

PLANT STRUCTURE AND DEVELOPMENT

M.Sc. BOTANY

SEMESTER-II, PAPER-IV

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FOREWORD

Since its establishment in 1976, Acharya Nagarjuna University has been forging ahead in the path of progress and dynamism, offering a variety of courses and research contributions. I am extremely happy that by gaining 'A+' grade from the NAAC in the year 2024, Acharya Nagarjuna University is offering educational opportunities at the UG, PG levels apart from research degrees to students from over 221 affiliated colleges spread over the two districts of Guntur and Prakasam.

The University has also started the Centre for Distance Education in 2003-04 with the aim of taking higher education to the door step of all the sectors of the society. The centre will be a great help to those who cannot join in colleges, those who cannot afford the exorbitant fees as regular students, and even to housewives desirous of pursuing higher studies. Acharya Nagarjuna University has started offering B.Sc., B.A., B.B.A., and B.Com. courses at the Degree level and M.A., M.Com., M.Sc., M.B.A., and L.L.M., courses at the PG level from the academic year 2003-2004 onwards.

To facilitate easier understanding by students studying through the distance mode, these self-instruction materials have been prepared by eminent and experienced teachers. The lessons have been drafted with great care and expertise in the stipulated time by these teachers. Constructive ideas and scholarly suggestions are welcome from students and teachers involved respectively. Such ideas will be incorporated for the greater efficacy of this distance mode of education. For clarification of doubts and feedback, weekly classes and contact classes will be arranged at the UG and PG levels respectively.

It is my aim that students getting higher education through the Centre for Distance Education should improve their qualification, have better employment opportunities and in turn be part of country's progress. It is my fond desire that in the years to come, the Centre for Distance Education will go from strength to strength in the form of new courses and by catering to larger number of people. My congratulations to all the Directors, Academic Coordinators, Editors and Lesson-writers of the Centre who have helped in these endeavors.

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M.Sc. BOTANY
SEMESTER-II, PAPER-IV
204BO24-PLANT STRUCTURE AND DEVELOPMENT

SYLLABUS

UNIT-I

Lesson 1: Types and Functions of Meristems, Organization of Shoot Apical Meristem (SAM)

Lesson 2: Root Apical Meristem (RAM), and Floral Meristems and MADS-Box Genes.

Lesson 3: Structure and Function of Vascular Cambium; and Xylem

Lesson 4: Structure and Functions of Phloem

UNIT-II

Lesson 5: Anatomy of the Stem

Lesson 6: Secondary Growth in Dicots and Monocots.

Lesson 7: Wood: Heart Wood and Sap Wood, Porous and Nonporous Wood, Reaction Wood

Lesson 8: Anomalous Secondary Growth in Dicots and Monocots.

UNIT-III

Lesson 9: Anatomy of the Root

Lesson 10: Structure, Development and Evolution of Leaf and Stomata

Lesson 11: Structure, Development and Evolution of Nodes

UNIT-IV

Lesson 12: Plant Endosperm Development, Stages, Cell Division and Pattern Formation in Embryo

Lesson 13: Plant Embryo Development, Stages, Cell Division and Pattern Formation in Embryo

Lesson 14: Seed Structure and Anatomy of Seed Formation.

UNIT- V

Lesson 15: Seed Dormancy and Barriers Effect Seed Dormancy

Lesson 16: Applications of Anatomy

Lesson 17: Applications of Anatomy in Taxonomy

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MODEL QUESTION PAPER

(204BO24)

M.Sc. DEGREE EXAMINATION, BOTANY - SECOND SEMESTER PLANT STRUCTURE AND DEVELOPMENT

Time: Three hours

Maximum: 70 marks

Answer All Questions

5 × 14 = 70M

Each Question carries equal marks

UNIT-I

- 1) a) Give a detailed note on shoot apical meristems

OR

- b) Give a detailed note on root apical meristems

UNIT-II

- 2) a) Give a detailed note on different types of wood.

OR

- b) Give a detailed note on the structure, types and functions of special tissues

UNIT-III

- 3) a) Give a detailed note on the anatomical adaptations of the Kranz pathway

OR

- b) Give a detailed note on the anatomical adaptations of the CAM pathway

UNIT-IV

- 4) a) Give a detailed note on plant embryo development.

OR

- b) Give a detailed note on the seed germination process

UNIT-V

- 5) a) Give a detailed note on the seed germination process

OR

- b) Give a detailed note on senescence

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LESSON-1

TYPES AND FUNCTIONS OF MERISTEMS AND SHOOT APICAL MERISTEM (SAM)

1.0. OBJECTIVE:

- In this chapter history of plant anatomy various types of meristems and theories with reference to their organization and function of Shoot Apical Meristem (SAM) and have been discussed.

STRUCTURE:

- 1.1 Introduction**
- 1.2 Classification of Meristems Based on Origin and Development**
- 1.3 Classification on the Basis of Position**
- 1.4 Classification on the Basis of Function**
- 1.5 Based on Plane of Cell Division**
- 1.6 Shoot Apex**
- 1.7 NEWMAN'S Classification of Shoot Apices**
- 1.8 Summary**
- 1.9 Model Questions**
- 1.10 References**

1.1. INTRODUCTION:

Plants are multicellular eukaryotes with tissue systems made of various cell types that carry out specific functions. Plant tissue systems fall into two general types: Meristematic tissue, and permanent (or non-meristematic) tissue. Cells of the meristematic tissue are found in meristems, which are plant regions of continuous cell division and growth. Meristematic tissue cells are either undifferentiated or incompletely differentiated, and they continue to divide and contribute to the growth of the plant. In contrast, permanent tissue consists of plant cells that are no longer actively dividing. Meristems produce cells that quickly differentiate, or specialize, and become permanent tissue. Such cells take on specific roles and lose their ability to divide further. They differentiate into three main types: dermal, vascular, and ground tissue.

Meristematic Tissues:

In the early stages of the embryo development, cell division occurs throughout the young plant let. But as soon as the embryo develops and converts into an independent plant, the addition of new cells is restricted to certain localized parts of the plant body. The growth of plants occurs only in certain specific regions. This is because the dividing tissue, also known as meristematic tissue, is located only at the growing points. These juvenile tissues, primarily concerned with growth, are known as the meristems. Because of activity of meristematic cells, growth occurs throughout the life of the plant. In this respect, plants differ from animals.

The term 'meristem' was derived from the Greek Word 'meristos' which means 'divisible'. It was coined by C. NAGELI in 1858. A meristematic tissue consists of a group of young cells that are in a continuous state of division (or) retain their power of division.

Cells of the Meristematic Tissues show the following features:

- 1) The meristematic tissue consists of young cells which are in a state of active division and cause growth.
- 2) The cells may be rounded, oval or rectangular in shape.
- 3) The cells are compactly arranged without inter- cellular spaces. The cells have thin walls.
- 4) The cells possess abundant cytoplasm and a prominent nucleus.
- 5) These cells do not show any reserve food material and are in an active state of metabolism.
- 6) The vacuoles in the cells are smaller in size or may be absent.
- 7) The cells show immature plastids called Proplastids and poorly developed endoplasmic reticulum.

1.2. CLASSIFICATION OF MERISTEMS BASED ON ORIGIN AND DEVELOPMENT:

On the basis of origin and development of initiating cells, three types have been recognized.

- (i) Promeristem or primordial meristem - It is a group of earliest and youngest meristematic cells of a growing organ, it is the early embryonic meristem from which other advanced meristems, such as shoot apex and root apex, are derived. Promeristem P further divides and forms primary meristem.
- (ii) Primary meristem - It is found at the tips of shoot, root and appendages. Cambium is also a primary meristem. It is responsible for formation of primary plant body.
- (iii) Secondary meristem - It is derived from the primary permanent tissues. Vascular cambium and cork cambium are the examples of secondary meristem and they are located at the lateral side of organ. It is responsible for formation of secondary plant body.

1.3. CLASSIFICATION ON THE BASIS OF POSITION:

On the basis, of their position in, the plant body, meristems are recognized into three.

(i) Apical Meristems:

They found in the apices of shoot (Fig. 1.1, 1.2) and root, and bring about increase in length. It includes both promeristem and primary meristem meristematic cells undergo divisions and give rise to derivatives. These derivatives are differentiated into tissue and tissue systems (Fig. 1.1) of various organs of the plant body.

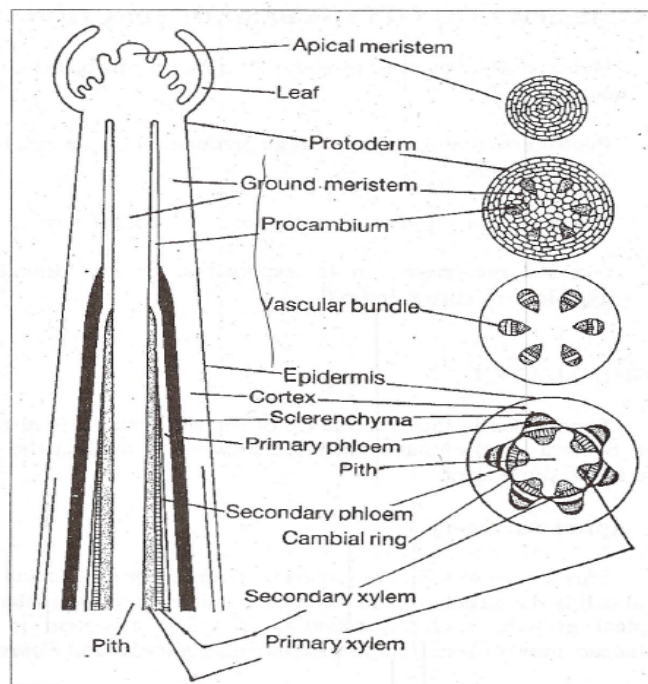


Fig. 1.1: Longitudinal and Transverse, Sections of Various Regions of Shoot Apex showing Different Stages of Tissue Differentiation

(ii) Intercalary Meristem:

It is also a primary meristem and lies in between the permanent tissues (Fig. 1.2). It is found in various places, e.g. at the base of leaf in *Pinus*, at the base of internode in grasses and *Equisetum*, and below the node of *Mentha*.

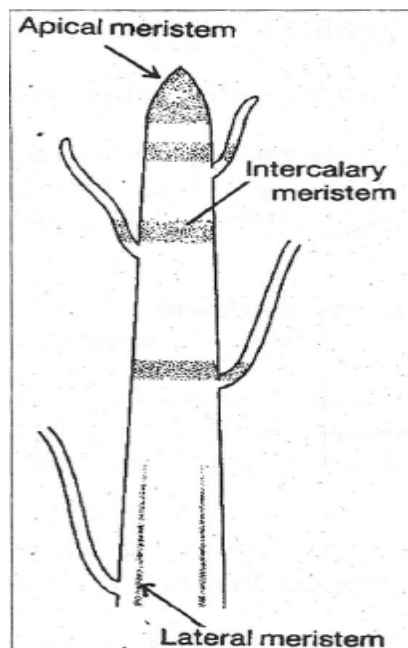


Fig. 1.2. Schematic Representation of Position of Different Meristems

(iii) Lateral Meristem:

It is a secondary meristem, arranged parallel to the sides of organs (Fig; 1.2) and normally divide periclinally or radially: Vascular cambium and cork cambium are common examples of lateral meristem, responsible for the formation of secondary structures and involve in the increase of diameter of the organ.

1.4. CLASSIFICATION ON THE BASIS OF FUNCTION:

Heberland recognized three types of meristems based on their functions.

- i) Protoderm - It is a meristematic precursor for epidermal tissue system.
- ii) Pro Cambium - It gives rise to primary vascular tissues.
- iii) Ground Meristem - It is responsible for the formation of ground tissue system, i.e., hypodermis, cortex and pith.

1.5. BASED ON PLANE OF CELL DIVISION:

The plane of division in meristematic cells is of considerable importance in determining growth patterns. On the basis of the plane of cell division, three types of meristems are recognized. They include -

- 1) **Rib (or) File Meristem:** The cells of the rib meristem divide only anticlinally, at right angles to the surface of axis of a growing organ. This results in the formation of long rows (or) of cells. The cortex and pith of young stems and roots originate from the cells of rib meristem.
- 2) **Plate meristem:** These cells divide chiefly anticlinally in two planes, so that new cells are formed but the number of layers does not increase. It helps in the formation of flat structures such as leaf blades and epidermis.
- 3) **Mass meristem:** The cells divide in all planes resulting in an increase in volume. This meristem plays an important role in the early development of embryo, endosperm, sporangia etc.,

1.6. SHOOT APEX:

Shoot apex is found at the tip of the shoot and it is responsible for the formation of entire shoot. Several theories have been put forward to explain the organization and mode of growth found in the shoot apex.

Apical Cell Theory:

This theory was first proposed by Hofmeister (1857) and advanced by Naegeli (1878). Single apical cell is the structural and functional unit of apical meristem which governs the entire process of apical growth, such organization of apical meristem is found in the algae, bryophytes, Psilotaceae most of ferns, some species of Selaginella and Equisetum.

Histogen Theory:

Hanstein (1868) postulated this theory and recognized three meristematic zones, also known as histogens or tissue builders, in the apical region (Figs. 1.3; L11). The histogens

arise from separate group of initials and have different mode of development, these three histogens are (a) dermatogen, the outermost uniseriate layer, (b) periblem, the middle region composed of isodiametric cells (c) Plerome, the central mass of cells. Each histogen has definite function. The dermatogen cells divide anticlinal direction and give rise to epidermis, the periblem forms the cortex and Plerome forms the stele (vascular tissues, pericycle, pith, rays etc.). There is another histogen, known as calyptragen, that gives rise to the root cap, in monocots. In dicots, calyptragen, responsible for the formation of both epidermis and root cap is found, e.g. members of Rosaceae, Solanaceae Cruciferae, Scrophulariaceae, Compositae etc.

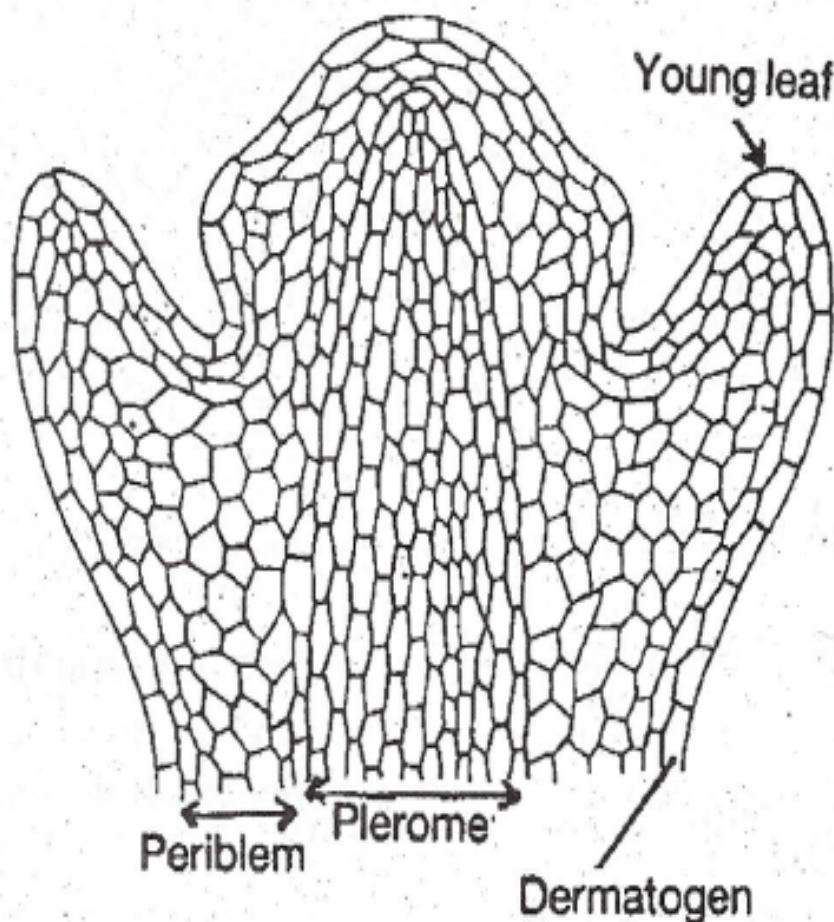


Fig. 1.3: Longitudinal Section of Growing Shoot Apex showing Histogens

Tunica-Corpus Theory:

This theory was proposed by Schmidt (1924). According to him, there are two zones in the apical meristem, (a) **tunica**, the cells of which undergo anticlinal divisions only and responsible for the formation of the epidermis; (b) **corpus** in which cells are undergoing divisions in various planes and form the central part of the shoot (Fig. 1.4). Corpus contains undifferentiated, multi layered mass of cells surrounded by tunica. Tunica and corpus have their own initials. The number of tiers of apical initials is varied from species to species. In angiosperm shoot apices, there are 3 tiers of apical initials, the first two tiers are **tunica initials** and third one is **corpus** initials.

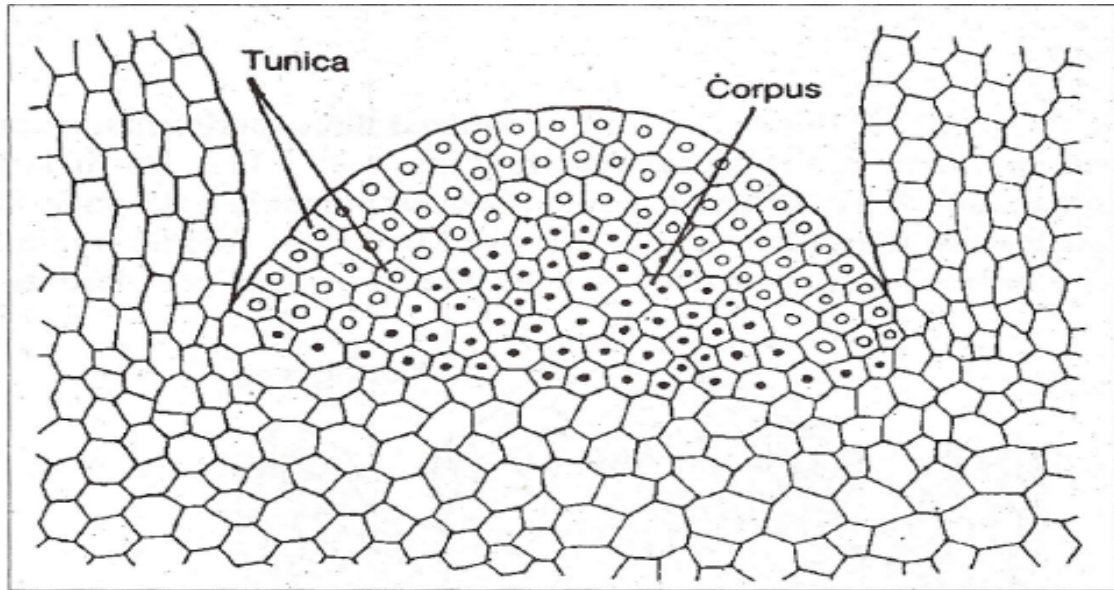


Fig. 1.4: Longi Section Through Shoot Apex showing Tunica - Corpus Organization

As the Tunica-corpus theory is based on plane of divisions, **mantle-core** hypothesis of Popham and Chan (1950) does not give importance of plane of divisions. The term **mantle** equiva to tunica includes all the outer layers of apex and **core** (equivalent to corpus) to the mass of cells surrounded by mantle (Fig. 1.5).

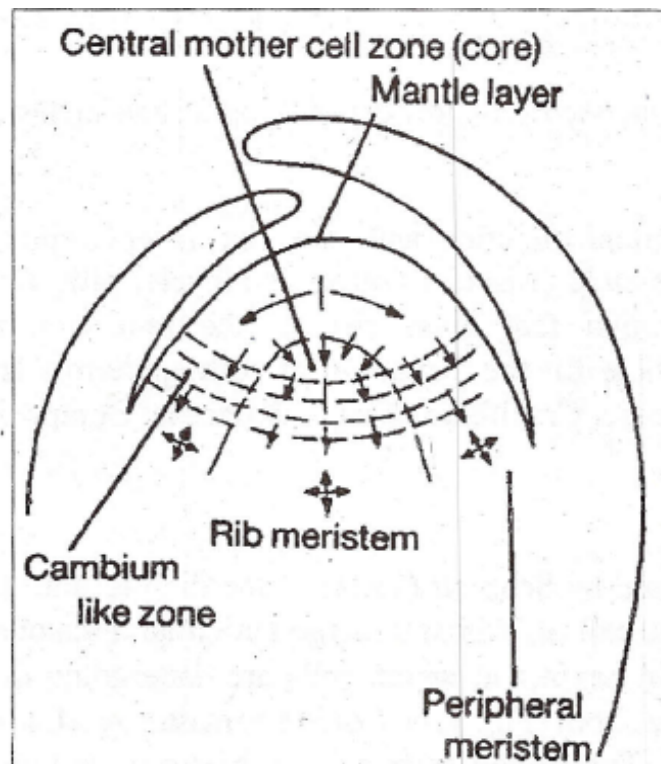


Fig. 1.5: Cytohistological Zonation of Gymnosperm Shoot Apex proposed by Foster (1941)

Forster (1939) has recognised cytohistological zonation in the shoot apex of *Ginkgo biloba* using dyes. Similar zonation had also observed by Clowes (1961) in angiosperms. According to Foster, four cytologically and histologically differentiated zonation are found in the shoot apex (Fig. 1.6).

These are as follows:

- a) Group of apical initials at the distal end of shoot apex contribute cells to surface layer by anticlinal divisions and, central mother cell zone by periclinal divisions.
- b) Central mother cell zone is sustaining and maintaining the organization of shoot apex; these cells are larger and lightly stained but contribute cells to peripheral meristem.
- c) Peripheral of flank. Meristem is located on either side of the central mother cell zone. These cells are smaller with densely stained larger nucleus. It is an actively dividing zone, also described as *EU meristem* (true meristem) from which all the tissues and tissue systems including leaf primordia are differentiated.
- d) Rib meristem cells are smaller and arranged in TOWS; cells with smaller nucleus stained scanty. It is responsible for the formation of pith region of stem.

Apical Initial Group:

According to Buvat (1955) the peripheral and subterminal regions are real initiating zones whereas distal zone is inert in nature. French School recognised three distinct regions in apical meristem (FigJ.7). These are as follows:

- i) The annual initial (*ai*; initiating ring) is peripheral active zone from which all the tissues and tissue systems, and leaf primordia are differentiated.
- ii) The meristem attente (*ma*, waiting meristem) is said to be waiting for the change from vegetative to reproductive stage before taking up its meristematic activity. It consists of two subzones: (a) promeristeme sporogene (*pursp*) and (b) promeristeme recepticulaire (*pmr*). These two subzones are active during reproductive phase of the shoot apex.
- iii) The meristem medullaire (Pith meristem) gives rise to the pith region of the stem. Promeristeme

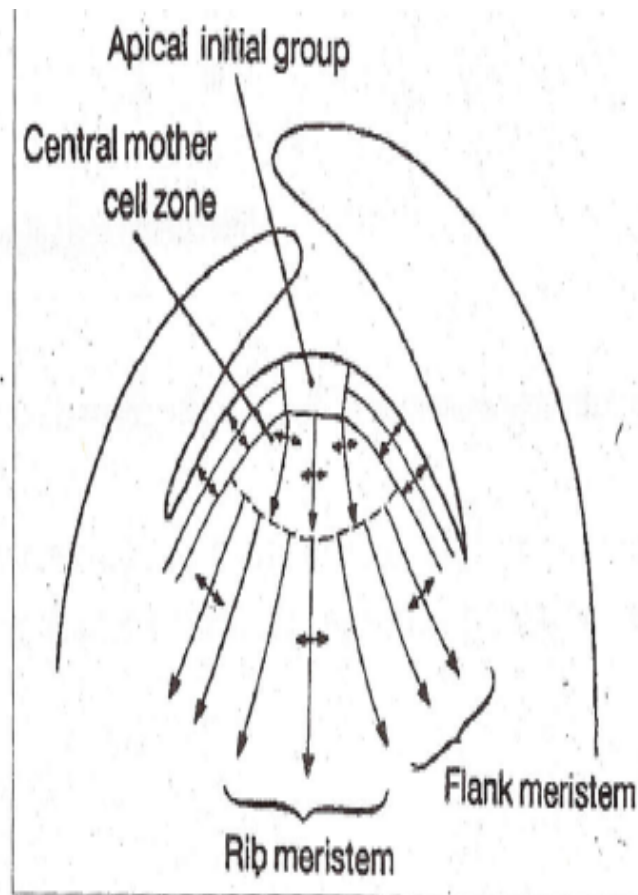


Fig. 1.6: L.S. of Shoot Apex of *Ginkgo biloba* showing Cytohistological zones

1.3...5 Buvat's (French School) Concept of Shoot Apex Organization:

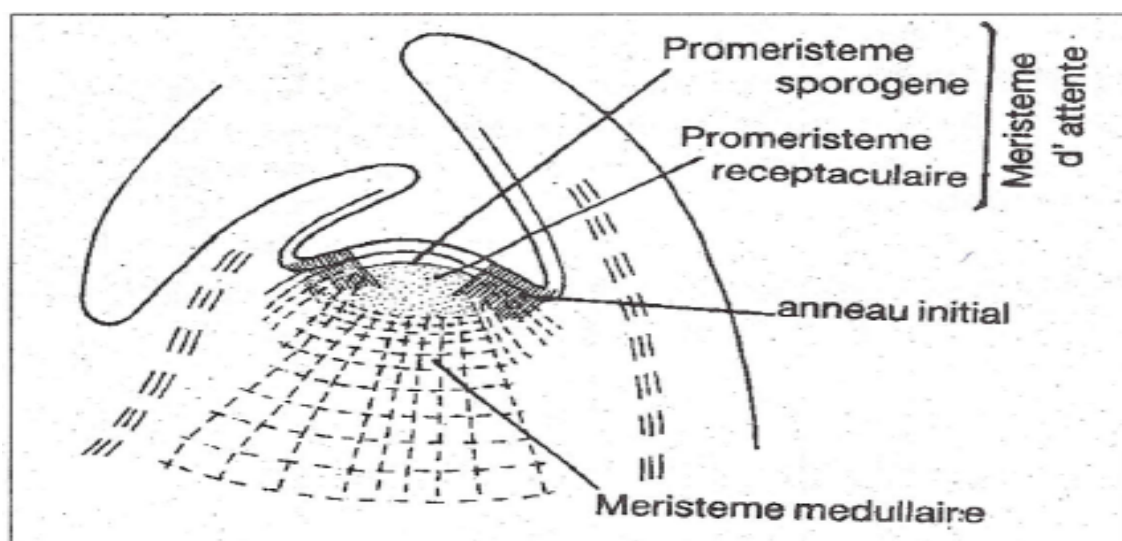


Fig. 1.7. Schematic Representation of Buvat's Concept of Shoot Apex Organization

The concept of the inactive distal zone in the apical meristem was extended from the shoots of angiosperms to those of the gymnosperms and the lower vascular plants.

3...5 Origin of Leaf:

Leaf primordium is initiated by periclinal divisions in peripheral meristem. In angiosperms, both tunica and corpus are responsible for leaf initiation. The time taken between the initiation of two successive leaf primordia is known as plastochron. During plastochron period, shoot apex undergoes some changes; these changes are known as plastochronic changes.

These are:

(A) minimal phase and (B) maximal phase of shoot apex. Before the initiation of leaf primordium, the apical meristem appears as a small, rounded mound (Fig. 1.8 A, B), this is the minimal phase during which shoot apex is preparing for the initiation of leaf. It gradually widens and reached to maximal phase (Fig. 1.8 C, D). Now leaf buttresses are initiated in its sides. Once the leaf buttress is initiated, then it again reaches to minimal phase. Leaf buttress later forms the leaf axis, eventually it develops into leaf. Similar changes are taken place in the shoot apex during 'formation of branches.

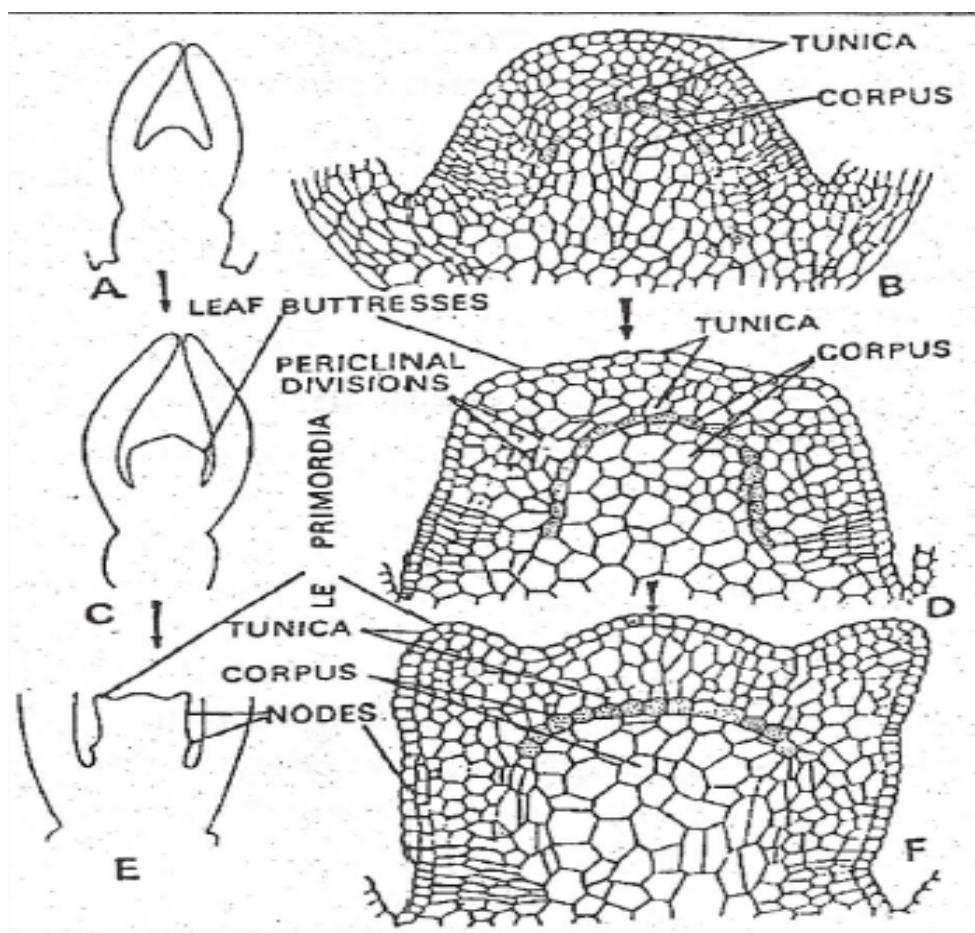


Fig. 1.8 A-F. Leaf Initiation in Shoot Apex of *Hypericum*. A, B. Minimal Phase; C, D. Maximal Phase; E, F. Minimal Phase

1.7. NEWMAN'S CLASSIFICATION OF SHOOT APICES:

Newman (1965) used the term continuous meristematic residue (*cmr*) to refer to a group of permanent initials in the shoot apex, and on the basis of form of the *cmr*, shoot apices are divided into following types:

- i) Monoplex type is the characteristic of ferns, in which *cmr* is in the superficial layer only. Any one cell contributes to growth in both length and breadth (Fig. 1.9A).

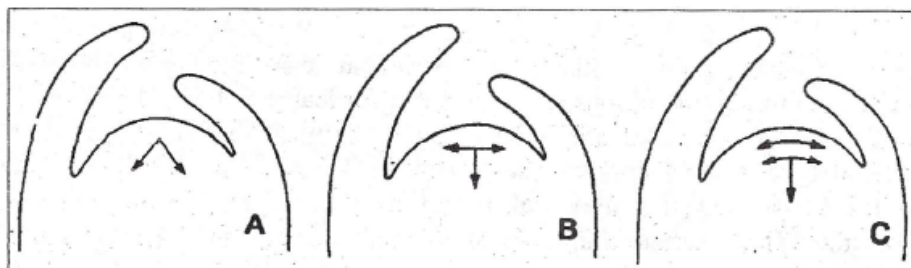


Fig. 1.9. Schematic Representation of Newman's Shoot Apices
A. Monoplex, B. Simplex, C. Duplex

- ii) Simplex type is common in gymnosperms. The *cmr* is restricted to a single layer. Cells are undergoing divisions both periclinal and anticlinal (Fig. 1.9B). Both the divisions are necessary for bulk growth.
- iii) Duplex is common in Angiosperms. The *cmr* is present in two layers, the first layer undergoes anticlinal divisions and second layer periclinal divisions. Thus, two contrasted mode of growth are evident, hence this renowned as duplex type of shoot apex (Fig. 1.9C)

1.8. SUMMARY:

Meristem is undifferentiated tissue capable of undergoing divisions. Primary meristems (derived from embryonic tissues) such as shoot apex and root apex are responsible for formation of primary plant body, whereas secondary meristems (secondarily originated) are for the secondary plant body. Based on their position, meristems are classified as apical, intercalary and lateral meristems. Vascular cambium and periderm are the examples of lateral meristem that are responsible for secondary plant body

There are several theories explaining the organization and function of shoot apices: (i) Apical cell theory, (ii) Histogen theory, (iii) Tunica - corpus theory (iv) Foster's cytohistological zonation of gymnosperm shoot apex, and (v) Buvat's concept. (French School). Among these, tunica - corpus theory is directly applicable to angiosperm shoot apices. Tunica cells undergo only anticlinal divisions and give rise to epidermis whereas corpus cells in various planes and form the central part of the shoot. According to French School, the distal zone, known as meristematic attitude, is said to be waiting for the change from vegetative to reproductive stage before taking up its meristematic activity. The anther initial is a peripheral active zone from which all the tissues and tissue systems, and leaf primordia are differentiated. Vascular cambium and periderm are the examples of lateral meristem that are responsible for secondary plant body

1.9. MODEL QUESTIONS:

- 1) Describe the Apical Cell Theory
- 2) Describe Histogen's Theory
- 3) Describe the Tunica- Corpus Theory
- 4) Explaining Cytological Zonation of Gymnosperm Shoot Apex
- 5) Buvat's Concept
- 6) Describe the Classification of Meristems based on Origin and Development
- 7) Explain the Classification on the Basis of Position
- 8) Explain the Classification on the Basis of Function

1.10. REFERENCES:

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Prof. K. Mallikarjuna

LESSON-2

ROOT APICAL MERISTEM (RAM) AND FLORAL MERISTEMS AND MADS-BOX GENES

2.0 OBJECTIVE:

- In this chapter. history of plant anatomy, various types of shoot apical meristems and theories with reference to their organization and function have been discussed.

STRUCTURE:

2.1 Root Apex

2.1.1 Cellular Organisation of Distal Zone of Root Apex

2.1.2 Theories related to Root Apex Organization

2.2 Floral Meristem: Introduction

2.2.1 Floral Meristems

2.3 MADS-Box Genes

2.4 Floral Organ Identity

2.5 Mads-Box Genes are Involved in Floral Development and Evolution

2.6 The Floral Bauplan

2.7 Functions of Mad Box Genes

2.8 Summary

2.9 Model Questions

2.10 Reference Books

2.1. ROOT APEX

Root apex differs from shoot apex in certain aspects: (a) due to presence of root cap, root apex is subterminal in position; (b) it does not form lateral appendages comparable to leaves, branches etc., (c) it does not show any periodic changes, and (d) it does not produce nodes and internodes.

2.1.1. Cellular Organisation of Distal Zone of Root Apex

The principal configuration of root apex is given in Fig. 2.1, in which the distal zone is represented as containing the initials (shown in black). In the lower vascular plants all tissues are derived from a single apical initial (Fig. 2.1 A), e.g. members of Equisetaceae, Polypodiaceae etc.

In *Pseudotsuga*, several initials arranged in a single tier (Fig. 2.1) initiate the mother-cell zones *Adiantum*.

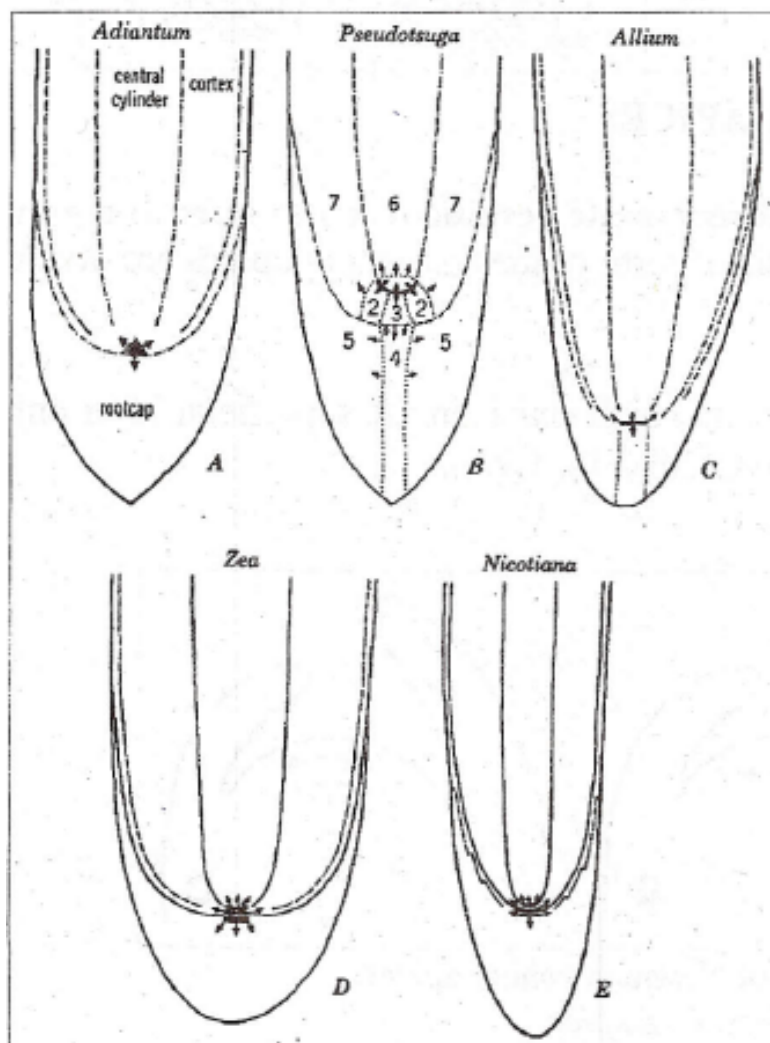


Fig. 2.1: A-E. Cellular Organisation of Root Apex:

- A. A single apical initial responsible for all parts of root and root-cap;
- B. A single tier of initials (black arc) initiates mother-cell zones of various parts of root as follows: 1 of central cylinder (6), 2 of cortex (7), 3 of column of root cap (4); C. a single tier of initials without clear mother-cell zones is the source of central cylinder, cortex and column;
- D. three tiers of initials in the initial zone, first related to central cylinder, second to cortex and third to root cap and epidermis differentiates from the outermost layer of the cortex;
- E. similar to D but epidermis originates from the root cap by periclinal divisions.

In *Allium* (Fig. 2.1 c), a single tier of initials, without clear-cut mother cell zones, is the source of root and root cap. In angiosperms, various parts of root are derived from separate tiers of initials. In monocots, three tiers of initials are located on the root apex, first gives rise to central cylinder, second to cortex and third tier (also known as calyptragen of Hanstein) to the root cap; epidermis differentiates from the outer most layer of the cortex (Fig. 2.1D). Similar type of cellular organization is found in dicots also but epidermis differentiates from the root cap by periclinal divisions (Fig. 2.1E). According to Hanstein, the histogen which gives rise to both root cap and epidermis, is known as *dermato calyptragen*. Presence of dermato calyptragen is the characteristic feature of dicots, e.g. members of Compositae, Cruciferae, Rosaceae, Scrophulariaceae and Rosaceae.

2.1.2. Theories related to Root Apex Organization:

Several theories have been proposed to describe the organization of root apex.

These are

- (i) Haustein's Histogen Theory,
- (ii) Korper-Kappe Theory, and
- (iii) Concept of Quiescent Centre.

i) **Histogen Theory** - please see section (ii) of this chapter for details.

This theory is more appropriate to explain the organization of root apex

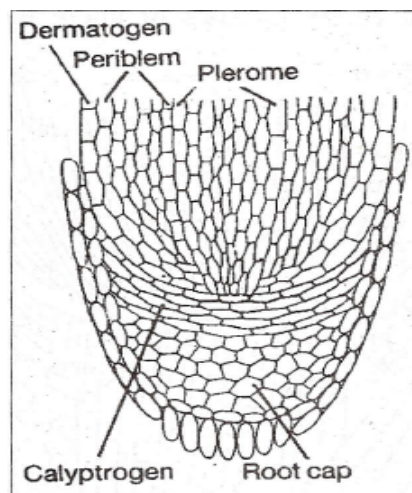


Fig. 2.2: Longisection of Root apex showing Different Histogens

ii) **Korper-Kappe theory (Body - Cap Concept)** - Schoepp (1917) proposed that the cells at the root apex divide into two planes (Fig. 2.2). The zone with inverted 'T' type of division is referred to as Korper (body) and in the body part, daughter cell away from apex undergoes division; whereas other with straight 'T' as Kappe (cap). This type of organization is found in some ferns.

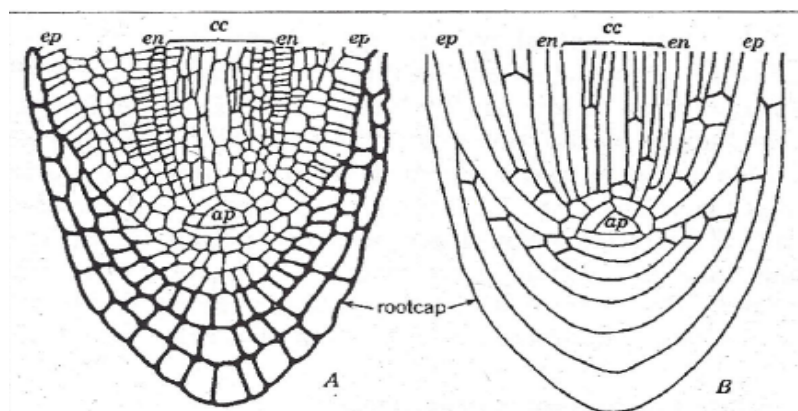


Fig. 2.3. A-B. Root tip of a fern. A. Organization of root apex with an apical cell (cp), B. Interpretation of Korper-Kappa concept i.e., epidermis; cc, central cylinder; en, endodermis).

iii) Concept of Quiescent Centre - Clowes (1958) reported that the distal region enclosed by the cup-shaped group of initials is quiescent (inactive) (Fig. 2.4). Clowes in his autoradiographic studies of DNA synthesis noted that the cells of this inactive zone have fewer mitochondria and endoplasmic reticulum, very small, faintly stained nuclei and low rate of DNA and protein synthesis.

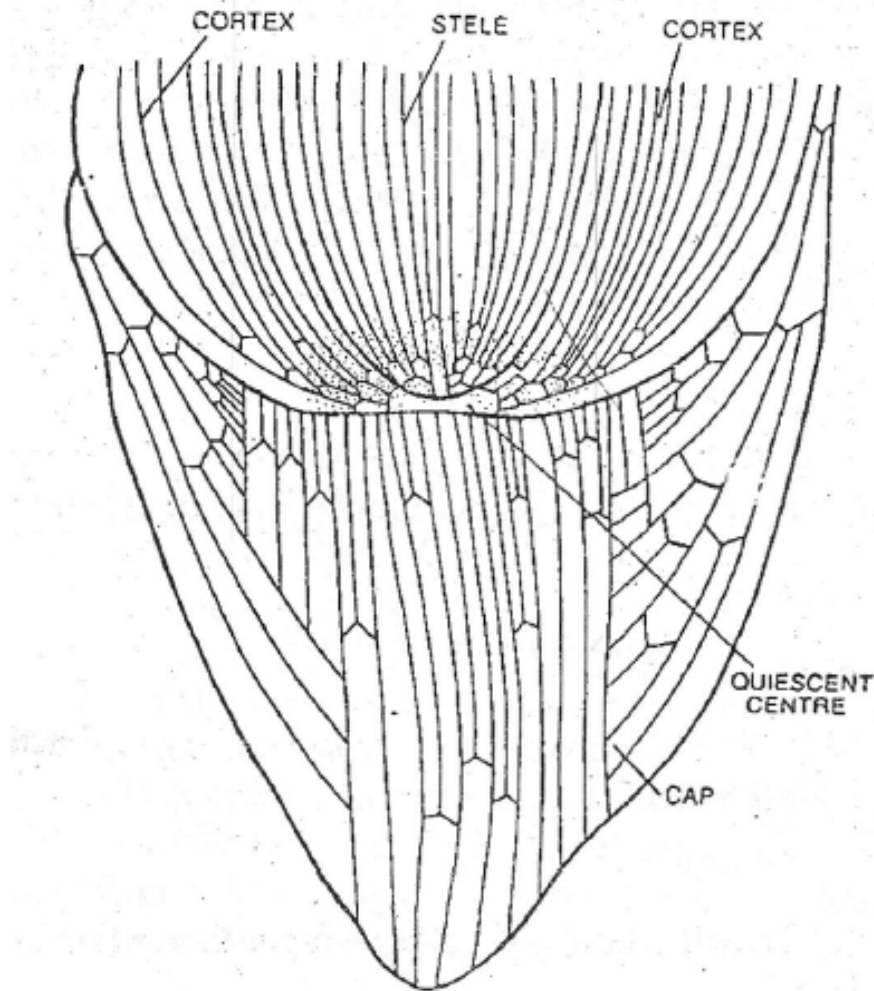


Fig.2.4: Root Apex in *Zea mays* indicating Quiescent Centre

Quiescent centre consists of about 500 cells in *Zea mays*, 600 in *Sinapis alba* and 1100 in *Vicia faba*. Generally, the cells of quiescent centre do not divide, but may divide occasionally when previously active initials are damaged. Thus, this region acts as reservoir of cells, relatively resistant to damage and irradiations because of their inactivity.

2.2. FLORAL MERISTEMS: INTRODUCTION

Floral meristems are the cell clusters that give rise to flowers, and MADS-box genes are a family of genes that are crucial for this process. MADS-box genes act as transcription factors to specify both the floral meristem's identity and the identity of the individual floral organs, such as sepals, petals, stamens, and carpels, in a process described by the ABC Model of floral development.

2.2.1. Floral Meristems:

A floral meristem is a type of shoot apical meristem that forms flowers. It is identified by its larger size compared to a vegetative meristem due to rapid cell division. MADS-box genes are involved in specifying its identity and regulating its transition from vegetative to generative growth.

2.3. MADS-BOX GENES:

These genes encode transcription factors that control a wide range of developmental processes, with a major role in floral development. They are named after a conserved region called the "MADS-box" found in genes from various organisms. In plants, the proteins encoded by MADS-box genes (especially the MIKC type) have a DNA-binding M-domain and a keratin-like K-domain.

Role in floral development

2.4. FLORAL ORGAN IDENTITY:

A combination of different MADS-box genes determines which type of organ forms at each position in the flower. The ABCDE model describes how different combinations of these genes, grouped into classes A, B, C, D, and E, specify the development of sepals, petals, stamens, and carpels. For example, loss-of-function mutants in certain MADS-box genes can result in the formation of incorrect floral organs, such as petals instead of sepals or stamens instead of carpels.

Meristem Determinacy:

MADS-box genes, such as the AGAMOUS (~~AG~~AG) gene, also regulate the "determinacy" of the floral meristem, which controls the number of floral organs that are produced before the meristem switches from producing flowers to producing a new meristem.

2.5. MADS-BOX GENES ARE INVOLVED IN FLORAL DEVELOPMENT AND EVOLUTION:

In higher plants most of the well-characterized genes are involved in floral development. They control the transition from vegetative to generative growth and determine inflorescence meristem identity. They specify floral organ identity as outlined in the ABC model of floral development. Moreover, in *Antirrhinum majus* the MADS-box gene products DEF/GLO and PLE control cell proliferation in the developing flower bud. In this species the DEF/GLO and the SQUA proteins form a ternary complex which determines the overall Bauplan of the flower. Phylogenetic reconstructions of MADS-box sequences obtained from ferns, gymnosperms and higher eudicots reveal that, although ferns possess already MIKC type genes, these are not orthologous to the well characterized MADS-box genes from gymnosperms or angiosperms. Putative orthologs of floral homeotic B- and C-function genes have been identified in different gymnosperms suggesting that these genes evolved some 300-400 million years ago. Both gymnosperms and angiosperms also contain a hitherto unknown sister clade of the B-genes, which we termed Bsister. A novel hypothesis will be described suggesting that B and Bsister might be involved in sex determination of male and female reproductive organs, respectively. If the default program of plant growth is flowering,

then a repressor is required to ensure vegetative growth of the plant. Indeed, recessive mutations are known in *Arabidopsis*

Two such repressor-encoding genes were identified to belong to the MADS-box gene family of transcription factors. However, in a certain developmental stage of plant growth and upon receiving the correct environmental signal phase transition occurs leading to the formation of an inflorescence thus initiating the generative mode of growth.

At the base of floral development two genes both in *Arabidopsis thaliana* and in *Antirrhinum majus* are of importance, *Leafy/ Apetala 1* and *Floricula/Squamosa* respectively. Recessive mutants do not form floral primordia but instead produce secondary inflorescences. Hence the above genes control flower meristem identity. *Apetala 1* and *Squamosa* encode MADS-box proteins. Further floral development is guided by a series of interacting MADS-box proteins.

How they act and how they specify the floral “Bauplan” will be described for *Antirrhinum majus*. In addition, the phylogeny of MADS-box genes will be described as well as possible scenarios for the origin of angiosperm flowers.

2.6. THE FLORAL BAUPLAN:

Floral organs in most eudicots are arranged in whorls, as in *Antirrhinum majus*, a representative of this group of plants. Its floral “Bauplan” is shown in Fig. 2.5.

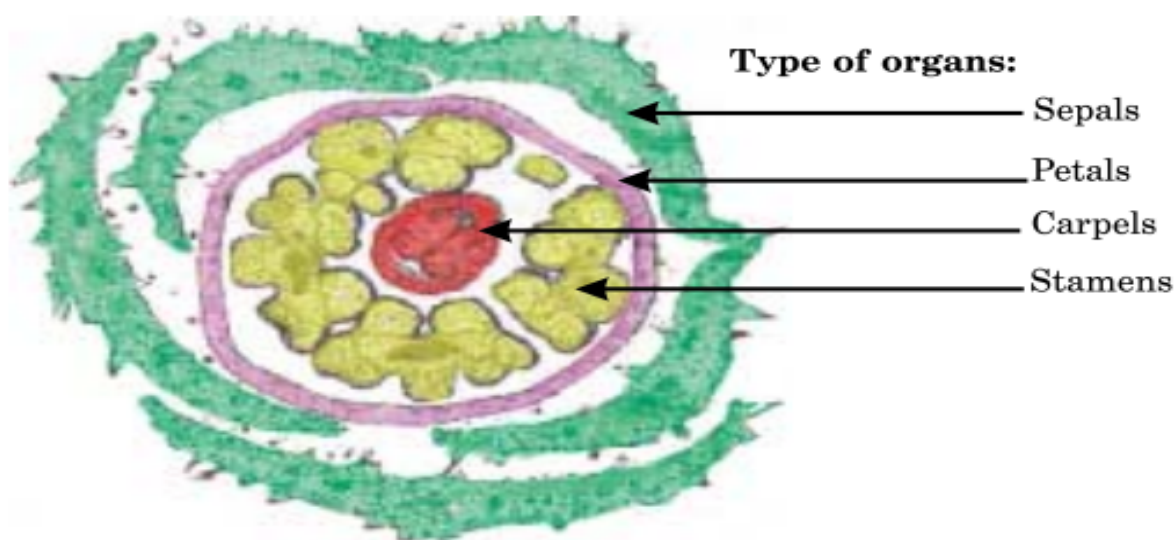


Fig. 2.5: Bauplan of Antirrhinum Majus

Number of organs / whorl. In this case are 5 for w1, w2 (fused to a tube and seen here as a ring) and w3, while w4 has only 2 carpels. Arrangement of organs either is whorled as shown here, decussate or spiral as in some other plants

The outermost whorl (w1) features five green sepals, while w2 holds five colored petals, which are fused to form a tubular structure with protruding lobes (Fig. 3a). These two whorls form the perianth, the protective organs. Further inside follow the sexual organs: w3 is male and features 4 stamens and 1 stamenoid, while the innermost female whorl (w4) contains a bilocular gynoecium. The numbers of organs, the types of organs and their

arrangement characterize the “Bauplan”. MADS-box genes seem to control these features. This is the subject of what follows. **THE ABC MODEL** The model is based on homeotic mutations in *Antirrhinum majus* and *Arabidopsis thaliana*, resulting in phenotypic replacements of organs in two adjacent whorls. Three classes of mutants are observed leading to the ABC model (Fig. 2.5):

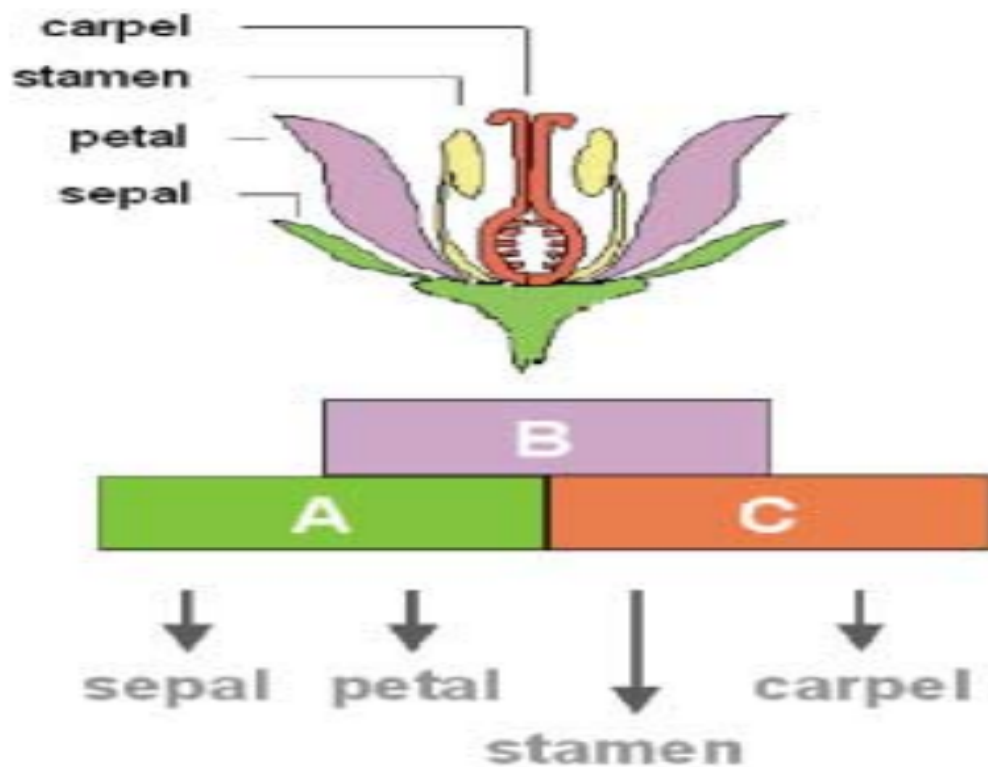


Fig. 2.6: The ABC Model

352 MADS-box genes 2001 Figure 1. Bauplan of *Antirrhinum majus*. Number of organs/whorls. In this case are 5 for w1, w2 (fused to a tube and seen here as a ring) and w3, while w4 has only 2 carpels. Arrangement of organs either is whorled as shown here, or decussate or spiral as in some other plants. Cross-section through a flower. uA-function mutants have organ replacements in w1 and w2... Instead of sepals and petals they feature carpeloid and stamenoid organs, respectively. uB-mutants have altered organs in w2 and w3 where sepals and carpels are formed; these are thus male sterile. uC-mutants feature no sexual organs at all; petals and sepals replace stamens and carpels in w3 and w4, respectively. All said, the three functions seem to specify organ identity in a combinatorial way: The A-function specifies sepals and together with the B-function petals, while B- and C-functions are needed for stamens and C-function alone determines carpel formation. However, there are also differences between species. In *Antirrhinum* for example, no recessive A-function mutations are found. Rather the A mutant phenotype is triggered in this species by a dominant mutation in a C-function gene indicating that the ABC model may be of mnemotechnic value, but certainly is not applicable to all species in its simplistic form. Nonetheless, MADS-box genes encode ABC functions, which will be described below for *Antirrhinum majus*.

2.7. FUNCTION OF THE MADS-BOX GENES:

Plant MADS-box genes encode transcription factors with MIKC domain structure. The M-domain represents the DNA-binding domain, while I is an intervening and K is a Keratin-like domain and is involved in protein–protein interactions as is the C-terminal domain in certain MADS-box proteins. A-function genes The *Squamosa* gene of *Antirrhinum majus* (Huijser et. al., 1992) encodes a protein orthologous to *Apetala 1* (Mandel et. al., 1992), one of the A-function genes of *Arabidopsis thaliana*. Nonetheless, *squamosa* mutants do not reveal an A-function deficient phenotype, but they produce secondary inflorescences instead of flowers. Therefore, *Squamosa* seems to be involved in floral meristem identity. On top of that, in conjunction with B-function genes, *Squamosa* is also involved in determining the floral “Bauplan”. B-function genes *Deficient* and *Globosa* are two genes located on different chromosomes in *A. majus* (Sommer et. al., 1990; Schwarz-Sommer et. al., 1990; Tröbner et. al., 1992)

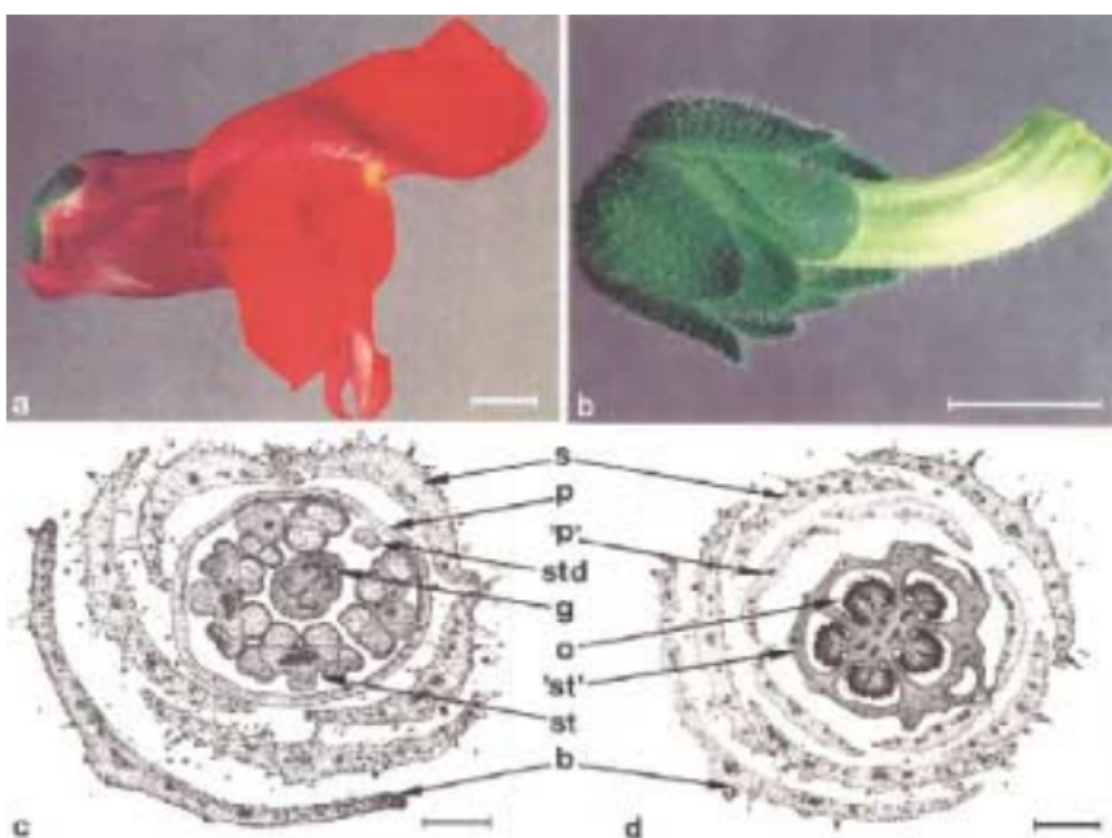


Fig. 2.7: Mutant Phenotype of B-Function Genes

Mutant phenotype of B-function genes (b, d) compared to wild type (a, c) in *Antirrhinum* mutants in each of them result in the almost same homeotic phenotype. Instead of petals a second whorl of sepals is formed in *w2*, and in *w3* carpels replace stamens and form a tubular structure (Fig. 3b and d). *w4* is missing altogether as can be seen in the cross section in Fig. 3d. *DEF* and *GLO* form the B-function and determine organ identity.

The ABC model note cell proliferation and as will be shown later they are involved in determining the floral “Bauplan” as well.

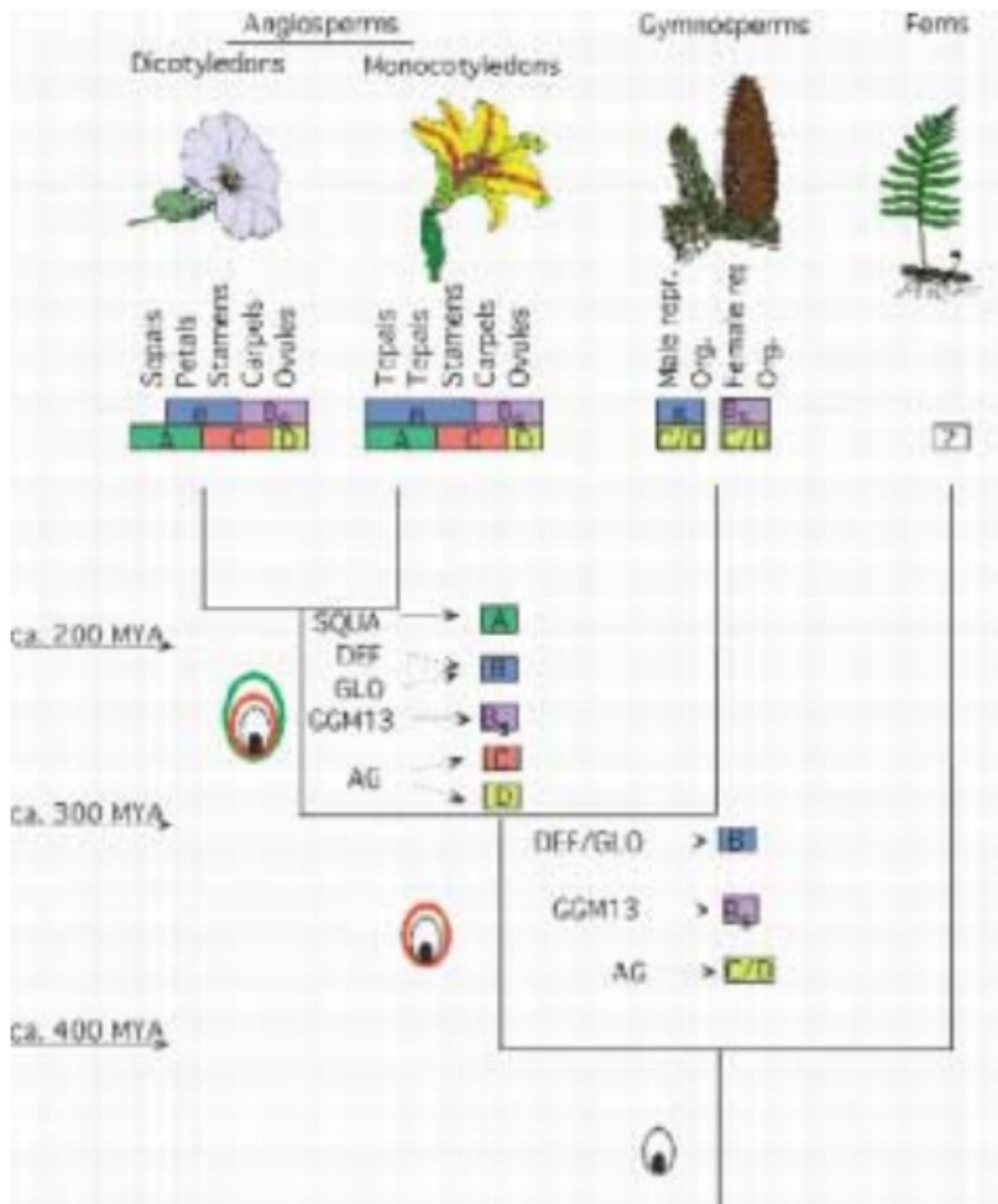


Fig. 2.8: Phylogeny of Major Land Plant Taxa and the Evolution of Floral Homeotic Functions

Phylogeny of major land plant taxa and the evolution of floral homeotic functions. EXPRESSION OF B AND Bs in contrast to the B genes, which are predominantly expressed in male reproductive organs in both gymnosperms and angiosperms, expression of the Bs genes was found to be predominantly in female reproductive organs in *Gnetum gnemon* (Fig.2.8).



Fig. 2.9: Expression of B and B's Gene of *Gnetumgnemoin*

Moreover, we could show that a Bs gene isolated from *Zea mays* was also predominantly expressed in female organs. A

2.8. SUMMARY:

The organization and function of root apex is explained by (i) Hanstein's Histogen theory; (ii) Schuepp's Korper-Kappe theory, and (iii) Clowes quiescent centre concept. The above-mentioned data suggest an ancestral system for the specification of reproductive organ identity which was established at the base of extant seed plants, about 300 MYA. We assume that it is the ancestral function of C genes to distinguish between reproductive (C expression on) and non-reproductive organs (C expression off). Superimposed is the differential expression of B (and probably also Bs) genes to discriminate between male and female reproductive organs. This possibly represents the ancestral sex determination system of extant seed plants. A superclade of B and Bs genes played an important role during two key innovative events in the evolution of seed plant reproductive structures. First, the establishment of distinct male B and female Bs gene lineages after duplication of an ancestral gene may have been a crucial event during the origin of male macrosporophylls and female megasporophylls (400-300 MYA). Second, during flower origin (300-200 MYA), expression of the Bs genes expanded into one of the key structures of angiosperms, the carpel, while B expression and function expanded into the petal, another evolutionary novelty of flowering plants. These hypotheses provide novel starting points for scenarios, which describe how flowers may have evolved out of gymnosperm cones.

2.9. MODEL QUESTIONS:

- 1) Explain Theories related to Root Apex
- 2) Short Answer Questions
- 3) Histogen theory, (B) French School (C) Tunica-Corpus theory (D) Quiescent Centre Concept (E) Korper-Kappe theory

- 4) Write about Floral Meristems, 2.3 MAD-Box Genes and Floral Identity
- 5) Explain how Mads-Box Genes Are Involved in Floral Development and Evolution
- 6) What is the Floral Bauplan
- 7) Write about the functions of Mad Box Genes

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LESSON-3

STRUCTURE AND FUNCTION OF VASCULAR CAMBIUM, XYLEM

3.0 OBJECTIVE:

- This lesson able to understand Structure and function of vascular cambium and complex tissues.

STRUCTURE:

3.1 Structure and Function of Vascular Cambium

3.1.1 Organization

3.1.2. Fusiform Initial

3.1.3. Ray Initials

3.1.4. Developmental Changes

3.1.5 Seasonal Changes

3.2 Xylem

3.3 Elements of the Xylem

3.3.1. Tracheary Elements

3.4 Vessels or Trachea

3.5 Xylem Fibres

3.6 Xylem Parenchyma

3.7 Phylogenetic and Ontogenetic Specializations of Xylem

3.8 Morphological Specialization in the Primitive Vessel Element

3.9 Axial Parenchyma

3.10 Ray Parenchyma

3.11 Summary

3.12 Model Question Papers

3.13 References

3.1. STRUCTURE AND FUNCTION OF VASCULAR CAMBIUM:

Vascular cambium produces; 1. Internally xylem (wood) a complex tissue that contains vessels, tracheids. wood fibers (libriform tracheids and fiber tracheids) and parenchyma (rays and axial parenchyma)

3... Externally 2° phloem - inner bark, a complex tissue. phloem, composed of companion cells and sieve tube members or albuminous cells and sieve cells, fibers and parenchyma - (rays and axial parenchyma)

3.1.1 Organization:

Meristematic cells of the vascular cambium somewhat different from those seen in the apical meristem ((Figure 3.1). Two types of initials in the vascular cambium: fusiform and ray initials

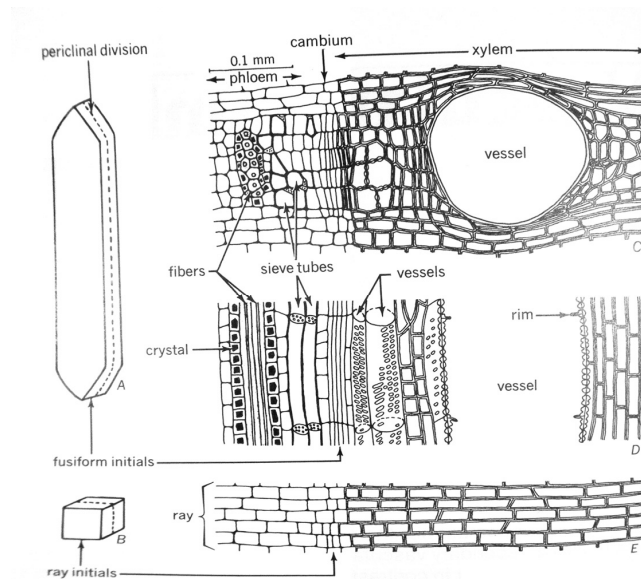


Fig. 3.1: Meristematic Cells of the Vascular Cambium

3.1.2. Fusiform Initial:

Fusiform initials are elongated to isodiametric in shape, fusiform = spindle shaped, really prismatic, wedge-shaped ends. How they look in section: fusiform shape in tangential section, rectangular in radial section, smaller rectangle in transverse (cross) section. Derivatives of fusiform initials constitute the axial and radial systems. Produce the axial elements, i.e. those oriented longitudinally. The cambium cell arrangement determines the organization of the secondary vascular tissues.

Eg. In the transverse section of *Pinus* wood, the tracheids form uniform pattern of radial rows, each tracheid being the daughter cell of the same fusiform initial. Another good example of this is the storied wood of *Wisteria* and the non-storied wood of *Rhus* (fig 3.1)

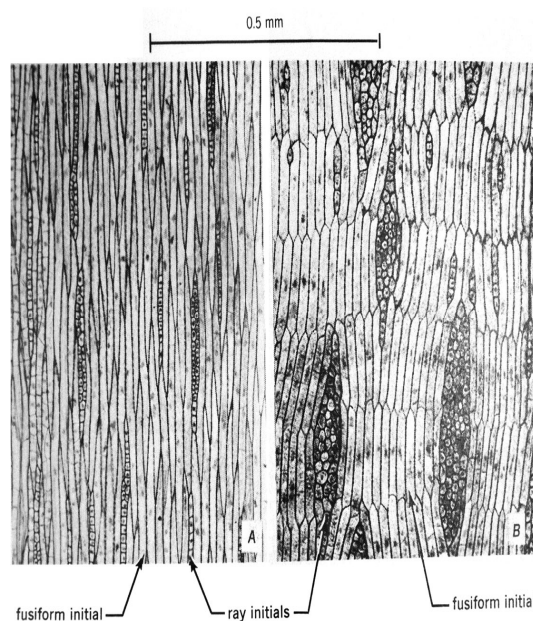


Fig. 3.2: Fusiform Initial and Ray Initials

Cambial initials are usually bifacial, which means they produce cells off of two sides. They divide periclinally to produce xylem to the inside and phloem to the outside, sometimes alternating. Periclinal divisions that add to the diameter (width) of the stem are called Additive (also called Proliferative) Divisions. They give radial files of the cells as seen in XS of the stem. 2) If cells are on only one side, the vascular cambium is called unifacial. Unifacial vascular cambia make either 2° xylem or 2° phloem, as was the case with early fossil land plants, pteridophytes, lycophytes, and in leaf veins.

3.1.3. Ray Initials

Ray initials produce ray cells - ray parenchyma and are present in groups. Ray initials are rectangular in tangential, radial and cross sections. Ray initials form at a constant rate from the fusiform initials. Cell division patterns are complex and vary between different plant taxa. Transverse divisions of the fusiform initial results in several cells, only some of which may survive and become ray initials.

Rays begin as a group of only 1-2 cells but they increase in height through later transverse divisions and by fusion with other rays. To become multiseriate, radial anticlinal divisions and fusions occur.

3.1.4. Developmental Changes

- 1) As the stem increases in width, the vascular cambium must adjust. How it does this is complex, involving anticlinal (not periclinal, as above) cell divisions, intrusive growth, elimination of initials, and conversion of fusiform initial to ray initials.
- 2) Anticlinal divisions = multiplicative divisions. These increase the number of cells in the vascular cambium. Example for *Pinus* (at arrow). Several types (Figure 3.....)
 - a) Radial anticlinal. Cell divided longitudinally, new wall connects to radial walls (ends)
 - b) Lateral anticlinal. Cell divided longitudinally, new wall connects to opposite ends of same lateral wall.
 - c) Oblique anticlinal (= pseudo transverse). Cell divided longitudinally, new wall connects in an inclined fashion between two different lateral walls. Example: *Juglans* (Figure 3...4).
- 3) Radial anticlinal divisions give more vascular cambium cells that are arranged in stacks, gives rise to storied wood (considered an advanced condition). The oblique divisions result in non-storied wood, no tiers of cells.

3.1.5. Seasonal Changes:

- 1) Fusiform initials, and their derivatives, are shorter at the end of the growing season compared with the cells formed at the beginning.
- 2) In conifers, spiral grain is caused by periodic changes in the orientations of the walls set up during the anticlinal cell divisions - forms panels or domains of cells. Figure 12.12 from Evert.
- 3) Cytokinesis in fusiform initials. See Figure 3.7 which shows the phragmoplast and cell plate in these cells that must divide longitudinally. Figure 3.6 B shows periclinal divisions in the cambium of *Cryptocarya* forking and invasion of rays (Figure 3.5 H-L, Figure 3.6 C) which may result in the ray splitting.

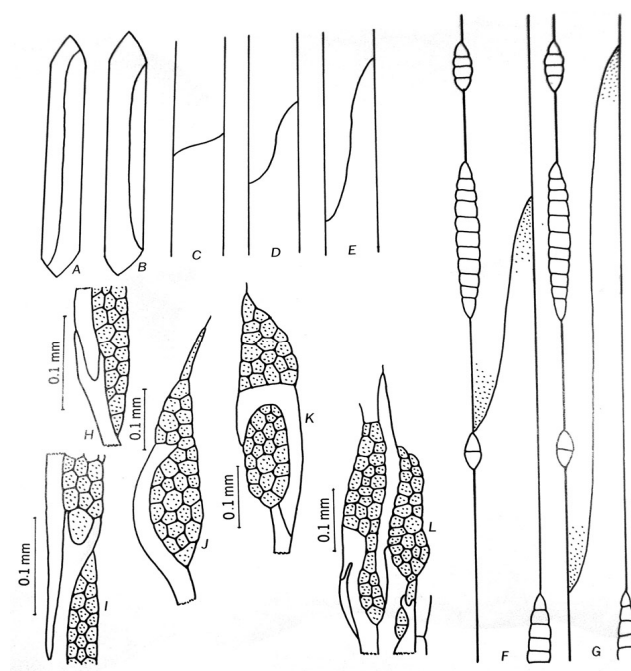


Fig. 3.3: Types of Cells in the Vascular Cambium of Pinus

3.2. XYLEM

The vascular system of plant is composed of two types of complex tissues, namely xylem and phloem. Xylem involves in the conduction of water and provides mechanical strength to the plant body whereas phloem in conduction of food materials. Both are found in Tracheophyte. Structurally xylem consists of both living and non-living cells. The most important components of xylem are tracheary elements which include tracheids and vessels; other constituents are the xylem fibres and xylem Parenchyma. Generally, primary xylem is derived from pro cambium whereas secondary xylem from vascular cambium.

3.3. ELEMENTS OF THE XYLEM:

3.3.1. Tracheary Elements:

The term Tracheary element is derived from 'trachea', a name originally applied to certain primary xylem elements resembling insect trachea. Tracheids and vessel members are two fundamental types of tracheary elements. Both are devoid of protoplast and hence these are dead cells.

Tracheids:

Tracheid is an elongated structure with tapering ends. It has got hard; thick and lignified walls and a large lumen. The tracheids are considered as primitive and found in the ancient vascular plants. These are the only elements found in the fossil seed plants.

A tracheid differs from xylem fibres in having: (i) the cell wall comparatively less lignified, (ii) large number of pits, (iii) bordered pits and (iv) a very large lumen. Lignified secondary walls are highly characteristic and these are deposited in different pattern such as annular (ring type, Fig. 3.1A), spiral (Fig. 3.1D); scalariform (ladder type, Fig. 3.1E), reticulate and pitted (Fig. 3.1F).

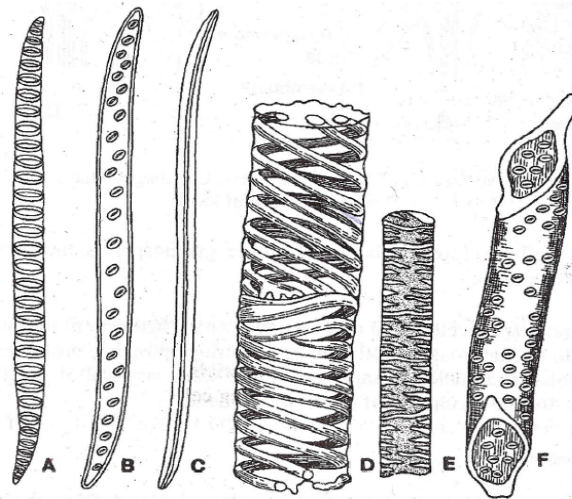


Fig. 3.4 Different types of Tracheids.

A. annular, Band C. Tracheidal fibres, D. Spiral, E. Scalariform and F. Pitted

Generally, tracheids with annular and spiral thickenings are found in the early formed primary xylem whereas scalariform and pitted tracheids in later formed primary xylem and also in secondary xylem. Pitted tracheids are common in tracheophyte. In this case, the entire inner surface of the cell wall is thickened except for certain unthickened circular areas which are known as pits (Fig. 3.4 F).

Two types of pits are recognised; these are simple and bordered. Simple pits are the areas with only primary wall without any secondary thickening. The bordered pits are, however, complicated with secondary wall thickenings, bordering the small perforation in the middle (Fig. 3.4 A, B). The primary wall develops a thickening in the central part of the pit, known as torus (Fig. 3.5 B, C, D).

Pitted Vessel

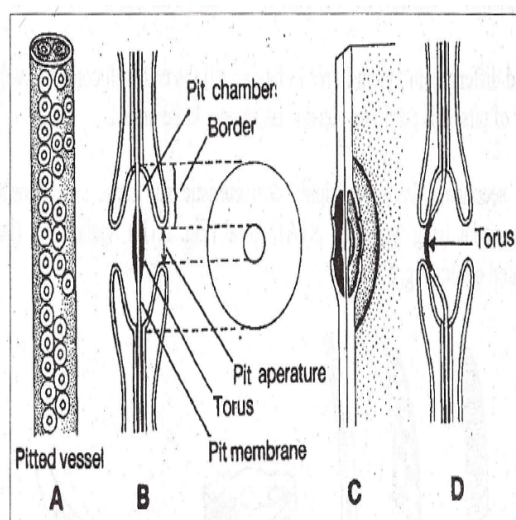


Fig. 3.5: Bordered Pits: (A) Surface View, (B) Sectional View, (C) A Diagrammatic 3-D Appearance of a Pit, (D) Sectional View of Torus

The torus is well developed in bordered pits of gymnosperms and remains surrounded by microfibrils, known as *margo*. During *xylogenesis* (development of xylem elements), fusiform initials of vascular cambium are differentiated into tracheids and vessel members. During ontogeny, protoplast of fusiform initial becomes non-functional and nucleus disappears. Later secondary wall deposition takes place in a pattern characteristic for the given type of tracheary element.

3.4. VESSELS OR TRACHEA:

Vessel members are joined one end to another end and form the vessel. It is long, cylindrical, tube-like structure with lignified walls and a wide lumen. The vessel members are arranged in longitudinal series, in which partitioned walls are perforated, so that entire structure look-like a water pipe. So, the characteristic feature of vessel members is that they have perforation plates (end walls) (Fig. 3.6.). If perforation plate containing one large pore, it is called simple perforation plate; if there are several pores, it is known as compound (multiple, perforation plate. In compound perforation plates, pores are arranged in several patterns (Fig.3.6). When the pores are arranged in ladder-like manner, it is called *scalariform* (Fig. 3.6. A, B). In some cases, perforations are circular and grouped together, the perforation 'plate' is called *foraminate* scalariform type, C. simple type, D-F. Complete vessel members, D. scalariform perforation plates, E. simple perforation plates, F. simple perforation plates, (*ip*-inter vessel pitting; *r*- ray contact areas; *sp*- spiral thickenings).

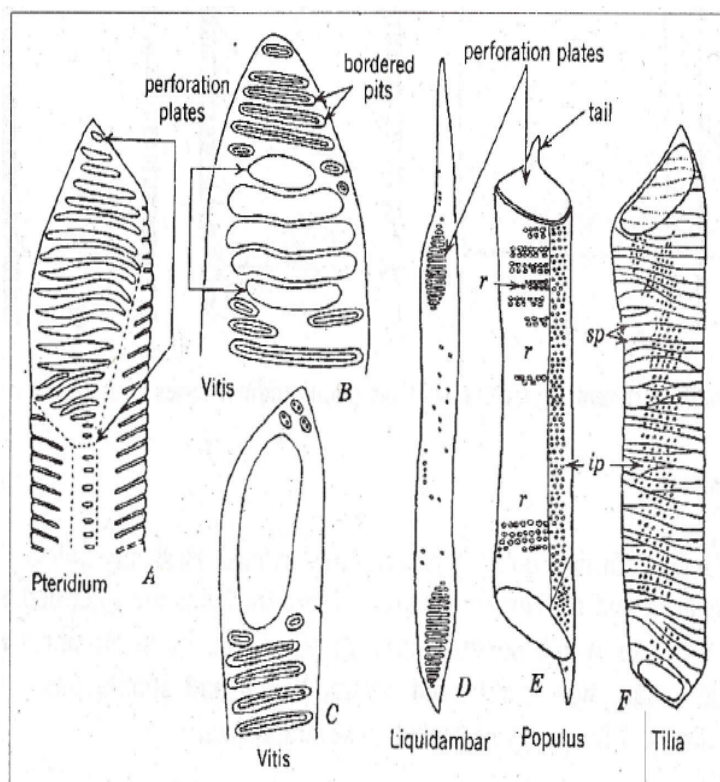


Fig. 3.6 A-C. End walls of vessel member showing various types of perforation plates. A. and B.

Vessels are commonly distributed in angiosperms. These are also present in few pteridophytes (e.g. *Selaginella*) and some gymnosperms (Gnetopsida members). Vessels are considered as phylogenetically advanced than tracheids. A vessel originates ontogenetically from a longitudinal series of meristematic cells. The primordial vessel member is usually expanded laterally. After this growth is completed, secondary wall layers are deposited (lignin deposition) in a characteristic pattern. The portion of the primary wall that later perforated, are not covered by secondary wall material. With the deposition of lignin, the cell undergoes lysis with the help of hydrolytic enzymes which attack the primary walls which are not covered by lignin. As a result, the primary wall disappears at the site of future perforations.

3.5. XYLEM FIBRES:

These are found both in primary and secondary xylem. Basically, xylem fibres are of two types, the *fibre tracheids* and the *libriform fibres*. Fibre tracheids are intermediate type between typical fibres and tracheids which possess bordered pits. The libriform fibres are narrow with highly thickened secondary wall, obliterated central lumen and simple pits. These are more common in woody dicots. Fibres may be septate in several dicots.

3.6. XYLEM PARENCHYMA:

The parenchymatous cells are found both in primary and secondary xylem. The parenchyma found in secondary xylem is classified into two types: (i) Axial parenchyma derived from fusiform initials, is somewhat elongated and form the vertical system of plant body along with tracheary elements; (ii) Ray Parenchyma derived from ray initials, is responsible for formation of rays. Ray may be heterogenous, made up of procumbent and erect cells or homogeneous with single type of cell. Ray may be uniseriate (unicelled thickness) or multiseriate (multi-celled thickness). In general, ray parenchyma involves in radial conduction of water.

Some parenchyma cells with wall ingrowths are extensively involved in transfer of solutes. These cells are known as transfer cells. Xylem parenchyma store reserved food materials in the form of starch, fats tannins, crystals and other secondary products.

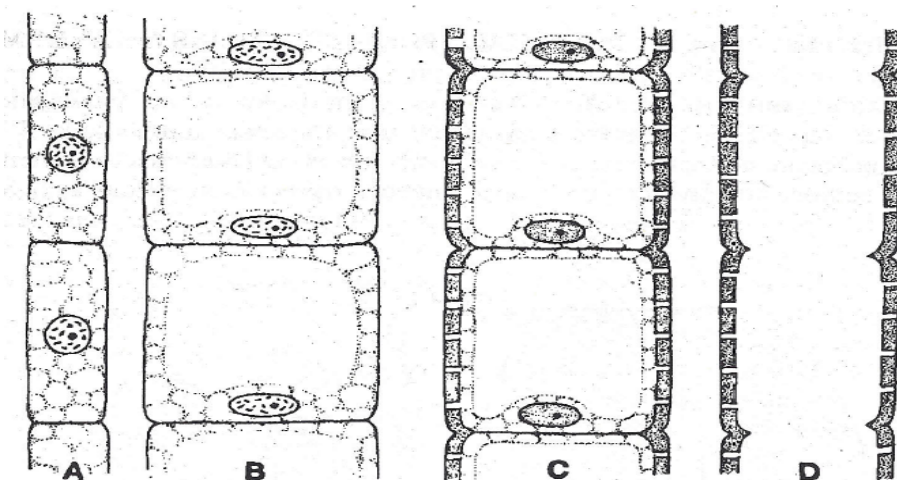


Fig. 3.7: A-D Differentiation of Vessel from a Longitudinal Series of Meristematic Cells

3.7. PHYLOGENETIC AND ONTOGENETIC SPECIALIZATIONS OF XYLEM:

Many morphologists opined that vessel element must have arisen phylogenetically from tracheid. The evidence for this hypothesis depends upon the great morphological similarity of primitive vessel elements to tracheids. This primitive tracheid-like vessel elements have been reported in the members of Winteraceae, Tetracentrace, Amborellaceae and also *Sarcandra* of Chlorophyceae. This primitive vessel element has got following tracheid-like features (Fig. 3.75A).

These are:

- i) Great length with comparatively narrow width,
- ii) Long overlapping end walls
- iii) Sclariform perforation plate with many bordered pits,
- iv) Sclariform pitting on lateral walls,
- v) Vessels angular in transactional view

3.8. MORPHOLOGICAL SPECIALIZATION IN THE PRIMITIVE VESSEL ELEMENT:

- i) Length - There has been a tendency for phylogenetic decrease in length of vessel element in angiosperms corresponding to advancement (Fig. 3...5). This tendency occurs not merely in secondary xylem but also in primary xylem of dicots and monocots.
- ii) End wall- There has been a alteration of end wall from highly oblique (Fig. 3.5 A) to a nearly transverse (Fig. 3.6 E) angle.
- iii) Perforation plate- In the course of advancement scalari form perforation plate has become the simple perforation plate. There have been a loss of borders and a loss of bars, that resulted into simple perforation plate. The final stage in the evolution of the end wall appears to be loss of perforation resulting into a degenerated vessel element, termed as vascular tracheids, that are found in advanced families such as Cactaceae and Compositae.
- iv) Lateral wall pitting ~ Lateral walls of vessels exhibit a similar series in specialization, showing following evolutionary sequence in pitting type: scalariform, transitional, opposite and alternate (Fig. 3.6 B, C, D, E). This trend applies both to intervacular and vessel-ray pitting. Besides, there has been a tendency from fully bordered vessel-ray pit pairs to half-bordered (border on vessel side only and finally to non-bordered pit pairs.
- v) Transectional outline - Primitive vascular elements which show angular in outline has become circular in the vessel member in the course of advancement.
- vi) The diameter of the vessel element - There has been a phylogenetic increase in diameter of vascular element right from the tracheid to advanced vessel member. It is obvious that tracheids are primitive and these are found in fossil seed plants, pteridosperms, the living lower vascular plants and gymnosperms. Vessel members which have evolved from tracheids, are occurred in Gnetales (gymnosperms), certain ferns, *Selaginella* of Lycopsidea, *Equisetum dictos* and monocots.

According to Bailey (1944b), vessels arose independently through parallel evolution in the above six groups of plants. In dicots specialization of tracheids into vessels occurred first in secondary xylem and then gradually proceeded into primary xylem. Organographically vessels first appeared in stem, then proceeded to root in dicots. In mono cots vessels evolved first in the ontogenetically latest part like primary xylem; first appeared in root, later in stems, inflorescence axes and leaves in that order.

In *Pteridium*, *Selaginella* and in secondary xylem of dicots, vessels arose from tracheids with scalariform bordered pitting; in Gnetales from tracheids with circular bordered pits of coniferous type. The vessel members of the primary xylem of mono cots evolved not only from scalariform pitted tracheids but also from tracheids with reticulate and helical thickenings.

According to Bailey (1944) origin and evolution of vessel is irreversible. Vessel evolution, together with the correlative evolution of other xylem elements, such as axial and ray parenchyma; constitutes the major trends of xylem evolution.

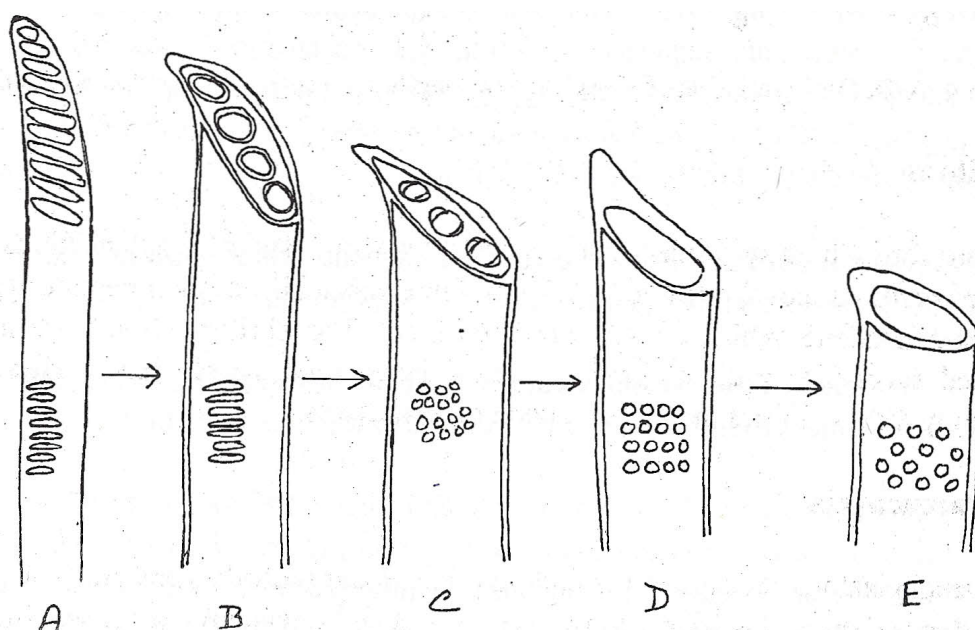


Fig. 3.8 A-E. Morphological Specializations

Morphological specializations occurred in tracheid-like vessel and formation of vessel member with simple perforation plate. A. Tracheid-like vessel; B-D. Vessel member formation. B. Vessel member with highly oblique end wall, C. with transitional lateral wall pitting, D; with slightly oblique, simple perforation plate and opposite lateral wall pitting, E. with transverse, simple perforation plate and alternate pitting.

3.9. AXIAL PARENCHYMA

Axial parenchyma forms the axial or vertical system of the plant body along with tracheids and vessels. Two basic types of distribution of axial parenchyma distinguished in dicot woods are apotracheal type, in which the position of the parenchyma is independent to that of vessels and paratracheal in which these two elements are closely associated with each other. In vessel less woods of Winteraceae, axial parenchyma is completely absent.; Apotracheal parenchyma may be diffuse (Fig. 3.9), that is dispersed throughout the grc. ring or

banded (Fig. 3.8) appearing in bands; or marginal (Fig. 3.7), that is, restricted either to the end of the growth ring (terminal parenchyma) or to the beginning of the growth ring (initial parenchyma). Para tracheal parenchyma may be scanty; Vasicentric (Fig. 3.9), surrounding the vessels aliform (Fig. 3.6), vasicentric with wing-like tangential extensions; and confluent (Fig. 3.9), coalesced aliform forming broad bands. The phylogenetic sequence of the distribution pattern of wood parenchyma is from the. Diffuse arrangement to the other apotracheal and the paratracheal types (Fig. 3.10).

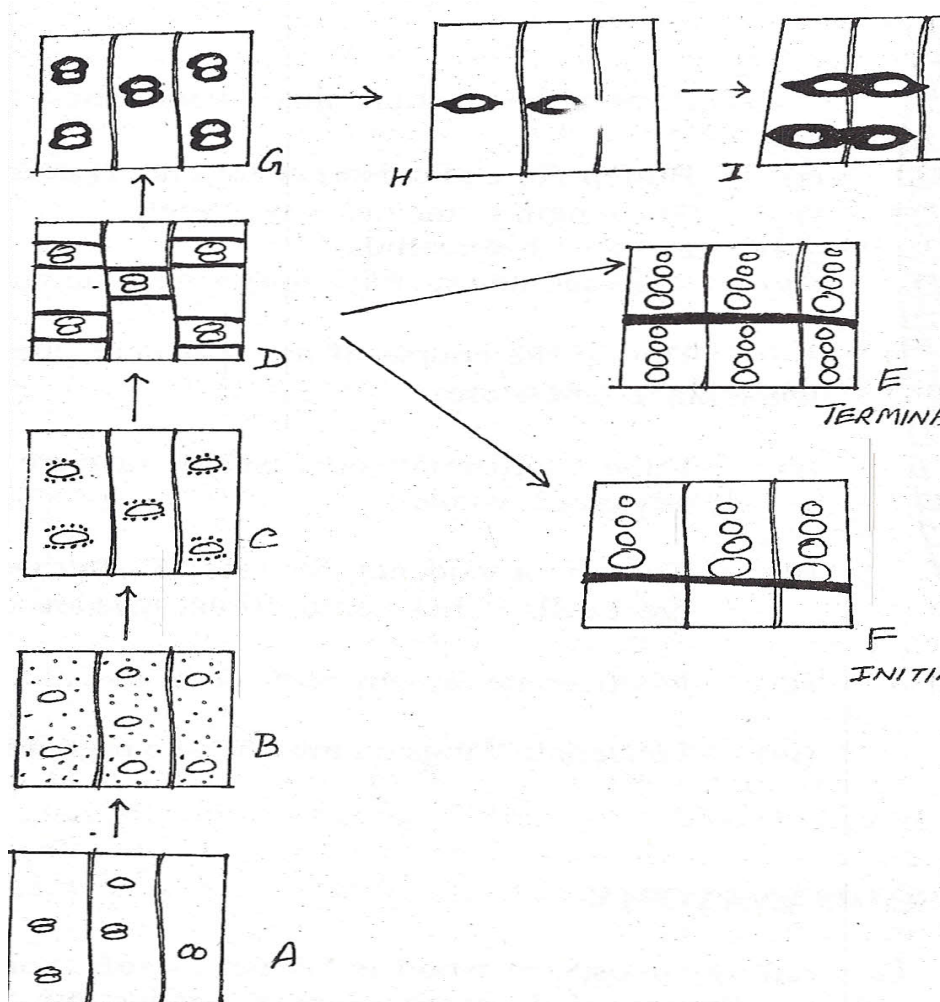


Fig. 3.9 A-I. Axial Parenchyma Distribution in Angiosperm Woods

A. Vessel less woods without axial parenchyma; B. diffuse parenchyma; C. diffuse-aggregate; D. Apotracheal wide banded; E, F. Marginal parenchyma (terminal and initial parenchyma respectively); G. Paratracheal vasicentric; H. Paratracheal aliform; I. Paratracheal confluent type.

3.10. RAY PARENCHYMA

This forms the transverse system in secondary woods. The two main types of ray parenchyma cells, the procumbent and the upright, occur in various combinations. The ray is homocellular, if it consists of only one type of cells, hetero cellular if it contains both types of

cells: Uniseriate or multiseriate rays may be either homo cellular or heterocellular. Ray system is classified into two: (1) homogeneous in which all rays are homo cellular; (2) heterogeneous, all rays are either heterocellular or some are heterocellular, others heterocellular.

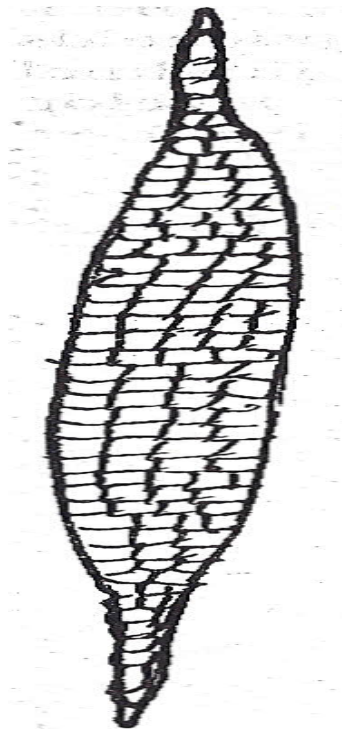


Fig. 3.10: Multiseriate Ray with Long Uniseriate wing

Rays in the most primitive woods show the following features. These are: Both multi and uniseriate rays appeared in primitive woods. The length of the ray is very high Rays are heterocellular Multiseriate rays have long uniseriate wings, e.g. *Drymis* (Winteraceae). During the course of advancement, the following changes in rays have been taken place. These are:

- i) Either multiseriate or uniseriate rays are lost. Only one type of ray is present in advanced woods.
- ii) There is a tendency for loss of heterogeneity. in ray cells, particularly loss of erect cells. Thus, homo cellular rays ~re advanced.
- iii) Multiseriate rays are reduced in size and number.
- iv) Uniseriate wings on multiseriate rays are reduced, ultimately to a single cell.

3.11. SUMMARY:

Tracheids and vessel members are two fundamental types of tracheary elements. Both are devoid of protoplast; hence these are dead cells. Tracheid .is an elongated structure with tapering ends whereas vessel members are broad with perforation plate. Vessel members are joined one end to another end to form the vessel. Both tracheids and vessels have got lignified wall thickenings and large lumen. If perforation plate containing one large pore, it is called simple perforation plate. If there are several pores, it is known as compound perforation plate.

Phylogenetic and ontogenetic specializations of xylem Many morphologists opined that vessels arose from the primitive vessel element, known as tracheid-like vessel. This tracheid-like vessel has undergone many morphological specializations mainly in length, end wall, perforation plate and, lateral wall pitting. Two basic types of distribution of axial parenchyma, distinguished in dicot woods are apotracheal type, in which the position of parenchyma is independent to that of vessels and paratracheal in which these two elements are closely associated with each other.

3.12. MODEL QUESTIONS:

- 1) Describe the Structure and function of vascular cambium
- 2) Explain the Structure of the Xylem
- 3) Describe the Phylogenetic and Ontogenetic Specializations of Xylem
- 4) Describe the Morphological specialization in the primitive vessel element
- 5) Explain Axial Parenchyma and Ray Parenchyma

3.13. REFERENCES:

- 1) K. Esau, 1996, Plant Anatomy, Wiley Eastern Limited, New Delhi.
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Prof. K. Mallikarjuna

LESSON-4

PHLOEM

4.0. OBJECTIVE: To understand its role in **translocation**, the process of transporting organic compounds, principally sugars (sucrose), from their source (e.g., leaves where photosynthesis occurs) to sink tissues (e.g., roots, fruits, and developing organs) throughout the plant.

STRUCTURE:

4.1 Introduction

4.2 Sieve Elements

4.2.1 Sieve Cells

4.2.2. Sieve Tube

4.2.3. The Cell Wall

4.2.4 Protoplast and Function of the Cell

4.3 Companion Cells

4.4 Phloem Parenchyma

4.5 Phloem Fibre

4.6 Phylogenetic Specialization of Phloem

4.7 Summary

4.8 Model Questions

4.9 Reference Books

4.1. INTRODUCTION:

Phloem is another complex tissue next to xylene found in the vascular system, also be called bast or leptome. Phloem consists of (i) sieve elements, such as sieve cells and sieve-tube members, (ii) companion cells, (iii) phloem parenchyma, and (iv) phloem fibres. As usually, primary phloem is derived from procambium and secondary phloem from vascular cambium.

Phloem is generally found outside to the cambium. However, in some dicotyledonous stems, patches of primary phloem are found towards the pith region, i.e., inner to the xylem; it is known as internal phloem or intraxylary phloem / commonly found in the members of Apocynaceae, Asclepiadaceae, Convolvulaceae, Myrtaceae and Solanaceae. In some members of Amaranthaceae, Chenopodiaceae and Nyctaginaceae, the phloem patches are found included in the secondary xylem and are known as included phloem or interxylary phloem. The basic components of phloem are sieve elements (sieve cells and sieve-tube members), companion cells, phloem fibres and selereids.

4.2. SIEVE ELEMENTS:

Sieve elements include two types of cells, the less specialized sieve cells and the more specialized sieve-tube members. The longitudinal series of sieve-tube members constitute the sieve tube. The most characteristic features of sieve elements are the sieve areas on their walls and disappearance of nucleus in their protoplasts.

4.2.1. Sieve Cells:

These are narrow elongated cells without conspicuous sieve areas and without sieve plate. They have tapering end walls and overlap one another. These are found in lower vascular plants and gymnosperms.

4.2.2. Sieve Tube:

Sieve-tube members have got highly specialized sieve areas and these are localized in the form of sieve plates. The sieve plates occur mainly on end walls which vary from much inclined to transverse. Sieve areas are the wall areas with cluster of pores through which the adjacent sieve elements are interconnected by strand-like prolongations of their protoplasts. Sieve areas are nothing but the modified primary pit-fields. Sieve areas are distinguished from primary pit-fields by two features: (i) in sieve areas the connecting strands are much thicker than the plasmodesmata that occur in the primary pit-fields, and (ii) several pores are found in the sieve area, each pore usually contains a small cylinder of callose which surrounds the connecting strand (Fig. 4.1).

Sieve-tube members are usually disposed end to end in long series; the common wall parts bear the sieve plates. The sieve plate may be either simple, if it has only one sieve area or compound, if it has several sieve areas (Fig. 4.2). The walls of laterally adjacent sieve tubes bear sieve areas of lower degree of specialization than those of sieve plates; In sectioned material, the sieve areas are commonly associated with the carbohydrate material, known as callose which stains a clear blue with aniline blue or resorcin blue. There are evidences that, in response to injury, callose is deposited very rapidly on walls so as to heal-off the injury very quickly to prevent further infection. Presence of callose can be served as a diagnostic feature of sieve elements.

In mature sieve tube, there is a thin layer of parietal cytoplasm, a large central vacuole and a large number of groups of longitudinally running transcellular strands. Transcellular strands are the aggregates of tubules made-up of P-protein (phloem protein).

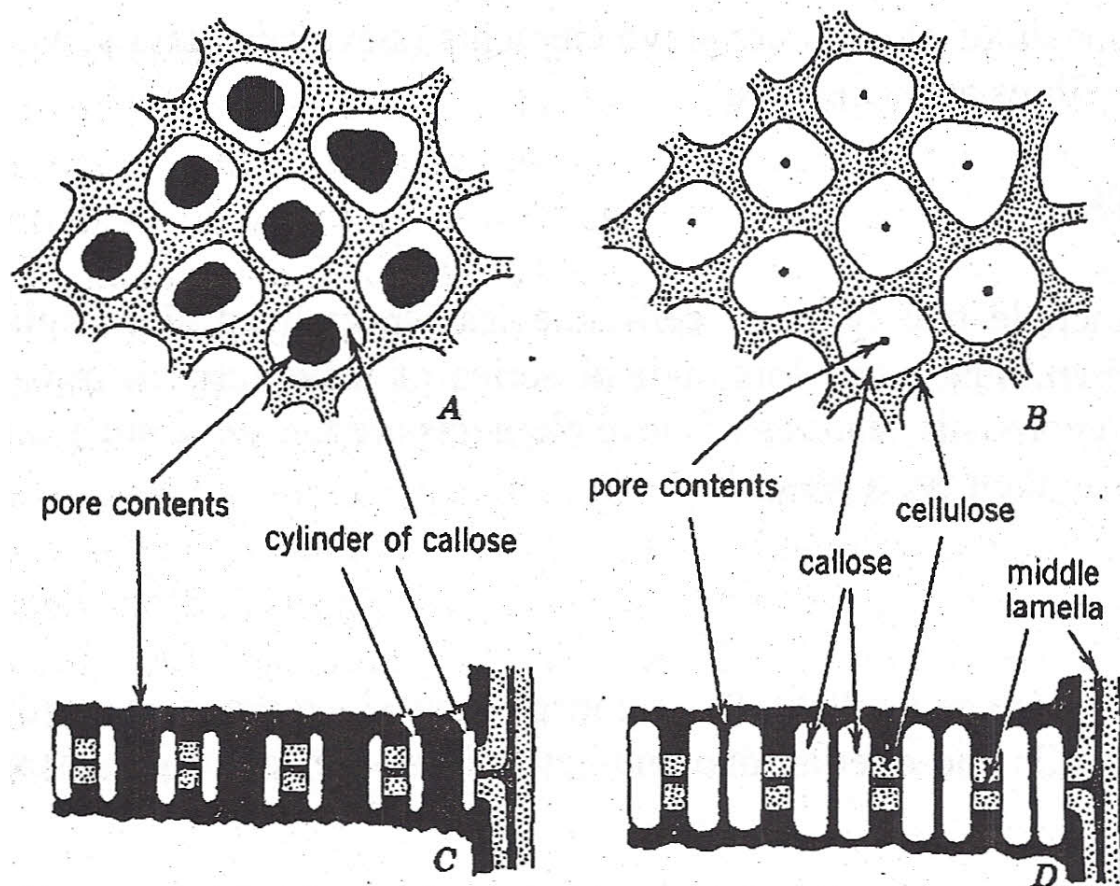


Fig. 4.1. A-D. Sieve Areas in Angiosperm Sieve Tube.

A, B. Surface Views, C, D. Sectional Views. A, C. Illustrate Younger Sieve Areas; B, D. Older Sieve Areas

Development of Sieve Tube:

In meristematic cells the future sieve plates resemble primary pit-fields. During differentiation of sieve tube, cell wall undergoes certain distinctive changes. It develops sieve areas with several pores in transverse wall or end walls. The less specialized sieve areas, that are with relatively small pores, differ at maturity from primary-pit-fields in the greater conspicuous of the pore contents and the usual presence of callose. Enlargement of pore occurs during their differentiation. Each pore has a single strand of cytoplasm extending through it and connect to the protoplast of adjoining sieve tube. In the more highly specialized sieve areas, pore formation follows a complex sequence as seen with the electron microscope (Esau, 1993). The future pore site is at first occupied by a single plasmodesmata strand. Sheets of endoplasmic reticulum (ER) and platelets of callose become localized on the opposing surfaces of each pore site, with the ectoplast interposed between the ER and the callose. The sheets and platelets increase in diameter, and eventually the two opposing platelets at each pore site-fuse because of the disappearance of the original separating wall. Hence, a hole- appears in the middle of the fused platelets and enlarges centrifugally (Fig: 4.3). Like this, a pore appears to be lined with callose since its inception.

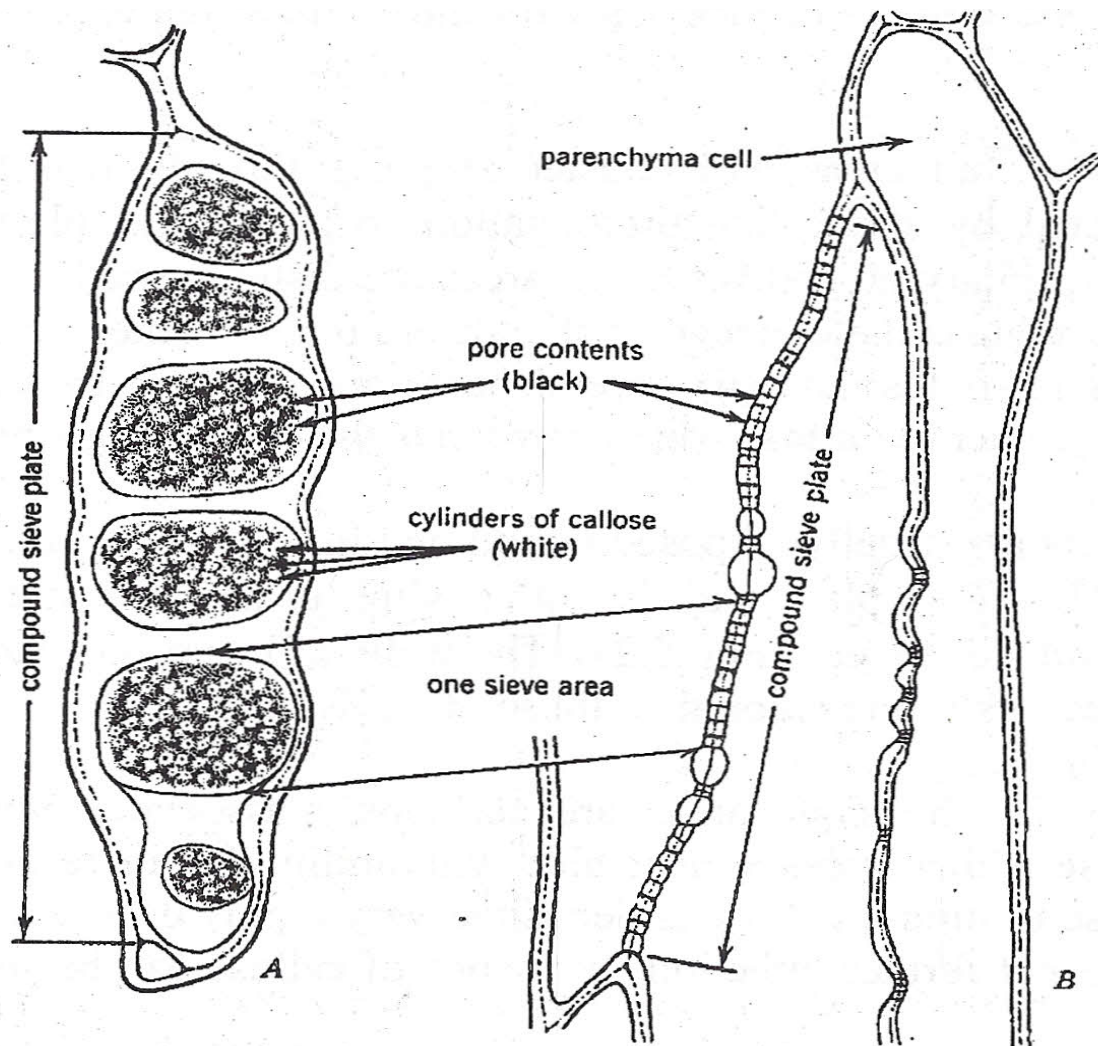


Fig. 4.2: Compound sieve plate of *Nicotiana*. A. in surface view, B. longitudinal section (After Esau, 1938).

As the sieve element ages, the amount of callose in the sieve area is increased (Fig. 4.3). Its mass increases within the pores. There is also a massive accumulation of callose on the surface of sieve area, it becomes thickened, and eventually it projects above the surface of the wall. Such extensive accumulation of callose is known as definitive callose (Fig. 4.3G) and it indicates cessation of activity of the sieve element. When the protoplast of inactive sieve element completely disorganizes, the sieve-area strands disappear. The definitive callose commonly separates from the sieve area and later it also disappears (Fig. 4.3H). The sieve area freed of callose represents a thin portion of cellulose wall with open perforations (Fig. 4.3H).

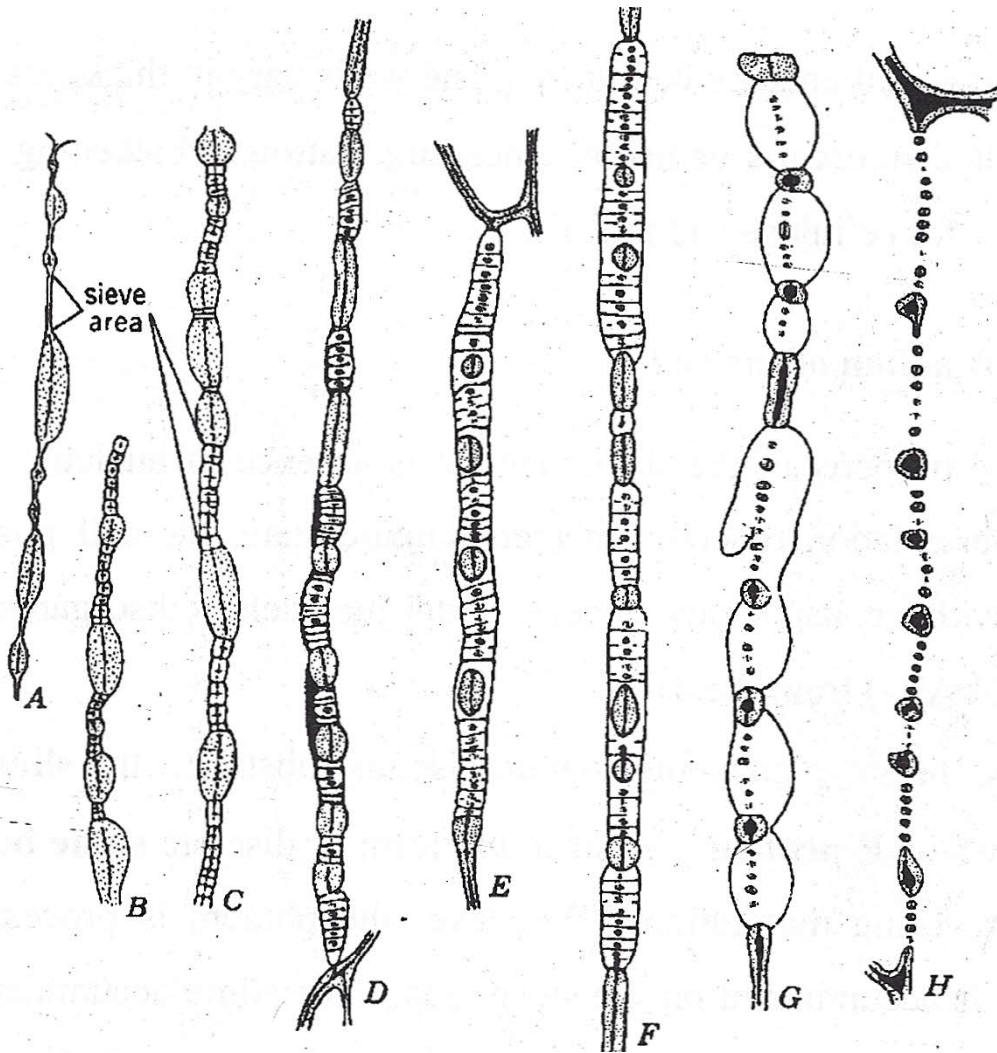


Fig. 4.3: A.JI. Development of compound sieve plate in *Nicotiana*. A. Cambial wall with

(less specialized sieve area; traversed by plasmodesmata); B-D. accumulation of callose (white) and resulting thickening of sieve areas; E, F. increase in amount of callose; G. most massive callose accumulation (definitive callose), pore contents have disappeared with death of protoplasts; sieve plate with no callose and with open pores from non-functional sieve tube (adopted from Esau, 1939)

4.2.3. The Cell Wall:

The walls of sieve elements are cellulosic. The walls vary in thickness. In many species, a distinct thickening, called nacreous or nacre (meaning lustrous) thickening is present. It gives positive reaction to tests for cellulose and pectins.

4.2.4. Protoplast and function of the Cell:

The well-known property of the sieve-element is absence of nucleus. The loss of nucleus occurs during the differentiation of cell. In meristematic state, the cell possesses more or less vacuolated protoplast with a conspicuous nucleus. Later the nucleus disorganizes and disappears as a discrete body (Fig. 4.4 A-G) from the cell.

In dicotyledons, the sieve elements contain viscous substance, the slime, which is made of protein. It is also known as P-protein present in the form of discrete slime bodies. These tend to fuse with one another during maturation. Whenever the phloem is processed for microscopic observation, the slime is accumulated on the sieve area. The slime accumulation on sieve area is called slime plug (P-protein plug). Slime plugs appear to stop the exudation of contents from the cut phloem in the first stages of wound reaction. Later, the sieve areas become plugged by wound callose.

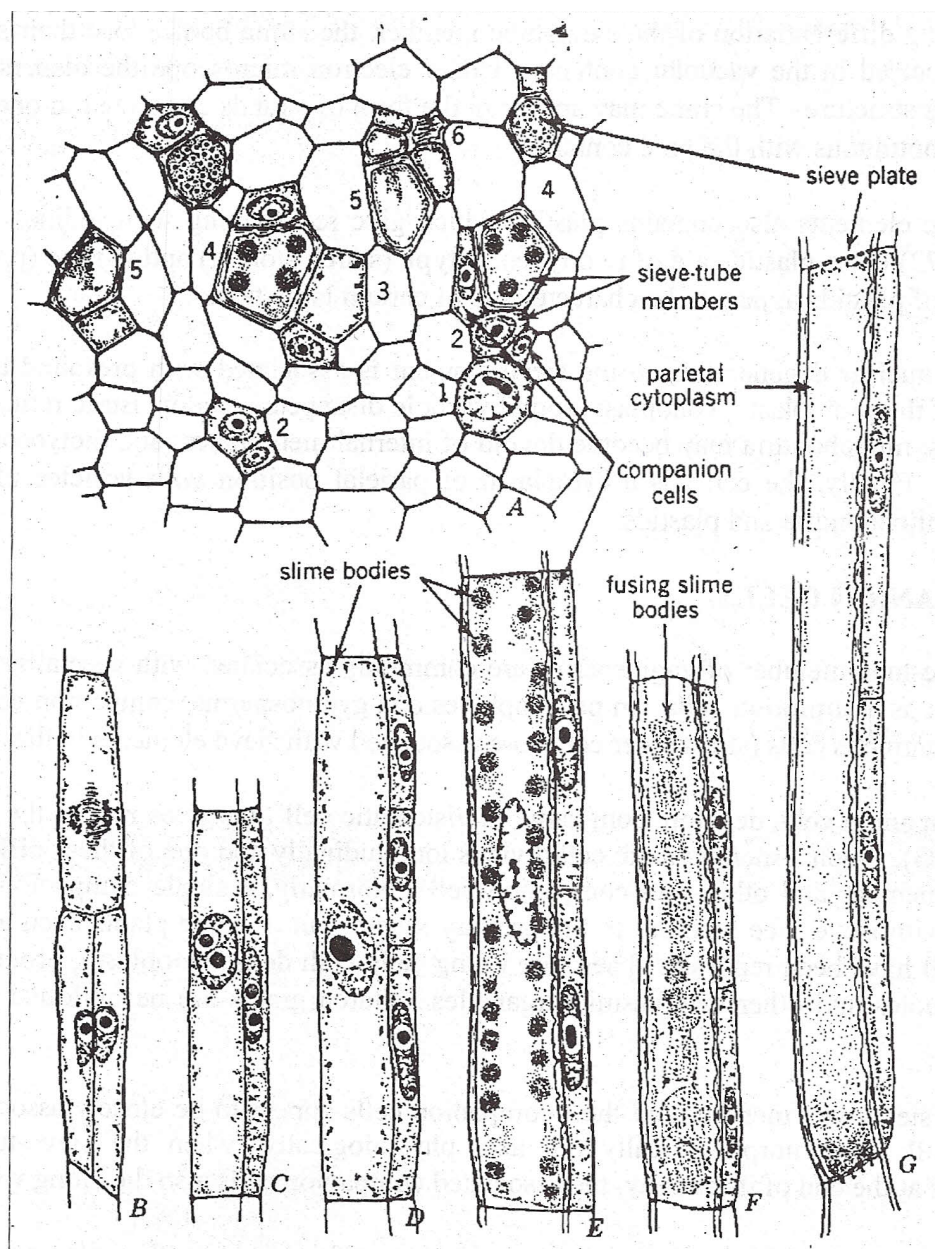


Fig. 4.4: A-G. Differentiation of sieve-tube members in primary phloem of *Cucurbita*.

- A. Transection with details: (1) cell before division, (2) after division into sieve-tube member and companion cell, (3) slime bodies have appeared in sieve element protoplast, (4) larger slime bodies and thick wall in sieve element, (5) slime bodies dispersed, (6) sieve element partly obliterated. Longitudinal sections.

- B. Cells in division (above) and after division (below) into sieve-tube member and precursor of companion cells.
- C. Young sieve element and precursor of companion cells,
- D. Sieve-tube member with small slime bodies and with three companion cells,
- E. Slime bodies of maximal size, nucleus highly vacuolated, thick walls in sieve element,
- F. Slime bodies partly fused and nucleus absent,
- G. Mature sieve element with sieve plate (Adopted from Esau, 1993).

During differentiation of the sieve-tube member, the slime bodies lose their sharp outlines, dispersed in the vacuolar contents. Under electron microscope the dispersed slime may show fibrous structure. The slime may appear in the form of strands connected to one or both sieve plates and continuous with the pore contents.

Sieve elements also contain plastids, which give red staining with iodine. According to Behnke (1972) these plastids are of two types, S-type (starch storing) and PS type (protein storing). S or P-type of plastids appear to be characteristic of certain large taxa. The nuclear degeneration in the sieve element is associated with profound changes in the condition of the protoplast. Tonoplast, around vacuole disappears; endoplasmic reticulum breaks up into masses; mitochondria may become devoid of internal membranes; and dictyosomes disappear completely. Finally, the cell has a cytoplasm of parietal position with vesicles of endoplasmic reticulum, mitochondria and plastids.

4.3. COMPANION CELLS:

Sieve-tube members of angiosperms are commonly associated with specialized parenchyma cells known as companion cells. In pteridophytes and gymnosperms, companion cells are absent; instead, albuminous cells (Strasburger cells) are associated with sieve elements in these plants. Companion cells develop from same meristematic cell that gives rise to the sieve element (Fig. 4.4 A-G). Such a meristematic cell divides longitudinally and one of them differentiates into sieve-tube member and other into companion cell. Normally, a single companion cell is found associated with sieve-tube member in the primary xylem, but in some plants such as carrot, more than one cell has been reported. These are living cells with dense cytoplasm, prominent nucleus, several vacuoles and other cytoplasmic organelles. Starch grains are never found in companion cells.

The sieve-tube member and their companion cells appear to be closely associated not only ontogenetically and morphologically but also physiologically; when the sieve-tube protoplast disorganises at the end of its activity, the associated companion cells also die along with it. The function of companion cells is not known so far, however, they play an important role in maintenance of a pressure gradient in the sieve tubes. Companion cells control the passage of materials and provide energy to sieve tubes in loading and unloading of assimilates, thus help in conduction of food along with sieve elements.

4.4. PHLOEM PARENCHYMA:

The phloem contains parenchyma cells other than companion and albuminous cells. These are living cells which have dense cytoplasm and nucleus, and are concerned with many

of the activity's characteristic of living parenchyma cells, such as storage of starch, fat and other organic food materials, and accumulation of tannins and resins.

The parenchyma cells of the primary phloem are elongated and are oriented along with sieve elements. In the secondary phloem, parenchyma occurs in two systems, the axial and ray systems. The parenchyma of the axial system is called axial phloem parenchyma whereas parenchyma of ray system is ray phloem parenchyma.

In the active phloem, the parenchyma and ray cells apparently have primary unthickened walls. After the tissue ceases to function, they may become sclerified. The cell walls of both kinds of parenchyma have numerous primary pit-fields, interconnecting axial and ray cells and also between companion cells and sieve-tube members. Usually, the pit-fields on the sieve element side is called a sieve area since it develops callose.

4.5. PHLOEM FIBRES (BAST FIBRES):

Phloem fibres (bast fibres) are found both in primary and secondary phloem. They provide mechanical strength to the plant body.

4.6. PHYLOGENETIC SPECIALIZATION OF PHLOEM:

- i) Sieve cells found in lower vascular plants and gymnosperms are considered as primitive and sieve-tube member of angiosperms are highly advanced in phylogenetic point of view.
- ii) In the course of evolution, there has been a progressive localization of specialized sieve areas on the cross walls led to the formation of sieve plates.
- iii) There has been a gradual change in the orientation of the end wall from oblique to transverse (horizontal).
- iv) A stepwise change from compound sieve plate to simple sieve plate have been occurred in the course of evolution.
- v) There has been a gradual decrease in conspicuousness of the sieve area on the side walls also. Phylogenetic enlargement of pores has taken place; and also increase in the transverse area occupied by the sieve areas.
- vi) Specialization of sieve elements also involved in the development of thick connecting strands traversing in between the sieve elements, right from lower vascular plants to highly advanced angiosperms.
- vii) The phylogenetic specialization of sieve elements shows some parallelism with that of tracheary elements.

These are as follows:

- i) The sieve cells lacking sieve plates can be compared with the pitted tracheids.
- ii) Sieve plate of sieve element can be compared with perforation plate of vessel member.
- iii) In both kinds of elements, there has been a change in the orientation of the end walls from oblique to transverse.

- iv) Simple sieve plate can be compared with the simple perforation plate of xylem and this is considered as phylogenetically advanced element.

Table 4.1: Comparison between Sieve Tubes and Vessels

Sl. No.	Sieve tubes	Vessels
Structural comparison		
1	Sieve tubes are very narrow	Vessels are wider
2	Sieve plates (simple or compound) are found on the end walls	Perforation plates (simple or compound) are found on the end walls
3	They have thin and cellulosic cell wall	They have thick, rigid and lignified walls
4	They have no specialized thickenings on their cell walls	They have various types of thickenings on their walls
Physiological comparison		
5	They are alive when mature and functional	They are dead but functional
6	They are semi-permeable in nature	They are permeable to both solute and solvent
7	They have high sap concentration	They have low sap concentration
8	The turgid cells have high turgor pressure	They do not have turgor pressure
9	They exudate cell sap when cut	They absorb water or air when cut
10	They translocate only solute	They translocate both solutes and solvents
11	Their translocation speed is upto 5 cm/min (maximum)	Their translocation speed is upto 75 cm/min.

4.7. SUMMARY:

Phloem consists of sieve elements, such as sieve cells and sieve-tube members, Companion cells, phloem parenchyma and phloem fibres. The most characteristic features of sieve elements are the sieve areas on their walls (sieve plates) and disappearance of nucleus in their protoplasts.

Sieve-tube members are usually disposed end to end in long series. They have got highly specialized sieve areas and these are localized in the form of sieve plates. The sieve areas are commonly associated with the carbohydrate material, callose.

As the sieve element ages, the amount of callose in the sieve area is increased. Development of definitive callose (extensive accumulation of callose) indicates cessation of activity of the sieve element. In dicots, the sieve element contains viscous substance, the slime, also known as P-protein.

The slime accumulation on sieve area whenever the phloem is cut, is called slime plug (P-protein plug). Later cut phloem is healed off by wound callose. The sieve-tube member and their companion cells appear to be closely associated not only ontogenetically and morphologically but also physiologically; when the sieve-tube protoplast disorganises at the end of its activity, the associated companion cells also die along with it. Sieve cells found in lower vascular plants and gymnosperms are considered as primitive and sieve-tube members of angiosperms are highly advanced in phylogenetic point of view.

4.8. MODEL QUESTIONS:**Essay Question:**

- 1) Give an account on phloem and its differentiation in angiosperms.

Short Answer Questions:

- 1) P-Protein
- 2) Sieve elements
- 3) Sieve-tube member and its differentiation
- 4) Companion cell
- 5) Structural similarities of phloem with xylem.

4.9. REFERENCE BOOKS:

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Prof. A. Amrutha Valli

LESSON-5

THE STEM

5.0 OBJECTIVE:

- In this chapter, root-stem transition, nodal anatomy and primary and secondary structures of angiosperm stem have been discussed.

STRUCTURE:

5.1 Introduction

5.2 Root Stem Transition

5.3 Nodal Anatomy

5.3.1 Types of Nodes

5.4 Anatomy of Dicotyledonous Stems

5.5 Summary

5.6 Model Questions

5.7 Reference Books

5.1. INTRODUCTION:

The part of the axis, which is aerial in nature and bears nodes; internodes and reproductive structures is called the stem. The difference between stem and root lies chiefly in the arrangement of the xylem and the phloem. In the root, the strands of primary xylem and phloem lie in different radii, separated from one another; in the stem, the strands lie side by side in the same radius, that is, they are conjoint and collateral. The xylem of the root is always exarch, whereas in stem it is endarch or mesarch. There are some fundamental differences in structure of dicot and monocot stems. Some comparative characteristics of both of these stems are given in the Table 5.1.

Table 5.1: Some Characteristic Features of Dicot and Monocot Stems

	Dicot Stem		Monocot Stem
1	Several multicellular hairs usually arise from epidermis in dicot stem	1	Epidermal hairs are usually not found
2	Hypodermis consists of collenchymatous cells	2	Hypodermis is usually sclerenchymatous
3	Cortex is distinct	3	Hypodermis and cortex are not well distinguishable and ground tissue is present next to hypodermis
4	Endodermis and pericycle are distinctly present	4	Endodermis and pericycle are not present
5	Vascular bundles are arranged in a ring	5	Vascular bundles are found scattered in the ground tissue
6	Vascular bundles are conjoint, collateral and open type.	6	Vascular bundles are conjoint, collateral and closed type.
7	Sclerenchymatous bundle sheath is not found	7	Each vascular bundle remains surrounded by sclerenchymatous sheath
8	In vascular bundles, several vessels are present and are linearly arranged	8	Vessels in each vascular bundle are arranged in V-shape and are fewer in number.
9	Phloem parenchyma is found.	9	Phloem parenchyma is absent.
10	Lysigenous cavity in vascular bundle is absent	10	Lysigenous cavity in each vascular bundle is present
11	Both pith (medulla) and medullary rays are present	11	Medulla and medullary rays are absent
12	Secondary growth is found	12	Secondary growth is not found

5.2. ROOT-STEM TRANSITION:

The root and stem make a continuous structure called the axis of the plant. The vascular bundles and other tissues are continuous from root to stem. However, the arrangement of vascular "bundles is quite different in the two organs. Root possesses radial bundles with exarch 'xylem -whereas stem has collateral bundles with endarch xylem. The place where vascular transition takes place is known as transition zone. Inversion and twisting of xylem strands from exarch to endarch is referred to as vascular transition. The transition may be of four main types.

Type A:

In *Dipsacus*, *Funaria* and *Mirabilis* etc., each xylem strand of the root divides by radial division and gives rise to the two branches. These branches pass upward and swing in their lateral direction; -one goes to right and other to left. Later these branches join the phloem strands on the inside (Fig, 5.1A). The phloem strands, however, remain unchanged and they remain in the form of straight strands continuously from the root into the stem. In this type, the number of vascular bundles' is equivalent to the number of phloem strands of root.

Type B:

In *Acer*, *Cucurbita*, *Phaseolus*, *Trapaeolum* etc., both xylem and phloem divide branches of both strands swing in their lateral direction and pass upward to join in pairs (Fig. 5.1B). The xylem strands become inverted, but phloem remain unchanged in their orientation. This way, in stem, number of vascular bundles becomes doubled of the phloem strands of root. This type is very common in angiosperms.

Type C:

In *Lathyrus*, *Madicago*, *Phoenix* etc., xylem strands do not fork but twist through 180°. The phloem strands divide soon and, the resulting halves swing in the lateral direction and join the xylem strands on the outside (Fig. 5.1 C). In this type, number of vascular bundles in stem is equivalent to number of phloem strands of root.

Type D:

This type is rarely found in monocotyledons, eg: *Anemarrhena*. In this type, half of the xylem strands fork and the branches swing in their lateral direction to join the other undivided strands of xylem. Later xylem strands become inverted. However, phloem strands do not divide, but on the other hand they become united in pairs. Simultaneously, these united phloem strands unite with the triple strands of the xylem (Fig. 5.1D). This way, the number of vascular bundles becomes half of the phloem strands of roots.

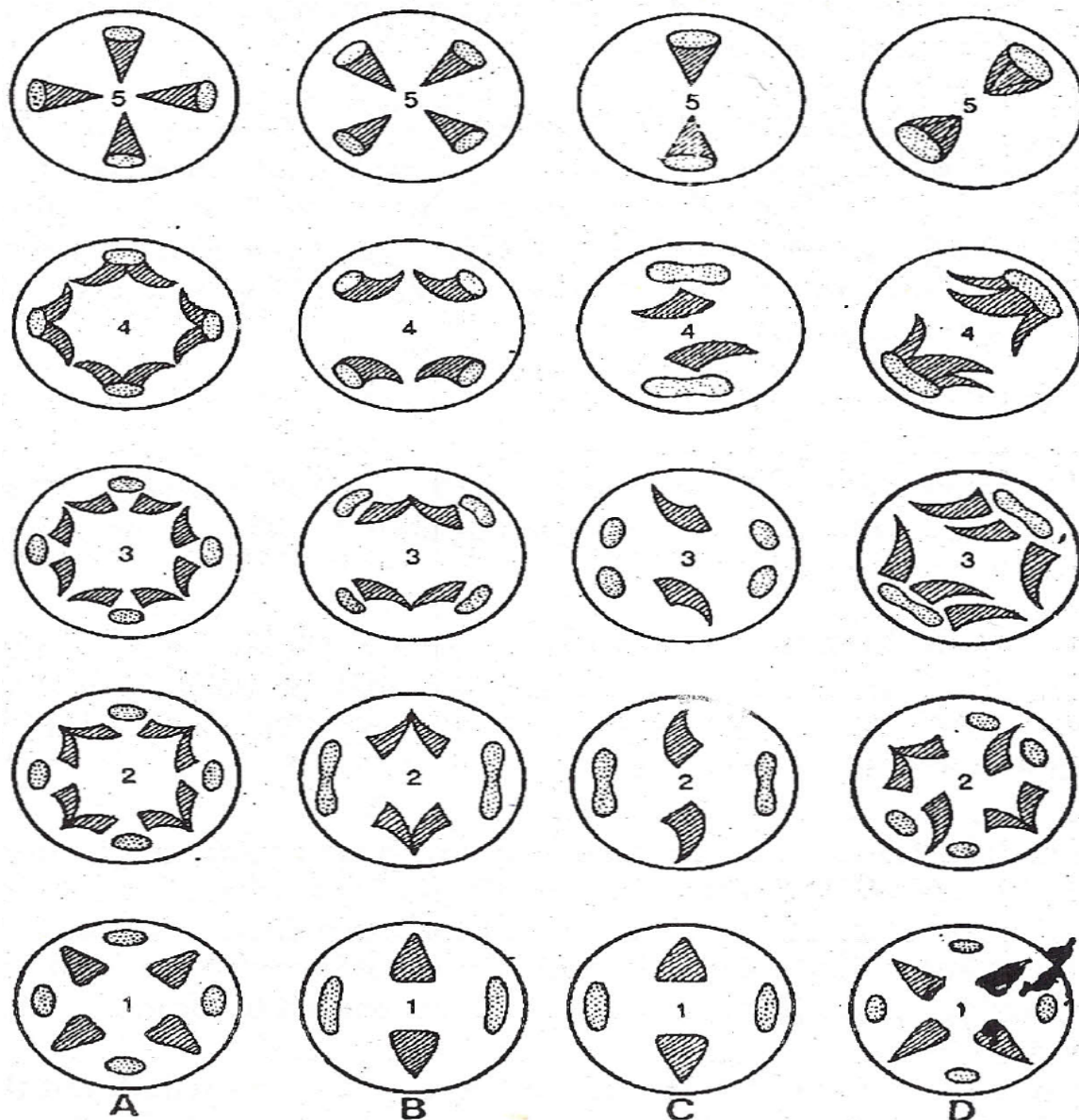


Fig. 5.1: A-D. Root-Stem Transition. A. *Funaria* type, B. *Cucurbita* type, c. *Lathyrus* type, D. *Anemarrhena* type (After Eames and McDaniels)

5.3. NODAL ANATOMY:

In angiosperms, stem possesses nodes and internodes. The place where leaf traces or branch traces arise is referred to as node. The structure of vascular cylinder shows variations in the regions of nodes and internodes.

Leaf traces - In the nodal region, part of the vascular cylinder enter into the leaf is known as leaf trace {vascular supply to the leaf. Leaf trace may also be defined as a vascular bundle ~ that connects the vascular bundle of the leaf with that of the stem. The vascular supply that goes to branch at the nodal region, is known as branch trace.

Leaf gaps - In higher plants such as ferns, gymnosperms and angiosperms, there is a discontinuity of vascular cylinder of stem just above the diverging leaf traces. This break up region of vascular cylinder made up of parenchyma is, known as leaf gap (nodal lacuna). Leaf traces are always accompanied by leaf gaps. However, in Lycopsidea leaf gaps are absent and these nodes are known as Cladosiphonic nodes. Branch traces are also accompanied by branch gaps.

In some ferns, such as *Pteridium* and *Iteris*, the leaves are so crowded that the gaps formed at the successive nodes overlap one another, as a result actual vascular cylinder becomes dissected.

Presence of branch gaps further complicates the structure. In general, at the internodal region solid vascular cylinder is present whereas at the node it becomes dissected due to presence of leaf gaps and branch gaps.

5.3.1 Types of Nodes:

The arrangement of leaf traces and their complexes vary in different groups of plants and, is related to phyllotaxis. There are four basic types of nodes found in dicotyledons. These are as follows:

- i) **Unilocular** node with a single gap and a single leaf trace, e.g. *Spiraea* (Fig. 5.1.A), and it is found in the opposite and whorled phyllotaxy.
- ii) Unilocular **two** trace is found in opposite leaves, e.g., *Clerodendron*, *Veronica* etc.
- iii) **Trilocular node** with a three leaf gaps and. three leaf traces, e.g., *Salix*. (Fig. 5.1.B), *Brassica* (Fig. 5.1.C), *Leptadenia* etc.
- iv) **Multilocular node** with several leaf gaps and leaf traces associated with a single leaf, e.g.: *Rumex* (Fig. 5.1.D), *Ricinus* etc. above nodes

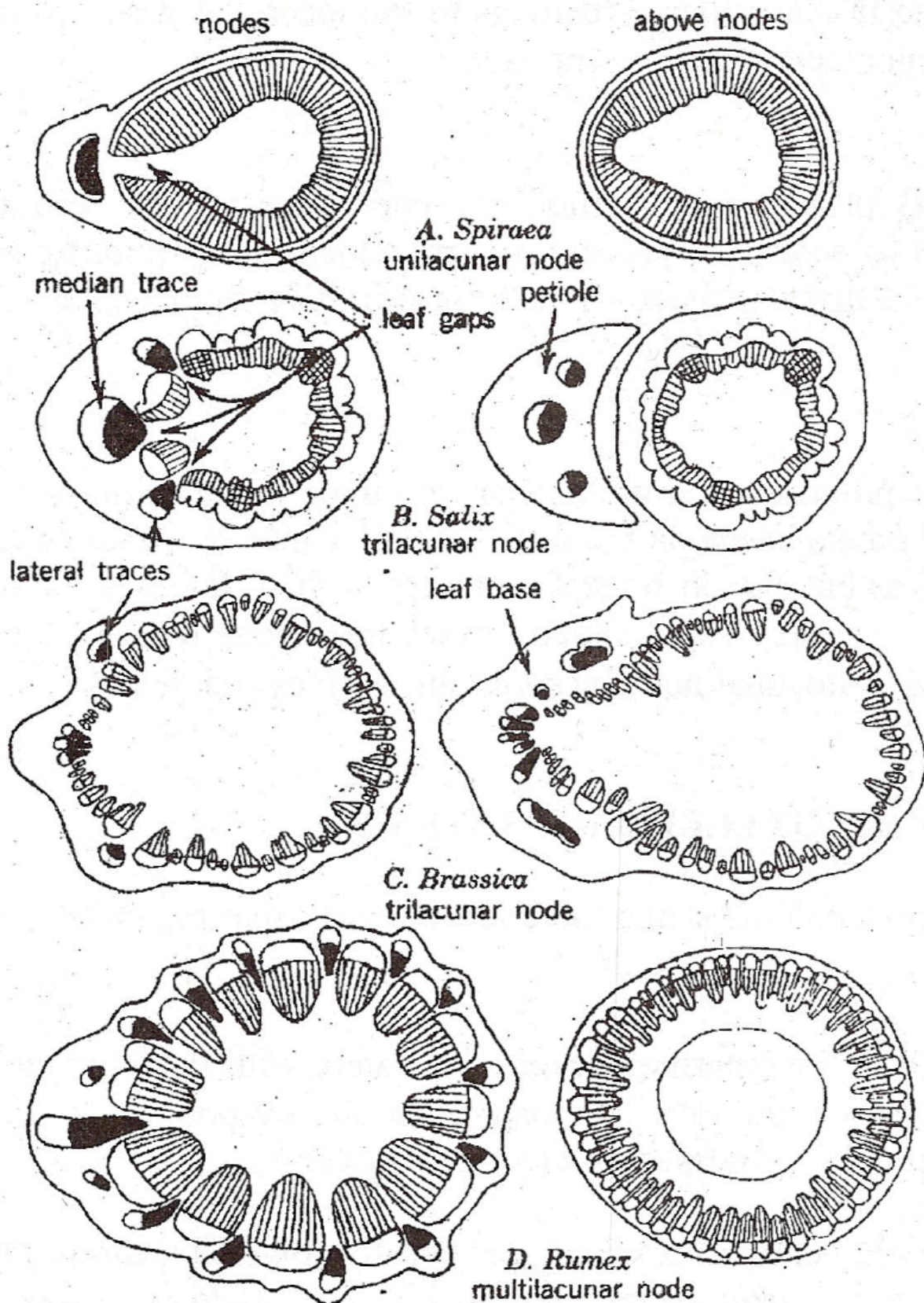


Fig. 5.5: A-D. Transection of Stems of Dicotyledons Showing Different Types of Nodes

In most monocotyledon leaves with sheathing leaf bases are found, which receives large number of leaf traces that are peripherally arranged around the stem. In gymnosperms, unilocular node is common. In ferns, variable number of leaf traces enter the leaf but they are always associated with single gap.

Nodal structure is thought to be of phylogenetic importance and is also valuable in systematics of dicotyledons. Unilocular node is found characteristically among members of several families such as Anonaceae, Apocynaceae, Ericaceae, Lauraceae, Solanaceae and Verbanaceae. Trilocular node is characteristically found in Meliaceae, Polygonaceae, Ranunculaceae and Winteraceae, and also in Amentiferae (belongs to Monocotyledonae). Multilocular node is found in Araliaceae, Chenopodiaceae and Degeneriaceae.

Sinnot (1914) proposed that trilocular node is the most primitive from which arose unilocular condition by reduction process and multilocular by amplification process. However, Ozenda (1949) opined that multilocular node is primitive from which arose tri- and unilocular nodes.

Bailey (1956) proposed that unilocular two trace is the primitive among angiosperms. It supported by several others because unilocular two trace is characteristic not only in gymnosperms and ferns but also in several members of dicot families such as Labiatae, Lauraceae, Solanaceae and Verbanaceae. This unilocular two trace node had given rise to unilocular single trace, trilocular and multilocular node by additions, fusions and deletions of leaf traces.

5.4. ANATOMY OF DICOTYLEDONOUS STEMS:

In young dicotyledonous stems there are three distinct regions - the epidermis, the cortex and the stele. Epidermis - It is the outermost layer of the stem with thick cuticle. It gives protection to the plant body and restricts the rate of transpiration and evaporation of the water. The cells are compactly arranged and do not possess intercellular spaces.

Hypodermis - In herbaceous stems, it is usually collenchymatous which may be in the form of a continuous ring, e.g. *Aristolochia*, *Ricinus* (Fig. 5.4.), *Helianthus annuus* (Fig. 5.5), or in the form of patches in angular stems such as *Cucurbita* (Fig. 5.4) and *Peristrophe*. Its primary functions to provide mechanical strength to the plant body.

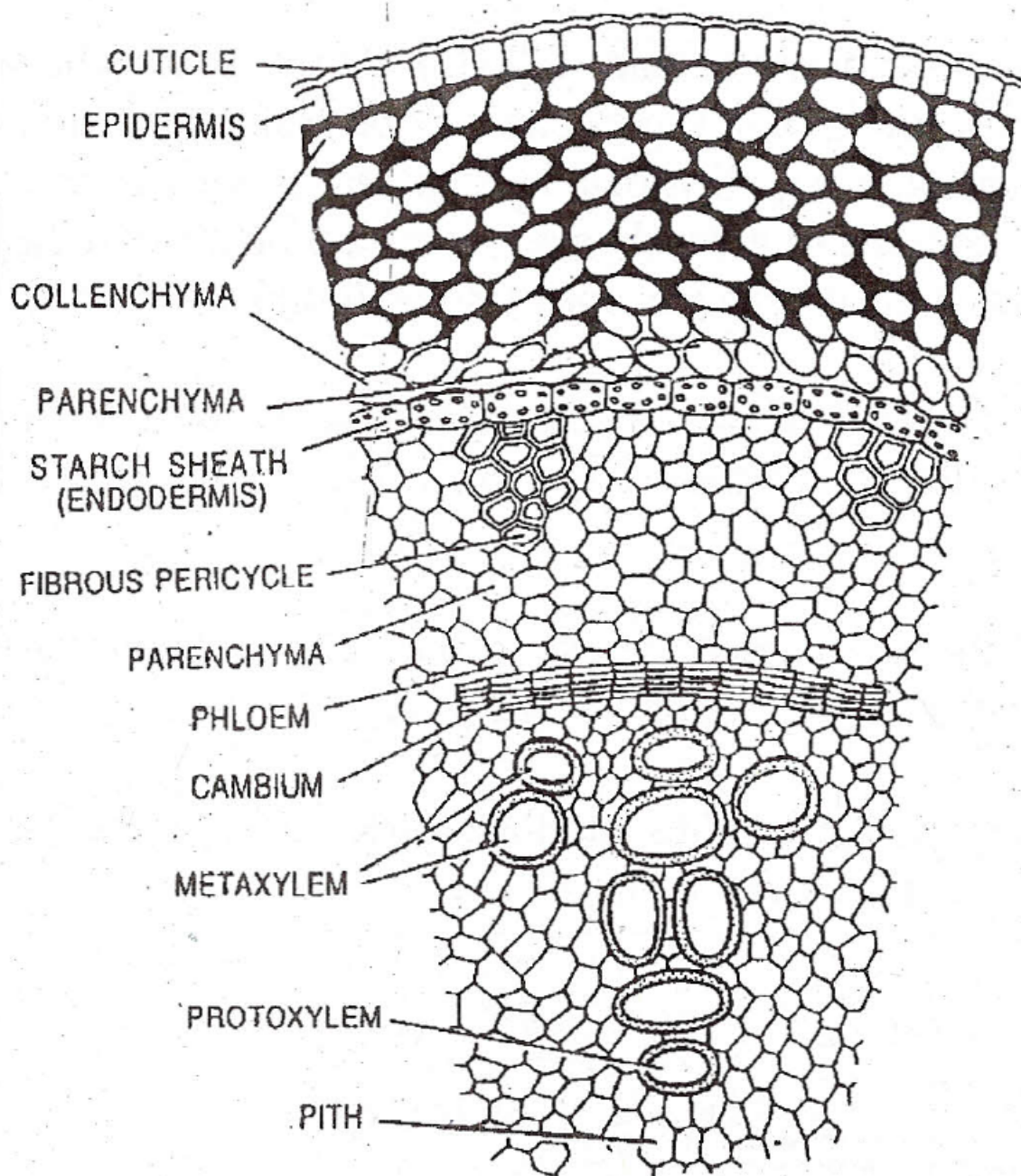


Fig.5.3 Transection of stem of *Ricinus communis* showing Collenchyma

Cortex:

It is parenchymatous and consists of thin-walled, round or oval cells with large number of intercellular spaces. Outer few layers of cortical cells may be assimilatory in nature due to presence of chloroplasts (chlorenchymatous), e.g. Phylloclade (stem) of *Euphorbia tirucalli*. The cortex in most of aquatic plants mainly consists of aerenchyma. In certain plants, laticiferous cells or ducts, mucilaginous canals, resin ducts, tannin cells etc., may also be found in cortex.

Endodermis:

It is the innermost layer of the cortex. It consists of cells with Casparian strips: However, in certain plants, the cells of innermost layer are rich in starch grains, hence this layer is called **Starch Sheath** (Fig. 5.4).

Stele:

It is central portion of the stem, located next to the cortex. It consists of three regions, these are the pericycle, the vascular bundle region and the pith.

Pericycle:

Pericycle is located between the vascular bundles and the cortex. It is generally composed of parenchyma and sclerenchymatous cells (Fig. 5.4 & 5.5).

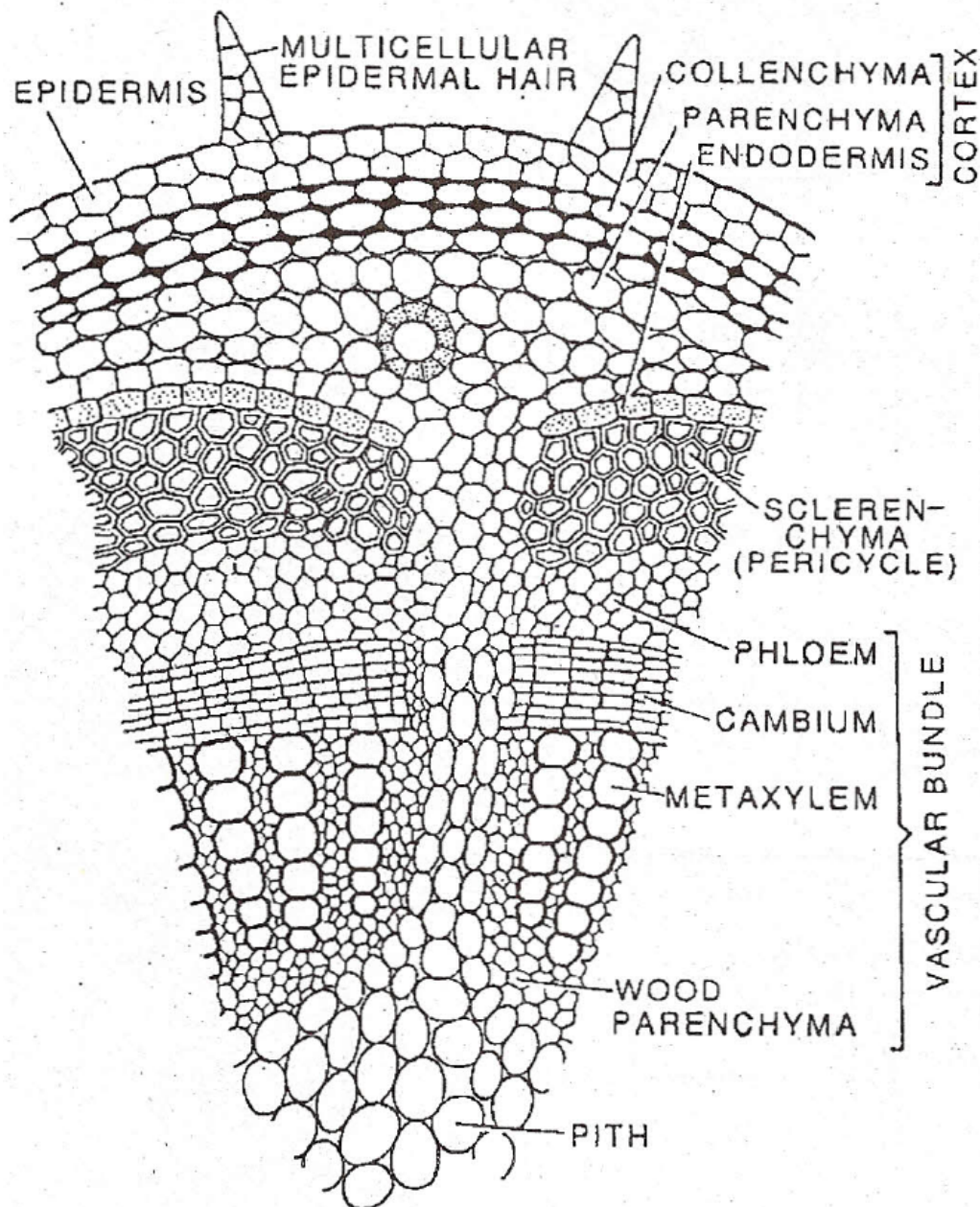


Fig. 5.5: Transection of Stem of *Helianthus Annuus* Showing Continuous Ring of Collenchyma and Sclerenchymatous Pericycle

A

CHLOROPHYLLOUS CELLS
COLLENGHYMA
SCLERENCHYMA (PERICYCLE)
PHLOEM (OUTER)
CAMBIUM
XYLEM
PHLOEM (INNER)
STOMA

B

EPIDERMIS
COLLENGHYMA
CHLOROPHYLLOUS CELLS
SCLERENCHYMA (PERICYCLE)
GROUND TISSUE

C

UTER LOEM
SIEVE TUBE
SIEVE PLATE
PHLOEM
PARENCHYMA
CAMBIUM
MARY LEM
METAXYLEM
XYLEM
PARENCHYMA
PROTOXYLEM
NER LOEM
SIEVE TUBE
COMPANION CELL
PHLOEM
PARENCHYMA
SIEVE PLATE
MEDULLARY RAY

Fig. 5.6: Transection of Bryonia Stem (Cucurbitaceae)

The xylem consists of tracheids, vessels, xylem fibres and xylem parenchyma. The phloem consists of sieve tubes, companion cells and phloem parenchyma. Pith rays are made up of radial rows of parenchyma cells. They separate the vascular bundles from each other. Pith rays involve in the conduction of food and water. Pith is the central portion of the stem and composed of thin-walled parenchyma cells. They may have intercellular spaces.

5.5. SUMMARY:

The part of the axis, which is aerial in nature and bears nodes, internodes and reproductive structures is called the stem. Root-stem transition: The root and stem make a continuous structure called the axis of the plant. The vascular bundles and other tissues are continuous from, root to stem. Root possesses radial bundles with exarch xylem whereas stem has collateral bundles with endarch xylem. The place where vascular transition takes place is known as transition zone: Inversion and twisting of xylem strands from exarch to endarch is referred to as vascular transition.

Nodal Anatomy: There are four basic types of nodes found in dicots. These are (i) Unilocular node with a single leaf gap and a single leaf trace, (2) unilocular with two trace, (3) trilocular with three leaf gaps, (4) multilocular node. Anatomy of Dicotyledonous stem: In young dicot stem, there are three distinct regions – the epidermis, the cortex and the stele. Vascular bundles are conjoint, collateral and open. The primary plant body is derived from primary meristems, such as shoot apex and root apex. Procambium is responsible for the formation of primary vascular tissues.

5.6. MODEL QUESTIONS:

Essay Questions

- 1) Write an essay on primary and secondary structures of dicot stem.
- 2) Discuss the structure of node and its phylogenetic significance in tracheophyta.

Short Answer Questions:

- 1) Root-Stem Transition

5.7. REFERENCES:

- 1) K. Esau, 1996. Plant Anatomy, Wiley Earn Limited, New Delhi.
- 2) A. Fahn, 1967. Plant Anatomy, Pergamon Press, Oxford.
- 3) P.C. Vasishta, Plant Anatomy. Pradeep Publications, Jalandhar.

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LESSON-6

SECONDARY GROWTH IN THE STEM

6.0 OBJECTIVE:

- To understand the secondary growth in dicotyledonous stemy.

STRUCTURE:

6.1 Secondary Growth in Dicotyledonous Stem

6.2 Action of Vascular Camium

6.3 Annual Rings

6.4 Periderm

6.5 Bark

6.6 Lenticel

6.7 Summary

6.8 Model Questions

6.9 References

6.1. SECONDARY GROWTH IN DICOTYLEDONOUS STEM:

The primary plant body is derived from primary meristems, such as shoot apex and root apex. Pro cambium is responsible for the formation of primary vascular tissues. Later, secondary growth takes place in gymnosperms and dicots by the activity of lateral meristems such as vascular cambium and phellogen. By the activity of lateral meristem, the girth of the stem is increasing and giving rise to secondary plant body.

Cambium is present in between the xylem and phloem of vascular bundles in dicotyledonous stems. The part of the cambium within the vascular bundle is known as fascicular (fascicle = bundle) cambium. Besides, the cambial strips are also differentiated in between the vascular bundles. These newly formed cambial strips which occur in the gaps between the bundles are called interfascicular cambium. Later fascicular and interfascicular cambial strips are joined one another and forming a complete ring of vascular cambium (Fig. 6.1B).

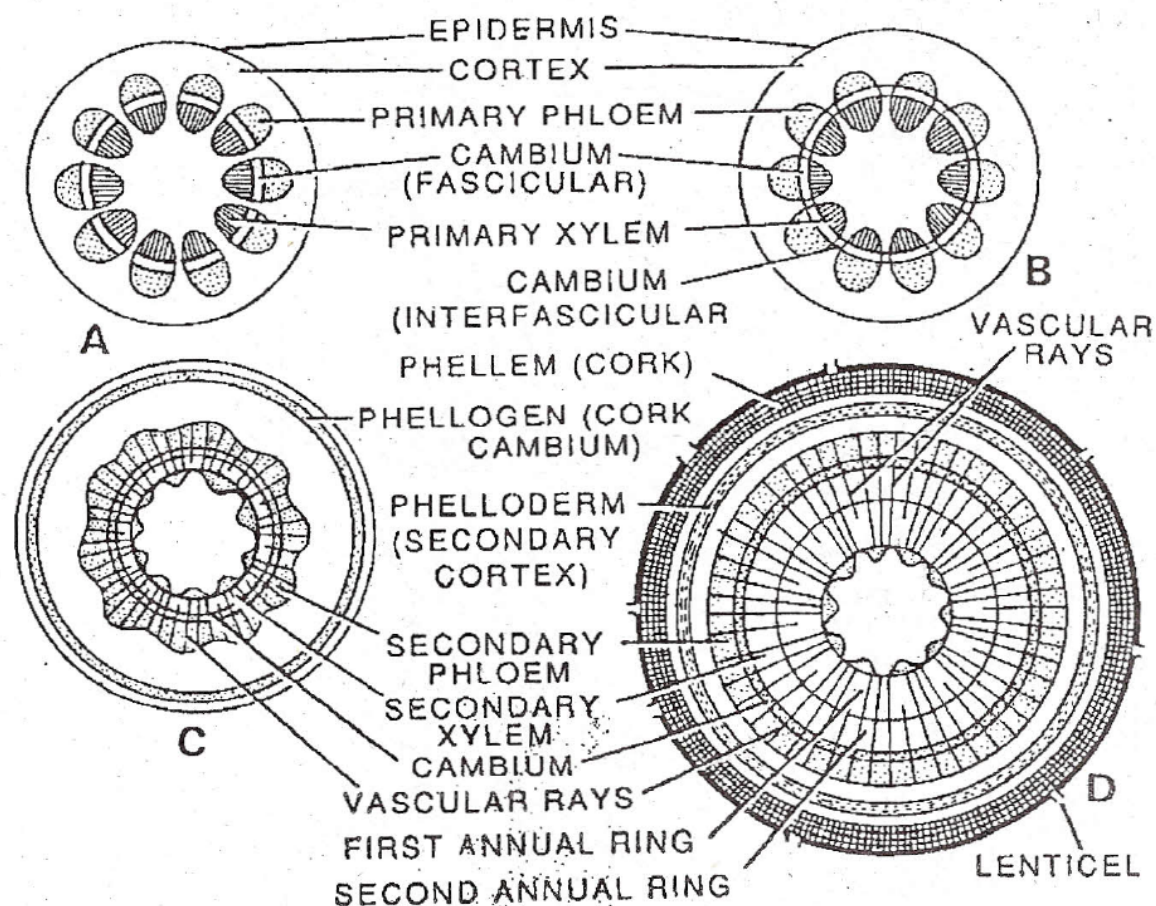


Fig. 6.1 A-D. Secondary Growth in Dicot Stem

6.2. ACTION OF VASCULAR CAMIUM:

Vascular cambium consists of two types of initials, **fusiform initials** and **ray initials**. The differentiation of long fusiform and short ray cells may not be distinct in procambium, but these initials are very distinct in the vascular cambium. Fusiform initials are responsible for the formation of vertically oriented axial system that consists of tracheids, vessels and sieve elements. These initials are elongated with tapering ends; these cells are very long up to 7 mm in old trunks of *equoia sempervirens*. Ray initials give rise to rays in the dicot stems. Initially vascular cambium consists of a single layer of cells. During its activity, number of layers increased. Cambium shows seasonal activity. In trees growing in tropical regions, it is active throughout the year, whereas in temperate trees it becomes dormant during winter and reactivates in spring. When it reactivates, widening of cambial zone takes place (increase in Number of layers; Fig.6.2).

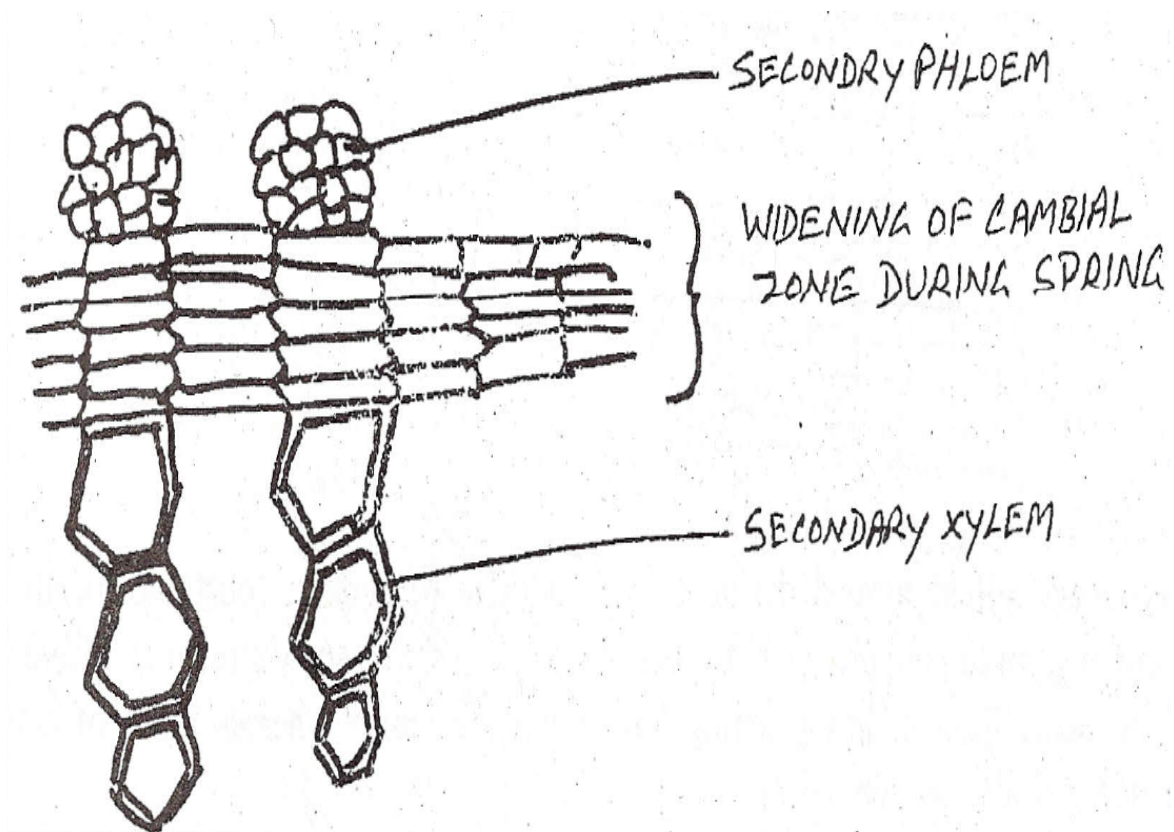


Fig. 6.2: Widening of Cambial Zone

Cambial initials undergo divisions and give rise to immediate and later derivatives. These later derivatives differentiate into sieve elements (secondary phloem) at the outer side and tracheary elements (secondary xylem) at the inner side (Fig. 6.3).

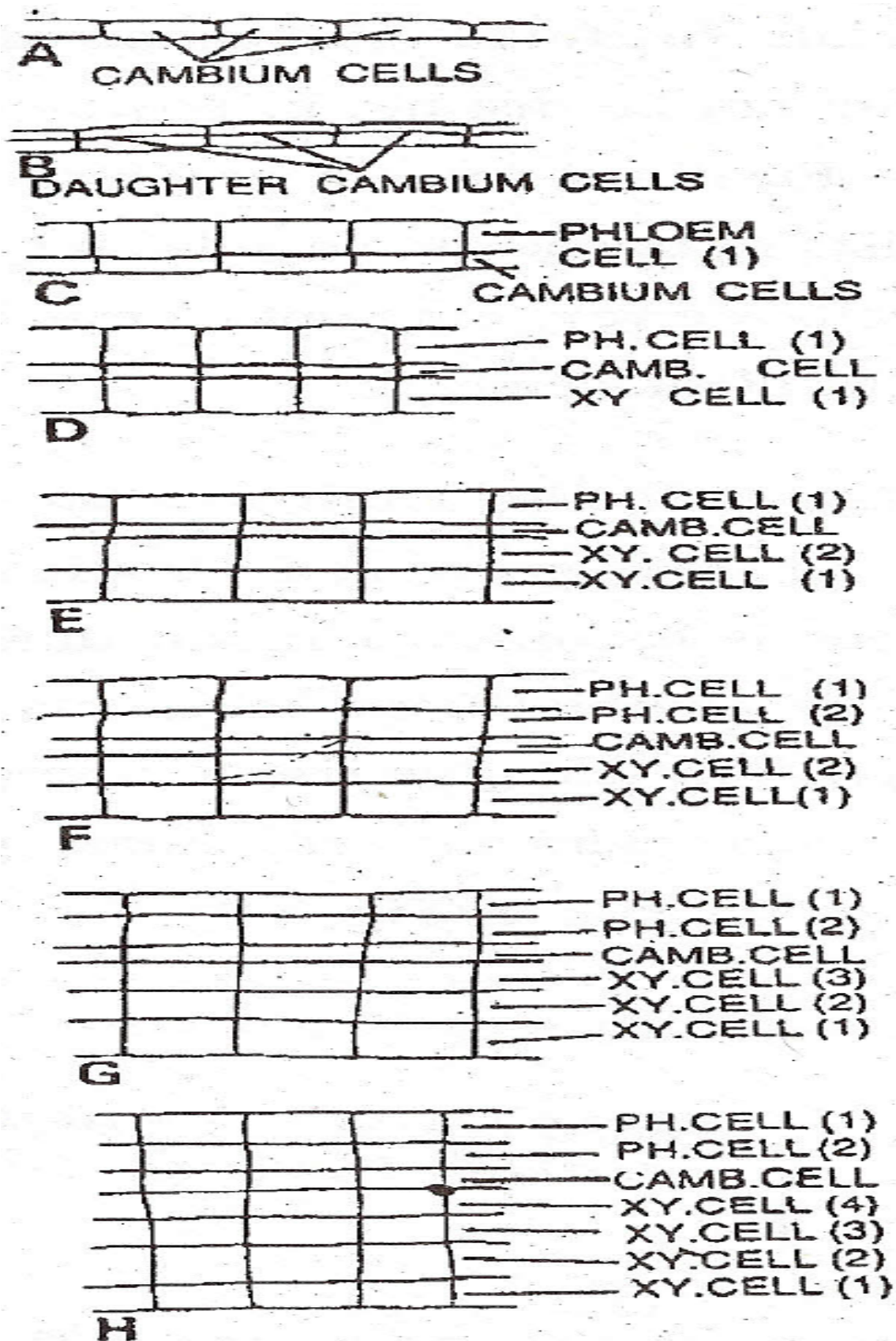


Fig. 6.3: A-H. The Active Cambium Showing Differentiation of Phloem and Xylem from its Derivatives

6.3. ANNUAL RINGS:

Secondary xylem formed during spring and autumn constitute together to form *r* annual ring or growth ring (Fig. 6.4). Secondary xylem shows some structural differences; those tracheary elements formed during spring have got wide lumen whereas those of autumn have narrow lumen

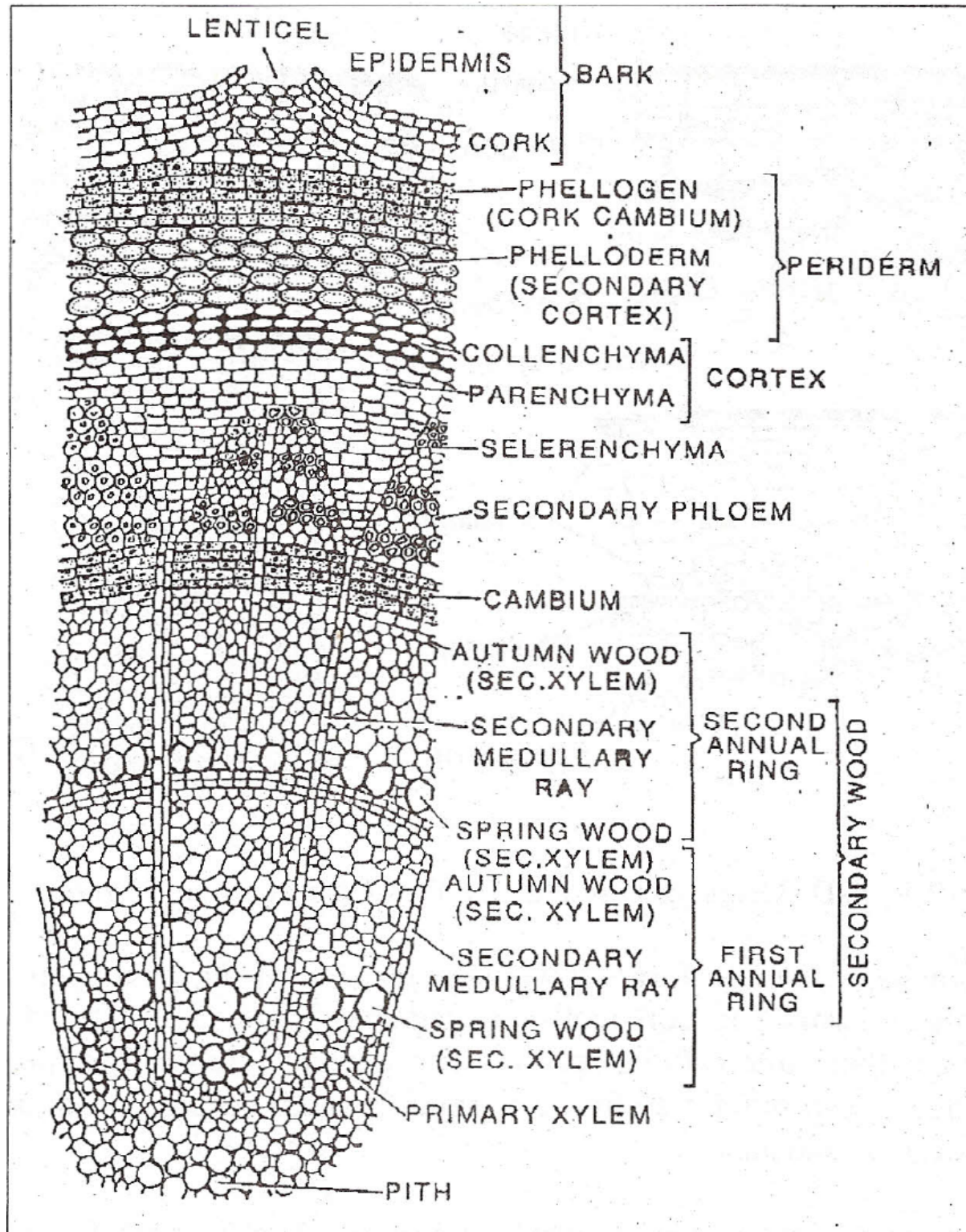


Fig 6.4: Transection of Two Years Old Dicot Stem showing Annual Rings

6.4. PERIDERM:

It is formed by the activity of a secondary lateral meristem called cork cambium or phellogen. It serves as a secondary protective tissue against desiccation and mechanical injuries due to its compact arrangement and suberised walls. Periderm may develop soon after the initiation of secondary growth or it may develop later. Periderm ruptures when it does not keep pace with the enlarging diameter of the stem by continuous increment of secondary vascular tissues.

The periderm consists of three types of tissues, these are (i) phellogen or cork cambium, (ii) phellem or cork and (iii) phelloderm or secondary' cortex.

(i) Phellogen (Cork Cambium):

Phellogen originates as a single layer of initiating cells either in the sub-epidermal portion, or in the epidermis itself, or in the cortex and or sometimes may even extend to the phloem. Phellogen cells behave like cambial cells which divide tangentially producing new tissues both towards the inner as well as outer side. The cells towards outer side form the phellem or cork and towards inner side form the phelloderm or secondary cortex (Fig .6.5)

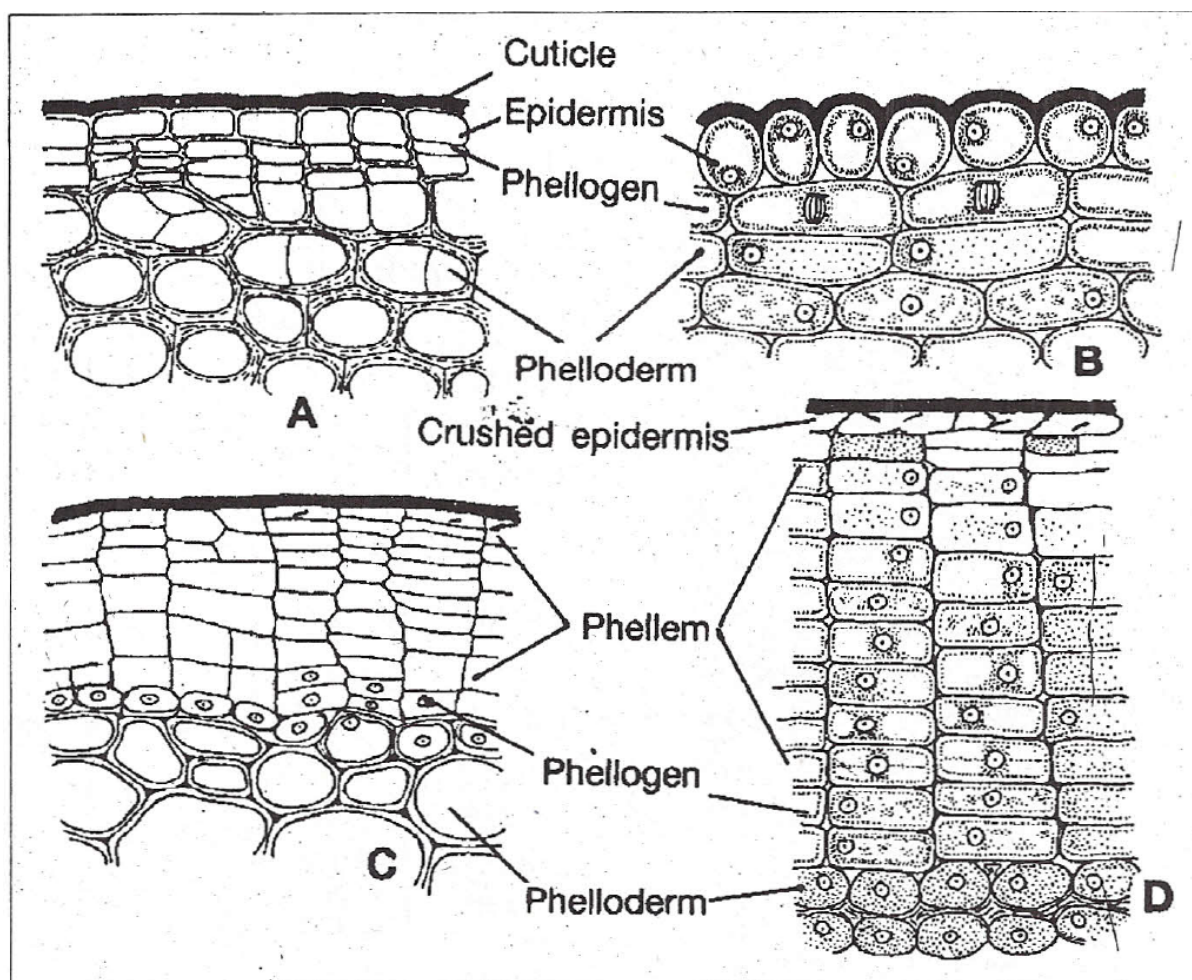


Fig 6.5.

(ii) Phellem (Cork):

Phellem forms towards outer side of the phellogen¹ and produces in more quantity than phelloderm. The cork cells are suberised and thick-walled and compactly arranged in radial rows without intercellular spaces. These characteristically appear rectangular in transverse section. They lose protoplasts after differentiation and become dead and, remain filled with air and coloured organic substances.

Suberin in cork cells is impervious to water and gases, thus the cork has more commercial value. *Quercus suber* yields bottle cork; the cavities of these cells are filled with air; hence it is light in weight. Air in the cavities gives thermal insulating qualities. Suberin is resistant to action of pathogens. These qualities of the cork make it a wonderful protective layer around the stem, and it is also a useful commercial product.

(iii) Phelloderm (Secondary Cortex):

It is formed inner side of the phellogen. The cells of phelloderm are thin-walled and living, consisting of starch and chloroplasts. Cells are arranged in definite radial rows. These cells are similar to cortex and involved in storage of food materials.

6.5. BARK:

In non-technical sense, the term bark means all the tissues outside the cambium. According to Esau, tissues of living and dead cells that are found external to the secondary phloem, includes pericycle, cortex, periderm and layers of dead cells external to periderm, are considered as bark. Some anatomists prefer to use the term *rhytidome* for outer bark.

Cork cambium is active throughout the life of the plant, e.g. *Quercus suber*, *Fagus sylvaticus*. First layer of phellogen forms below the epidermis and produces periderm and after some time, it becomes inactive. Later second layer of phellogen forms below the middle cortex and produces cortex and becomes inactive. Like this phellogen forms in deeper layers like pericycle.'

Secondary phloem etc. In such cases, the living and dead tissues produced by the successive layers of phellogen, external to wood, are all of secondary in origin and referred to as bark. These tissues are cut off from the supply of water and nutrients, and so the bark is no longer take part in the expansion of stem and root. When trees become old, it is shed or it becomes longitudinally fissured.

Bark is of two types, the ring bark and the scale bark. If the bark is found in the form of concentric rings surrounding the entire stem, it is called ring bark, e.g. *Vitis*, *Betula*, *Clematis* etc., if it is found in the form of separate strips or patches, it is called scale bark, e.g. *Ficus*, *Platanus* etc.

6.6. LENTICELS:

During the continuous secondary growth, protective tissue, *periderm* is formed. The cork cells of periderm are impervious to water and gases. Thus, the gaseous exchange

between the internal cells and outer atmosphere becomes difficult and is brought about by lenticels. These are the pore-like openings, look-like lens-shaped 'raised spots' on the surface of the stem. Lenticels are developed in most woody plants. During their origin the phellogen instead of cork cells, contributes loosely arranged cells on outer side. Besides, substomatal parenchyma cells also actively dividing and gives rise to loose parenchyma cells. Both of these loosely arranged parenchyma cells derived from sub stomatal parenchyma and phellogen are collectively called complementary cells (Fig. 6.6). These cells are thin, oval in shape and loosely arranged with intercellular spaces. As the new complementary cells are added towards the outer side, the overlying epidermis ruptures and exposes the underlying complementary cells, thus facilitates gaseous exchange. In some cases, loosely arranged complementary cells are lined by the compactly arranged suberised layer, known as closing layer, e.g. *Prunus*. A closing layer is helpful in keeping the loosely arranged complementary cells in position.

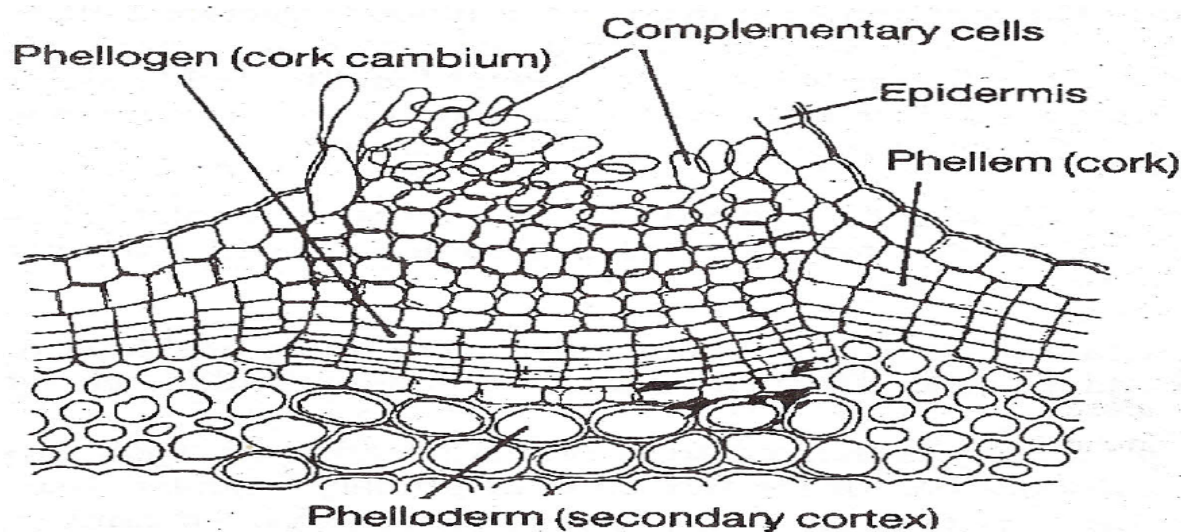


Fig. 6.6: Structure of Lenticell

The arrangement and the cell wall deposition of complementary cells show variation. In some cases, these are somewhat compactly arranged with less distinct intercellular spaces, e.g. *Magnolia*; in *Quercus* and *Sambucus*, the cells are thin-walled, unsuberised and loosely arranged; in *Prunus*, both suberised and unsuberised complementary cells are found.

6.7. SUMMARY:

Later, secondary growth takes place by the activity of lateral meristems, such as vascular cambium and phellogen. Vascular cambium consists of two types of initials, fusiform initials and ray initials. Fusiform initials give rise to the axial system that consists of tracheids, vessels and sieve elements, Ray initials give rise to rays. Vascular cambium cuts off the secondary xylem outside and secondary phloem inside. Secondary xylem formed during spring and also of autumn constitute together to form annual ring or growth ring.

Periderm: Periderm is formed by the activity of phellogen or cork cambium. It serves as a secondary protective tissue against desiccation and mechanical injuries. The periderm consists of three types of tissues, these are: (i) Phellogen or cork cambium, (ii) Phellem or cork, and (iii) Phelloderm or secondary cortex.

Lenticels consist of loosely arranged parenchyma cells, known as complementary cells. They provide gaseous exchange when the bark is formed.

6.8. MODEL QUESTIONS:

- 1) Seasonal activity of vascular cambium
- 2) Cork cambium
- 3) Lenticels
- 4) Cucurbita stem

6.9. REFERENCE BOOKS:

- 1) K. Esau, 1996... Plant Anatomy, Wiley Earrn Limited, New Delhi.
- 2) A. Fahn, 1967. Plant Anatomy. Pergamon Press, Oxford.
- 3) P.C. Vasishta, Plant Anatomy. Pradeep Publications, Jalandhar

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LESSON-7

WOOD ANATOMY

7.0 OBJECTIVE:

- This lesson helps to understand the formation of different types of wood and its evolutionary significance.

STRUCTURE:

7.1 Introduction

7.2 Gymnosperm Wood (Soft Wood)

7.3 Angiosperm Wood (Hard Wood)

7.4 Summary

7.5 Model Questions

7.6 Reference Books

7.1. INTRODUCTION:

Generally, gymnosperm wood is known as soft wood and angiosperm wood hard wood. Sap wood is a living wood, functioning in conduction of water whereas heart wood is non-functional.

7.2. GYMNOSPERM WOOD (SOFT WOOD):

The xylem of gymnosperms is generally simpler and more homogeneous than that of angiosperms. The chief distinction between the two kinds of wood is the absence of vessels in gymnosperms and their presence in the most angiosperms. The other, outstanding peculiarity of gymnosperm wood is the relatively small amount of parenchyma, particularly axial parenchyma, Axial system: In gymnosperms, axial system mainly consists of tracheids. Tracheids are elongated with tapering ends, often forked tips (Fig.7.1A). They are varied in their length from 0.5 to 11mm. Because of great length each tracheid comes into contact with one or more rays. The tracheids overlap one another and form non-storied wood. Neighbouring tracheids are joined by longitudinal row or in a few rows; the pitting may be opposite or alternate. The late-wood tracheids develop relatively thick walls and pits with reduced borders; these are formed fibre tracheids. Libriform fibres are absent.

In bordered pits (Fig. 7.2) *torus* (pit membrane thickening) is present in *Ginkgo*, coniferales, *Ephedra* whereas absent in *Gnetum*, *Welwitschia*, *Cycas revoluta* and *Encephalartos*.

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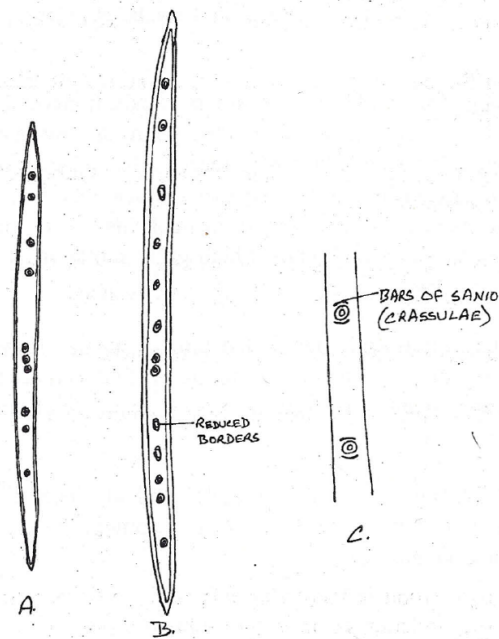


Fig. 7.1: A-C. Tracheid (A) Fibre-Tracheid (B) Tracheid with Crassulae

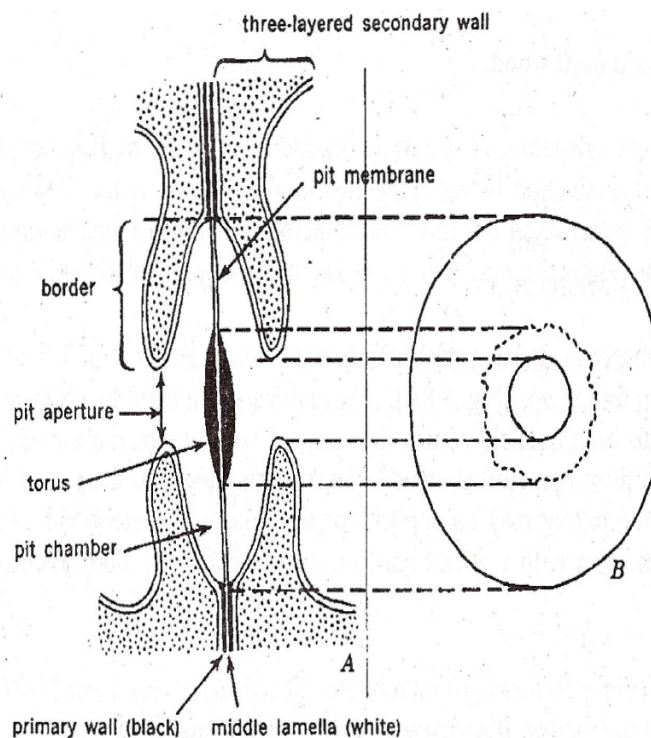


Fig. 7.2: Bordered P A. Sectional View, B. Face View

In radial longi section of most of the gymnosperm woods, transversely oriented thickenings of wall can be observed above and below the pit-pairs.

These are the thickenings of middle lamella and primary wall, and they' are termed Crassulae or bars of Sanyo (Fig. 7.8C). Another characteristic feature of gymnosperm wood is the presence of arbuscule in tracheids. These are rod-shaped outgrowths of the tangential cell walls which grow across the cell lumen so as to connect the tangential walls.

The axial parenchyma is uniformly distributed throughout the growth ring in Coniferales. Parenchyma is conspicuous in many Podocarpaceae, Toxodiaceae and Cupressaceae; scanty in Pinaceae; absent in Araucariaceae and Taxaceae.

Ray system - Rays 'are 'uniseriate in Coniferales and biseriate (Fig. 7.10) and multi seriate in Gnetales. These may be homogeneous or heterogeneous (heterocellular in *Gnetum*).

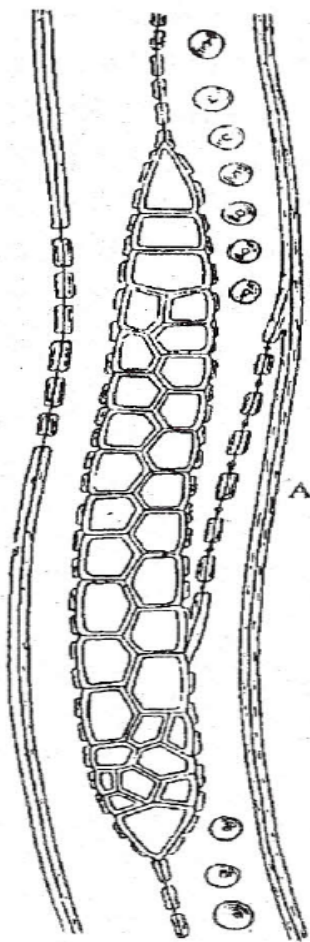


Fig. 7.3: Multiseriate Ray in *Gnetum*.

Rays of gymnosperms are composed either of parenchyma cells alone or of parenchyma cells and tracheids. Ray tracheids are distinguished from ray parenchyma cells chiefly by their bordered pits and lack of protoplasts.

When the vertical tracheid come in contact with ray parenchyma, the pit-pairs are usually half- bordered, i.e., the bordered pit is situated at the side of the tracheid and the simple pit on the side of the parenchyma cells. This area of contact between a ray parenchyma cell and a single vertical tracheid is known as cross-field. The type of pits, their number and distribution in the cross-field important features in the identification of gymnosperm woods.

Resin Ducts:

In certain gymnosperms, such as *Pinus*, *Picea*, *Pseudotsuga* etc., the resin ducts are found both in axial and ray parenchyma. The resin ducts arise as schizogenous intercellular spaces by separation of resin producing parenchyma cells from each other. These cells make the lining, the epithelium, of the resin duct (Fig. 7.4 B) and, secrete the resin. A resin duct may become closed by the enlarging epithelial cells in non-functional woods (heart woods). These are known as *tylosoids* (Fig. 7.2B).

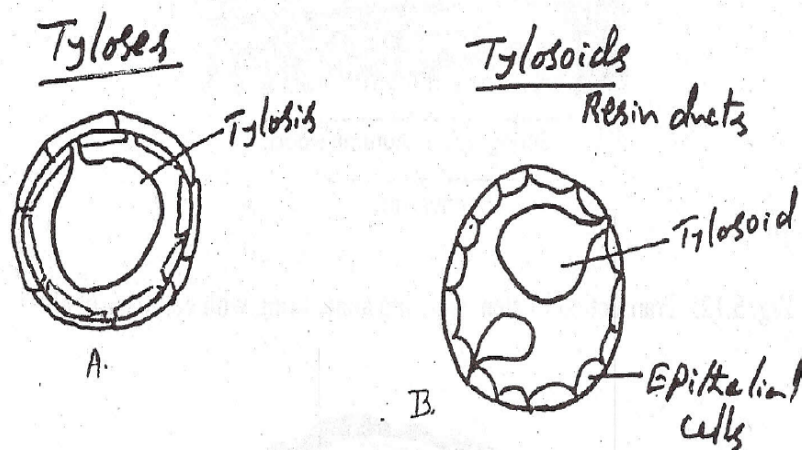


Fig. 7.5: Resin duct. A. Tyloses, B. Tylosoids

7.3. ANGIOSPERM WOOD (HARD WOOD):

The angiosperm wood commonly refers to secondary xylem of dicotyledons. Angiosperm wood is generally more complex than the gymnosperm wood, since its elements are more varied in size, kind, form and arrangement. The most complex dicotyledonous woods, such as oak, may contain vessel members, tracheids, fibre-tracheids, libriform fibres, axial parenchyma and ray parenchyma. Because of the complexity of structure of dicotyledonous woods many characters may be used in their identification, such as presence or absence of vessels and their distribution pattern types of perforation plate in vessels, distribution of axial parenchyma, types of rays, presence of storied or non-storied structure etc.

Growth Rings:

Cambial activity is influenced by environmental fluctuations. In temperate regions, cambium reactivates in spring season during which more leaves and flowers are formed, so the plant requires large amount of water and mineral salts, Hence, the wood formed during this period shows more number. of xylem vessels with wide lumen (Fig. 7.6) and it is known as spring wood (early wood) which is light in colour. During the unfavourable season, i.e. in autumn, the cambium is less active and produce less number of vessels with narrow lumen (Fig. 7.7), it is called autumn wood (latewood) and is dark coloured. Both spring and autumn woods are constituted as annual ring or growth ring or seasonal ring (Fig. 7.6).

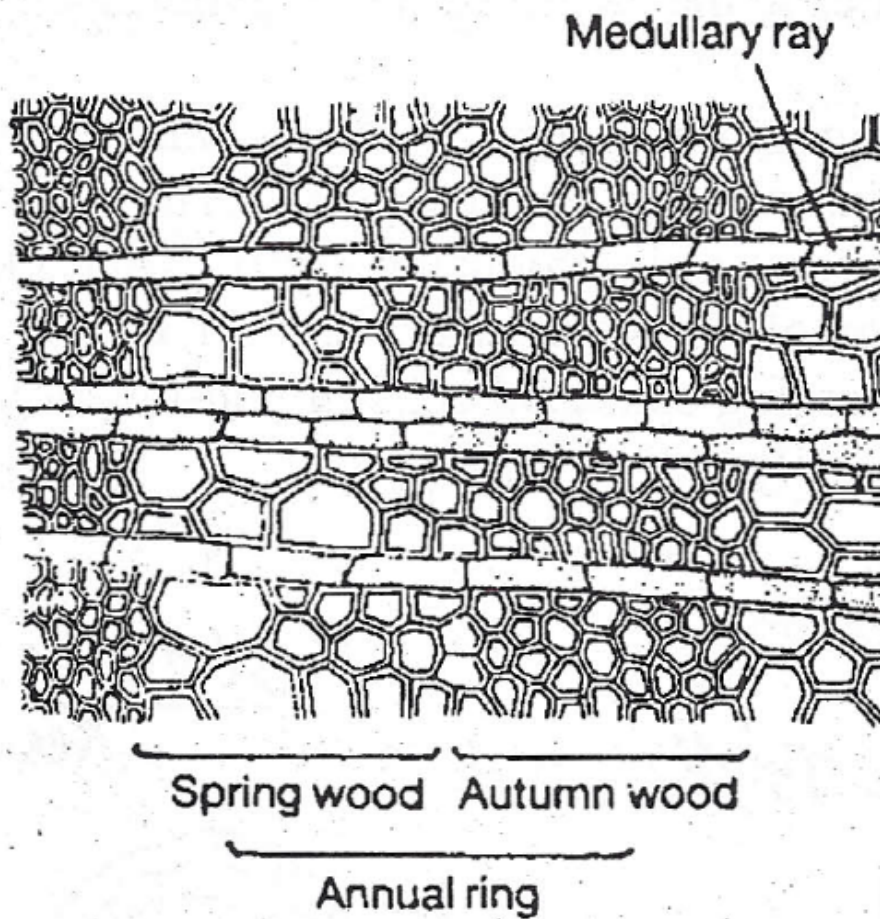


Fig. 7.6: Transection of Stem showing Annual Ring with Cellular Details



Fig. 7.7: Transection of Old Dicot Stem Showing Annual Rings

By counting the number of annual rings, the approximate age of trees can be estimated. The branch of biology dealing with the estimation of age of tree on the basis of number of growth rings is known as Dendrochronology. The tree *Sequoia sempervirens*, considered to be the tallest tree in the world located in *Sequoia* National Park, California is estimated to be 3,000 years old; *Sequoiadendron giganteum* (giant sequoia) has got 3,500 years of age.

In tropical countries like India, the climate is normally uniform, so the number of growth rings formed does not correlate with age of the tree. Such growth rings are called growth marks. Sometimes, two rings may be produced in a year in tropical trees. Sometimes, the annual rings are formed due to hormonal changes or heavy rainfall or due to diseases. They are called "pseudo-annual rings". So, the number of annual rings is not always an accurate parameter to estimate the age of trees.

Distribution of Vessels:

The arrangement of vessel in dicotyledonous woods show two main patterns, these are diffuse-porous and ring-porous. In diffuse-porous woods, the vessels are essentially equal in diameter and are uniformly distributed throughout the growth ring (Fig. 7.8 A), e.g. *Acer*, *Betula*, *Liriodendron*, *Eucalyptus*, *Populus* etc., whereas in ring-porous woods; the vessels of unequal diameter with largest vessels localized in the early wood are present, e.g. *Fraxinus*, *Robinia*; *Quercus* etc. The vessels in ring-porous wood are longer than that of in the diffuse-porous wood.

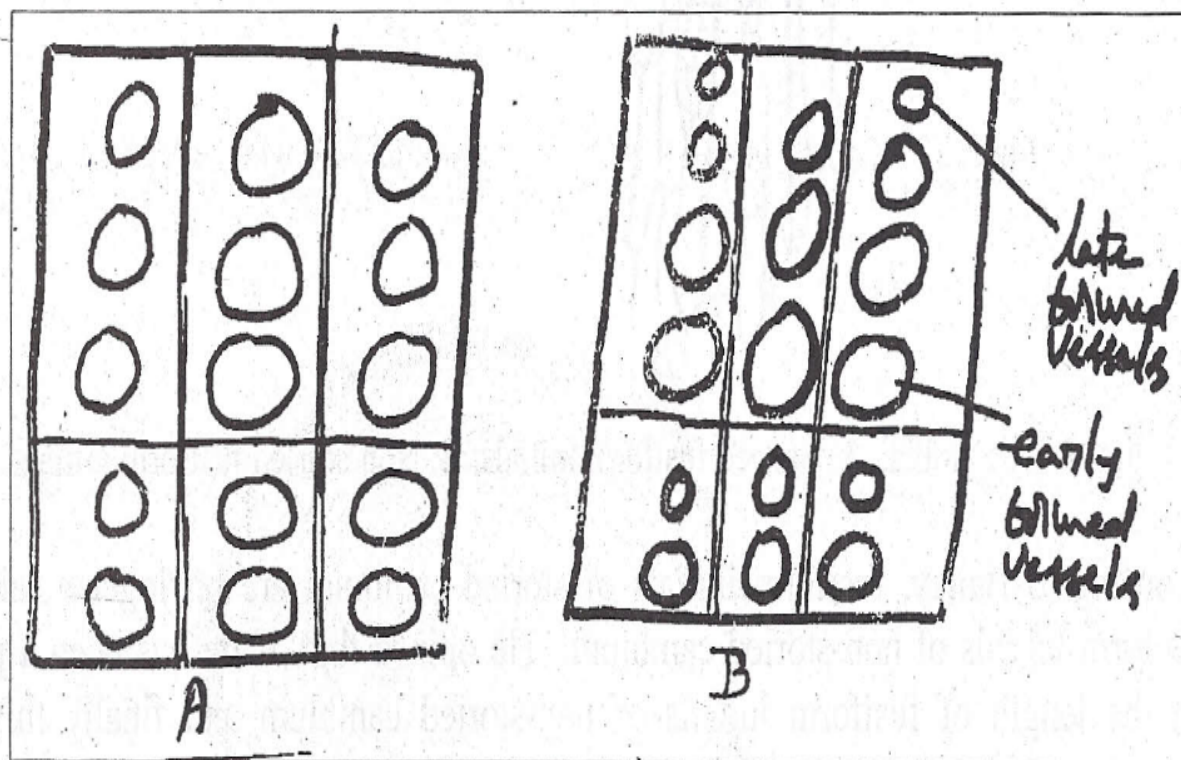


Fig. 7.8 A, B. Dicotyledonous Woods

A. Diffuse Porous Wood; B. Ring Porous Wood

The physiological studies indicate the specialized nature of ring-porous wood. Flow of water in ring-porous wood is about ten times, faster than that of diffuse-porous wood. Trees with ring-porous wood appear to produce their early-wood vessel system rapidly, whereas species with diffuse-porous wood form their new xylem slowly. An early development of tyloses in ring-porous woods indicate that these highly specialized vessels are functional for a short period only.

Stored and Non-Stored Woods:

These woods are formed on the basis of arrangement of fusiform initials present in the cambium. Stored wood is derived from stored cambium, in which fusiform initials (140-250 in length) arranged in horizontal rows (Fig. 7.9 A), e.g. *Tamarix*, *Robinia* etc., whereas non-stored wood from non-stored cambium where fusiform initials (7.10)

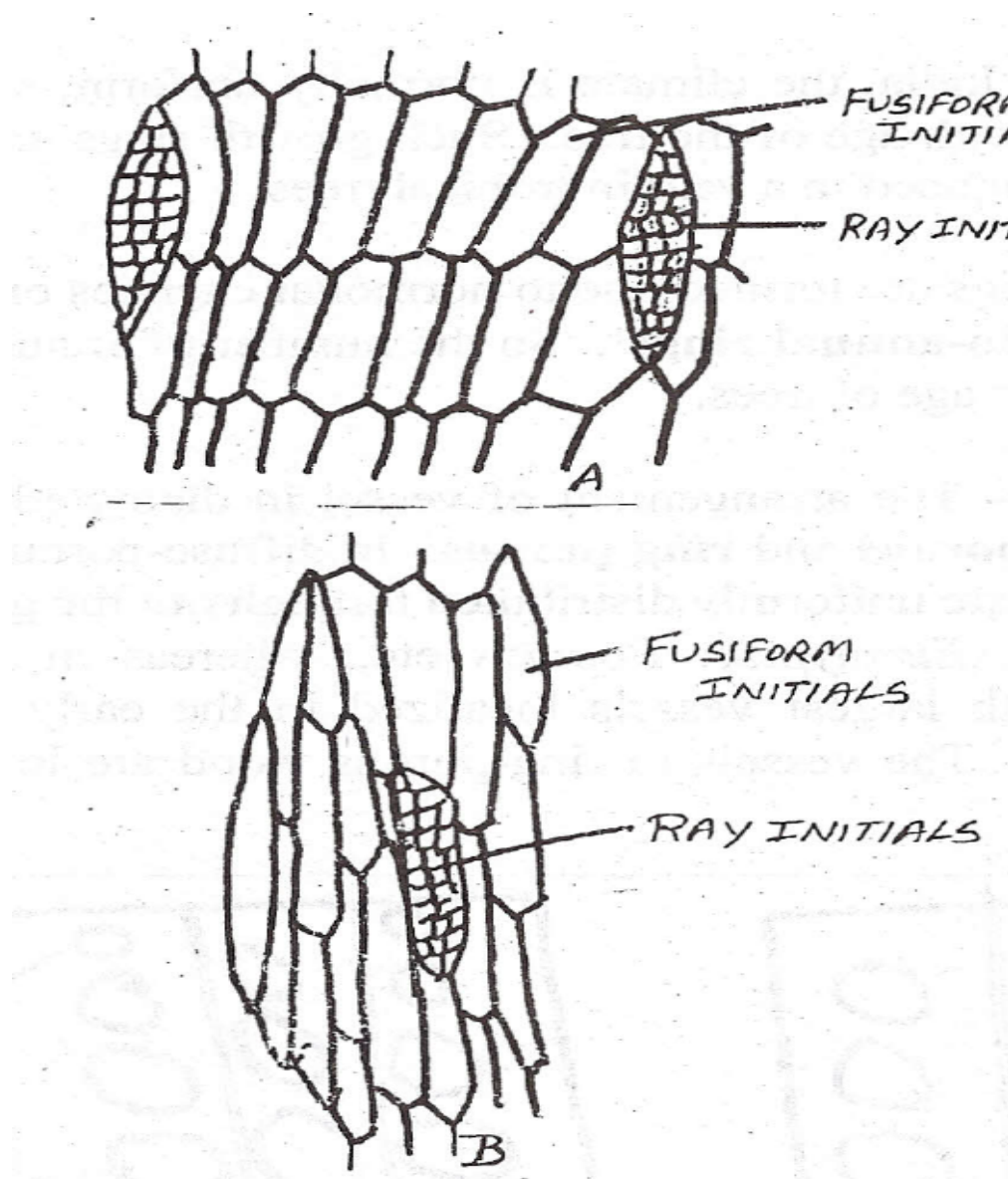


Fig. 7.8: Cambia. A. Stored Fusiform Initials; B. Non-Stored Fusiform Initials

According to Bailey, fusiform initials of storied cambium are phylogenetically advanced than the fusiform initials of non-storied cambium. He opined that, there has been a phylogenetic decrease in the 'length of fusiform initials of non-storied cambium and finally this led to the development of storied cambium.

Axial Parenchyma Distribution:

As it has already mentioned in section 7.2 both *Apotracheal* and *paratracheal* types of axial parenchyma distribution are found in dicotyledonous woods. In each distributional type subordinate variations are recognized (see section 7.2).

Sapwood and Heartwood:

In transection of wood two regions are distinct, the outer light coloured, known as *sapwood* (alburnum) (Fig. 7.9) and central dark coloured, *heartwood* (duramen) (Fig. 7.9). The sapwood consists of living and functional cells involved in conduction of water.

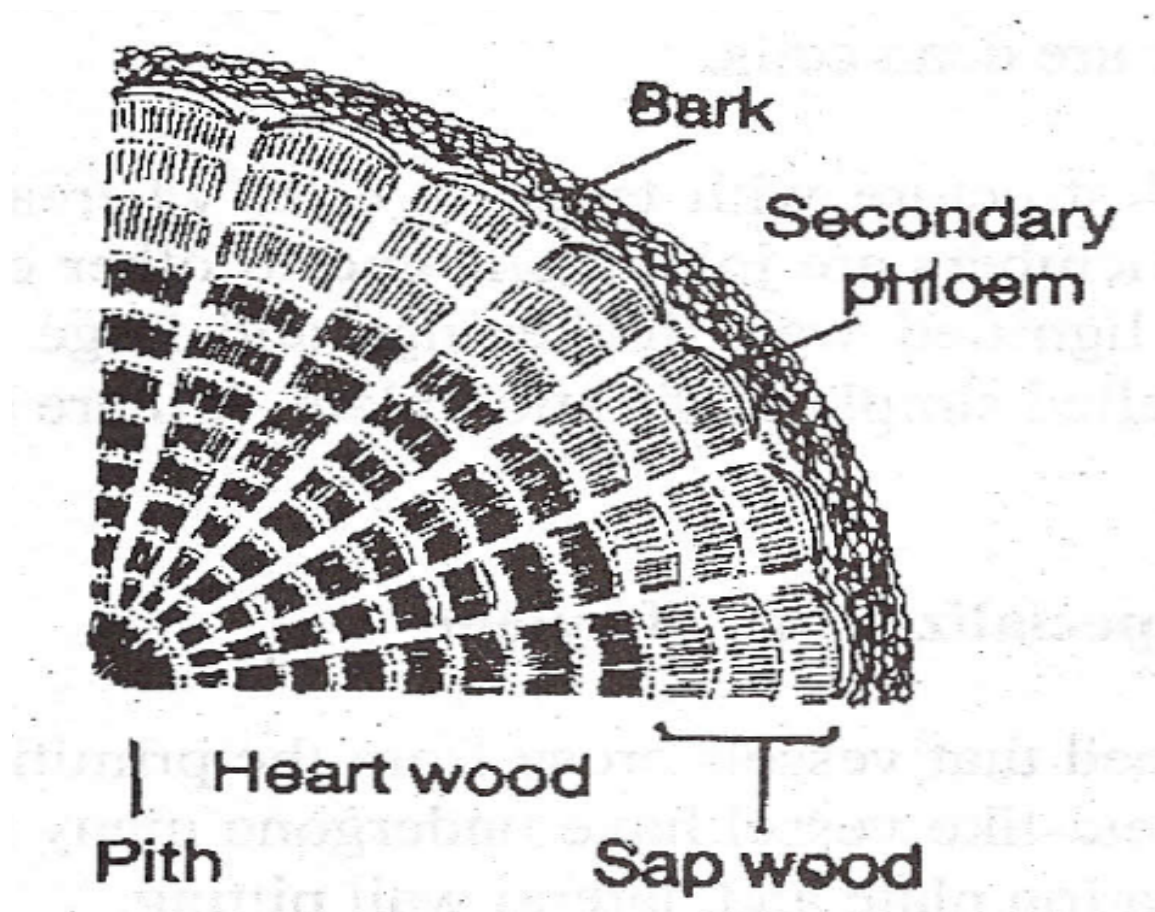


Fig. 7.9: A Sector of Transection of Old Dicotyledonous Stem Showing Sapwood and Heartwood

The heartwood consists of dead cells and becomes non-functional. With increasing age, the wood loses water and store food substances, and becomes infiltrated with various organic compounds, such as oils, gums, resins, tannins and aromatic and coloured substances. The development of the colour in the heartwood is a slow process dependent on oxidation of phenols. The pigments found in heartwood in certain cases are of commercial importance, e.g. haematoxylin (*Haematoxylon campechianum* brasil in (*Caesalpinia sappan*), santalin (*Pterocarpus santalinus*) etc. Formation of tyloses, (Fig. 7.3A; 7.10) make the xylem vessels non-functional. In gymnosperms, tori appressed to the border and close the pit aperture. All these changes do not affect the strength of the wood but make it more durable than the sapwood, less easily attacked by decay organisms and less penetrable to various liquids.

7.4. SUMMARY:

Generally, gymnosperm wood is known as soft wood and angiosperm wood is hardwood. Sap wood is living and functioning in conduction. of water whereas heart and is non-functional. The gymnosperm wood is generally simpler and more homogeneous than that of angiosperms. Storied wood is derived from storied cambium, in which fusiform initials arranged in horizontal rows; whereas non-storied from non-storied cambium where fusiform initials overlap partially one another.

7.5. MODEL QUESTIONS:

- 1) Give an account on gymnosperm and Angiosperm woods.
- 2) Annual rings
- 3) Sap Wood and Heart Wood.

7.6. REFERENCE BOOKS:

- 1) L S. Carlquist, 1961. Comparative Plant Anatomy. Hold, Rehart and Winston, New York.
- 2) K. Esau, 1997. Plant Anatomy, Second Edition, Wiley Eastern Limited; New Delhi.
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LESSON-8

ANOMALOUS SECONDARY GROWTH

8.0 OBJECTIVE:

- In this chapter, anomalous secondary growth in angiosperms has been discussed.

STRUCTURE:

8.1 Introduction

8.2 Normal Cambium with Abnormal Activity

8.2.1 Presence of Phloem Wedges in the Xylem in *Bignonia* Stem

8.2.2 Presence of Fissured Xylem in *Aristolochia*

8.3 Abnormal Behaviour of the Abnormal Cambium

8.3.1 Formation of Extra Stelar cambium from Pericycle and Cortical Tissue

8.3.2 Formation of Accessory Cambia

8.3.3 Formation of Interxylary Phloem (Included Phloem)

8.4 Anomalous Secondary Growth in Monocot Stem

8.5 Summary

8.6 Model Questions

8.7 Reference Books

8.1. INTRODUCTION

The process of secondary, growth that gives rise to the secondary plant body may be termed the common type of secondary growth. However, in many angiosperms there are deviations from 'this type of secondary growth. Such deviated pattern of secondary growth is described as anomalous.' secondary growth. With the result of the combinations of unusual structure, certain anomalous and extremely complex structures are formed. These complex structures are referred to as anomalies.

The Anomalies can be listed as follows:

(i) Anomalies in Primary Plant Body

- A. Occurrence of scattered vascular bundles in dicotyledons, e.g. members of Nymphaeaceae, Papaveraceae and Piperaceae.
- B. Vascular bundles arranged in a ring in monocotyledons, e.g. *Hordeum*, *Oryza*, *Triticum* etc.
- C. Presence of medullary bundles, e.g., *Amaranthus*, *Boerhavia*, *Bougainvillaea*.
- D. Occurrence of cortical bundles, e.g., *Nyctanthes*, *Casuarina*, members of Rutaceae etc.
- E. Presence of intraxylary phloem (bicollateral vascular bundles), e.g. members of Apocyanaceae, Cucurbitaceae and Solanaceae.

(ii) Anomalies in Secondary Plant Body

- A. Abnormal behaviour of the normal cambium e.g., *Aristolochia*, *Bignonia* etc.
- B. Abnormal behaviour of abnormal cambium.
 - a) Formation of exstrastelar cambium from the pericycle e.g, *Achyranthes*, *Amaranthes*,
 - b) *Chenopodium* etc.
 - c) Formation of accessory cambia from the cortex, e.g. *Boerhavia*, *Bougainvillea* etc.
 - d) Formation of interxylary phloem (included phloem); e.g, *Combretum*, *Leptadenia*, *Strychnos* etc.

(iii) Anomalies in monocotyledons, e.g. *Dracaena*, *Musa* etc.**8.2. NORMAL CAMBIUM WITH ABNORMAL ACTIVITY:**

The vascular cambium is formed normally, that is by the union of the fascicular and inter fascicular cambium but behaves in an abnormal manner. Sometimes, the normal cambium starts cutting cells at several places irregularly, and forms at certain places much larger portions of xylem than phloem; at other places more phloem than xylem, that-leads to formation of ridged and furrowed xylem cylinder.

8.2.1. Presence of Phloem wedges in the Xylem in *Bignonia* Stem (Fig. 8.1)

In *Bignonia*, the cambium ring behaves normally in the beginning, cutting the secondary xylem towards outside and secondary phloem inside. However, after some time, there are four furrows at four equidistant points appeared in the xylem, extending almost to the pith. The cambium is situated inside of these furrows and acts abnormally. At these points, extensive amount of secondary phloem with little or no secondary xylem is formed. These phloem masses intrude inwards forming four deep wedges of irregular width and supported by transverse bands of sclerenchyma (Fig. 8.1). Later, these four furrows become closed. The four radial groups of phloem tissue (also known as phloem wedges) are united by medullary rays.

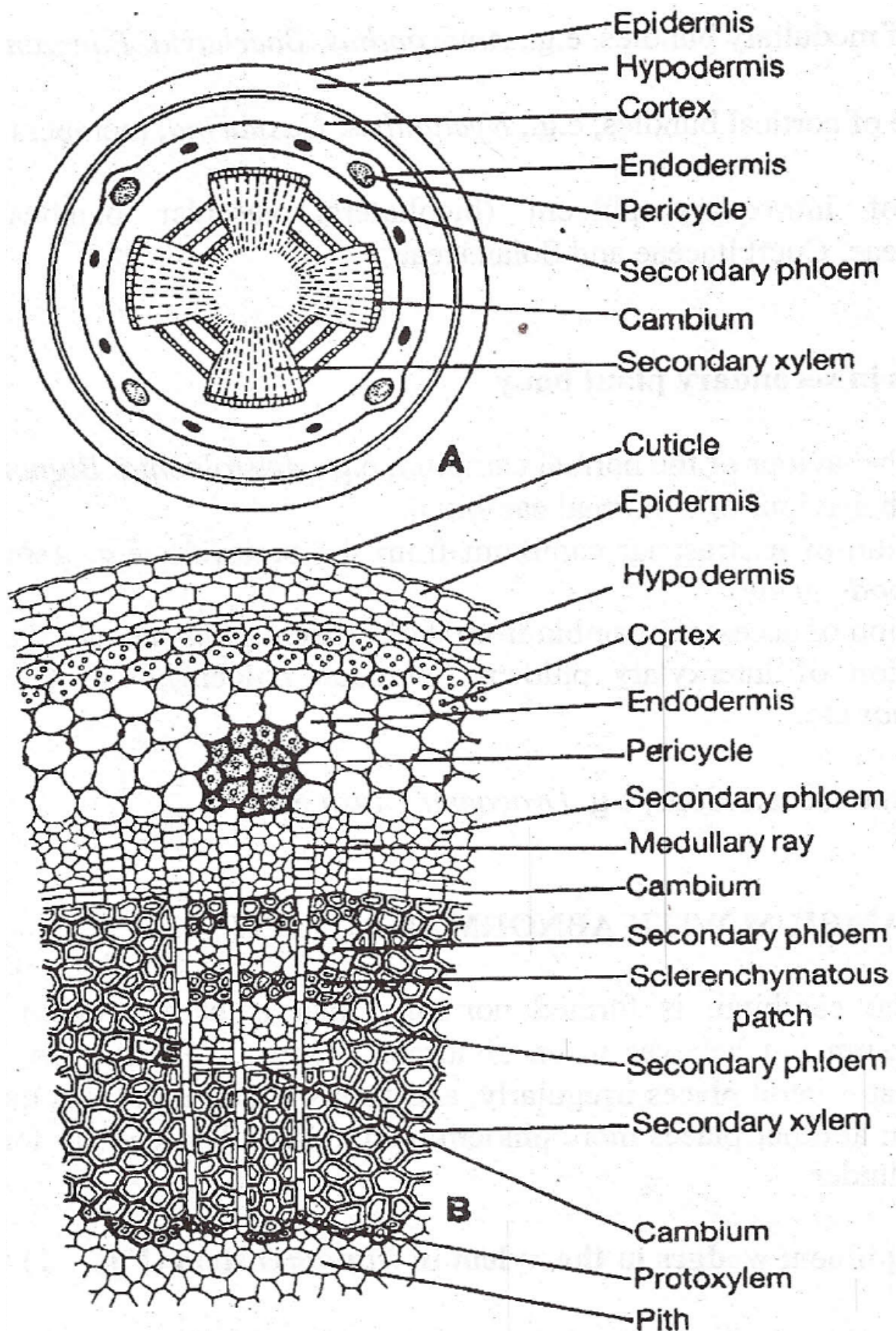


Fig. 8.1: T.S. of *Bigonia* stem. A. Transection in Outline, B. Enlarged Sector

8.1.2. Presence of Fissured xylem in *Aristolochia* (Fig. 8.2):

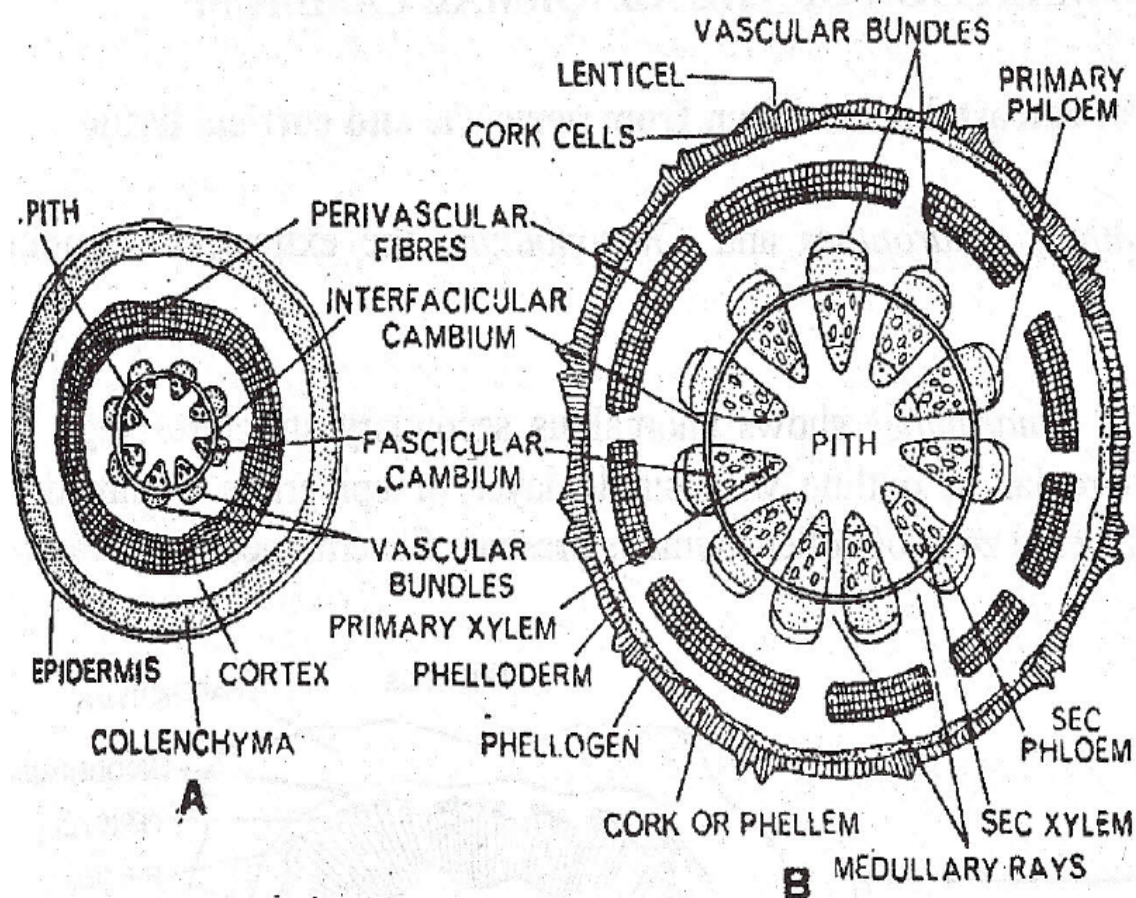


Fig. 8.2: A-B. T.S. of *Aristolochia* Stem Showing early and Later Stages of Secondary Growth

The fissured xylem is seen in the fairly old stems. In *Aristolochia*, as usually cambium cuts off secondary phloem towards outside and secondary xylem inside. Later in old stems, segment of the cambium act abnormally and cut only parenchyma cells both on outer and inner sides, thus they form ray-like parenchyma. The new cambial segments constantly form the rays of parenchyma and increase in diameter of stem. As the vascular cylinder, broken by wide rays, increases in circumference, the cylinder of sclerenchyma that encircled the vascular bundles becomes ruptured (Fig. 8.2) and adjacent parenchyma is intruded into the gaps. As a result, very fluted vascular cylinder is formed (Fig. 8.3). Woody climbers (lianes) are also showed the fissured xylem in their fairly old stems.

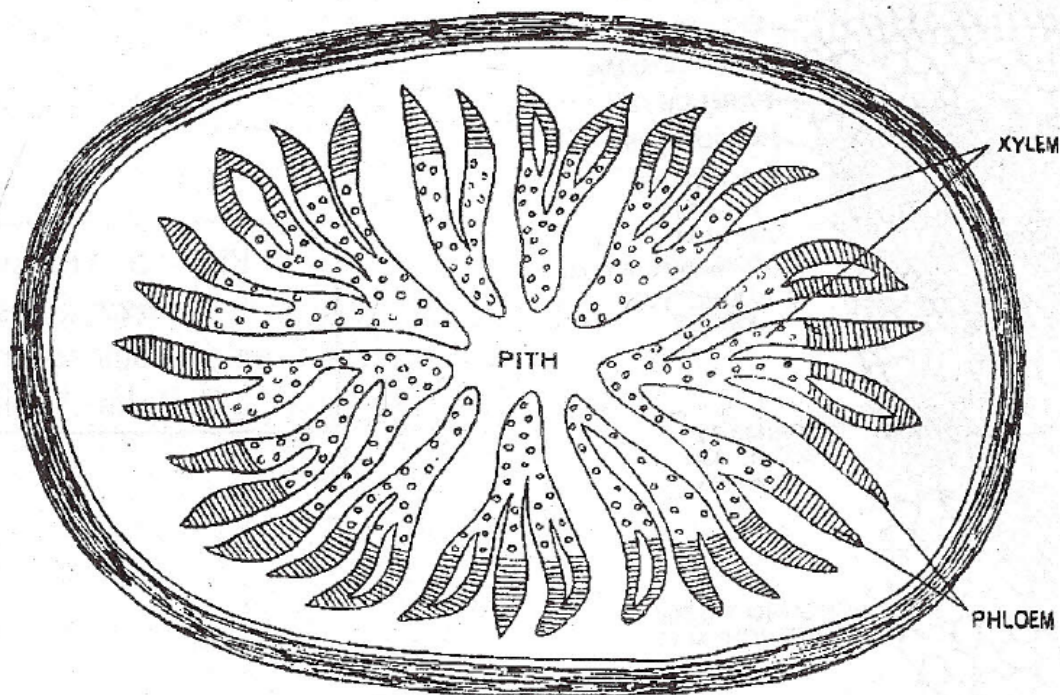


Fig. 8.3: T.S. of Old Stem of *Aristolochia* Showing Anomalous Secondary Growth

8.3. ABNORMAL BEHAVIOR OF THE ABNORMAL CAMBIUM:

8.3.1 Formation of Extra Stellar Cambium from Pericycle and Cortical Tissue

In *Achyranthes*, *Amaranthes* and *Chenopodium*, the extra stellar cambium arises in the pericycle. The stem of *Amaranthes* shows anomalous secondary structure (Fig. 8.4 and Fig. 8.5). In transection, it is circular in outline with single layer of epidermis. Immediately beneath the epidermis, a multi layered zone of collenchyma is present. Several medullary vascular bundles remain scattered in the cortex and pith regions. Cambial activity is found only in individual bundles which are collateral and open. Later their activity is ceased. Anomalous secondary growth takes place due to the development of a new extra stellar cambium, i.e., the cambium outside the stele, in the pericycle region. this newly formed cambium cuts off secondary vascular bundles and inter fascicular parenchymatous conjunctive tissue. Hence, several secondary vascular bundles remained embedded in conjunctive tissue.

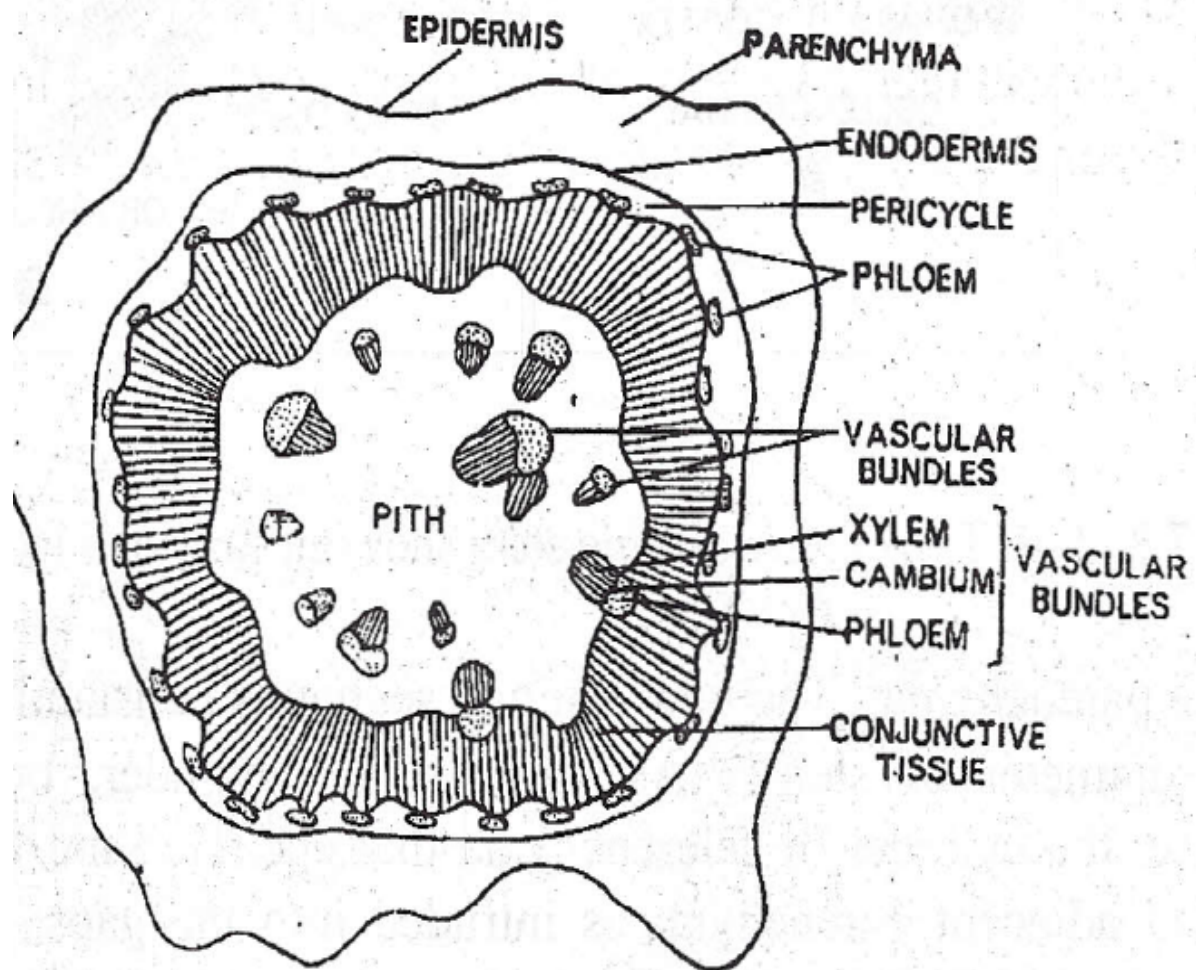


Fig. 8.4: Outline of Transverse Section of *Amaranthus* Stem Showing Anomalous Secondary Structure

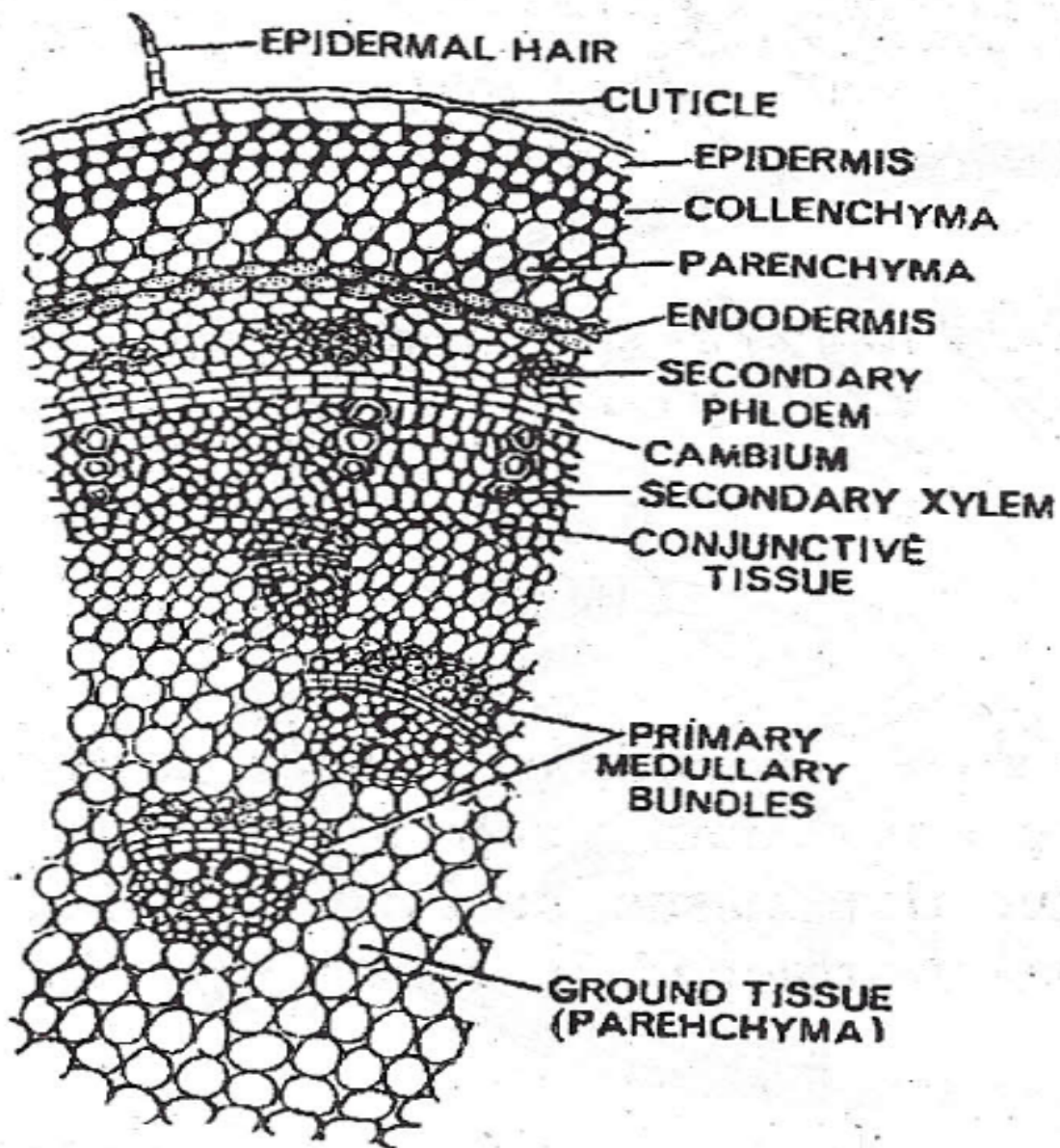


Fig. 8.5: Transverse Section of *Amaranthus* Stem showing Anomalous Secondary Structure - Cellular Details of a Sector

In *Achyranthes* stem, the extra stelar secondary arcs or rings of meristematic cells (cambium) appear in the pericycle that give rise to secondary vascular bundles (Fig. 8.6 and 8.7). If bundles originate from closed ring of cambium, they are arranged in concentric rings. When they are formed from cambial arcs, they are irregularly distributed in the ground tissue. The conjunctive tissue in between the bundles consists of parenchyma in some species and of lignified or unlignified in others.

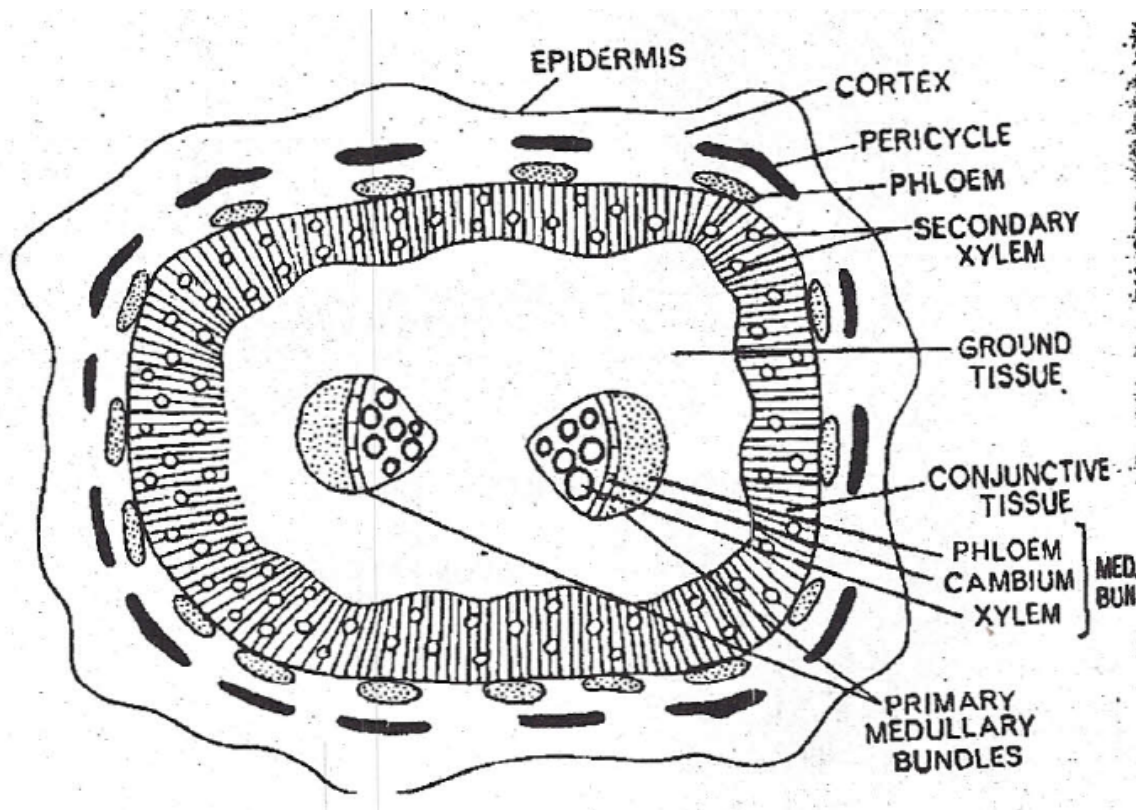


Fig. 8.6: Outline Diagram of Transection of *Achyranthes* Stem Showing Anomalous Secondary Thickening and Medullary Bundles

8.3.2. Formation of Accessory Cambia:

In the stems of *Boerhavia* and other members of Nyctaginaceae (*Bougainvillea*, *Mirabilis* etc.) several cambia arise successively in a centrifugal direction. Each cambium cuts off xylem and conjunctive tissue inside, and phloem and conjunctive tissue outside. In this way, there is continuous increment of secondary vascular tissues arranged in concentric rings; as a result, diameter of stem is increased.

Boerhavia Stem:

Secondary xylem and phloem are formed as usually by the activity of vascular cambium (Fig. 8.8). After the formation of secondary tissues, the cambium ceases its activity and a new cambium ring arises from the parenchyma cells, that is outside the phloem. This first accessory cambium behaves similarly to the vascular cambium, cutting off secondary xylem alternating with lignified conjunctive tissue on the inner side and secondary phloem opposite to secondary xylem and parenchyma on outer side. In this way, many accessory cambia are formed, resulting into continuous increment of secondary vascular tissues (Fig. 8.9).

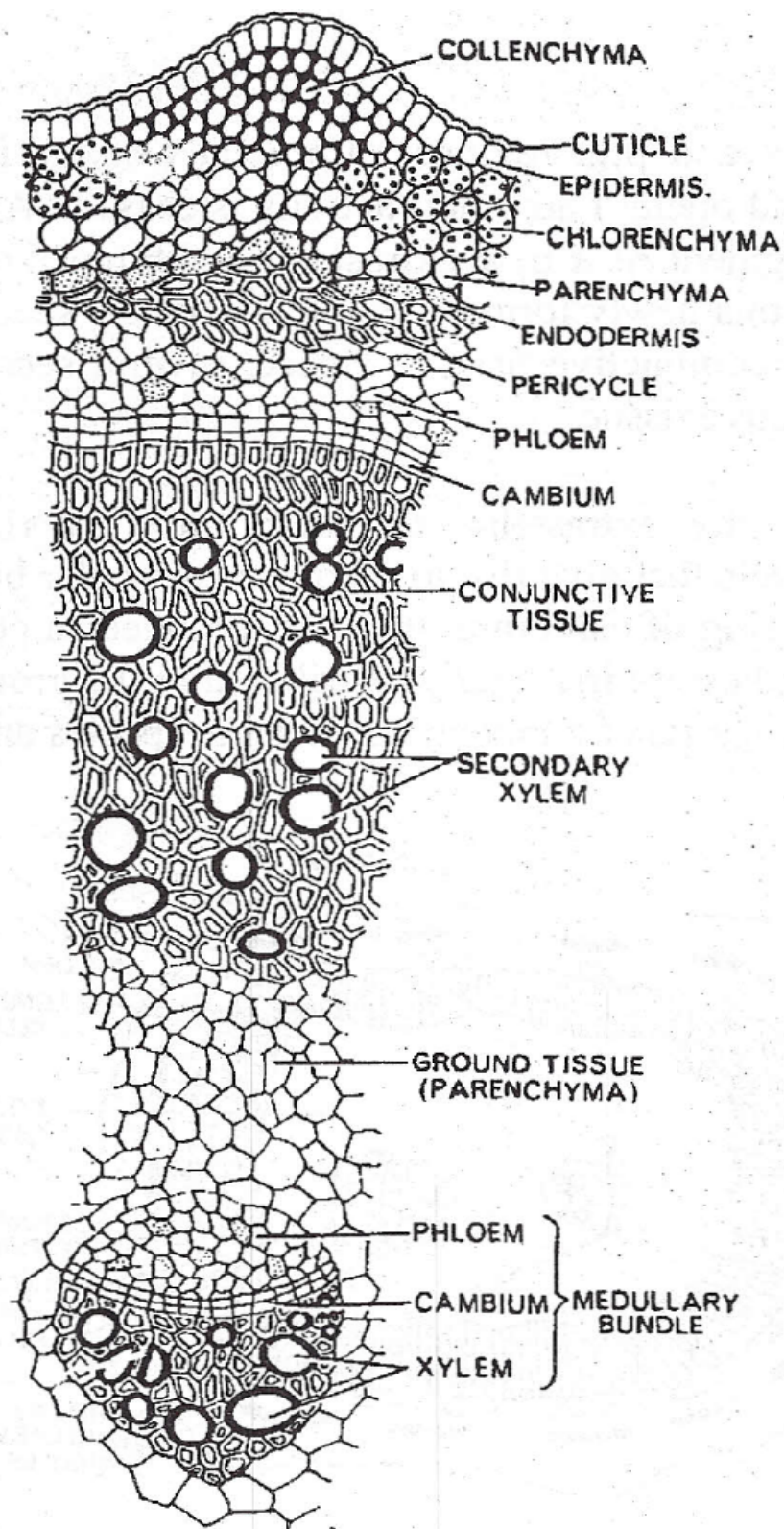


Fig. 8.7: Transection of *Achyranthes* Stem Showing Anomalous Secondary Structure - Details of A Sector

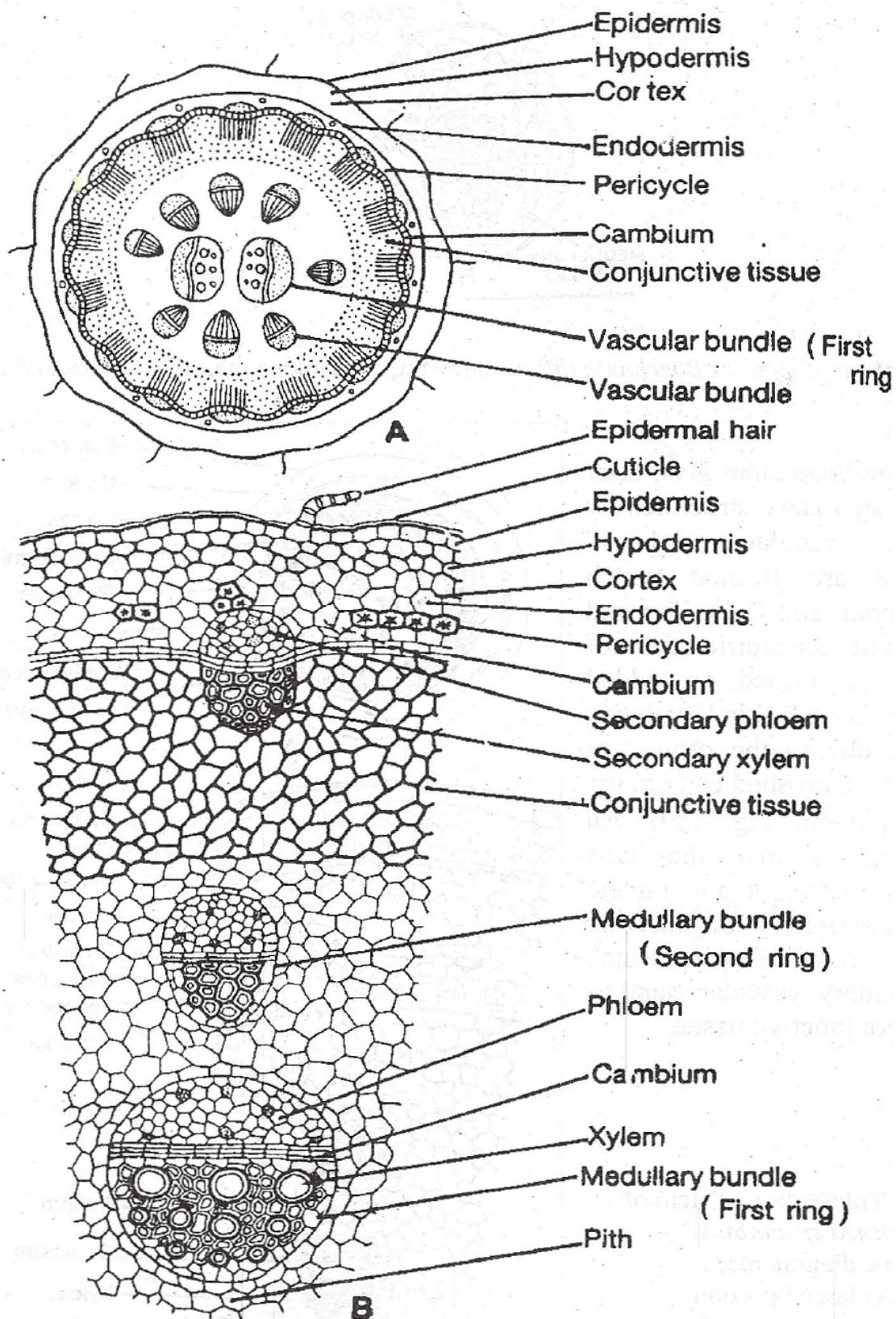


Fig. 8.8: A-B. Transection of Stem of *Boerhavia diffusa*. A. Outline Diagram, B. Cellular Details

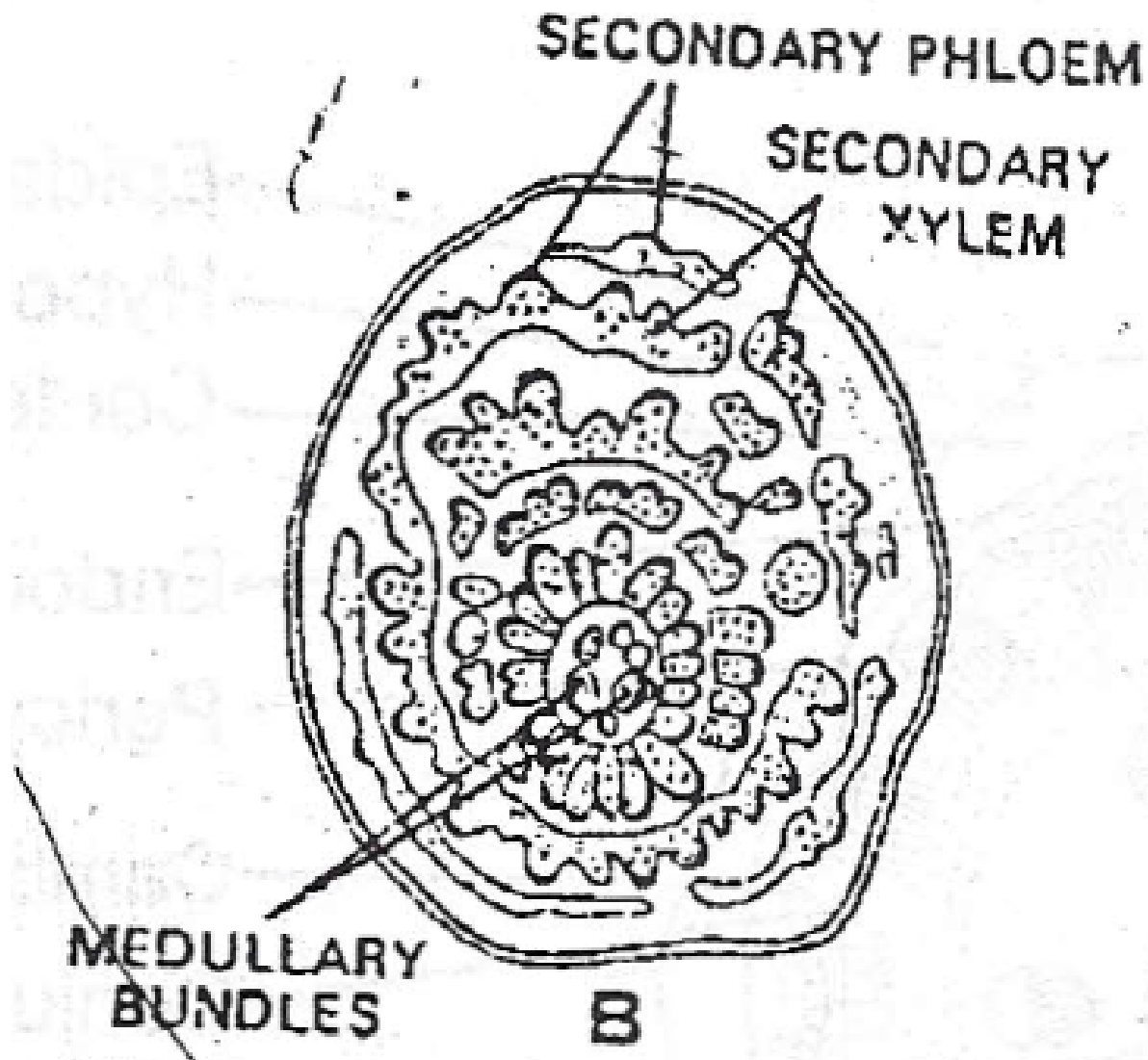


Fig. 8.9: Transection of Stem of *Boerhavia* Showing Continuous Increment of Secondary Tissues

In *Bougainvillea* stem also, after the formation of secondary structures. By the activity of vascular cambium, accessory cambia are formed which behave in a manner similar to normal cambium; as a result, concentric layers of vascular bundles are formed, embedded in the conjunctive tissue. This layering is very conspicuous due to the prominent xylem vessels and the crushed cells in the oldest part of the phloem (Fig. 8.10). An interesting feature is that the 'new cambium' does not arise as a complete ring around the periphery of vascular cylinder but in the form of strips which give rise to secondary vascular bundles embedded in the conjunctive tissue.

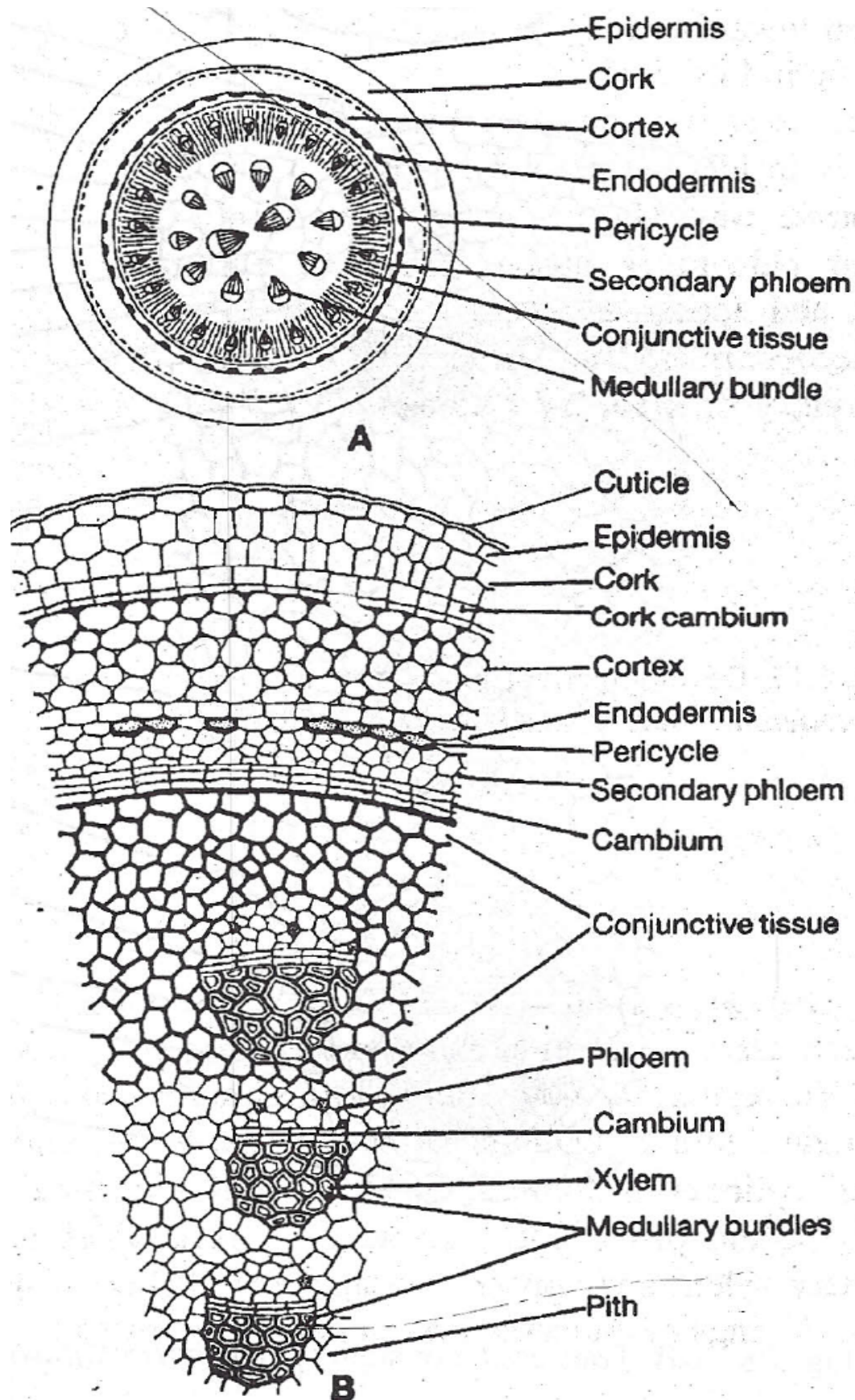


Fig. 8.10: A-B. Transection of stem of *Bougainvillea spectabilis*. A. Outline Diagramme

8.3.3. Formation of Interxylary Phloem (Included Phloem):

Interxylary or included phloem is formed by the abnormal activity of cambium. The interxylary phloem is always secondary in origin and is found in the form of islands, embedded in the secondary xylem.

Leptadenia Stem:

In *Leptadenia* and other species of *Combretum*, *Entada* and *Salvadora*, certain small segments of the cambium behave abnormally and cut only the phloem towards inner side, instead of xylem, for a short, period of time. Later, the entire cambium regains its activity and cuts off secondary xylem towards inside and secondary phloem outside in its normal way. In this process, the abnormally formed phloem's pushed into the secondary xylem and appear as islands remain included in the secondary xylem, hence it is known as interxylary or included phloem (Fig. 8.11 and Fig. 8.12).

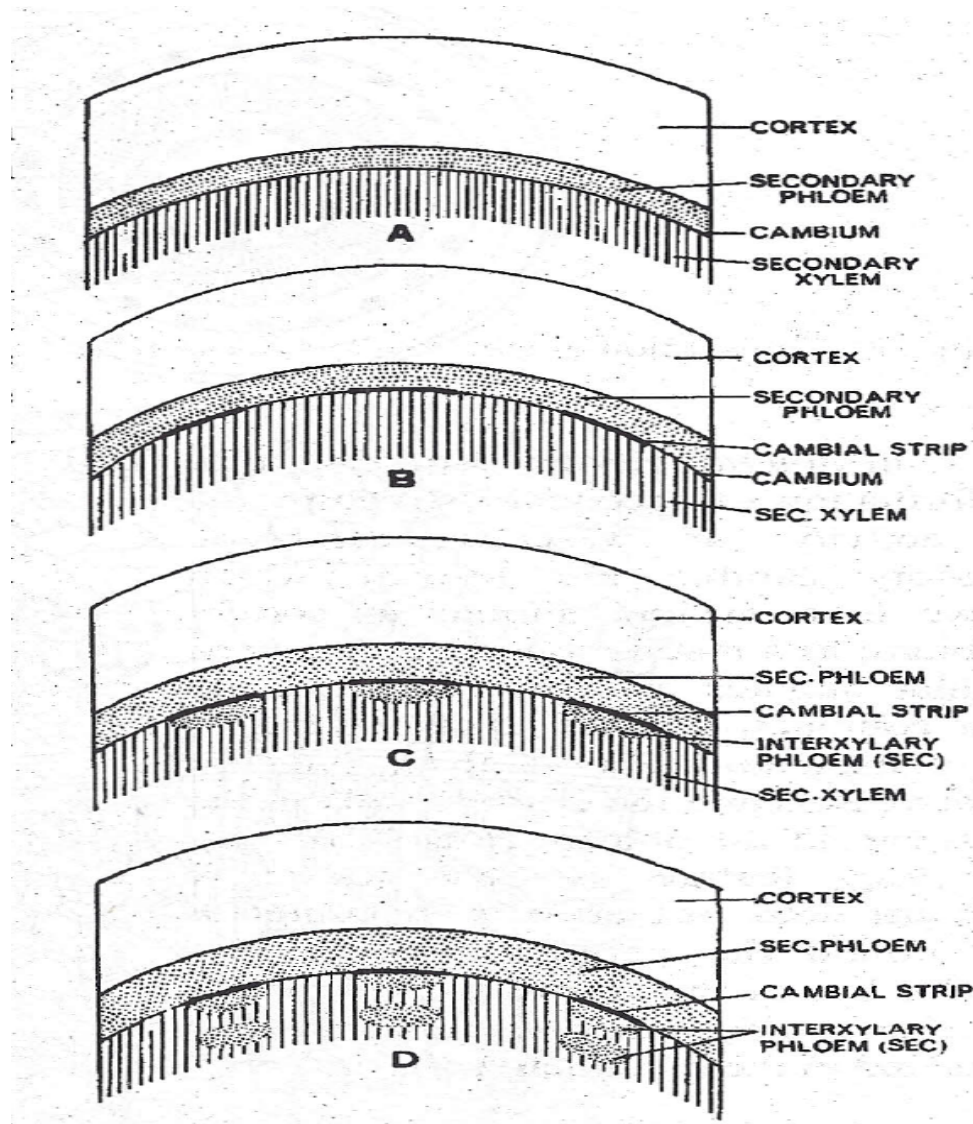
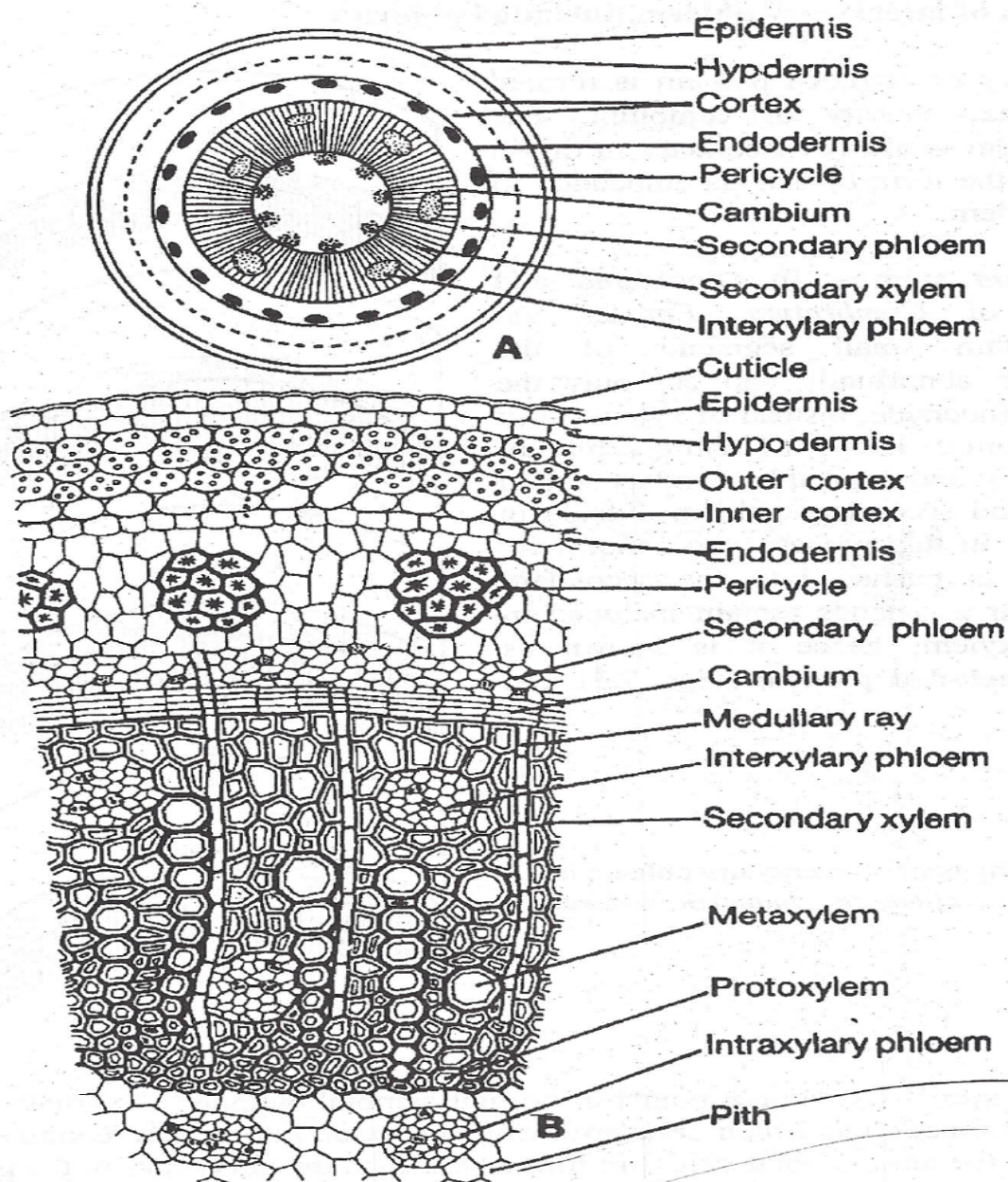


Fig. 8.11: Development of Interxylary Phloem in *Leptadenia*, *Combretum*, *Entada* and *Salvadora*

Strychnos Stem:

At certain points of normal cambial cylinder, the small segments of the cambium cease to function and their cells are being converted into mature conducting tissue (Fig. 8.13). Thereafter, the new cambial strips are formed either in the phloem or in the pericycle. Later, these newly formed cambial strips unite with the edges of the normal cambium. Thus, a wavy cambial cylinder is formed. Soon after, this cambial cylinder becomes stretched and regains its activity; in this process, the secondary phloem which is already formed earlier, is pushed into the secondary xylem and appear as islands (Fig. 8.14) This process is repeated and forming several concentric rings of interxylary or included phloem patches which are purely secondary in origin.



**Fig. 8.18: Transection of Stem of *Leptadenia* showing Interxylary Phloem.
A. Outline Diagram. B. Cellular Details of the Sector**

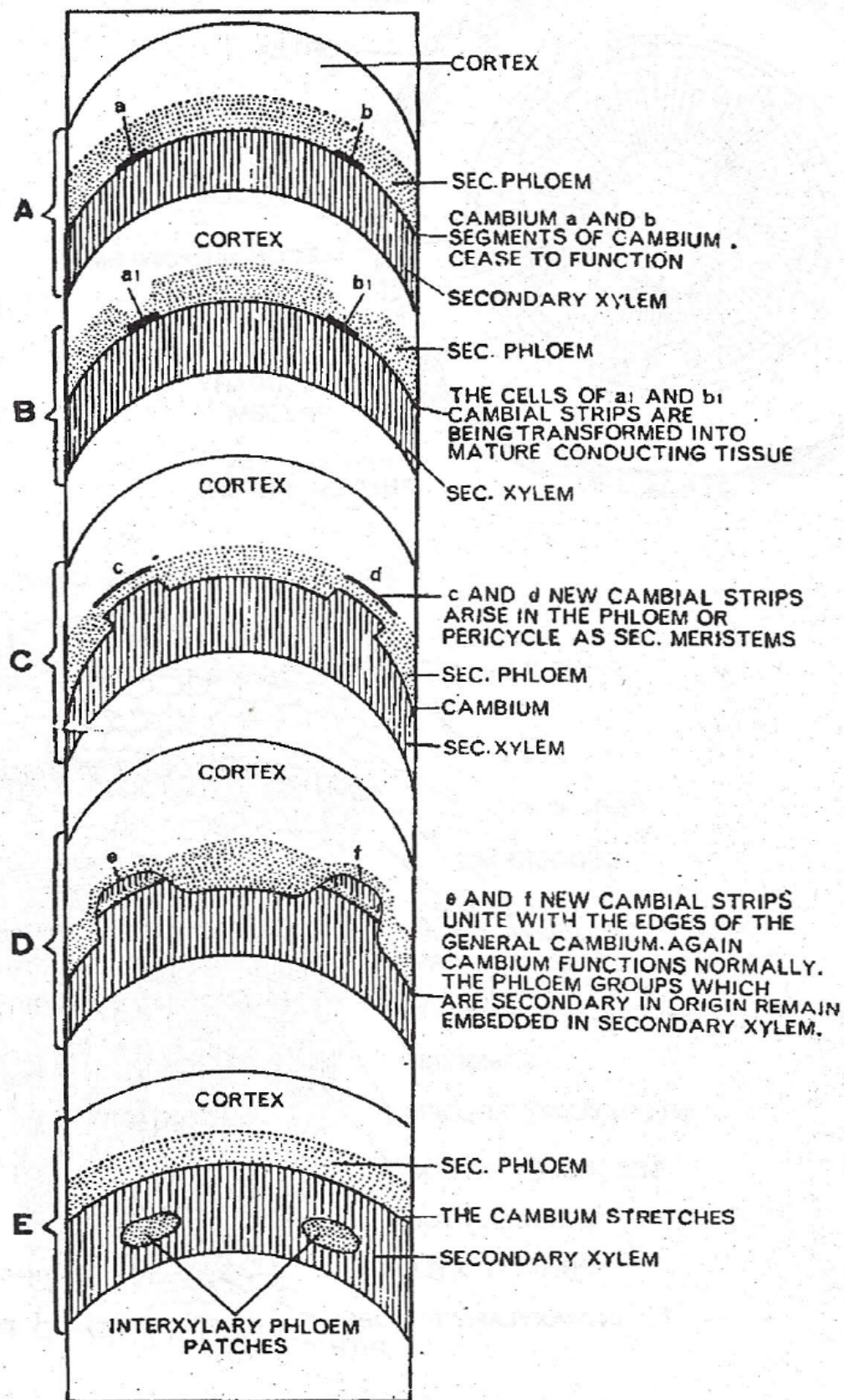


Fig. 8.13: Development of Inter Xylary Phloem in the Stem of *Strychnos*

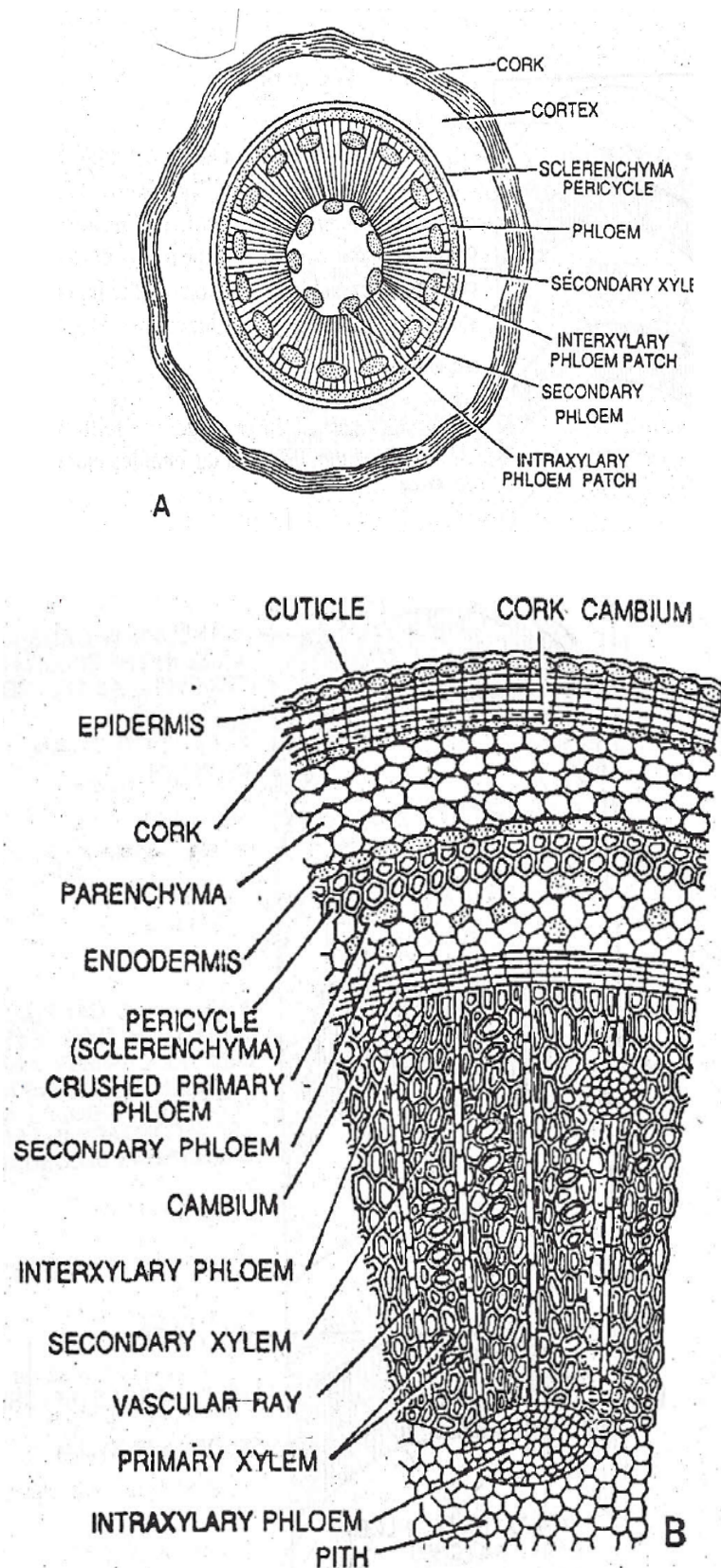


Fig. 8.14: Transection of Stem of *Strychnos* Showing Interxylary Phloem

A) Outline Diagram, B) Cellular Details of a Sector

Interxylary or included phloem patches are found in several families, such as Asclepiadaceae, Amaranthaceae, Loganiaceae, Nyctaginaceae, Onagraceae, Salvadoraceae etc.

8.4. ANOMALOUS SECONDARY GROWTH IN MONOCOT STEM:

In monocotyledons, secondary growth is absent because vascular bundles are closed type, i.e. without cambium. But Some plants such as *Dracaena*, *Yucca*, *Aloe*, *Sansevieria* (Family: Liliaceae), *Agave* (Amaryllidaceae) and, *Lomandra*, *Xanthorrhoea* and *Kingia* (Xanthorrhoea) exhibit anomalous growth which is secondary in nature. The cambium appears to be a direct continuation of a primary thickening meristem. However, the cambium functions in the part of the axis, that has completed its elongation. The cambium originates in the parenchyma outside the vascular bundles. *Dracaena* stem (Fam. Liliaceae) - The young stem has an outer 'epidermis followed by sclerenchymatous hypodermis and a large number of closed, collateral vascular bundles embedded in parenchymatous ground tissue (Fig. 8.15).

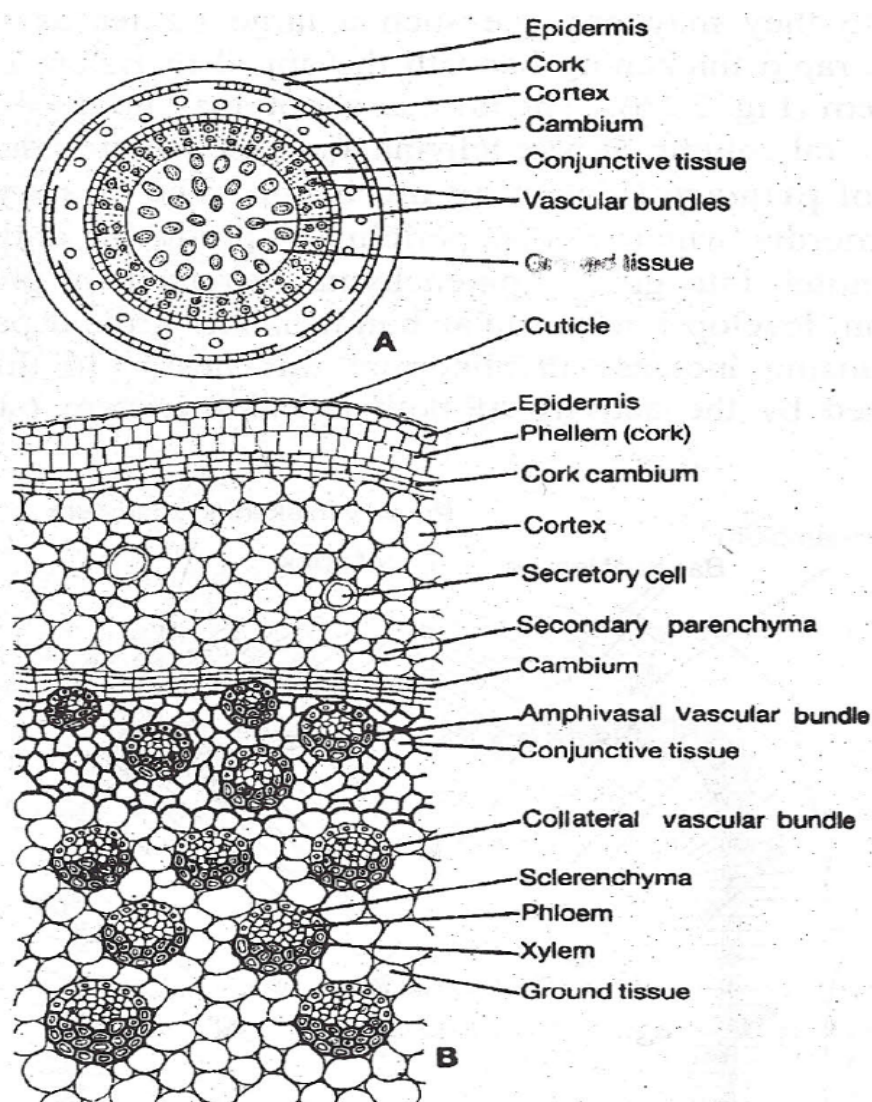


Fig. 8.15: A-B. Transection of Stem of *Dracaena*. A. Outline Diagram, B. Cellular Details of a Sector

Dracaena shows anomalous secondary growth. The cambium originates in the parenchyma outside the vascular bundles. This region in which the cambium appears is sometimes identified as cortex or pericycle. The newly formed cambium cuts off cells towards outside and inside both. The tissue developed on the inner side of the cambium is usually differentiated into vascular bundles and they remain separated from each other by lignified or unlignified tissue. The cells develop on the outer side of the cambium may be differentiated into parenchyma. Hence, in mature stem of *Dracaena*, very closely arranged numerous vascular bundles are appeared in the ground tissue region.

Anomalous Growth in Palms:

In palms there is no secondary growth but thickening is due to the gradual increase in size of cells and intercellular spaces, and sometimes of the proliferation of fibre tissue. Majority of monocotyledons lack secondary growth, but with the result of intense and long continuing primary growth they may produce such a large body as those of the palms. In monocots often produce a rapid thickening beneath the apical meristem by means of a peripheral primary thickening meristem (Fig. 8.16). The normal shoot apex produces only a small part of the primary body including central column of parenchyma and vascular strands. Most of the plant body is formed by the activity of **primary thickening meristem**. The primary thickening meristem is found beneath the leaf primordia, which are periclinal producing anticlinal rows of cells (Fig. 8.16). These cells differentiate into parenchyma traversed by procambial strands. These procambial strands later develop into vascular bundles. The ground parenchyma cells enlarge, and divide repeatedly, causing increase in abnormal thickness. In this way, huge trunks of monocotyledons are formed by the activity of both apical meristem (shoot apex) and primary thickening meristem.

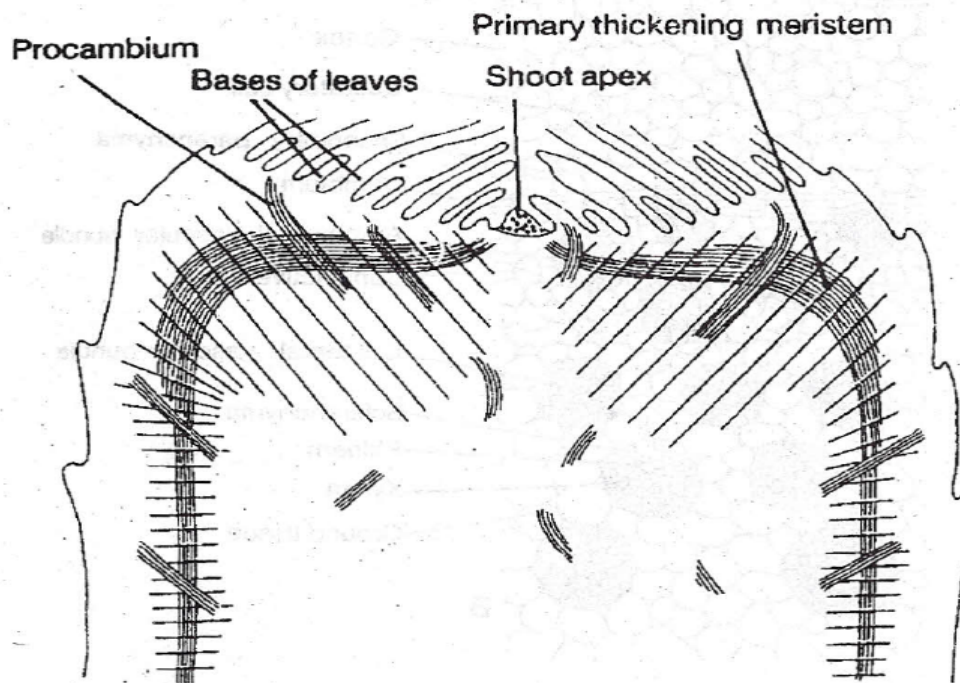


Fig. 8.16: Anomalous Growth in Monocotyledon Stem showing Primary Thickening Meristem

8.5. SUMMARY:

The deviated pattern from the normal secondary growth is described as anomalous secondary growth. Some of the anomalous structures are phloem wedges in xylem in *Bignonia*, fissured xylem in *Aristolochia* and, interxylary phloem (included phloem) in *Leptadenia*, *Strychnos* etc.

In *Boerhavia* and members of Nyctaginaceae, several cambia arise successively in the outside of the phloem. There is a continuous increment of secondary vascular tissues by the activity of these accessory cambia. In Palms, secondary growth is absent. However, the large bodies are formed due to continuous activity of primary thickening meristem.

8.6. MODEL QUESTIONS:**Essay Question:**

- 1) Write an account on anomalous secondary growth in angiosperms.

Short Answer Questions:

- 1) Anomalous growth in palms
- 2) *Dracaena*
- 3) *Strychnos*
- 4) Included phloem
- 5) Abnormal activity of cambium in *Aristolochia*.

8.7. REFERENCE BOOKS:

- 1) A. Fahn, 1968. Plant Anatomy. Pergamon Press, Oxford.
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- 3) P.C. Vasishta, 1988. Plant Anatomy. Pradeep Publications, Jalandhar.

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LESSON-9

ANATOMY OF THE ROOT

9.0 OBJECTIVE:

- In this chapter internal structure of angiosperm root, lateral root origin and storage roots have been discussed.

STRUCTURE:

9.1 Introduction

9.2 Anatomy of Dicotyledonous Roots

9.3 Anatomy of Monocotyledonous Roots

9.4 Lateral Root Origin

9.5 Storage Roots

9.6 Summary

9.7 Model Questions

9.8 Reference Books

9.1. INTRODUCTION:

The roots are generally of two types. (1) Primary, normal roots, which originate from the embryo, and persist throughout the life; (2) adventitious roots which arise secondarily from stem, leaf or others and these may be either permanent or temporary. The functions of primary roots are to anchor the plant body in the soil, to absorb water and soluble substances, and to serve as storehouses of food materials. Adventitious roots are varied in their function; they may act as primary roots or may be modified into climbing organs, stilts or props, thorns/ haustoria etc.

Root shows the Following Characteristic Features:

- 1) Roots show the tendency to grow downwards against gravitational force or sideways rather than upwards,
- 2) Absence of chlorophyll,
- 3) Absence of nodes and internodes,
- 4) Absence of leaves or any other appendages,
- 5) Presence of root cap,
- 6) The endogenous origin of lateral roots and branches,
- 7) Xylem and phloem/strands situated in different radii.

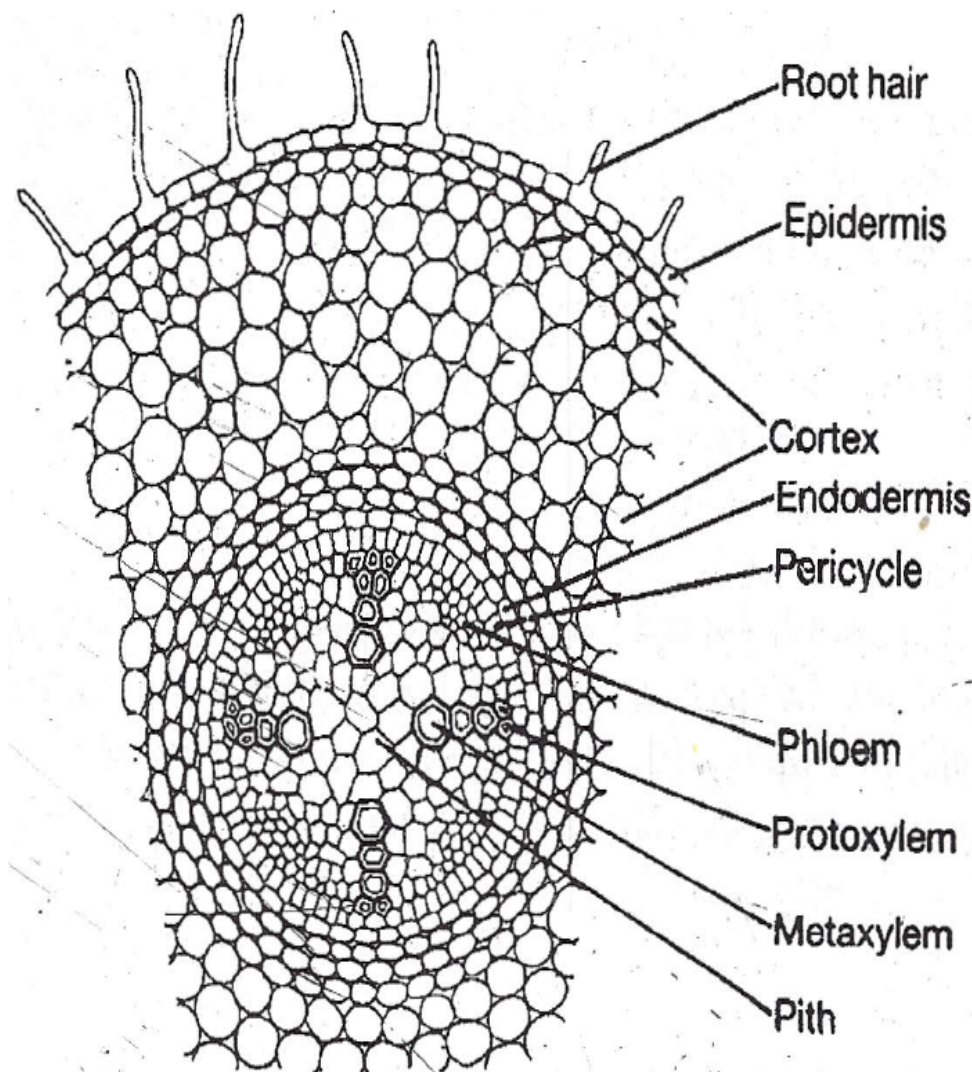
Anatomical differences between the dicotyledonous and monocotyledonous roots are given in Table 9.1.

Table. 9.1: Difference between Roots of Dicots and Monocots

Character	Dicotyledonous Root	Monocotyledonous Root
1. Vascular bundles	The number varies from two to six (di-to hexarch), rarely more	They are numerous, rarely limited (e.g. onion)
2. Xylem vessels	They appear circular in outline	They are usually polygonal in outline
3. Pith	It may be absent or highly reduced due to presence of metaxylem elements in the central portion of root	It is very distinct, well developed
4. Secondary growth	Present	Absent
5. Pericycle	It gives rise to lateral roots and secondary meristems such as cambium and cork cambium	It gives rise to lateral roots only

9.2. ANATOMY OF DICOTYLEDONOUS ROOT:

Basically, primary root consists of three distinct layers (1) *Epidermis* (*Epiblema*), (2) *Cortex* and (3) *stele*-*Epidermis* (*Epiblema*) - The root epidermis, also known as epiblema or piliferous layer or rhizodermis is typically uniseriate. Epidermis consists of closely packed thin-walled, parenchyma cells. Most of the epidermal cells extend out in the form of tubular unicellular root hairs which are thin-walled and, absorb water and minerals from the soil.

**Fig. 9.1** Transection of Root (Sunflower'(*Helianthus annuus*'))

Cortex - The cortex consists of, thin-walled rounded or polygonal parenchyma cells with intercellular spaces (Fig. 9.1). In aquatic plants like *Hydrilla* (Fig. 9.6), and others, it is largely aerenchymatous enclosing air cavities which help in maintaining the buoyancy of plant.

Cortical cells usually store reserve foods (Fig. 9.2). Chloroplast is absent but it may be present in few aquatic plants e.g. *Trapa*. Some of the aerial climbers such as *Tinospora* have got assimilatory roots and chloroplasts -are found in the cortical cells (Fig. 9.2). In several gymnosperms and some members of Cruciferae, Rosaceae and Caprifoliaceae, the cortical cells possess lignified reticulate thickenings.

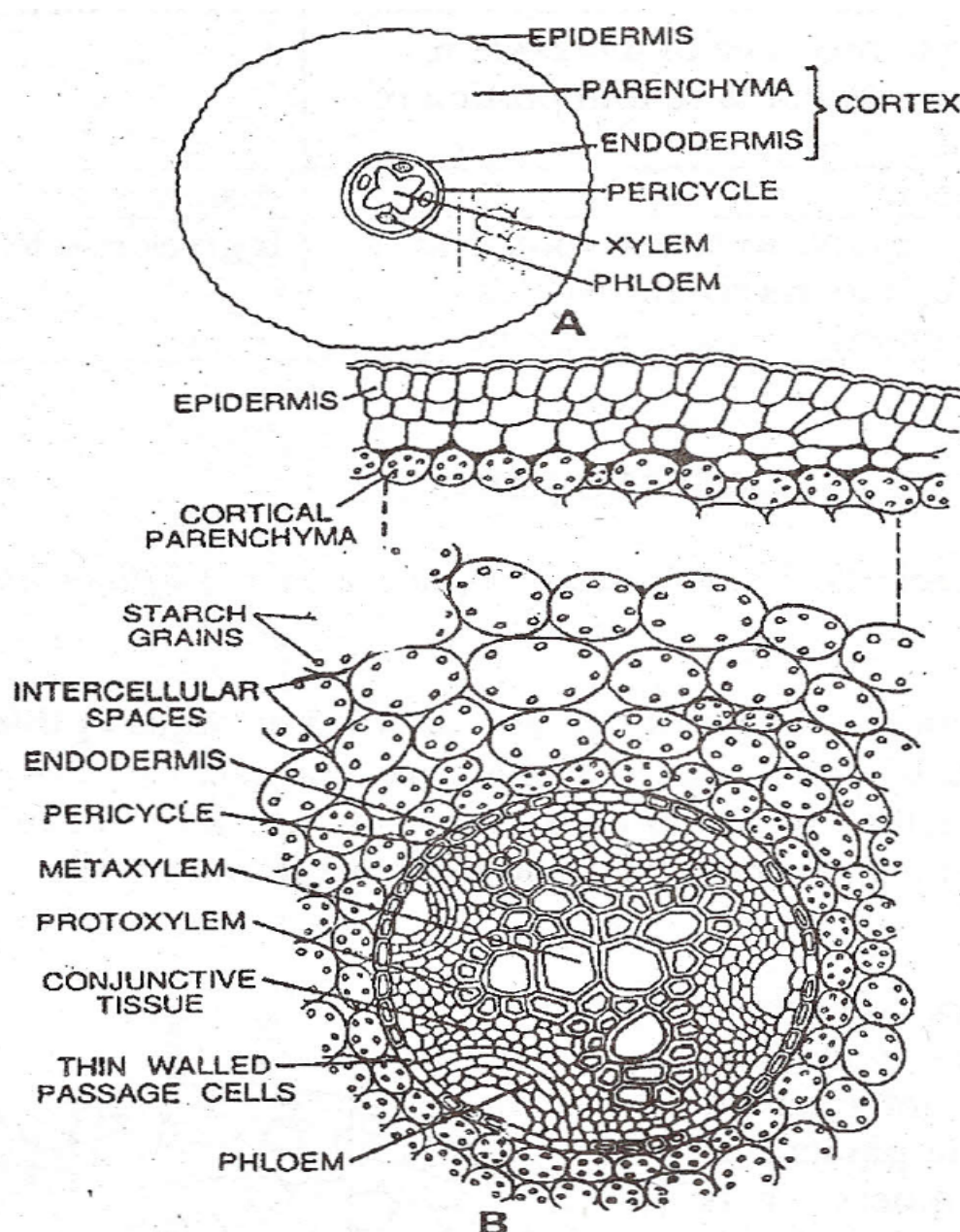


Fig. 9.2: A-B. Transection of Root of *Ranunculus Rapens* Showing Starch Granules

Endodermis:

The innermost layer of the cortex is known as endodermis. The endodermal cells are living- characterized by the presence of **casparian strips or casparian bands** on their anticlinal walls. The casparian thickening is formed due to deposition of suberin and lignin. Some of the -endodermal cells are thin-walled and these are called **passage cells** located against the protoxylem strands.

Pericycle:

The layer next to the endodermis is known as pericycle. It makes the outer boundary of primary vascular cylinder of dicotyledonous roots. The pericycle of young roots consists of thin-walled parenchyma. The lateral roots in dicots arise from this tissue.

Vascular System:

Vascular bundles in root are radial type in which xylem and phloem strands are placed on different radii and alternate in their position. The root typically shows an exarch xylem, i.e., the protoxylem is located near the periphery of the vascular cylinder and the metaxylem towards centre. The phloem is also centripetally differentiated (that is, protophloem towards periphery and metaphloem towards centre). Most dicotyledons have few xylem strands.

The tap root is frequently di-, tri-, or tetrach, or it may have more poles (e.g., members of mentiferae, *Castanea*). Only one xylem strand occurs in the slender root of hydrophyte, *Trapa natans*. In *Raphanus*, *Daucus*, *Linum*, *Lycopersicon* and *Nicotiana*, the roots are diarch. In *Pisum*, the root is triarch. In *Cicer*, *Vicia*, *Helianthus* (Fig. 9.1), *Gossypium* and *Ranunculus* the roots are tetrarch. In certain dicots the root of the same plant may show di-, tri- and tetrach xylem, e.g., *Nymphaea chilensis*, *Enhydrafluctuans* etc. Such roots are known as heteroarchic roots.

The protoxylem consists of annular and spiral thickenings whereas metaxylem of reticulate and pitted thickenings. The phloem consists of sieve tubes, companion cells and phloem parenchyma. The parenchymatous conjunctive tissue occurs in. between the xylem and phloem strands.

The central portion of the young root is pith which consists of few parenchymatous, Is without intercellular spaces. In older root, the pith may be altogether absent due to development of metaxylem.

9.3. ANATOMY OF MONOCOTYLEDONOUS ROOTS:

The epidermis of monocotyledonous root is similar to that of dicotyledonous root. However, in orchids and epiphytic aroids, multiseriate epidermis, known as velamen is found.

Velamen:

It is a multiple epidermis. The Velamen, consists of several layers of dead cells often with multi-spirally thickened (Fig. 9.3B) and perforated walls. Velamen acts as a sponge, absorbs water and moisture from the atmosphere. It also acts as a protective tissue, preventing undue water loss from the delicate cortical cells of the exposed aerial root.

Exodermis:

Just below the velamen, a layer of exodermis is present. It consists of alternate long thick-walled and short thin-walled, passage cells (Fig. 9.3B). Movements of solutes takes place through the passage cells: thick-walled cells prevent the water loss from the interior tissues of the root.

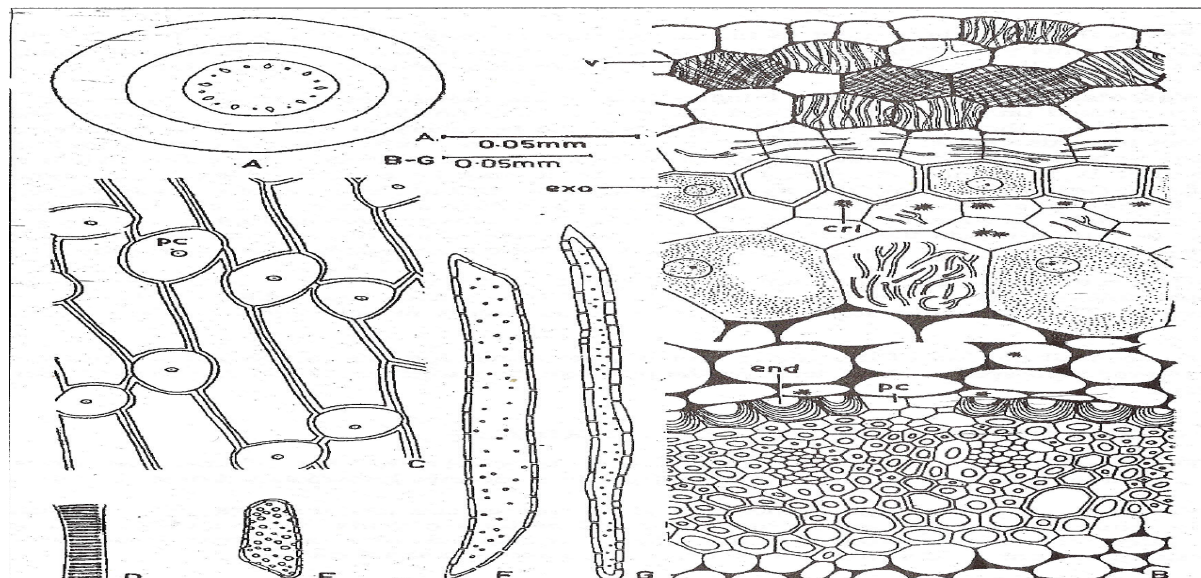


Fig. 9.3: A-G. Root of *Panisea uniflora*. A. Transection of root in outline, B. Cellular details of root transection, C. exodermis in surface view, D. tracheid, E. thick-walled cortical cells, F. xylem fibre, G. phloem fibre. Cryl, crystal, end, endodermis; exo, exodermis; pc, passage cell; v, velamen.

Cortex:

Cortex is massive (Fig.9.4) with large air spaces (Fig, 9.5) and similar to that of dicotyledonous root. However, some of the cortical cells are highly thickened and provide mechanical strength to the plant body (Fig. 9.3 B, E). Some of middle cortical cells show hypertrophs due to the presence of endotrophic micorrhiza (Fig. 9.3B). Stegmata (crystals) are also found in outer and inner most cortical cells in some orchids (Fig: 9.3B).

Endodermis:

The uniseriate endodermis consists of thick-walled and also thin-walled passage cells. In some cases, casparian strips are found on their anticlinal walls. In some plants, like epiphytic orchids, endodermal cells possess L-shaped thickenings on their inner tangential and radial walls (Fig 9.4.and Fig. 9.5). Thin-walled, passage cells are also formed opposite the protoxylem poles. These passage cells are meant for diffusion and also called transfusion cells.

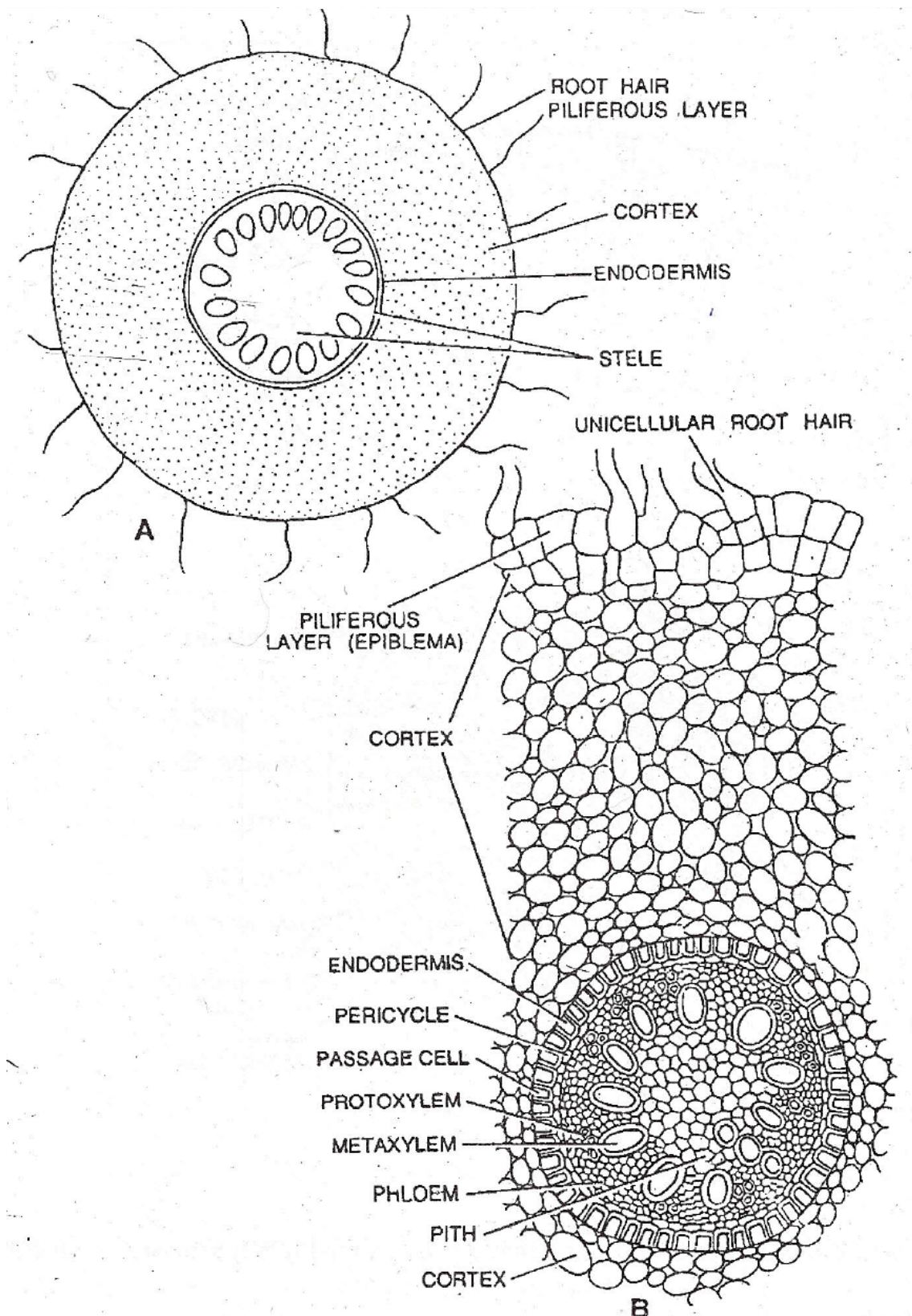


Fig. 9.4: Transection of Mono Cot Root of *Iris* A. Root Outline and B. Cellular Details

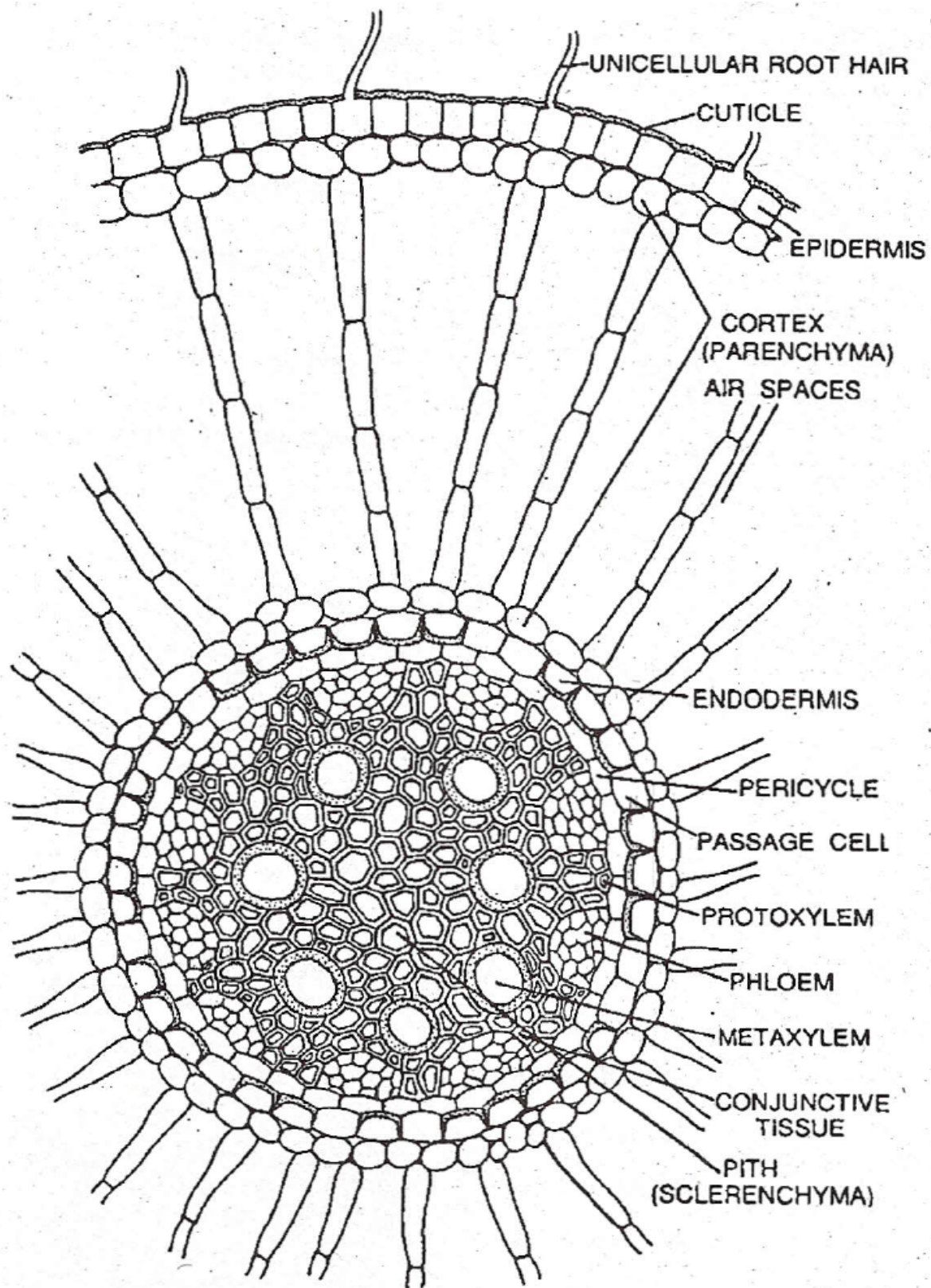


Fig. 9.5: Transection of Mono Cot Root of *Oryza Sativa* showing Large Airspaces in Cortex and Sclerenchymatous Pith

Pericycle:

It is usually uniseriate with thin-walled parenchymatous cells. In some cases, it is sclerified. In many monocotyledons (e.g. some Graminae, *Smilax*, *Agave*, *Dracaena*, Palms) pericycle consists of several layers.

Vascular System:

The vascular system composes of alternating strands of xylem and phloem. Vascular bundles are numerous and it is referred to as polyarch condition. The adventitious roots of Palmae and Pandanaceae have *considerably* higher number of vascular bundles, up to 100 or more. In some roots (e.g. *Hydrilla*, *Triticum*), a single vessel occupies the centre (Fig. 9.6) and is separated by non-tracheary elements from the peripheral strands.

In *Zea mays*, large metaxylem vessels are arranged in a circle around the pith (Fig. 9.7). In some monocotyledons (e.g., *Cordyline*, *Musa*, Pandanaceae): Phloem strands are scattered among the tracheary elements in the central portion of the root. Conjunctive tissue is present in between the xylem and phloem.

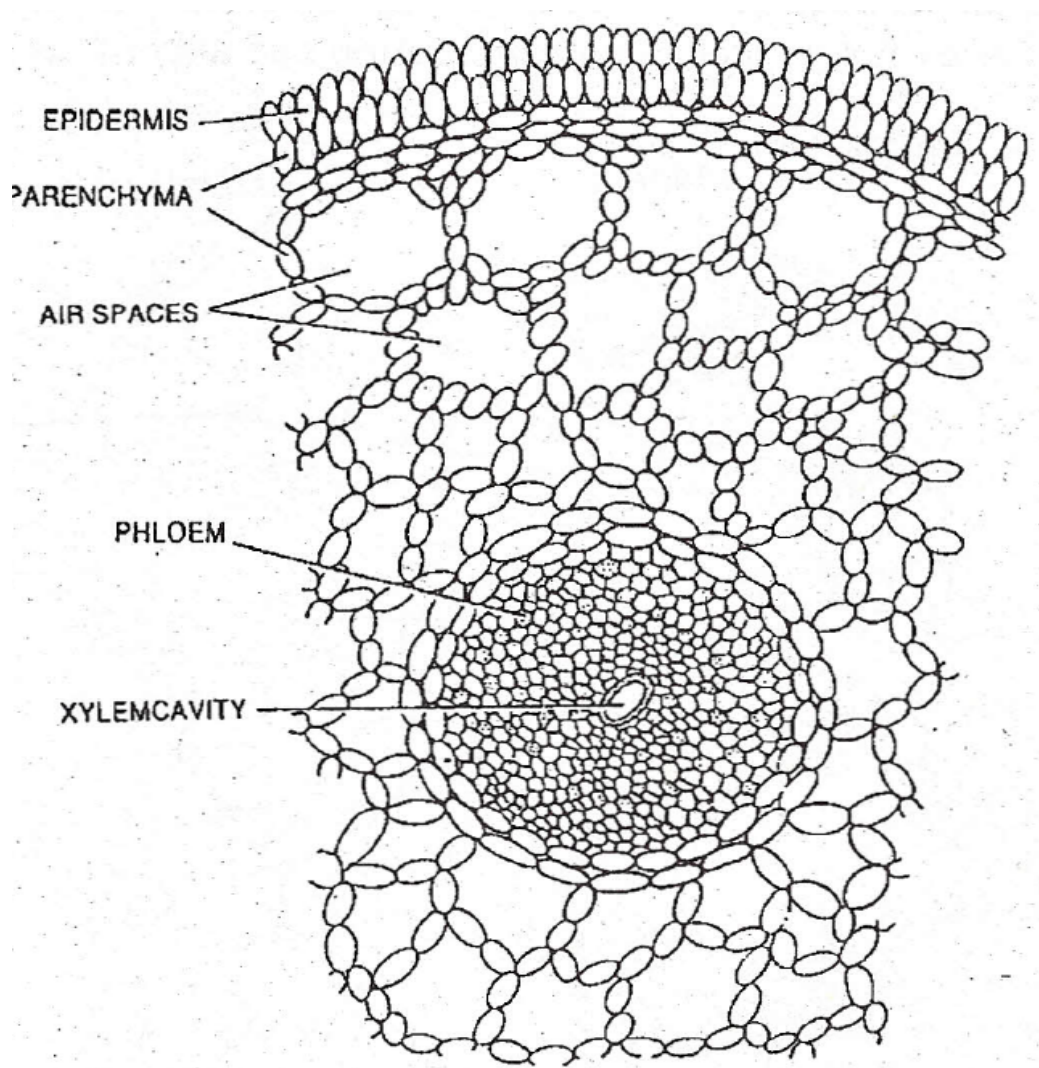


Fig. 9.6 Transection of Monocot Root of *Hydrilla* showing Large Air Spaces in Cortex and Single Metaxylem Element

The xylem is exarch. It consists of tracheids, vessels, xylem fibres (Fig. 9.3F) and xylem parenchyma. The phloem consists of sieve tubes, companion cells, phloem fibres (Fig. 9.3G) and phloem parenchyma. The central part of the stele is called pith. It is sclerenchymatous in *Avena sativa*, *Canna* and *Oryza sativa*.

9.4. LATERAL ROOT ORIGIN:

Lateral roots of both gymnosperms and angiosperms arise endogenously from the pericycle and grow through the cortex (Fig. 9.7). It arises between the xylem and phloem strands in diarch roots, opposite the protoxylem in triarch to pentarch roots and, opposite the protophloem in polyarch roots.

During the development of lateral root, some of the pericycle cells get meristematic activity and undergo anticlinal and periclinal divisions. As a result, a root primordium is formed. This primordium later grows and makes its way by piercing the cortex and epiblema. The passage of lateral root through the cortex is by mechanical penetration and also by enzyme action.

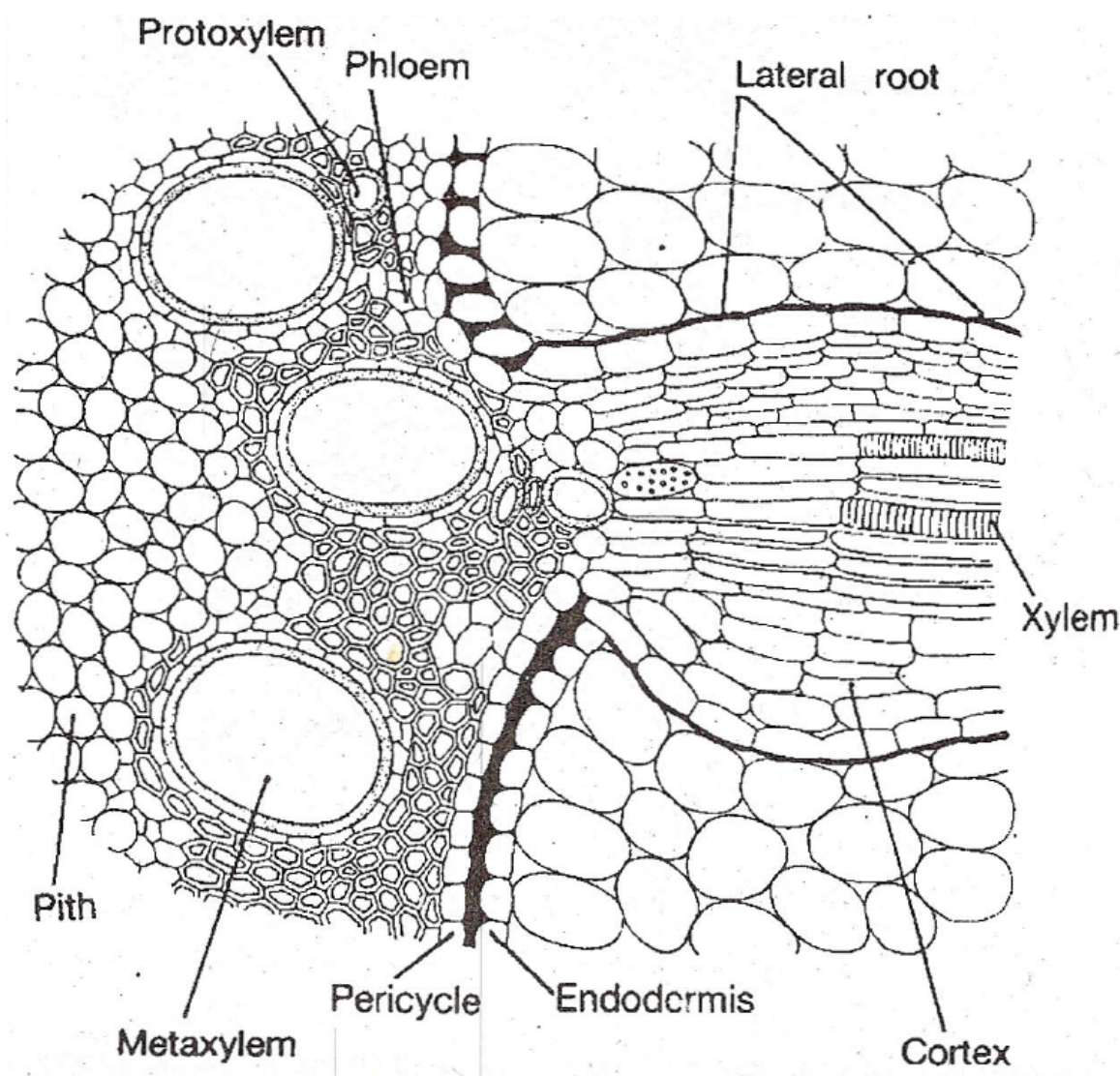


Fig. 9.9 Transection of Maize Root Showing Lateral Root

The primordium with initial of various histogens, later develops into lateral root. Vascular elements of lateral root are directly connected with that of parental root through the pericycle cells. In few cases, endodermis is also involved in the development of lateral root. The lateral roots usually develop in acropetalous manner i.e., older at the base and younger towards the apex.

9.5. STORAGE ROOTS:

The underground roots may serve as organs for the storage of food materials. In storage roots of sweet potato, radish, turnip, carrot and dahlias, food may be stored "largely in the cortex or xylem region or in both.

9.5.1. Beta Vulgaris (Beetroot Chenopodiaceae-Dicot):

The young root possesses a diarch protoxylem plates. The sugar beet. forms fleshy hypocotyl root by anomalous growth. It shows a usual type of primary and early secondary development. The primary cambium that gives rise to the innermost vascular ring in the beet root develops in the interstitial parenchyma except opposite the two protoxylem pole where it is derived from the pericycle. The first secondary cambium arises in the -phloem parenchyma or in the pericycle. Later, however; a series of supernumerary cambia arise outside the normal vascular cylinder and produce several increments of vascular tissue each consisting of a layer of parenchyma, parenchymatous xylem and parenchymatous Figs. 9.8 and 9.9). Anomalous produced parenchyma is storage in function.

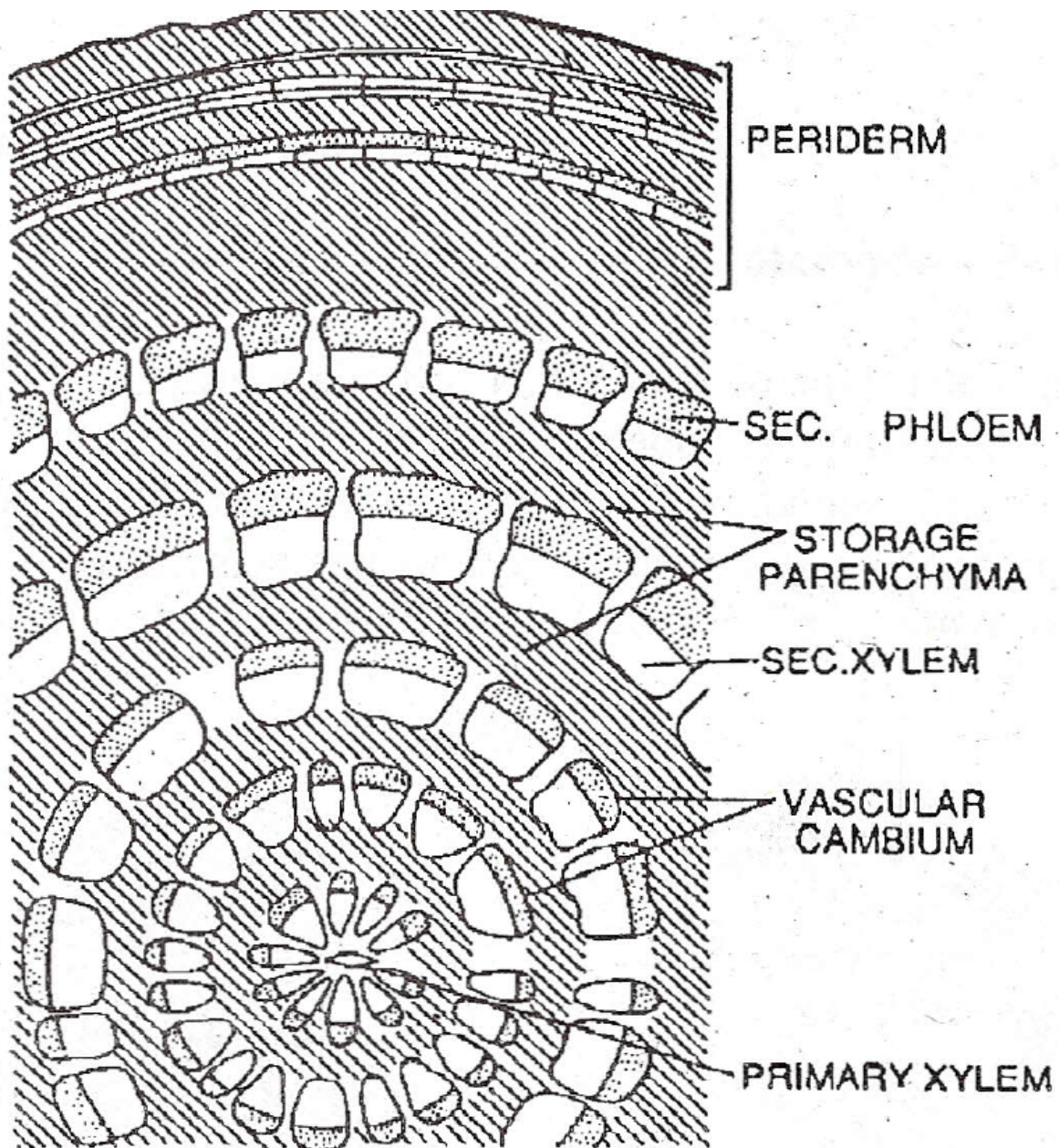


Fig. 9.8 Transection of *Beta vulgaris* root showing anomalous secondary growth
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Fig. 9.9 Transection of *B. vulgaris* root showing growth layers

9.5.2. *Ipomoeabatatas* (Sweet potato - Convolvulaceae -Dicot):

It shows a complicated type of anomalous secondary growth. In primary state, the root is pentarch or hexarch. A distinct endodermis is present. In normal development, abundant parenchymatous primary and secondary xylem is formed. Anomalous cambia are formed around vessels or vessel groups and produce phloem rich in parenchyma with some laticifers. Massive amount of storage parenchyma (Fig. 9.10 and 9.11) is developed, thus forming the tuberous roots.

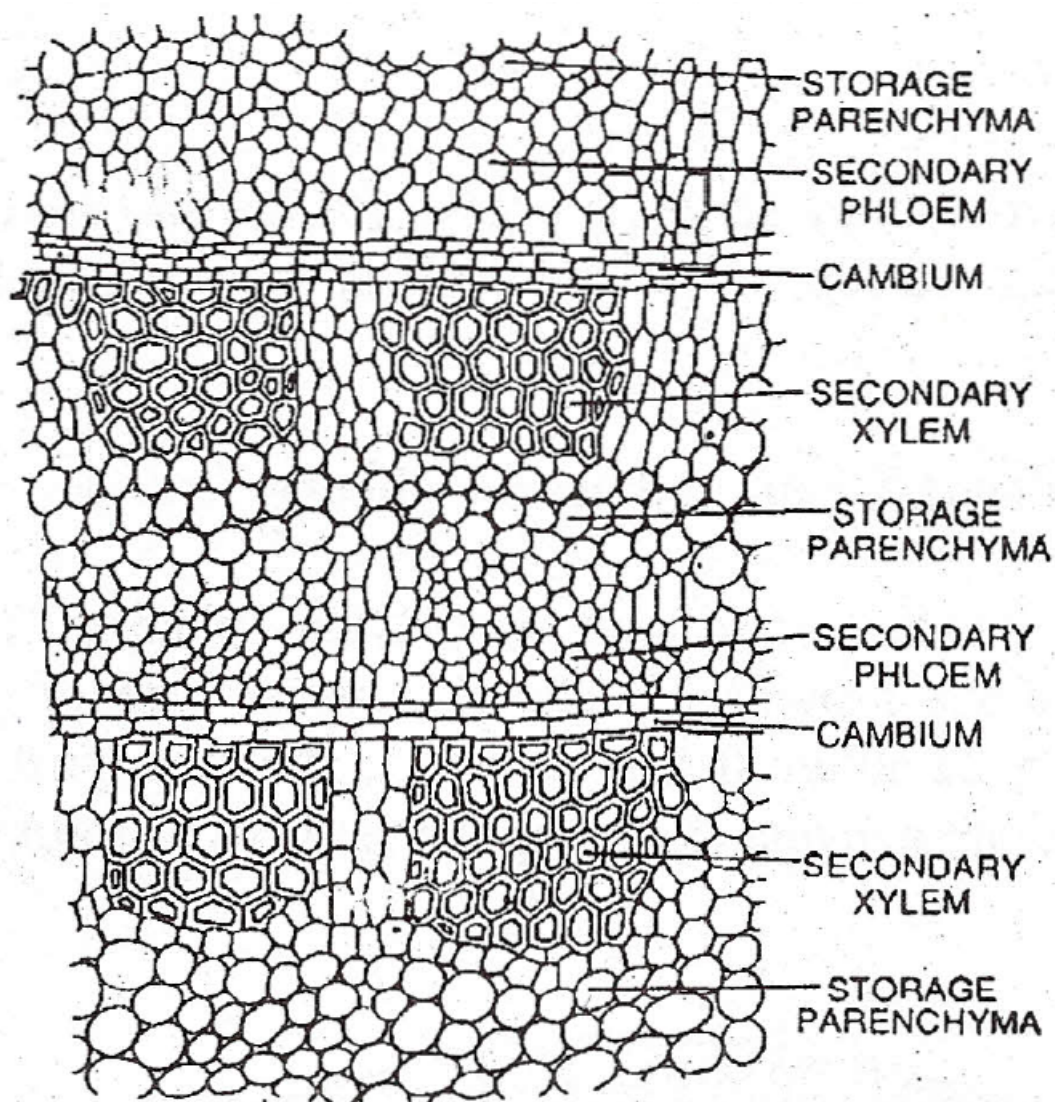


Fig. 9.10: Transection Roots. Left-*Ipomoea Batatas*; Right - *Daucus Carota*

9.5.3. *Daucus Carota* (Carrot Tmbelliferae - Dicot):

In this case, the hypocotyl and base of taproot form jointly the fleshy structure. The fleshy organ consists of large amount of storage parenchyma associated with ordinary arrangement or tissues. After sloughing off the cortex, organ becomes fleshy by the massive development of parenchyma in the. phloem and xylem. Besides the cambial activity, massive development of parenchyma adds to the thickness of the root.

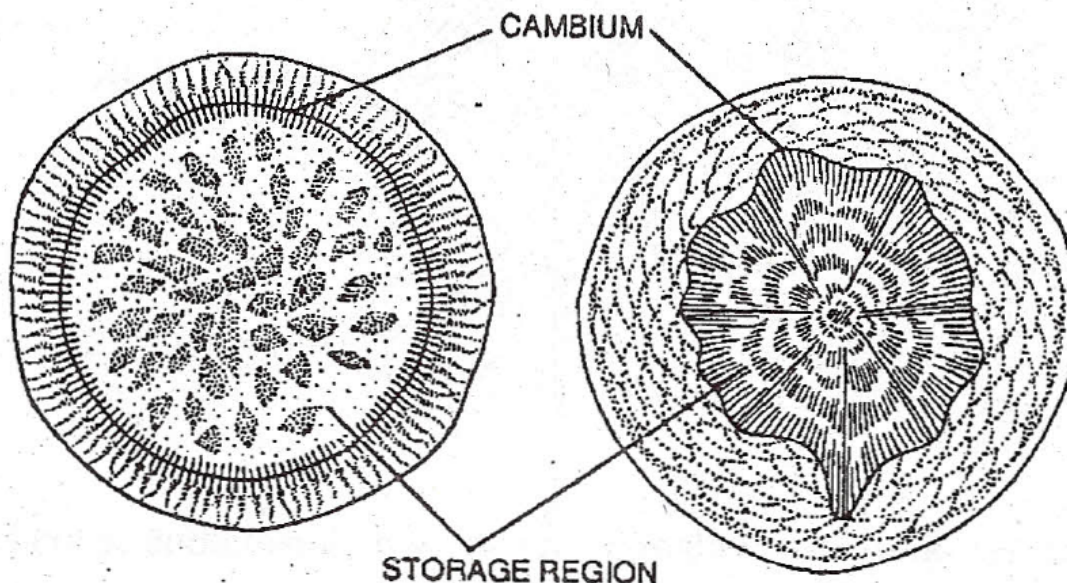


Fig.9.11: Transection of Storage Root of *Ipomoea Batatas* showing Cellular Details

9.6. SUMMARY:

The important functions of primary roots are to anchor the plant body in the soil, to absorb water and soluble substances, and to serve as storehouses of food materials.

Dicotyledonous Roots: Basically, primary root consists of epidermis (epiblema), cortex and stele. Vascular bundles are radial type in which xylem and phloem strands are placed on different radii and alternate in their position. Root shows an exarch xylem. i.e., the protoxylem located near the periphery of the vascular cylinder, the metaxylem towards centre. Most dicots have few xylem strands (di-, tri-, or tetrarch or more xylem poles). The central portion of the young root is pith which is made up of parenchymatous cells without intercellular spaces. In older roots, the pith may be absent due to development of metaxylem. **Lateral Root origin:** Lateral roots arise endogenously from the pericycle and grow through the cortex. During its development root primordium is formed from the pericycle. This primordium later develops into lateral root.

9.7. MODEL QUESTIONS:

Essay Questions:

- 1) Write an essay on structure of dicot root and give a note on lateral root origin.
- 2) Explain the anatomy of Storage roots

9.8. REFERENCE BOOKS:

- 1) K. Esau, 1999. Plant Anatomy, Wiley Eastern Limited, New Delhi.
- 2) P.C. Vasishta, Plant Anatomy. Pradeep Publications, Jalandhar.

Prof V. Umamaheswara Rao

LESSON-10

THE LEAF

10.0 OBJECTIVE:

- In this chapter, structure and development of angiosperm leaves have been discussed.

STRUCTURE:

10.1 Introduction

10.2 Structure of Leaf

10.3 Ontogeny of Leaf

10.4 Summary

10.5 Model Questions

10.6 Reference Books

10.1. INTRODUCTION:

Morphologically and anatomically the leaf is the most variable plant organ. The collective term for all types of leaves appearing on plants is the Phyllome (Aber, 1950). The different phyllomes of the Spermatophyta are extremely variable both in external and internal structure and function. The phyllomes have been classified into *foliage leaves*, *cataphylls*, *hypsophylls*, *cotyledons* and others. The foliage Leaves are the principal Photosynthetic organs. the cataphylls are the scales that appear on buds and underground stems, and their function is protection or storage of reserve food materials. The hypsophylls are various types of bracts that accompany flowers and their function is, apparently protection. The cotyledons are first leaves of plant. The first lowermost leaves of a side branch are termed prophylls in monocots only one prophyll is usually present and in dicots two.

In general, leaves are Classified into three groups based on their position on the stem, radical (arising as if from root, *e.g. Raphanus*) Cauline (from unbranched axis directly, as in maize and sugarcane) and ramal (from the branches as in most dicot trees).

Structurally leaves may also be classified as (i) Dorsiventral or bifacial type with dissimilar upper and lower leaf surfaces (with heterogeneous mesophyll), (ii) isobilateral or unifacial with similar type of upper and lower surfaces (with homogeneous mesophyll) and (iii) centric which are circular in outline and are with tissue distributed evenly as in *Allium cepa*. Dorsiventral leaves are characteristic of dicots whereas isobilateral of monocots.

10.2. STRUCTURE OF LEAF:

The internal organization of leaf lamina shows the differentiation into epidermis, mesophyll and vascular tissues.

Epidermis:

Epidermis forms the dermal tissue system of leaf. Generally, adaxial epidermal cells (upper epidermal cells) are comparative larger in their size than the abaxial epidermal cells

(lower epidermal cells). In orchids, e.g., *Paphiopedilum fairrieatum*, the adaxial epidermal cells are 2 to 3 times larger than the abaxial cells (Fig. 10.1) and they involve in storage and conservation of water.

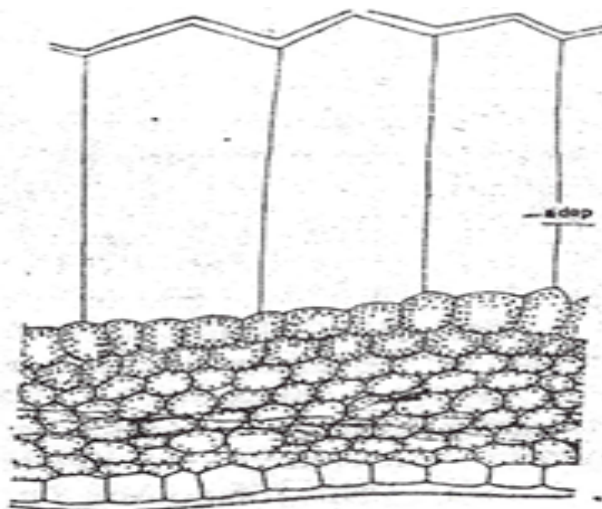


Fig. 10.1: T.S. of Leaf of *Paphiopedilum Fairrieatum* showing Larger Adaxial Epidermal Cells (Adep - Adaxial Epidermis)

A group of epidermal cells which are slightly larger but with thin flexible walls, are found in grasses and these cells are called bulliform cells or motor cells (Fig. 10.7 and 10.8). These help in rolling of leaves during dry weather, thus preventing the loss of water via transpiration.

Both adaxial and abaxial epidermis are usually uniseriate composed of compactly arranged cells. / In *Ficus* the upper epidermis is multiseriate (Fig. 10.2), whereas in *Nerium*, both upper and lower epidermis are multiseriate (10.3).

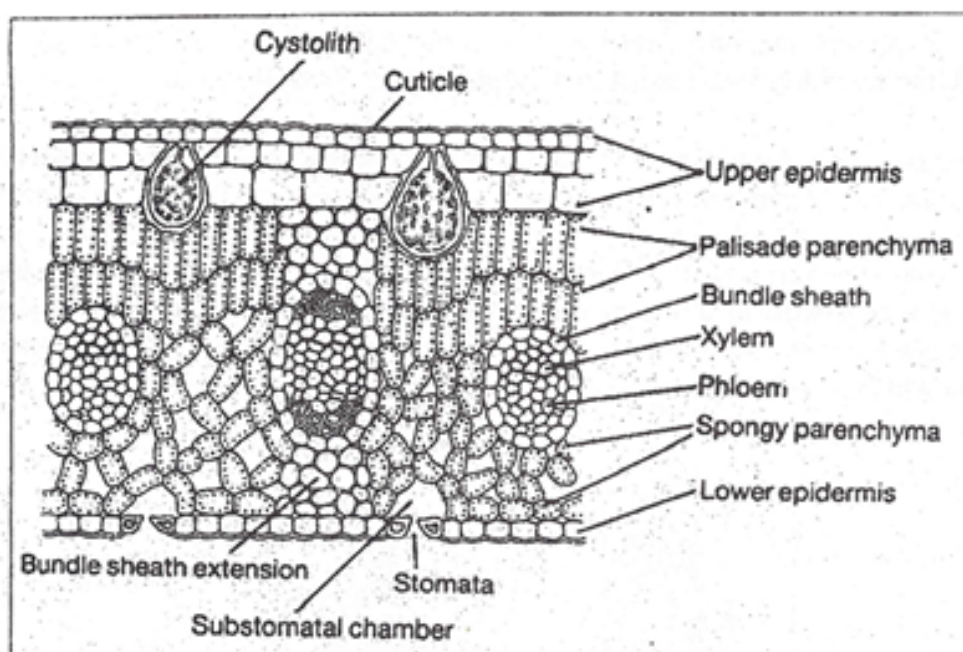


Fig.10.2: T.S. of Leaf of Banyan (*Ficus Bengalensis*) showing Multilayered Upper Epidermis)

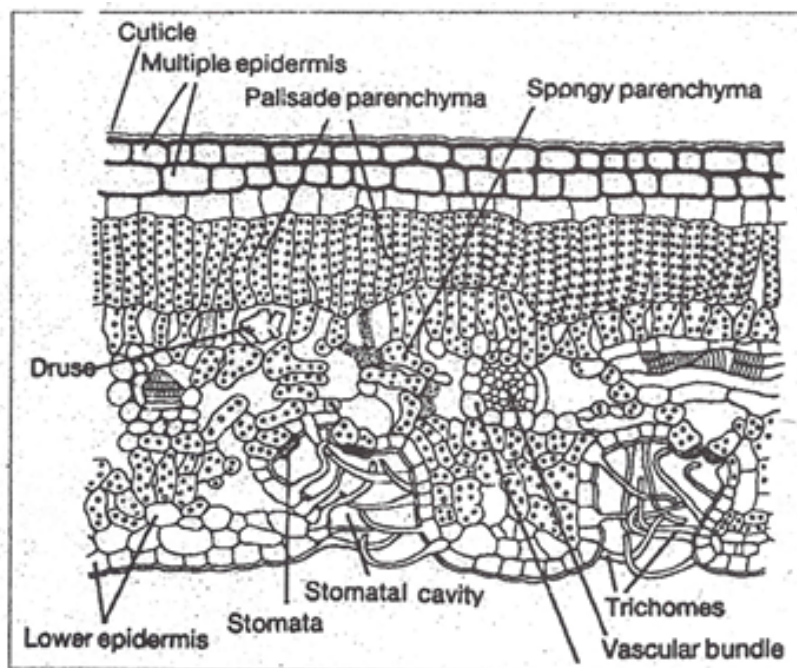


Fig. 10.3: T.S. of leaf of *Nerium* showing Multiseriate Upper and Lower Epidermis

Cuticles are present on outer walls of epidermal cells. It is very thick and distinct in xerophytic leaf, and relatively less distinct in mesophytic leaf. Cuticle is absent in hydrophytic leaf.

Stomata found in epidermis. If stomata are distributed only on upper surface, the leaf is called epistomatic, e.g. *Nymphaea*; if only on lower surface, it is called hypostomatic, e.g., *Mangifera indica*, *Ficus bengalensis* etc. if on both the surfaces, it is amphistomatic (isobilateral leaves): Each stoma is surrounded by a pair of highly specialized cells, known as guard cells, which may be kidney-shaped in dicots or dumbbell-shaped in Graminae members (Fig. 10.4). The stomata may be present at the same level as epidermis as in mesophytic leaves, or may be sunken as in *Cycas*, *Pinus*, *Allium*, *Nerium* (Fig. 10.3) etc.

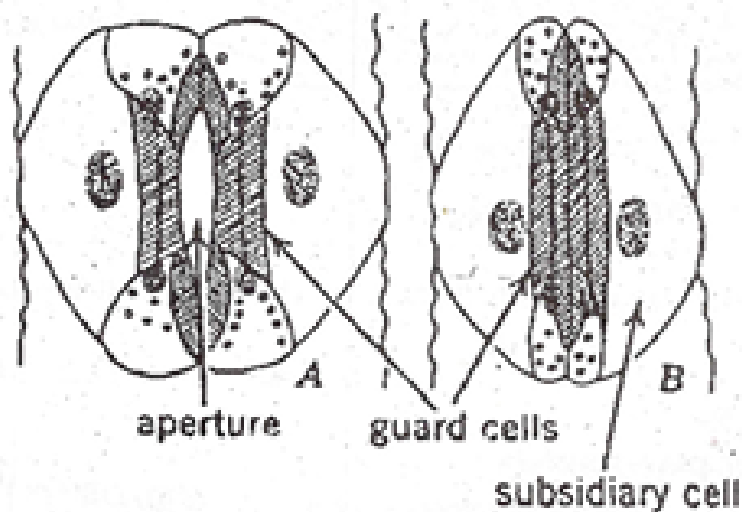


Fig. 10.4 Stomata of *Saccharum* showing Double-Dumbbell Shaped Guard Cells

In certain species, glandular and non-glandular hairs arise from epidermis. Some epidermal cells contain *cystoliths* as in *Ficus* (Fig. 10.2) and *Momordica*. Some silica cells are also present in epidermis.

Hypodermis:

In certain cases, a layer of hypodermis is present just below, the epidermis. In *Phaius mukulatus* (orchid) hypodermal cells with cellulosic thickenings (Fig.10.5) function in storage of water and provide mechanical strength to the plant organ.

Mesophyll:

It forms the important internal tissue of the leaf, involving in photosynthesis. In dorsiventral leaves (dicots), it shows remarkable differentiation into Palisade and spongy parenchyma, extending from upper to lower epidermis (Fig. 10.6). Palisade cells are columnar and compactly arranged. Xerophytes have well developed palisade tissue in Centric Leaves

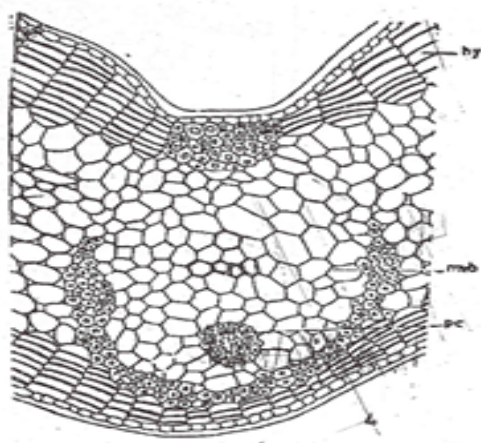


Fig. 10.5: Leaf, transection of *Phaius maculatus* showing hypodermal cells with cellulose thickening (hy, hypodermis; mvb, midrib vascular bundle; i pc, phloem cap)

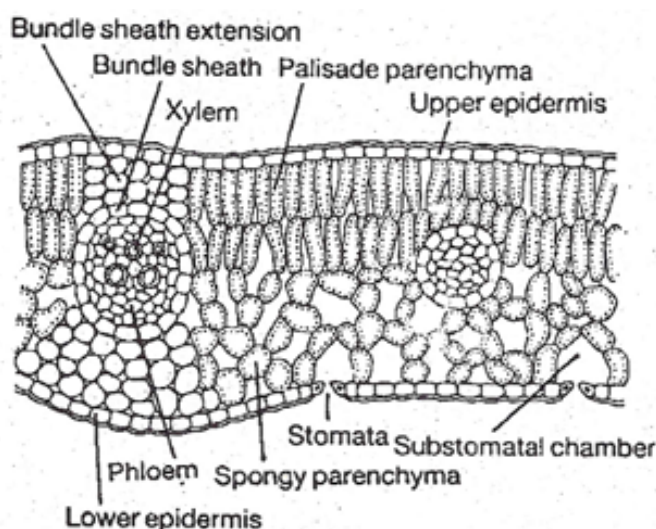


Fig.10.6: Transection of Dorsiventral Leaf of *Mangifera Indica*

such as *Allium* and *Juncus*, the palisade occurs all around the periphery of leaf. Spongy cells are of variable shapes and are loosely arranged with abundant intercellular spaces. The intercellular spaces which maintain continuity with stomatal chamber facilitate the gaseous exchange.

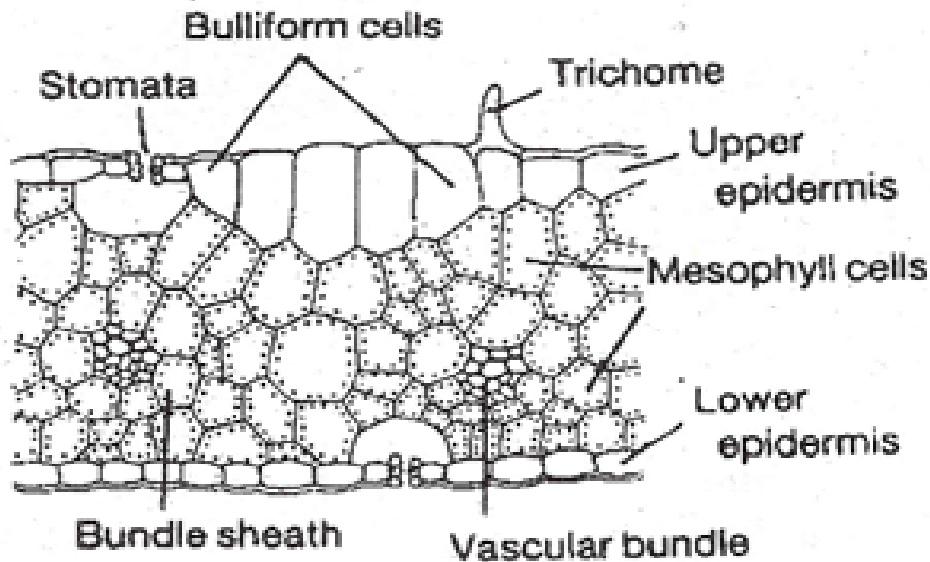


Fig.10.7: Transection of Isobilateral Leaf of *Zea Mays*

In isobilateral leaves (monocots), especially members of Graminae, mesophyll is homogeneous (Fig. 10.7 and 10.8) without differentiation of palisade and spongy parenchyma. These cells contain abundant chloroplasts. In orchids e.g. *Cirrhopetalum parvulum*, some of the mesophyll cells are modified into water storage cells (Fig. 10.9). These cells are circular or columnar in shape with multi-spiral cellulosic thickenings and protect the plant against desiccation.

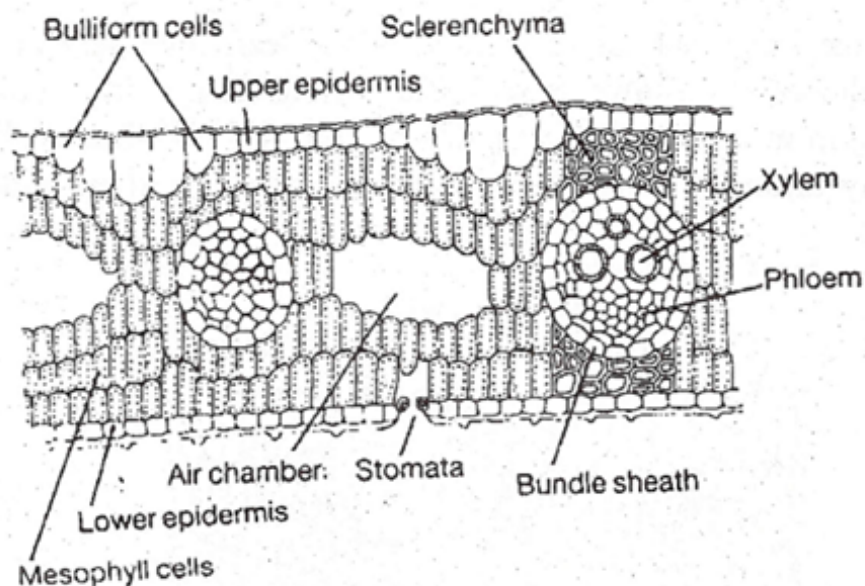


Fig. 10.8: Transection of Isobilateral Leaf of *Bambusa*

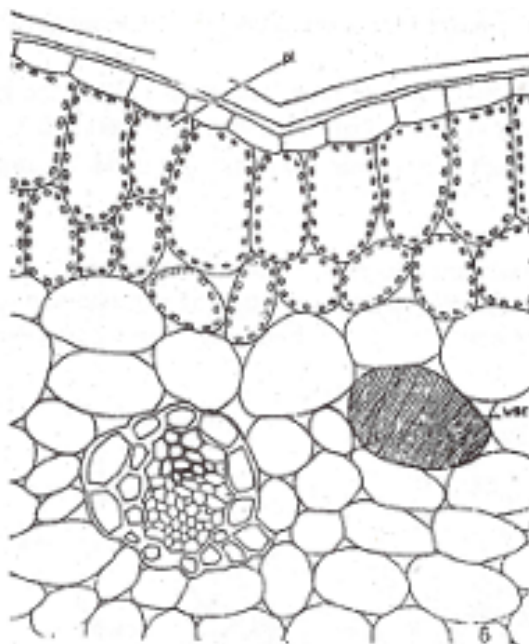


Fig. 10.9: Transection of Leaf of *Cirrhopetalum Pervulum* showing Water Storage Cells (wsc) and Loosely Arranged Palisade (PL)

In aquatic plants, mesophyll region accommodates large air chambers. surrounding them have fewer chloroplasts. Sometimes, various types of idioblasts are found in mesophyll regions. Presence of lithocytes in *Ficus*, oil glands in *Citrus* and laticifers in *Calotropis* are few such examples. In some species raphide bundles, and trichosclereids are present.

Vascular Bundles:

The arrangement of vascular bundles is known as venation. Venation pattern varies from one group to other group of plants. In dicotyledons reticulate venation is found whereas in monocotyledons parallel venation is present. In transection of leaf, a large midrib vascular bundle is present at the center, and large and small laminar vascular bundles are found on either side of it. The largest bundles with both xylem on the adaxial and phloem on the abaxial side are abundantly present. In smaller laminar bundles xylem is represented by tracheids and phloem by some sieve element. There is not much variation in structure of vascular bundles of dicots and monocots. All are conjoint, collateral and closed type of bundles.

Bundle Sheath:

The vascular bundles in leaf have characteristic bundle sheath. Parenchymatous or sclerenchymatous sheath is present around the vascular bundle in members of Melastomataceae and Winteraceae. In some cases, sheaths may be present at the xylem end, known as xylem cap or phloem end known as phloem cap. The xylem and phloem caps provide mechanical strength to the plant body.

In monocotyledons bundle sheath is made up of parenchymatous cells (Fig. 10.7) in which chloroplasts are present especially in C4 plants. Chloroplast dimorphism is found in C4 plants. Chloroplasts in mesophyll are normal with grana and stroma whereas chloroplasts of bundle sheath cells are lacking grana. Bundle sheath chloroplasts participate in C4 cycle,

an alternative pathway of C3 cycle photosynthesis. Thus, the structure of C4 leaf is known as Kranz anatomy. The C4 cycle enables these plants to carry on photosynthesis at low carbon dioxide concentrations and at relatively higher temperatures. In fact, C4 plants are more efficient in synthesizing the food through photosynthesis.

10.3. ONTOGENY OF LEAF:

Ontogeny (development) of leaf can be divided into three stages: (i) Initiation of leaf buttress, (ii) Formation of leaf axis, (iii) Formation of lamina.

(i) Initiation of Leaf Buttress:

Divisions in the peripheral zone of the apical meristem initiate a lateral protrusion, the leaf buttress (Fig. 10.10), upon which the erect portion of leaf later develops. The two growth zones of angiosperm shoot apices, the *tunica* and the *corpus*, variously participate in the formation of leaf primordium. The degree of their participation in leaf initiation varies from species to species. In *Scrophularia nodosa*, for example, the apical meristem has a single tunica layer, but the first division to initiate the leaf occur in the corpus; in *Vinca minor* with three layered tunica, leaf initiation takes place in the innermost layer of tunica; in *Acacia* both tunica and corpus involve in the initiation of phyllodes; in the members of Graminae first two layers of shoot apex involve in the leaf initiation.

The location of the initial divisions in the shoot apex depends on the phyllotaxis (spatial arrangement of leaves around the stem) of the shoot and on the circumferential spread of the future leaf. If the leaf has a narrow insertion and closely arranged, then the divisions have remained localized; if the leaf has a large base or completely 'ensheathes' the stem, the divisions are propagated circumferentially in both directions from the point of their initiation, which is more common in monocots with sheathing leaf bases.

It is already mentioned in lesson 1 that shoot apex undergoes some changes during plastochron, these changes are known as plastochronic changes.

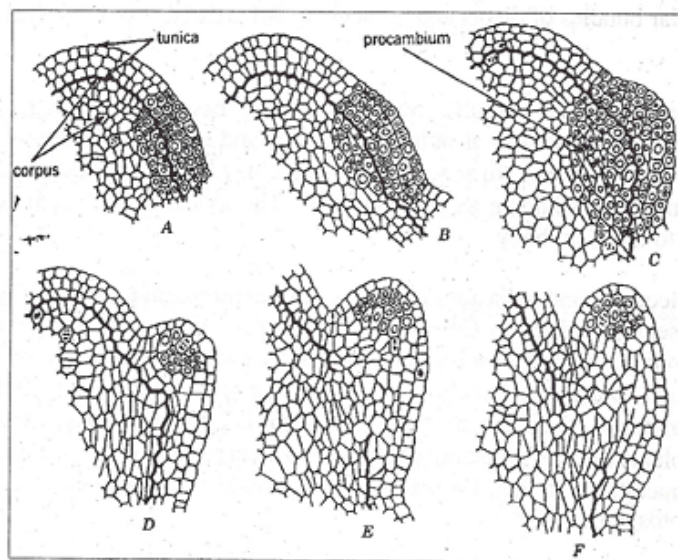


Fig. 10.10 A-E: Development of phyllode in *Acacia*. A. Periclinal divisions occurred in outer layer of corpus and third layer of tunica, .B. periclinal divisions spread into second layer of tunica, C. leaf buttress and procambium of leaf trace, D.' meristematic activity in

buttress initiates upward growth of primordium, E. F. Upward growth is continued, Periclinal and other divisions in subapical initials of Primordium and growth in surface of Protoderm (Adopted from Esau).

(ii) Formation of Leaf Axis:

An erect peg-like protuberance (Fig. 10.10 D-F), often flattened on the adaxial side (Fig. 10.11 A), arises by the change in the direction of growth of leaf buttress. This protuberance is the axis of leaf. It may be considered as midrib-petiole part of the primordium, bearing the meristematic precursors of the future lamina. The meristematic activity of the leaf axis is at first concentrated at the apex (Fig. 10.11 D-F). Later, it occurs throughout; that is, apical growth is followed by intercalary growth. As the leaf axis is elevated above, the buttress, procambium is differentiated in its median part, which is in continuity with procambium in the buttress and the internode below. The leaf axis also increases in thickness by the activity of *adaxial meristem* which is with strip of cells located beneath the *adaxial protoderm*.

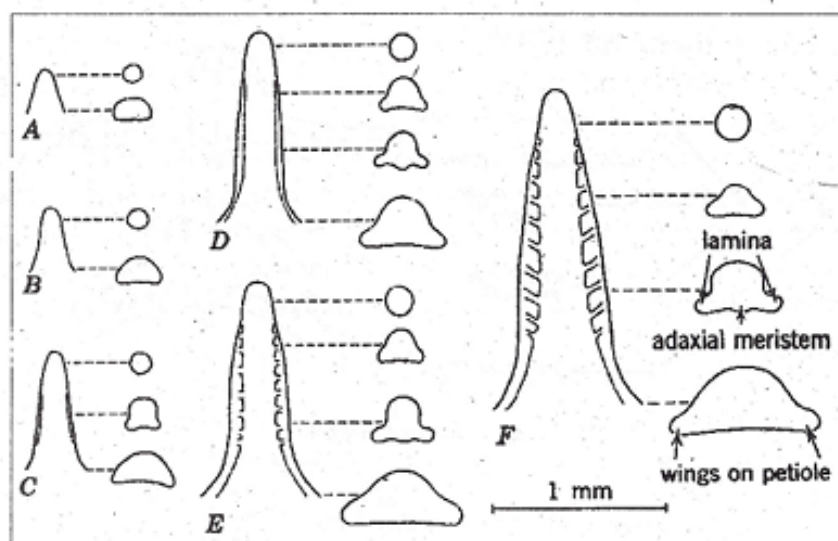


Fig. 10.11 A-F: Development of leaf of *Nicotiana tabacum*, longitudinal and transverse sections. A, B. growth of primordium in height, it is first an axis without blade; C-F. in later development, marginal meristem activity on two flanks begins to form blade; marginal activity of limited duration in petiole forms wings (Adopted from Esau, 1993).

(iii) Formation of Lamina:

The lamina is initiated in the early stages of elongation of the leaf axis by the activity of two bands of meristematic cells, which are marginally located, known as marginal meristem. The derivatives developing from the marginal meristem are differentiated eventually into various tissues of leaf.

Esau had developed the concept of the marginal meristem. Marginal meristem is composed of a file of superficial initials, the marginal initials which extend the protoderm of lamina by anticlinal divisions and a file of submarginal initials, located beneath the marginal. During marginal growth and after its cessation, the lamina expands also by intercalary

growth throughout its extent. A meristem composed of parallel cell layers growing in one plane, known as plate meristem is established close to the margin of leaf. Plate meristem is responsible for leaf expansion and also in maintaining the characteristic number of cell layers of leaf.

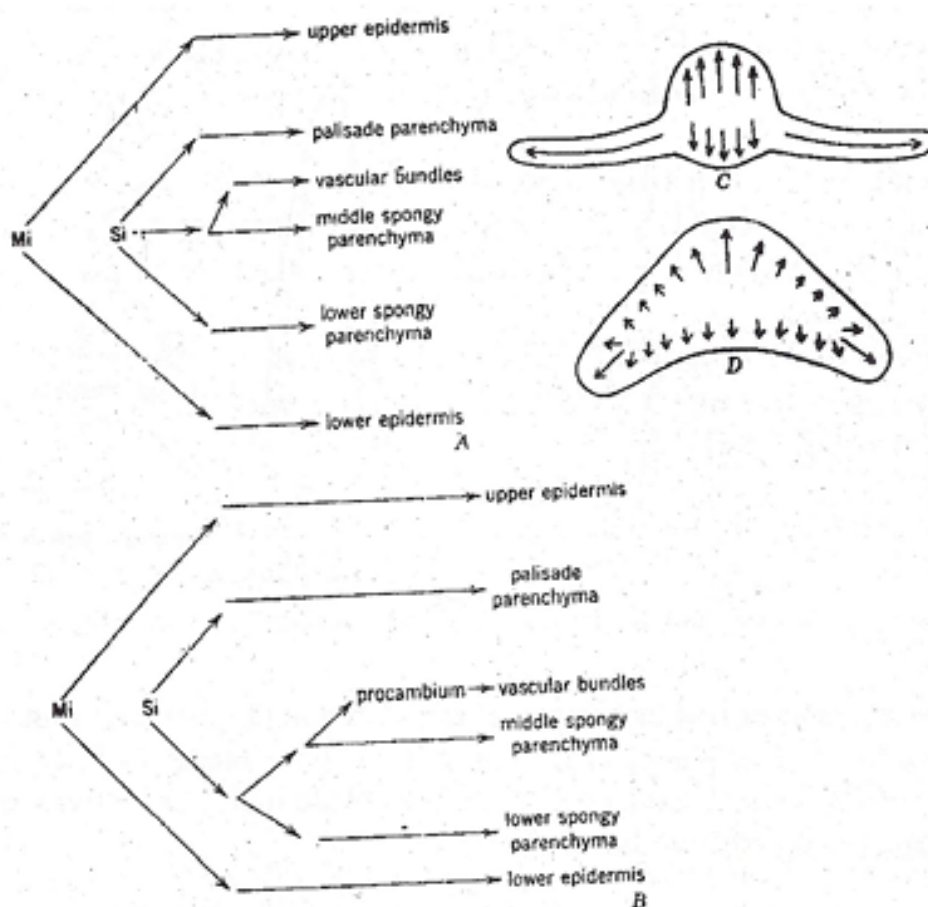


Fig. 10.12 A-D: Schematic representation of formation of various leaf tissues and tissue systems based on the assumption of presence of marginal and submarginal initials. A. *Nicotiana tabacum*, *Carya buckleyi*; C, D. Contrasting patterns of growth of leaf of *Oenothera* and *Honkenya* respectively (Adapted from Foster, 1936).

The above discussion is related to the development of simple, dicot leaves. A compound leaf is also initiated as a leaf axis upon a buttress. "This leaf axis is a primordium of petiole - rachis part of the leaf and bears meristem zones. Each meristem gives rise to a single leaflet. Each leaflet resembles a simple leaf in its development and histogenesis.

10.4. SUMMARY:

The collective term for all types of leaves appearing on plants is *Phyllome*. The phyllomes have been classified into foliage leaves, cataphylls, hypsophylls, cotyledons etc. Structurally leaves may also be classified into: (i) dorsiventral (bifacial), (ii) isobilateral (unifacial), and (iii) centric types. Mesophyll is well differentiated into palisade and spongy parenchyma in dorsiventral leaves where it is homogeneous in other two types of leaves.

The structure of C4 leaf in mono cots is known as Kranz anatomy, in which chloroplast dimorphism is evidently present. The C4 cycle enables these plants to carry photosynthesis at low carbondioxide concentration and at relatively higher temperature.

Ontogeny of leaf: Development of leaf can be divided into three stages: (i) initiation of leaf buttress, (ii) formation of leaf axis, and (iii) Formation of lamina. Leaf initiation takes place in the peripheral zone of the apical meristem.) Lamina is initiated by the activity of two bands of meristematic cells, known as marginal meristem. It consists of marginal and submarginal initials. Marginal initials are responsible for the formation of epidermis by undergoing anticlinal divisions whereas submarginal initials for internal tissues of lamina.

10.5. MODEL QUESTIONS:

A. Essay Questions:

- 1) Write an account on structure and ontogeny of angiosperm leaf.
- 2) Compare and contrast the structural differences between dicot and monocot leaf and add a note on the leaf differentiation of epidermis and mesophyll.

B. Short Answer Questions:

- 1) Dorsiventral leaf
- 2) Kranz anatomy
- 3) Plastochron
- 4) Lamina development

10.6. REFERENCE BOOKS:

- 1) K.Esau, 1993. Plant Anatomy, Wiley Eastern Limited, New Delhi.
- 2) A.Fahn, 1967. Plant Anatomy, Pergamon Press, Oxford.

Prof V. Umamaheswara Rao

LESSON-11

NODAL ANATOMY

11.0 OBJECTIVE:

- To understand the ontogeny of meristem to differentiate the stem into node.

STRUCTURE:

11.1 Introduction

11.2 Nodal Anatomy in Wheat (Monocot) Stem

11.3 Nodal Anatomy in Branch Traces and Branch Gaps

11.4 Summary

11.5 Model Questions

11.6 References

11.1. INTRODUCTION:

A shoot bears nodes and internodes. At each node, portions of the vascular system are deflected into the leaf, which is attached at this node. A vascular bundle located in the stem but directly related to a leaf, to represent the lower part of the vascular supply of this leaf, is termed the leaf trace.

The leaf trace is defined as follows - The leaf trace is a vascular bundle that connects the vascular system of the leaf with that of the stem. A leaf trace is extended between the base of a leaf and the point where it is completely merged with other parts of the vascular system in the stem. One or more leaf traces may be associated with each leaf.

In the shoot of a pteropsid (seed plants and ferns) where the leaf trace diverges into a leaf, it appears as though a portion of the vascular cylinder of the stem is deflected to one side. Immediately above the diverging trace, a parenchymatous tissue is being differentiated instead of vascular tissue in the vascular region of the stem for a limited distance.

The parenchymatous regions in the vascular system of the stem, located adaxially from the diverging leaf traces, are called leaf gaps or lacunae. Actually, these gaps are not breaking in the continuity of the vascular system of the axis. Lateral connections occur between the tissues above and below the gap. In transverse sections of an axis at the level of a leaf gap, the gap resembles an inter-fascicular area.

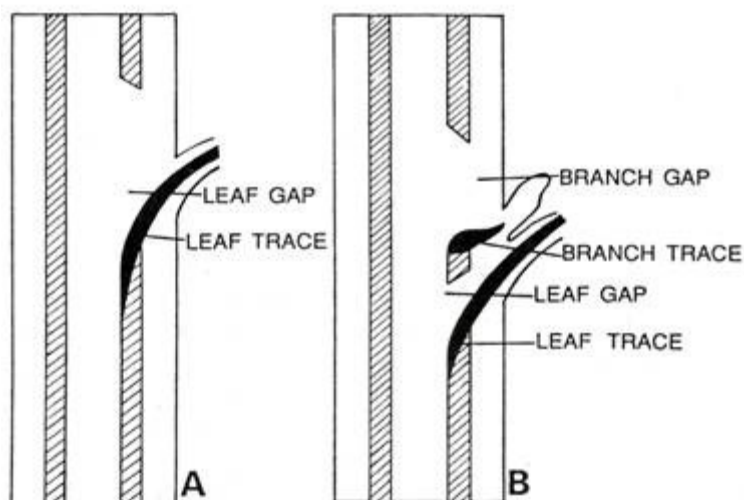


Fig. 11.1: Leaf and Branch Traces and Gaps, A, L.S. of Node through Leaf Trace and Gap; B, L.S. of Node through Branch Trace

The gaps are quite conspicuous in the ferns and angiosperms where the vascular system in the inter-nodal parts of the stem forms a more or less continuous cylinder. In some ferns the leaves are so crowded that the gaps formed at the successive nodes overlap one another and the vascular cylinder appears highly dissected.

The transverse sections of such stems show a circle of vascular bundles with the parenchymatous leaf gaps. In certain ferns, gymnosperms and most angiosperms the vascular system consists of anastomosing strands. In such cases, the parenchyma that occurs above the diverging leaf trace becomes confluent with the interfascicular areas, thus the recognition of the gaps become uncertain.

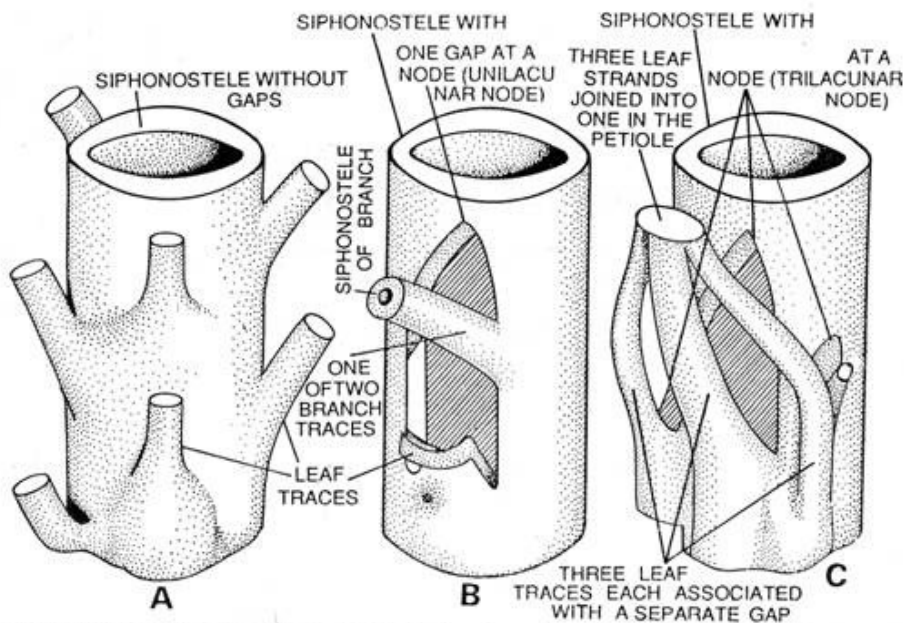


Fig. 11.2: Primary vascular system. A, Selaginella-three-dimensional view, siphonostelic type without leaf-gaps; B, Nicotiana-unilacunar node, siphonostelic with leaf gap; C, Salix-trilacunar node. siphonostelic type with leaf gaps. (After Esau).

There are three common types of nodes in the dicotyledons. The node with a single gap and a single trace to a leaf is known as unilacunar; the node with three gaps and three traces to a leaf (one median and two lateral) is known as trilacunar; and the node with several to many gaps and traces to a leaf is known as multi-lacunar.

The most accepted concept is that the trilacunar condition is primitive in the dicotyledons and that the unilacunar and the multi-lacunar have been derived from it. Several monocotyledonous plants possess leaves with sheathing bases and nodes with a large number of leaf traces separately inserted around the stem.

In ferns the number of traces to a leaf varies from one to many, but they are always associated with a single gap. In gymnosperms a unilacunar node is common.

The leaf trace relationships at the nodes are thought to be of phylogenetic importance, and therefore, nodal anatomy is concerned with the study of systematics and phylogeny of angiosperms.

11.2. NODAL ANATOMY IN WHEAT (MONOCOT) STEM:

In the wheat stem the course of the vascular bundles through the internode and the leaf sheath is almost parallel. Near the node the leaf sheath is considerably thick and attains its maximum thickness just above its union with the stem.

On the other hand, the stem has the smallest diameter above the junction with the leaf sheath. The stem is hollow in the internode and solid at the node. The sheath remains open on one side at higher levels, just near the node. Massive collenchymatous bundle caps are present in the bundles of leaf sheath.

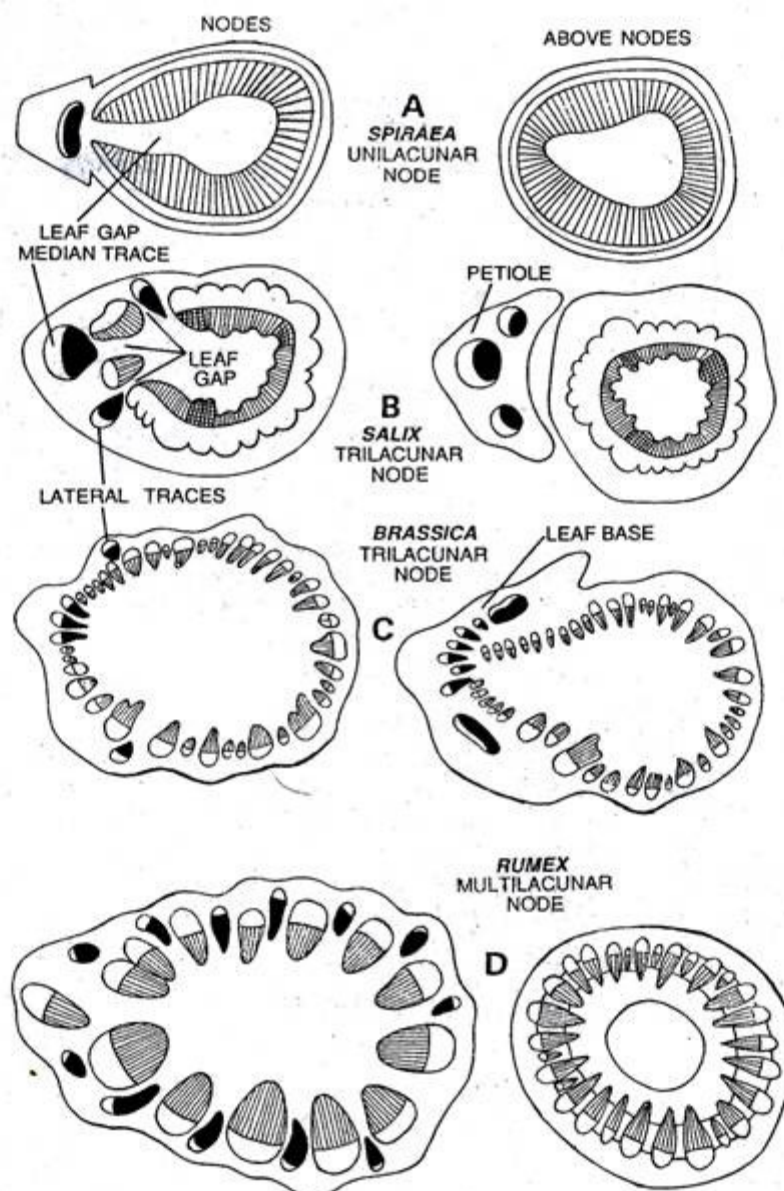


Fig. 11.3: Nodal anatomy of dicotyledons. A. *Spiraea*- each leaf has one leaf trace and one leaf gap (unilacunar node); B, *Salix*- each leaf has three leaf traces and three leaf gaps (trilacunar node); C. *Brassica*-three leaf traces and three leaf gaps per leaf (trilacunar node); D, *Rumex*-many leaf traces and many leaf gaps per leaf (multilacunar node).

Just beneath the junction of the leaf sheath and stem the smaller of the leaf traces are prolonged in the peripheral part of the axis, and the larger leaf traces become part of the inner cylinder of strands.

The inter-nodal bundles located above the leaf insertion assume, just above the node a horizontal and oblique course (Fig. 11.7 C, D), and are reoriented toward a more peripheral position in the node and below it (Fig. 11.7 D, E).

These horizontal and oblique bundles variously branch and coalesce, and their number reduces. The large leaf traces and the bundles from the internode above the insertion of the leaf make the inner cylinder of the bundles of the next lower internode (Fig. 11.7 E).

In this cylinder approximately, half of the bundles are leaf traces from the nearest leaf above and the other half of the bundles are from the internode above the insertion of the leaf (Fig. 11.7 E). The peripheral bundles are mostly leaf traces. The most conspicuous character of grass stems is the presence of transverse bundles in the nodal regions.

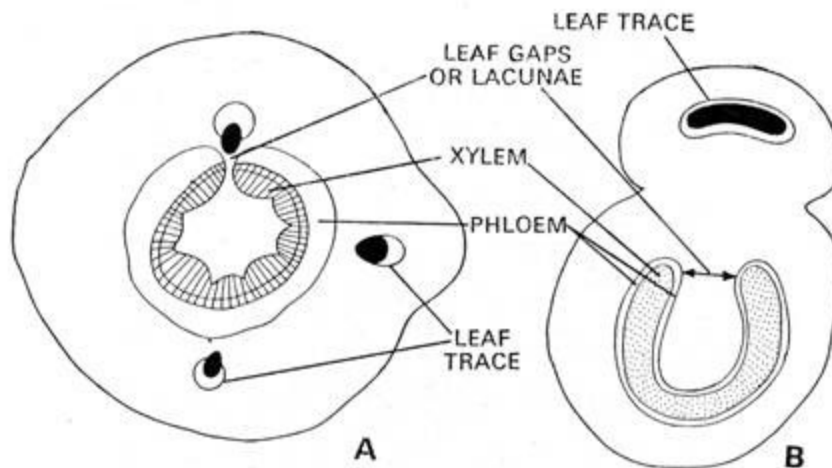


Fig. 11.4: Nodal anatomy. A, nodal anatomy of *Picea* (a conifer) in transection; B, nodal anatomy of *Adiantum* (a fern) in transection. Both possess alternate leaf arrangement, single traces to leaves, and single leaf gaps at the nodes. A, has some secondary growth; B, has phloem on both sides of xylem.

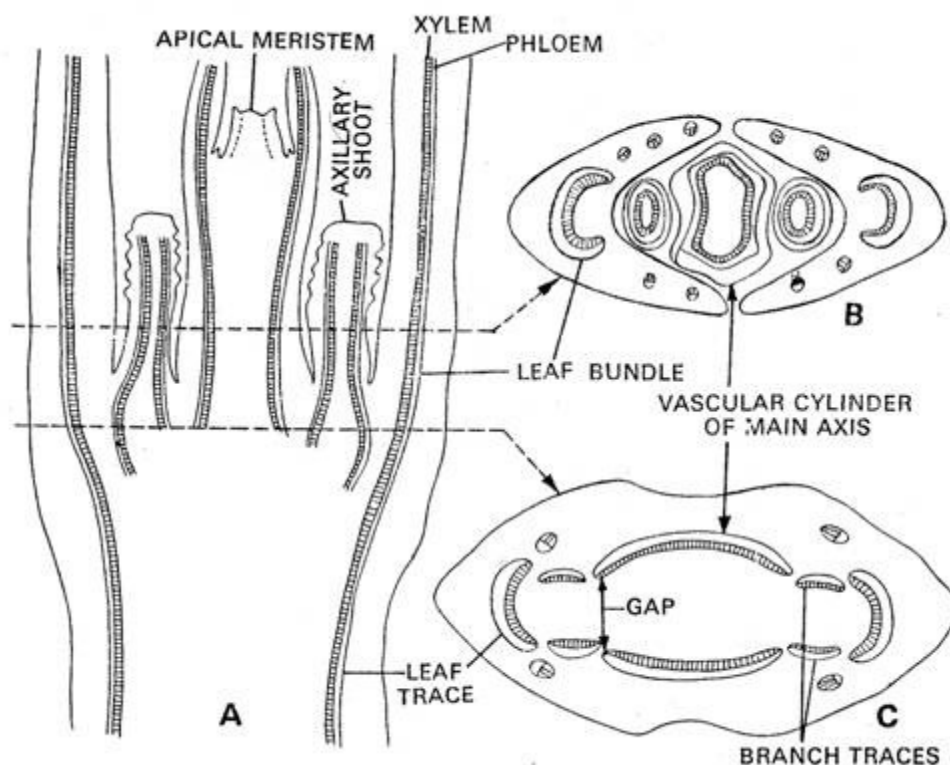


Fig. 11.5: Nodal anatomy. The diagrams depict the primary vascular system of plant with an opposite (decussate) leaf arrangement in L.S. (A) and T.S. (B and C). The branches present in the axils of the leaves are inflorescences. The leaf trace and branch traces in its axil are associated with one common gap. The two branch traces of level C are united into a tubular vascular cylinder in B.

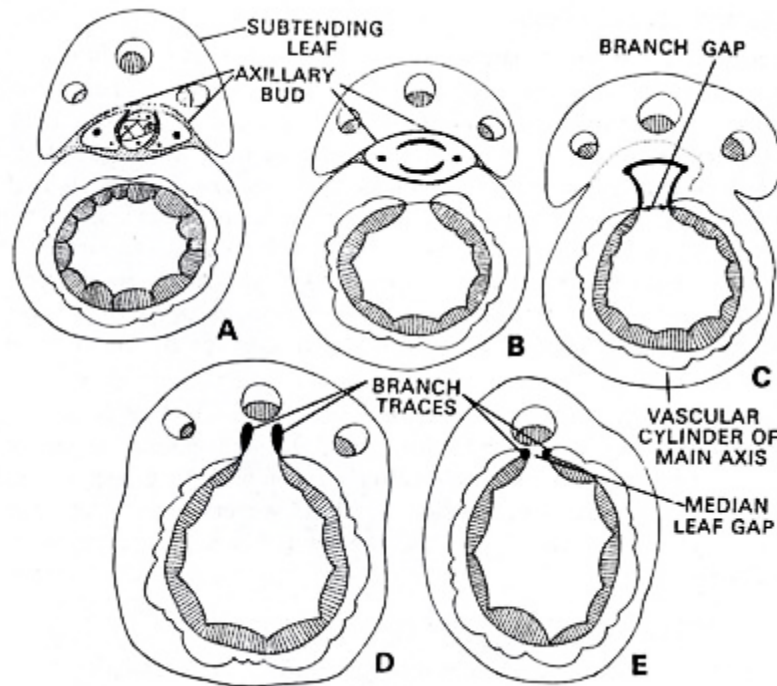


Fig. 11.6: Branch traces and gaps. Diagrams showing vascular connection between an axillary branch (bud) and the main axis in *Salix*. Vascular system of bud is shown in black in the diagram. First two leaves of bud are opposite. The branch gap and the median gap of the subtending leaf are confluent.

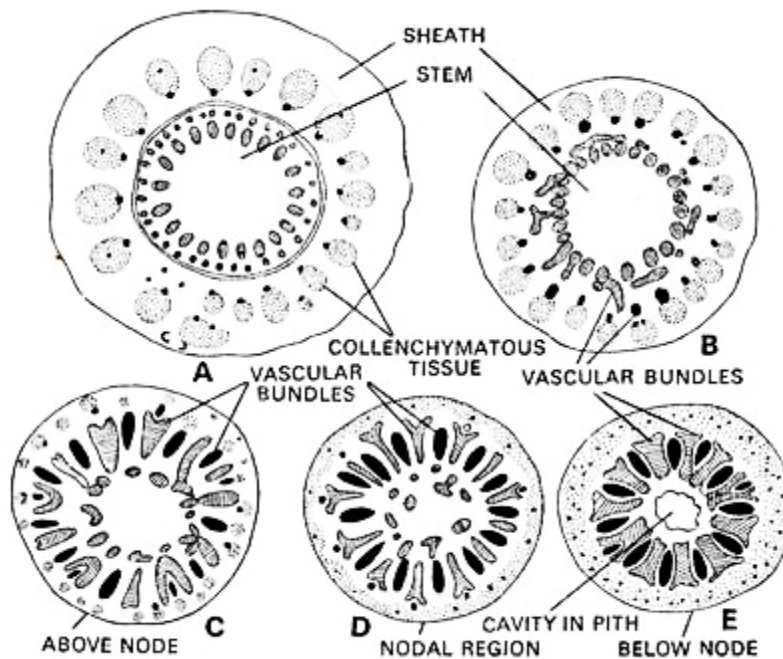


Fig. 11.7: Nodal anatomy of *Triticum* stem. Bundles of sheath and their traces in stem are depicted in black: vascular tissue of internode and its continuation through node is hatched. A-E, transactions of stem at various levels. Toward node, sheath increases and stem decreases in thickness.

11.3. NODAL ANATOMY IN BRANCH TRACES AND BRANCH GAPS:

The primary vascular supply to lateral branches is also derived from the vascular system of the main axis, usually in the form of two bundles, less often, one bundle. These strands are known as branch traces or ramular traces (Eames and Mac Daniels, 1947).

Dicotyledons and gymnosperms commonly have two branch traces, connecting the vascular system of the branch to that of the main stem. In monocotyledons the connection of the axillary shoot with the main stem consists of many strands.

The branch traces are extended within the main axis and appendages are tied together by a primary vascular system.

When the branch possesses two traces, these bundles unite within a short distance, forming a complete vascular cylinder; when one trace occurs, this strand usually possesses the cross-sectional form of a horse-shoe shaped structure with the opening downward, and the vascular cylinder of the branch is formed by the closure of the opening as the branch traces passes out.

In most of vascular plants the outward passage of a branch trace is associated with the formation of a break in the vascular cylinder around and above the point of departure of the trace. This opening is known as branch gap, which always accompanies a branch trace.

Branch gaps are present in all vascular plants which possess a pith. However, in protosteles the gaps do not occur because there is no pith. Branch gaps are commonly lower than leaf gaps and extend for greater distances in the axis.

Nodal Anatomy - Closing of Leaf Gaps:

The features which characterize the nodal structure do not perpetuate in the secondary body. A cambium develops in the parenchyma of the leaf gap and forms vascular tissues in continuity with those bordering the gap. This phenomenon is known as closing of the gap.

The parenchyma cells near the margin of the gap are the first to change into cambium and those in the inner portion change later. This process takes place gradually, and the gap parenchyma is maintained as such within the secondary body until and cambium is differentiated throughout the entire tangential width of the gap.

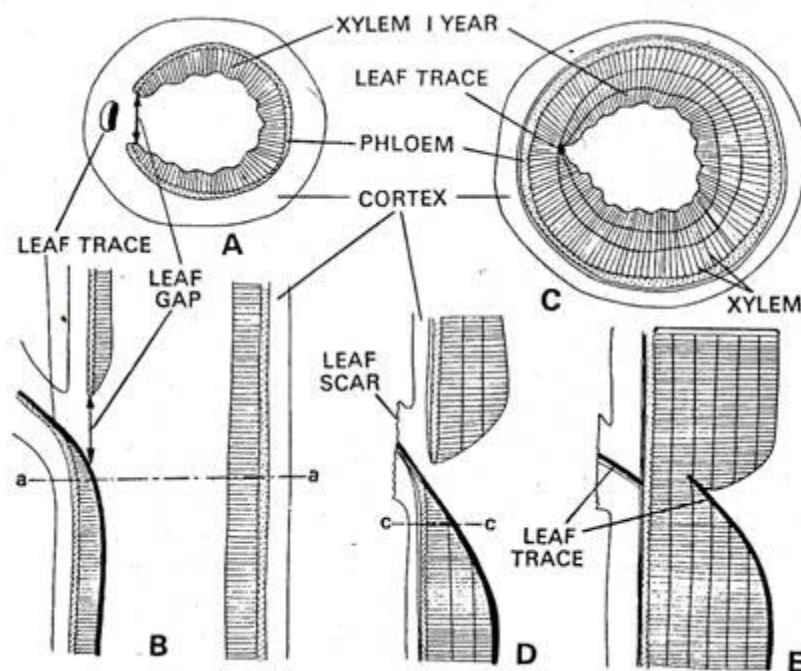


Fig. 11.8: Closing of leaf gaps by secondary growth. A and B, T.S. and L.S. through nodal region of stems in first year of growth; C-E, T.S. and L.S. through stems several years old; D and E. depict stages in closing of gaps and rupture of leaf trace (E).

In the leaf trace itself complicated changes take place during secondary growth. The primary xylem is buried by the secondary tissues while the phloem is pushed outward. The upper part of the trace diverges outwardly and crosses the plane of the cambium. The part of the cambium that differentiates above the trace in the gap region produces vascular tissue between the trace and the vascular cylinder.

This tissue which increases in amount exerts a pressure upon the trace and ultimately causes its rupture. The break is filled with parenchyma which is changed into cambium and connects the cambium of the lower part of the trace with that formed in the gap. After this cambium has formed some secondary tissues, the end of the trace below the break becomes embedded in secondary xylem (Fig. 11.8 E).

The upper severed end is carried outward, and in time it may be thrown off, together with the cortex, by the activity of the periderm. Since the cambium within the trace itself pushes the trace phloem outward, the buried part of the trace consists of xylem only.

11.4. SUMMARY:

The primary vascular supply to lateral branches is also derived from the vascular system of the main axis, usually in the form of two bundles, less often, one bundle. These strands are known as branch traces or ramular traces (Eames and Mac Daniels, 1947).

Dicotyledons and gymnosperms commonly have two branch traces, connecting the vascular system of the branch to that of the main stem. In monocotyledons the connection of the axillary shoot with the main stem consists of many strands.

The branch traces are extended within the main axis and appendages are tied together by a primary vascular system.

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Branch gaps are present in all vascular plants which possess a pith. However, in protosteles the gaps do not occur because there is no pith. Branch gaps are commonly lower than leaf gaps and extend for greater distances in the axis.

11.5. MODEL QUESTIONS:

- 1) Nodal Anatomy in Wheat (Monocot) Stem
- 2) Nodal Anatomy in Branch Traces and Branch Gaps

11.6. REFERENCE BOOKS:

- 1) K.Esau, 1993. Plant Anatomy, Wiley Eastern Limited, New Delhi.
- 2) A.Fahn, 1967. Plant Anatomy, Pergamon Press, Oxford.

Prof V. Umamaheswara Rao

LESSON-12

ENDOSPERM ANATOMY

12.0 OBJECTIVE:

- To understand the anatomy of endosperm during the development of seed.

STRUCTURE:

12.1 Introduction

12.2 Types of Endosperm

12.2.1. Nuclear Endosperm

12.2.2. Cellular Endosperm

12.2.3. Helobial Endosperm

12.2.4. Ruminant Endosperm

12.3 Cytology of Endosperm

12.4 Functions of Endosperm

12.5 Model Questions

12.6 References

12.1. INTRODUCTION:

Endosperm is the most common nutrition tissue for the developing embryos in angiosperms. Functionally, it is comparable to the female gametophytes in Gymnosperms but has a unique origin. Whereas the female gametophytes in gymnosperms differentiate before fertilization and, is haploid, the endosperm is the product of fertilization and is usually triploid. After double fertilization the egg is called zygote, and the fusion product of polars and the second male gamete is termed primary endosperm nucleus. The former develops into an organised embryo whereas the latter gives rise to an almost formless tissue, the endosperm. The only angiosperms which do not form endosperm are the members of the families Orchidaceae, Podostemaceae, and Trapaceae where present, the endosperm may either be consumed by the developing embryo, so that the seeds are non-endospermous (Pea, beans) or it may persist in mature seeds and continue to support the growth of embryo during seed germination. Common example of endospermous seeds are cereals, castorbean and coconut. Endosperm forms the edible part of cereals and coconut and it is the source of commercial castor-oil in castor-beans.

Depending on its mode of development the endosperm may be (a) Nuclear, (b) Cellular (c) Helobial. According to the data of Davis (1996) of the 288 families of Angiosperms for which information was available at the time 161 families show nuclear endosperm, 72 cellular endosperm and only 17 helobial endosperm. Cellular endosperm is largely restricted to dicotyledonous families. In monocots it occurs only in Araceae and Lemnaceae. Similarly, of the 17 families, showing Helobial endosperms are non-cotyledonous.

12.2. TYPES OF ENDOSPERM:

12.2.1. Nuclear Endosperm:

In this type of endosperm, the division of the primary endosperm nucleus and a few subsequent nuclear divisions are not accompanied by wall formation. This results in a condition on where the central cell of the embryo sac has formed a few to several thousand nuclei freely suspended in its sap. Such a condition of endosperm may persist until it is consumed by the developing embryo (*Floerkea*, *Limnanthes*, *Oxyspora*) or it may become cellular at a later stage (Fig 12.1). When the latter is the case, which is more common, the wall formation is mostly centripetal, i.e., from the periphery toward the centre. The degree of cellularization varies a great deal. Mostly the endosperm becomes completely cellular but in *Phaseolus* cellularization occurs only around the embryo. In *Crotalaria*, the wall formation is confined to the upper region of the embryo sac, the chalazal region remains free-nuclear, and it often elongates and behaves like a haustorium (Fig. 12.2).

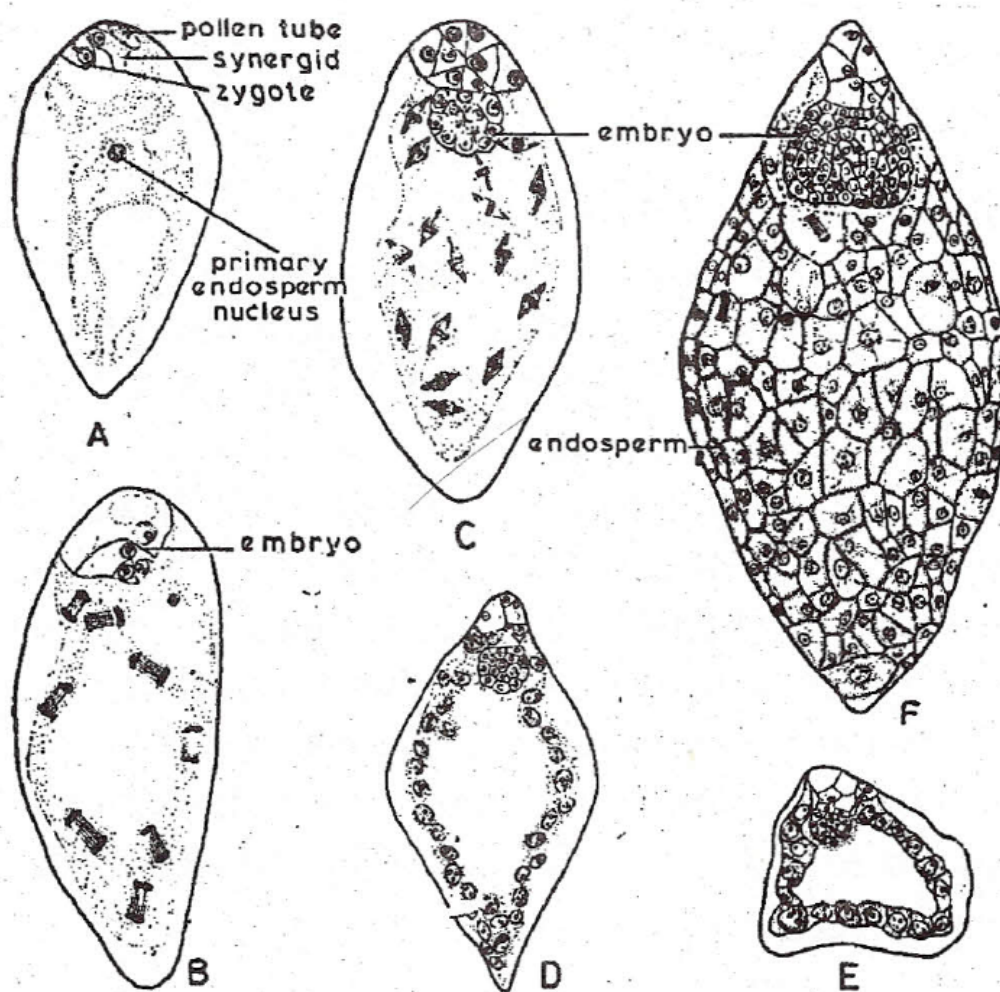


Fig. 12.1: Nuclear endosperm in *Acalypha indica*. A. Embryo sac after fertilization, the primary endosperm nucleus and the zygote have not yet divided. B, C. Embryo sac showing synchronous divisions of the endosperm nuclei. D. The endosperm nuclei have moved to the periphery. E. The peripheral part of the embryo sac has become cellular. F. Completely cellular endosperm.

Using the technique of dissections Karsik (1941), for the first time, reported the presence of a vermiform appendage at the chalazal end of the endosperm in *Grevillea robusta* (Fig. 12.3).

Since then, endosperm haustoria have been reported in several members of Cucurbitaceae, Leguminosae, and Proteaceae. Whereas in *Grevillea*, the chalazal endosperm haustorium remains free nuclear throughout. In *Coccinea* and *Citrullus fistulosus*, it becomes partitioned into multinucleate chambers. The longest endosperm haustorium is reported in *Echinocystis lobata* of the Cucurbitaceae. It measures upto 16mm in length (Seth, 1962).

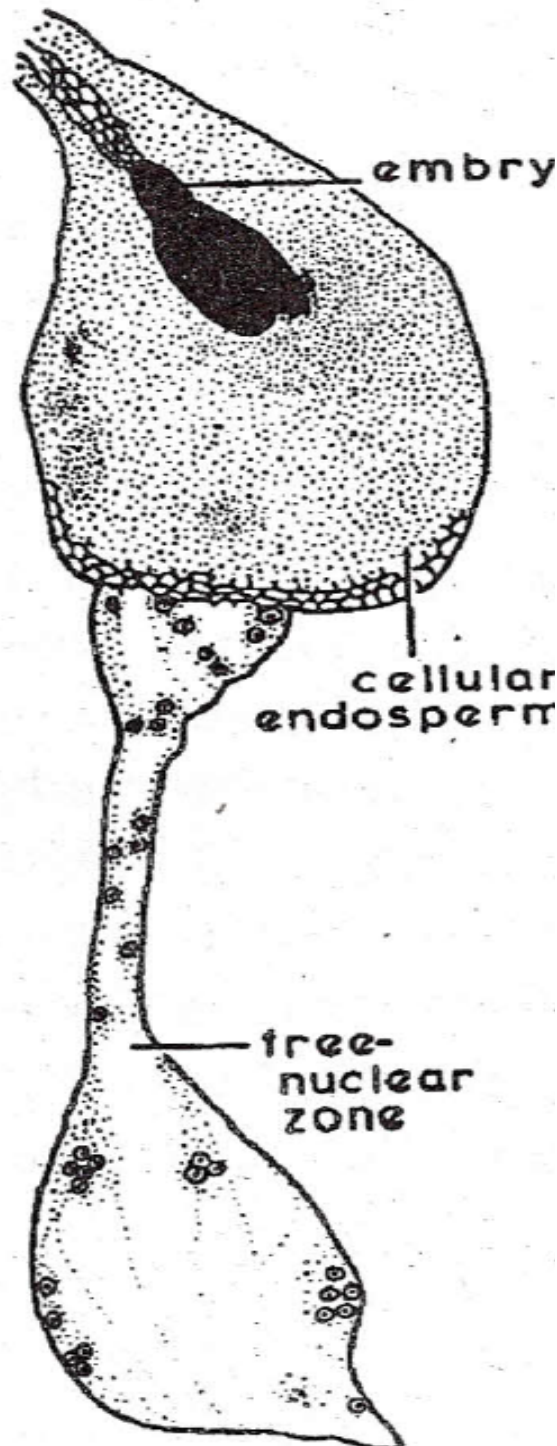


Fig. 12.3: Endosperm in *Grevillea*

Note the free-nuclear, vermiform, haustorium at the chalazal end of the cellular part of the endosperm. Contour endosperm In *Lomatia* besides the main chalazal haustorium,

numerous single-celled finger-shaped projections are present all over the endosperm. (Fig.12.4). This increases the absorbing surface of the endosperm. Contour endosperm

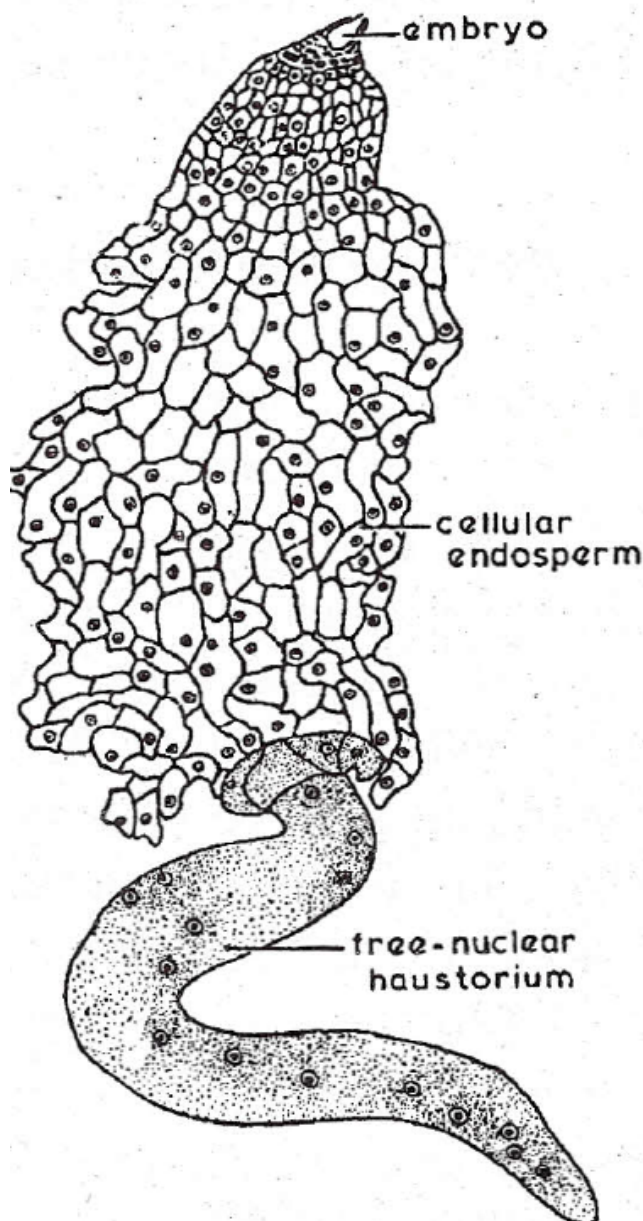


Fig. 12.4: *Lomatia Polymorpha*

Endosperm enclosing the embryo dissected out from a young seed. Several uninucleate projections are present on the surface of the endosperm as well as the haustorium.

Development of endosperm in coconut deserves special mention. The primary endosperm nucleus undergoes a number of free nuclear divisions. When the fruit is 50 mm long the embryo sac gets filled with a clear fluid in which float numerous nuclei of various sizes. At a later stage (about 100 mm long fruit), the suspension shows, in addition to free nuclei, several cells each enclosing variable number of nuclei. Gradually these cells and free nuclei start settling at the periphery of the cavity, and layers of cellular endosperm starts appearing. This forms the coconut meat. The quantity of the cellular endosperm increases further by the divisions of the cells.

12.2.2. Cellular Endosperm:

The cellular endosperm is characterised by the absence of free-nuclear stage. The division of the primary endosperm nucleus and a few subsequent nuclear divisions are followed regularly, by wall formation. (Fig. 12.5). The occurrence of haustoria is a common feature of this type of endosperm, it is more varied than that in the nuclear endosperm. The haustoria may be micropylar or chalazal. Occasionally, both types of haustoria are present in the same plant.

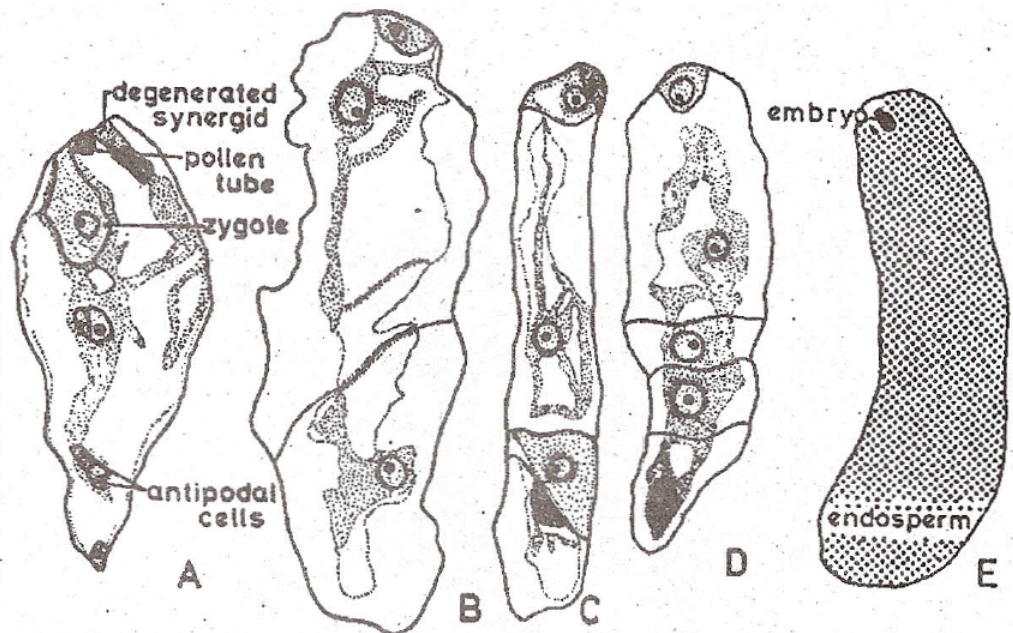


Fig. 12.5: Cellular endosperm in *Drimys Winteri*. A. Embryo sac after fertilization. B-D. Two-celled, 3-celled, and 4-celled endosperm, respectively. E. Older embryo sac completely filled with cellular endosperm.

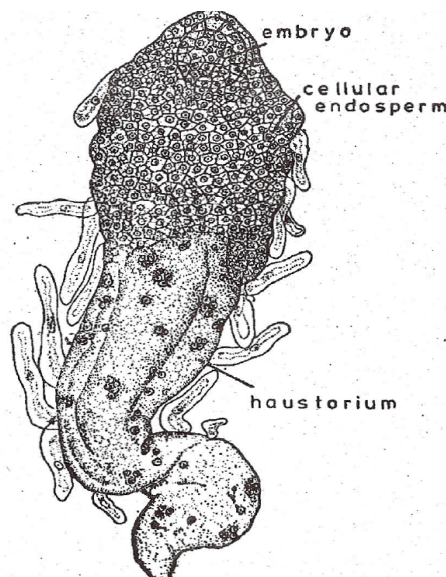


Fig. 12.6: Endosperm development in *Magnolia obovata*. A. Two-celled endosperm B. Thirteen-celled endosperm; note that the zygote has not yet divided. C. Diagram of endosperm at the globular stage of embryo to show 2-celled chalazal haustorium. D. A portion from C enlarged to show the chalazal haustorium with a few cells of the endosperm proper.

Micropylar haustoria are known to occur in *Impatiens roylei* and *Hydroceratriflora*. Development of 6 celled chalazal haustorium in *Magnolia obovate* is shown (Fig. 12.6). The first division of the primary endosperm nucleus is followed by a transverse wall resulting into two chambers of almost equal size

- a) Division in the micropylar chamber are rapid and, in all directions,
- b) The chalazal chamber divides transversely and at a comparatively slow rate. This results in a tail like chalazal part attached to the more massive tissue at the micropylar end. Further divisions-occur in the upper part of the tail and add to the endosperm tissue. The basal two or three cells of the tail elongate to form a haustorium (Fig. 12.6 C, D) which penetrates into the chalazal part of the nucellus.

A very aggressive chalazal haustorium is formed in *Iodina rhombifolia* Bhatnagar and Sabharwal, 1969). The haustorium is actually formed before fertilization. The chalazal end of the unfertilized embryo sac forms an extensive caecum, the lower end of which extends into the placenta and branches. After fertilization, the- division of the primary endosperm nucleus is followed by transverse partitioning of the central cell, resulting in the formation of a micropylar chamber and a chalazal chamber. The endosperm proper is derived from the micropylar chamber alone. The chalazal chamber functions as an aggressive, uninucleate haustorium. The nucleus migrates into the caecum and becomes much hypertrophied. Profuse branching at the free-end gives the haustorium coralloid: appearance. (Fig. 12.7).

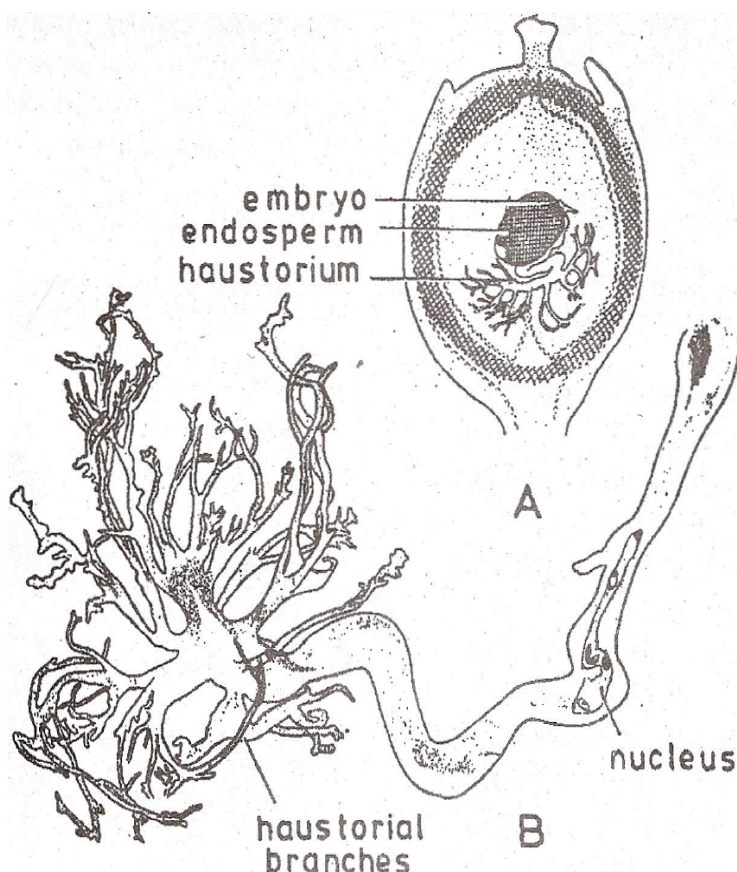


Fig. 12.7: *Iodina rhombifolia*. A. Longisection of the fruit at the globular stage of the embryo; note the aggressive nature of the chalazal haustorium. B, Enlarged view of the haustorium with branched lower end and hypertrophied nucleus.

In *Melampyrum*, the micropyle haustorium comprises a single, 4-nucleate cell with many tubular processes. (Fig 12.8). One of the processes enlarges and enters the funiculus (Arekal, 1963). The chalazal haustorium is a binucleate cell, broader above and narrow below. In the *Acanthaceae*, the endosperm development is asymmetric, and It shows characteristic micropylar and chalazal haustoria. The general pattern of endosperm development in this family is as follows. The primary endosperm nucleus moves to the chalazal end of the embryo sac and divides forming a smaller chalazal chamber and a larger upper chamber.

- a) The upper chamber again divides transversely, so that a linear row of three cells is formed.
- b) The chalazal chamber and the micropylar chamber develop into haustoria and the central cell forms the endosperm proper. (Fig 12.9).
- c) Variation

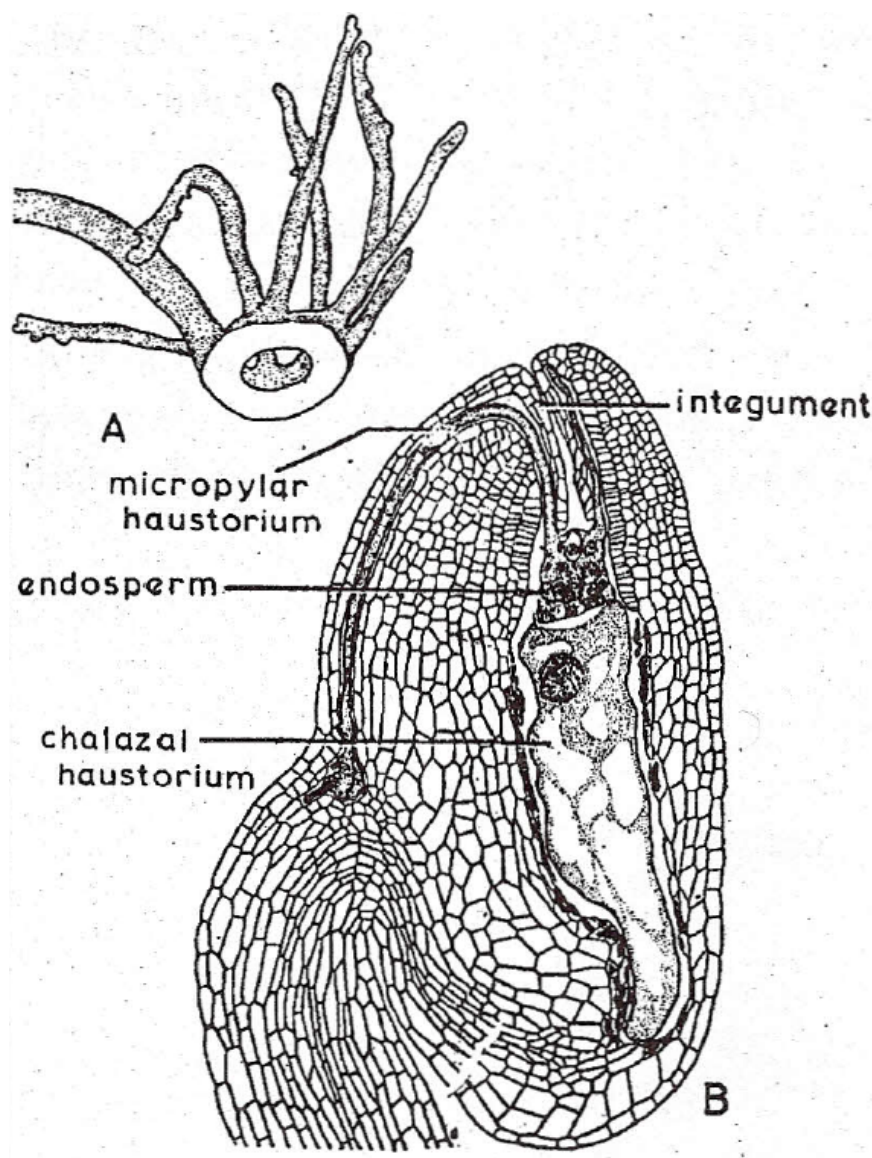


Fig. 12.8: Endosperm haustorium In *Melampyrum lineare*. A. Dissected out micropylar haustorium. B. Longitudinal section of a young seed showing extension of one of the micropylar haustoria processes grown into the funiculus. Single-celled chalazal haustorium is also seen in the figure

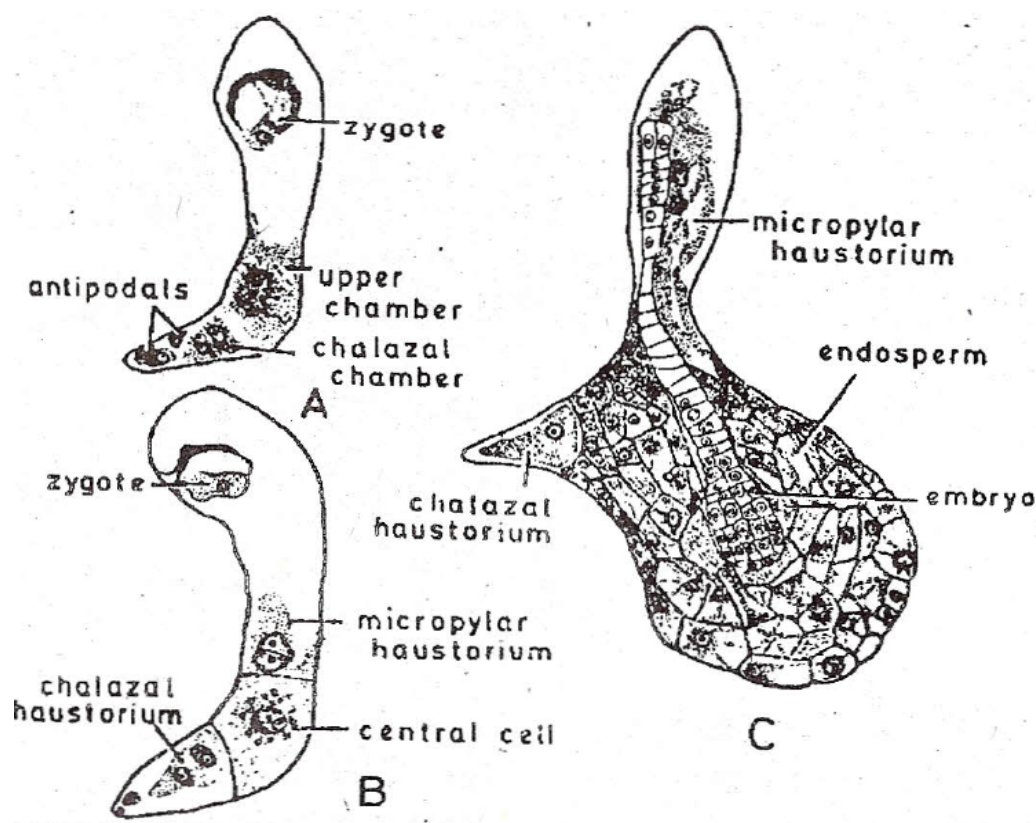


Fig. 12.9: Endosperm development in *Barleria cristata*. A. Two-celled stage; the chalazal chamber is binucleate. B. Three-celled stage. C. The central cell has formed cellular endosperm; also note the micropylar and chalazal haustoria.

exists in the behaviour of the central cell, Nuclear divisions in the central cell may be accompanied by wall formation right from the beginning so that the endosperm is ab initio cellular (*Barleria*, *Prioritis*, *Elytraria*), or wall formation may occur after a few free nuclear divisions. When latter is the condition, cellularization of the central may be complete (*Barleria cristata*, *Schaveria*) or partial (*Ruellia tuberosa*), the lower free nuclear portion being termed "basal apparatus".

Deviation from the general pattern of endosperm development in the Acanthaceae is shown by *Zhumbergia* and *Blepharis*. The linear three celled stage, present in all other members of the family, does not occur in these plants. They also lack the chalazal haustorium. After the division of the primary endosperm nucleus a micropylar chamber and a chalazal chamber are formed. The former grows into a haustorium whereas the latter gives rise to the endosperm proper. In *Zhumbergia* the micropylar haustorium is a branched coenocytic structure *Klugianotoniana* shows an interesting pattern of haustorium development (Arekal, 1961) Both chalazal and micropylar haustoria occur in this plant (Fig 12.10).

The chalazal haustorium is initially a binucleate cell but, eventually, becomes uni-nucleate due to the fusion of the two nuclei. The uni-nucleate haustorium grows laterally and

upward consuming the sub-epidermal cells of the integuments. The micropylar haustorium comprises two uninucleate cells. It becomes active only during later stages of seed development, when the activity of the chalazal haustorium begins to decline.

The development of endosperm in the Lorantheceae is unique. There being no true ovule, all the embryo sacs in an ovary lie close to each other. After fertilization, the primary endosperm nucleus moves to the lower part of the embryo sac where it divides. During their development, the endosperms of all the embryo sacs in an ovary fuse to form a composite endosperm (Fig. 12.11).

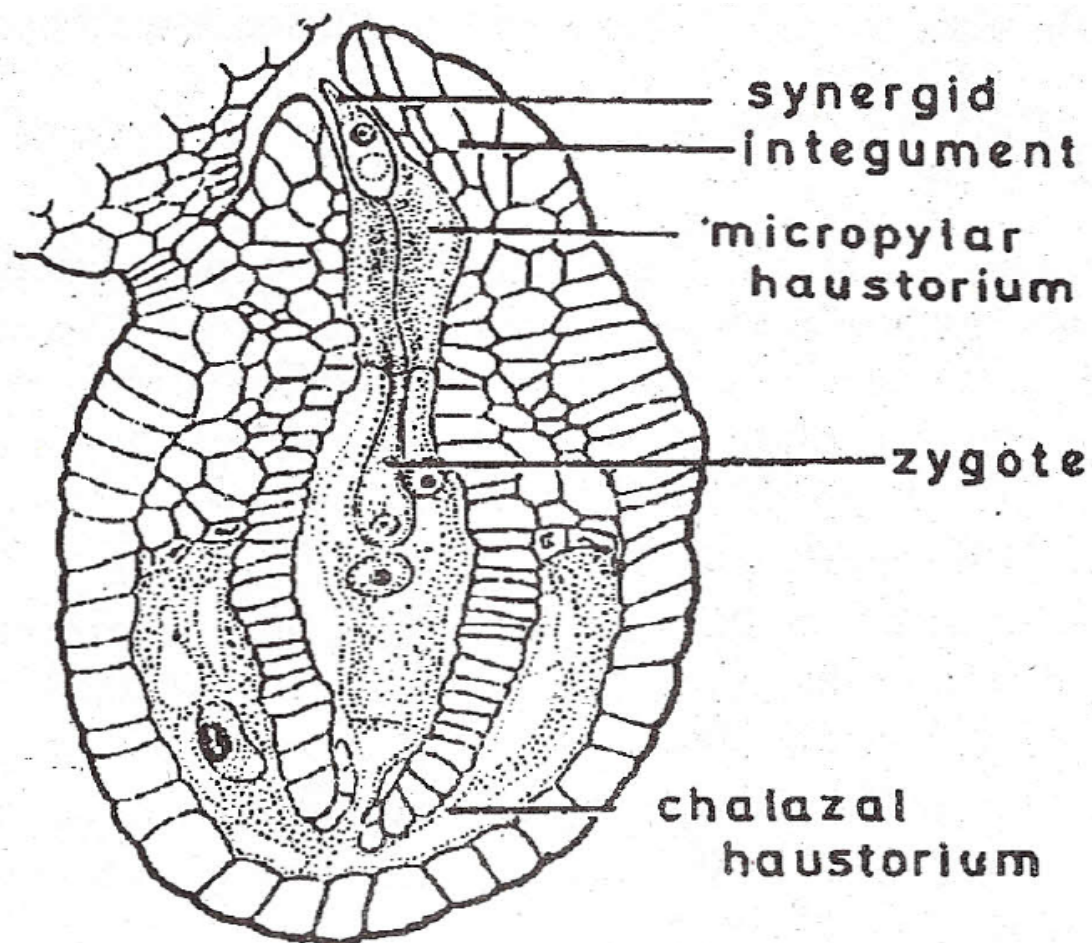


Fig. 12.10: Endosperm haustoria in *Klugiamotoniana*. L.S. of the ovule showing laterally upward growing chalazal haustorium, and the micropylar haustorium.

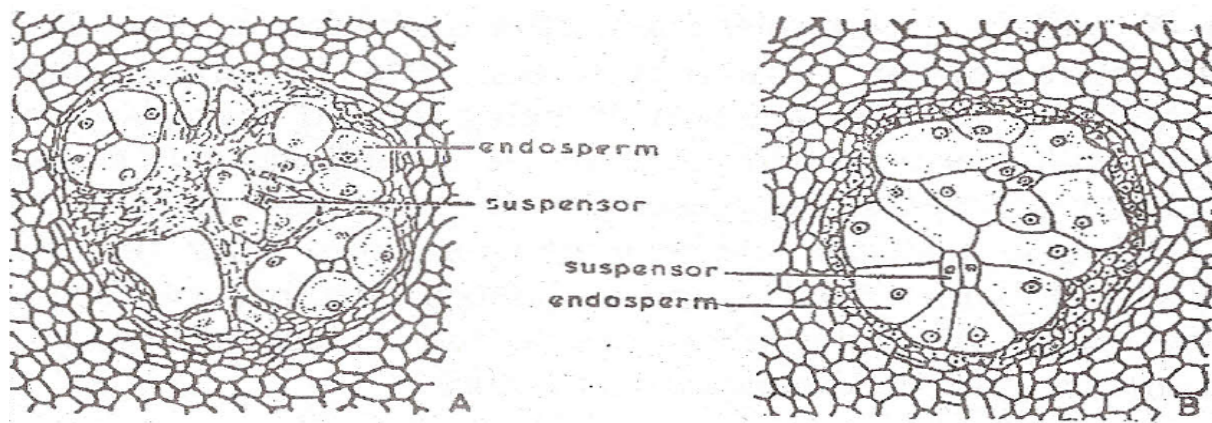


Fig. 12.11: Composite endosperm in *Tolypanthus involucratus*. A. Transverse section of ovary showing four embryo sacs, each with 4-sedate endosperm and a biseriate suspensor. B. Same, at a later stage of development. All the endosperms in the ovary have fused and formed a composite structure.

12.2.3. Helobial Endosperm:

This type of endosperm is restricted largely to the monocotyledons. The primary endosperm nucleus moves to the chalazal end of the embryo sac where it divides forming a large micropylar chamber and a small chalazal chamber. In the micropylar chamber, as a rule, free nuclear divisions, and cell formation, if any start at a much latter stage. In the chalazal chamber the nucleus either remains undivided or divides, only a few times. If latter is the situation the divisions are usually free-nuclear. However, sometimes as in *Philydrum lanuginosum* it may become cellular.

12.2.4. Ruminant Endosperm:

Mature endosperm with any degree of irregularity and unevenness in its surface contour is called ruminant endosperm. (Fig. 12.12). This is not the fourth type of endosperm development.

Rumination starts at a late stage of endosperm development and it may belong to anyone of the three categories described above Ruminant endosperm is known to occur in about 12. families of angiosperms.

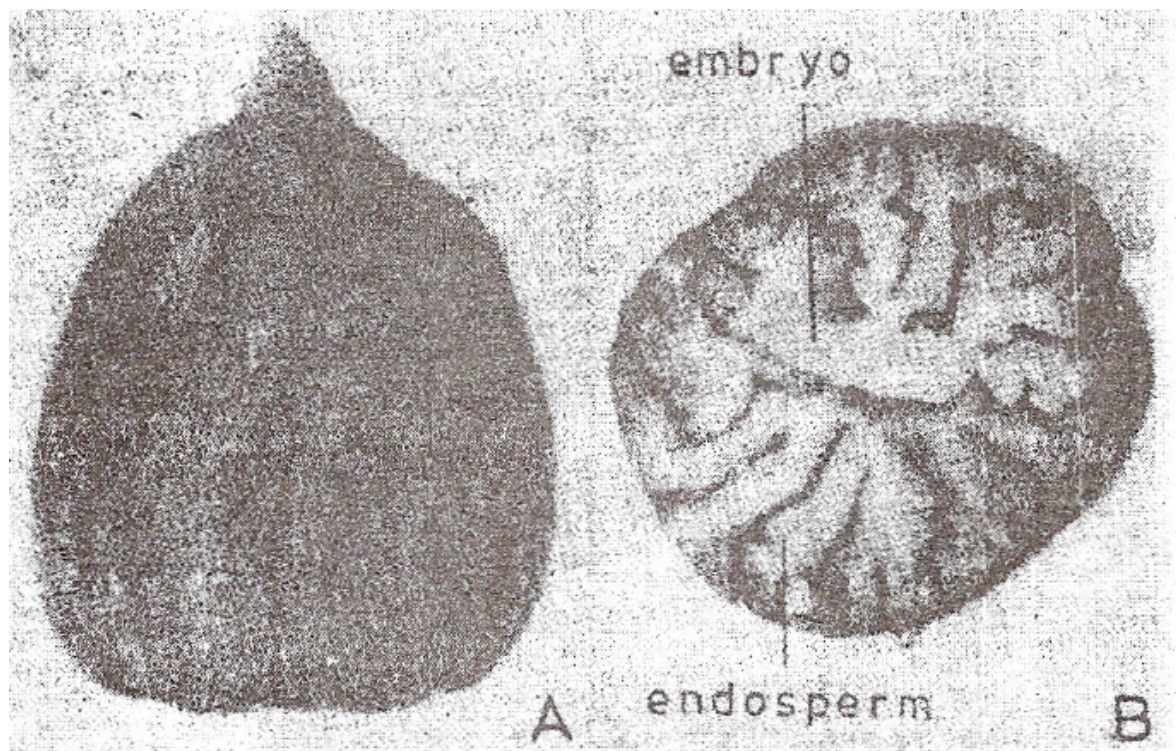


Fig. 12.12: Ruminant endosperm of *Antigonon*. A. Surface view, B. Same in L.S.; note the irregular structure of the endosperm.

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: (a) unequal radial elongation of any one or the only layer of the seed coat. *Passiflora carata*, or (b) definite increase in growth or in folding of the seed coat. The second cause is of more common occurrence and is found in the -Annonaceae, Aristolochiaceae etc. Rumination of endosperm by its own activity occurs in *Myristica*, *Coccoloba* etc. In these plants, the endosperm begins to increase in volume simultaneously with the increase in volume of the seed. It soon absorbs the nucellus and comes in direct contact with the seed coat. During further growth of the endosperm the irregular inner surface of the seed coat makes it to ruminate. On the other hand, in *Elytraria* and *Andrographis*, the endosperm exhibits unequal peripheral activity during late stage of its development and causes the seed coat to attain an irregular configuration.

12.3 CYTOLOGY OF ENDOSPERM:

In the majority of plants the endosperm is initially triploid because it is derived from the fusion product of three haploid -nuclei one from the male gametophyte and two from female gametophyte. Whereas the number of nuclei contributed by the male gametophyte in the formation of the endosperm is constant throughout the angiosperms, the number of nuclei contributed by the female gametophyte varies with the type of embryo sac. In *Oenothera* it is just one, and the endosperm is diploid whereas in *Peperomia* it is eight, and the endosperm is $9n$.

The endosperm tissue is well known for high degree of polyploidization of its cells during development. Erbrich (1965) studied endosperm cytology in many flowering plants. The ploidy of the nucleus of the endosperm haustorium in *Thesium malpinum* is up to 384 n. The highest ploidy, however, is reported in *Arum maculatum* where the nucleus becomes 2457 n.

The occurrence of various mitotic irregularities, such as chromosome bridges, lagging chromosomes, spontaneous breakage of the chromosomes and fragmentation of the nuclei is quite common in the endosperm tissue (Kapoor, 1962) (Fig. 12.13). Size of the nuclei and number of nucleoli per nucleus also exhibit great variation (C).

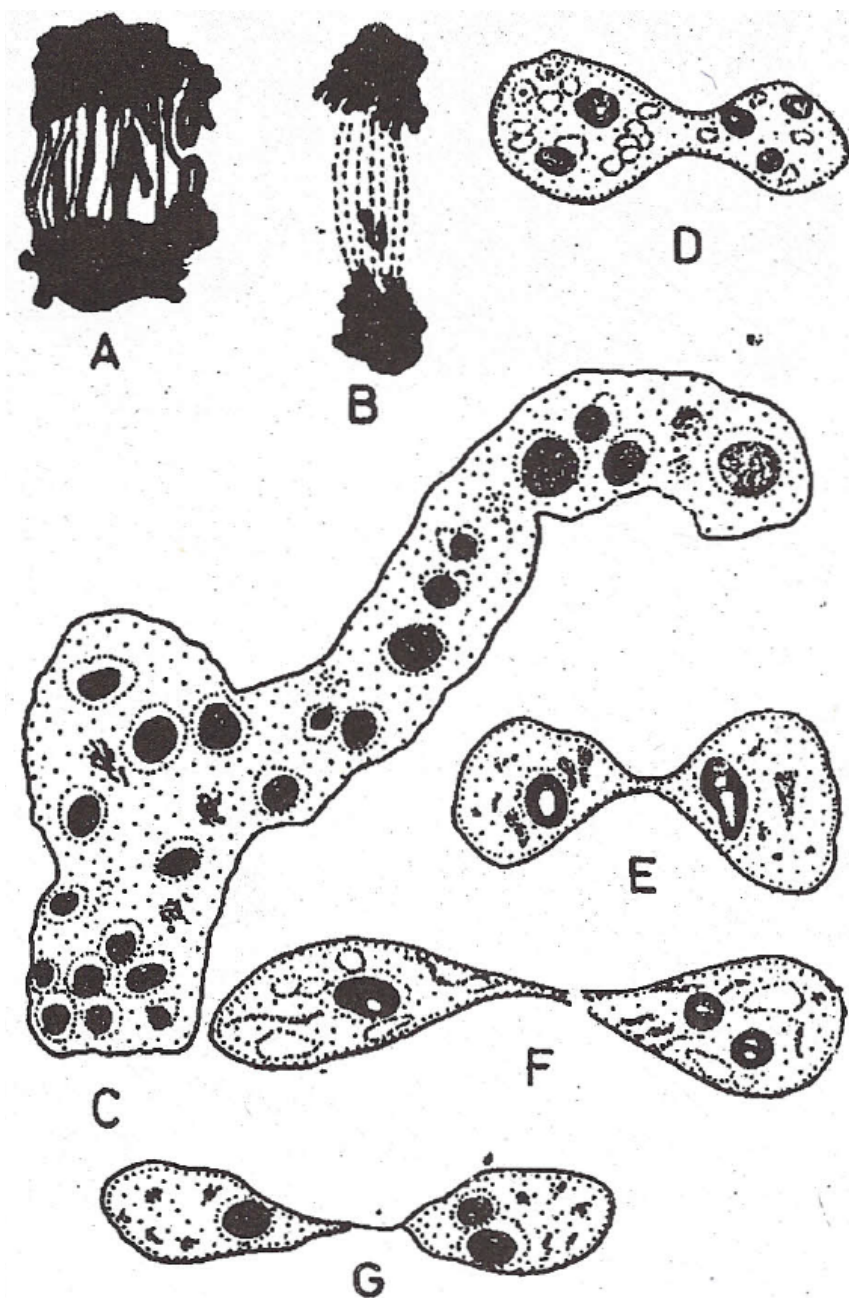


Fig. 12.13: Cytology of the endosperm. A. *Nothoscordum*; B, C. *Zephyranthes*; and D-G. *Vicia*. A. Late anaphase showing chromosome bridges. B. Late anaphase showing lagging chromosomes. C. An exceptionally large nucleus with 23 nucleoli. D-G. Stages in the fragmentation of the nucleus.

Endosperm is usually non-chlorophyllous, In *Crinum* during seed development, the seed coats as well as fruit wall are absorbed and the endosperm is exposed to sun light. Consequently, it becomes green; Chlorophyllous endosperm also occurs in *Mathiola*, *Raphanus*, *Viscum* etc.

Aleurone Tissue:

In cereals one or a few outer most layers of the endosperm become highly specialized morphologically and physiologically, and constitute the aleurone tissue. In barley the aleurone tissue is 3 or A-layered. In mature grams, the aleurone cells are alive whereas the starchy part of the endosperm, surrounded by the aleurone cells, has been regarded as dead by plant physiologists (Varner, 1972).

The aleurone cells are characterized by the presence of thick walls and non-vacuolated cytoplasm. They are interconnected by plasmodesmata. The most prominent organelles of these cells are aleurone grains followed by spherosomes. (Fig. 12.14). Aleurone grains are 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 is localized in discrete particles (Jacobsone et al, 1971). Structurally, the aleurone grains possess two kinds of inclusions, beside the ground substance (B). (a) Globoids present within the globoidal cavities they contain phytin and lipids. (b) protein-carbohydrate bodies, which are 1-1.5µm in diameter. The ground substance also contains high concentration of protein, but it is less than that in the protein-carbohydrate bodies.

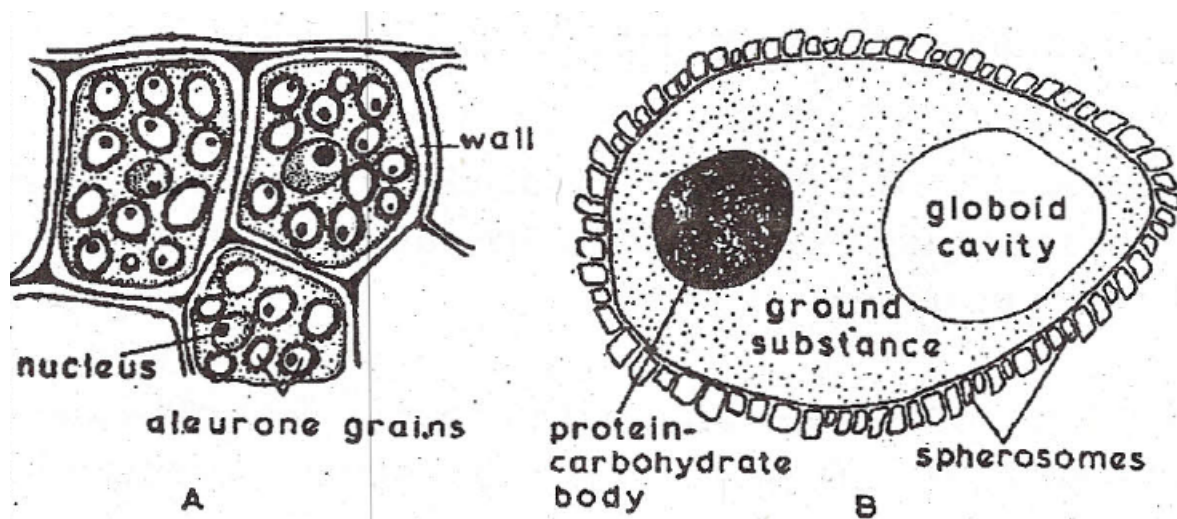


Fig.12.14: A. Aleurone cell of barley. B. A single aleurone grain enlarged

Recently aleurone tissue has received considerable importance in the studies of plant hormone action. During seed germination the reserve food (starch and protein) in the endosperm cells is digested by the activity of certain hydrolytic enzymes (amylases and proteases) which are secreted by the aleurone cells. Gibberellins have been shown to activate these enzymes or induce their de novo synthesis.

12.4. FUNCTIONS OF ENDOSPERM:

Where the endosperm persists in mature, seeds, it is rich in reserve food materials in the form of carbohydrates, fats and/or proteins. During seed germination these substances are digested and utilized for the growth of the seedling until the latter develops the green pigments and is able to manufacture its own food. The more important contribution of endosperm is in the nutrition of embryo during the early stages of development (from zygote to globular embryo). Maheshwari and Rangaswamy (1965) have given following points to support this view.

- 1) At the time of fertilization, the embryo sac having very little nutritive material. After the endosperm advances in development it stores enough food substances to ensure an adequate supply for the developing embryo.
- 2) In the majority of angiosperms, the zygote divides only after the endosperm has reached a reasonable stage of development. Even in, those cases where the zygote" divides before or simultaneously with the endosperm the latter soon stir 'passes the embryo ingrowth.
- 3) Generally, the embryo grows only when the endosperm develops properly. If the endosperin aborts, as it happens in many incompatible crosses, the growth of the embryo is adversely affected.
- 4) In the absence of the endosperm (Orchidaceae, Podostemaceae and Trapaceae) special, provisions exist to ensure the nutrition of the developing embryo.
- 5) During its growth the embryo depletes the surrounding cells of the endosperm of their contents. In many plants, such as legumes and cucurbits, the embryo consumes the endosperm completely before the seed attains maturity.

During early stages the endosperm as a nurse tissue, does not show specificity for its own embryo but can also nourish the embryos of other angiosperms. Coconut milk collected from green fruits has been successfully employed for growing embryos of many plants. Immature endosperm is also potent for inducing divisions in highly differentiated and mature cells such as the cells of secondary phloem in carrot. Besides coconut, such a property of endosperm has been shown for the extract of corn endosperm in the milk stage, liquid endosperm of horse-chest nut and walnut.

Added to the basic nutrient medium, coconut milk also induces the differentiation of embryos (embryoids) and plant lets from various plant tissues. nuclear, endosperm, as a rule, lacks these stimulation properties, it may even proves inhibitory, 'This may be correlated with the fact that young endosperm is rich in various growth hormones, such as auxins, cytokinin, and gibberellins whose concentration decreases after certain age of the tissue. Zeatin, now a well-known cytokinin, is extracted from young endosperm of maize.

Apart from being a nutrition tissue endosperm also regulates the precise mode of embryo development. Removed from the influences of the endosperm very young embryos fail to mature in richest artificial nutrient medium: Moreover; the isolated, older embryos often skip the normal stages of embryogeny and show precocious germination in cultures.

12.5. MODEL QUESTIONS:

- 1) Types of Endosperm
- 2) Cytology of Endosperm
- 3) Functions of Endosperm.

12.6. REFERENCE BOOKS:

- 1) The Embryology of Angiosperms; S.S; Bhojwani, S.P. Bhatnagar, Vikas Publishing House Pvt. Ltd., 2000.
- 2) Textbook. of Embryology of Angiosperms, T. Pullaiah, K. Lakshmi Narayana and Hanumantha Rao.

Dr. Madhuri Vajha

LESSON-13

CELLULAR ORGANIZATION AND DIFFERENTIATION IN THE ANATOMY OF EMBRYO

13.0 OBJECTIVE:

- To understand the cellular organization and differentiation in the anatomy of Embryo.

STRUCTURE:

- 13.1 Embryogeny
- 13.2 Proembryo
- 13.3 Embryogeny in Dicotyledons
- 13.4 Developmental Stages of *Ceratocephallus Falcatus*
 - 13.4.1. Asterad Type
 - 13.4.2. Chenopodial Type
 - 13.4.3. Caryophyllod Type
 - 13.4.4. Solanad Type
- 13.5 Embryogeny in Monocotyledons
- 13.6 Grass Embryo
- 13.7 Suspensor
- 13.8 Role of Suspensor
- 13.9 Nutrition of the Embryo
- 13.10 Model Questions
- 13.11 Reference Books

13.1. EMBRYOGENY:

In many angiosperms, the zygote divides transversely, resulting into a small apical cell (ca) toward the interior of the embryo sac and a large basal cell (cb) toward the micropyle. Rarely, the division of the zygote may be vertical (Loranthaceae) or oblique (Triticum sp), The variations in the developmental pattern of embryo during early embryogeny are common to monocotyledons' and dicotyledons. Differences appear when the initials of plumule and cotyledon are laid down. From the 2-celled stage until the initiation of the organs the embryo is commonly called pro embryo.

13.2. PRO-EMBRYO:

In a 2-celled pro embryo the based cell (cb) either remains undivided, or it undergoes a transverse division to form two' cells, m and ci. In the latter case, depending on whether the division of the apical cell (ca) is transverse or vertical the 4-celled pro embryo is linear or T-

shaped.; respectively (Fig 13.1). In the linear pro embryo, the two daughter cells of ca (l_1 and l_2) by two vertical divisions at right angles to each other, give rise to, octant with two superposed tiers (l , l_1) of four cells each (A). An octant of similar configuration is formed by the T-shaped pro embryo by one transverse division and one vertical division (B).

The T-shaped pro embryo can also form an octant of a different configuration, in which all the eight cells are included in the same tier (q), an axial quadrant is surrounded by four peripheral cells (Fig. 13.1 C). Thus, in angiosperms two types of octant BI configurations occur. a) The component cells are ci arranged in two superposed tiers of 4-cells each. (*Capsella beta*, *Sagitharia*, *Poa*), and b) all the 8-cells occur in a single tier (*Lactuca*, *Muscar*). As is evident from the cited examples, both types of octant occur in monocotyledons as well as in dicotyledons. It is at the octant stage of the proembryo that the destinies of various cells become determined. Octant

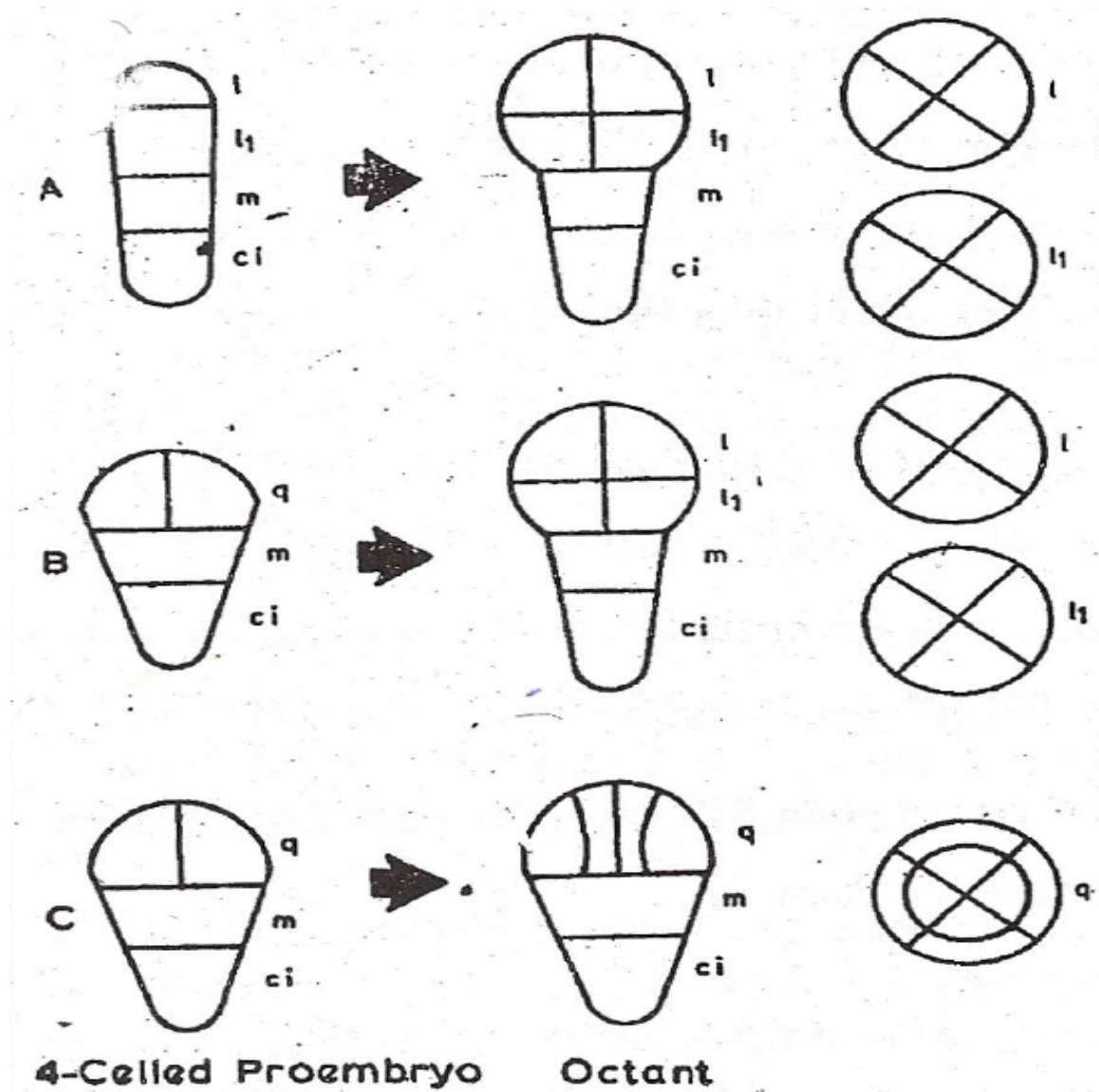


Fig. 13.1: Formation of two different types of octants. On the extreme right are transverse sections of the tiers l , l_1 , and q of the octants.

13.3. EMBRYOGENY IN DICOTYLEDONS:

Based on the plane of division of the apical cell in the 2-celled pro embryo, and the contribution of the basal cell (cb) and the apical cell (ca) in the formation of embryo proper five chief type of embryogeny have been recognised by Maheshwari (1950). A) The apical cell of the 2-celled pro embryo divides longitudinally.

- 1) The basal cell plays only a minor role or none in the subsequent development of the embryo proper Crucifer Type or Onagrad Type (e.g. Ranunculaceae, Annonaceae, Onagraceae, Cruciferae, Pedaliaceae, Scrophulariaceae).
- 2) The basal cell and apical cell both contribute to the development of embryo-Asterad Type (e.g. Balsaminaceae, Vitaceae, Violaceae, Compositae).
- 3) The apical cell of the 2-celled pro embryo divides transversely.
 - a) The basal cell plays only a minor role - none in the subsequent development of embryo proper.
 - b) The basal cell usually forms a suspensor-Solanad Type (e.g. Campanulaceae, Theaceae, Linaceae, Solanaceae).
- 4) The basal cell undergoes no further division, and the suspensor, if present, is always derived from the apical cell – Caryophyllad Type (e.g. Crassulaceae, Haloragaceae, Caryophyllaceae).
- 5) The basal and terminal cells both contribute to the development of embryo - Cheropodial Type (e.g. Boraginaceae, Cheropodiaceae).

These five types of embryogeny refer to those plants where first division of the zygote is transverse, so that an apical cell and a basal cell are formed. Johanson (1950) has recognised a sixth type of embryogeny called piperad type which includes those cases where first division of the zygote is vertical (Loranthaceae, Piperaceae). Often the type of embryogeny is constant throughout a family. Rarely, however the same species may show more than one well established trend of embryo development. For example, in *Monerularia* solanad type as well as crucifer type of embryogeny occurs regularly.

To illustrate complete development of a dicotyledonous embryo the work of Bhandari and Asnani (1968) on *Ceratocephalus falcatus* (Ranunculaceae) is described. In this species the embryogeny is of Onagrad type.

13.4. DEVELOPMENTAL STAGES OF CERATOCEPHALUS FALCATUS:

The zygote (Fig A) divides transversely forming a small apical cell (ca) and a large basal cell. (cb, Fig 13.2 B). Cell cb divides transversely forming two superposed cells ci and m (Fig 13.2C), and cell ca undergoes a vertical division giving rise to two juxtaposed cells (Fig 13.2 D). Thus; a T-shaped 4-celled pro-embryo is formed. Of the two daughter cells of cb, cell ci divides transversely giving rise to n and n¹ (Fig. 13.2 D). These two cells further divide forming a linear row of 3 or 4-celled suspension cell.m and its derivations divide by a vertical division to form 4-6 cells. Oblique periclinal divisions in each of these cells result in an inner set of cells (the initials of root apex) and an outer set of cells, the initials of root cap (Fig. 13.2 H-K).

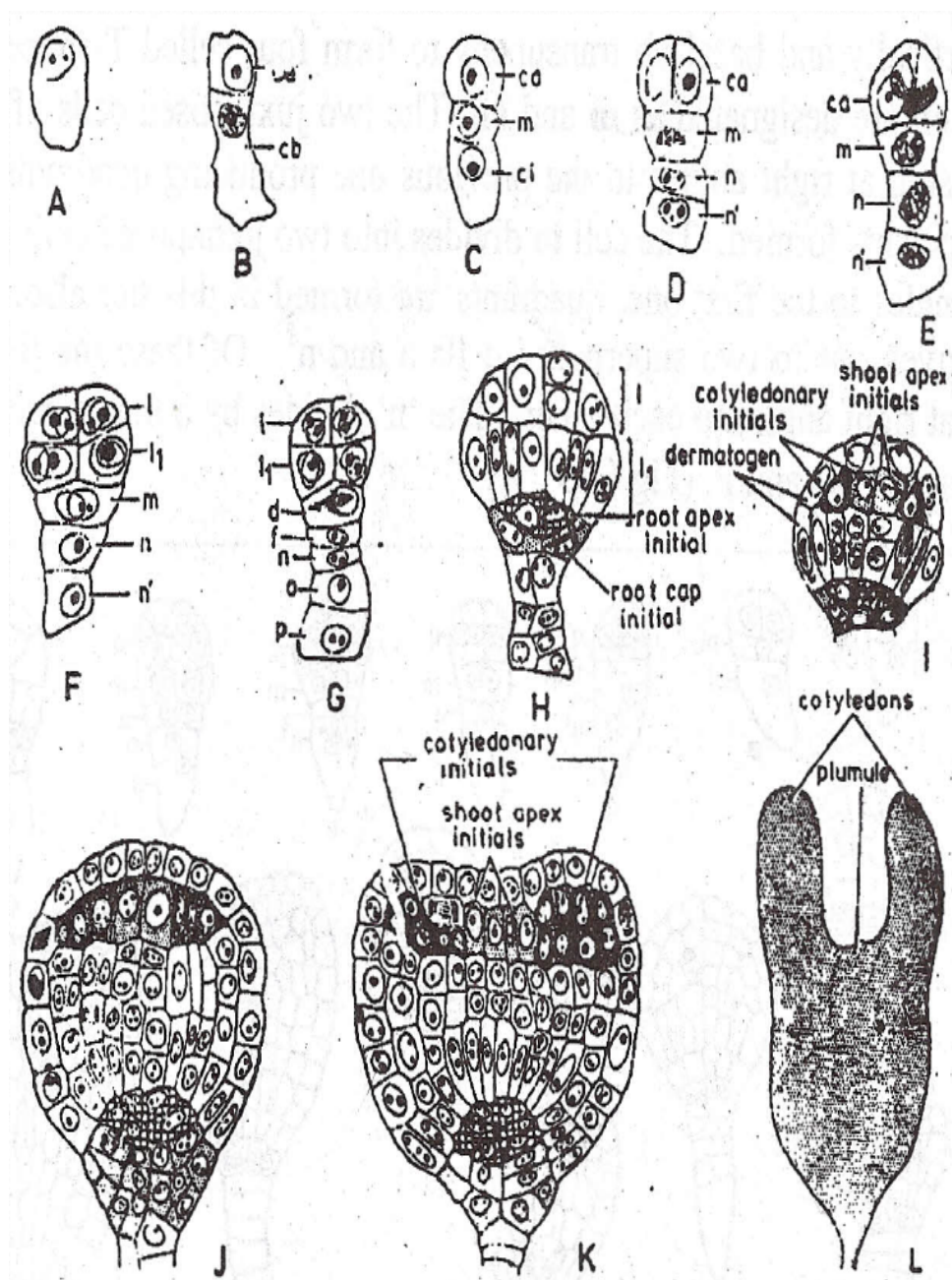


Fig. 13.2: Development of Embryo in *Ceratocephalus Falcatus*.

In the meantime, the daughter cells of apical cell divide by another vertical division at right angles to the first division (Fig. 13.2 E), forming a quadrant q. A transverse division of the quadrant result in an octant arranged in two tiers (I, II) of four cells each (Fig. 13.2 F, G). Vertical divisions in tiers (I and II) give rise to a globular pro embryo (Fig. 13.2 H), Periclinal divisions in the peripheral cells of the globular pro embryo demarcate a single-layered dermatogen, the further epidermis (Fig 13.2 I). Cells of the tier I differentiate the initials of plumule and the two cotyledons.

The latter flank the former on either side (Fig 13.2 I-K). Growth in the cotyledonous zones is much faster than that in the plumular- zone. As a result, in the mature embryo and plumule is enclosed at the base of the two cotyledons (Fig 13.2 L). The tier II finally forms the hypocotyl-radicle axis.

13.4.1. Asterad Type:

Soueges (1920) gave a detailed account of developme~1 of embryo in *Senecio Vulgaris*. Since then several other members of this family have been studied and all of them follow uniform pattern of embryo development (Pullaiah, 1984).

The zygote divides transversely to form a terminal cell ca and a basal cell cb. The terminal cell ca divides vertically and basal cb transversely to form four-celled T-shaped pro embryo. The two deviations of cb are designated as m and ci. The two juxtaposed cells of tier ca undergo one more vertical division at right angles to the previous, one producing quadrants. Due to oblique divisions in them octants formed. The cell m divides into two juxtaposed cells. By another vertical division at right angles to the first one quadrants are formed in, this tier also. The cell ci divides transversely and gives rise to two superposed cells n and n'. The former undergoes two vertical divisions at right angles to each other. The 'n' divides by a transverse wall and forms two superposed cells, namely a. and P. (Fig 13.3)

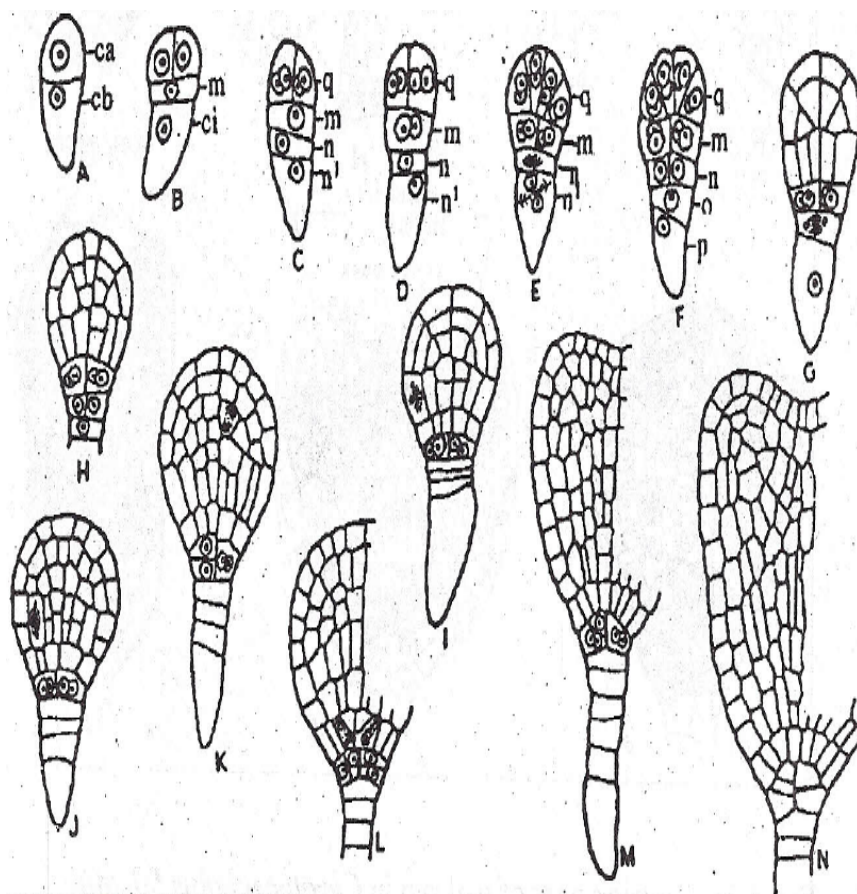


Fig. 13.3: Embryo Development in *Senecio Vulgaris*

13.4.2. Chenopodium Type:

Maheswari Devi and Pullaiah (1975) described Chenopodium type of embryo development in *Basella rubra*. The zygote undergoes transverse division resulting in a terminal cell ca and a based cell cb (Fig. 13.4A) which undergo one more transverse division resulting in a linear 4-celled pro embryo (Fig. 13.4 B). These cells are designated as 1,1', m and. ci. Now 1, i and m undergo vertical divisions twice at right angles to one another to form quadrants in each tier (Fig. 13.4 C-E) while ci undergoes transverse division to produce n and n'. The cell will divide further transverse division resulting in two cells 0 and P. During

further development in tier 1 gives rise to stem tip and cotyledons, 11 and m to the hypocotyl 1 (Fig. 13.4 H-P). The derivatives of n: function as the hypo physical initials and contribute to the formation of root tip. The cells 0 and P undergo further divisions and form suspensor (Fig. 13.4 J-P).

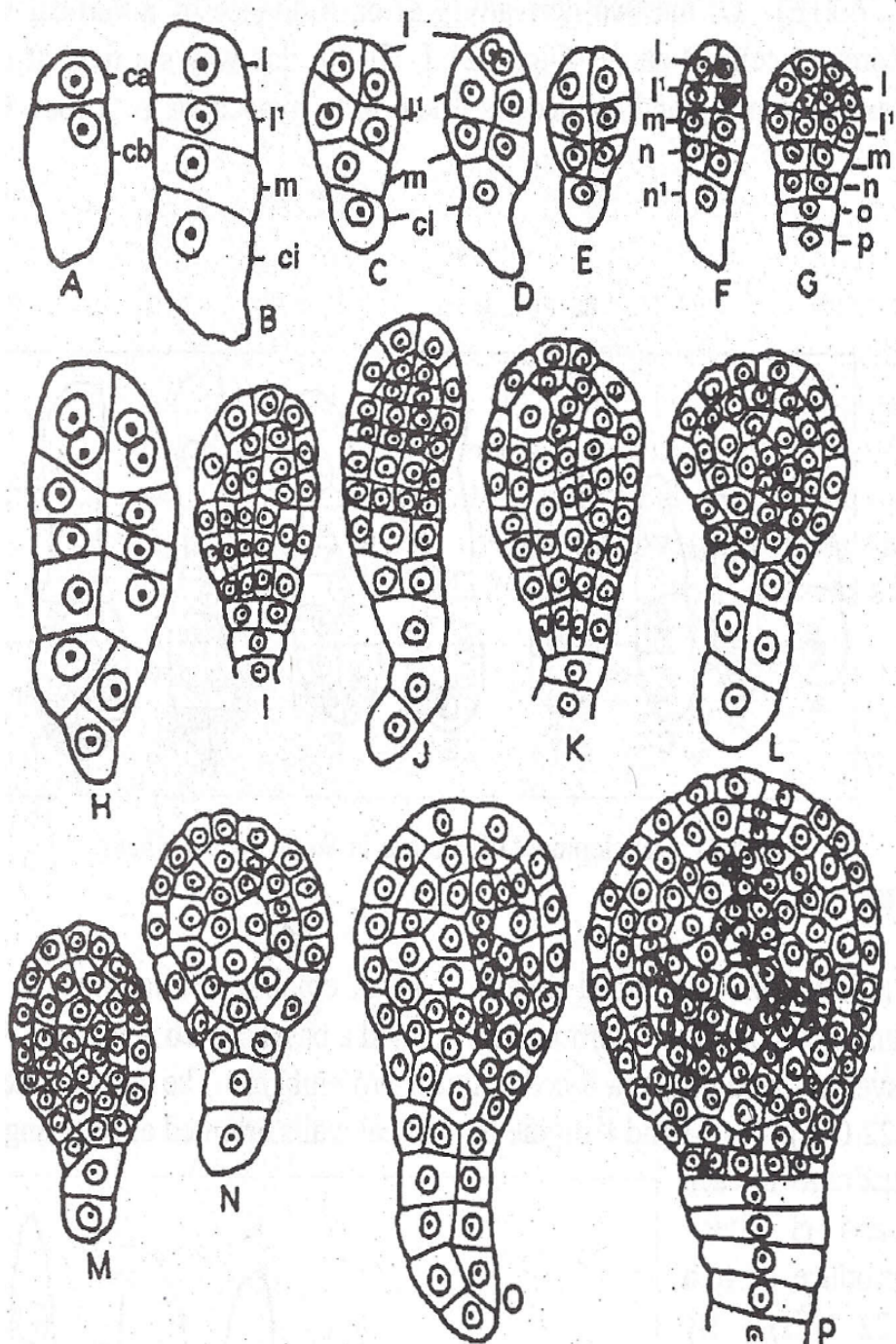


Fig. 13.4: Embryo Development in *Basella Rubra*

13.4.3. Caryophyllad Type:

Soueqes (1924) described caryophyllad type of embryo development in *Sagina procumbens*. The zygote divides by a transverse division forming a terminal cell **ea** and basal cell **cb** (Fig.13.5 A). The basal cell **cb** remains undivided which does not take part in the

development of embryo and forms a large vesicular structure (Fig. 13.5 B,H). The terminal cell undergoes transverse division and thus two cells are formed, an upper cc and lower cd (Fig. 13.5 B).

The cell cd again undergoes transverse division and gives rise to ci and m (Fig. 13.5 C). The cell cc also divides transversely to form I and I' (fig. 13.5 D). Thus, a row of four cells ci, m, I and I' is formed from cd and cc. Of these the three cells m and I divide by a vertical division and the cell ci transversely (Fig. 13.5 E). Of the two derivatives of ci, n divides by a vertical wall and by a transverse wall forming cells o and p (Fig. 13.5 F-H). In this way six tiers of cells are formed. The tier I gives rise to stem tip and cotyledons I' and m to hypocotyl n to root, o and p to short suspensor.

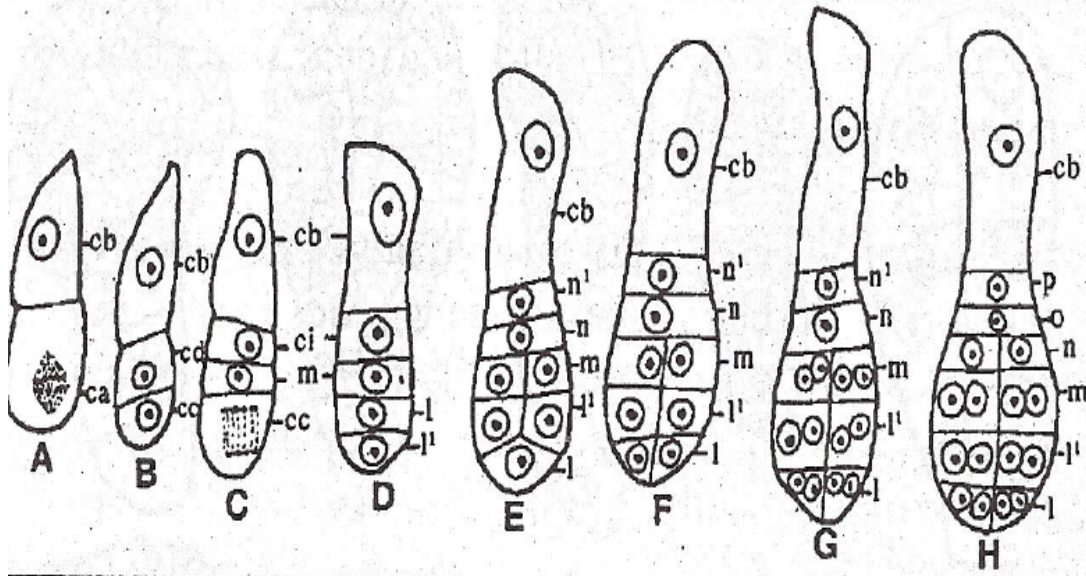


Fig. 13.5: Development of Embryo in *Sagina Procumbens* (d) Solanad Type

Soueges (1920, 1922) described Solanad type of embryo development in *Nicotiana*. The zygote divide transversely forming a terminal cell.ca and a basal cell cb (Fig. 13.6 A, B). Both these cells divide transversely resulting in a 4-celled linear pro embryo. The cells are designated as I, 11, m and ci (Fig. 13.6 C-F). Now I and 11 divide by vertical walls oriented at right angles to each other to give rise to quadrants in each tier, while m and ci divide transversely to produce d, f, n. l .and n (Fig. 13.6 G, H). By subsequent divisions I gives rise to stem tip and' cotyledons 11 to hypocotyl and to the perilem and plerome of the root, d to the root tip and. root cap. The remaining cells f, n and nl produce suspensor (Fig. 13.6).

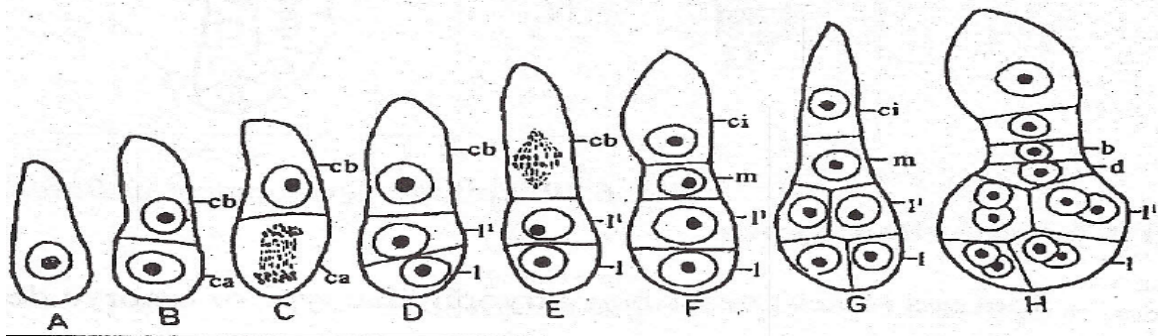


Fig. 13.6: Development of Embryo in *Nicotiana*

13.5. EMBRYOGENY IN MONOCOTYLEDONS:

As mentioned earlier, the development of embryo up to the octant stage is almost similar in monocotyledons and dicotyledons. This difference appears later. The main difference between the mature embryos of monocotyledons and dicotyledons is in the number of cotyledons. The single cotyledon in monocotyledons has been regarded by many authors as a terminal structure. Wardlaw (1955) has remarked. In the dicotyledonous embryo the plumule is typically distal and is situated symmetrically between two equivalent cotyledons in the monocotyledonous embryo the shoot apex occupies a lateral position in the somewhat cylindrical embryo and the cotyledon is terminal". However, extensive onto genetic work on monocot embryos by Swamy (Madras) and his co-workers (Lakshmanan, 1972) has established that the epicotyl in monocotyledonous embryo is truly. a terminal structure, both. epicotyl and cotyledon arise from the same terminal tier. The apparent lateral position of the epicotyl is due to early growth of the cotyledon, the epicotyl, after initiation, shows slow' growth. This is well illustrated by the embryogeny in *Najas*.

According to Lakshmanan (1972) the chief difference between embryos of the two groups. lies in the number of cells of the terminal quadrant which contribute to the formation of cotyledon(s) and epicotyl where the number of cells forming cotyledons) in the two types of embryos is same the relative position of the cells in the quadrant may be different. In dicotyledons .it is the two opposite cells of the terminal quadrant that give rise to the two cotyledons (Fig. 13.7).

In monocotyledons the number of cells involved in cotyledon formation is variable. It is practically all the four cells (except a few cells derived from one of the quadrant cells) in the Philodraceae (Fig.13.7 A) three cells of the quadrant in the Pontederiaceae. Spraganiaceae, and Iridaceae (Fig. 13.7 B) and turn adjacent cells in the Hydrocharitaceae Potamogetonaceae, and Amryllideaceae (Fig. 13.7C).

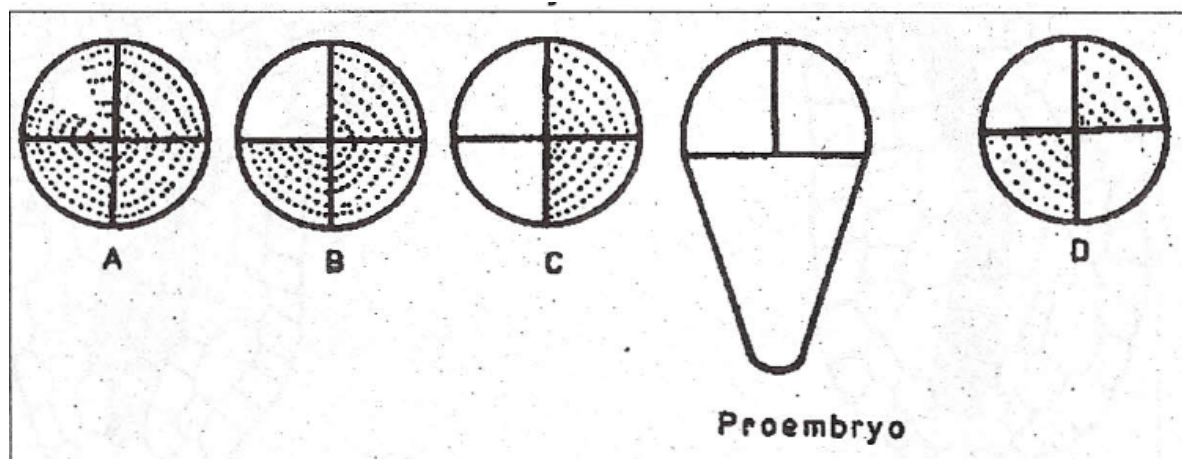


Fig. 13.7: Proembryo at the quadrant stage. A-D. Transverse sections of the terminal tier. Stippled parts of the quadrants represent the portion of the quadrant: contributing to the formation of cotyledon(s).

In monocotyledons, more than three sectors (A), three sectors (B), or two adjacent sectors (C) form the single cotyledon. whereas in dicotyledons two opposite sector (D) develop into a pair of cotyledons. To illustrate complete development of a monocotyledonous embryo the work of Swamy and Lakshmanan, (1942) on *Najaslacerata* is described here.

In *N. lacerate* transverse division of the zygote results in a large basal (cb) and a small apical cell (ca). The basal cell, without dividing even once, enlarges to form a single-celled haustorium (Fig. 13.8 A-D). Thus, the entire embryo is derived from the apical cell. It (ca) divides transversely into two cells, c and d. Of these the cell d once again divides transversely. In this way a linear pro embryo of four cells (c, m, ci, cb) is formed (Fig. 13.8 B). Two vertical divisions at right angles to each other in the two distal cells (c, m) lead to formation of two superposed tiers (q, m) of four cells each (Fig. 13.8 C, D). In the meantime, cell ci divides transversely to give rise to o and oi CD). Whereas cell. o divides vertically oi undergoes transverse division giving rise to two cells (o, p, h and s) cells (Fig. 13.8 F).

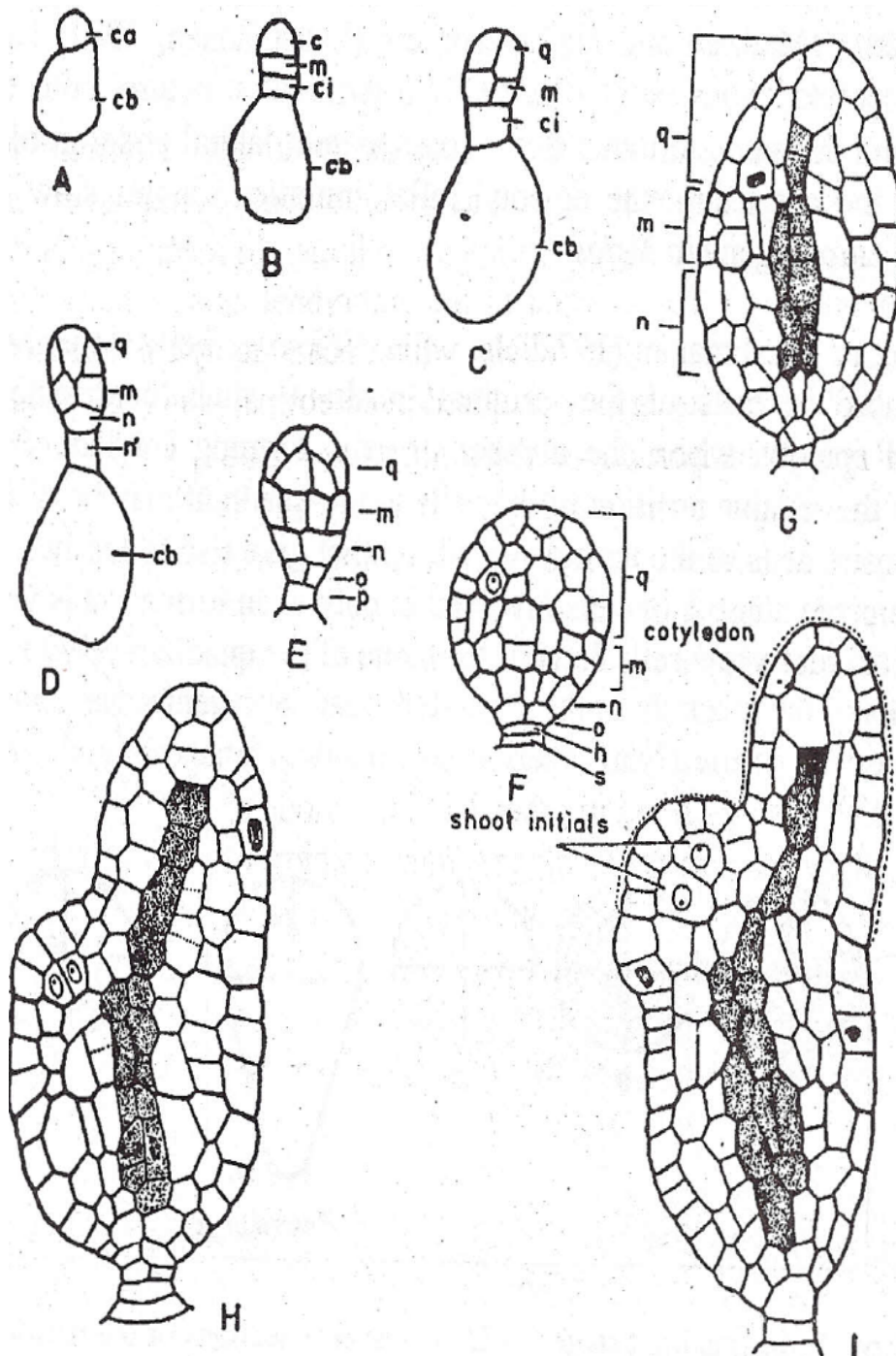


Fig. 13.8: Development of Embryo in *Najaslacerata*.

The quadrant q divides by a periclinal division cutting a four-celled dermatogen surrounding the four axial cells. (Fig. 13.8 E). The cells in the tier m divide by vertical and transfer, divisions and become two-tiered. At this stage, the pro embryo is slightly spherical (Fig. 13.8F). Now onwards, it elongates appreciably due to mainly transverse divisions in the tiers and D. At the stage when embryo becomes oval the central core of cells in the tier q, m and D differentiate into pleurome initials ss tipped cells in Fig: 13.8 G).

At the eight celled stage of the tier q (axial cells and four circum axial cells) three of the axial cells divide faster than the fourth one. This disturbs the symmetry of the pro embryo, and its top becomes notched. (Fig. 13.8 H). The rapidly growing portion of the tier q forms the single cotyledon (Fig. 13.8 I), and the slow growing tissue derived from the fourth axial cell, gives rise to the initials of epicotyl. The radicle is organised from the derivatives on n. Thus, in *Najas* the single cotyledon and the epicotyl are distinctly terminal structures, ontogenetically.

13.6. GRASS EMBRYO:

The monocotyledons embryo of grasses is strikingly different from that of other monocotyledons in its mature structure as well as development. A mature embryo of *Triticum* (Fig.13.9) for example, has. a single cotyledon called scutellum. In medium longitudinal section.

mature embryo it appears laterally attached 'to the embryonal axis. The portion of the embryonal axis below the level of scutellum is the radicle, which bears. an apical meristem and a root cap at the lower end. The radicle and its cap are enclosed in coleorhiza, which is the undifferentiated lower part of the preembryo. The portion of the embryo and axis above the level of scutellum is the epicotyle. It comprises a scutellum shoot apex with some leaf primordia enclosed in a shallow foliar structure, the coleoptile. The latter has an apical pore. The epiblast on one side of the. embryo is an outgrowth of the Coleorhiza.

Batygina (1969) has described in great detail the mode of embryo development in *Triticums*. All the four species of *Triticums* examined by her show a fixed pattern of embryogeny; which is so different from that in dicotyledons and, other monocotyledons that marked the unique mode of embryogenesis in Gramineae may allow the separation of a new type of embryogeny is Graminad Type. The early part of embryogeny. In *Triticum* is characterised by the regular occurrence of oblique divisions.

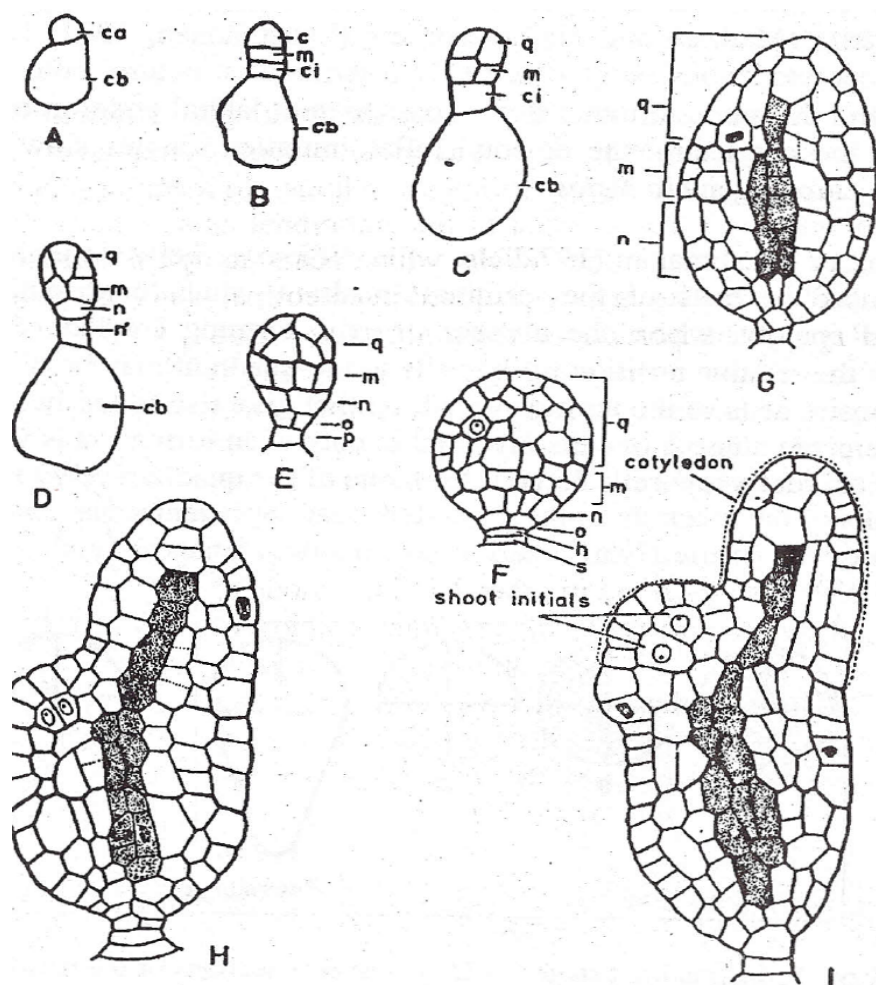


Fig. 13.9: Mature Embryo of *Triticum* as Seen in Median Longitudinal Section

The first nuclear division of the zygote (Fig. 13.9 A) is followed, by laying down of an oblique wall, cutting a small apical cell (ca) and a large based cell cb (Fig. 13.9 B). Cell cb again divides obliquely forming cells ci and m (Fig. 13.9 C, D). The upper end of the wall formed during the divisions connects with the walls separating ca and cb. The third division occurs in the cell ca, in a plane perpendicular to the first division of the zygote. Thus, T-shaped pro embryo (4-celled) is formed (Fig. 13.9 D). However, the orientation of the walls are very different from the T-shaped tetrads in either dicotyledons or other monocotyledons. This characterizes the wheat embryogeny.

Cell ci divides by a wall at right angles to the wall between ci and m, resulting in the formation of cells n and n1 (Fig. 13.26 E). Divisions of the daughter cells of ca are in the same plane as the first division in ca but at right angles to it, forming the typical quadrant q (Fig. 13.9 E, F). The cell m divides vertically into two cells (Fig. 13.9 E-H). Further divisions go on in various planes (Fig. 13.9 G-J).

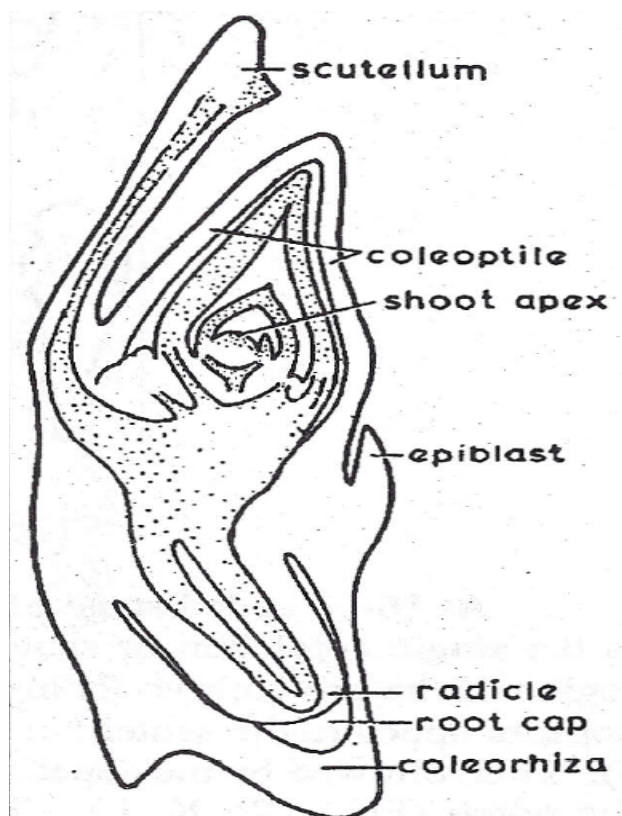


Fig. 13.10: Development of Embryo in *Triticum*

At 16-13 celled stage of the pro embryo organogenesis sets in the first organ to be initiated is the single cotyledon or scutellum. Its differentiation starts with a growth in the apical lateral region of the pro embryo. (1) involving sector q, m and n. With further development a constriction appears opposite the scutellum (in the sector ca) demarcating it from rest of the embryo (Fig. 13.9J). This followed by the appearance of the primordia of coleoptile and, then the shoot apex close to the notch (Fig. 13.26 K, L).

The radicle differentiates endogenously in the central zone of the embryo (Fig. 13.9, M). As in *Najas* in *Triticum* also the epicotyl is formed by the terminal tier (q). Its apparent lateral position in the mature embryo is a secondary feature. It arises due to active growth of the cotyledon leaving behind the epicotyl.

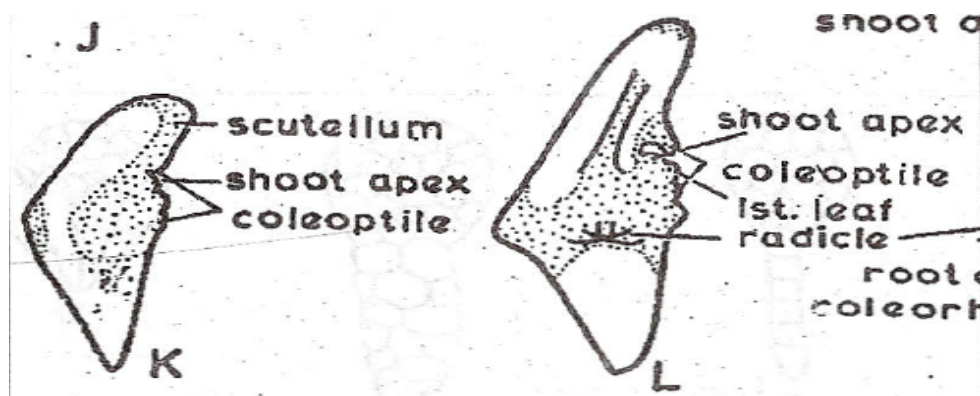


Fig. 13.11: Development of Embryo in *Triticum*

13.7. SUSPENSOR:

In most of the angiosperms, the early pro embryo is differentiated into two distinct regions namely the suspensor and the embryo. proper. The suspensor is an ephemeral structure and is present on the radicular part of the embryo. In the early stages of development, the suspensor grows much faster than the embryo and it reaches its maximum development by the globular or heart shaped stage of the embryo. Only the remnants of the suspensor may be seen in the mature seed. The early embryologists are of the opinion that the suspensor is an organ, which merely pushes the embryo proper into a nutritionally rich environment, namely the endosperm. But recent studies have indicated that the suspensor by itself takes up the nutritive function in some cases. The suspensor shows a lot of variation in its size, shape and in the number of cells.

In some taxa like *Lycopodium*, *Penaeia*, *Tilia* etc., there is no suspensor at all. A reduced suspensor is seen in *Bryonia*, *Euphorbia*, *Ruta* etc. In the plants, which produce the micropylar endosperm haustoria, the suspensor is not prominent or short lived. A long filamentous suspensor is characteristically present in *Brassicaceae* and certain taxa like *Pedicularis* of *Scrophulariaceae*. In certain families like *Crassulaceae*, *Fumariaceae*, *Rubiaceae* etc., the suspensor becomes massive and haustorial. The suspensor shows wide variation in the family *Fabaceae* from its virtual absence to a very massive structure, which may be filamentous or clustered like a bunch of grapes. In *Loranthaceae*, it is exceptionally long.

In the families *Orchidaceae*, *Podostemaceae* and *Trapaceae*, where the endosperm is absent, the embryo possesses extensively developed suspensor haustoria. A large variety of organisations is met within the *Orchidaceae*. It may be a) Single-celled enlarged to become sac-like, conical, tubular or crest-like (Fig. 13.12A) e.g. *Dendrobium*, *Cypripedium*. b) Uniseriate filament of 5-10 cells which grows beyond the micropyle, and upon reaching the placenta, penetrates it by issuing haustorial branches (Fig. 13.12B). e.g. *Satyriscum*, *Habenaria*, *Ophrys*. c) Looking like a bunch of grapes (Fig. 13.12C) e.g. *Sobralia*, *Epidendrum*. d) The suspensor's initial divides by three vertical divisions and the eight cells thus formed elongate downward to envelop more than half of the embryo (Fig. 13.12D). e.g. *Vanda*, *Lusitana*, *Cottonia*. e) The zygote divides to produce an irregular mass of 6-10 cells, some of which situated towards the micropylar end elongate and form tubular structures (Fig. 13.12E). e.g. *Eulophia*, *Cymbidium*.

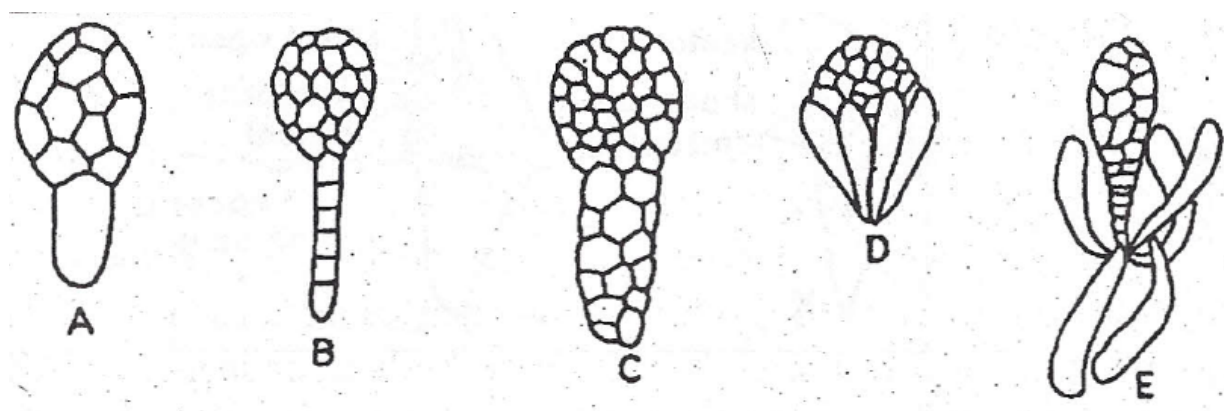


Fig.13.12: Some Suspensor Types Found in Orchids

13.8. ROLE OF SUSPENSOR:

a) Absorption of Nutrition Substances:

The suspensor plays a very important role in the nutritive of the embryo. The suspensor - cells are metabolically very active and consists of abundant cells organelles. The basal cells of the suspensor show wall labyrinths, which indicate that its main function is the absorption of nutrients from the maternal tissues.

b) Synthesis of Phytohormones:

Several growth regulators have been observed in suspensor cells. Alpi *et. al.*, (1975) extracted Gibberellic acid like substance from the cells of the suspensor and embryo Gibberellic acid concentration was found to be more in the suspensor at the heart shaped stage of the embryo. In *phaseolus*, biologically active cytokinin are found in suspensor cells.

c) Synthesis of Nutritive Substances:

Satina and Rietsema (1959) have noted the presence of oil globules in the basal cell of the pro embryo. In *Stellaria*, Proteinaceous materials were reported by Pritchard (1964). Several hydrolytic and oxidative enzymes are also found .in the suspensor cells indicating high metabolically active state.

d) Transport of Nutrients:

The presence of Plasmodesmata connections in the cell of the suspensor has indicated its role in the transport of nutrients to the embryo. Thus, the suspensor plays a very dynamic role riot only in nourishing the embryo proper at specific developmental stage, but also in, exercising control on its growth by supplying several important phyto hormones.

13.9. NUTRITION OF EMBRYO:

During the earlier stages of development, the embryo receives nourishment from the surrounding cells of the embryo sac, namely nucellus and integuments. The disappearance of plasmodesmata connections during fertilization -causes breaking up of the nutrient flow from the material tissue to the embryo. Sometimes the plasmodesmata reappear at the heart shapes stages of the embryo and assist in the, absorption of food from the cells of endosperm. After fertilization, the suspensor also pushes the embryo deep into the endosperm in order to enable to. embryo in a nutritionally favourable condition.

The nutrition of the embryo can be understood in two different ways:

- By examining the different structures that are associated with the nutrition of the embryo in nature and their chemical analysis (*in vitro* studies)
- By culturing the excised embryos at various stages of its development so as to understand its nutritional requirements (*in vitro* studies).

13.10. MODEL QUESTIONS:

- 1) Embryogeny in Dicotyledonous
- 2) Grass embryo
- 3) Role of suspensor

13.11. REFERENCE BOOKS:

- 1) The Embryology of Angiosperms; S.S; Bhojwani, S.P. Bhatnagar, Vikas Publishing House Pvt. Ltd., 2000.
- 2) Textbook. of Embryology of Angiosperms, T. Pullaiah, K. Lakshmi Narayana and Hanumantha Rao.

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LESSON-14

SEED STRUCTURE AND ANATOMY OF SEED FORMATION

14.0 OBJECTIVE:

- To gain the knowledge of seed anatomy and development of the seed from fertilized ovule.

STRUCTURE:

- 14.1 Introduction
- 14.2 Variation of The Seed
- 14.3 Seed Development
- 14.4 Post-Fertilization Changes
- 14.5 Functions of Seed Coat
- 14.6 Classification of Seeds
- 14.7 Importance of Seeds
- 14.8 Summary
- 14.9 Model Questions
- 14.10 Reference Books

14.1. INTRODUCTION:

A true seed is defined as a fertilized mature ovule that possesses an embryonic plant, stored material (sometimes absent) and a protective coat or coats (Kozlowski and Gunn, 1972). However, in popular sense the term seed is also applied to single-seeded dry fruits (caryopsis of cereals, capsella of composites, etc.,) and negative propagules (bulbils, pieces of potato tubers, etc.)

After fertilization growth sets in various parts of the ovule resulting into a seed. The zygote grows into an embryo; the primary endosperm nucleus gives rise to the endosperm; and the integuments from the protective coats. Thus, a seed has a basic structure of an ovule with some parts lost and some new ones developed. It is seldom that all the ovules in an ovary mature into for example, the cherry and almond there are two ovules per ovary but, regularly, only one matures into seed. Occasionally, however, both may develop.

14.2. VARIATION OF THE SEED:

There are innumerable variations in the seed size, shape, colour and surface. The seeds range in size from tiny dust particles, as found in some orchids, to large double coconuts (*Lodoicea maldivica*). Fresh weight of an orchid seed may be 20.33 .ug, and that of a double coconut about 6 kilograms. The seed surface may be smooth, wrinkled, striate, ribbed, furrowed, reticulate, tuberculate, alveolate, hairy, pulpy or having patterns like finger prints. In certain plants the seeds are so characteristic that they help identifying species or variety.

Pea has been chosen to describe the parts of a seed. In a mature pod of pea there are a number of seeds arranged 'in two rows. (Fig. 14.1 A, B). The seeds are attached to the fruit wall by a small stalk, the funiculus (Fig. 14.1B). At maturity the funiculus abscises leaving a scar, called hilum (Fig. 14.1 C). Slightly below the hilum is located a small pore, the micropyle. The seed has a smooth and papery seed-coat. In some plants such as *Casterbean*, the seed-coat shows to distinct layers (a) the outer one, called testa, and (b) the inner one, called tegmen. In pea these layers cannot distinguished clearly. Upon removing the seed-coat, two green and massive cotyledons are seen (Fig. 14.1 D). They are attached laterally to the embryonal axis. A portion of the embryonal axis projects beyond the cotyledons, the pointed end of which is the embryonic root (radicle). The other end of the axis, which is embryonic shoot (plumule), is seen only after separating to the cotyledons (Fig. 14.1 E). The portion of the axis between the radicle and the point of attachment of the cotyledons to the axis is called hypocotyl, and the portion between the plumule and the cotyledons: is known as epicotyl.

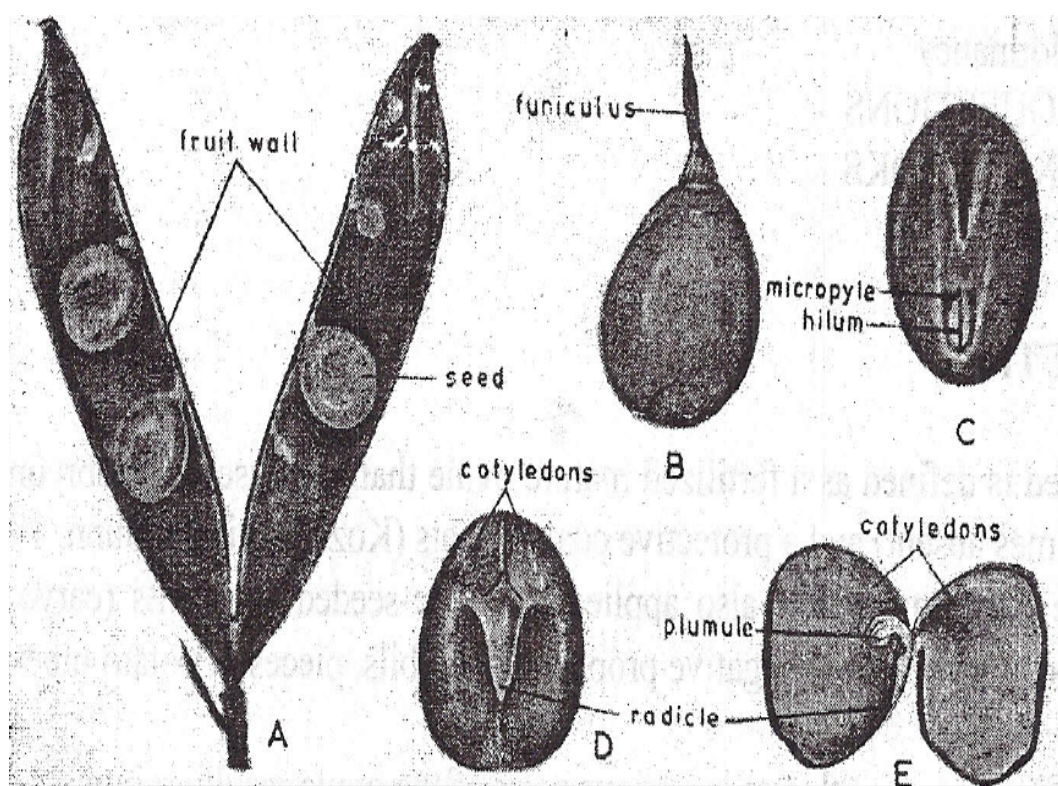


Fig. 14.1: Parts of a pea seed. A. Opened fruit, bearing three well developed seeds. Some abortive seeds are also seen. B. A seed detached from the fruit wall along with the funiculus. C. The seed after removing the funiculus, to show the micropyle and the hilum. D. Decorated seed; note the two massive cotyledons and the radicular end of the embryonal axis projecting beyond them. E. The cotyledons separated apart to expose the plumular end of the embryonal axis.

In pea the cotyledons themselves function as the storage organs. This is also true of many other plants such as the cucurbits and beans. However, there is another group of plants where the cotyledons are thin, and the reserve food is stored in the persistent endosperm. Castor bean (*Ricinus communis*) and coconut (*Cocos nucifera*) may be cited as examples of the latter type of seeds.

14.3. SEED DEVELOPMENT:

The main parts of seed are embryo, endosperm (if present), and seed coat.

14.3.1. Seed Coat:

As the ovule develops into seed, the integuments mature into seed-coats. With very few exceptions, the ovule has either two integuments or just one. During the transformation into seedcoats the integuments undergo significant histological changes. In bitegmic ovules the seed-coat may be derived from both the integuments, or the inner integument may be lost, and the seed-coat is formed by the outer integument alone.

In *Cotton* (*Gossypium* spp.) the ovule has two integuments (bitegmic) and both contribute to the formation of seed-coat. At the mature embryo sac the outer integument consists of 1-6 layers of thin-walled cells (Fig. 14.2 B). Six days after pollination it can be distinguished into three zones. (Fig. 14.2 D). (a) Outer epidermis. (b) Outer pigmented zone of 2-5 layers with some tannin and starch filled cells, and (c) inner epidermis. As the seed matures, the cells undergo considerable enlargement. The inner epidermis either remains single-layered. (*G. arboreum*) or divides to form 2- or 3-layers (*G. hirsutum*, *G. herbaceum*). Abundant compound starch grains accumulate in the cells of these layers which constitute the outer colourless zone (Fig. 14.2 F). The cells of the outer epidermis get filled with tannin. The inner integument at the mature embryo sac stage, is 8 to 15 layers (Fig. 14.2 B)

For three days after Pollination there is no, significant change except for slight elongation of, the cells and deposition of starch grains in 3 or 4 layers next to the Outer epidermis (C). In the next two or three days the cells of the outer epidermis start elongating radially, and within twenty days after pollination they enlarge many times their original size (Fig. 14.2 E). They become thick-walled, and their nuclei and cytoplasm become restricted, to their outer end (Fig. 14.2 F). This forms the palisade layer of the mature seed-coat, Cells of the inner epidermis also show slight radial elongation, they develop plate like thickenings on their walls, and form the finger layer (Fig. 14.2 F). In mature seedcoat the inner, Integument is distinguished into four zones, (a) Outer palisade layer (b) inner pigmented zone of 4 or 5 layers. (c) inner colourless zone of 9 or 10 layers and (d) Fringe layer. Thus, the mature seed-coat comprises 7 distinct zones.

The cotton fibers of commerce are formed by the outer epidermis of the outer integument. These hairs are single-celled and thin-walled, and attain a length of up to 45 mm. These fibers also show the characteristic twists and are called lint hairs (Fig 14.2 G). Intermingled with lint hairs are some fuzz hairs. The maximum length attained by the latter is 10mm. They are thick-walled with a narrow lumen and lack the twists (Fig. 14.2 H).

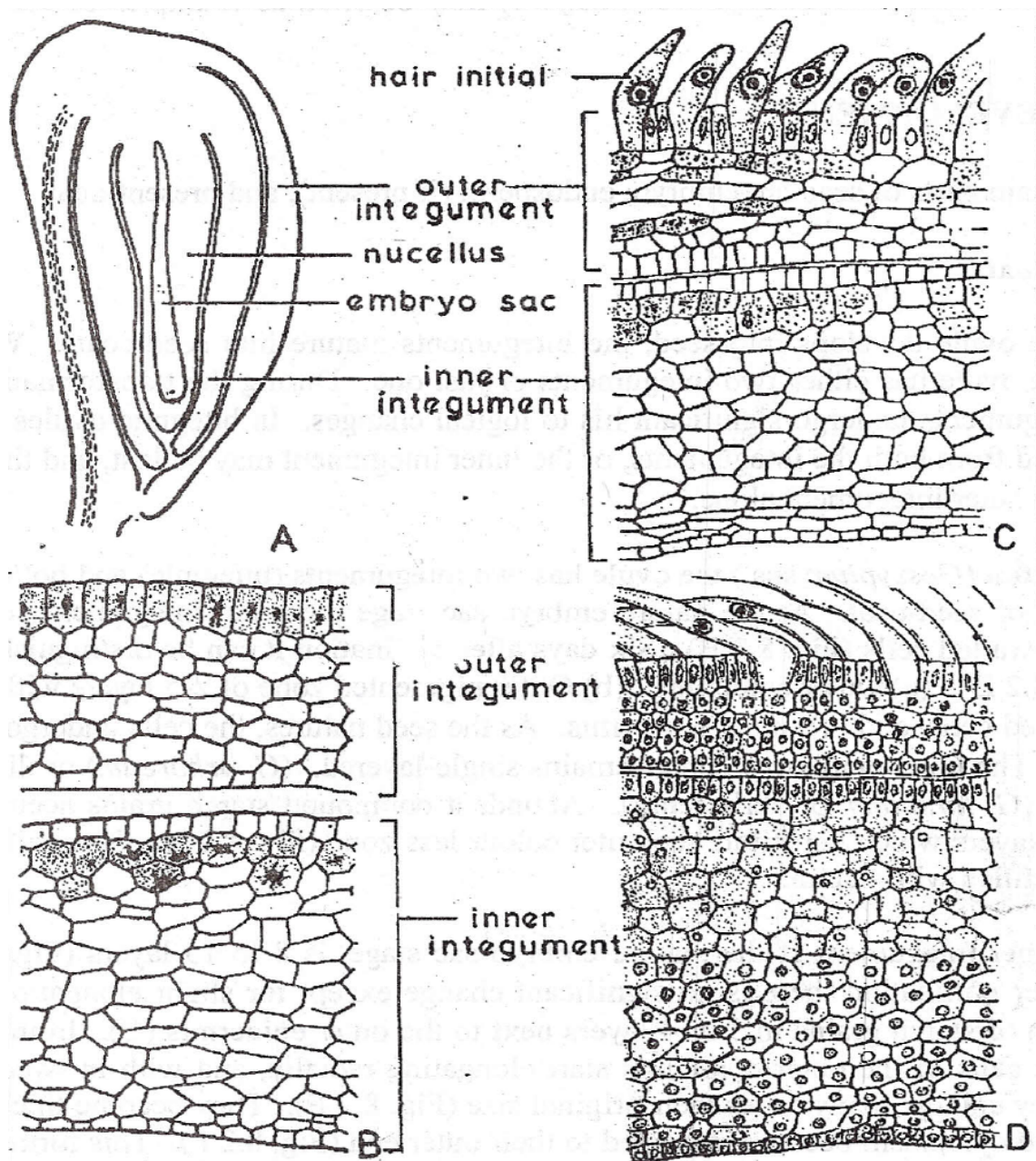


Fig. 14.2: Seed coat development in *Gossypium herbaceum*. A. L. S of ovule at the mature embryo sac stage. B. Portions of the outer and inner integuments enlarged from A to show their cellular details. C, D. Portion of integuments from ovules 2-3 and 5-6 days after pollination, respectively.

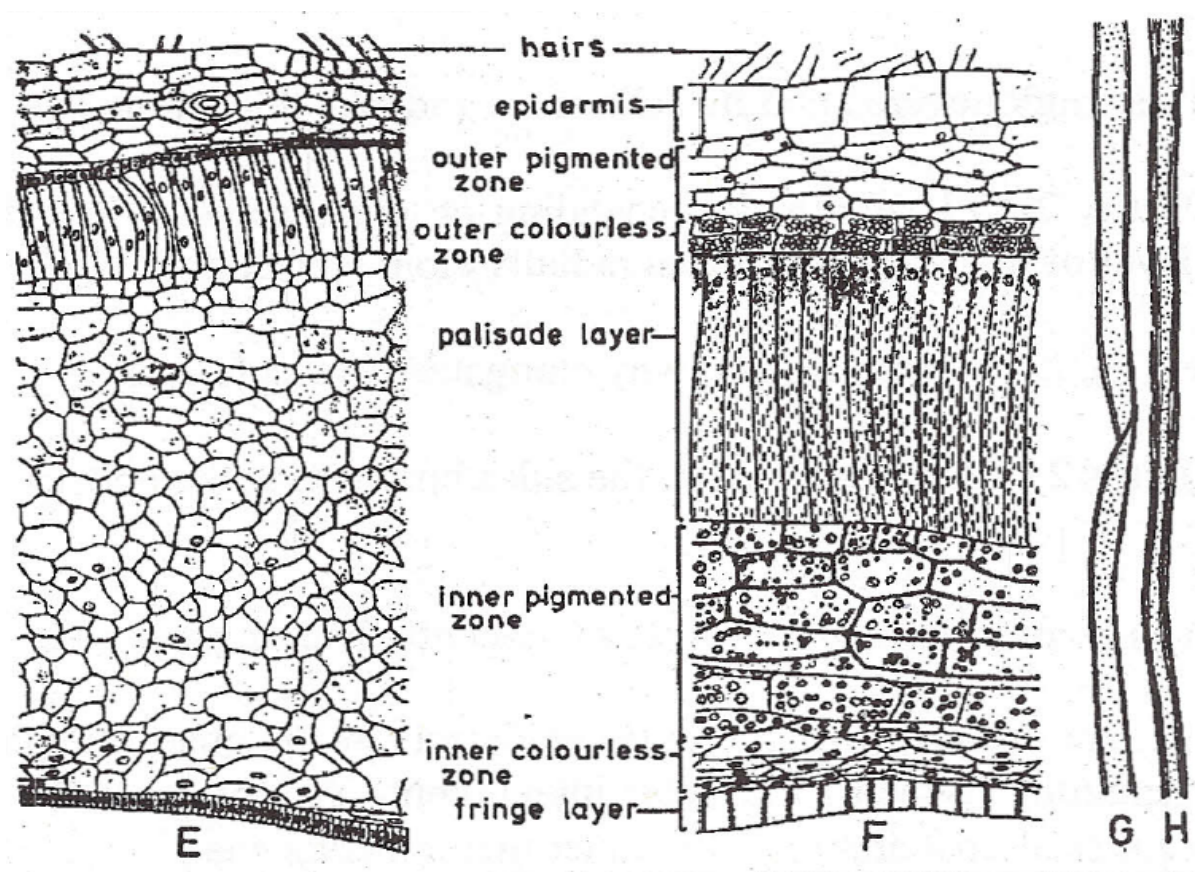


Fig. 14.3: (contd.) Seed-coat development in *Gossypium herbaceum*. E. Portion of integuments from an ovule 15 days after pollination. F. Portion of the mature seed-coat, G. A lint hair, H. A fuzz hair.

In the Cucurbitaceae, the ovules are bitegmic but the outer integuments alone form the seed-coat. (Fig. 14.3 A, B). The inner integument degenerates. Seed-coat development in some species of *Luffa* has been described by Singh (1971). In an unfertilized ovule, at the mature embryo sac stage, the outer integuments are 10-15 layers thick and the inner integuments is only 3 layered. The mature seed-coat is differentiated into five zones in the following sequence, from outside inward. (Fig. B).

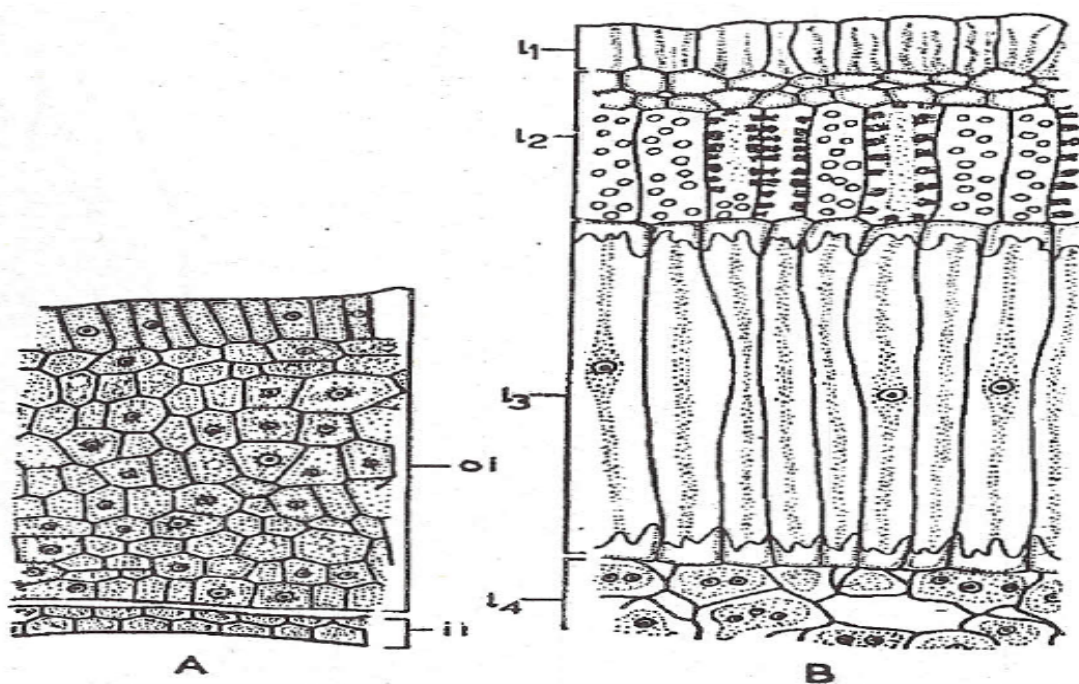


Fig. 14.3: Seed-coat development in *Luffa*. *ii*, inner integument; *oi*, outer integument; *l1* epidermis; *h*, hypodermis; *l1* sclerenchymatous layer; *l4*, aerenchyma) A Portion of L.S of integuments before fertilization in *L. hermaphrodita*. B. Portion of L.S of mature seed-coat in *L. graveolens*; chlorenchymatous zone is not drawn.

- 1) Epidermis (*l1*), it is single-layered and its cells show rod-like thickenings on radial walls.
- 2) Hypodermis (*h*), it is 2-10 layers thick, depending on the species of the cells are thick-walled.

The inner most layer of this zone comprises radially elongated-cells. Mechanical layer (*h*), it consists of many elongated osteosclerides, Aerenchyma (*l4*), it is 2 or 3 layers thick on the sides but more at the ends and the margins of the

The layers *l1*-*h* are derived from the outer epidermis of the outer integument and the layers *l4* and *l5* from the remaining tissue of the outer integument in dry seeds the layers *l4* and *l5* get detached from the main seed-coat and form the inner membranous coat.

In the Acanthaceae, the ovules are unitegmic. A large portion of the integuments is consumed by the developing endosperm, and only the epidermis persists in mature seed. In *Andrographis*, *Elytraria* and *Haplanthus*, the integument is completely digested so that the mature seed is devoid of seed-coat. The Loranthaceous parasites also have naked-seeds because integuments are altogether absent in these plants. In orchids the seed-co. forms a transparent sheath of thin-walled cells. (Fig. 14.4).

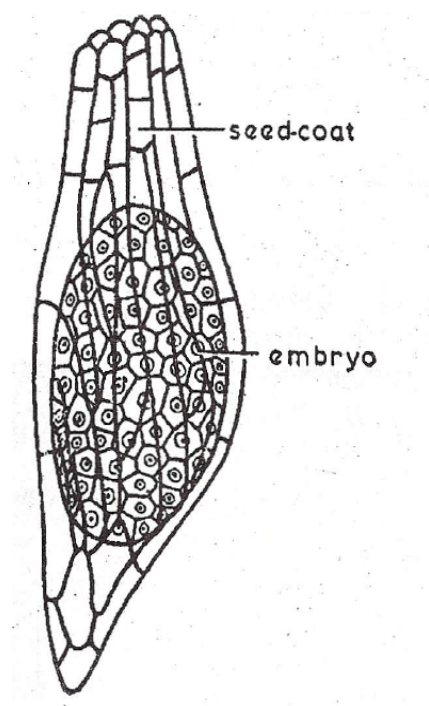


Fig. 14.4: A seed of *Cypripedium*; the embryo can be seen through the transparent seed-coat

In *Magnolia*, the inner integument forms the protective layer and the outer integument becomes fleshy and brightly coloured cells called sarcotesta, the cells are rich in fats. It functions as an attractant for the seed-dispersing agents. In *plantago*, the epidermis of seed-coat is hygroscopic and becomes mucilaginous upon coming in contact with water.

14.4. POST -FERTILIZATION CHANGES:

During post-fertilization changes development many special structures arise from various parts of the ovule. Some of these described below:

- 1) **Caruncle:** This is a fleshy, whitish structure present on the micropylar end of the seed. It arises due to the proliferation of cells at the tip of the outer integument, on the side of the funiculus or all-round the micropyle. It is common the Euphorbiaceae. At least two functions have been ascribed to caruncle (a) being sugary it is eaten by ants, which helps in seed dispersal, and (b) by virtue of being hygroscopic it absorbs water from the soil and passes it on to the embryo during germination.
- 2) **Operculum:** While the caruncle arises by the activity of the outer integument's operculum is formed by the proliferation of inner integument at its tip. In the Lemnaceae, at the mature embryo sac stage the inner integuments is two-layered except at the micropylar region where it becomes 3-layered due to divisions in the cells of the inner epidermis. After fertilization the cells in this region undergo remarkable expansion and organise a unique, dome shaped, stoppers-like structure, called operculum (Fig. 14.5). Cells in the operculum become thick-walled and contained a bright orange coloured substance of unknown nature.

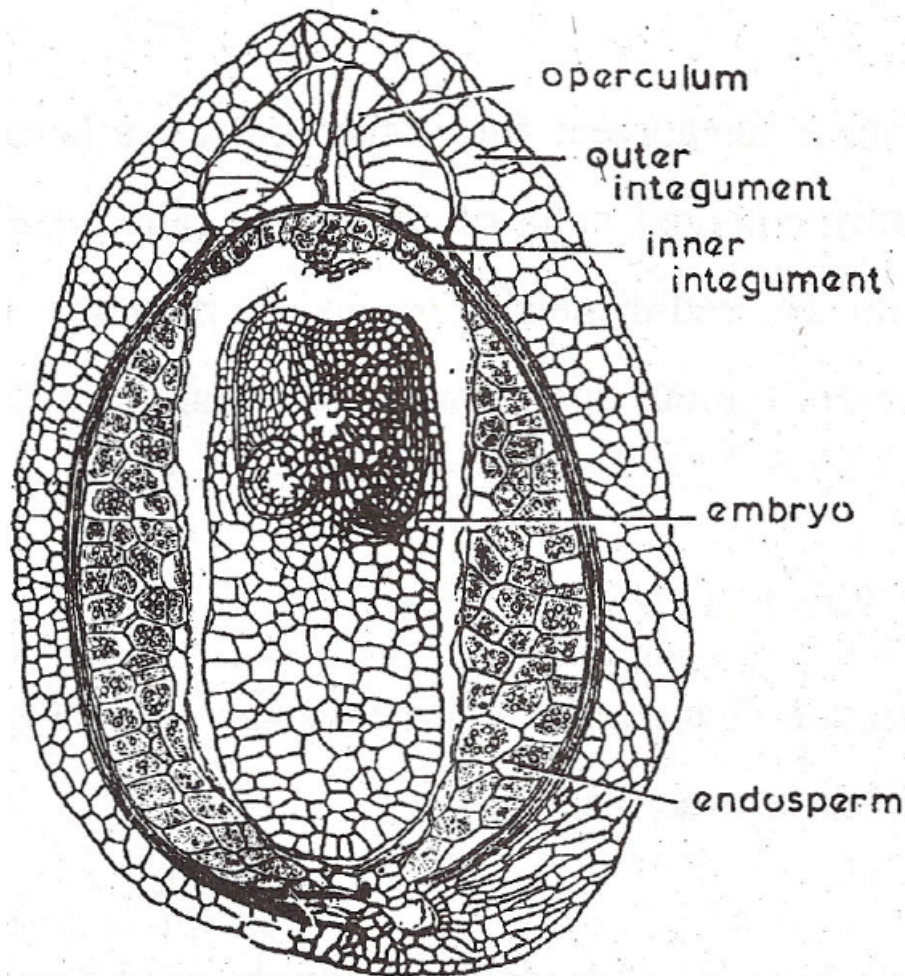


Fig. 14.14: Mature Seed of *Lemna Paucicostata* in Longisection

A prominent operculum is present at the micropylar end.

- 3) **Aril:** It arises from the funiculus and surrounds the ovule completely in postfertilization stage. Aril is regarded as the third integument. The edible part of *Litchi* fruit is aril. In *Passifloraceae*, the aril is thin-walled and contains oil, starch, and yellow-red pigment. In *Crossosoma californicum*, a fimbriate aril surrounds the seed on the sides (Fig. 14.6).

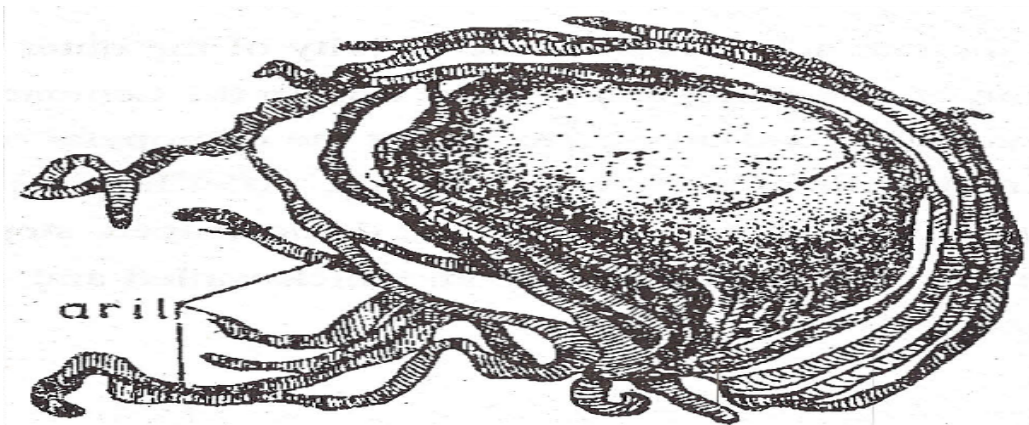


Fig. 14.6: Mature seed of *Crossosoma Californicum* Surrounded by Fimbriate Aril

14.5. FUNCTIONS OF SEED COAT:

At least two functions of seed-coat are distinct.

- 1) It protects the embryo and the endosperm (if present) from desiccation, mechanical injury unfavourable temperatures, and attacks by bacteria, fungi and insects.
- 2) It helps in the dispersal of seeds by acquiring special features, such as wings (Oroxylon) fleshy and brightly coloured tissue (Magnolia), hairs (Cotton), and air-filled cavities (*Enalus acoroides*).

Labyrinth seeds! The seeds that show ail irregular internal structure when cut in any plane are called labyrinth seeds (Van Heel, 1970). It may be due to the rumination of the endosperm (Annonaceae, Palmae, Myristicaceae), or lobing and folding of the cotyledons. However, the Labyrith appearance is most pronounced if the lobing of the cotyledons. Occurs is combination with intrusion of the seed-coat between the folds and lobes (Kingiodendron, Erycibe, Fig. 14.7).

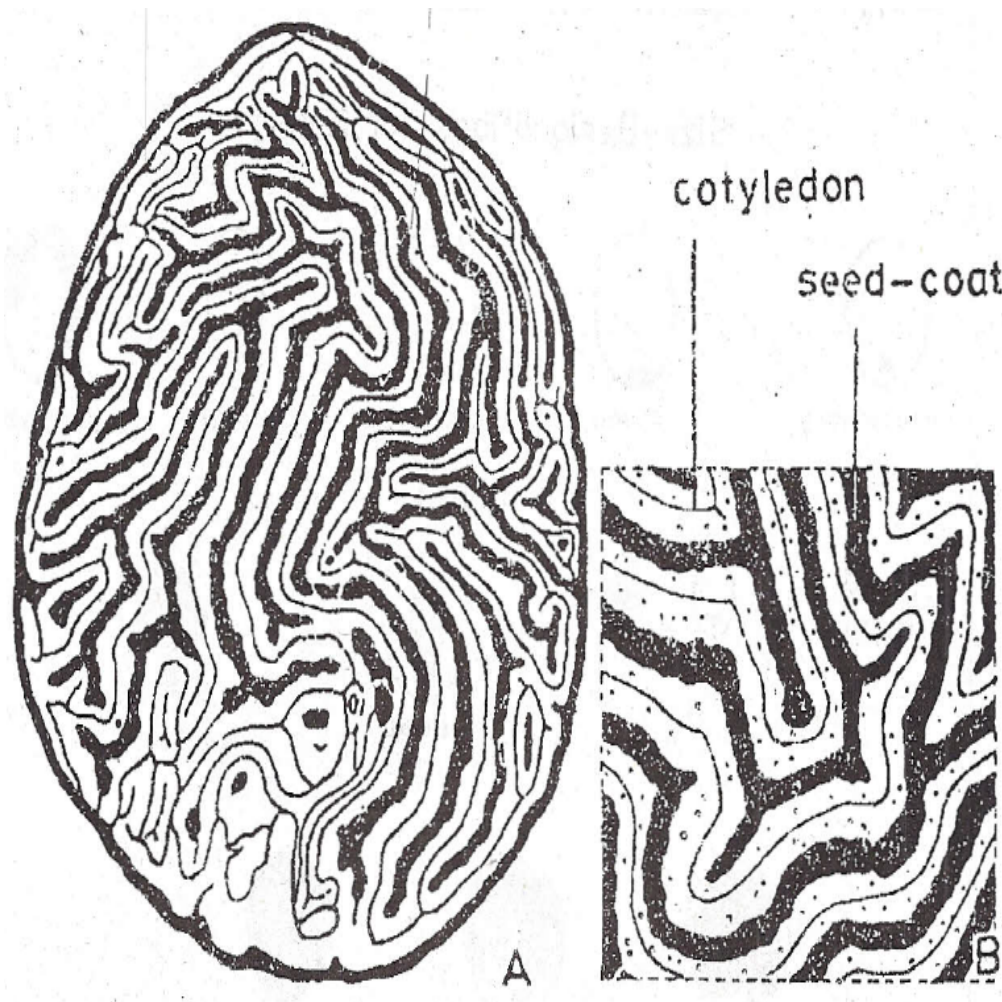


Fig. 14.7: A. Seed of *Kingiodendron pinnatutn* cut lengthwise, in median plane. B. A portion from A enlarged to show the intricate growth pattern of the seed-coat into the folds of the cotyledons.

14.6. CLASSIFICATION OF SEEDS:

Commonly, mature seeds are classified into two groups depending on the presence or absence of endosperm.

- 1) Albuminous or endospermous; where endosperm is present, as in mustard and castor bean.
- 2) Ex-albuminous or non-endospermous where endosperm is absent, as in beans and cucurbits.

Martha studied the internal morphology of seeds belonging to about 1287 genera of angiosperms, and proposed a classification of seeds (Martin, 1946) on the basis of (a) size of the embryo in relation to the endosperm, and (b) differences in the size, shape, and position of embryo in the seed.

With respect to embryo-endosperm ratio Martin has given five size-designations represented volumetrically in quarter units. Depending upon the size, shape, and position of embryo in the seed, it has been described as peripheral or axile. These are further sub divided into 12 types of which rudiment~ type has been considered an exception (Fig. 14.8).

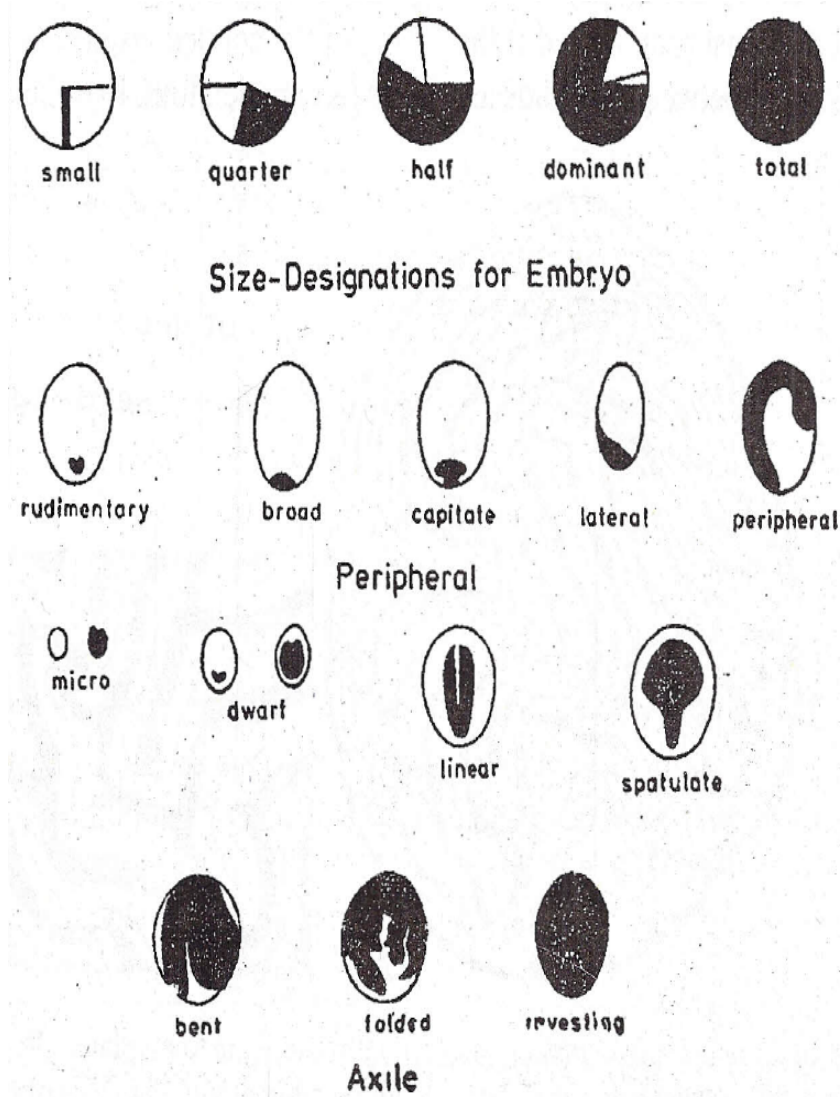


Fig. 14.8: Classification of seeds

14.7. IMPORTANCE OF SEEDS:

Seeds are probably more valuable than any other part of the plant for man as well as for the plant itself. Seeds are produced by plants to ensure the perpetuation of their types and for the spread of the species to newer areas. For most of the annual's seeds are the only means of multiplication and their continued existence. These plants live for a few months; the remaining part of the year being unfavourable for their survival they die and disappear. Before dying they produce numerous seeds each provided with a sufficient quantity of reserve food and protective covering around them. The seeds can remain dormant for years and produce individuals on the return of favourable conditions. The weeds which appear every year along with the crop plants are the sprouted seeds which scattered in the soil by the plants of the preceding season.

Cereals contribute the major part of human diet. It is because of the high food value of their seeds. They contain carbohydrates, proteins, minerals, vitamins, and little of fat stored in the endosperm. The greater part of the seed is endosperm. Another advantage with cereals is that the grain is compact and dry and therefore, can be stored for long periods without deterioration.

Seeds are also the source of several other items of human use, such as fibres, oils, beverages etc. Edible oils are obtained from the seeds of groundnut, coconut, mustard and cotton. Tung oil, obtained from the seeds of *Aleurites fordii* is a powerful drying agent and used in paints and varnishes. It has water-proofing and preservative qualities. **Seeds** of cardamom and mustard, and branched aril of nutmeg are common spices.

The cotton fibre, which is derived from the seed-coat of *Gossypium* species has been in use for more than the fibre of any other plant. Before the introduction of synthetic fibres cotton was the chief clothing material. Even today it is widely used, especially for summer clothing because of its water absorbing capacity.

14.8. SUMMARY:

A seed is a mature, fertilized ovule containing a protective seed coat, an embryo (miniature plant with root/shoot), and food storage (endosperm or cotyledons), formed after double fertilization in flowering plants; this structure ensures protection, nourishment, and propagation, with the embryo developing from the zygote and the coat from ovule integuments. Seed formation involves the ovule maturing into a seed, with the embryo's radicle emerging first during germination to form roots, triggered by water absorption through the micropyle. Seed Structure: Seed Coat (Testa/Tegmen): Tough outer layer protecting against injury, dehydration, and pests. Embryo: The baby plant, consisting of: Radicle: Embryonic root, grows downwards. Plumule: Embryonic shoot (stem and leaves). Hypocotyl: Connects radicle and plumule. Cotyledons: Seed leaves, store food (in non-endospermic seeds) or absorb nutrients. Endosperm: Nutritive tissue (triploid) for the embryo (e.g., maize). Cotyledons: Fleshy, store food (e.g., beans).

14.9. MODEL QUESTIONS:

- 1) Seed Development
- 2) Describe the Mature seed

14.10. REFERENCE BOOKS:

- 1) The Embryology of Angiosperms, S.S. Bhojwani, S.P. Bhatnagar -1971.
- 2) The Embryology of Angiosperms, S.S. Bhojwani, S.P. Bhatnagar - 2000. Vikas Publishing House Pvt. Ltd.
- 3) J. Text book of Embryology of Angiosperm, T. Puliaiah, K.Lakshmanan.

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LESSON-15

SEED DORMANCY AND BARRIERS EFFECT SEED DORMANCY

15.0 OBJECTIVE:

- To gain Knowledge on Seed Dormancy and Barriers Effect Seed Dormancy.

STRUCTURE:

15.1. Introduction

15.2. Seed Coat Dormancy

15.3. Embryo Dormancy

15.4. Barrier Effects of Seed Dormancy

15.4.1 Water Impermeability

15.4.2. Gas Impermeability

15.4.3. Mechanical Resistance

15.4.4. Rudimentary Embryo

15.4.5. Cellular Membranes

15.5. Summary

15.6. Model Questions

15.7. Reference Books

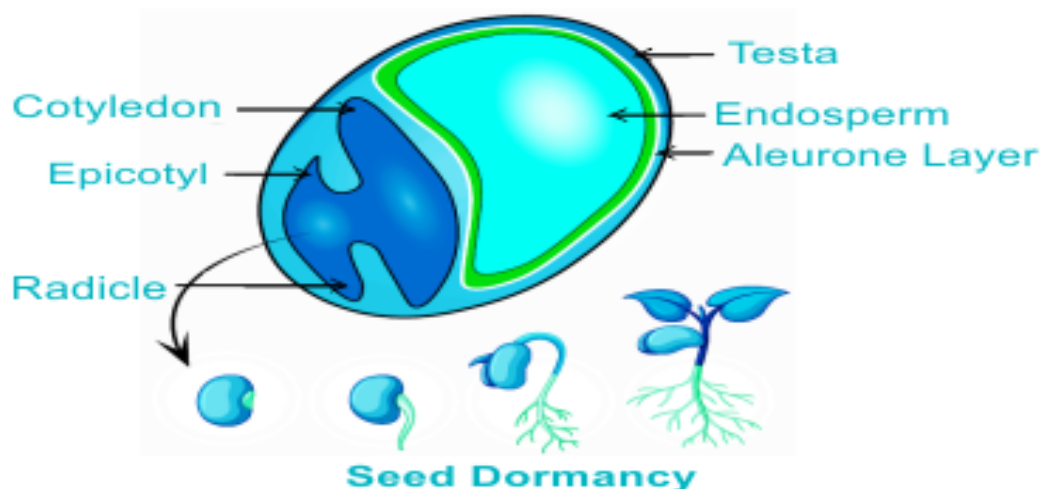
15.1. INTRODUCTION:

Plants, such as Rhizophora, the growth from zygote to embryo, and to seedling is almost continuous, the germinate while they are still enclosed with in the fruit attached to the parent plant. This phenomenon is of rare occurrence and is known as vivipary.

The seeds of many species (*Phascolus*, *Psium*, *Zeamays*) would germinate immediately after falling from the plant if favourable conditions of moisture, temperature and aeration are available. There are some other plants whose seeds fail to germinate, even under ideal conditions for germination, for some time after falling from the parent plant. This period, which varies from species to species, is called dormancy period. Seed dormancy is of considerable advantage to the plant. It enables the embryo to safely pass the unfavourable part of the year and germinate when the conditions are suitable for the establishment of seedling. In nature, dormancy coincides with the unfavourable period for the seedlings of the species.

Seed Dormancy is mainly two types namely:

- 1) Seed-coat dormancy, and
- 2) Embryo dormancy.



15.2. SEED COAT DORMANCY:

In many plants the cause of dormancy is the presence of hard seed-coat, which may offer mechanical resistance to embryo growth (Malvaceae, Leguminosae) or it may be impermeable to water (Melilotus, Trigonella) or oxygen (Xanthium). In nature such seeds are rendered germinable by the weakening or breaking-down of the seed-coat by microbial attacks, mechanical abrasions, passage through the digestive tract of animals, or exposure to alternating low and high temperatures. Some of the treatments used to break seed-coat dormancy artificially are (a) Scarification, which means scratching the seeds with abrasives (e.g. *Cassia*, *Melilotus*). (b) soaking the seeds in concentrated sulphuric acid for 15-16 minutes (e.g. *Cercocarpus*, *Gossypium*, *Pistacia*) and (c) washing the seeds with alcohol (e.g. *Cassia Parkinsonia*).

15.3. EMBRYO DORMANCY:

The most common type of seed dormancy is -one in which the embryo requires certain period after harvesting to be able to germinate. During this period, which is called after ripening period, the embryo may undergo structural maturation or physiological maturation.

At shedding, the seeds in some members of the Ranunculaceae contain an undifferentiated embryo. During the after-ripening period the embryo undergoes further development and acquires mature structure. In *Fraxinus excelsior*, a seed when shed contains a fully differentiated embryo -but it undergoes considerable enlargement before germination.

In the rosaceous plants, the embryo 'does not show any visible morphological or histological change during the after-ripening period. It is assumed that these seeds undergo physiological maturation during the dormancy period. The physiological changes may include the disappearance of growth inhibitions, appearance of growth promoters etc.

15.4. BARRIER EFFECTS OF SEED DORMANCY:

The degree of dormancy of seeds has been associated with hard seed coat. The barrier effect of seed coats can be due to physical and chemical characteristics of the seed coats as well as due to permeability changes to water, gases and solutes.

There are examples of seeds which have remained dormant for a few days to thousands of years without the loss of viability, i.e., ability of germination.

15.4.1. Water Impermeability:

Presence of hard and impervious seed coat is no doubt an important aspect of dormancy because less water is available for germination under this condition. Removal of the seed coat or weakening of the seed coat by various means leads to dormancy release. One mechanical method is scarification in which the seed coat is cracked to permit entry of water.

Under natural conditions in the soil, fungi and bacteria infecting the seeds hydrolyze the seed coat components and thereby soften them so that water can penetrate into the embryo. The testas can be made permeable by treatment for short periods with concentrated sulphuric acid.

15.4.2. Gas Impermeability:

Impermeability of seed coats to gases, such as oxygen and carbon dioxide is another characteristic of certain seeds showing dormancy.

Hard seed coat is likely to impose restriction of oxygen supply to the embryo, thereby impairing aerobic respiration. Respiration also involves the release of CO₂ from the embryo which cannot cross the permeability barrier imposed by the coat and the CO₂ thus accumulated would further inhibit germination.

Either removal or puncturing of the covering structures which facilitates diffusion of gases is most effective in removing dormancy. It is postulated that dormancy is related to the presence of phenol oxidase in the covering tissues and oxygen which is preferentially consumed by the enzyme there becomes less available to the embryo.

15.4.3. Mechanical Resistance:

Seed coats may also act as physical barriers, thereby restricting the expansion of the embryo. In such cases, a balance between the expansive force of the embryo and strength of the coats determine dormancy release. The balance may be modified by various seed treatments like light, hormones and oxygen. Mechanical scarification which weakens the seed coat will permit embryo growth.

15.4.4. Rudimentary Embryos:

Many species of plants have seeds in which the embryo does not develop as rapidly as the surrounding tissue so that when the seeds are shed, the embryo is still imperfectly developed.

In some other species, embryos have grown little beyond the egg stage. Germination of such seeds is usually delayed until the development of the immature embryo is complete. Seeds showing this type of dormancy include *Ficaria verna*, *Caltha palustris* and *Anemone nemorosa*.

The embryos of *Fraxinus excelsior* are morphologically developed but undergo considerable growth after shedding. A suitable after-ripening period during which the embryo completes its development is necessary for breaking dormancy of such seeds.

15.4.5. Cellular Membranes:

Some other factors have been recognized with seed coats and cellular membranes with respect to differential permeability of solutes along with the differential exchanges of anions and cations. Fusicoccin, a diterpene glucoside, produced by *Fusicoccum amygdale* has been shown to release dormancy in a number of seeds.

It has been interpreted that fusicoccin activates at the cell-membrane level an energy-dependent proton extrusion mechanism which is subject to hormonal regulation.

According to Marre, the effects of well-known plant hormones like auxin, gibberellin and cytokinin on the dormancy release process is mediated by the same mechanisms involved in fusicoccin action. Marre et al., proposed a model to explain the action of fusicoccin and plant hormones in removing some kind of factors impeding cell elongation.

15.5. SUMMARY:

Anatomical reasons for seed dormancy involve physical barriers like hard, impermeable seed coats blocking water/gas, or the seed coat offering mechanical resistance to embryo expansion, preventing germination. Other key anatomical factors include an immature embryo needing time to develop or the presence of inhibitory chemicals (like ABA) within seed tissues (coat, endosperm) that must break down, often aided by decay or specific triggers.

Physical/Structural Causes

Impermeable Seed Coat: The coat prevents water uptake (imbibition) and gas exchange (oxygen/CO₂), essential for respiration, as seen in legumes. **Mechanically Resistant Seed Coat:** A tough outer layer physically restricts the radicle (embryonic root) from pushing through, common in weeds.

Internal/Tissue-Based Causes

Embryo Immaturity (Morphological Dormancy): The embryo is underdeveloped at dispersal and needs more time/conditions (like after-ripening) to complete its growth within the seed.

Germination Inhibitors: Chemicals like abscisic acid (ABA), phenolic compounds, or coumarins are present in the seed coat or endosperm, preventing germination until degraded or leached out. **Endosperm/Embryo Interaction:** In some seeds, the endosperm (food storage) may hinder embryo growth until it decays or specific enzymes break it down.

15.6. MODEL QUESTIONS:

- 1) Explain types of seed dormancy
- 2) Describe the Barriers that effect seed Dormancy

15.7. REFERENCE BOOKS:

- 1) The Embryology of Angiosperms. Bhojwani, S.P. Bhatnagar -1975.
- 2) The Embryology of Angiosperms, S.S. Bhojwani, S.P. Bhatnagar - 2000. Vikas Publishing House Pvt. Ltd.
- 3) Text book of Angiosperm, T. Pullaiah, K. Lakshmanan.

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LESSON-16

APPLICATIONS OF ANATOMY

16.0. OBJECTIVE:

- To understand the anatomical characteristics that help in various applied branches of science.

STRUCTURE:

16.1. Introduction

16.2. Enables to Identify Fragmentary Plant Material

16.3. Enables to Detect Adulterants in Crude Drugs

16.4. Enables to Identify Wood

16.5. Enables to Identify Archaeological Plant Remains

16.6. Applied Aspects of Meristem Culture

16.7. Provides Evidences in Forensic Investigation

16.8. Provides Characters of Taxonomic Significance

16.9. Summary

16.10. Model Questions

16.11. Reference Books

16.1. INTRODUCTION:

Applications of plant anatomy are: 1. Enables to Identify Fragmentary Plant Materials 2. Enables to Detect Adulterants in Crude Drugs 3. Enables to Identify Wood 4. Enables to Identify Archaeological Plant Remains 5. Applied Aspects of Meristem Culture 6. Provides Evidences in Forensic Investigation 7. Provides Characters of Taxonomic Significance.

16.2. ENABLES TO IDENTIFY FRAGMENTARY PLANT MATERIALS:

Since the time of Linnaeus flowers and fruits provided the characters of identification. Sometimes situation arises where these characters are not available.

Example:

Fragments of herbarium specimens, leaf, dried and powdered medicinal plants etc. The prerequisite of any botanical research is the proper identification of the specimen.

Anyone dealing with plants for food, furniture, building materials, medicine etc. the plant breeders, geneticists and cytologists must have proper identifying characters of their source materials. These characters will identify parallel specimens, if required. They will be in a position to verify whether the parallel specimen is from the same species of the source material.

The characters that differentiate a species from other species are considered as of taxonomic significance. Apart from vegetative and reproductive organs plant anatomy provides characters that are of taxonomic significance.

Trichome anatomy, wood and leaf anatomy, leaf epidermis and cuticle etc. provide valuable characters in differentiation between species. As for example the different species of *Rhododendron* and *Ficus* can be differentiated by means of trichome characters.

16.3. ENABLES TO DETECT ADULTERANTS IN CRUDE DRUGS:

The medicinal plants provide the crude drug. Drug can be obtained from all parts of a plant (ex. *Swertia chirata*), leaves (ex. *Adhatoda vasica*, *Andrographis paniculata* etc.), roots (*Cephaelis ipecacuanha*), rhizome (ex. *Zingiber officinale*, *Rauwolfia serpentina* etc.), or bark (*Alstonia scholaris*). The crude drugs are imported in dry form and in some cases in dry powdered form.

In this condition it becomes difficult to identify the materials by macroscopic appearance only. For this reason, the microscopical along with morphological characters of drug materials are studied. They are described and published in pharmacopoeia. The pharmacopoeias may be of official publications.

Example:

European Pharmacopoeia, British Pharmacopoeia, British Pharmaceutical Codex, United States Dispensatory, Indian Pharmacopoeia, the Indian Pharmaceutical Codex etc.

A very brief and to the point description of drug material are given in the pharmacopoeias. The characters that will identify the drug specifically are mentioned only. Proper authentication of crude drug material is a prerequisite for importers. They must be sure about the quality, purity and if adulterated, the nature of the adulterants of materials.

Samples to be imported are studied morphologically and anatomically. Their authenticity is established by comparing with the descriptions published in pharmacopoeias. A crude drug may also be identified from its chemistry.

But the identification with the study of microscopical examination is much easier and quicker than that of chemical analysis. Mention may be made of a few drug plants with their uses and adulterants that can be detected microscopically.

Swertia chirata (Family: *Gentianaceae*), commonly known as chirata is an indigenous drug of India. It is used as stomachic bitter tonic, anthelmintic and in skin diseases. The root is used as a substitute of *Centiana lutea*, which is used as gastrointestinal tonic, because the root of chirata does not constipate the bowels. The most common adulterant is *Swertia angustifolia* commonly known as pahari chirata. The distinguishing characters between the two species are given below according to Prasad et al., (1960).

Apart from *Swertia angustifolia*, *Enicostema littorale*, roots of *Rubia cordifolia* and *Andrographis paniculata* are found to be mixed with *Swertia chirata*. *Andrographis paniculata* differs from *Swertia chirata* in having characteristic cystolith on leaves, diacytic type of stoma and phloem on the dorsal side of xylem only.

Zingiber officinale (Family: Zingiberaceae), commonly known as ginger is rhizome drug. The rhizome is used as carminative medicine. It is used in digestive disorders. It expels gas from stomach and intestine. It dilates the blood vessels causing a warm feeling. It increases the rate of perspiration and thus lowers the body temperature. It is mainly used as condiment.

The rhizome of *Zingiber officinale* contains abundant starch grains. They remain singly or in groups. Each grain is simple and the shape may be round, oval, oblong and flattened. The hilum is small and terminal. The striations are very faint. The common adulterant is *Zingiber mioga*. It has compound starch grains and thus can be differentiated.

Starch grains from wheat flower, *Curcuma* etc. are the other adulterants. The study of starch grains detects them. Adulteration may also occur with 'spent ginger' that is exhausted in the preparation of essence. This can be detected by chemical tests only.

Cephaelis ipecacuanha (Family: Rubiaceae) is the root drug and is used in cough mixture. The drug contains abundant starch grains that are mostly compound with 2-4 or five or up to 8 parts. The individual granule is fairly small, not more than 15 μm in diameter. The shape of the granules may be round or oval.

The vessels are moderately thick walled with narrow lumen and numerous bordered pits on walls. *Ionidium* (Family: Violaceae) and other roots are the adulterant of *Cephaelis ipecacuanha*. These adulterants have wide vessels and lack the characteristic starch granules. The other adulterant is *Cephaelis acuminata* that have starch granules up to 22 μm in diameter.

Adhatoda vasica (Family: Acanthaceae) is the leaf drug and is used as an expectorant medicine. It gives relief in bronchitis. The powdered leaf contains fragments of epidermis with diacytic stoma, non-glandular and glandular trichomes. The non-glandular trichomes are elongated, multicellular usually 3-4 celled, conical in shapes with wide bases and the apical cell is pointed.

The glandular trichome is sessile, more or less circular in shape from top view; quadricellular and the partition walls have cross like appearance. Cystoliths are present within the palisade tissues that are double layered. The cystoliths are cylindrical and have warty projections on the surface.

Adhatoda vasica plants grow profusely as a weed and the leaves are collected from natural sources. So, they are rarely adulterated. In Kerala *Adhatoda beddomei* is used as substitute. *Adhatoda vasica* leaves are used as adulterant of tea (*Camellia sinensis*).

Digitalis purpurea (Family: Scrophulariaceae) is a leaf drug. It is used as stimulant of heart and as diuretics. The drug makes the heart powerful and causes the complete contraction of heart, and thus the circulatory system is toned up. *Digitalis lanata* is also used medicinally. *D. purpurea* can be distinguished from *D. lanata*. In the former the anticlinal walls of abaxial epidermal cells are more beaded than the latter.

16.4. ENABLES TO IDENTIFY WOOD:

The anatomy of a wood sample reveals many characters that help in the identification of plant from which the wood comes. In each country there are several excellent books on wood anatomy. These books provide not only anatomical description of wood of the plants occurring at the particular part of the world, but also give the salient anatomical features that help in the identification of plants.

In India there are several volumes of book written on wood anatomy. Mention may be made of Indian woods, published by the Manager of Publications, Government of India, Delhi. In these volumes the anatomical description of woods, mostly from Indian origin, are given and the identifying characters are also mentioned.

In India the number of timbers available in large quantities is not more than sixty, among which the following three are most important-Tectona grandis (teak), Shorea robusta (sal) and Cedrus deodara (deodar).

A Brief Description of the Wood of Teak, Sal and Deodar is given below:

i. *Tectona grandis* Linn. f. (Family: Verbenaceae):

The sapwood and heartwood are sharply demarcated. The colour of sapwood may be white or pale yellow, whereas the heartwood may be of light golden brown or dark brown in colour. The growth rings are conspicuous with ring-porous wood. The vessels of early wood are large in diameter, oval in outline and mostly solitary.

The vessels of latewood are large to small in diameter, oval to round in outline and may occur as single, in radial pairs or radial multiples. The vessels have alternate pittings and simple perforation. The vessels are partly filled with tyloses and sometimes with white powdery deposits. The parenchyma cells are vasicentric and form a thin sheath around the vessel. The rays are moderately broad, 1-3 cells wide, heterocellular and uniformly distributed. The fibres are septate.

ii. *Shorea robusta* Gaertn. f. (Family: Dipterocarpaceae):

The growth rings are usually absent with diffuse-porous wood. The vessels are moderately large in diameter, moderately few (5-10/mm²) and occasionally numerous (10-20/mm²). The distribution of pores is more or less uniform. The pores are solitary and oval to round in shape and have simple perforation plate. Tyloses are present and they almost completely fill up the pore cavities.

Parenchyma vasicentric forming a narrow sheath round the pores or pore groups. The rays are fine to moderately broad, heterocellular. The gum ducts are present and they are vertical canals. The diameter of gum duct is usually smaller than pore. Each duct remains surrounded by thin-walled epithelial cell. The ducts are very irregularly spaced and occur in one or more rows. The ducts are often filled up with white gummy deposits.

iii. *Cedrus deodara* D. Don (Family: Pinaceae):

The sapwood and heartwood are sharply demarcated. The sapwood is white to creamy white in colour. The colour of heartwood is yellowish brown turning to purplish-brown on exposure.

The wood is non-porous. Growth rings are distinguishable. The transition from early wood to late wood is either gradual or abrupt. Resin canals are present and they are arranged in long tangential rows. Ray cells are numerous and they are arranged in closely-spaced line.

In the wood of *Eucalyptus* (Family: Myrtaceae) the vessels are solitary and occur in radial and oblique multiples. The vessels have simple perforation plates. Tyloses are present in lumen of vessels. Parenchyma cells are mostly amphivasal. The rays are wide and heterocellular.

It was previously mentioned that each country has its own publication of name of species from which the wood comes along with their wood anatomy. It is an authoritative work and provides the identifying characters of woods.

Any wood sample in question is studied anatomically and compared with the publications. Thus, the identity of wood sample can be established. For correct identification microscopic slides are prepared from wood samples under study and compared with those from reference microscopic slides.

For domestic purposes woods are best used in making furniture and building materials. Craftsman needs the identification of the antique furniture when repairs are necessary. The wood of doors and windows can be checked as declared.

Apart from making furniture and building materials, woods are used for many more specialized purposes. Sometimes normally used species become unavailable. Then search is made for substitute woods. By studying the anatomy of wood that is to be replaced, sometimes it is possible to suggest other species, from which similar properties can be expected.

Mention may be made of the followings from where specialized properties are obtained. The cricket bat is produced from *Salix Alba* var. *caerulea*. The wood is light and the cell walls are moderately thick. The walls are resilient and after denting recover their shape better than dense wood. The dense wood of *Guaiaecum officinale* is heavy and the fibres are thick walled.

It is used for making bowls and pulleys. The wood of *Ochroma lagopus* and *O. pyramidale* is very light and the wood of former is lighter than cork. The wood consists of large-thin walled parenchyma cells and thin walled fibres. It is used in life boat industries and making insulating materials in aircraft.

The wood of Leguminosae in tangential longitudinal section reveals that the rays and fibres are oriented in regular horizontal rows. This type of figure has decorative value. The wood of *Fraxinus* and *Carya* has straight grain, i.e. the elements of wood are oriented parallel to the longitudinal axis of the plant. The wood is resilient and so it is used in making handles of axe and similar tools.

Many woods have the property of resistance against decay, insect and fungus attack. Mention may be made of *Tectona*, where the heartwood is one of the most durable timbers of the world. The wood contains anthraquinones, which is effective in termites and fungi. The heartwood is used in boat building and it is one of the most important timbers in shipbuilding.

16.5. ENABLES TO IDENTIFY ARCHAEOLOGICAL PLANT REMAINS:

The wood-anatomy of present-day-plant provides characters to identify the fragmentary wood. These characters also enable to identify the wood and charcoal preserved in sites from antiquity.

A burnt wood or charcoal sample is collected from the site of excavation. Microscopic slides are prepared and examined thoroughly. The observation shows that the very delicate features like perforation plate and lateral wall pitting are still retained. The wood anatomy of archaeological sample is compared with that of present-day-wood and thus their identity can be detected.

After authentication it can be decided whether it was selected for burning purpose only. It may happen that the plants composed the vegetation of that area at that time. The plants, as they grew locally, were obtainable at ease and so were selected for burning purposes.

A wood is best preserved in those localities where continuous wet or dry conditions prevail. A fluctuating dry and wet atmosphere encourages the growth of pathogenic microorganisms that may attack the wood thus causing the wood to decay. It is not yet definitely known when the first use of wood began. It is assumed that the practice of using wood started in Old Stone Age for digging purposes in search of food.

For the first time, actual evidences of using wood have been recorded from the sites of New Stone Age. But no sites at this age in India produce any evidence of the use of wood. The Indus Valley civilization revealed the uses of wood for many purposes. The different use of wood was also recorded from the archaeological excavation of the proto-historic period in India namely, the Bronze Age civilization of Harappa and the Copper Age civilization of Hastinapura.

It has been reported that the Harappans used the wood of *Cedrus deodara* (Deodar) and *Dalbergia latifolia* (Rosewood) for making coffins. These durable and scented woods are still in use after thousands of years for the same purpose. *Zizyphus* was used as wooden mortar for pounding grains. This wood has the property of shock absorbing and the Harappans were quite aware of the fact.

Dalbergia sissoo (Sissoo) and *Holarrhena antidysenterica* (Kurchi) —these two timber-yielding plants were found in Hastinapura. These plants provide good fuel woods. It is not known whether these were used as firewood or charcoal. It is assumed that the Copper Age civilization was aware about the woods that have high calorific value.

In Iron Age the species of *Quercus* were used in making buildings and boats. At the site of excavation at Brigg at South Humberside a boat made up of *Quercus* wood was preserved. It was interesting to find that the main logs of the boat were sewn together with twigs of *Salix*.

The twigs were twisted and passed through the regularly made holes on the timbers. No nails were used to hold the timbers. *Corylus* were well preserved in waterlogged condition in Somerset at Bronze Age. These were used in building track ways across swampy grounds.

Apart from wood and charcoal other archaeological plant remains are also preserved. As for example a sandal was preserved in ancient Egypt. Anatomical studies reveal that it is composed of *Cyperus papyrus* and *Borassus* sp.

16.6. APPLIED ASPECTS OF MERISTEM CULTURE:

Meristems may be apical, intercalary and lateral. Each of the meristems is exploited in the improvement of plants.

i. Apical Meristem:

Apical meristems occur at the tips of root, leaf and shoot. The shoot apical meristems are particularly used in culture. In culture method the shoot apical meristem is excised out and placed in a glass container, containing nutrient. In a strict botanical sense the cells in the apical dome of shoot apex compose the meristem. In apical meristem culture the sub-millimetre shoot tip with 0.1 to 0.5 mm high apical dome is dissected out and placed in nutrient media.

Different media are used for different plants. The media usually consist of a carbohydrate source, minerals, vitamins, amino acids, growth regulators and the gelling agent agar. Perfect temperature, humidity, filtered air and controlled light are necessary during the culture. Aseptic condition is the prime importance in all the steps of culture to check the introduction of pathogens.

Sometimes circumstances arise when meristem culture becomes necessary for vegetative propagation. As for example the plant under study is infertile as in the case of triploid *Musa* sp., certain varieties of apple, tulips, iris, hyacinths etc. In breeding experiments the hybrid of first filial generation (F_1), when heterozygous, never breeds true, i.e. segregation of characters occur in the second filial generation (F_2).

The meristem culture of F_1 plant keeps the progeny alike. In many experiments on plant breeding the hybrid plants fail to produce normal seeds. The seeds are either abortive or nonviable. These hybrids are propagated through meristem culture. The haploid plants produced as a result of anther or pollen culture are always sterile. They become fertile when they are converted to homozygous diploid.

The haploid plants are propagated through apical meristem culture. In apical meristems viruses are either absent or present in a very low concentration because the cells of this region have fast mitotic activity. By apical meristem culture a clone of virus-free plant can be obtained. The clones can be multiplied vegetatively by meristem culture. The problems of plant tumors, especially the crown gall can be eradicated by meristem culture.

It is to note that a virus-free plant is not virus resistant. So aseptic measures are the dominant prerequisite for obtaining virus-free plant that serves as a source for propagation of other virus-free plants. Sometimes plants are imported or exported to other countries.

They are also exchanged in crop improvement programmed. In these cases quarantine laws are applicable. But the quarantine authorities relax the procedure of checking when the plants in question are derived from apical meristem culture.

The apical meristem culture is also useful in micropropagation. Micropropagation is the practice where a stock plant material is multiplied vegetatively into a large number of progeny plants. It is the true-to-type propagation of the selected genotype. Micropropagation

gives immediate results in contrast to traditional means of propagation and so it is used to overcome the limitations imposed by long breeding cycle.

The practice of micropropagation is extensively used in horticulture, agriculture, forestry and conservation of endangered plants. It was estimated in 1991 that the world production of micropropagated plants are about 600 million. In horticulture, floriculture especially in cut-flower industry the registered line of stalk plants is maintained by micropropagation.

In cut-flower industry India has bright future. India has more than 35000 hectares of land under flower cultivation and is gradually entering into export market. Traditional methods of plant multiplication are very slow and it takes long time of being commercially available. So micropropagation through apical meristem culture is necessary to meet the high demand of flower, for pathogen-free plants and for hybrid plants etc.

In forestry micropropagation through apical meristem culture is also practiced as it gives immediate result. By traditional means to obtain a homogeneous true seed might take over a hundred years.

The teak wood is obtained from *Tectona grandis*. This tree grows naturally in India. The other naturally growing species of *Tectona* occur in Burma, Thailand and the adjoining areas of Laos. *Tectona grandis* is one of the most important timbers of India. The wood is moderately hard, moderately heavy and strong timber. The heartwood has a reputation of being one of the most durable timbers of the world and is practically immune to fungus and termites.

The essential oil citronella is obtained from the leaves of *Eucalyptus citriodora* tree. These plants are micropropagated from where about 500 plants of teak and 1000 plants of *Eucalyptus citriodora* are raised from a single bud (Fig. 16.1) in a year. Apical meristem culture is widely used to raise virus-free plants.

Example:

Manihot esculentus, which is usually infected by Mosaic virus or Streak virus. A single meristem tip of *Manihot esculentus* provides a number of virus-free plants.

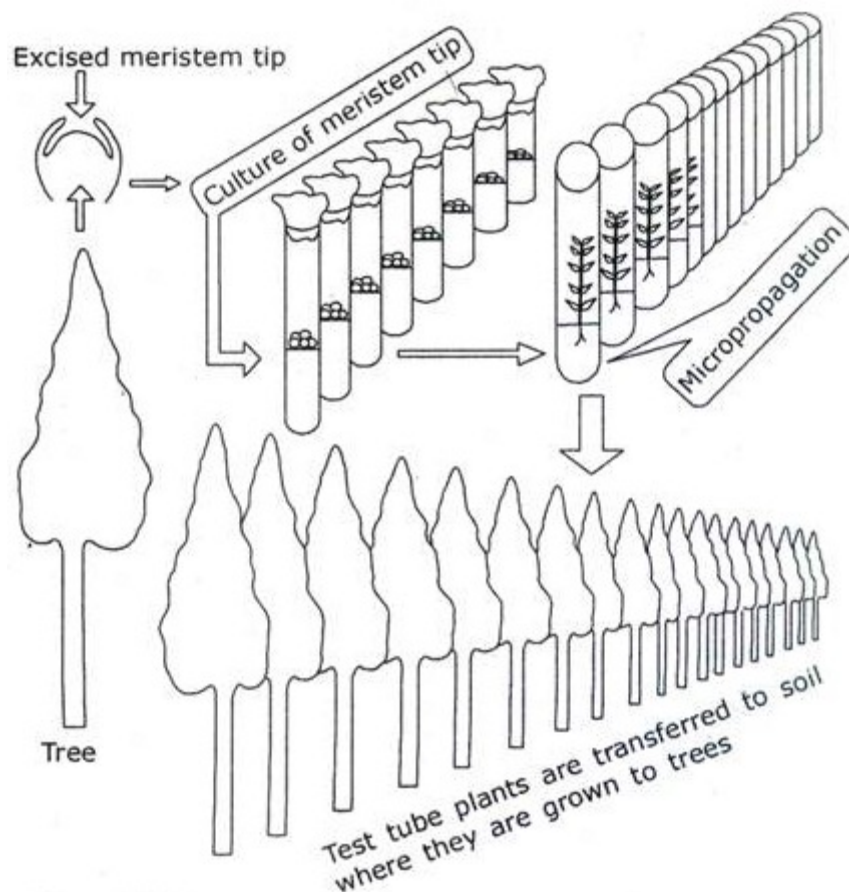


Figure 32.1

Fig. 16.1

Diagram Illustrating the Meristem Tip Culture for Rapid Propagation of Plants.

In the conservation of endangered species micropropagation technique plays an important role. Through this technique endangered plants are propagated and thus conserved. Mention may be made of the orchids *Liparis loeselii*, *Cypripedium calceolus* etc., carnivorous plants *Nepenthes*, *Drosera*, *Dionaea* etc. and the woody plant *Ramosmania rodriguesii*, *Hyophorbe lagenicaulis* etc.

ii. Intercalary Meristem:

A large number of plants have meristem adjacent to and just above most nodes. This meristem is derived from apical meristem. During the course of development of apical meristem of a plant, a portion of meristem becomes separated from apical meristem by more or less mature tissues. This is intercalary meristem. In many plants adventitious roots are formed at nodes from this meristem.

In horticulture this property is used in the propagation of plants by stem cuttings. Adventitious roots are formed in many plants which failed to grow upright and fell to the ground. Ex. *Triticum*, *Dianthus* etc. Adventitious roots grew at the nodes and made the plants upright again. The intercalary meristem is capable of producing adventitious roots.

This can be demonstrated by the following experiment. The experimental material is *Dianthus*. The plant is cut just below a node. The node is split longitudinally up to the intercalary zone. The split was kept apart by means of stick. Proper nutrition and aseptic condition were maintained as usual. It was observed that from the split sides adventitious roots develop (Fig. 16.2).

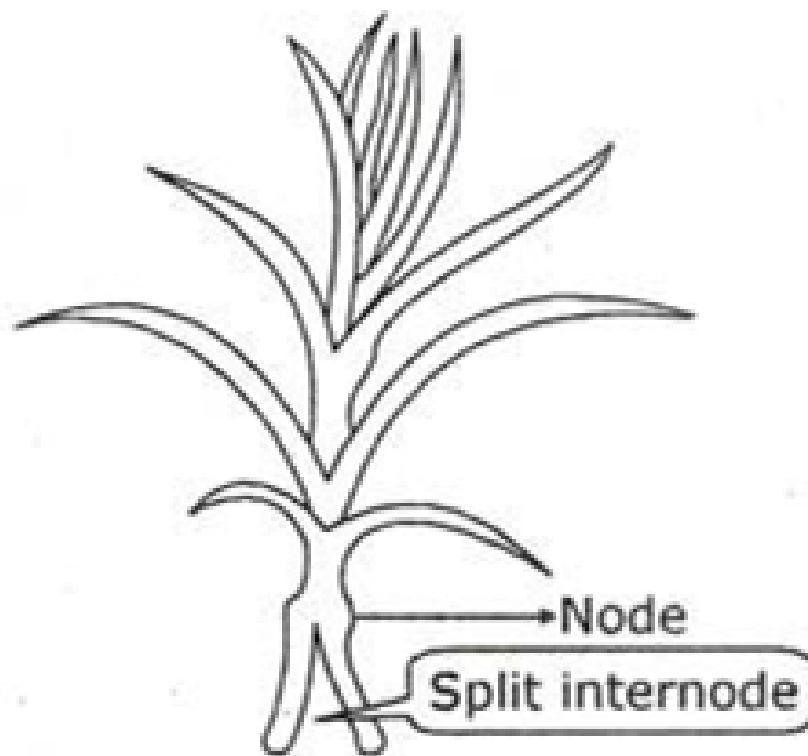


Fig. 16.2: A Portion of *Dianthus* with split internode. The split side of the internode is the site of adventitious root formation.

iii. Lateral Meristem:

Lateral meristem occurs on the lateral sides of a plant.

Example:

Phellogen or cork cambium, fascicular cambium that is present between xylem and phloem of a vascular bundle of dicot stem and the inter-fascicular cambium that develops at the time of secondary growth from the tissues present between the two vascular bundles.

The fascicular - and inter-fascicular cambium unites on lateral sides to form a complete cambium ring. The function of cambium ring and phellogen. These cambia, if wounded, normally can regenerate and form callus cells adjacent to them. The cambial continuity is regained and thus the wound is healed. This wound healing property is employed for commercial purposes.

The phellogen donates on the peripheral side phellem cells that are also known as cork. The bottle cork, which is used as stoppers, is obtained from the phellem. *Quercus suber* provides most of the cork. The bottle corks that are used as stoppers are made sizes by tangential cut to stop leakage from vertically oriented lenticels (Fig. 16.3).

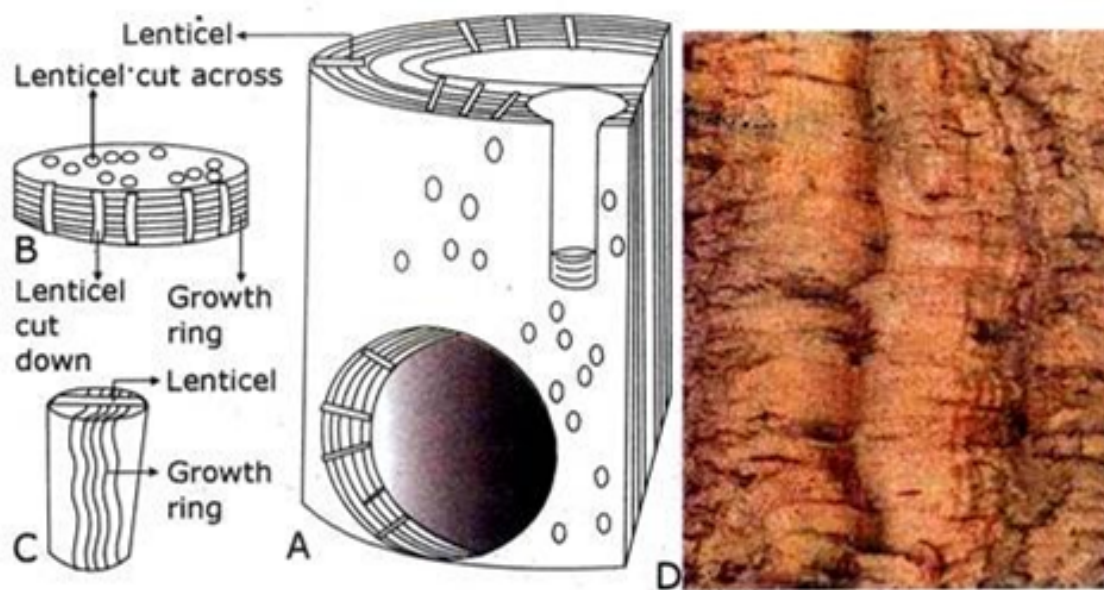


Fig. 16.3: (A) Cavities in a cork sheet from which have been cut. (B) A piece of cork indicating the position of lenticel. (C). A Piece of cork for a bottle. (D) Photograph of the bark of *Quercus suber*. The tree is present at Hopetoun Gardens, Elsternwick, VIC, Australia.

The phellogen of *Q. suber* persists indefinitely and forms mass of cork tissue externally. After about twenty years of age of the plant the cork tissues are removed by stripping. This cork, also known as virgin cork, consists of phellem cells only and sometimes phellogen and phelloderm may be present. The virgin corks are nearly useless.

After stripping, the underlying phelloderm and cortical cells are exposed and they gradually die. This wound is healed by a cork cambium or phellogen, which originates in the deeper layer of cortex. Phellogen forms new layers of cork, which is harvested after about ten years. This cork is not of good quality but definitely better than the virgin cork.

The better quality of cork is obtained from the third and subsequent stripping. The cork layers are harvested at intervals of nine to ten years until the tree becomes 150 or more years old. Portugal is the centre of cork industry. The recent use of plastic corks is reducing the demand of oak-cork.

The other lateral meristems, fascicular - and inter-fascicular cambium are also employed in plant propagation. This is usually done by cuttings and grafting. Cutting is a method where a shoot is cut away from a desired plant and planted to soil for rooting. Thus, a new individual is produced. In horticulture this method is employed to propagate plants thus maintaining similar genotype.

In stem grafting the cut away shoot of a plant, also called scion, is inserted to the stem of another plants, also called stock. In grafting both scion and stock are wounded and the two are joined in such a way that the exposed meristematic cambial cells of them are brought into close contact. The inherent ability of wounds to heal causes the formation of callus tissue.

Through the callus the cambia of stock and scion become continuous and form the secondary vascular tissues as usual. Thus, the scion becomes a permanent part of stock. The plants like *Mangifera indica*, apples, *Nephelium litchi* etc. are propagated by grafting. This device can regulate the size of the plant and earlier fruiting can be induced.

The gourd root, which is *Verticillium* wilt resistant, is used as stock where the watermelon with wilt-prone root is grafted. Thus, the wilt disease can be avoided in watermelon. *Juniperus glauca* has vigorous roots whereas the root of *J. virginiana* is weak. The latter is the desirable species and so it is grafted to the stock of *J. glauca*.

In conifers the growth ring is continuous at an early stage below lower branch. At the branch region the continuity of growth ring is interrupted where gap is present. In forestry there is a practice to remove the lower branches of conifers at an early stage. This enables the growth ring to become continuous over the discontinuous growth ring. Thus, a sound new wood can be formed.

16.7. PROVIDES EVIDENCES IN FORENSIC INVESTIGATION:

The application of forensic science is indispensable in investigating a crime. Forensic science has many disciplines and forensic botany is one of them. Forensic botany encompasses many sub-disciplines, which include plant anatomy, plant systematic (taxonomy and species identification), palynology (the study of spores and pollen) etc. They refer the use of plant materials in solving crimes or resolving other legal problems.

Plants remains are present everywhere. In a crime scene they may occur in the form of macroscopic pieces (ex. wood, twigs, leaves, flowers, fruits, seeds etc.) or microscopic forms (ex. pollen, spores, trichomes, cell walls in stomach contents etc.). The morphological and anatomical diversity expressed by plant species provide characters to identify plant parts. Species identification is a prerequisite in analyzing botanical evidences for casework.

Plant anatomy provides characters such as trichomes, stomata, cuticular pattern, leaf venation, wood anatomy, growth rings etc. to aid in species identification and in performing physical matches of evidence. The identified plant materials help the investigators of criminal cases to determine whether a suspect was present in a crime scene, in which season the crime occurred, how long the body has been buried, whether the body has been moved etc.

The following is an example of one of the earliest and famous case in which botanical evidence was used and accepted in court. In 1932, in the evening of March 1st the infant son of famous American aviation hero Charles Lindbergh was kidnapped from his home in Hopewell, New Jersey, US. For the release of their son, the family paid \$50,000. But the kidnapper did not return their son. Two months later the dead body of the son was discovered a few miles away from the family home.

The son was kidnapped from a second-story nursery. The kidnapper used wooden ladders to gain the access there. The ladders were the only evidence left at the scene. They were homemade and crude.

Xylotomist Arthur Koehler of United state Forest Services in Wisconsin examined the wood of the ladder both morphologically and anatomically. Four years later, when the case finally came to trial, Koehler offered the evidences from plant anatomy, which was ever to be heard and accepted in American court.

The ladders had been constructed in three sections. It was presumed that they were made such for ease of transport. Koehler numbered each piece of rungs and side rails. Koehler identified each piece to species. The following four species were used to construct the ladder-namely Yellow pine, *Pinus ponderosa*, Douglas fir and *Betula* sp. The basis of identification was the microscopic analysis of grain patterns of the woods.

Next Koehler analyzed the tool marks left on the wood. Koehler was able to differentiate the woods with mill plain marks and hand plane marks. The hand plane marks were distinct by their dull and nicked appearance. The nick was distinct when the wood was placed in oblique light in a dark room. The wood of rail #16 was very distinct from others.

It was from Pinus wood with hand planed marks and had four very prominent marks of square nail holes. Moreover, the rail #16 was not weathered suggesting that the wood was removed from some interior construction like shed. Finally, Koehler analyzed the growth ring patterns and knots present on the wood and especially on the rail #16.

The progress of the case was very slow as no suspect was identified. Sometimes in September of 1934 a gas station received some currency notes and it was detected that those were once used to pay the ransom for the release the infant son. Bruno Richard Hauptman, a carpenter from Bronx, New York city paid the notes to the gas station.

Then search was made at Hauptman's house and \$14,600 of the ransom was found in the garage. So, Hauptman was arrested. Further search was continued for the recovery of more money of the ransom. During investigation it was noticed that one of the joists of floorboards of Hauptman's attic was shorter of about eight feet than the others.

This joist had four square nail hole marks and the growth ring patterns and knots were studied. Amazingly it was found that the four-square nail hole marks, growth ring patterns and knots matched with rail #16. The hand plane marks of rail #16 matched with the wood of a homemade shelf present in the Hauptman's garage. A hand plane was recovered from the garage and it made identical nick that was present in rail #16 and wood that constructed the shelf.

Hauptman was convicted and executed on 3rd April 1936.

In the above case the features of plant anatomy provided evidences in solving the kidnapping of infant son of Lindbergh and involvement of Hauptman in the crime.

The anatomical features like silica bodies, starch grains, raphides, sclereids, druse etc. found in edible plants are used to identify the stomach contents and last meal of a victim.

This is necessary to find the victims' whereabouts and actions prior to death. In the analysis of stomach contents, the cell wall provides important identifying characters of many food materials because the cell walls are not easily digested and persist longer time period than other anatomical features. Moreover, the characteristic thickening of cell walls is sometimes taxon-specific.

Many dicotyledonous roots show growth rings or annual rings. The number of rings reveals the age of the tree. This property is utilized in forensic anthropology to estimate the time since skeletal remains had been in their present location. In one case living roots were found in the cavity of a skull.

The anatomy and growth ring pattern revealed that the root belongs to *Ranunculus ficaria* and the plant was approximately one year old. These findings enabled to determine that the skeleton had been there for at least one year. When a grave is dug roots can be damaged but still continue to grow leaving a permanent lesion.

In dicotyledonous roots growth rings are formed as usual and the number of rings formed after the lesion indicates the number of years passed since the damage. So, growth rings can indicate the number of years passed since burial. From the number of growth rings

or annual rings of root that are in contact with the bones can also indicate minimum time passed since death.

Dendrochronology or tree-ring dating is a method of scientific dating of a tree based on the analysis of annual growth ring patterns. The number of growth ring gives the age of the tree. The growth ring analysts can pinpoint the exact age of a tree and the year when the tree was cut. This enables to detect any art fraud, the provenance of wood arts objects, wood of musical instruments etc.

Many European painters used to paint directly on wood. Dendrochronology techniques enable to date the wood and so the year of painting. These techniques are also used to detect when the wood was used to make art objects or musical instruments etc.

Marijuana is a controlled drug and obtained from *Cannabis sativa*. In powdered form it is identified microscopically by the presence of characteristic cystolith and hairs. Drug enforcement confirms the drug by chemical tests in combination with microscopic observations. Apart from *Cannabis sativa* there are large number of plant species, which are used as drugs, substitutes and adulterants.

Most of them are used in a very finely powdered form. Quite a lot of time and effort is needed to authenticate them. There exists enormous genetic diversity among plant populations. Forensic scientists take the advantage of the property of genetic diversity to identify plant species by molecular biology techniques.

The development of DNA typing methods for plant species enables to identify plant species and thus helps in solving criminal and civil cases. Though the traditional microscopic anatomical identification is not always conclusive, it is still in use for preliminary identification. Moreover, the anatomical techniques are simple and inexpensive.

16.8. PROVIDES CHARACTERS OF TAXONOMIC SIGNIFICANCE:

It is the prime importance to know exactly to which species a plant specimen belongs. This is necessary for a natural and reliable classification. Most of the plants are classified according to their macro-morphological features. But an accurate classification results when the information from diverse sources are utilized.

The sources may be from anatomical features, palynology, biochemistry, embryology, cytogenetics, phytogeography, physiology etc. It is now realized that alpha taxonomy can form a natural, accurate and reliable classification.

Once morphology and anatomy formed the backbone of taxonomy. Anatomical features provide characters to supplement the macro-morphological characters of plant species.

The following important anatomical features those are often good indicators of the family, genera and sometimes species are discussed below:

i. Trichomes:

Trichomes are the collective term of hairs and papillae. They occur on all organs of a plant. There exists much morphological diversity among them. This property and the simple means of preparation of slides for study enabled the taxonomists to employ the trichome

characters for systematic comparisons and individual identification. Metcalfe and Chalk (1950) provided the diverse types of trichome with their structure, nomenclature and distribution. Trichomes are of taxonomic significance especially at generic and specific level.

The families like Restionaceae and Centrolepidaceae can be recognized by the presence of distinctive type(s) of trichomes that are simple and unbranched. The hair of *Aphelia cyperoides* (Centrolepidaceae) has a boat-hook-shaped end (Fig. 32.4A) that characterizes the species. *Leptocarpus* (Restionaceae) has flattened multi-cellular stem hairs with short stalk.

There are two major categories of hairs-the glandular and non-glandular. Each of the categories is sub-divided according to their gross structure, cellular constitution, nature of branching etc. There exist much diversities and varied forms in non-glandular hairs than the glandular hair. A few types of hair are illustrated in Fig 32.4.

16.9. SUMMARY:

Plant anatomy helps identify plants (even fragments), detect fake medicines (pharmacognosy), understand evolution (systematics), solve crimes (forensics), and improve plant science like breeding and tissue culture, by examining internal structures like cells, tissues, and wood to reveal identity, relationships, and function in medicine, law, and agriculture.

16.10. MODEL QUESTIONS:

- 1) Describe how plant anatomy helps to Identify Fragmentary Plant Material
- 2) Describe how plant anatomy helps to Detect Adulterants in Crude Drugs
- 3) Describe how plant anatomy helps to Identify Wood
- 4) Describe how plant anatomy helps to Archaeological Plant Remains
- 5) Describe how plant anatomy helps in Applied Aspects of Meristem Culture
- 6) Describe how plant anatomy helps to in Forensic Investigation

16.11. REFERENCE BOOKS:

- 1) K.Esau, 1993. Plant Anatomy, Wiley Eastern Limited, New Delhi.
- 2) A.Fahn, 1967. Plant Anatomy, Pergamon Press, Oxford.

Dr. K. Babu

LESSON-17

APPLICATIONS OF PLANT ANATOMY IN TAXONOMY

17.0. OBJECTIVE:

- To gain Knowledge on the supplication of Plant anatomy in biomedical and plant systematics.

STRUCTURE:

17.1 Introduction

17.2 Anatomical Evidence can be Useful in Systematics in Several Ways

17.3 Types of Anatomy

17.4 Stem Anatomy

17.5 Petiole Anatomy

17.6 Nodal Anatomy

17.7 Wood Anatomy

17.8 Sclereids

17.9 Cellular Contents

17.10 Floral Anatomy

17.11 Ultra Structural Systematics of Anatomy

17.12 Summary

17.13 Model Questions

17.14 Reference Books

17.1. INTRODUCTION:

Anatomical characters of vegetative and floral parts of flowering plants have been successfully employed to solve taxonomic problems and for the elucidation of phylogenetic relationships. It was Bureau, who for the first time used anatomical characters in plant classification for the delimitation of taxa of various levels, within the family Bignoniaceae.

However, anatomical data have been used extensively as a taxonomic tool only after the nineteenth century. Anatomical data has not only been useful at the higher levels but in certain instances, have been successfully employed even at the specific level. Auguste Mathiew is one of the pioneer taxonomists, who used features of wood anatomy in the description of forest plants in *Florae forestiere*.

Later, another taxonomist Solereder, discussed the systematic value of anatomical structures in dicotyledons in his classic book *Systematische Anatomie der Dicotyledonen*, the English translation of which was later published in a modified form in the two-volume book *Anatomy of the Dicotyledons* by Metcalfe and Chalk.

17.2. ANATOMICAL EVIDENCE CAN BE USEFUL IN SYSTEMATICS IN SEVERAL WAYS:

- i) It can well be exploited taxonomically in the identification of fragmentary material, say a piece of wood.
- ii) When morphological characters prove to be of no help in the preliminary identification of herbarium material, anatomical study may prove helpful.
- iii) Anatomical data has proved to be very useful in discerning evolutionary trends and interrelationships of taxa at and above the species level and at higher taxonomic categories. They are most useful in determining relationship between different genera, families, orders and other taxonomic categories.

While studying anatomical data, it is advised to study the ranges of variability of these characters within the same individual and between different individuals of the same species and not rely on data from a single sample of an organ or tissue, as similarities in structural organization may not necessarily reflect close relationship but may be the result of parallel and convergent evolution.

17.3. TYPES OF ANATOMY:

1. Vegetative Anatomy:

(a) Leaf Anatomy:

Leaf anatomy provides various characters of taxonomic importance as has been rightly stated by Carlquist, that **“the leaf is perhaps anatomically most varied organ of angiosperms and its anatomical variations often concur closely with generic and specific and occasionally familial lines”**.

Leaf anatomy has been used widely in several taxonomically different groups such as Euphorbiaceae, Cyperaceae and Gramineae of Angiosperms and Coniferae of Gymnosperms.

It has been one of the most reliable characters in grass systematics. For example, the leaf anatomy of several species of Cyperaceae, was studied by Koyama and Govindrajalu and they formulated keys to identify various species of Cyperus, Fuirena, etc. Brown surveyed, 72 genera of grasses and on the basis of their tissue arrangement, six main types were recognized.

However, they could not, be segregated into the two traditional subfamilies, Pooideae and Panicoideae. Similarly, Vidakovic have used several characters of leaf anatomy in differentiating species in Pinus. Taxonomic implication of leaf anatomy of several genera of Musaceae, Zingiberaceae, Xanthorrhoeaceae and Ericaceae have also been established by several workers.

Some of the Important Characters of Taxonomic Significance in Leaf Anatomy include the following:

(i) Nature and Thickness of Epidermis:

The size and shape of epidermal cells is of great value in the taxonomy of several taxa (Fig. 8.2). Cuticular characters of the epidermis and stomata have also proved to be of great value.

For example, Conde studied 5 species of the genus *Opuntia* with respect to cuticular thickness, epidermal papillosity, stomatal size and frequency, hypodermal thickness, vessel number, etc. and found that each species was distinct in respect of the degree of papillosity of epidermal cells, hypodermal thickness and vessel width.

The information from trichome anatomy has also proved useful in certain taxa, e.g. trichomes have furnished as diagnostic characters in certain species of *Veronica*.

(ii) Structure and Types of Mesophyll, Storage Parenchyma, Mid Vein Structure, Bundle Sheath, Secretory Apparatus, etc:

For example, Anderson & Crech suggested precise groupings of *Solidago* and other species of *Asteraceae* based on their study of leaf anatomy, including qualitative and quantitative differences in mesophyll, storage parenchyma, secretory apparatus, bundle-sheath extension and midvein structure.

(iii) Pattern of Sclerenchyma:

Patterns of the distribution of sclerenchyma in *Carex* and *Festuca* have been used in distinguishing species.

(iv) Silica Bodies:

Silica bodies in the epidermal cells of members of certain families like *Zingiberaceae*, *Musaceae* and *Palmae* among Monocotyledons and *Rosaceae* in the Dicotyledons have been used as diagnostic character in systematics at generic as well as specific levels.

(v) Chloroplast Structure can also prove to be of Taxonomic Significance.

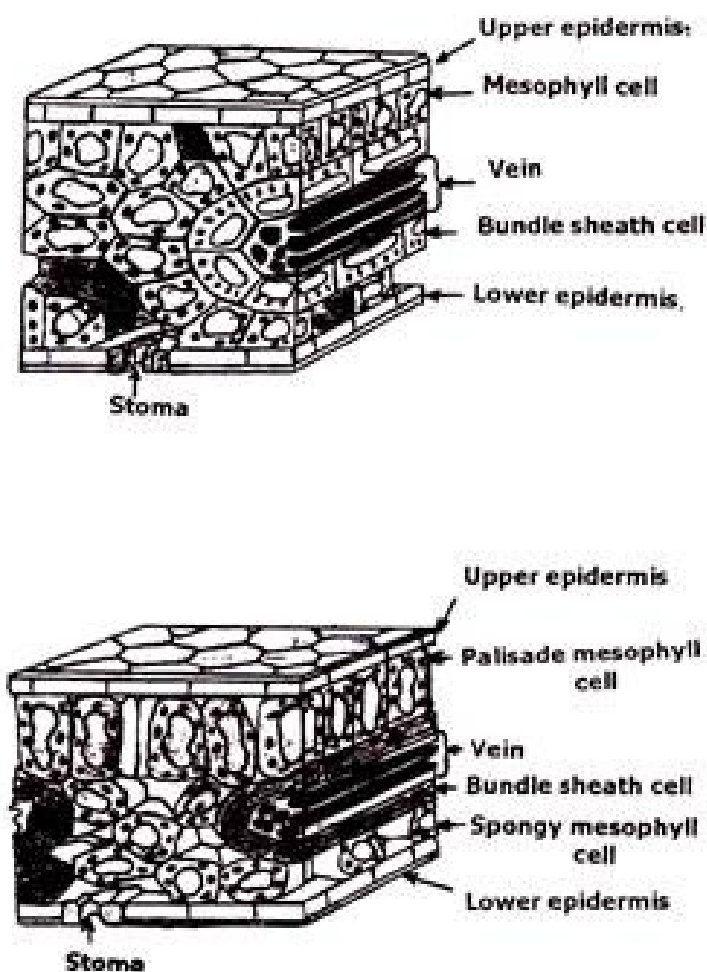


Fig. 17.1: Cross-Section of Different Types of Leaves showing Anatomical Characters of Taxonomic Significance

17.4. STEM ANATOMY:

Stem anatomy has also been long relied on as a taxonomic tool (Fig. 8.3). The two-volume work by Metcalfe & Chalk is an excellent example of an illustrated encyclopaedia of this and of other aspects of plant anatomy, which reveals the taxonomical significance of anatomical characters in plant classification and can be used at various levels from Dicotyledon-

Monocotyledon distinction, to the separation of various species of the same genus. Stem anatomy has particularly proved to be of diagnostic value in the herbaceous members. For example, anatomy of stems has been successfully employed in the delimitation of species of *Dioscorea* which otherwise are not easily separable on exomorphic grounds.

Carlquist has used anatomical features of the genus *Fitchia* (Asteraceae) in the classification of various species. Further, it is also possible to identify parents of several hybrids on anatomical grounds.

The anatomical features, which can be taken into account as diagnostically useful characters of the stem include:

- i) Degree of elevation of stem ridges.
- ii) The distribution and abundance of collenchyma.
- iii) Pattern of collenchyma thickenings.
- iv) Transformation of ground tissue cells of cortex into transfusion cells - e.g. *Casuarina*.
- v) Distribution of fibres - e.g. *Genista*.
- vi) Variation in the structure of the cells of stem endodermis - e.g. in families like *Piperaceae*, *Asteraceae* and *Lamiaceae*.
- vii) Features of the stem pith - e.g. species of *Dubantia* and *Fitchia* have been distinguished on the basis of anatomical differences in pith.
- viii) Shape and size of sclerenchyma girders - e.g. used to distinguish species of the subgenus *Genuini* of *Juncus*.
- ix) Arrangement and type of vascular bundles - e.g. two species of *Dioscorea*, viz. *D. cayenensis* and *D. rotundata* have been distinguished on the basis of arrangement of vascular bundles in the stem, which otherwise are difficult to distinguish on exomorphic grounds.

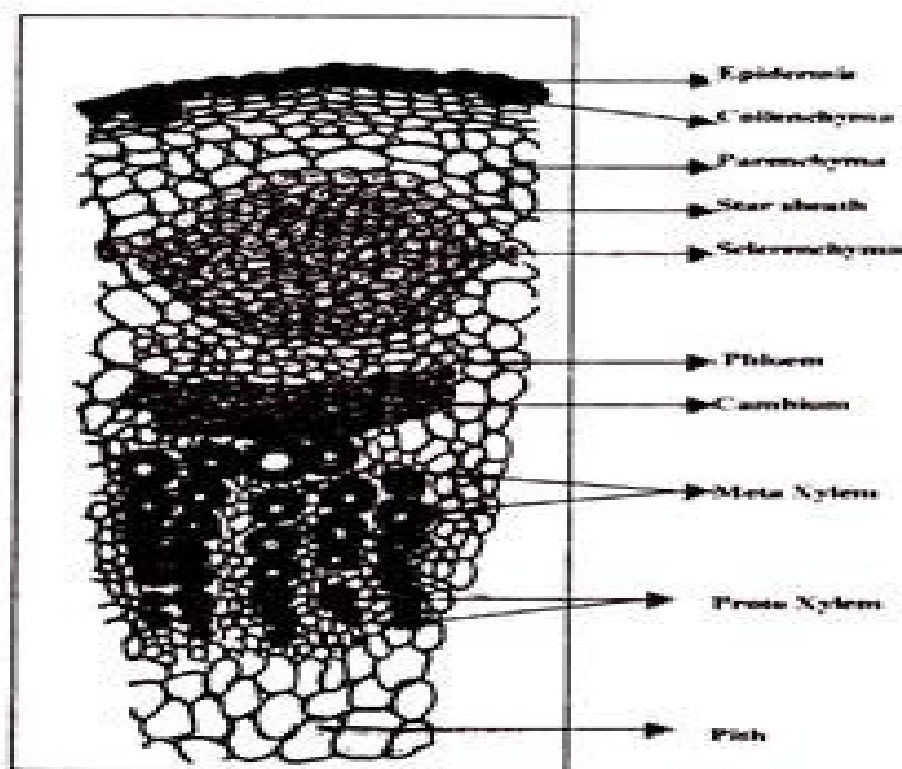


Fig. 17.2: T.S. of Dicot Stem Showing Anatomical Features of Taxonomic Significance

17.5. PETIOLE ANATOMY:

Metcalf and Chalk and Howard have suggested that the petiole anatomy might also be of taxonomic significance (Fig. 8.4). According to Howard families, genera and even species in some cases may be identified by petiole characters.

Some of the important diagnostic characters of petiole anatomy include:

- i) Position of petiole on stem.
- ii) Presence or absence of stipules.
- iii) Petiole outline.
- iv) Number of layers of parenchyma in the cortex.
- v) Vascularization of petioles.
- vi) Distribution of perivascular fibres.
- vii) Number of traces.

Example:

Petiole anatomy of 64 species of *Baphia* of Leguminosae have been studied by Soladoye, and some species of *Phlomis* and *Eremostachys* of Labiatae by Azizian and Cutler, which provide clear support of its use in the taxonomy of these genera.

17.6. NODAL ANATOMY:

Nodal anatomy has also gained much importance in taxonomy and phylogeny of angiosperms in recent years. Correlations of nodal anatomy with some other features might help significantly in tracing the phylogeny of angiosperms. A comparative study of nodal anatomy may show important relationships or distinctness of genera or even species (Fig. 8.4).

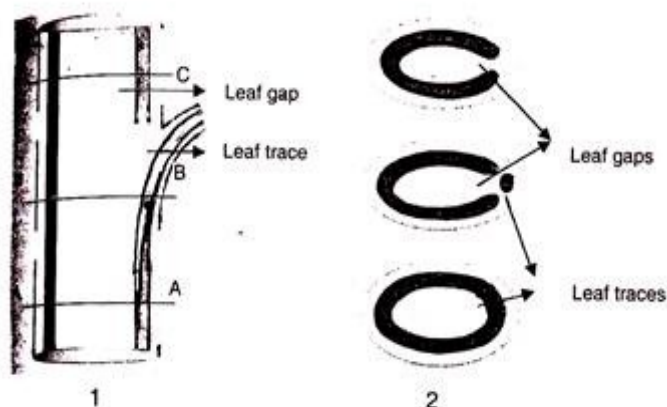


Fig. 17.3: Diagrammatic representation of Leaf Trace and Leaf Gaps; (1) L.S. through a node showing leaf trace and leaf gap, (2) T.S. through the node illustrated in 1 at levels A-A, B-B and C-C respectively

Based on his studies on megaphyllous plants, provided a classification of nodal types. In general, there are three major types of nodes:

- a) Unilacunar - occur in Laurales, Caryophyllales, Ericales, Ebenales, Primulales, Myrtales, some families of Tubiflorae and a majority of families of Asteridae.
- b) Trilacunar - occur in the majority of Dicotyledons.
- c) Multilacunar - occur in the primitive orders such as Magnoliales, Piperales, Trochodendrales and a few advanced orders such as Umbellales and Asterales.

Sinnot considered the tri-lacunar node as primitive, and unilacunar and multi-lacunar nodes as advanced. A fourth type of node was discovered by Marsden & Bailey, viz.

- d) Unilacunar two trace - It is now considered as the basic type of node found in angiosperms.

Usually, the mode of nodal vasculature is uniform in the family, but exceptions have also been reported, where different types of node occur even in the same individual plant.

Example:

On the basis of nodal structure, the subfamily Icacinoidae of the family Icacinaceae has been divided into two distinct groups i.e., one section, which is characterized by trilacunar nodes, while the other section, which is characterized by unilacunar nodes.

17.7. WOOD ANATOMY:

Wood anatomy has been used at almost all taxonomic levels. Because of their conservative nature, anatomical features of the secondary wood have been very useful in taxonomy and phylogeny.

Along with other lines of evidence, it has been successfully used in deciding the systematic position of primitive vessel less families such as Amborellaceae, Tetracentraceae, Trochodendraceae and Winteraceae, all included under the Magnoliales of angiosperms.

Similarly, due to the presence of specialized wood, it has been agreed by all phylogenists that the Englerian group of primitive angiosperms, namely, Amentiferae (including families like the Salicaceae, Betulaceae, Fagaceae, Juglandaceae, etc.) cannot be considered primitive.

Some of the Important Features of Wood Anatomy of Taxonomical Significance are as follows:

1. Vessel Elements:

They are considered to have been derived from the tracheids and their evolution (advancement) is considered to have occurred along the following lines:

- (i) Decrease in the length of vessel element.
- (ii) Transition from vessels with angular outline to nearly circular outline.
- (iii) Loss of borders and decrease of bars on perforation plates.
- (iv) Alteration from oblique to nearly transverse angle of end wall.
- (v) Pitting of lateral walls of vessels showing evolutionary series from scalariform to transitional to opposite to alternate.

Apart from the structure, the abundance of vessels, distribution of vessels, and sculpturing on vessel walls have also proved to be of taxonomic significance (Fig. 8.4). Thus, solitary vessels are considered to be primitive to aggregate groupings, such as pore clusters, pore multiples and pore chains. Similarly, diffuse-porous woods are considered primitive to ring-porous woods.

2. Axial Parenchyma:

The distribution and characteristics of the cells of axial parenchyma and the length and thickness and lignification of their walls, can be useful in taxonomic considerations.

Like vessel elements, evolution (advancement) is considered to have occurred along the following lines:

- (i) Absence of parenchyma is primitive at least in some cases e.g., Winteraceae.
- (ii) Diffuse arrangement is primitive to diffuse-in-aggregates, such as apotracheal or paratracheal types.

Based on the distribution of parenchyma cells, they can be of two types:

- (i) Apotracheal - Parenchyma distributed without any specific relation to vessels.
- (ii) Paratracheal - Parenchyma distributed in close association with vessels.

3. Vascular Rays:

The characteristics of vascular rays, which can prove useful as taxonomic criteria include ray abundance, cellular composition of rays, dimensions of rays in tangential section, degree of wall thickness and pitting of ray parenchyma cells. Rays with all the cells radially elongated i.e., homogeneous rays are considered advanced to the heterogeneous rays, i.e. rays with both vertically and radially elongated cells.

4. Storied Wood:

Storied structure of wood refers to the planes of divisions of cambial initials. Woods with non-stratified cells are considered primitive to storied structures.

5. Presence or absence of latex vessels, resins, gums, crystals, etc. in the wood are also the characters of taxonomic importance.

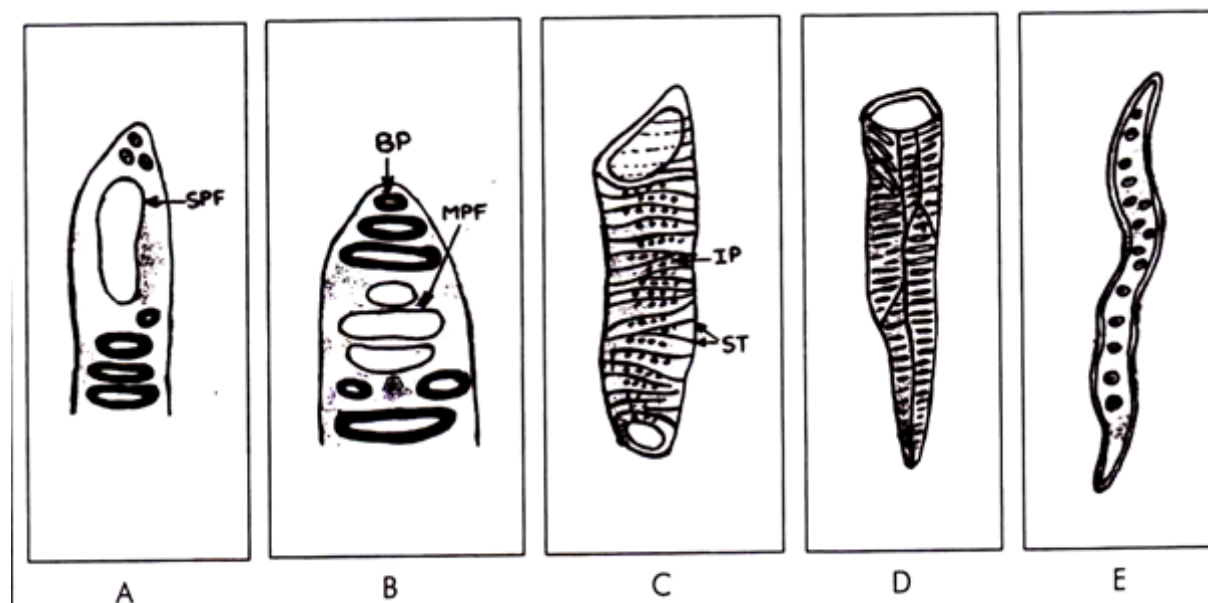


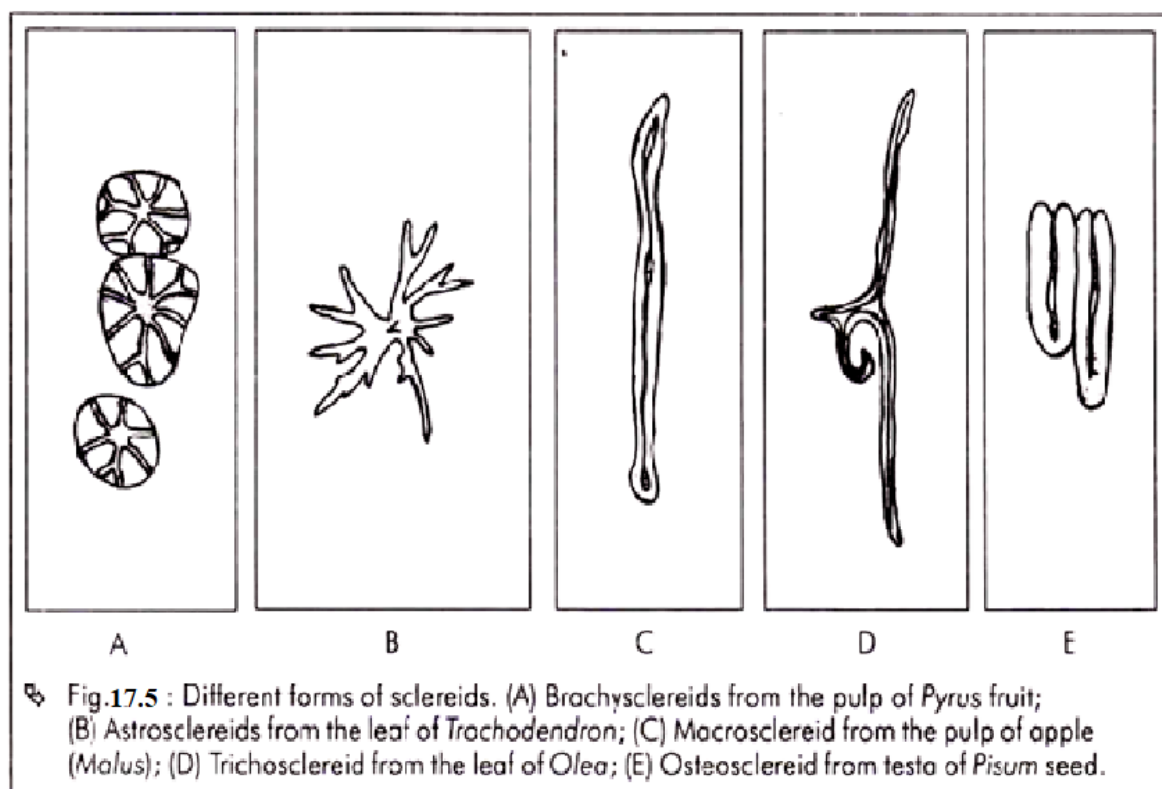
Fig. 17.4: End walls of some tracheae (vessel members) – (A) With simple perforation plate (SPF); (B) with multile (scalariform) perforation plates (MPF); (C) Complete tracheae with simple perforation plates, intervessel pitting (IP) and spiral thickening (ST); Tracheids – (D) with scalariform (E) with bordered pits (BP)

17.8. SCLEREIDS:

Sclereids, i.e. cells with very thick lignified walls, which are widely distributed in the plant body, have been used as diagnostic tools in several taxa like Connaraceae, Nymphaeaceae, Oleaceae, Theaceae, Umoniaceae, and a few genera of Araceae, Acanthaceae, Ericaceae and Melastomaceae (Fig. 17.5).

In dicots, they are more common in woody forms than in herbaceous ones, but they are extremely rare in monocots, except in certain genera of Araceae, Agavaceae, Arecaceae and a few other families. As they exhibit various shapes, sizes and characteristics of their walls, they have been of some taxonomic significance.

Two main types of sclereids have been recognized, viz. isomorphic and polymorphic types. The sclereid forms may be characteristic of a particular species and thus of taxonomic value.



17.9. CELLULAR CONTENTS:

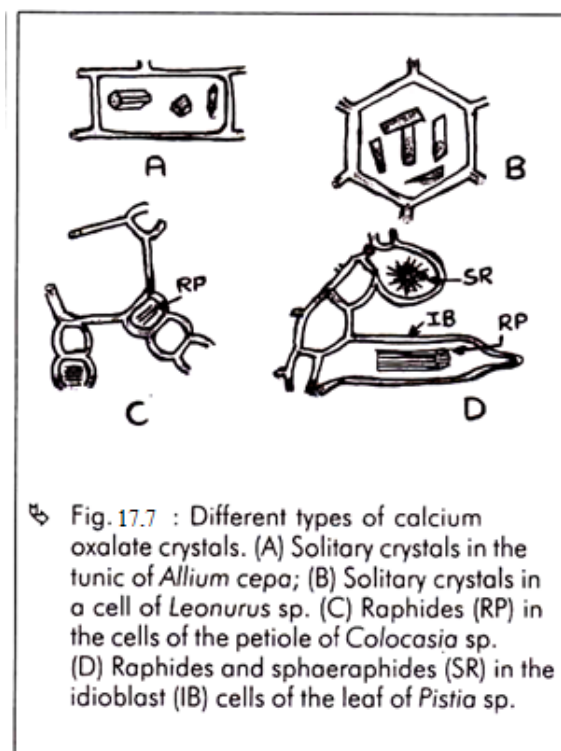
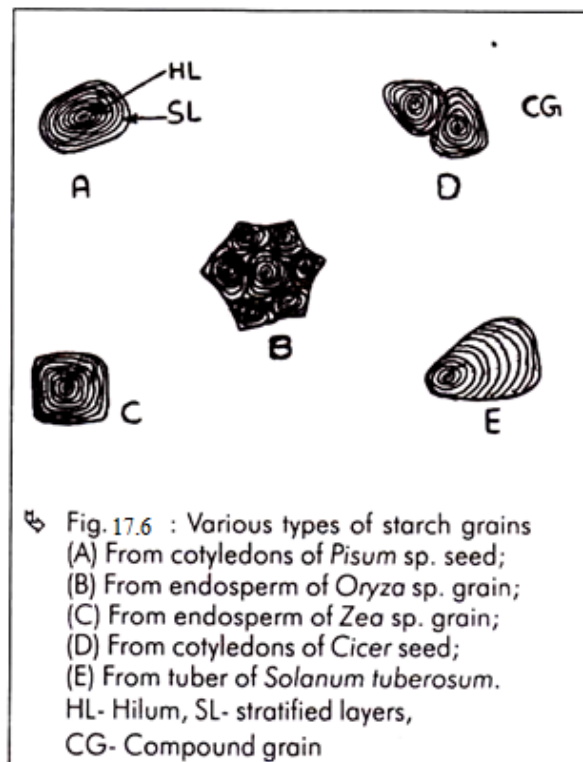
Many types of microscopic characters of cell contents i.e., chemical deposits, can serve as important diagnostic tools, and at times prove extremely helpful in delineating species, genera and families.

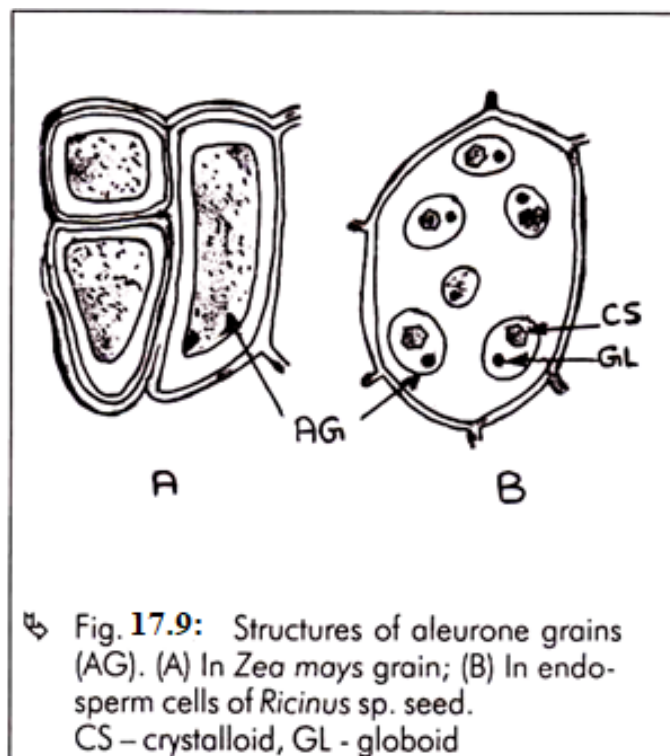
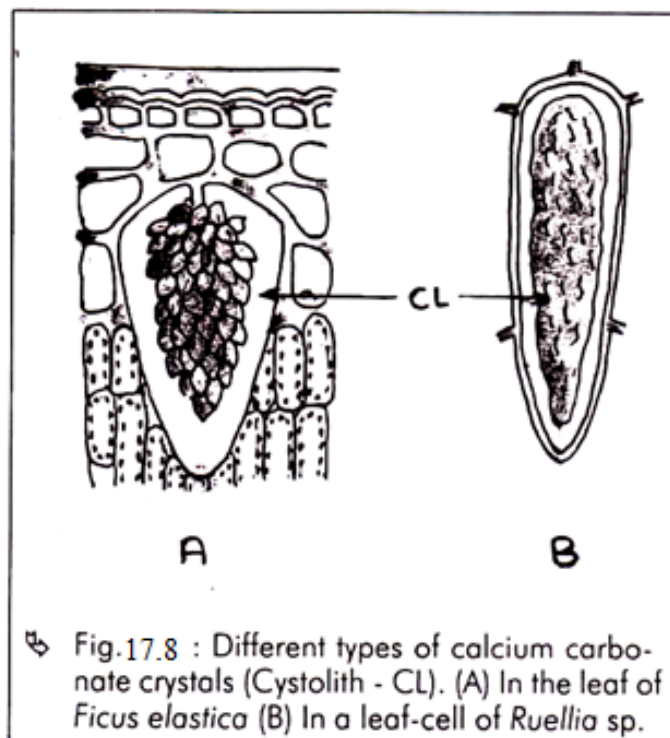
Crystals and crystalliferous cells have been found to be of systematic importance in several families of angiosperms such as Euphorbiaceae, Leguminosae, Verbenaceae, etc.

Some of the Important Chemical Deposits of Systematic Significance are as follows:

- Albuminoids - e.g. Laportea.
- Starch grains - The immense diversity in the types of starch grains (Fig. 17.6) may turn out to be a good taxonomic character for the angiosperms in general, e.g. *Solarium tuberosum*.
- Protein bodies - Deposition of solid protein depositions have systematic use, e.g. some Cactaceae.
- Large silica bodies - Silica bodies in the epidermal cells of various families like Arecaceae, Musaceae and Zingiberaceae and Rosaceae can be used at generic as well as specific levels.
- Calcium oxalate crystals - They are widely distributed in plants and are of different types, like prismatic, styloid and idioblasts (Fig. 17.7). Their distribution is very specific for a particular taxon and hence of taxonomic importance, e.g. *Eichhornia*, - *Allium*.

- f) Cystoliths (calcium carbonate crystals) (Fig. 17.8) - e.g. Cannabinaceae, Moraceae and Urticaceae.
- g) Tanniniferous cells - e.g. The presence and absence of tanniniferous cells in the root cortex of related families of Rapateaceae and Xyridaceae can be used as systematic criterion.





Apart from these, presence or absence of Laticifers, which are cells or a series of fused cells containing latex, and their structure, has also been of some taxonomic value. They are common features of many succulent plants and other plants of arid regions, and vary widely in their structure and the latex in their composition.

For example, certain species in Aroideae lack laticifers or any related structures, while others have longitudinal rows of elongated, cylindrical, sac-like cells.

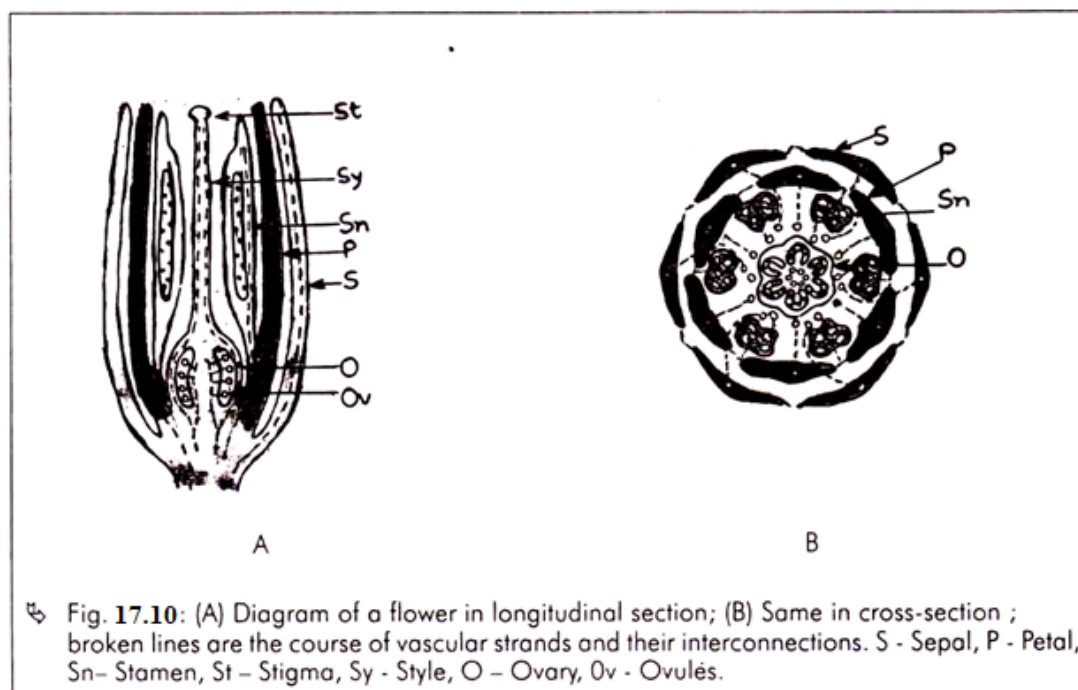
17.10. FLORAL ANATOMY:

As the reproductive organs show a high degree of conservation, they have been widely used in the classifications (Fig. 17.10A). At the same time, it is also quite likely that the vascular supply to these floral organs is also conservative and thus more reliable in taxonomic and phylogenetic interpretations (Fig. 17.11B).

The distribution and course of vascular bundles within the receptacle and floral parts have proved to be of systematic significance, particularly in ranking taxa of higher order such as genera and families. Even specific characters may be quite clear in some cases.

The significant role played by the floral anatomy in the solution of morphological problems has been greatly emphasized by Puri. Unlike other branches of anatomy, the application of floral anatomy to taxonomy is limited due to technical and interpretative difficulties.

However, with the development of rapid clearing techniques, this branch of investigation received a great impetus. The floral anatomical characters of families and genera are generally well marked and have been useful in solving some fundamental questions, like the nature of flower, carpel, inferior ovary and also several problems related with homologies, phylogeny and taxonomy.



Following are some of the examples of the contribution of floral anatomy in resolving the taxonomic position of some disputed taxa:

- a) Confirmation of the origin of the families of Annonaceae, Calycanthaceae and Menispermaceae from Ranunculaceae.
- b) Separation of Paeonia from Ranunculaceae and its inclusion under a separate family Paeoniaceae.
- c) Derivation of Polemoniaceae and Caryophyllaceae from a caryophyllaceous stock.
- d) Cyperaceae and Poaceae were formerly treated together in one single order. Later Hutchinson separated them and placed them in Cyperales and Poales respectively, which has been confirmed by floral anatomical studies of both the families.
- e) Inclusion of Solanaceae and Scrophulariaceae under one single order, Scrophulariales due to uniformity in floral vasculature.
- f) Confirmation of the close relationship between Cyrtandromoea and members of Scrophulariaceae based on the presence of several lateral traces in carpels, a bilocular ovary, and absence of a disc in both.
- g) Support for the removal of Lilaea from Scheuchzeriaceae and be placed under an independent family Lilaeaceae, because both differ in their vascular supply of flower and number of ovules.
- h) Confirmation of the transfer of *Hydrocotyle asiatica* L. to the genus *Centella* in the form of *Centella asiatica* L.

17.11. ULTRA STRUCTURAL SYSTEMATICS OF ANATOMY:

Electron microscopy has brought revolution in all biological fields, and so also in the field of taxonomy. Heywood and Dakhshini and Meywood have demonstrated and reviewed the benefits of scanning electron microscopy to plant systematics and have suggested that this ultra-structural device represents one of the most powerful taxonomic tools now available for systematic research.

Like the role of SEM in plant micromorphology, Transmission electron microscopy (TEM), aided by ultra-microtome techniques, have proved a powerful tool in studying various anatomical aspects of taxonomic significance. However, till date only a few ultra-structural characters have been exploited and applied in plant classification.

Some of These Characters are as follows:

(a) Dilated Cisternae (DC):

These structures are of common occurrence in the Cruciferae and of the order Capparales. Dilated Cisternae (DC) in the endoplasmic reticulum was first reported by Bonnet & Newcomb in the root cells of *Raphanus sativus* (radish).

Later they were also reported in the phloem parenchyma of foliar veins in *Brassica chinensis* and in *Capparis cynophallophora*. The significance of the endoplasmic reticulum in sieve elements has been focused by Spanner & Moattari, in the light of its evolutionary origin.

Depending upon their location in the cells, the internal structure of Dilated Cisternae is of following types:

They usually contain filamentous structures when present in the root cells. They contain protein tubules when present in other parts.

(b) Sieve-Tube Plastids:

The potential uses of ultra-structural features of sieve-element plastids, which are of systematic value, were noted almost a decade ago. Since then more than 1500 species from 380 families have been investigated by Behnke with regard to this character.

The plastid elements are of following types, depending upon their accumulation of starch and protein:

i. S-type—:

They are the plastid elements, which accumulate starch. About 65% of the flowering plants have such plastids in the sieve tube elements. They are present in the subclasses Dilleniidae, Hamamelidae, Ranunculidae, a great majority of the orders in the Rosidae, half the members of the Magnoliidae, a few orders in Caryophyllidae, Rhamnaceae.

ii. P-type—:

They are the plastid elements, which accumulate protein. They are further differentiated on the basis of their number and shape of the crystalloids as well as the nature of the filaments surrounding them.

They are present only in Pinaceae among Gymnosperms and among the Angiosperms, in all the 21 families of Monocotyledons and a few groups among Dicotyledons, such as Vitaceae and Leeaceae and half the members of the Magnoliidae.

iii. S₀-type—:

They are the plastid elements, which have neither starch, nor protein accumulations, e.g. Crassulaceae, Rafflesiaceae and some species of Moraceae, Ulmaceae and Urticaceae. According to Behnke, classification and delimitation of higher taxa in flowering plants can be aided by utilizing the different types of sieve-element plastids.

P-type is considered to be ancestral and the S-type is considered to have been derived from the P-type by loss of protein.

The heterogeneity of the Magnoliidae as to its plastid types is attributed to its basal position in the evolution of flowering plants. The presence of P-type plastids in all groups of Monocotyledons, and the preponderance of S-type in the basal groups of Dicotyledons, have been interpreted as an additional evidence for the independent origin of Monocotyledons and Dicotyledons.

A very good example of the use of plastids has been made in elucidating the inter-relationships and circumscribing the order Caryophyllales (Centrospermae).

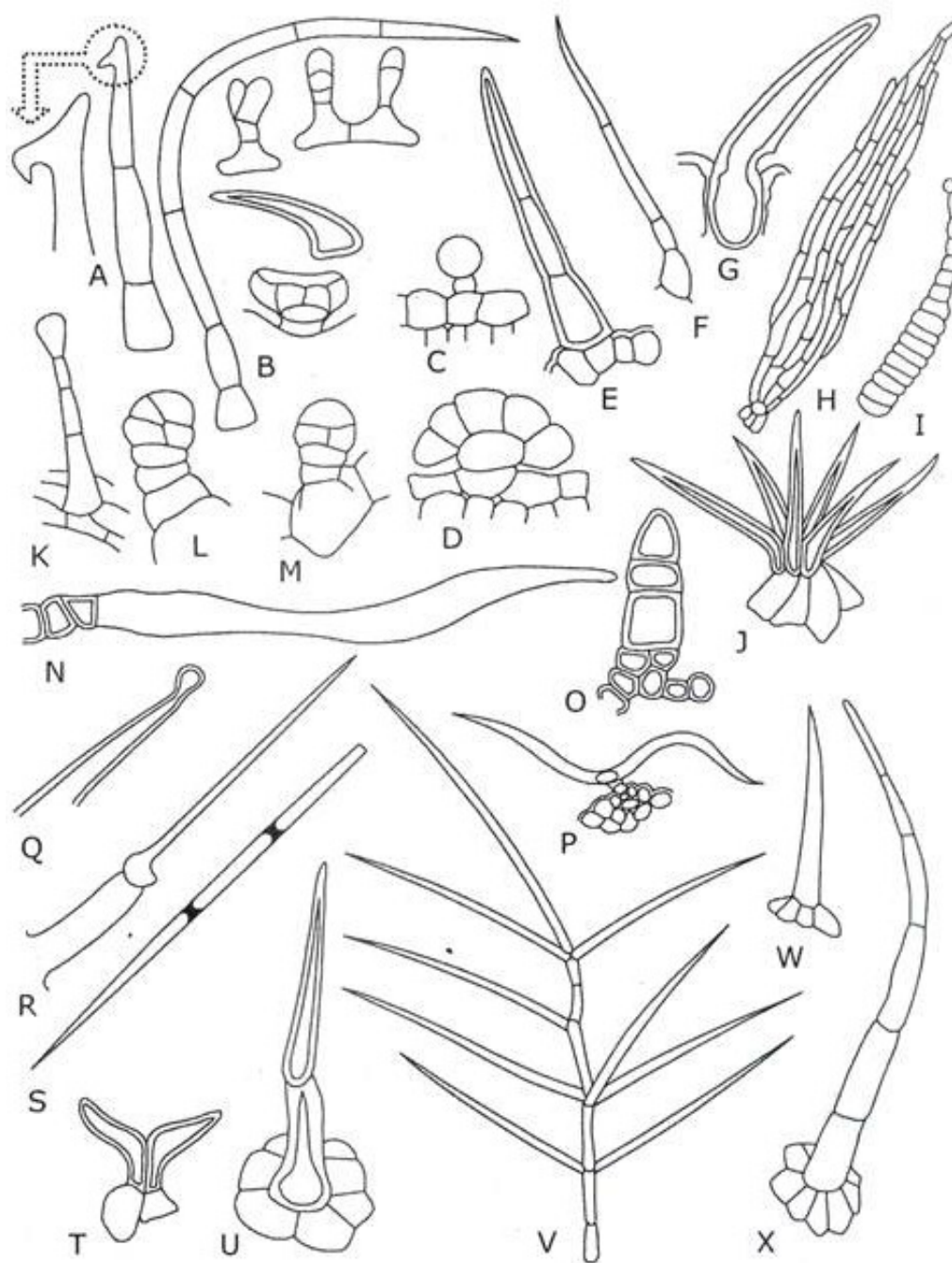


Fig. 17.11:

A. Hair of *Aphelia cyperoides*; B. Different hair types in *Mentha spicata*; C. Bicellular hair of *Salvia officinalis*; D. Multicellular hair of *Salvia officinalis*; E. Non-glandular hair of *Salvia officinalis*; F. Hair of *Centrolepis*; G. Hair of *Thamnochortus*; H. Surface view of hair of *Leptocarpus*; I. Glandular hair of *Cistus*; J. Dendritic hair of *Cistus*; K. Glandular trichome of *Pelargonium*; L. & M. Glandular trichome of *Cucurbita*; N. Hair of *Loxocarya*; O. & P. Hair of *Artemisia*; Q. & R. Glandular hair of *Urtica dioica*; S. Glandular hair of *Mucuna* containing irritant oil droplets; T. Hair of *Trigonobalanus*; U. Non-glandular hair of *Justicia*; V. Non-glandular hair of *Verbascum*; W. Non-glandular hair of *Coldenia*; X. Hair of *Origanum*.

A particular type of hair is constant in a species. This property is used as an aid to identify the different species of Oleaceae, Ficus and Rhododendron to some extent. Presence of T-shaped hair diagnoses the family Malpighiaceae. Trichomes provide the distinguishing characters within the family Icacinaceae where the genus *Ottoschulzia* is segregated from *Poraqueiba* on the basis of trichome characters.

Trichome types with their distribution pattern can be correlated with the sub-generic and specific distinction in *Nicotiana*. In Sparganiaceae and Typhaceae, the presence of sessile glandular trichomes provides a link between these families. Trichome anatomy is of immense significance in the separation of species and even varieties in the tropical family Combretaceae.

ii. Stomata:

Stoma has been shown to have great value in the taxonomy of several taxa. The distribution, morphology and ontogeny of a stoma are of taxonomic significance. Stoma is absent in roots. In exceptional cases it is reported from *Ceratonia siliqua* and *Pisum arvense* seedling roots.

Stomata are also absent from the chlorophyll-less parasitic angiosperm like *Monotropa* and *Neottia*. The submerged hydrophytes lack stoma. The floating hydrophytes i.e. *Nymphaea*, *Victoria* etc. are epistomatic (= stoma is present on upper surface of a leaf). Hypostomatic (stoma is present on lower surface of a leaf) leaf occurs on those plants that have xeromorphic habit.

Amphistomatic (= stoma occurs on both upper and lower surfaces of a leaf) leaf is observed in mesophytes. The stomatal frequency and stomatal index have taxonomic importance. The taxonomic groups and the different species of a genus can be differentiated on the basis of stomatal index.

The different morphologic and ontogenetic types of angiosperm stoma. They are of immense taxonomic significance. Metcalfe and Chalk provide a list of angiosperm families where different morphological types of stoma occur. It is shown that paracytic stomata characterize woody Ranales. So, it is regarded that such stoma is primitive among dicotyledons.

Sen and De (1992a) recognized 24 types of stoma in ferns among which polocytic stoma is regarded as the basic form from which the other types have ontogenetically been derived. The polocytic stoma is found in *Diplazium polypodioides* (Fig. 17.12G), *Cyathea contaminans* etc. This type of stoma has single subsidiary cell. The stoma is attached to the distal side of the subsidiary cell.

Thus, the subsidiary cell appears U-shaped or horseshoe shaped. Pant (1965) and Payne provide the different ontogenetic types of stoma. The diameristic and mesoperigenous stoma are thought to be primitive in the Embryophyta. It is to note that monocotyledons are characterized by the above patterns of stoma. In monocots stoma with two or more subsidiaries appears to be more primitive than those with none.

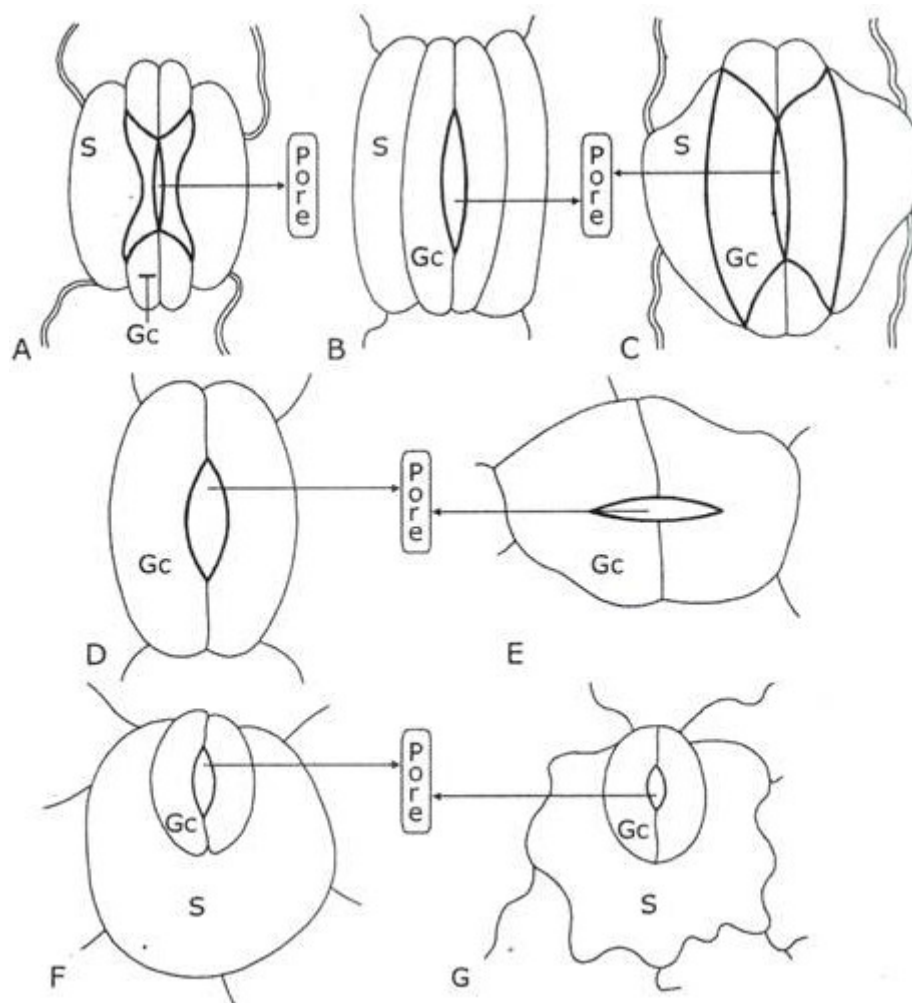


Fig. 17.12:

Diagram illustrating the types of guard cell and polycytic stoma. A. Dumb-bell type: The cell wall of guard cell is thinner at the polar ends than the other walls. Each guard cell is much narrowed in the middle and so it has dumb-bell like appearance in surface view. B. Rectangular type-A: The cell wall of guard cell is uniformly thick. Each guard cell is of uniform breadth in surface view. C. Rectangular type-B: The cell wall of guard cell is thinner at the polar ends than the rest of the walls. Each guard cell is of uniform breadth. D. Elliptic type: Each guard cell is as broad as long or longer than broad. The cell is reniform or more or less uniformly wide. Pore of stoma occurs parallel to guard cells. E. Right-angle type: Each guard cell is shaped like U or V. The contiguous wall of guard cells determines the stomatal axis, also referred to as polar axis of stoma. The pore of stoma occurs approximately at right angles to stomatal axis. The polar axis is frequently shorter than the equatorial diameter. F. Polycytic stoma (diagrammatic). G. Polycytic stoma of *Diplazium polypodioides*.

The surface view of guard cells of a stoma can be of taxonomic significance. Rajagopal and Ramayya classified five types of guard cells on the basis of their appearance in surface view under light microscope (Fig. 17.12). The types are (a) dumb-bell type (ex. *Cyanodon*), (b) rectangular type-A (ex. *Eriocaulon*), (c) rectangular type-B (ex. *Cyperus*), (d) elliptic type (ex. *Scilla*, *Mollugo*) and (e) right-angle type (ex. *Azolla*).

The dumb-bell type guard cells characterize the family Gramineae. The monocotyledonous families like Cyperaceae, Restionaceae, Juncaceae, Marantaceae etc. show rectangular type-B guard cells. In dicotyledon rectangular type-B guard cell is reported from *Haloxylon articulatum* (Chenopodiaceae) only. The rectangular type-A guard cells occur in the monocotyledonous families like Xyridaceae, Eriocaulaceae and Palmae.

The elliptic type of stoma is the characteristic of gymnosperms, dicotyledons, most of pteridophytes and some monocotyledonous families like Dioscoriaceae and Liliaceae. Rajagopal and Ramayya regarded that within the monocotyledons the above types of guard cell might have value at higher taxonomic levels. The leaf of *Pinus pinea* shows circular raised rim above the stoma. The epidermal cells form the rim. It is revealed by the scanning electron micrograph. The raised rim is termed as Florin ring.

iii. Veins:

The veins and their innumerable variations in leaf venation pattern provide various characters of taxonomic importance. The anatomical division of Angiosperm into dicotyledon and monocotyledon is based on venation pattern.

With a few exceptions' dicots have reticulate venation and monocots show parallel venation. The veins are the vascular strands or traces that diverge from the vascular cylinder of stem at the nodes. In dicotyledons they may consist of one, three or many traces. These traces and other accessory strands collectively form diverse patterns or types of venation.

In a dicotyledonous leaf the veins may be primary, secondary and tertiary. The primary vein is the widest vein in the leaf. It originates at or just above the petiole. It is usually symbolized as 1° veins. The secondary veins are narrower than the primary. It originates from the primary vein. It is usually symbolized as 2° veins. The tertiary veins are narrower than the secondary.

It may originate from secondary and primaries. It is usually symbolized as 3° veins. (Fig. 32.6). The primary and secondary veins are the structural veins of a leaf. The tertiary veins fill the field of the leaf. The primary and secondary veins gradually taper towards the margin. The tertiary veins connect primary and secondary veins thus forming a more or less regular polygonal field over the leaf area.

A polygonal field is usually designated as vein-islet. Apart from above types most dicotyledonous leaves have higher orders of veins, i.e. after tertiary there are 4°, 5° veins category and they may be up to 7°. In the lamina of many leaves the vein terminates blindly as veinlets in the mesophyll. These veinlets are termed as vein endings. The sieve tube elements are absent from vein endings.

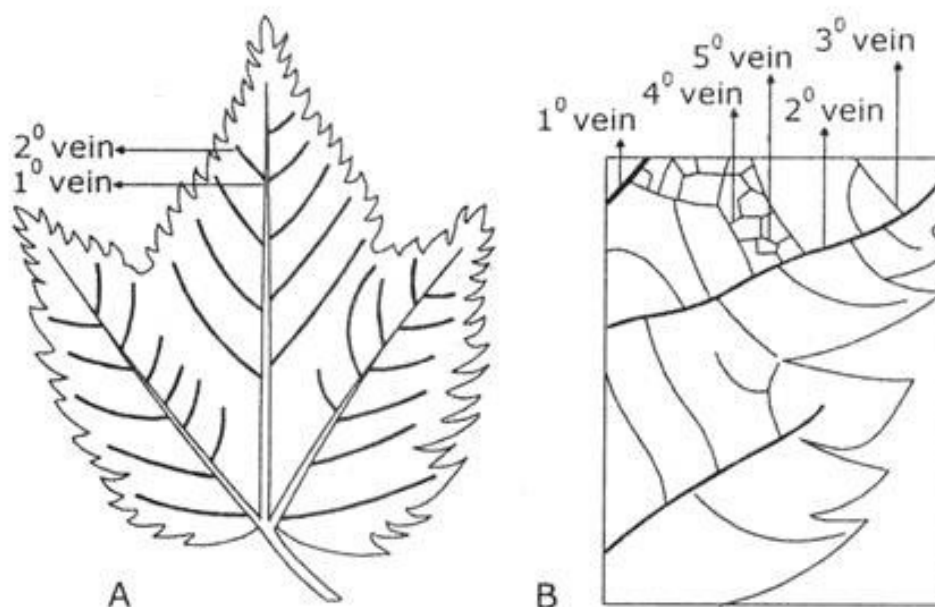


Fig. 17.13:

A. Diagram of a leaf of *Acer argutum* showing 1° and 2° veins. B. A portion of A enlarged showing 1°, 2°, 3°, 4° and 5° vein.

The different categories of vein provide many characters that are very useful in leaf identification. The 1° veins may be single, three or more. The 2° veins form an angle with 1°. The angles are constant in a species. The angles may be uniform, abruptly increasing towards the base, smoothly decreasing towards base etc.

The spacing between 2° veins is also of taxonomic significance. It may be uniform, irregular and increasing or decreasing towards the base. The 3° veins show different angles to 1° (Fig. 32.14A, B, C, & D). The course of 3° veins may be straight, convex and sinuous (Fig. 32.14E, F, and G). The number of vein-islets in a unit area is species-specific.

Usually four-square millimetre area of a leaf is considered as a unit in counting the vein-islet numbers. The ultimate free endings of vein-lets have diagnostic value. They may be unbranched, linear or curved 1-branched, 2 or more branched etc. The following features of veins provide taxonomic information.

The veins may or may not be raised above the two epidermises of a leaf. Bundle sheath may be absent or present in vascular bundle, which is the cross-section of veins. When present it surrounds the vascular bundle and may be one or two layered, parenchymatous or sclerenchymatous.

In two-layered bundle sheath both the layers may be parenchymatous or sclerenchymatous, or the inner layer is parenchymatous and the outer layer is composed of sclerenchyma. Chloroplastids may be present or absent from the cells of bundle sheath. Bundle sheath extension may be absent or present and when present it may be composed of parenchyma, collenchyma or sclerenchyma.

It is taxon specific. Hickey (1973, 1974) provides terminologies for the description of leaf form and venation. This enables to identify and classify dispersed leaves. The foliar characters may or may not offer conclusive evidences of affinities, but generally they do allow distinguishing the closely related species.

Moreover, the diverse patterns of venation can be utilized in the morphological interpretation of such organs as bracts, sepals and petals. The leaf epidermal characters such as pattern of epidermal cells, cuticular ornamentation, and the patterns of leaf wax structure as revealed by means of electron microscopy have, of late, been demonstrated to be of taxonomic importance of many taxa.

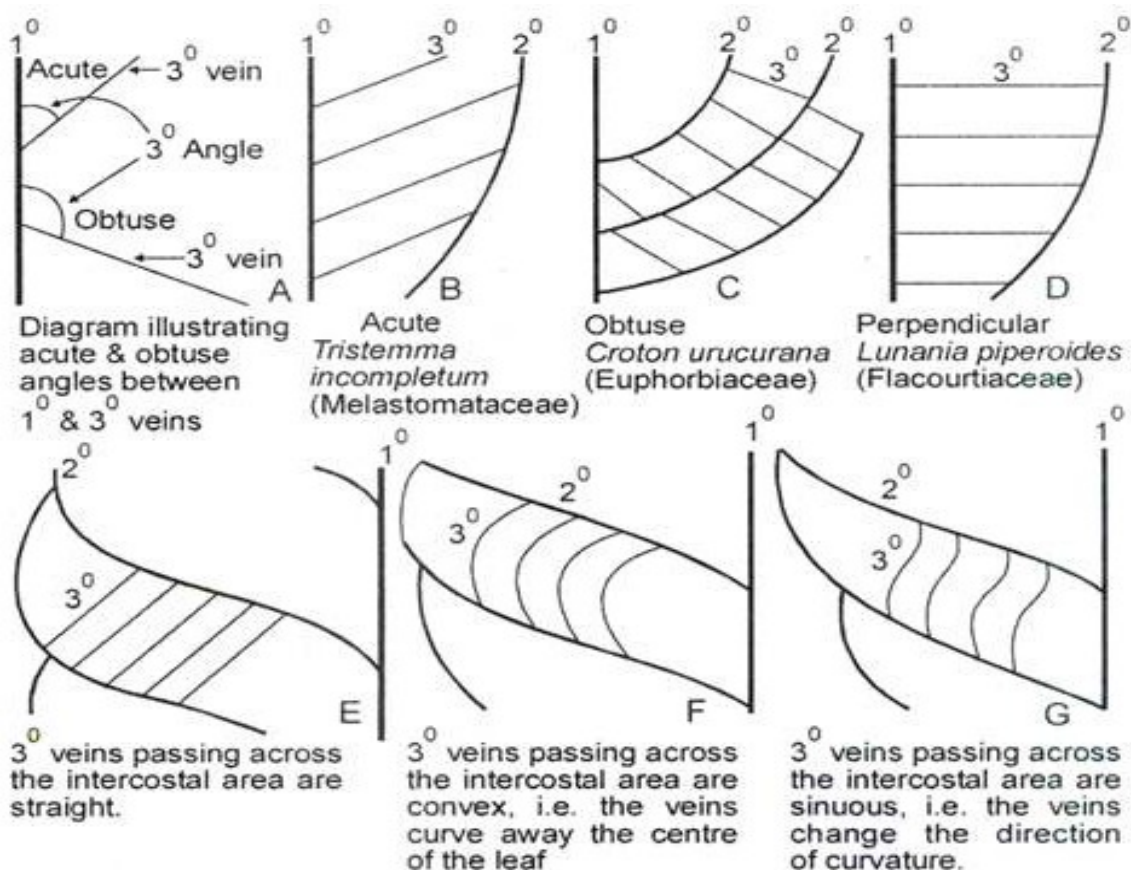


Fig. 17.14:

Diagram illustrating the angles formed between 1^0 and 3^0 veins (A, B, C, D) with terminology and the course of 3^0 veins in the intercostal areas (E, F, G).

Crystals, especially calcium oxalate crystals, silica bodies on the epidermal cells, foliar sclereids with their types and distribution are taxon specific and hence taxonomically useful.

The measurement called palisade ratio is taxon-specific and hence it is often used to identify a leaf or fragments of leaf. Pharmacognosists frequently use this measurement to authenticate the leaf drug that is mostly obtained in powdered forms. The palisade ratio indicates the number of palisade cells present beneath each epidermal cell.

The cells of epidermis and palisade are observed and counted from surface views. A large number of counts are recorded and an average number is determined from the counts. The average number obtained from a statistically sound count provides a fairly reliable identifying datum of materials.

Example:

The palisade ratio of *Swertia angustifolia*, *S. chirata*, *S. paniculata* and *S. dilatata* is 2.94, 2.06, 3.27 and 6.5 respectively.

The other taxonomically useful anatomical features are stem, leaf and root anatomy, nodal anatomy, wood anatomy, primary and secondary anomalous structure, ultra-structure of sieve tube, plastids etc.

Examples where Anatomical Features Solved Taxonomic Problems:

There are numerous examples where the anatomical features were used in solving taxonomic disputes, a few of which are mentioned below.

The ultra-structure of sieve tube plastids was used in circumscribing taxa. Sieve tube plastids are broadly of two types-starch accumulating (S-type) and protein accumulating (P-type). The S-type occurs in Polygonaceae, Plumbaginaceae, Batqceae, Theligoniaceae etc. whereas the P-type is found in Phytolaccaceae, Molluginaceae etc.

There are certain families like Rafflesiaceae, Crassulaceae, and some species of Moraceae etc. where the sieve tube plastids accumulate neither starch nor protein. The ultra-structural details of sieve tube plastids are taxon-specific and hence taxonomically useful. It was best used in elucidating the inter-relationships in the order Caryophyllales.

Mabry (1976) segregated the order into two sub-orders - Chenopodiineae and Caryophyllineae, on the basis of pigment biochemistry. Chenopodiineae comprises the betalain containing families and Caryophyllineae includes the anthocyanin containing families - Caryophyllaceae and Molluginaceae.

The nature and character of the ultra-structure of sieve tube plastids suggest that the betalain and anthocyanin families are closely related since all of them possess P-type plastids with a peripheral ring-shaped bundle of proteinaceous filaments. Betalain and anthocyanin families both have characteristic anomalous secondary thickenings and primary anomalous structure.

Moreover, anatomical and palynological evidences provide no basis for splitting the Caryophyllales into Chenopodiineae and Caryophyllineae. Gisekia has been included under the anthocyanin family Molluginaceae. Unlike other Molluginaceae Gisekia possesses betalain instead of anthocyanin.

So Takhtajan (1980) preferred to shift the genus to the Phytolaccaceae that has several characters common with Gisekia. Gisekia shows globular crystalloid P-type plastids in sieve elements like Molluginaceae and Phytolaccaceae. From the available data from plastid structure, pigmentation and palynology its alignment with Phytolaccaceae is indicated.

The monotypic species *Halophytum ameghinoi* has often been associated with Chenopodiaceae. Chenopodiaceae and *Halophytum* both possess P-type plastids with ring shaped bundle of filaments. But Chenopodiaceae lacks the crystalloid in the ring-shaped bundle of filaments. In contrast *Halophytum* possesses globular crystalloid in the ring-shaped bundle of filaments.

So, the structure of sieve element plastids does not favour its association with the Chenopodiaceae. Thelegoniaceae had been placed often close to or even into Caryophyllales.

The presence of S-type plastid and anthocyanin argues against its incorporation into the Caryophyllales. On the basis of the plastid data *Dysphania* can be included in the Chenopodiaceae. It possesses P-type of plastid with ring-shaped bundle of filament; but it lacks the central crystalloid.

Anarthria and *Ecdeiocolea* were included under the family Restionaceae. Later a survey on anatomical and macro-morphological features of these two genera resulted in the recognition of two families - Anarthriaceae and Ecdeiocoleaceae. The stem anatomy of most Restionaceae shows a continuous parenchymatous cylinder that is absent in the other two families.

Below the epidermis there exists a zone of chlorenchyma in all the three families. The stem anatomy of Ecdeiocoleaceae shows the presence of hypodermal sclerenchyma, which is absent from Restionaceae. In Anarthriaceae there exists the sub-epidermal fibre strands associated with vascular bundles.

17.12. SUMMARY:

Plant anatomy is crucial in taxonomy for classification and understanding evolution, using stable internal features like leaf venation, stomata type, wood structure, vascular bundles, and trichomes to resolve identification issues, define groups (like monocots vs. dicots), and reveal evolutionary relationships beyond simple external morphology. It helps distinguish species, families, and higher taxa, especially when visual traits are ambiguous, providing reliable evidence for phylogenetic studies and confirming modern molecular data.

Key Applications in Taxonomy are

- 1) **Resolving Ambiguities:** Provides consistent characteristics (e.g., epidermal patterns, sclereids) to separate plants with similar external features.
- 2) **Defining Taxa:** Helps establish scientific criteria for defining and separating plant genera, families, and orders, as seen with the recognition of new families.
- 3) **Phylogenetic Studies:** Reveals evolutionary relationships by analyzing structural differences and similarities, supporting or refining classifications based on other data (morphological, molecular).
- 4) **Identifying Fragmentary Material:** Essential for identifying plant parts (wood, pollen, leaves) in forensic, archaeological, or economic contexts, linking specimens to broader taxonomic groups.
- 5) **Distinguishing Major Groups:** Key features, like parallel leaf venation in monocots vs. reticulate in dicots, help differentiate major plant types. In essence, plant anatomy offers a stable, microscopic layer of evidence, supplementing external features to build robust and accurate plant classification systems.

17.13. MODEL QUESTIONS:

- 1) Explain in detail the Anatomical evidence can be useful in systematics in several ways
- 2) Describe different types of Anatomy
- 3) Explain Ultra Structural Systematics of Anatomy

17.14. REFERENCE BOOKS:

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