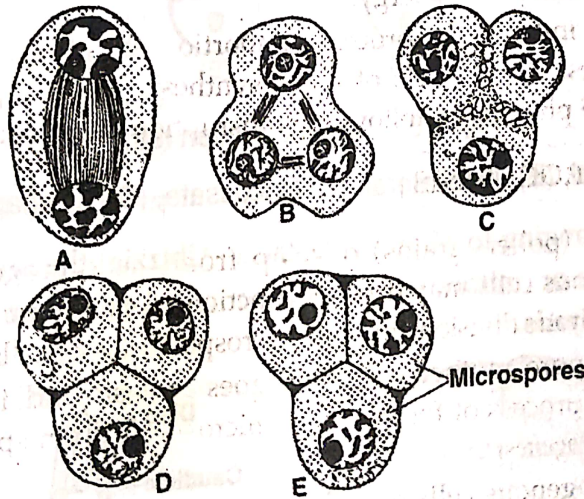


Fig. 2-7 : Simultaneous division of Cytoplasm in Microspore Mother Cell

II Pollen Tetrads :

The four microspores formed from a microspore mother cell are usually arranged in *tetrahedral* or *isobilateral* tetrads. In *tetrahedral* tetrads, which are formed as a result of simultaneous division, the four microspores lie at the four corners of a tetrahedron. When seen from one angle, only three microspores are visible and the fourth one lies at the back. In *isobilateral* tetrads, which are formed by successive division, the four microspores are arranged in one plane in two tiers of 2 each.

Besides the above two types, microspores may be arranged in decussate (e.g. *Magnolia*, *Crocus*, *Atriplex*), T - shaped (e.g. *Aristolochia*, *Butomopsis*) or linear (e.g. *Asclepiadaceae*) tetrads. Interesting all the five types of tetrads have been observed in *Aristolochia elegans*.

The microspores of a tetrad usually separate from each other as the anther matures. But sometimes, the tetrads stuck together in groups to form compound pollen grains. The compound pollen grains may contain 16, 32, 64 spores (e.g. *Drymis*, *Annona*, *Acacia*, *Drosera*, *Typha*, *Elodea* etc.) In *Asclepiadaceae*, all the pollen in a pollen sac are united in a single compact mass known as pollinia. Pollinia are also formed in *Orchidaceae*. But in certain members of this family, the pollinium is less compact as it comprises smaller groups of pollen grains. Such loose groups are termed as *massulae*. The pollen grains of a *massulae* are loosely joined among themselves by means of a viscin thread.

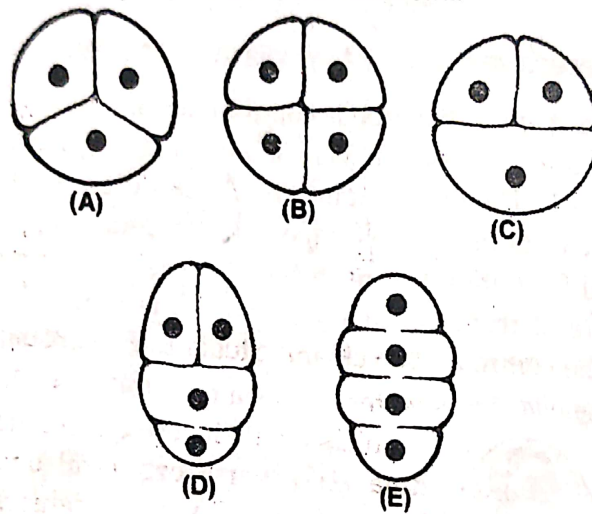


Fig. 2-8 : Types of Pollen tetrads

(A) Tetrahedral, (B) Isobilateral, (C) Decussate, (D) T - shaped, (E) Linear

In Plants belonging to Mimosae (*Acacia*, *Albizzia*) the four microspores in a tetrad undergo one or more mitotic divisions to form 4+4 or 8+8 or 16+16 spores. Such units are called Polyads.

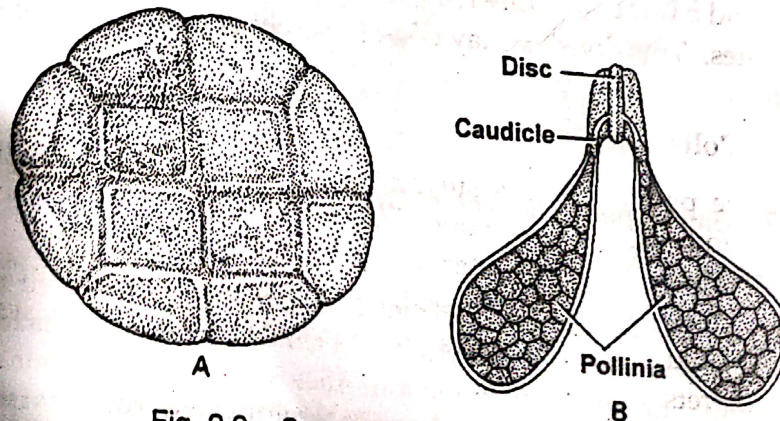


Fig. 2-9 : Special Types of Microspores

(A) Compound Pollen grain (*Acacia*) (B) Pollinium (*Calotropis*)

III Dehiscence of Anther :

At maturity, the endothelial cells develop fibrous thickenings all around the anther locule, except along the line of dehiscence. This region which is characterized by the presence of thin-walled cells, is called *stomium*.

The middle layers and tapetum disappear, and the ripe sporangial wall now consists of epidermis and endothecium. The sterile tissue present between two pollen sacs dissolves, so that pollen sacs unite with each other.

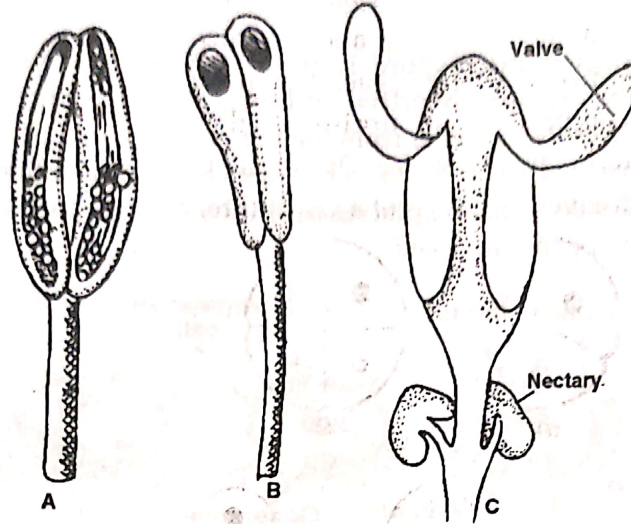


Fig. 2-10 : Anther dehiscence - (A) Longitudinal; (B) Porous; (C) Valvular

Now the anther wall loses water and as a result of this, all the external walls of endothecium shrink inwards which result in the dehiscence of anther. The dehiscence slit may be longitudinal, transverse or lateral depending upon the position of stomium cells. In *Solanum nigrum*, *Cassia* sp., dehiscence takes place at the top of the anther by apical pores.

2-3 MALE GAMETOPHYTE

The microspore (pollen grain) is the mother cell of the male gametophyte. During gametogenesis, the nucleus of pollen grain divides into a small lenticular *generative* cell, and a large *vegetative* cell. The generative cell again divides and forms two male gametes. This division may take place either inside the pollen grain or in the pollen tube.

I Structure of Pollen Grain :

The mature pollen grain is surrounded by a well defined wall, which is differentiated into two layers - the outer *exine* and the inner *intine*. The exine first appears as a thin layer, but later becomes considerably thick. It can be differentiated into two layers (outer *sexine* and *inner layer nexine*). The sexine is further differentiated into three layers - the basal *foot layer*, a middle *bacula* and an upper roof like spret called *tectum*.

The bacula, which consists of radially elongated rods, forms various sculpturing patterns on the exine. The exine is chiefly composed of sporopollenin, an oxidative polymer of carotenoids. It is a tough substance and provides

resistance to physical and biological decomposition of pollen wall. Thus it is the natural decay of pollen grains.

The exine is provided with small *apertures* or *pores*. These are thin areas in the exine is completely absent or represented by endexine only. The aperture is associated with the germination of pollen grain. Through the aperture, the pollen comes out and forms the *pollen tube*.

The nexine can be differentiated into two layers called Nexine - I and Nexine - II. In some gymnosperms, the nexine - I extends to form one or two sac like wings, e.g., Pinus.

A freshly formed microspore is rich in cytoplasm and centrally placed nucleus. Dictyosomes, mitochondria, endoplasmic reticulum are present in the cytoplasm. Soon after their release from the tetrad, the pollen grain enlarges rapidly in volume. As a result, their cytoplasm becomes highly vacuolated. The nucleus is shifted to a lateral side. This displacement is always in a particular direction and marks the position of generative cell.

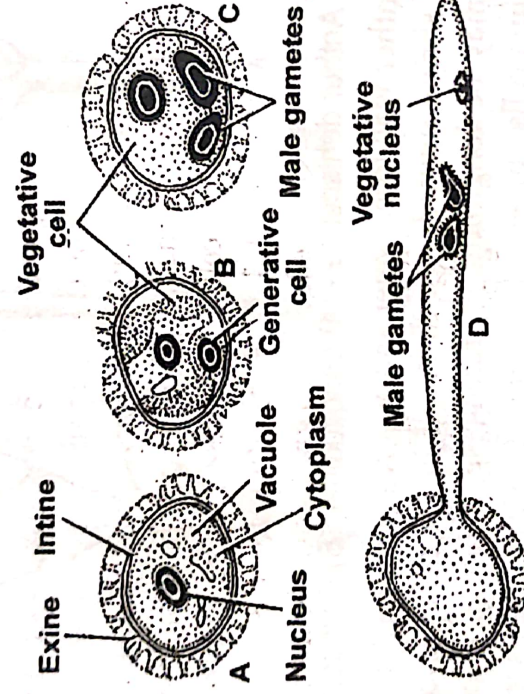


Fig. 2-11 : Development of male gametophyte

II Development of Male Gametophyte :

The first mitotic division in a pollen grain results in two unequal cells. The larger one is the *vegetative cell*, which eventually forms the pollen tube. The smaller one is the *generative cell* which forms male gametes by another mitotic division.

Initially, the generative cell is attached to the intine of the pollen wall, but it gets detached from the pollen wall and lies free in the cytoplasm of the vegetative cell. The generative cell is usually biconvex or elliptical in shape. But sometimes in *Cuscuta*, the generative nucleus becomes very long and occupy the entire length of the pollen grain.

(A) Vegetative Cell : The nucleus of the vegetative cell is spherical or irregular in outline with thin chromatin material. It has one or two nucleoli. The cytoplasm of the vegetative cell contains ribosomes, much ER, plastids, mitochondria, fat and starch grains. RNA is present in lesser quantity. The vegetative cell normally does not divide, although it is capable of DNA synthesis.

In the past, it was assumed that the vegetative nucleus directs the growth of the pollen tube.

But there are several objections to this view since -

- (i) In several species the vegetative nucleus gets degenerated soon after of its formation.
- (ii) In some cases it lies behind the generative cell in the pollen tube and
- (iii) In others, where the pollen tube is branched, the generative cell and vegetative nucleus are in different branches.

Therefore, Maheswari (1950) regarded the vegetative nucleus as a degenerating structure without any function.

(B) Generative Cell : The generative cell is surrounded by a wall. There is no cytoplasmic connection between the vegetative cell and the generative cell. The cytoplasm is relatively dense and contains usually cell organelles. In most of the species, plastids are absent in the generative cell. But in some species like *Oenothera hookeri*, the generative cell contains plastids, but they do not contain starch. The nucleus contains a small nucleolus.

(C) Formation of male gametes : The male gametes are formed by mitotic division of the generative cell. The division usually occurs before the pollen is shed from the anther (e.g. *Beta*, *Hordeum*) but in some species the generative cell divides only after the pollen have been shed. In the former condition, the pollen are shed at the 3 - celled stage (vegetative cell + 2 generative cells) and in the later at the 2 - celled stage (1 vegetative cell + 1 gamete). In some cases, (e.g. *Viola*, *Dionea*, *Nicotiana*) both 2 - celled and 3 - celled pollen grains have been reported in the same plant.

In those plants, where pollen grains are shed at the 2 - celled stage, the generative cell may divide after the pollen have reached the stigma (e.g. *Holoptelea integrifolia*, *Portulaca*) or in the pollen tube (e.g. *Euphorbia terracina*, *Lilium*, *Impatiens*).

The division of the generative cell within the pollen grain is associated with normal mitosis. Cytokinesis occurs through cell plate formation or through a process of furrowing. However, metaphase plate and spindle formation are absent in those plants where the generative cell divides in the pollen tube.

Mitotic division of the generative cell results in the formation of two non - motile *male gametes*. Each male gamete consists of a large nucleus surrounded by a thin sheath of cytoplasm, externally limited by a cell membrane. Cell wall is usually absent, hence the male gametes are *naked*.

The two male cells of a gametophyte do have physical contact with each other. Such a contact is important as it helps in co - ordinated development of both the cells. It is also important from the point of view of double fertilization.

2-4 ABNORMAL FEATURES

I Pollen development in Cyperaceae :

In majority of angiosperms, the pollen mother cell divides by meiotic division to form four haploid microspores. However, the members of Cyperaceae show a special method of pollen development (Staut, 1912). The microspore mother cell

... of angiosperms. A typical embryo sac contains eight haploid nuclei. Of these eight nuclei, three nuclei at the chalazal end organize into three *antipodal cells*, three at the micropylar end form the *egg - apparatus*, the two median nuclei are called *polar nuclei*. The egg apparatus has an *egg - cell*, and two *synergids*. The egg - cell represents the female gamete.

3-2 TYPES OF OVULES

Many types of ovules are found in angiosperms. Based on position of micropyle in relation to the funiculus and other parts of the ovule, six types of ovules are recognized.

1. **Atropous or Orthotropous ovules** : It is a straight ovule with micropyle, chalaza and funiculus arranged in one straight line. It is supposed to be primitive type and not very common in angiosperms. e.g. Polygonaceae, Piperaceae, Urticaceae Xyridaceae, Araceae.
2. **Anatropous ovule** : Due to unilateral growth of funicle, the whole body of the ovule is inverted through 180° . As a result the micropyle comes close to the base of the funicle. The nucellus remains straight i.e., micropyle and chalaza lie in one line and the funicle lies parallel to it. It is the most common type and found in several families of both dicotyledons and monocotyledons. e.g. *Helianthus*, *Tridax*.
3. **Hemi anatropous or Hemitropous ovule** : In this type, the body of the ovule takes a turn by 90° only so that it is horizontally placed on the funicle. Hence, the micropyle and chalaza are on a horizontal line and the funicle lies at right angles to this line. e.g. Ranunculaceae and Primulaceae.

(4) **Campylotropous ovule** : Like hemitropous ovule, the body of the ovule is bent more or less at right angles to the funicle. But here, the micropylar part of the ovule becomes curved, without any curvature in the embryo sac. e.g. Fabaceae, Brassicaceae.

(5) **Amphitropous ovule** : Here, the curvature of the body of ovule is more prominent, so that the embryo sac within the ovule also bends and becomes horse - shoe shaped e.g. Alismataceae, Butomeaceae and Centrospermae.

(6) **Circinotropous ovule** : In this type of ovule the funicle is very long and it coils like a watch spring around the body of the ovule. e.g. Plumbaginaceae (*Plumbago*) and Cactaceae (*Opuntia*).

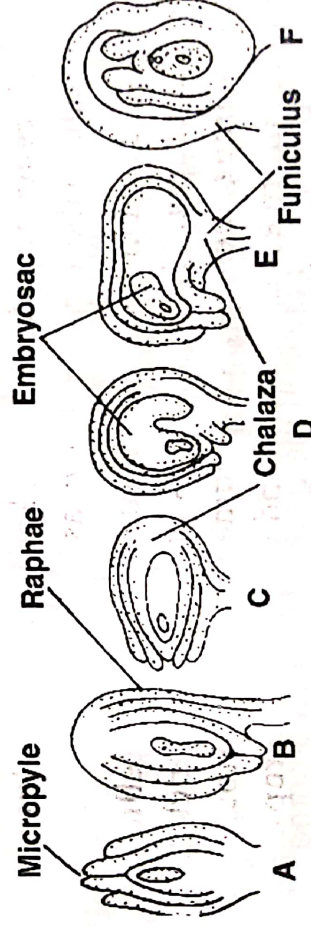


Fig. 3-2 : Types of Ovules

(A) Orthotropous, (B) Anatropous, (C) Hemi - anatropous (D) Amphitropous, (E) Campylotropous, (F) Circinotropous

(Rutaceae), some epidermal cells of the funiculus as well as placenta elongate into elongate and function as obturator. In Thymeliaceae, the cells of the stylar canal Some workers believe that obturator provides nutrition to the pollen tube.

3-4 MEGASPOROGENESIS

A single hypodermal cell at the apex of the nucellus differentiates as *archesporial cell*. It is distinguishable from the other cells by its conspicuous large size, dense cytoplasm and prominent nucleus.

In tenuinucellate ovules, the archesporial cell directly functions as *megaspore mother cell*. But in crassinucellate ovules, this cell divides by a periclinal wall forming an **outer primary parietal cell** and an **inner primary sporogenous cell**. The latter functions as megaspore mother cell. Primary parietal cell. Undergoes both periclinal and anticlinal divisions and forms a multiseriate parietal tissue.

Usually the archesporium is single - celled, but in Onagraceae, Fagaceae, Apiaceae, Salicaceae, Poaceae and Liliaceae, the archesporium consists of several cells. Of these, usually the central cell alone is functional.

The megaspore mother cell is the last cell of the sporophytic division. It undergoes a reduction division (meiosis) to form four haploid **megaspores**. This process is known as **megasporogenesis**. The first division of megaspore mother cell is always transverse resulting in the formation of two cells (dyads). Second division is also transverse, resulting in a linear tetrad of megaspores.

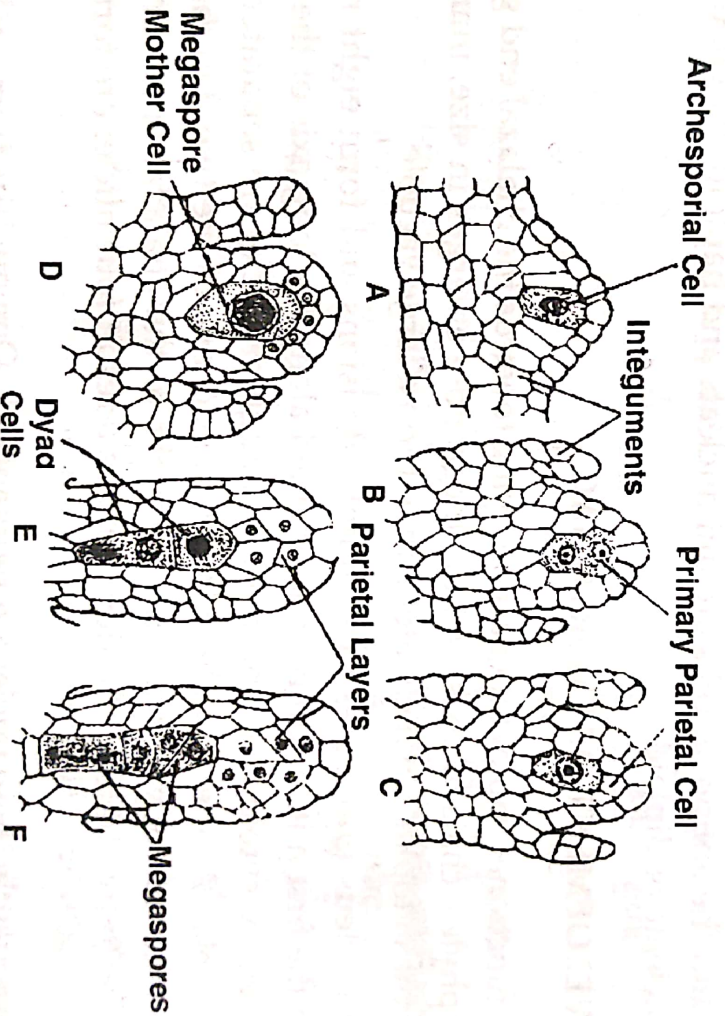


Fig. 3-10 : Stages in Megasporogenesis

Orchis macula, *Rheum* and *Rumex* usually form T-shaped tetrads. They are due to vertical division in the micropylar dyad cell and transverse division in the chalazal dyad cell.

Of the four megaspores of a tetrad, only the lowest spore (chalazal) is functional and forms female gametophyte. The remaining three megaspores degenerate. This type of embryo sac development is known as *monosporic* type of embryo sac. In *Onagraceae*, the micropylar megaspore is functional and forms nucleate embryo sac. e.g. *Oenothera*.

In *Bisporic type* of embryo sac development, the second meiotic division is not followed by wall formation. One of the dyad cells with two haploid megaspore nuclei takes part in the formation of embryo sac. The other dyad cell degenerates. e.g. *Allium*.

In *tetrasporic* type of embryo sac, no wall formation occurs through meiosis. All the four megaspore nuclei remain in a single cell (coenomegaspore) and participate in the formation of embryo sac e.g. *Plumbago*, *Peperomia*.

Female Gametophyte

3-5 INTRODUCTION

The haploid megaspore is the first cell of the female gametophytic generation. It germinates within the nucellus of the ovule and develops into the female gametophyte known as the *embryo sac*. The embryo sac is dependent on the surrounding sporophytic tissues for its nourishment.

The organized embryo sac typically consists of an **egg cell**, two **synergids**, three **antipodal cells** and two **polar nuclei**. The egg apparatus is situated towards the micropylar end and the antipodals lie on the chalazal side. Cells of the egg apparatus and the antipodal cells are uni-nucleate and haploid, whereas the central cell is binucleate or diploid.

3-6 DEVELOPMENT OF EMBRYO SAC

The functional haploid megaspore lying towards the chalazal end grows along the micropylar - chalazal axis. As the megaspore enlarges in size, many vacuoles appear in the cytoplasm which later join to form a large vacuole.

The nucleus undergoes three mitotic divisions and forms eight nuclei. The spindle of the first mitotic division is oriented along the long axis of the ovule. It is not followed by cytokinesis and the two daughter nuclei are separated by a large central vacuole. As the vacuole enlarges in size, one of the two daughter nuclei is pushed to the micropylar end and the other to the chalazal end. Both of these nuclei undergo two mitotic divisions, and as a result four nuclei are formed at each pole.

Subsequently these nuclei are reorganized. One nucleus from each group migrates to the centre of the cell. These two nuclei are called **polar nuclei**. These two polar nuclei fuse to form the **secondary nucleus** ($2n$). The three nuclei

OVULE - STRUCTURE AND TYPES

The chalazal end are surrounded by wall cells. At the micropylar end, one serves as **synergids**. These three cells together form the **egg apparatus**. The structure with two polar nuclei, three antipodal cells, and the egg apparatus is known as the mature female gametophyte.

Since this type of embryo sac development was first described by S. G. N. S. in 1898, it is known as *Polygonum type* of embryo sac and is found in about 81% of angiosperms.

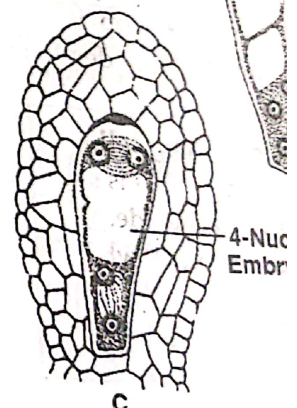
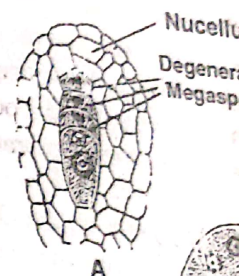


Fig. 3-11 : Mon

(A) Megasporogenesis, (B) 2-Nucleate, (C) 4-Nucleate, (D) 8-Nucleate

3-7 TYPES OF EMBRYO SAC

In majority of angiosperms, the embryo sac develops from a single functional megaspore. However, in many cases two functional megaspores participate in the development of embryo sac. The basis of the number of functional megaspores is the basis of the development of embryo sac.

(1) Monosporic (2) Bisporic (3) Tetrasporic

One type of embryo sac name

the chalazal end are surrounded by walls and form *antipodals*. Of the three nuclei located at the micropylar end, one serves as *egg or female gamete* and the other two act as *synergids*. These three cells together constitute the *egg apparatus*. The whole structure with two polar nuclei, three antipodals, one egg and two synergids, is known as the mature *female gametophyte or embryo sac*.

Since this type of embryo sac develops from a single megaspore and has a 8 - nuclei, it is called *monosporic 8 - nucleate embryo sac*. This type of embryo sac development was first described by Strassburger (1879) in *Polygonum divaricatum*. Hence it is known as *Polygonum type* of embryo sac. It is the most common type of embryo sac and is found in about 81% of the flowering plants. (Davis, 1966).

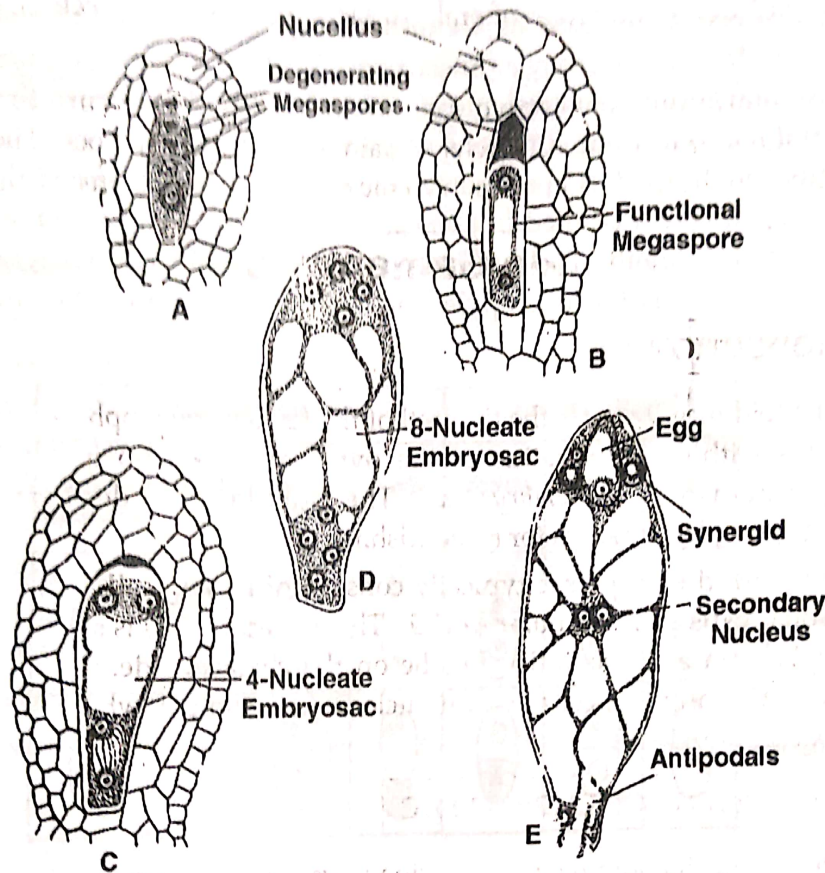


Fig. 3.11 : Monosporic embryo sac - development

(A) Megasporogenesis, (B) 2 - Nucleate Embryo sac, (C) 4 - Nucleate Embryo sac, (D) 8 - Nucleate Embryo sac, (E) Mature Embryo sac

3-7 TYPES OF EMBRYO SACS

In majority of angiosperms, the embryo sac develops from a single megaspore. However, in many cases two or all the four megaspore nuclei take part in the development of embryo sac. Three types of embryo sacs have been recognised on the basis of the number of functional megaspores nuclei taking part in the development of embryo sac. They are :

(1) Monosporic (2) Bisporic and (3) Tetrasporic. Each group has more than one type of embryo sac named after the genus in which it was first described.

I Monosporic Embryo Sacs :

A monosporic embryo sac develops from a single megaspore and as such the nuclei present in the embryo sac are genetically alike. Monosporic embryo sacs are of two types :

1. **Monosporic 8 - nucleate or Polygonum type :** This type of embryo sac develops from the chalazal megaspore. Its nucleus divides thrice to form eight nuclei. The mature embryo sac comprises of a 3- celled egg apparatus, antipodals and a bi - nucleate central cell (i.e. $3 + 2 + 3$). This type is referred to as *normal type* of embryo sac. It is also called Polygonum type as it was first time described in *Polygonum divaricatum* by Strasburger (1879).

2. **Monosporic 4-nucleate or Oenothera type :** This type of embryo sac usually develops from the micropylar megaspore. The functional megaspore nucleus divides twice and forms four free nuclei. Out of these, three organise the egg apparatus and the fourth one functions as polar nucleus (i.e. $3 + 1$). The second polar nucleus and antipodals are absent. This type is characteristic of the family Onagraceae and was first studied in *Oenothera lamarckiana*. *Schisandra* is the example outside this family. The difference is that whereas in the Onagraceae functional megaspore is the micropyla one and in Schigandha, the functional megaspore is the chalazal one.

	Megasporogenesis			Megagametogenesis		
	Megaspore mother cell	Meiosis I	Meiosis II	Mitosis I	Mitosis II	Mitosis III
Polygonum						
Oenothera						

Fig. 3-12 : Monosporic embryo sac development

II Bisporic Embryo Sacs :

The bisporic embryo sac develops from one of the two dyads formed as a result of the first meiotic division (Meiosis I) of megaspore mother cell. The other dyad cell degenerates. In the functional dyad cell, wall formation does not occur after the second division and both nuclei of the functional dyad take part in the formation of embryo sac. Each nucleus undergoes two mitotic divisions, as such the mature embryo sac is 8 - nucleate. The eight nuclei get organised as antipodals, egg apparatus and polar nuclei as in Polygonum type of embryo sac. In this type, the four megaspore nuclei derived from one megaspore nucleus are genetically different from the other four derived from the second megaspore nucleus.

On the basis of the position of functional dyad, the following two types have been recognised in bisporic embryo sacs.

1. *Allium* type : This type develops from the chalazal dyad cell. It was first described by Strasburger (1879) in *Allium fistulosum*.

2. *Endymion* type : This type develops from the micropylar dyad cell. e.g. *Scilla*.

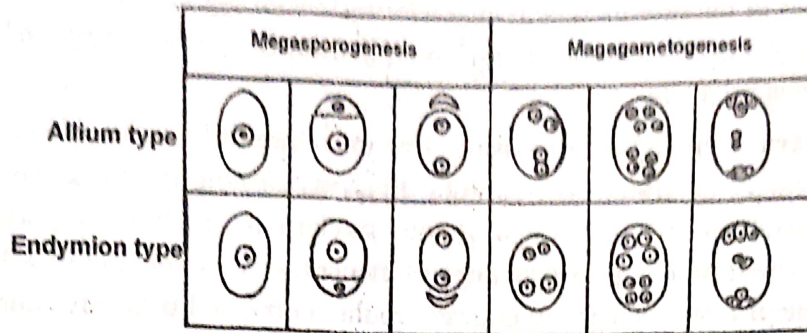


Fig. 3-13 : Bisporic embryo sac development

III Tetrasporic Embryo Sacs :

Sometimes meiotic division of the megaspore mother cell is not accompanied by cytokinesis. Hence all the four haploid nuclei remain in a common cytoplasm. Such a four nucleate megaspore is known as *coeno - megaspore*. All the four nuclei of *coeno - megaspore* participate in the formation of embryo sac. This type of embryo sac is called *tetrasporic* and it is genetically more heterogeneous than the bisporic type of embryo sac.

The four haploid megaspore nuclei divide one or two times to form 8 - nucleate or 16 - nucleate embryo sacs. Tetrasporic type of embryo sacs are of 7 types. They include :

(A) 16 - nucleate Embryo sac Types :

(1) *Peperomia* type ; (2) *Penaea* type ; (3) *Drusa* type.

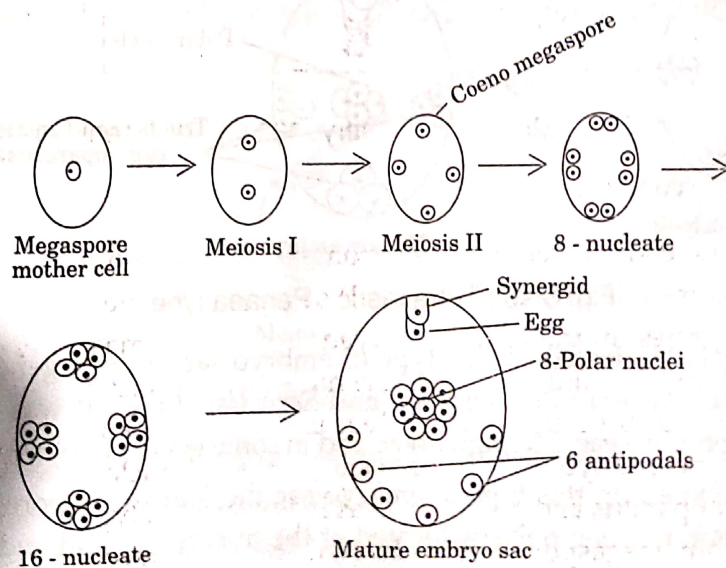


Fig. 3-14 : Tetrasporic *Peperomia* Type

1. Peperomia type : The four haploid nuclei of coeno - megaspore undergo two successive mitotic divisions forming 16 nuclei. These nuclei arrange themselves in four groups of four nuclei each in a cross - wise manner ($4 + 4 + 4 + 4$). Of the two nuclei at the micropylar end form egg and a synergid. Eight nuclei come to the central region resulting into secondary nucleus ($8n$). The remaining six nuclei form antipodal cells near the periphery of the embryo sac at the chalazal end. The embryo sac of Peperomia type is characterised by an egg apparatus with egg and one synergid cell. Campbell (1901) and Johnson (1900) described such embryo sac in *Peperomia pellucida*.

2. Penaea Type : In this type, the four haploid nuclei of the coeno megaspore undergo two successive mitotic divisions forming 16 nuclei. These nuclei arrange themselves in four groups of four nuclei each in the cytoplasm of megaspore. The four groups are arranged in a cross - wise manner ($4 + 4 + 4 + 4$). Now one nucleus from each group migrates to the centre, and these four nuclei in the centre form a secondary nucleus ($4n$). The three nuclei at the micropylar end are of by membranes and form the egg apparatus. The remaining three groups of nuclei (one chalazal and two lateral) usually degenerate or may form non - functional apparatus at each pole. Thus at maturity, the *Penaea* type of embryo sac has an apparatus and four polar nuclei. There are no antipodals.

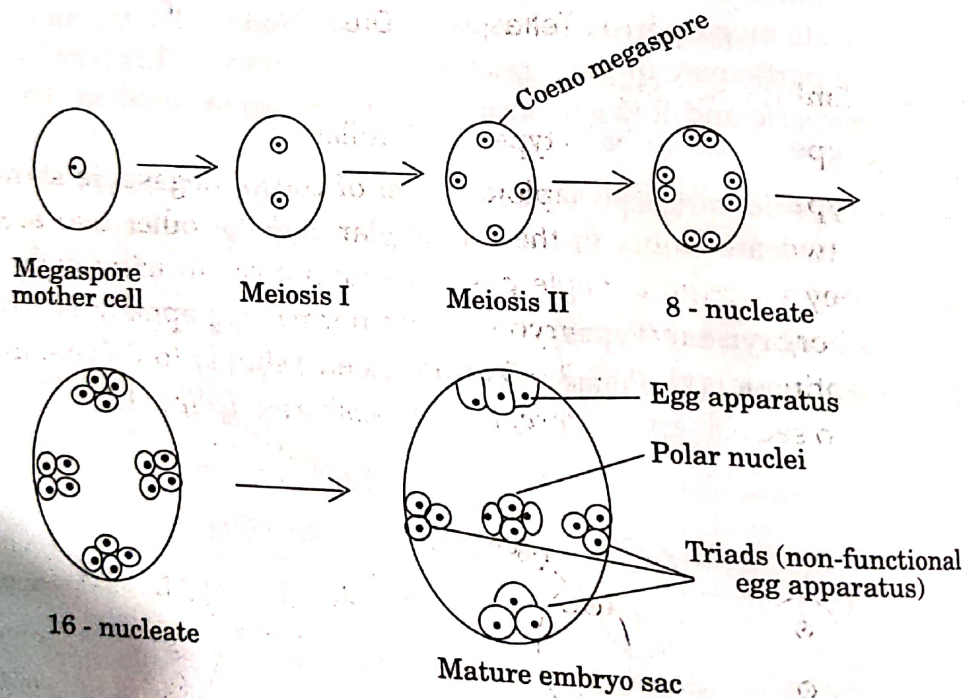


Fig. 3-15 : Tetrasporic - Penaea type

Stephens (1909) described this type of embryo sac in three genera of far Penaeaceae, viz., *Penaea*, *Brachysiphon* and *Sarcolla*. Later, it was observed in members of Euphorbiaceae, Malpighiaceae and in some genera of other families.

3. Drusa Type : In this type of embryo sac the four megaspore nuclei are in a $1 + 3$ arrangement, i.e., one nucleus located at the micropylar end and three at the chalazal end. The four nuclei undergo two successive mitotic divisions forming

nuclei at the micropolar end and twelve nuclei give rise to egg apparatus and upper polar nucleus and eleven antipodals to lower polar nucleus and upper polar apparatus + 2 polar nuclei + 11 antipodals is found in *Drusa*, *Chrysanthemum*, *Ulm*

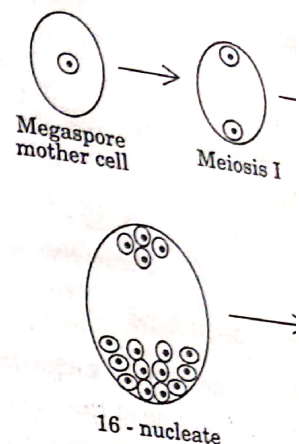


Fig. 3-16 :

(B) 8 - nucleate Embryo sac Types:

(1) Adoxa type ; (2) Plumbago type

1. Adoxa Type : The four nuclei are arranged i.e. two nuclei are at the chalazal end. They undergo a $1 + 3$ arrangement. These eight nuclei organise into one egg apparatus and three antipodals (i.e. $1 + 3$). This type of embryo sac occurs in

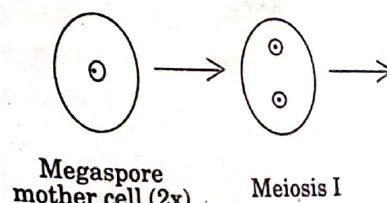


Fig. 3-

2. Plumbago Type : The four nuclei are arranged in a $1 + 1 + 1 + 1$ arrangement. Each nucleus undergoes two successive mitotic divisions forming sixteen nuclei in four pairs. One of the nuclei

nuclei at the micropylar end and twelve at the chalazal end. The four micropylar nuclei give rise to egg apparatus and upper polar nucleus. The chalazal nuclei give rise to lower polar nucleus and eleven antipodal cells. Thus a 16-nucleate embryo sac (Egg apparatus + 2 polar nuclei + 11 antipodal cells) is formed. This type of embryo sac is found in *Drusa*, *Chrysanthemum*, *Ulmus* etc.

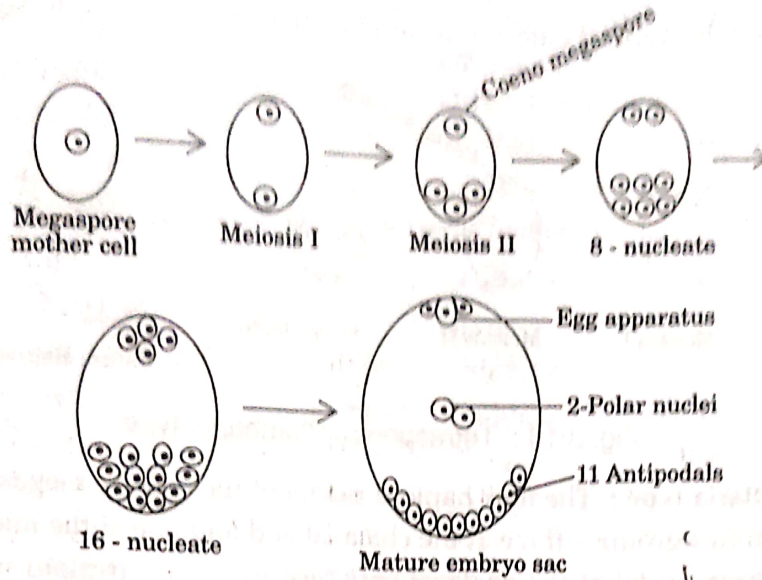


Fig. 3-16 : Tetrasporic - Drusa type

(B) 8-nucleate Embryo sac Types :

(1) Adoxa type ; (2) Plumbago type ; (3) Fritillaria type.

1. Adoxa Type : The four haploid nuclei of coeno megaspore show 2 + 2 arrangement i.e. two nuclei are at the micropylar and the other two are at the chalazal end. They undergo a single post meiotic mitosis forming eight nuclei. These eight nuclei organise into embryo sac with normal egg apparatus, two polar nuclei and three antipodals (i.e. 3 + 2 + 3 arrangement) similar to *Polygonum* type. This type of embryo sac occurs in *Adoxa*, *Ulmus*, *Sambucus*, *Tulipa* etc.

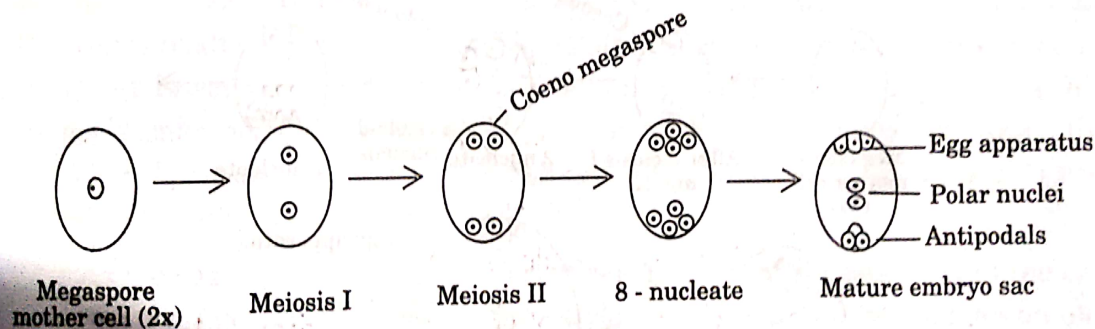


Fig. 3-17 : Tetrasporic - Adoxa type

2. Plumbago Type : The four haploid nuclei move towards the periphery of the cytoplasm of coeno-megaspore and get arranged in a cross-wise manner (1 + 1 + 1 + 1 arrangement). Each of these four nuclei divides again to form eight nuclei in four pairs. One of the nucleus from each group moves to the centre of the cell and

OVULE - STRUCTURE AND TYPE

form the secondary nucleus ($4n$). The remaining nucleus at the micropylar end is cut off by a membrane and forms the egg. There are no synergids. The other nuclei (i.e., one chalazal and two lateral) usually disappear, but occasionally may cut off by membranes and appear as accessory egg cells. The *Plumbago* embryo sac is thus characterised by the absence of synergids and antipodals. (1934) reported this type of embryo sac in *Plumbago capensis* of Plumbaginaceae.

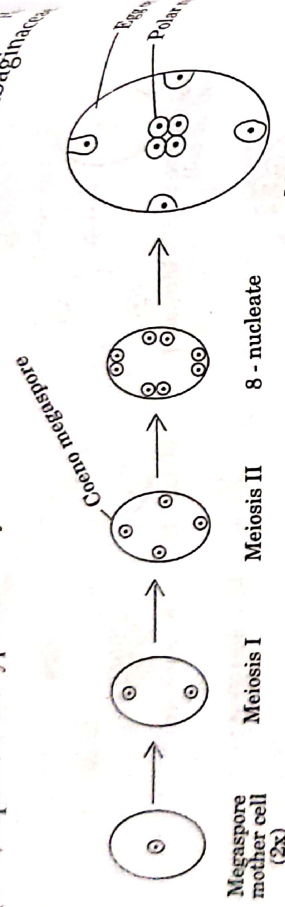


Fig. 3-18 : Tetrasporic - Plumbago type

3. Fritillaria type : The four haploid nuclei of the coeno - megaspore are themselves in two groups - three at the chalazal end and one at the micropylar end (1+3). The three nuclei at the chalazal end fuse to form a triploid nucleus, triploid chalazal and haploid micropylar nucleus undergo two mitotic divisions, a result four triploid nuclei are formed at the chalazal end and four haploid nuclei at the micropylar end. In the mature embryo sac three haploid nuclei organise an apparatus, and three triploid nuclei into antipodal cells. The remaining one haploid and one triploid nuclei move to the centre where they fuse to form a tetraploid nucleus. Thus in this type the antipodal nuclei are triploid and the polar nuclei are tetraploid. Trueb and Melink (1880) reported such embryo sac in various species of *Lilium*.

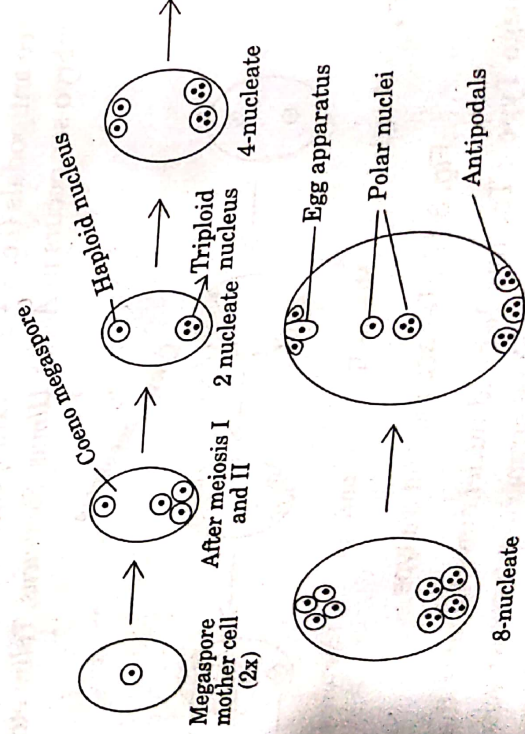


Fig. 3-19 : Tetrasporic - Fritillaria type

OVULE - STRUCTURE AND TYPES

(C) 4 - nucleate Embryo sac Types :

Plumbagella Type : The initial development is similar to Fritillaria type. After meiosis, the nuclei are arranged at the chalazal end and a haploid nucleus at the micropylar end (groups of two nuclei each. Each of these nuclei undergoes two mitotic divisions, and one triploid nucleus each. One haploid nucleus and two triploid nuclei move to the centre and form a tetraploid nucleus. Thus in this type the antipodal nuclei are triploid and the polar nuclei are tetraploid. (1938) reported this type of embryo sac, there are no synergids observed by Fagerlind (1938) in *Plumbago capensis*.

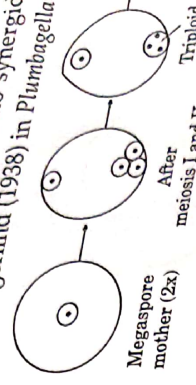


Fig. 3-20 : Tetrasporic - Plumbagella type

3-8 STRUCTURE OF MATURE EMBRYO SAC

The mature embryo sac is an ellipsoid structure with a well defined boundary and is surrounded by a thin wall. The embryo sac consists of an egg apparatus at the micropylar end and two polar nuclei at the chalazal end and two synergids in the middle. There is however a variation in the number of synergids and in the polar nuclei in different species.

I The Egg cell :

The egg cell, along with the two synergids, forms the egg apparatus at the micropylar end of the embryo sac. The wall is relatively thick and contains a large nucleus. But in the lower portion towards the chalazal end, the plasma membrane is thin. On the other hand, the egg cell in *Epidendrum scutella*. The central cell by plasmodesmata.

As the egg matures, polarity is established. The nucleus lies at the chalazal end, whereas the egg nucleus is also situated in the lower portion. Mitochondria are poorly developed.

In those embryo sacs, where the egg cell develops prominent polar filiform outgrowths, generally four synergids, the egg cell itself takes on

(C) 4 - nucleate Embryo sac Types :

Plumbagella Type: The initial development of this type of embryo sac is similar to Fritillaria type. After meiosis, the megaspore nuclei form a triploid nucleus at the chalazal end and a haploid nucleus at the micropylar end (1 + 3 arrangement). Each of these nuclei undergo a single mitotic division and form two groups of two nuclei each. One haploid nucleus at the micropylar end form the egg and one triploid nucleus at the chalazal end form single *antipodal cell*. The other two nuclei move to the centre and form a tetraploid secondary nucleus. Thus in this type of embryo sac, there are no synergids. This type of embryo sac was first observed by Fagerlind (1938) in *Plumbagella micrantha*.

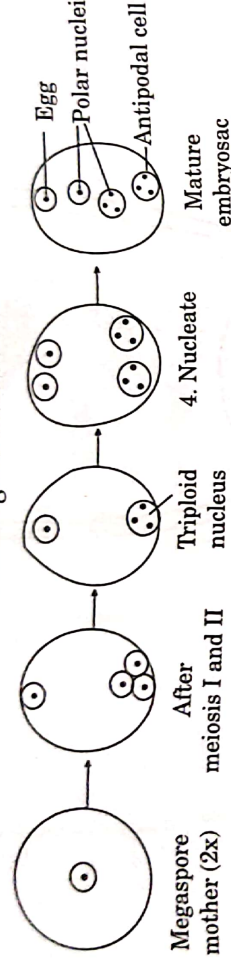


Fig. 3-20 : Tetrasporic - Plumbagella Type

3-8 STRUCTURE OF MATURE EMBRYO SAC

The mature embryo sac is an ellipsoidal structure with tapering ends. It has a well defined boundary and is surrounded by a thin cellulosic wall. A typical embryo sac consists of an *egg apparatus* at the micropylar end, three *antipodal cells* at the chalazal end and two *polar nuclei* in the centre. The egg apparatus consists of an egg and two *synergids*. There is however, a considerable variation in the number of synergids and in the polar nuclei in different types of embryo sacs.

I The Egg cell :

The egg cell, along with the two synergids, forms the egg apparatus at the micropylar end of the embryo sac. The egg cell is partly surrounded by the wall. The wall is relatively thick and contains cellulose where it is contact with synergids. But in the lower portion towards the chalazal end, it is bounded only by a thin plasma membrane. On the otherhand, uniformly thick wall is found all around the egg cell in *Epidendrum scutella*. The egg cell is connected with the synergids and central cell by plasmodesmata.

As the egg matures, polarity is established. The entire cytoplasm of the cell lies at the chalazal end, whereas the micropylar end is occupied by a large vacuole. The nucleus is also situated in the lower end. The cytoplasm contains plastids, and ribosomes. Mitochondria are poorly developed.

In those embryo sacs, where synergids are absent (e.g. *Plumbago*, *Plumbagella*), the egg cell develops prominent projections at it micropylar end. They resemble the filiform outgrowths, generally found in synergids. It shows that, in the absence of synergids, the egg cell itself takes over the role of synergids.

On the basis of their development, the following three types of endosperm have been recognised:

(1) Nuclear endosperm; (2) Cellular endosperm; (3) Helobial endosperm. Of these three types, nuclear endosperm is the most common and is found in about 50% families of angiosperms. Cellular endosperm occurs in 25% families and helobial endosperm in 19% families. Further, cellular endosperm is mostly confined to the dicotyledonous families (in monocots it occurs only in *Araceae* and *Lemnaceae*) and helobial endosperm to the monocotyledonous families.

I Nuclear Endosperm:

In the development of nuclear endosperm the first few divisions of the primary endosperm nucleus are not accompanied by cell wall formation. The nuclei thus formed remain free in the cytoplasm of the embryo sac. The wall formation occurs subsequently, or the nuclei may remain free indefinitely as in *Linum*, *Antirrhinum*, *Agave* and *Floerkea* etc.

The first four divisions of the primary endosperm nucleus are synchronous but the later divisions are irregular. The number of successive divisions usually depends upon the size of the embryo sac, larger the embryo sac more the divisions. When several nuclei are formed, they arrange themselves peripherally in a layer in the cytoplasm. Wall formation starts from periphery towards the center or from apex to base. Eventually, the entire endosperm becomes cellular. The degree of cellularization, however, varies in different taxa. In *Phaseolus*, and *Cassia*, cellularization is restricted only to the micropylar part of the sac around the embryo and in *Crotalaria*, the endosperm is cellular at the micropylar end, the chalazal end is free nuclear and it often elongates and behaves like an haustorium.

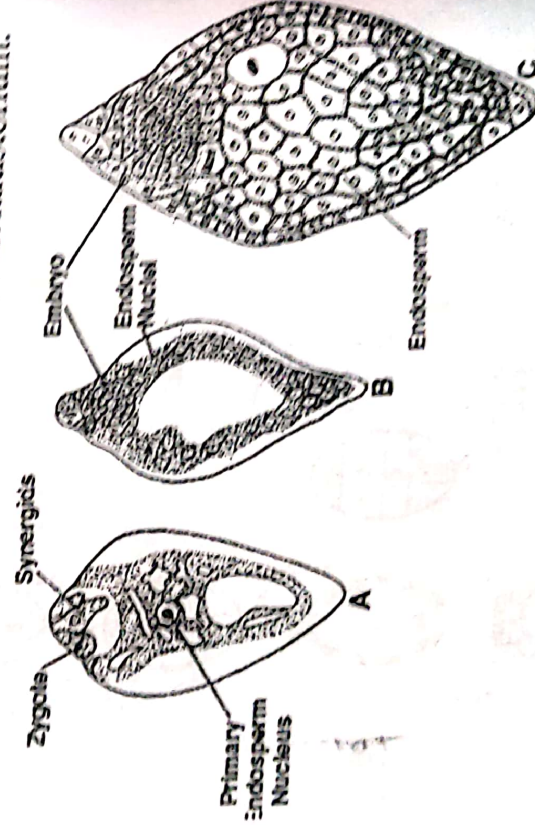


Fig. 6-2 : Nuclear type of endosperm - *Acalypha indica*

Cocos nucifera is the classical example of nuclear endosperm. The PEN undergoes a number of free nuclear divisions. When the fruit is 50 mm. long, the embryo sac is filled with liquid endosperm which contains many free nuclei and cytoplasm. It is called *liquid syncytium*. The ploidy of the nuclei in the syncytium

from $2n$ to $10n$. Mitotic activity in the nuclei of syncytium is rapid and varies by wall formation. The cellular endosperm thus formed, is called *coconut*. Similar type of endosperm development is found in *Azeca catechu*. The embryo sac cavity is small and it becomes completely filled with endosperm. It later becomes extremely hard.

Endosperm haustoria : In families like Cucurbitaceae, Fabaceae and Proteaceae, the cellularization of endosperm is restricted to the micropylar end of the embryo sac. The nuclei at the chalazal end are free and embedded in a common cytoplasm. This chalazal coenocytic part of the embryo sac grows into a tubular haustorium.

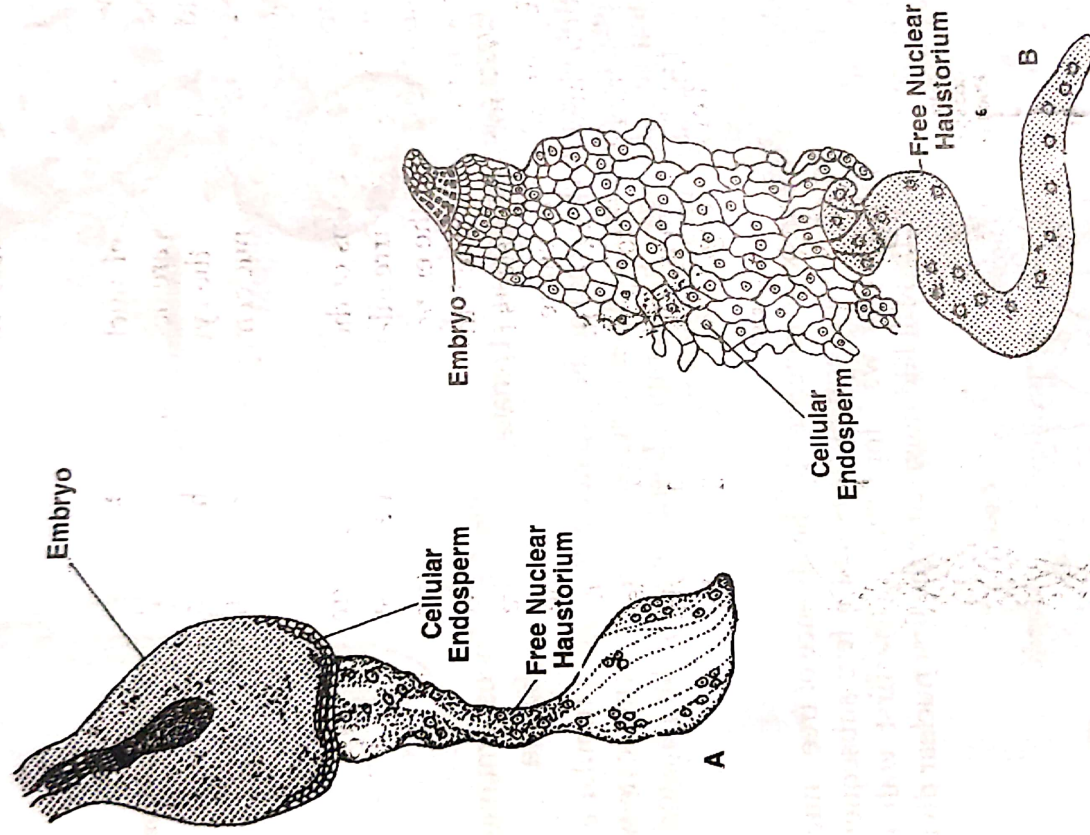


Fig. 6-3 : Endosperm haustoria – (A) *Crotalaria* (B) *Grevillea*

In *Grevillea*, a Vermiform appendage is formed at the chalazal end of the endosperm and functions as haustorium. It remains free nuclear throughout. In *Coccinia* and *Citrullus* the haustorium becomes cellular with multinucleate cells. In *Lomatia*, besides the main chalazal haustorium, numerous single-celled, finger-like outgrowths develop all over the surface of the endosperm. This increases the absorbing surface of the endosperm.

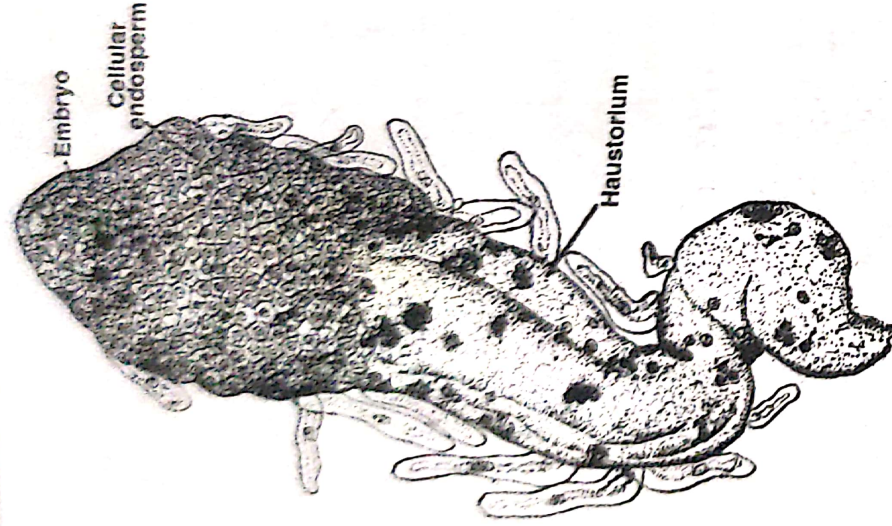


Fig. 6.4 : Endosperm haustorium - Lomatia

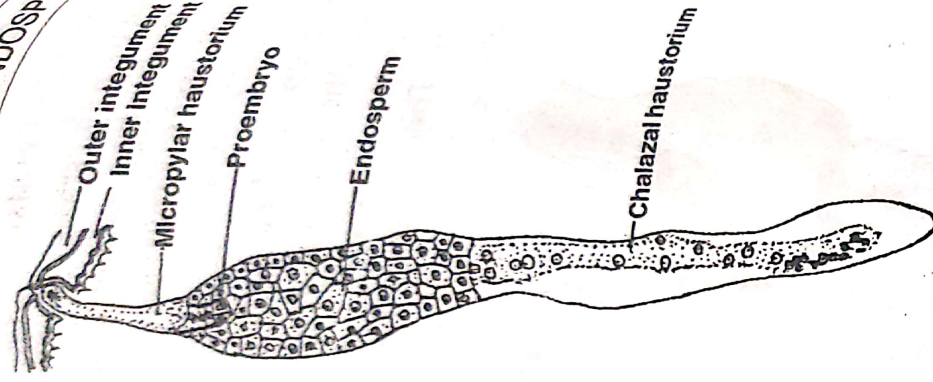


Fig. 6.5 : Endosperm haustorium - Scleria

In *Scleria foliosa* (Cyperaceae) at the two nucleate stage, a tubular extension is formed at the micropylar end of the embryo sac. It remains enucleate with scant cytoplasm, and functions as a haustorium. Besides micropylar haustorium, a free nuclear chalazal haustorium also develops.

II Cellular Endosperm :

The cellular endosperm is characterized by the absence of free - nuclear stage. The division of the primary endosperm nucleus and a few subsequent nuclear divisions are followed by regular wall formation. The first wall is usually transverse. But occasionally the wall laid down after the first nuclear division, may be oblique or vertical.

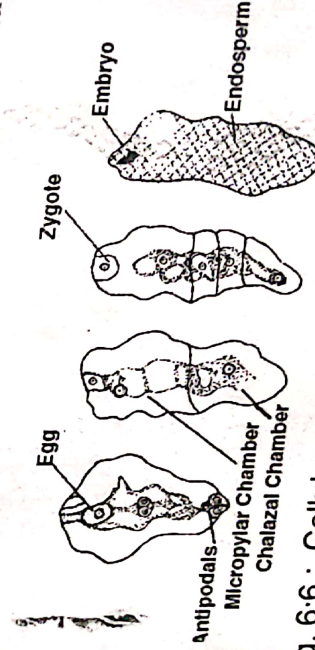


Fig. 6.6 : Cellular type of endosperm - Drimys winterii

The first transverse division results in the formation of two unequal or equal chambers - micropylar chamber and chalazal chamber. Subsequent nuclear divisions are followed by regular wall formation giving rise to cellular endosperm. Such endosperm formation occurs chiefly in dicotyledons.

Endosperm haustoria : The occurrence of haustoria is a common feature of this type of endosperm. One or more cells become specialized to function as haustoria. The haustoria are formed at the micropylar or chalazal or at both the ends and penetrate the nucellar tissue to absorb nutrition.

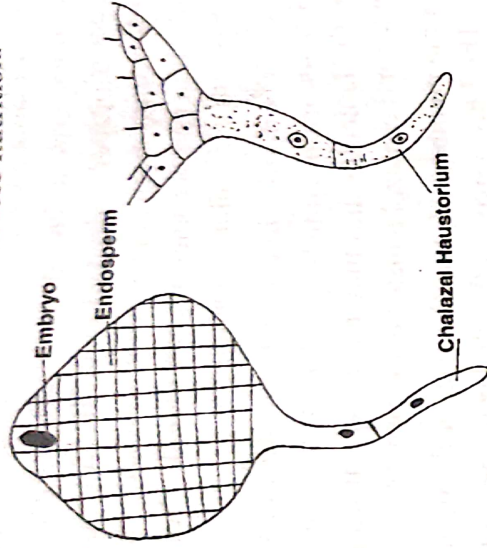


Fig. 6-7 : Endosperm haustorium - *Magnolia obovata*

Micropylar haustoria are known to occur in *Impatiens roylei* and *Hydrocera triflora*. In *Magnolia obovata*, the chalazal haustorium is 2-celled. The first division of PEN is followed by a transverse wall resulting into two equal chambers. Divisions in the micropylar chamber are rapid and in all directions. This results in a chamber divides transversely and at a comparatively slow rate. The micropylar tail-like chalazal part attached to the massive nucellar tissue at the micropylar end.

In *Melampyrum lineare* (*Orobanchaceae*) and *Blumenbachia insignis*, (*Loasaceae*) both chalazal and micropylar haustoria are present. In *Melampyrum*, the micropylar

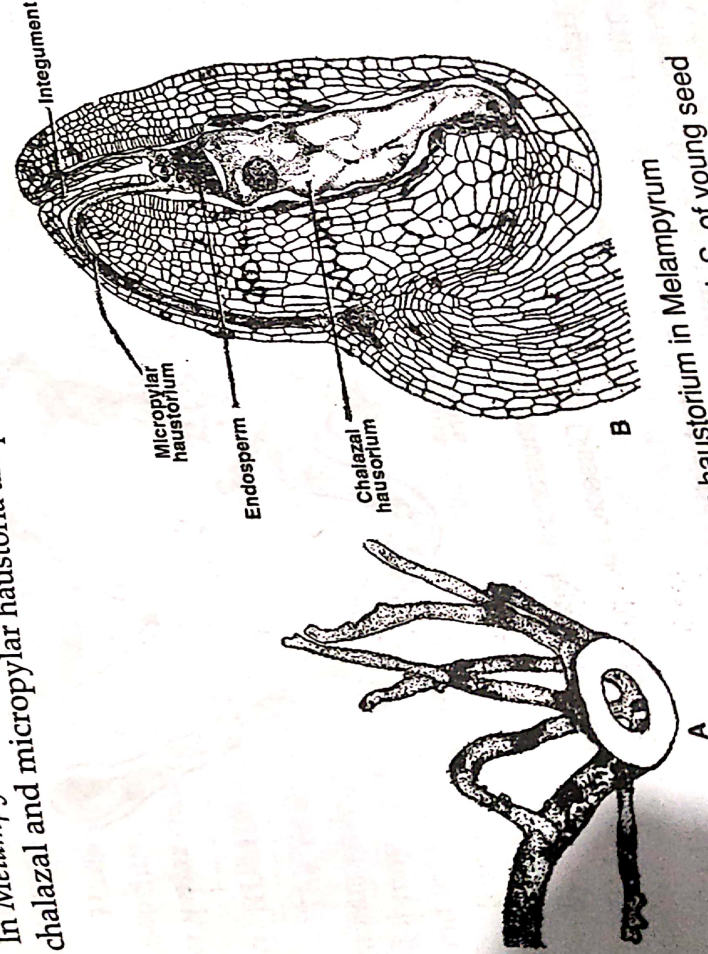


Fig. 6-8 : Endosperm haustorium in *Melampyrum*
(A) Dissected out micropylar haustorium ; (B) L.S. of young seed

haustorium comprises a single, 4-nucleate cell with many tubular processes. Some of these processes enlarge and enter the funiculus. The chalazal haustorium is a multinucleate cell, broader above and narrower below.

In *Iodina rhombifolia* (Santalaceae), a very aggressive chalazal haustorium is formed. The primary endosperm nucleus dives to form a micropylar and a chalazal chamber. The endosperm proper is derived from the micropylar and a chalazal chamber functions as an aggressive uninucleate chamber. The chalazal chamber migrates into the haustorium and becomes hypertrophied. Profuse branching at the free end gives the haustorium, a coralloid appearance.

In *Nemophila*, the PEN divides into two equal cells, of which the lower functions as chalazal haustorium sometimes, it may form a long lateral branch which penetrates into the funiculus and may reach even upto Placenta. In *Lobelia*, both micropylar and chalazal haustoria are formed.

In *Ruellia* and some members of *Acanthaceae*, both micropylar and chalazal haustoria are formed. The PEN moves to the chalazal end of the embryo-sac, divides forming a smaller chalazal chamber and a larger upper chamber. The chalazal chamber gives rise to haustorium that remains coenocytic. The micropylar chamber divides transversely and its upper cell gives rise to micropylar haustorium. The central cells forms the endosperm proper.

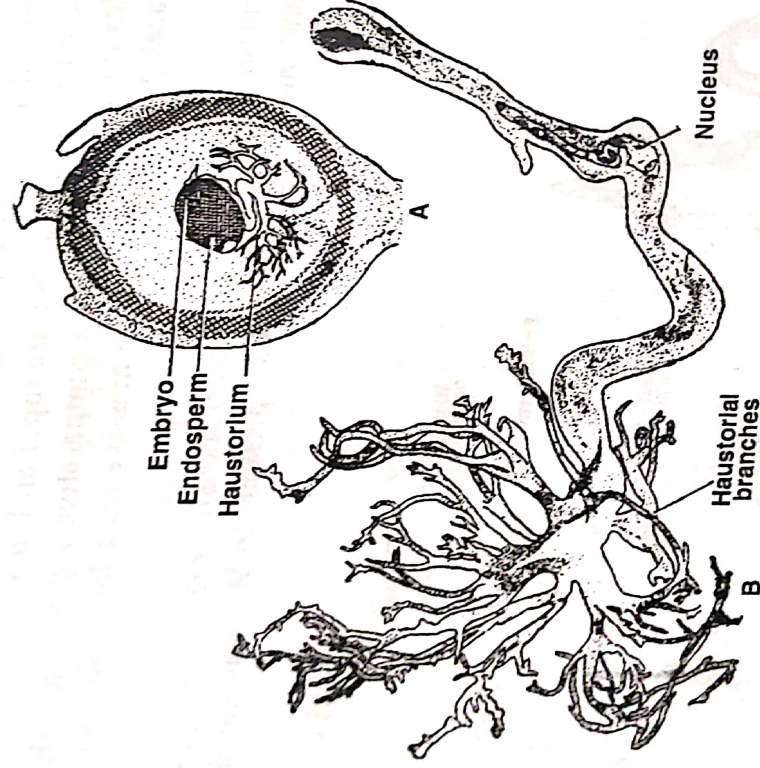


Fig. 6-9 : Endosperm haustorium - *Iodina rhombifolia*
(A) L.S. of fruit (B) Dissected out haustorium

III Helobial Endosperm :

This type of endosperm is characteristic of the Helobiae and confined only to some monocotyledonous families. e.g. *Haemanthus*, *Zephyranthes*, *Juncus*, *Eremurus*, *Asphodelus*. This is an intermediate type between nuclear and cellular endosperms.

The primary endosperm nucleus moves towards the chalazal end of the embryo sac. Here it divides to form a large micropylar and a small chalazal endosperm chamber. In the micropylar chamber several free nuclear divisions takes place ; cell wall formation, if any, begins at a much later stage. The chalazal chamber behaves differently and its nucleus may or may not divide. It usually remains coenocytic. In *Phyllidrum lanuginosum*, it may become cellular.

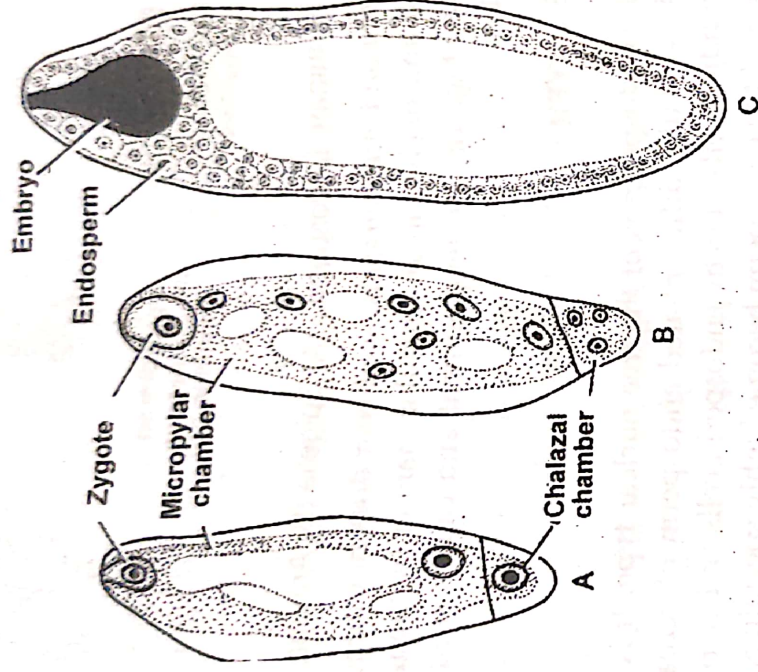


Fig. 6-10 : Helobial type of Endosperm - Eremurus

Haustoria : In *Asphodelus*, the chalazal chamber grows into a hedge - shaped haustorium. In *Monochoria*, the haustoria develop from the lateral sides of the micropylar chamber.

6-3 RUMINATE ENDOSPERM

The endosperm with uneven or irregularities on its surface is known as *ruminata endosperm*. Rumination starts at a later stage of endosperm development and it may be cellular, nuclear or helobial type. Ruminata endosperm is commonly found in Annonaceae, Myristicaceae, Araliaceae and many Arecaceae.

Rumination is caused by the activity of the seed coat or by the endosperm itself. In the former case, the irregularities on the inner surface of the seed coat may arise by :

- (i) Unequal radial elongation of cells of any one layer of the seed coat e.g. *Passiflora calcarata*.
- (ii) Definite ingrowth or infolding of the integuments (seed coat). This is brought about either by excessive elongation or enlargement of cells of the seed coat (e.g. *Annona squamosa*, *Artabotrys blumei*) or by localised meristematic activity of the cells of the seed coat (e.g. *Myristica fragrans*, *Diospyros chloroxylon* and ruminata seeds of palmae).

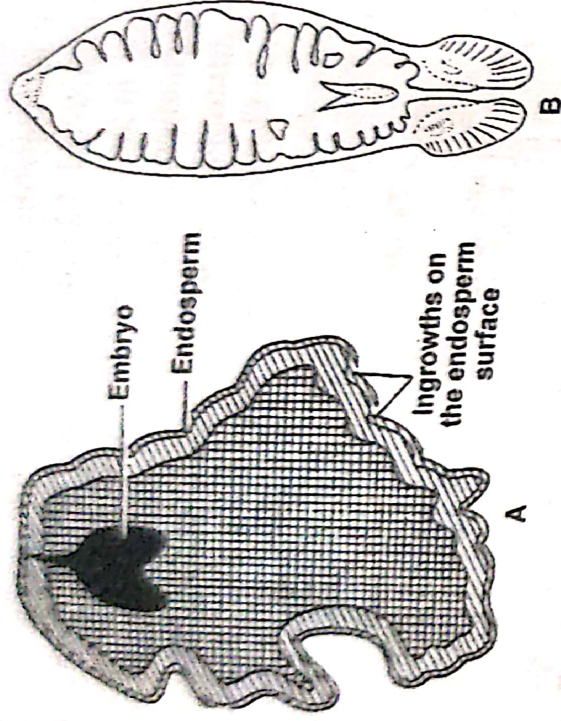


Fig. 6.11 : Ruminant Endosperm - (A) *Spigelia* (B) *Annona squamosa*

□ (iii) In *Elettaria* and *Andrographis*, seed coat does not form infoldings, but activity during late stage of its development and causes seed coat to attain an irregular configuration.

6-4 ALEURONE LAYER

In cereals, the endosperm is of the free nuclear type. It is generally starchy and dry at maturity. Fully differentiated endosperm of cereals show Transverse cells, Embryo surrounding cells, starchy endosperm cells and aleurone cells. One or two outermost layers of the endosperm become highly specialized morphologically and physiologically to form the aleurone tissue. In barley (*Hordeum vulgare*) the tissue is 3 - 4 layered. The aleurone cells are alive, whereas the starchy endosperm is surrounded by aleurone cells is a dead tissue. Aleurone layer protects the endosperm from desiccation and enables it to survive during seed drying.

Aleurone cells are morphologically distinct in different cereals. In *Setaria*, the aleurone cells near the placental vascular supply are columnar and show wall ingrowths. These cells help in transferring substances from the vascular tissue to the embryo proper and endosperm proper. So they have been named as *transfer cells* (T C). T C have also been observed in *Echinochloa* and *Zea mays*, but they are absent in rice and wheat.

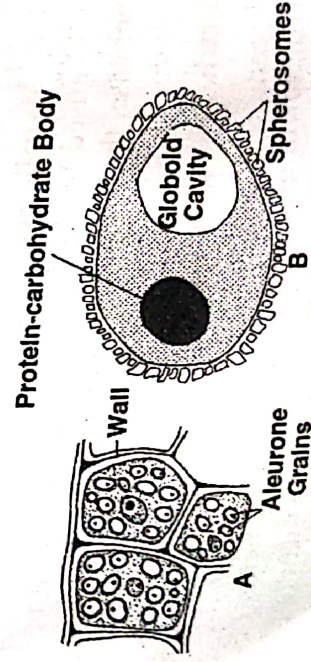


Fig. 6.12 : Aleurone layer of Barley
(A) Aleurone cells (B) Single grain enlarged

The aleurone cells show thick cellulose walls and non vacuolated dense cytoplasm. The cells are interconnected by plasmodesmata. The aleurone cells possess aleurone grains and spherosomes. An aleurone grain is surrounded by a single unit membrane, which is closely associated with spherosomes. The main components of the aleurone grains are proteins, phytin, phospholipids and some carbohydrates. Each of these components occur as discrete particles in the cells. In the matrix, a proteinaceous *crystalloid body* and a non - proteinaceous spherical body, the *globoid* are embedded. The globoids present within the globoid cavity contain phytin and lipids.

During seed germination, the reserve food (starch and protein) present in the endosperm cells is digested by the activity of hydrolytic enzymes (amylases, proteases) which are secreted by the aleurone cells. Gibberellins have been shown to activate these enzymes or induce their de - novo synthesis. Besides the biological importance, the aleurone layer us also of practical importance. Almost half of the cereal bran is composed of aleurone cells.

Functions of Endosperm:

1. The endosperm is an important nutrient medium for the successful development of the embryo. It is rich in fats, carbohydrates and proteins. During seed germination, these substances are digested and utilized for the growth of the seedling.
2. The young endosperm is rich in growth hormones like auxins, gibberellins and cytokinins. The young endosperm of maize contains a cytokinin called *zeatin*. Hence coconut milk and extracts of corn are frequently used as a nutrient medium in embryo culture technique.
3. Endosperm regulates the precise mode of embryo development. In the absence of endosperm, very young embryos often fail to mature even in the richest artificial nutrient medium.

Questions

1. Describe the structure and development of endosperm in angiosperms. Add a note on its significance.
2. Write short notes on :
 - (a) Nuclear endosperm.
 - (b) Cellular endosperm.
 - (c) Helobial endosperm.
 - (d) Endosperm haustoria.
 - (e) Ruminant endosperm.
 - (f) Aleurone layer.