

APICAL MERISTEMS

CC-4
UNIT-4

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Unit 4: Apical meristems

Evolution of concept of organization of shoot apex (Apical cell theory, Histogen theory, Tunica Corpus theory, continuing meristematic residue, cytohistological zonation); Types of vascular bundles; Structural differences of dicot and monocot stem, root & leaf, Kranz anatomy. Organization of root apex (Apical cell theory, Histogen theory, Korper-Kappe theory); Quiescent centre; Endodermis, exodermis and origin of lateral root.

Apical meristems

In higher plants, the shoot apical meristem (SAM) gives rise to all the above-ground organs. It is supposed to be the site of organogenesis in flowering plants.

It contains all the necessary information of shoot building and its pattern formation in the form of cell signalling.

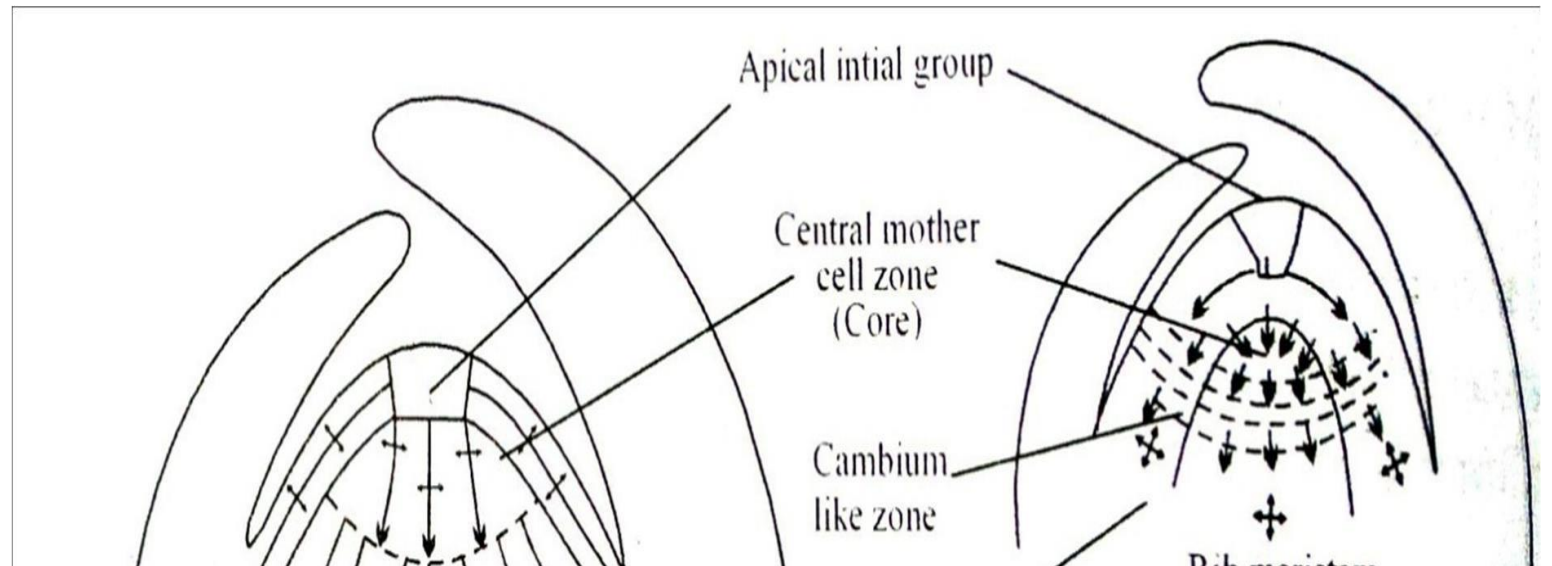
The SAM supplies cells that divide and differentiate to form the elements of the shoot. It also initiates the lateral organ formation and decides their anatomical features and cell division patterns.

Primordia of leaves, sepals, petals, stamens and ovaries are initiated at SAM. First indication of flower development appears in the form of loss of the apical dominance.

Shoot Apical meristems

The SAM gives rise to:

- (a) **Central zone:** It is located in the center of the SAM and acts as a pool of undifferentiated, indeterminate cells. Cells of this zone have a stem cell (initial cell) function and are essential for meristem maintenance. Here the cell division is less frequent.
- (b) **Peripheral zone:** This zone flanks the SAM, its cells divide more frequently and are incorporated into leaf primordia.
- (c) **Rib zone:** It is the proximal region. It supplies the cells that form the body of the stem.

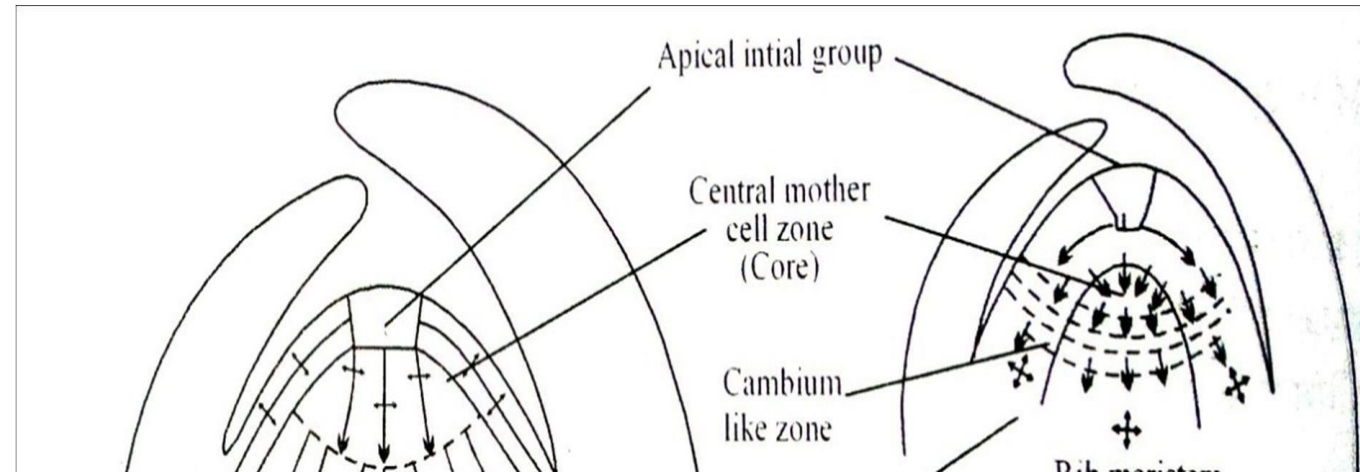


Gymnospermous shoot apical meristems

Here, cellular organization in different phases of development has not been seen.

But, Foster (1939) identified interrelated cellular regions in 4 different regions and named them as:

- (a) Apical initial group
- (b) Central mother cell zone
- (c) Rib meristem
- (d) meristem or flank meristem.



Further, Prophan and Chan (1950) and Singh and Singh (1970) proved a cambium like region below the youngest leaf primordium in *Chrysanthemum morifolium* and *Ricinus* sp., respectively.

Theories related to shoot apex organization

Multiple theories have been proposed to understand the structure and organization of shoot apical meristem:

1 Apical Cell Theory

2 Histogen Theory

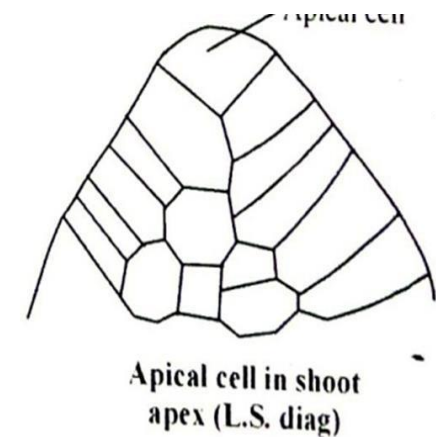
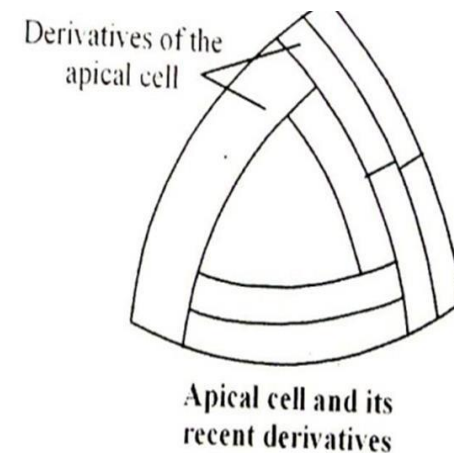
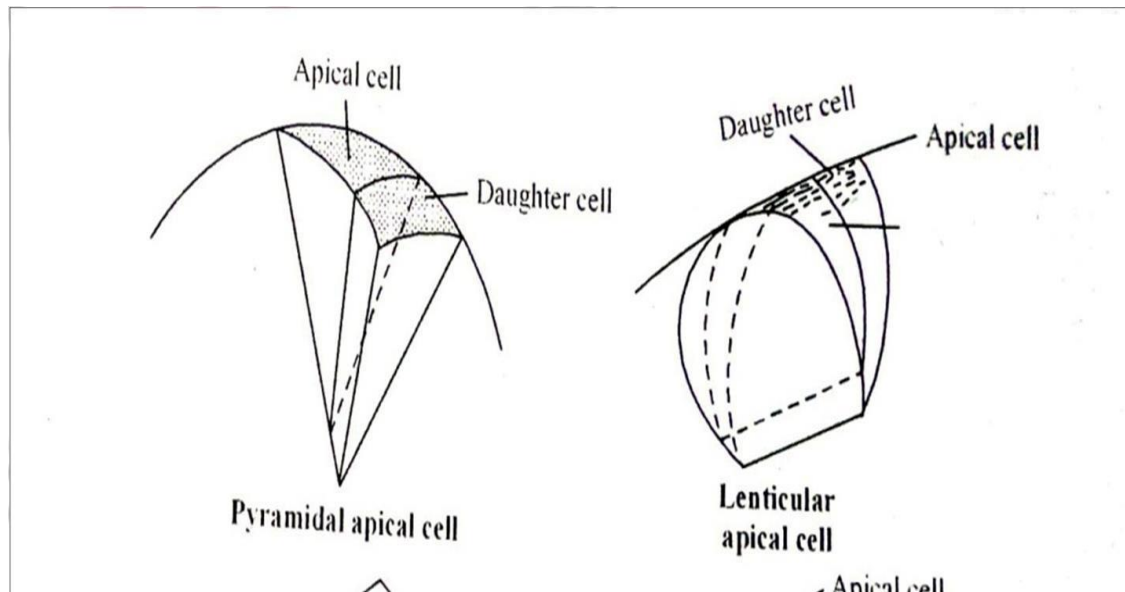
3 Tunica Corpus Theory

4 Mantle-Core Theory

5 Histogen Layer Theory

Apical Cell Theory

- This theory was proposed by Hofmeister (1957) and elaborated by Nageli (1978).
- According to this theory, the apical cell of shoot is always in most active state.
- Various tissues of shoots are formed by the activity of this apical cell.
- Apical cell of the shoot apex also exhibits differentiation and regulatory function necessary for pattern formation.
- The apical cell gives rise to new cells by cutting one or two cells on its posterior face. These cells transform into tissues in the later stage.



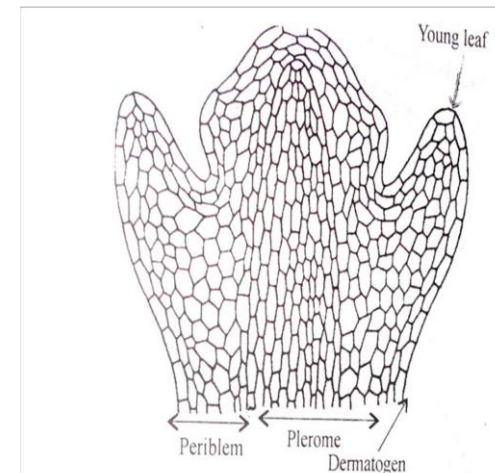
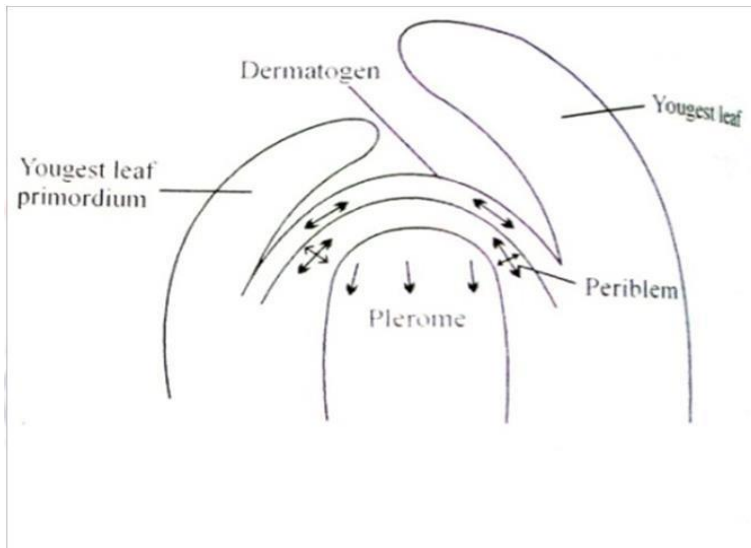
Apical Cell Theory

This theory efficiently explains growth and differentiation process in some higher algae, bryophytes and some pteridophytes, but failed to explain the structure and organization of shoot apex in phanerogams, i.e. gymnosperms and angiosperms, since the shoot apices of phanerogams consist of many cells.

Histogen Theory

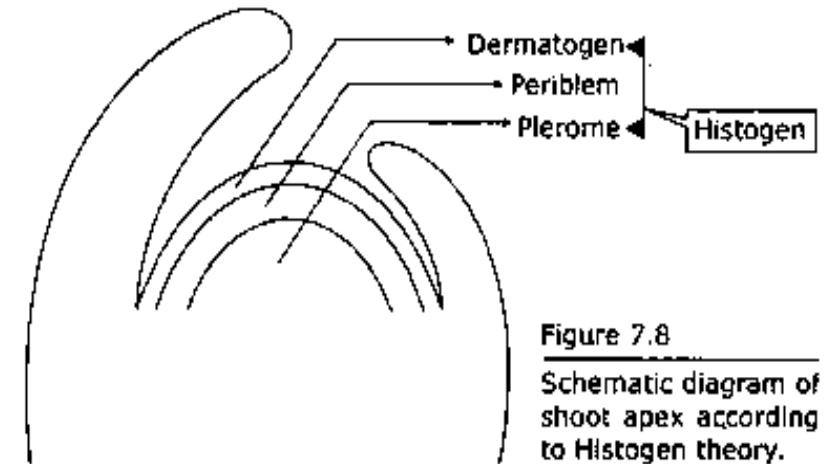
Hanstein (1970) proposed this theory after studying the shoots and embryos of many angiosperms. He identified 3 clear-cut regions in shoots and roots-

- (i) **Dermatogen:** This is the outermost layer of cells. It forms epidermis of the stems.
- (ii) **Periblem:** This region is just below the dermatogens. It is unilayered at apical regions but multilayered at lower regions. Division and differentiation of this region gives rise to hypodermis, general cortex and endodermis.
- (iii) **Plerome:** This is situated at inner side of periblem and middle part of the shoot apex. This is made of thin layered isodiametric cells. This forms the stellar tissues, viz. pericycle, primary vascular tissue, medullary rays and medulla. Additionally, it also gives rise to procambium situated at sub-apical region in the shoot.



Histogen Theory

- Histogen theory is not suitable for the explanation of shoot apex because there is no clear-cut demarcation between dermatogens and periblem.
- Thus, histogen theory is used to explain the growth of the root apices only.



Demerits Histogen Theory

Later investigations reveal that the sub-divisions — dermatogen, periblem and plerome have no universal application due to the following two reasons:

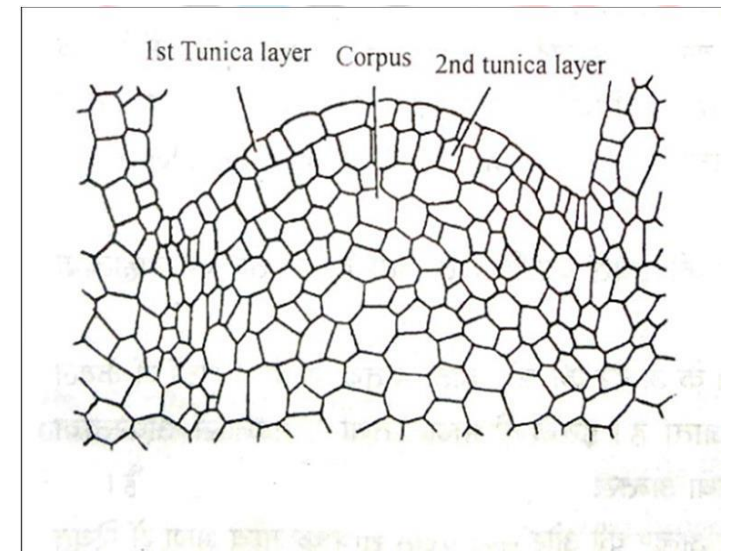
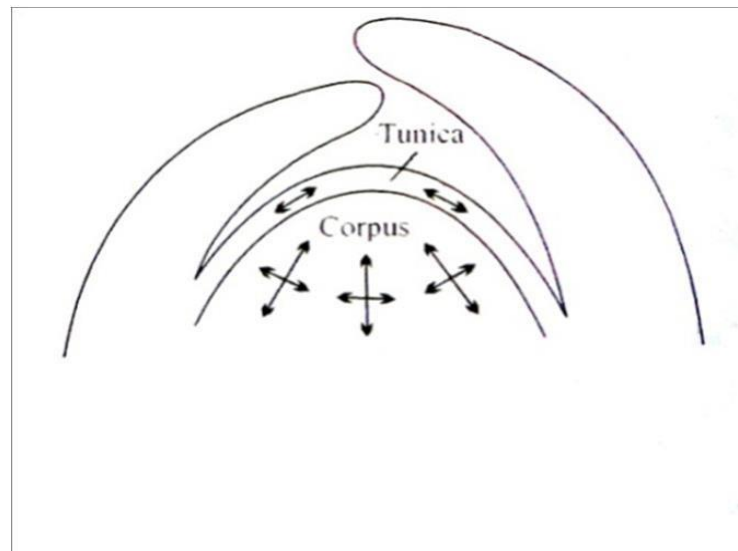
- (i) In gymnosperm and angiosperm there exists no clear distinction between periblem and plerome.
 - (ii) The respective roles of the three histogens cannot be demonstrated.
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- The main weakness of Hanstein's concept was to assign specific destinies of histogens.
 - The histogens — dermatogen, periblem and plerome are committal and respectfully give rise to epidermis, cortex and stele.
 - Later this theory was superseded by tunica- corpus theory.

Tunica Corpus Theory

- This theory was proposed by Schmidt in 1924 to explain the apical growing regions of shoots only (and not used to explain the growth of root apices).
- According to this theory, two regions viz. tunica and corpus are found in shoot apical regions.

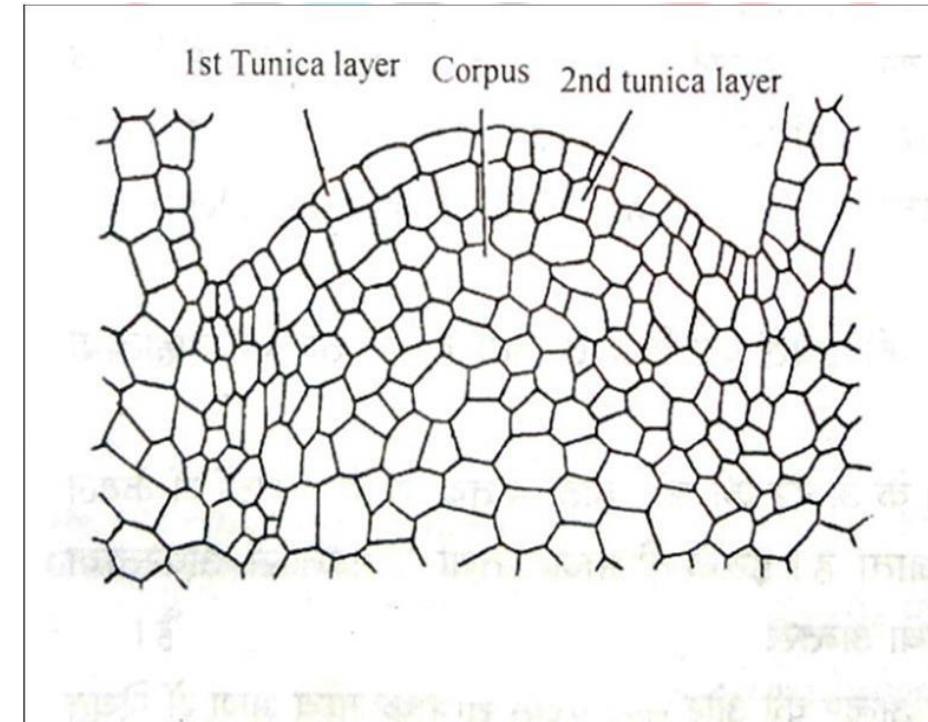
Tunica:

- Tunica comprises one or many outer layers of shoot apex. Cells of tunica region are cut only by anticlinal divisions.
- Tunica expands the surface of shoot apex, and its outer most layer gives rise to epidermal layer.



Tunica Corpus Theory

- Tunica covers the corpus wherein cells divide in all directions and volume of the shoot increases.
- By studying the shoot apex in many angiosperms, it becomes clear that in some special cases, tunica divides by periclinal divisions also along with anticlinal divisions.
- In monocots, the tunica determines the physical characters of the leaf edge and margin. In dicots, corpus determines the characteristics of the edge of the leaf.



Tunica Corpus Theory

Cytologically two zones are recognized in the tunica though all cells exhibit the same anticlinal cell division.

The first zone is central apical zone and the second occurs between the central apical zone and leaf primordium.

- 1. The central apical zone consists of one or few initial cells that are larger and contain large nuclei and vacuoles than the cells of the second zone.**
- 2. The cells of the second zone are small and more darkly staining than the cells of the first zone. In contrast to first zone periclinal division may occur in the second zone close to the leaf primordium in addition to anticlinal division.**

Tunica Corpus Theory

Corpus:

- Central moCorpus is the innermost bulky tissue zone of shoot apex. It consists of cells that are several cell layers deep. Tunica overarches corpus.
- Meristematic tissues composing this zone are larger than tunica.
- The cells of corpus are arranged haphazardly, as opposed a good the neat linear arrangement of tunica.
- cells of corpus show both anticlinal and periclinal division. It is destined to give rise cortex and vascular tissue.

Tunica Corpus Theory

- **Corpus:**
- **Usually corpus is not homogeneous. It consists of several zones. The corpus is composed of three zones:**
 - (a) the cells —the uppermost zone of corpus.**
 - (b) Pith-rib meristem that occurs below the central mother cell zone.**
 - (c) Flank meristem (also called peripheral meristem) surrounds both central mother cell zone and pith-rib meristem.**

The peripheral zone is shaped like a truncated hollow cone. The component cells of tunica and corpus differ in size, shape, plane of cell division and topography. Ultrastructurally each zone is composed of cells that have characteristic architectures as is revealed by quantitative techniques.

Merits of tunica-corporis theory

- It deals with one thing, i.e. planes of cell division. As a result the description of meristem becomes precise.**
- ii) It has topographical value in the studies of development of different tissue system in plants.**
 - iii) The destiny of derivatives of corpus is not predetermined.**
 - iv) The derivatives of the zones are not rigid like histogen theory.**
 - v) It explains clearly the growth pattern in the shoot apex of angiosperm.**
 - vi) It enables to understand the development of leaves as they arise close to apex.**
 - vii) The specific variation in the number of tunica layers may be of taxonomic significance, e.g. grasses.**

Limitations of tunica-corporis theory

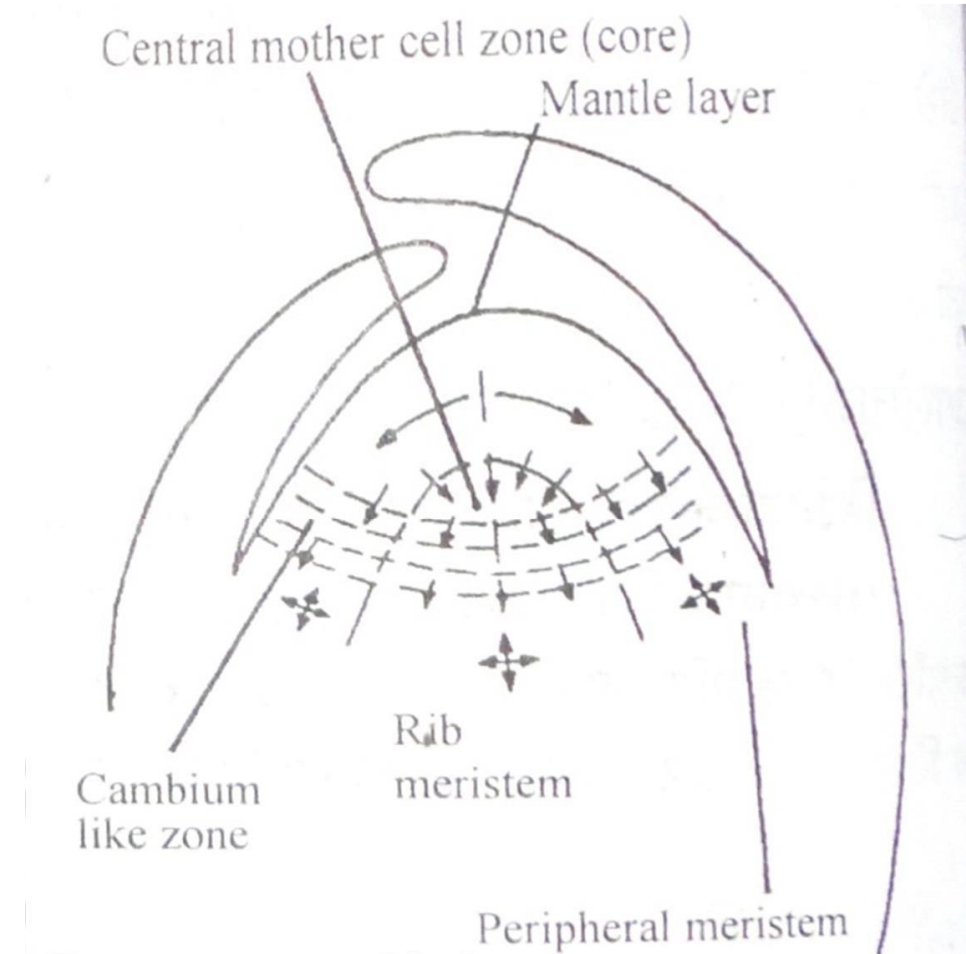
Tunica-corporis organization of shoot apical meristem is observed in angiosperm only. Cryptogams and majority of gymnosperm do not exhibit tunica-corporis organization. They do not have any stable surface layer that divides only by anticlinal division .

Mantle-Core Theory

Propham and Chan (1950) proposed this theory to explain the division in peripheral tissues in shoot apical regions of some angiosperms.

This theory is similar to tunica-corporis theory.

This theory does not rely upon the manner by which the cells divide; it only states that mantle is peripheral cellular region of the shoot apex. Mantle covers the central core region.



Histogen Layer Theory

Dermen (1947) defied tunica-corpus theory and proposed histogen layer theory.

According to this theory, shoot apex of angiosperms is organized in 3 layered structure. They may be called as L-I, L-II and L-III.

According to this theory, epidermis of leaves and stem develop from L-I; hypodermis, cortex and some of the vascular bundle regions develop from L-II; while vascular tissues and medulla develop from L-III.

Organizational form of shoot apex in 3 layers gives this theory a modified version of histogen theory.

Cyto-histological zonation

▪ The shoot apices of angiosperm exhibit cytohistological zonation in addition to tunica corpus zonation.

▪ zones are recognized namely:

- (1) Tunica initials-that consist of an apical group of cells,
- (2) Corpus initials-that occur below apical initials and are similar to central mother cells,
- (3) A peripheral zone and
- (4) Rib meristem.

- Tunica initials contribute cells to central mother cell zone and to peripheral meristem.
- The central mother cell zone donates cells to the rib meristem and pith.
- peripheral meristem is highly meristematic. Leaf primordia originate from this layer

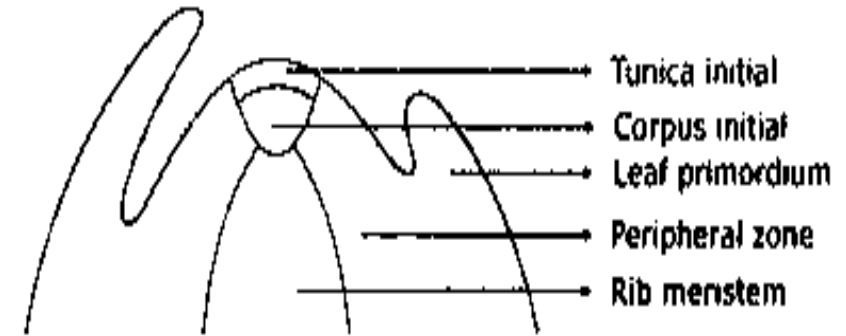


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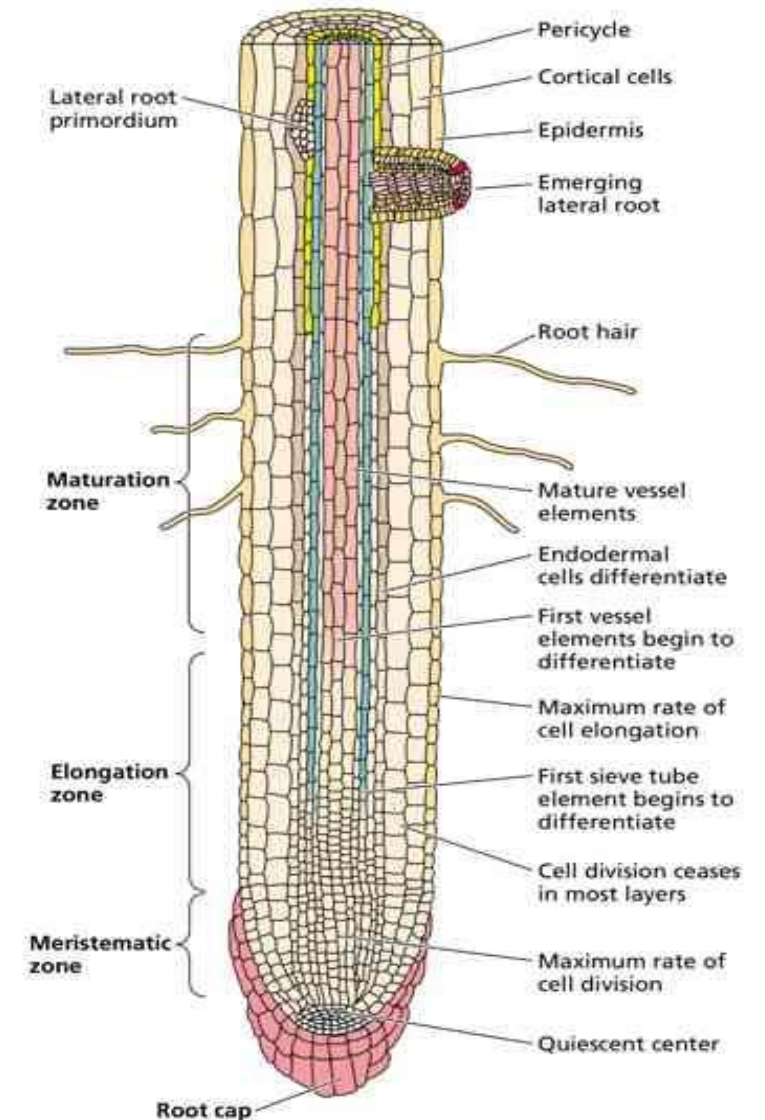
Diagram illustrating the cytohistological zonation of apical meristem.

Root Apical Meristem (RAM)

Root apical meristems

Root apical meristems (RAM) are the sub-apical region of apical portion of the roots wherein meristematic cells are situated. They produce different internal tissues of roots. This region has following distinctive features:

1. It is always sub-terminal region because it is covered by the root cap.
2. Neither any lateral appendage or branch or their growth zone, e.g. leaf or branch primordia are attached to the RAM.
3. It is smaller than the shoot apex.
4. The cells of RAM consistently divide and their activity enables the roots to grow in positively geotropic and negatively phototropic direction.



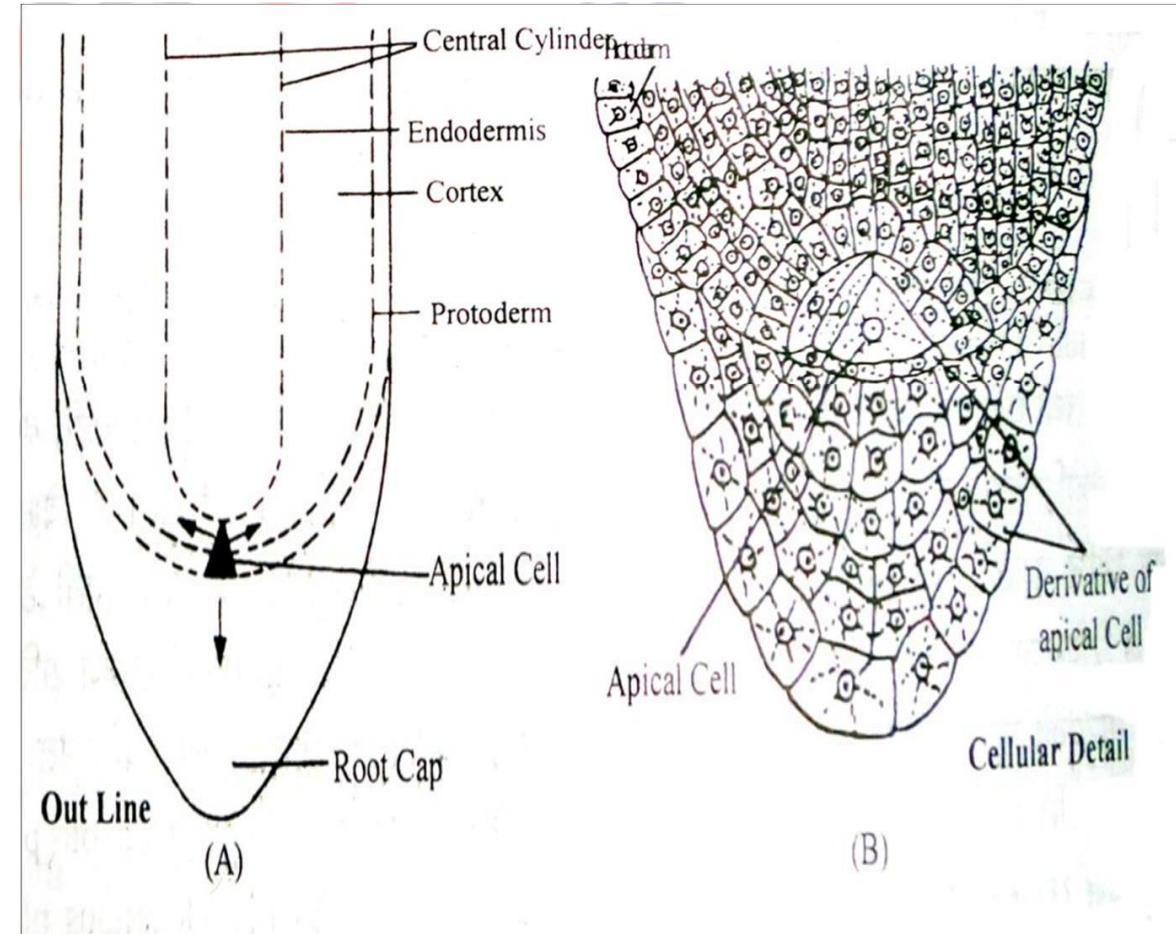
Theories related to root apex organization

Multiple theories have been proposed to understand the structure and organization of root apex:

- 1 Apical Cell Theory**
- 2 Histogen Theory**
- 3 Korper-Kappe Theory**
- 4 Quiscent Centre Concept**

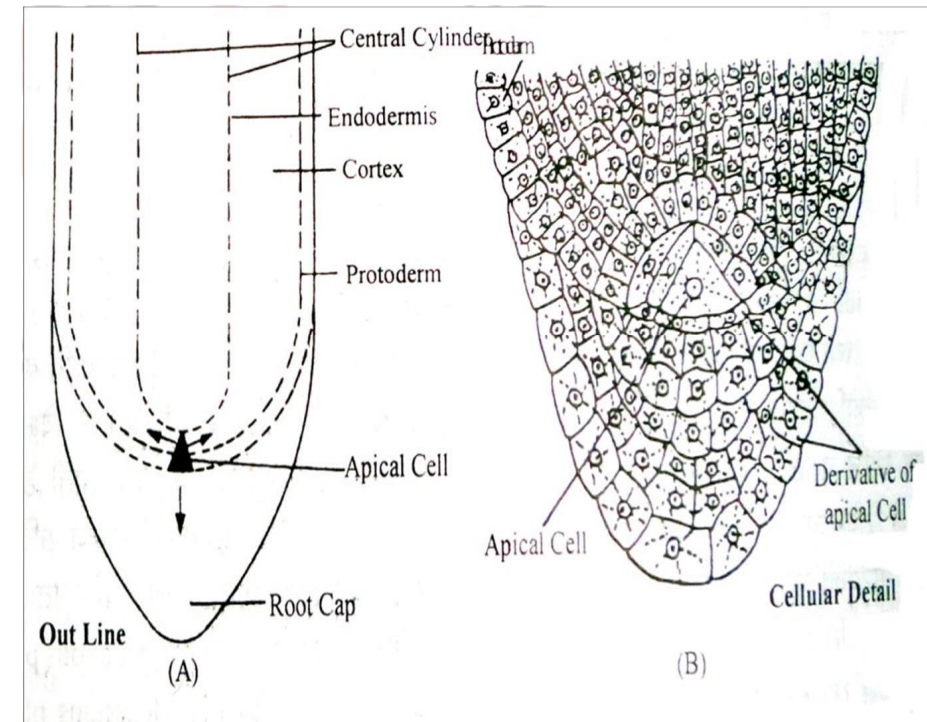
Apical Cell Theory

- This theory was proposed by Hofmeister (1957) and later elaborated by Nageli (1978).
- According to this theory, there is a tetrahedral cell in root apex which divides in three planes producing different tissues of roots.
- Division in the basal plane of this tetrahedral cell gives rise to root cap.



Apical Cell Theory

- This theory is acceptable for some of the pteridophytes, e.g. polypodiaceae, Ophioglossaceae, Equisetaceae and Azollaceae because the differentiation and formation of various tissues and related regions in these plant groups becomes possible due to the activity of one apical cell.
- For example, according to Gunning et al. (1978) and Hardham (1979), the apical cell of root apex in Azolla divides for about 55 times to initiate root growth.
- However, this theory failed to explain the structure and organization of root apex in spermatophytes, i.e. gymnosperms and angiosperms, because there are group of meristematic initial cells in and angiosperms in the apical portion of the root apex which actively divide differentiate to form different tissues of roots.



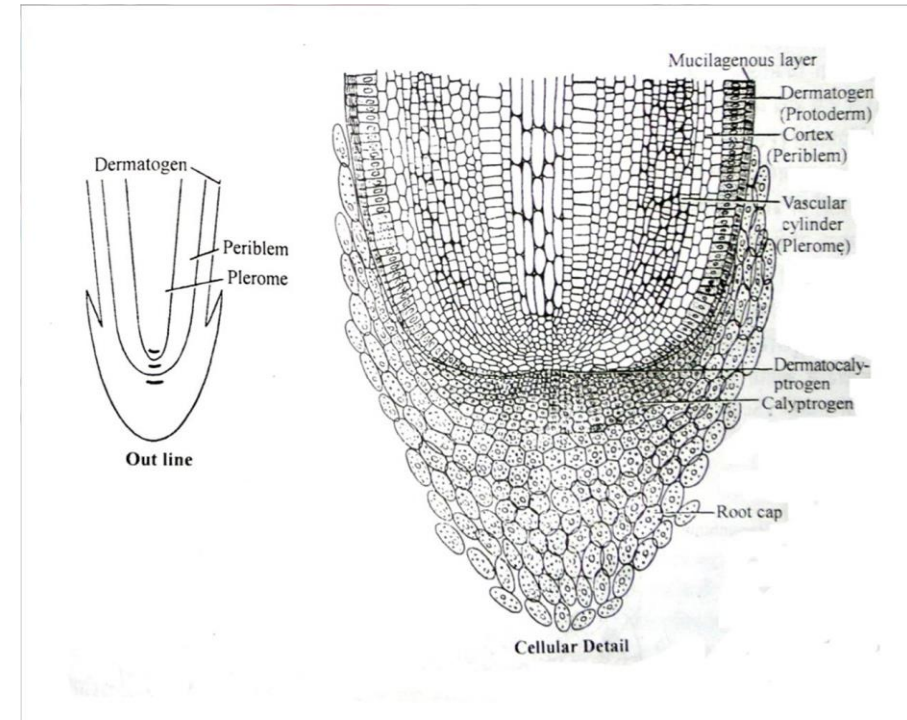
Histogen Theory

Hanstein (1970) proposed this theory after studying the shoots and embryos of many angiosperms.

He asserted that the meristematic cells of root apex are made of 3 layers exactly similar to shoot apical meristems.

He identified the presence of 3 regions in shoots and roots:

(i) Dermatogen: This is the outermost layer of the cells of root apex and divide to form new cells. Later it produces tissues consisting smaller cells, called as calyptrogens. Calyptrogen is also a kind of meristematic cell and its activity makes root cap. Dermatogen produces epidermis.

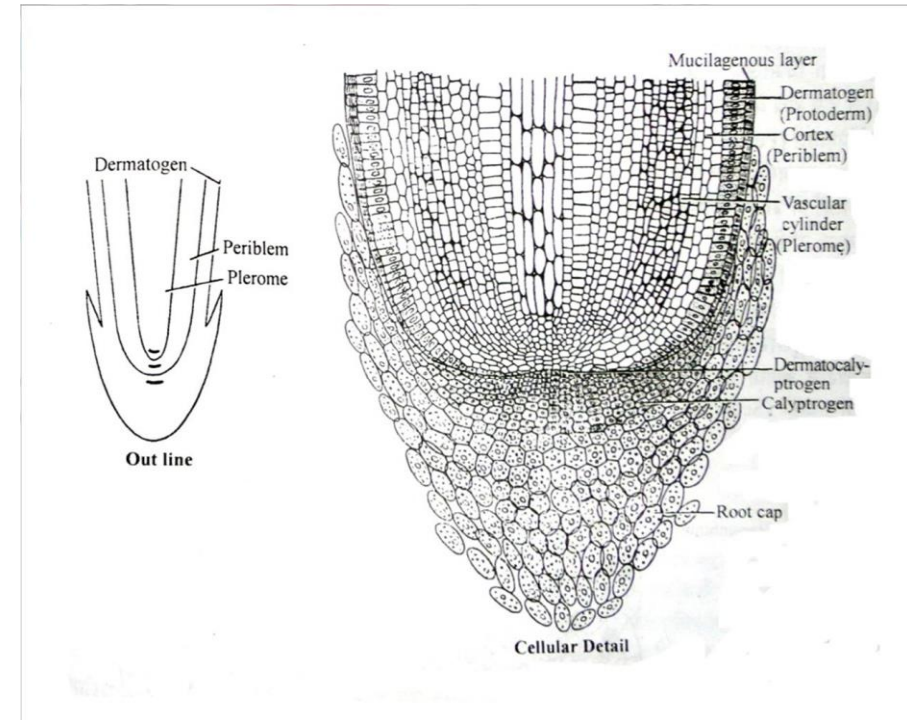


Histogen Theory

(ii) Periblem: This region is just below the dermatogen layer. This region is apical most or middle portion of the root apex. This is single layered at apical portion but becomes multilayered in middle portion. Division and differentiation of this region gives rise to cortical region of the roots.

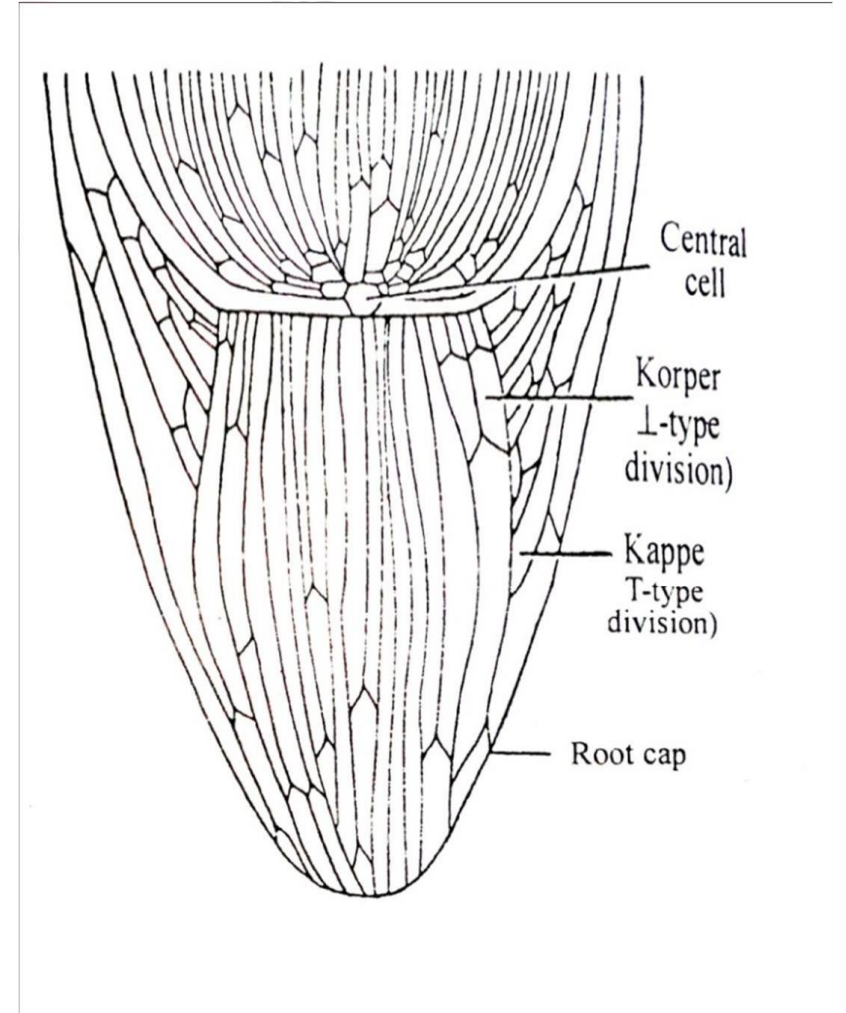
(iii) Plerome: Plerome is the central meristematic part of the apical meristem of the roots. This forms the stelar tissues, some parts of ground tissues like, pericycle, pith rays or medullary ray and pith.

These three layers were collectively called as histogen.



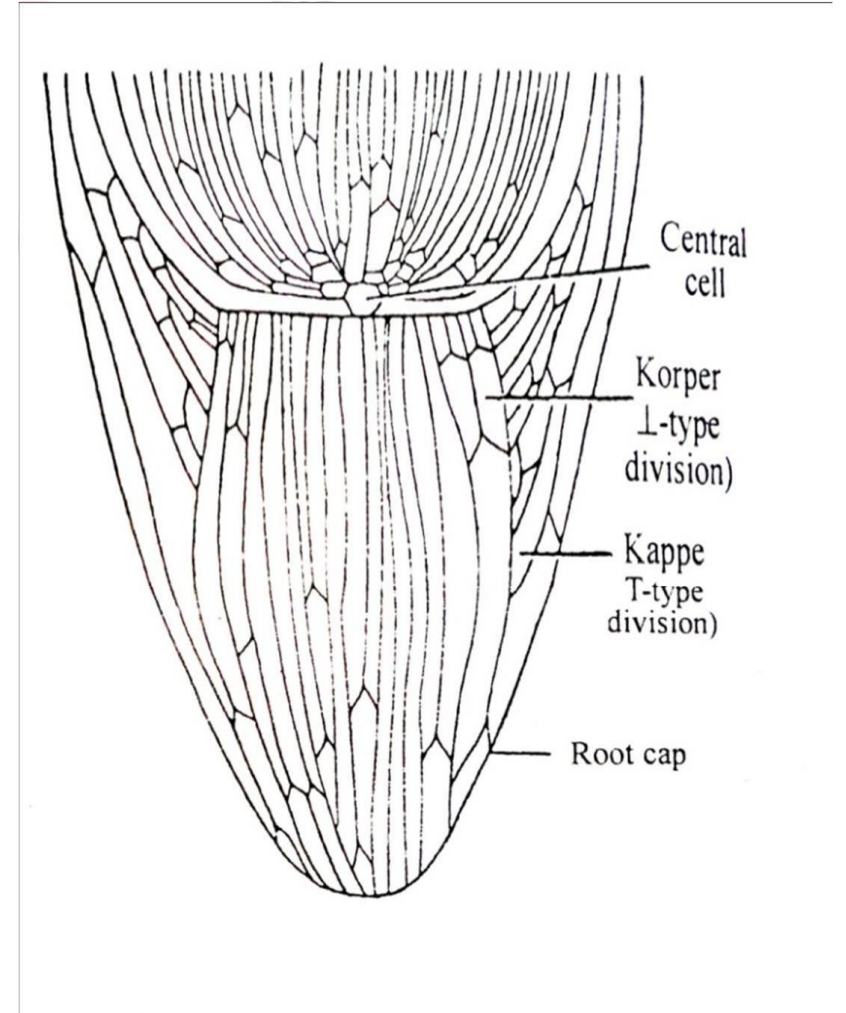
Korper-Kappe Theory

- This theory was proposed by Schuepp (1917).
- According to this theory, the cells of root apex are divided into two elements. The first division is of transverse type resulting into two cells, out of which one divides anticlinally, called as T- division.
- In some of the portions of the root apex, especially in the middle portion 'T' is seen upright while in rest of the regions, inverted T is seen (\perp).



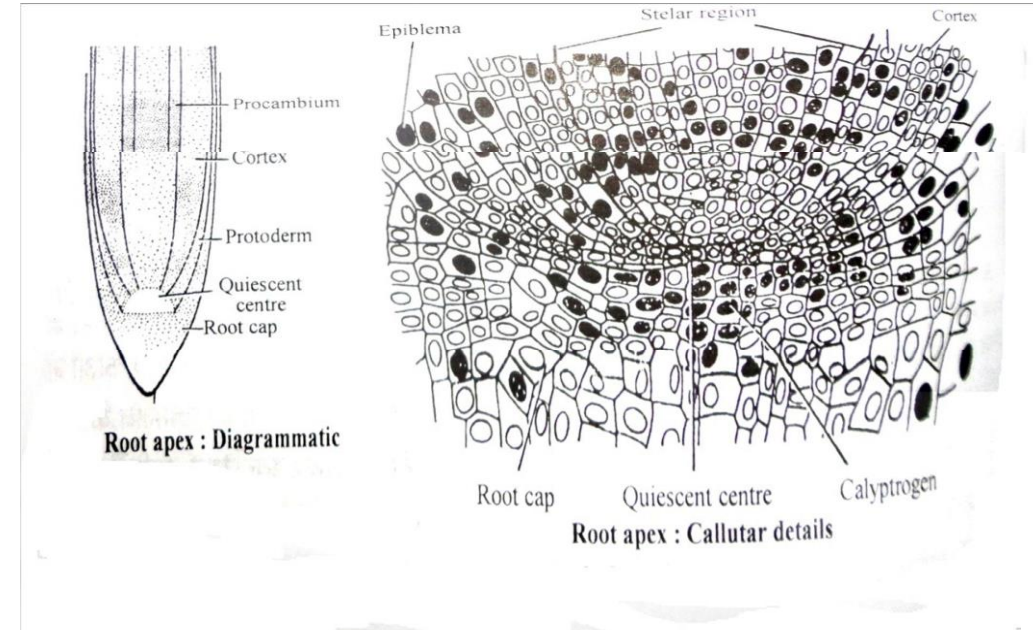
Korper-Kappe Theory

- When 'T' is upright, then this is directed towards the apical portion, but, when 'T' is inverted, it is directed opposite to the apical portion.
- Schuepp named upright 'T' as Korper or body while inverted 'T' was named as Kappy or cap.
- Such type of division is found in the members of poaceae.
- This theory is equivalent to the Tunica-Corpus Theory of shoot apex.



Quiescent Centre Concept

- This concept was given by Clowes (1958).
- He studied root apex in *Zea mays* and ascertained the presence a cellular region in between root cap and meristematic cells called as Quiescent Centre (QC).
- The cells of QC remain inactive and often do not divide.
- Unlike the shoot apical meristems, the root apical meristems which flank the QC produce cells in two dimensions at its periphery and together produce most of the cells in an adult root. He recognized these cells as constituent of promeristem.
- At its terminus, the root meristem is covered by the root cap, which protects and guides its growth trajectory.
- Cells are continuously shed-off the outer surface of the root cap.



Quiescent Centre Concept

- The cells of quiescent centre have lesser DNA, RNA and protein content.
- These cells have lesser number of ER and mitochondria.
- and nucleolus are smaller in size.
- The QC cells are characterized by their low mitotic activity as they are maintained at the G1/S checkpoint in the cell cycles.
- Rate of DNA replication is lesser than those of other cells.

Function: QC acts as a reservoir of root cells to recover whatever is lost or damaged. The QC cells are pluripotent and are the source of stem cell initials. The cells of quiescent centre remain inactive till the peripheral cells are in active stage of division, but start to divide in unfavorable condition, especially when roots are destroyed somehow and also when secondary roots are formed.