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Programme: M.Sc., Botany

Course Title: Anatomy, embryology and morphogenesis
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UNIT -III

Embryology

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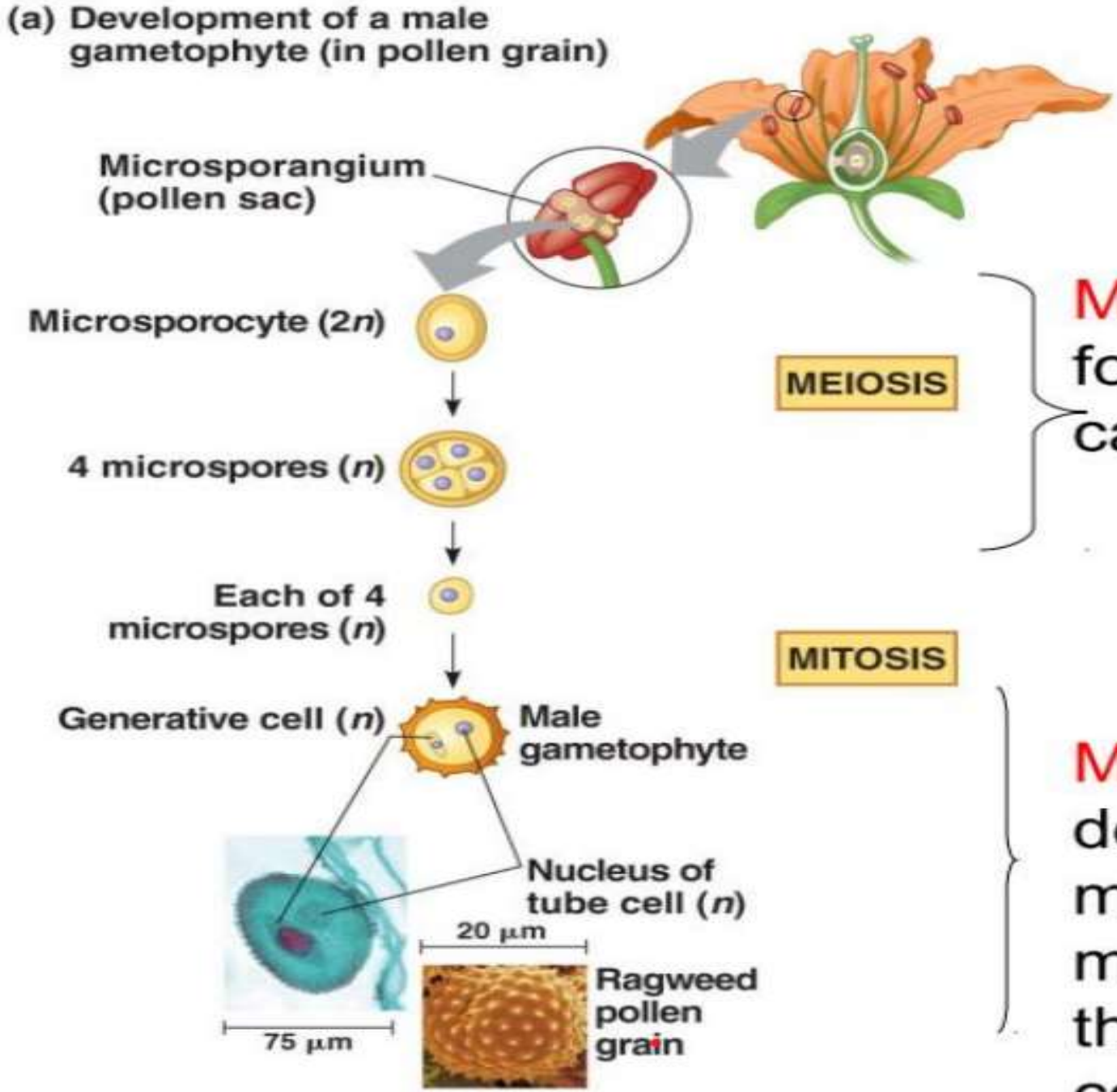
EMBRYOLOGY

Plant embryology is the study of the development of embryos, gametophytes, and sporangia in land plants. It covers the development of microsporangia, microspores, pollen grains, ovules, megaspores, female gametophytes, and seeds in seed plants.

MICROSPORANGIUM

Microsporangium is a structure in the plant’s male reproductive organ where the development of pollen takes place.

- Microsporophyll or the stamen is the male reproductive part of the flower, which consists filament, anther and connective.
- Anther is the fertile part of microsporophyll sometimes it is sterile called staminode.
- The filament is the slender stalk of the stamen and the anther is the expended head borne by the filament at its tip.



Microsporogenesis- formation of spores called microspores

Microgametogenesis- development of microspore into the microgametophyte or the pollen grain containing sperm cells

Structure of Stamen

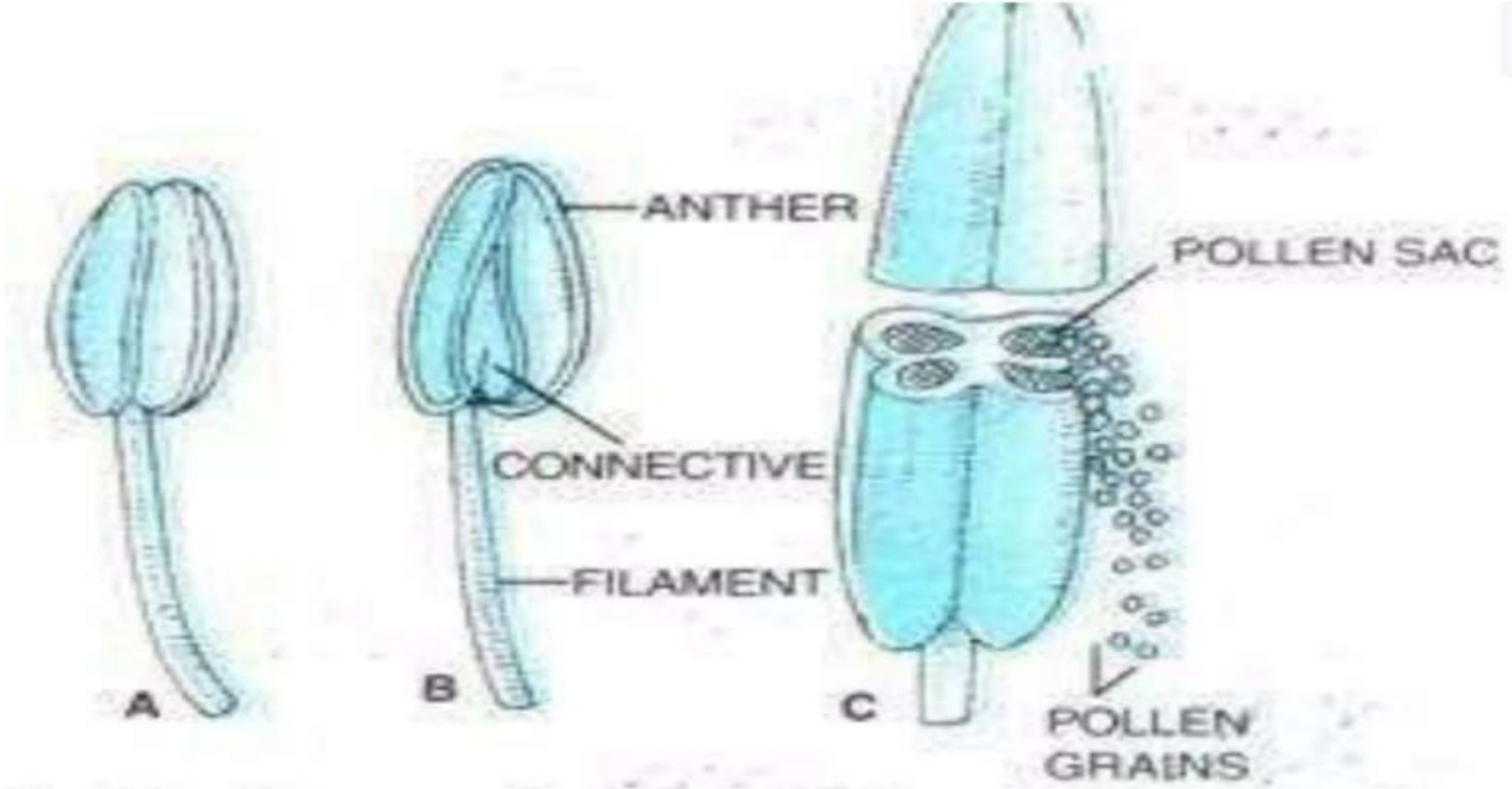
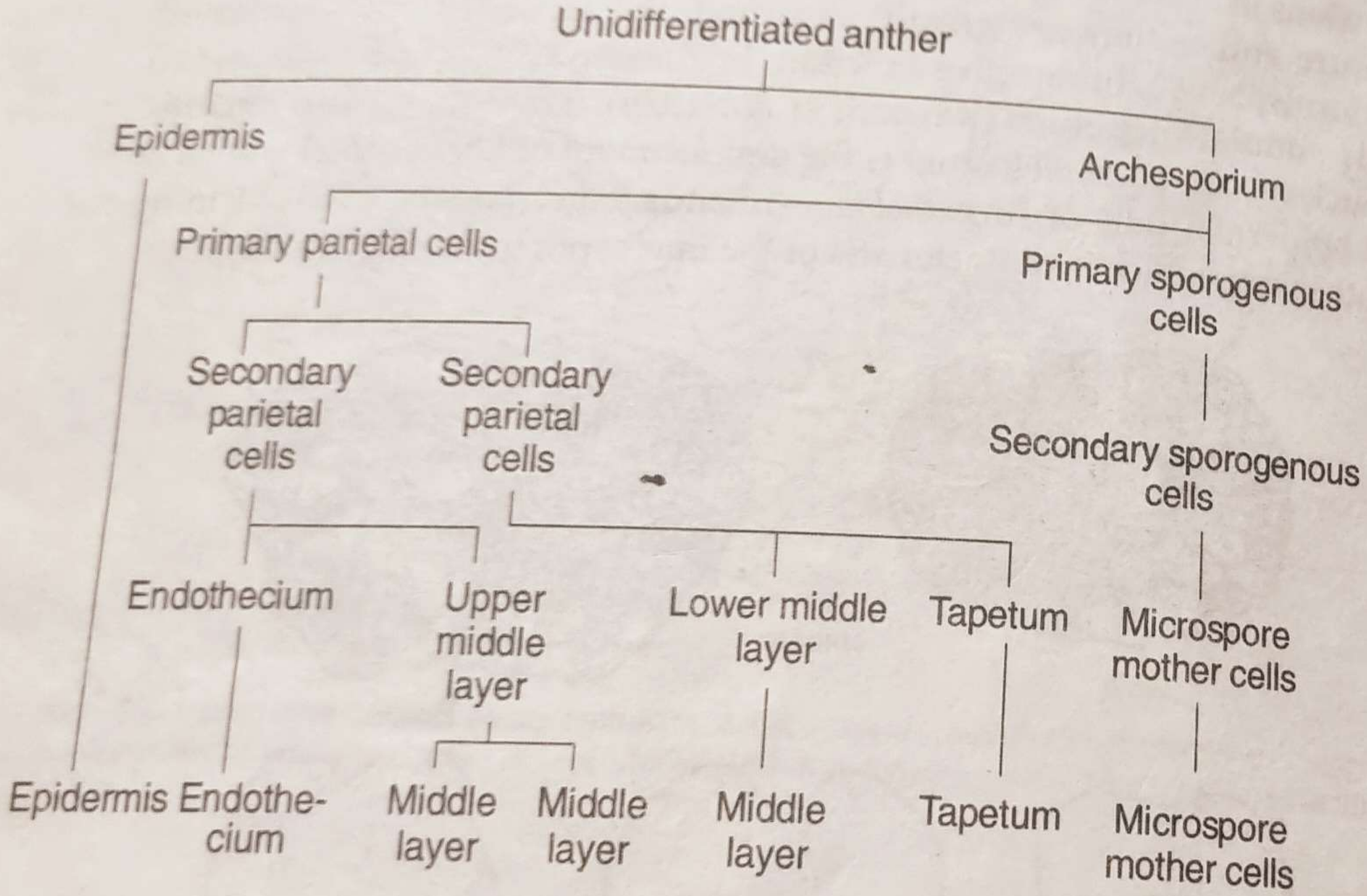


Fig. 2.3. Stamen. A. Ventral view; B. Dorsal view; C. Three dimensional cut section of Anther (Enlarged).

Development of microsporangium

- In each lobe a few cells in the hypodermal region become differentiated by their large size, radial growth, dense cytoplasm and conspicuous nuclei.
- There is much variation in the number of cells of archesporium.
- Generally, the archesporium consists of a two to three cell, wide plate running along the entire length of the lobe.
- The extent of archesporium varies both length wise and breadth wise.


Unidifferentiated anther
Epidermis
Archesporium
Primary parietal cells
Primary sporogenous cells
Secondary parietal cells
Secondary parietal cells
Secondary sporogenous cells
Endothecium
Upper middle layer
Lower middle layer
Tapetum
Microspore mother cells
Epidermis
Endothe-cium
Middle layer
Middle layer
Middle layer
Tapetum
Microspore mother cells

- In a flower, stamen is considered as the male reproductive organ. Each stamen consists of filament, connective and anther.
- Anther may be monothecous or dithecous. A monothecous anther consists of two locules or two sporangia. So it is said to be bilocular or bisporangiate.

- A dithecous anther consists of four locules or four sporangia. So it is said to be tetralocular or tetrasporangiate.
- Development of microsporangium is eusporangiate (= Sporangium developing from a group of cells).
- A very young anther in transverse section shows epidermis and archesporium.

- The archesporial cells divide periclinally giving rise to primary parietal cells on the outer side and sporogenous cells towards inner side.
- The cells of the parietal layer divide periclinally and anticlinally forms endothecium, middle layers and tapetum.
- The cells of the primary sporogenous tissue differentiated into pollen mother cells or microspore mother cells.

- The anther wall consists of following walls layers:
- 1.Epidermis
- 2. Endothecium
- 3. Middle Layers
- 4. Tapetum

1.Epidermis:

- Epidermis is the outermost single layer.
- It is compactly arranged and usually protective in function.
- Epidermal stomata was reported in **Alangium.**

2.Endothecium:

- The cells of the endothecium are radially elongated and shows fibrous bands.
- The fibrous bands are made up of callose an arise from the inner tangential walls.
- Usually fibrous bands are “U” shaped.
- The fibrous bands are hygroscopic in nature. Endothecial cells help in the dehiscence of anther at maturity.
- Because of the presence of fibrous bands, this layer is otherwise called fibrous layer. It is usually single layered.(Exception - **Coccinia** double layered.)

3.Middle layers:

- Below the endothecium 2-3 layers of cells are present which constitute middle layers.
- These layers are ephemeral and become crushed by early meiosis in pollen mother cells.
- These cells act as storage centres for starch.

4.Tapetum:

- Tapetum is the innermost layer of antherwalls, and it completely surrounds the sporogenous tissue.
- The cells contain dense cytoplasm with prominent nuclei.
- Usually tapetum consists of single layer of cells.
- As the tapetum completely surrounds the sporogenous tissue major part of it is derived from parietal cells and a small part developed from the sporogenous tissue.
- Tapetum transports the nutrients to the developing sporocytes. Tapetal cells are pigmented and it is red brown in Apple or violet in Anemone

- On the basis of behaviour, there are two kinds of tapetum.

a) Amoeboid tapetum:

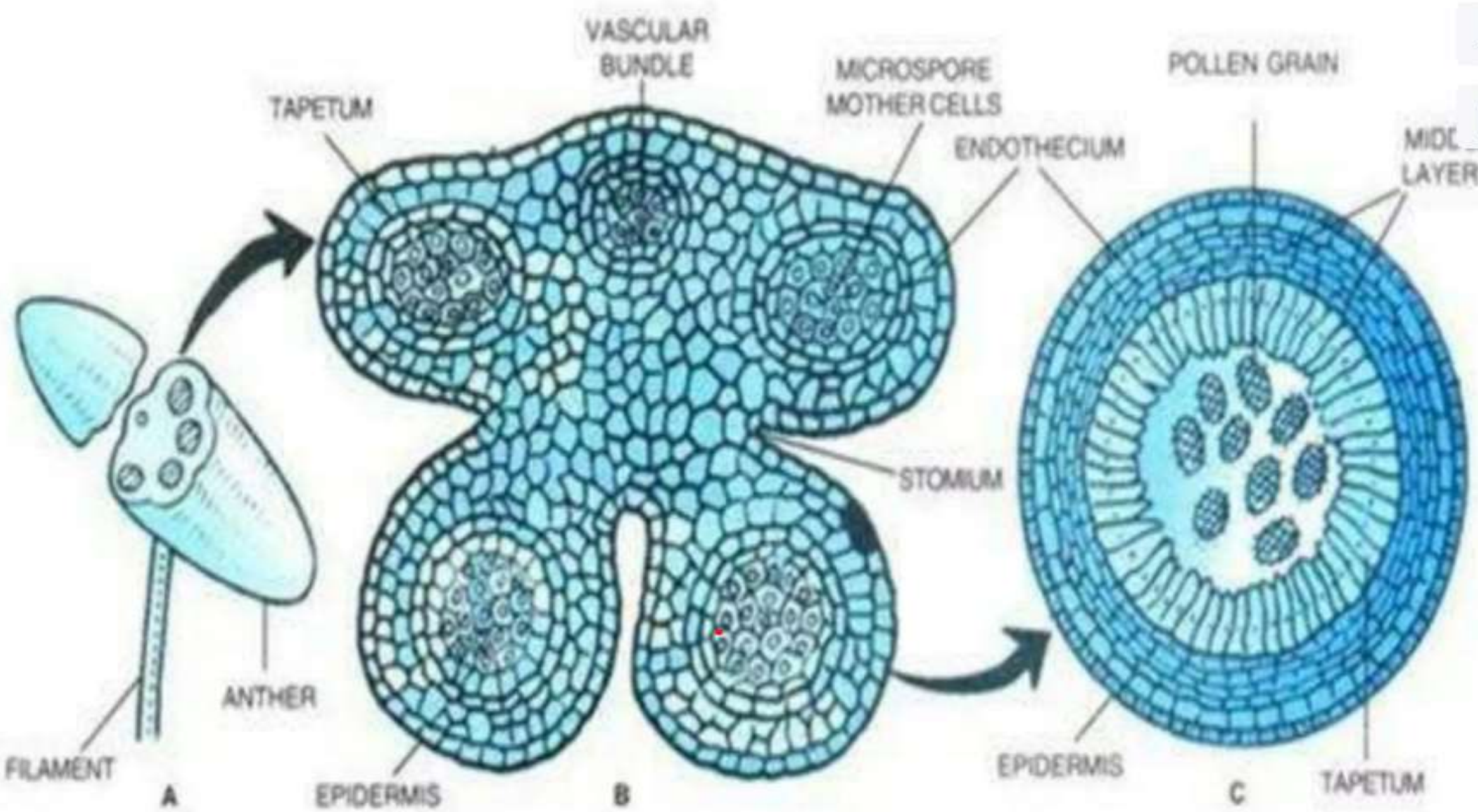
- The inner and radial walls of the tapetum break down due to the action of hydrolytic enzymes and their protoplast penetrates between the pollen mother cells and developing pollen grains.
- After intrusion, they fuse with each other and forms a mass of tapetal periplasmodium.
- This tapetal plasmodium remains associated with the pollengrains till their maturity.
- When the anther gets drying up the tapetal periplasmodium gets dehydrated and coated over the surface of pollengrains, thereby helping in the formation of exine.
- Amoeboid tapetum is considered as the primitive type.
- It is also called periplasmodial tapetum. Eg:- ***Alisma, Tradescantia, Typha, Saggitaria, Potamogeton.***

b) Glandular tapetum:

- The cells of glandular tapetum remains intact throughout microspore development.
- They secrete their substances from their inner faces. Secretary tapetal cells are thin and possess almost all cell organells like mitochondria, plastids, dictyosomes etc.
- Just before the pollen mother cells undergo meiosis, the walls of the tapetal cells become thick and there is considerable increase in the no. of ribosomes and pro-ubisch bodies with the completion of pollen development proubish bodies pass into the anther locule from the tapetal cells and they are now called ubisch bodies and they coated over the pollengrains
- Eg:- Higher monocots and many dicots.

Functions of tapetum:

- 1. The nutrients are transported through tapetum to the sporogenous tissue.
- 2. Tapetum is involved in the synthesis of callose which release microspores in a tetrad by degrading callose wall.
- 3. Tapetum plays an important role in the formation of exine.
- 4. Pollen kit (Lipids and carotenoids) is formed by tapetal layer. It is a insect attractant & protect pollen from ultra violet.



T.S. anther showing stomium and pollen grains

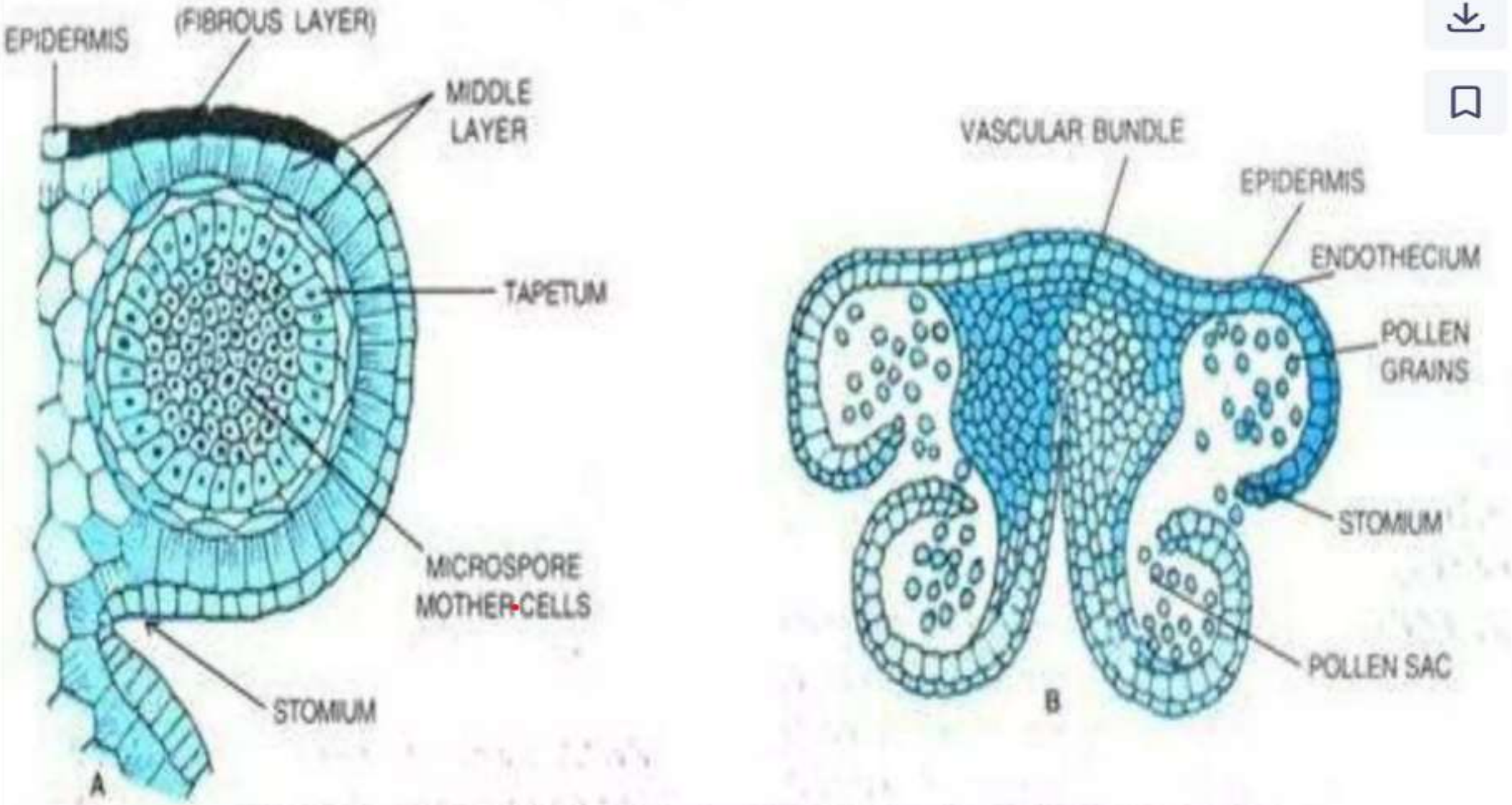


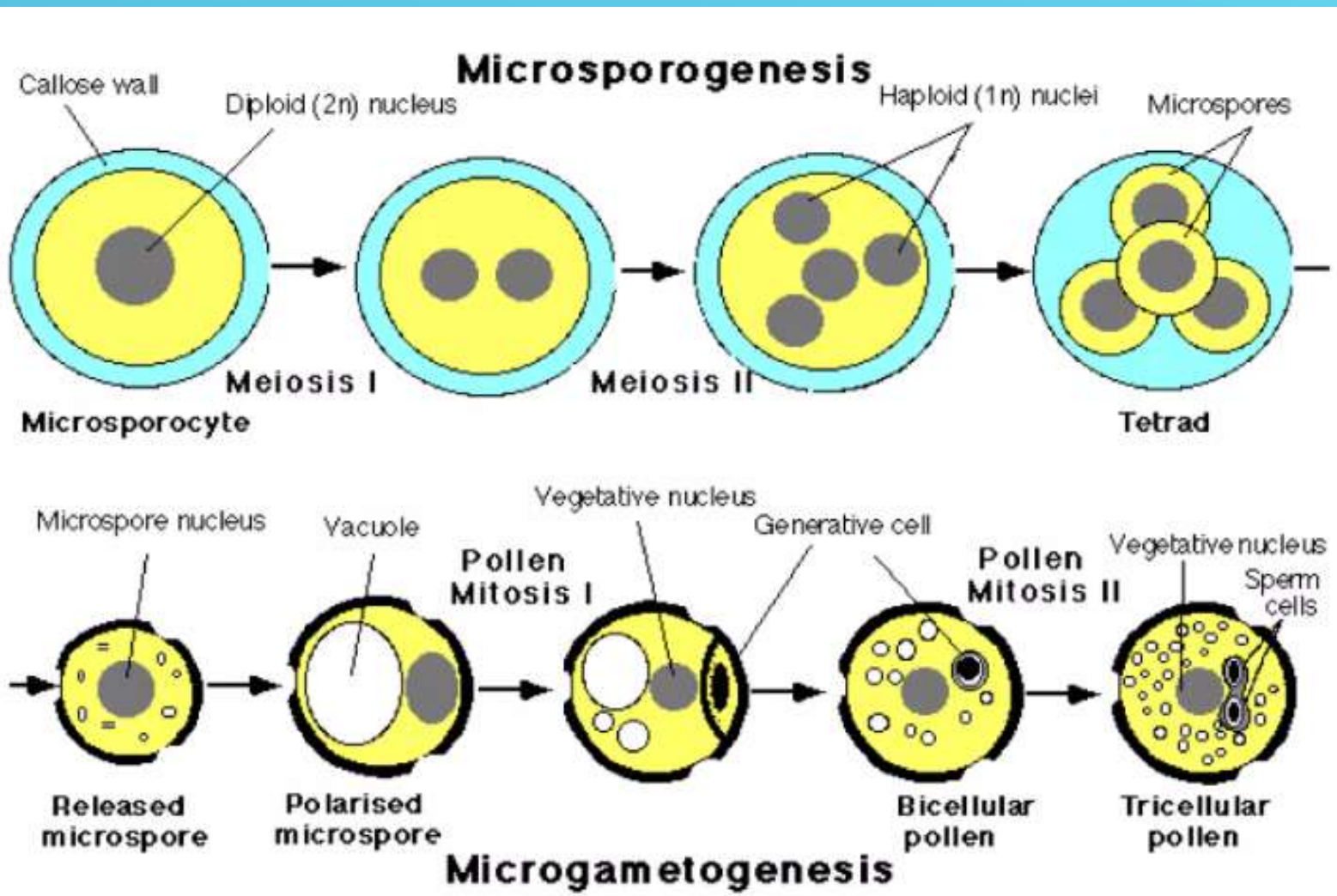
Fig. 2.5. A. Detailed structure of one young pollen sac; B. T.S. mature anther.

Sporogenous tissue

- The primary sporogenous layer forms the sporogenous tissue that gives rise to the ***microspore mother cells (MMC),*** or ***pollen mother cells (PMC).***
- The sporogenous cells may function directly as the microspore mother cells or undergo a series of mitotic divisions.
- The daughter cells of the last mitotic division function as microspore mother cells.
- Pollen mother cells are polygonal in shape and are closely packed.
- As the anther increases in size, these cells become loosely arranged and rounded in shape.
- All spore mother cells have the potential for forming microspores or pollen grains.
- However, some of them disintegrate and act as a nourishing tissue for the developing pollen grains.
- The formation of microspores from the MMC of sporogenous tissue is called ***microsporogenesis***.

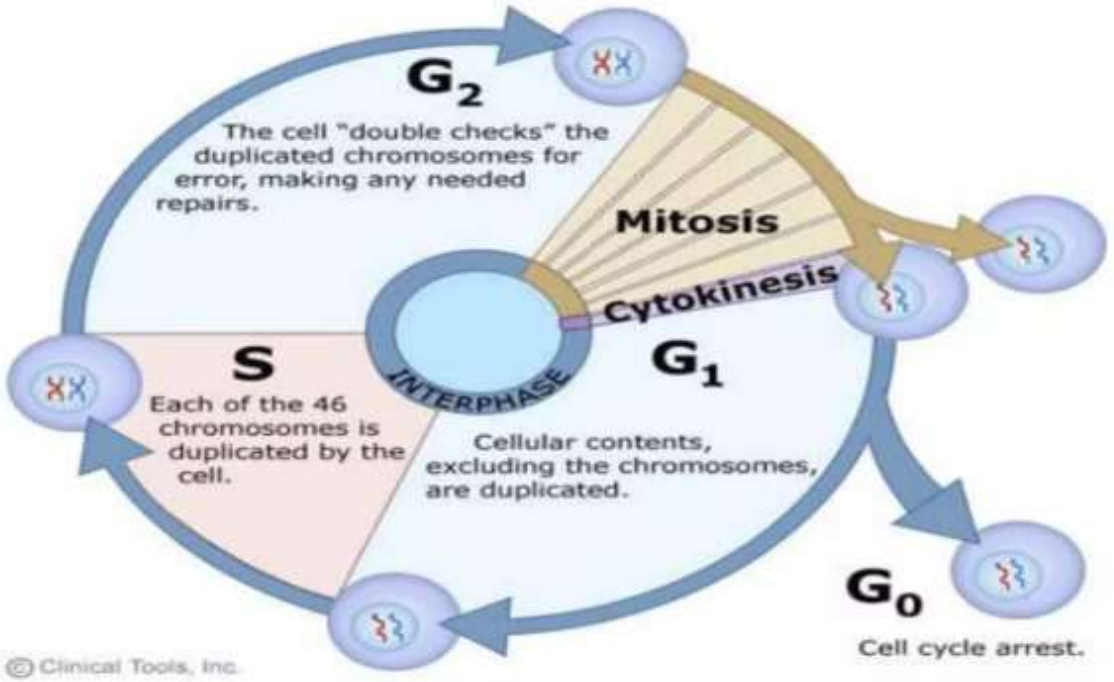
Microsporogenesis

- Microspores are formed by the meiotic (reduction) division of MMC.
- Each undergoes meiotic division and forms four haploid ***pollen cells or microspores***
- Initially, the microspores exist together in a tetrad condition, called ***microspore tetrad or pollen tetrad***, enclosed within a common wall of callose.
- Gradually, the micros separate from each other, develop an outer covering around each of them, and then mature to four ***pollen grains (microgametophytes or male gametophytes).***
- In Cyperaceae, out of the four microspores, only one matures as the functional pollen grain and the others degenerate.
- Thus, in Cyperaceae, a microspore mother cell gives rise to only a single pollen grain, instead of four.
- During the meiotic division of MMC, wall formation and cytokinesis take place in two ways, namely successive and simultaneous.


Microsporogenesis
Callose wall
Diploid (2n) nucleus
Haploid (1n) nuclei
Microspores
Meiosis I
Meiosis II
Microsporocyte
Tetrad
Microspore nucleus
Vacuole
Vegetative nucleus
Generative cell
Pollen Mitosis I
Pollen Mitosis II
Vegetative nucleus
Sperm cells
Released microspore
Polarised microspore
Bicellular pollen
Tricellular pollen
Microgametogenesis

The cell cycle

Actively dividing eukaryote cells pass through a series of stages known collectively as the **cell cycle**: two gap phases (G1 and G2); an S (for synthesis) phase, in which the genetic material is duplicated; and an M phase, in which mitosis partitions the genetic material and the cell divides.

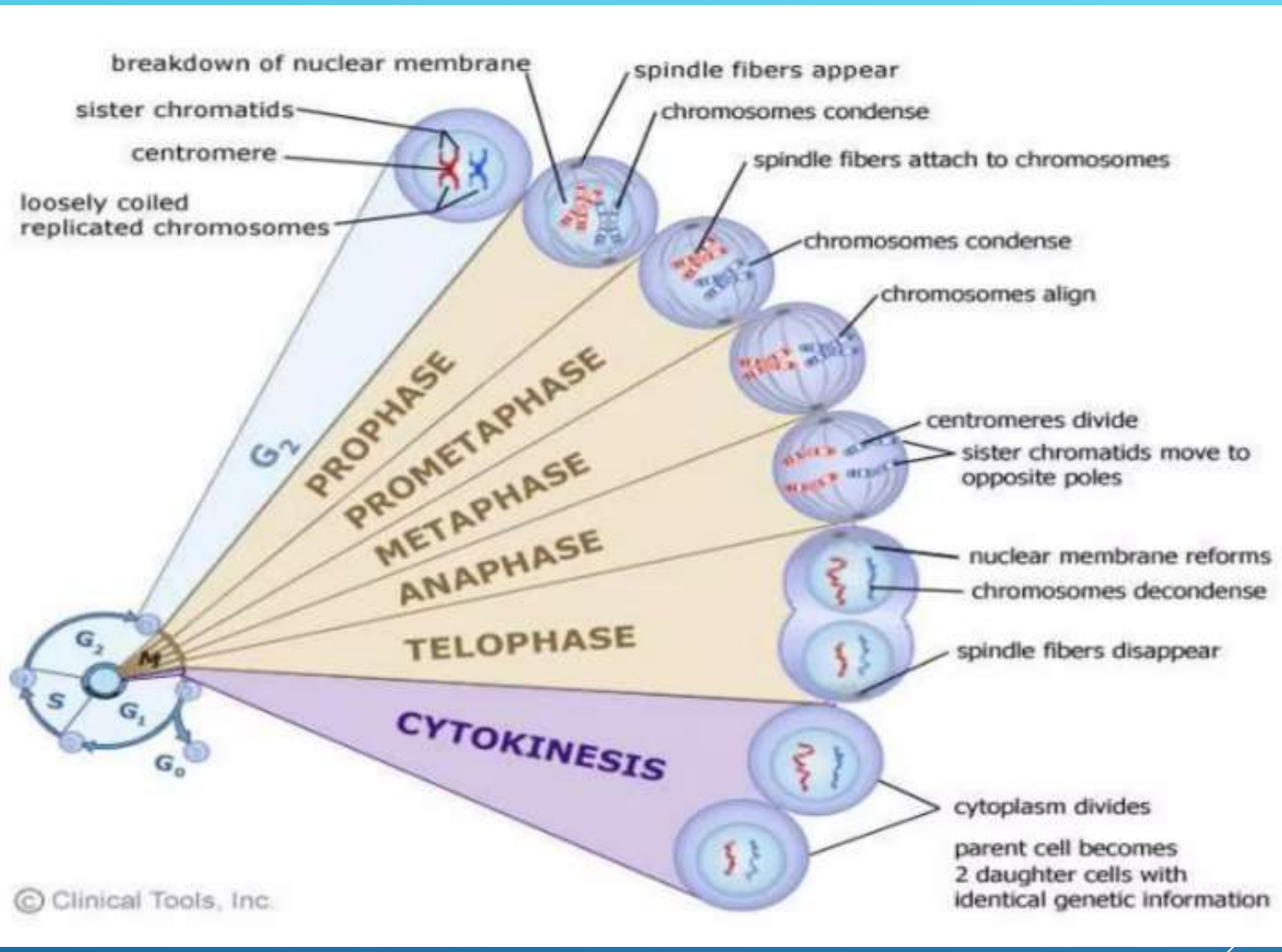


•**G1 phase.** Metabolic changes prepare the cell for division. At a certain point - the restriction point - the cell is committed to division and moves into the S phase.

•**S phase**. DNA synthesis replicates the genetic material. Each chromosome now consists of two sister chromatids.

•**G2 phase.** Metabolic changes assemble the cytoplasmic materials necessary for mitosis and cytokinesis.

•**M phase.** A nuclear division (mitosis) followed by a cell division (cytokinesis).
The period between mitotic divisions - that is, G1, S and G2 - is known as interphase.


breakdown of nuclear membrane
sister chromatids
centromere
loosely coiled
replicated chromosomes
spindle fibers appear
chromosomes condense
spindle fibers attach to chromosomes
chromosomes condense
chromosomes align
centromeres divide
sister chromatids move to
opposite poles
nuclear membrane reforms
chromosomes decondense
spindle fibers disappear
cytoplasm divides
parent cell becomes
2 daughter cells with
identical genetic information
G2
PROPHASE
PROMETAPHASE
METAPHASE
ANAPHASE
TELOPHASE
CYTOKINESIS
G2
M
S
G1
G0
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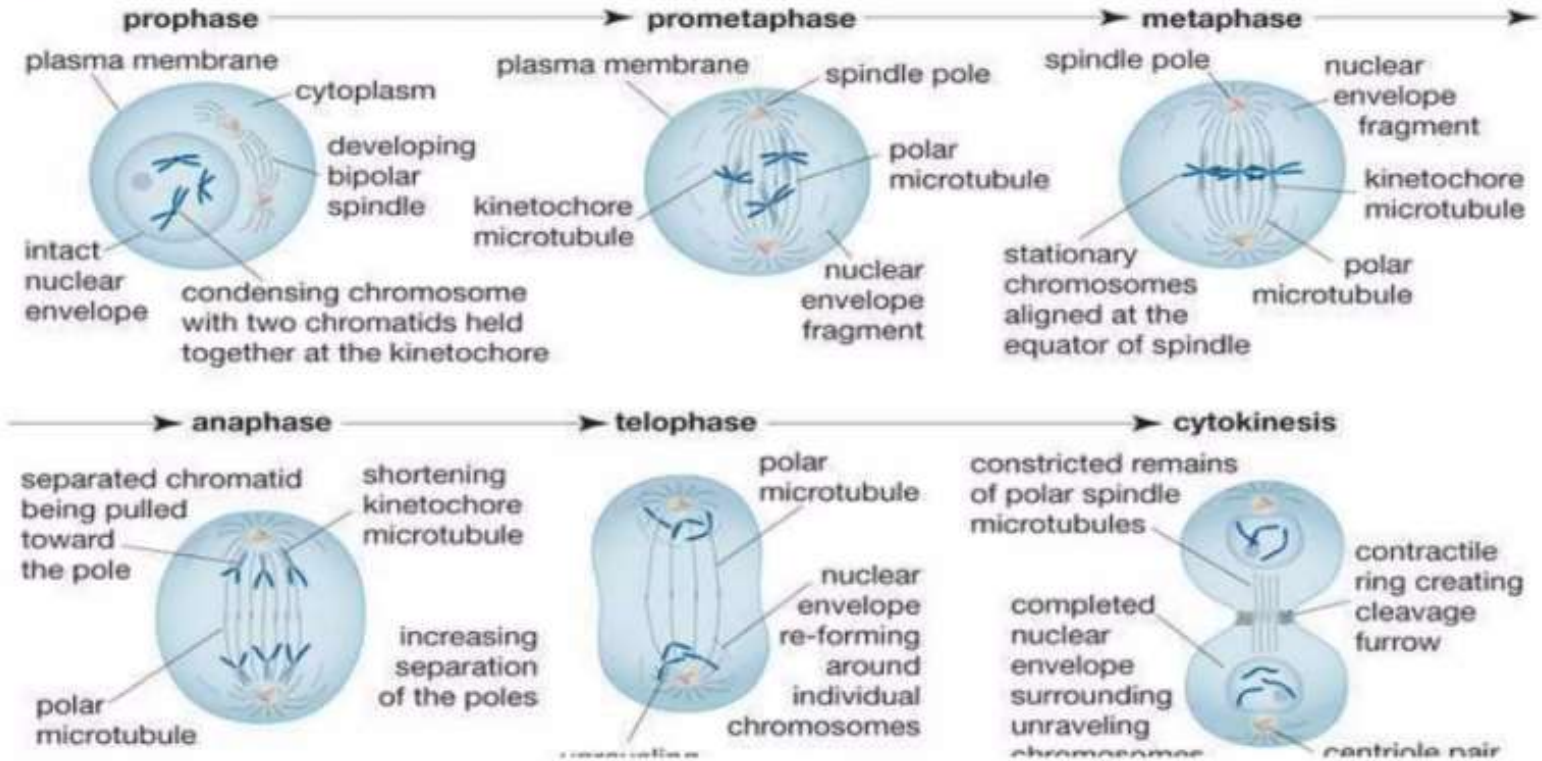
Mitosis, a process of cell duplication, or reproduction, during which one cell gives rise to two genetically identical daughter cells. Strictly applied, the term *mitosis* is used to describe the duplication and distribution of chromosomes, the structures that carry the genetic information.



Early **prophase**, the cell starts to break down some structures and build others up, setting the stage for division of the chromosomes.

- The chromosomes start to condense (making them easier to pull apart later on).
- The **mitotic spindle** begins to form. The spindle is a structure made of microtubules, strong fibers that are part of the cell's "skeleton." Its job is to organize the chromosomes and move them around during mitosis. The spindle grows between the centrosomes as they move apart.
- The **nucleolus** (or nucleoli, plural), a part of the nucleus where ribosomes are made, disappears. This is a sign that the nucleus is getting ready to break down.

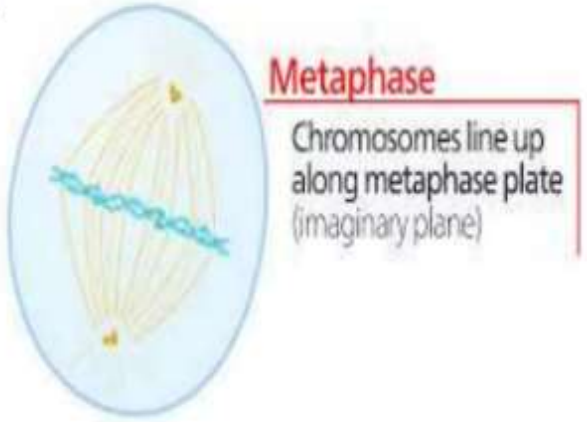
Late prophase (sometimes also called **prometaphase**), the mitotic spindle begins to capture and organize the chromosomes. The chromosomes become even more condensed, so they are very compact.

- The nuclear envelope breaks down, releasing the chromosomes.
- The mitotic spindle grows more, and some of the microtubules start to "capture" chromosomes.

- Microtubules can bind to chromosomes at the **kinetochore**, a patch of protein found on the centromere of each sister chromatid. (**Centromeres** are the regions of DNA where the sister chromatids are most tightly connected.)

Metaphase, the spindle has captured all the chromosomes and lined them up at the middle of the cell, ready to divide.

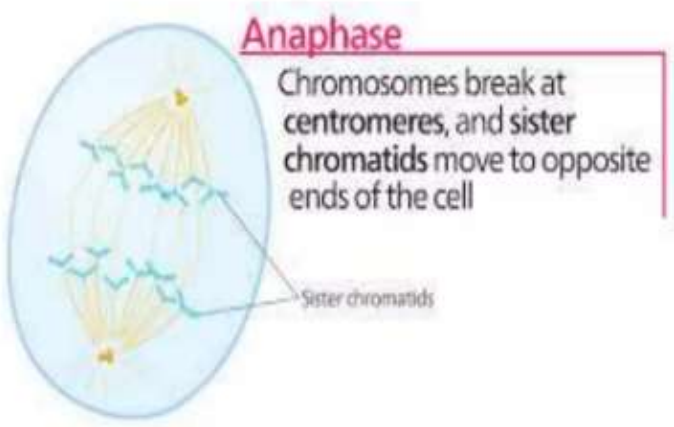
- All the chromosomes align at the **metaphase plate** (not a physical structure, just a term for the plane where the chromosomes line up).
- At this stage, the two kinetochores of each chromosome should be attached to r site spindle poles.



Anaphase, the sister chromatids separate from each other and are pulled towards opposite ends of the cell.

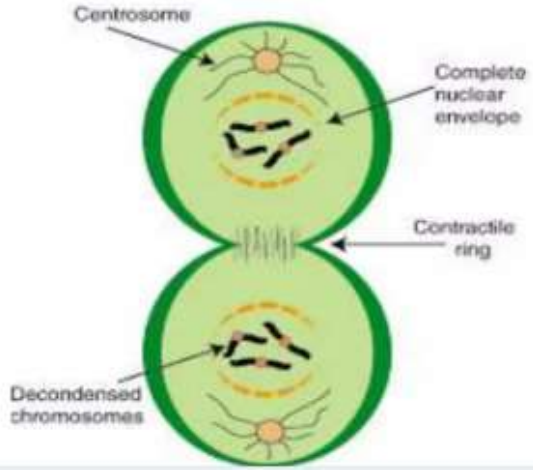
•The protein "glue" that holds the sister chromatids together is broken down, allowing them to separate. Each is now its own chromosome. The chromosomes of each pair are pulled towards opposite ends of the cell.

•Microtubules not attached to chromosomes elongate and push apart, separating the poles and making the cell longer.



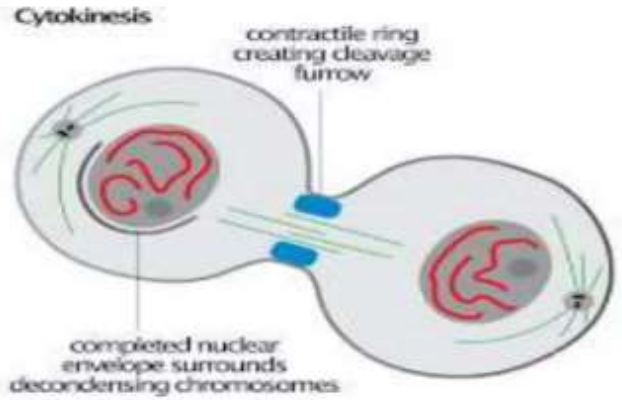
Telophase, the cell is nearly done dividing, and it starts to re-establish its normal structures as cytokinesis (division of the cell contents) takes place.

- The mitotic spindle is broken down into its building blocks.
- Two new nuclei form, one for each set of chromosomes. Nuclear membranes and nucleoli reappear.
- The chromosomes begin to decondense and return to their form.



Cytokinesis, the division of the cytoplasm to form two new cells, overlaps with the final stages of mitosis. It may start in either anaphase or telophase, depending on the cell, and finishes shortly after telophase.

Plant cells can't be divided because they have a cell wall and are too stiff. Instead, a structure called the **cell plate** forms down the middle of the cell, splitting it into two daughter cells separated by a new wall.



Meiosis

Meiosis is a lot like mitosis. The cell goes through similar stages and uses similar strategies to organize and separate chromosomes. In meiosis, however, the cell has a more complex task. It still needs to separate **sister chromatids** (the two halves of a duplicated chromosome), as in mitosis. But it must also separate **homologous chromosomes**, the similar but nonidentical chromosome pairs an organism receives from its two parents.

These goals are accomplished in meiosis using a two-step division process. Homologue pairs separate during a first round of cell division, called **meiosis I**. Sister chromatids separate during a second round, called **meiosis II**.

Since cell division occurs twice during meiosis, one starting cell can produce four gametes (eggs or sperm). In each round of division, cells go through four stages: prophase, metaphase, anaphase, and telophase.

MEIOSIS

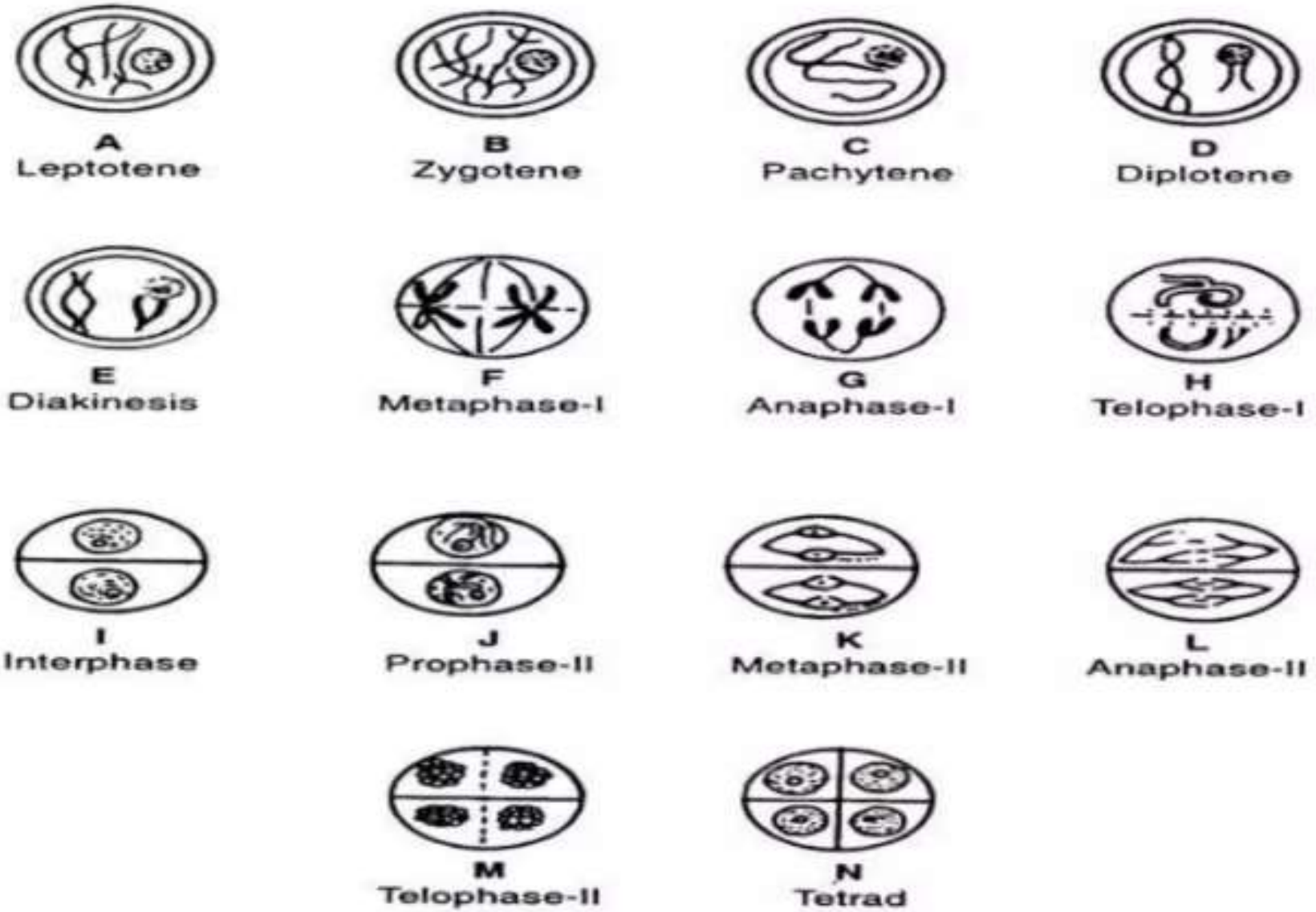


Fig. 3.3. Various stages of meiotic cell division in a reproductive plant cell ($2n = 4$).

Prophase I

The homologous chromosomes pair and exchange DNA to form recombinant chromosomes. Prophase I is divided into five phases:

- **Leptotene**: chromosomes start to condense.
- **Zygotene**: homologous chromosomes become closely associated (synapsis) to form pairs of chromosomes (bivalents) consisting of four chromatids (tetrads).
- **Pachytene**: crossing over between pairs of homologous chromosomes to form chiasmata (sing. chiasma).
- **Diplotene**: homologous chromosomes start to separate but remain attached by chiasmata.
- **Diakinesis**: homologous chromosomes continue to separate, and chiasmata move to the ends of the chromosomes.

Prometaphase I

Spindle apparatus formed, and chromosomes attached to spindle fibres by kinetochores.

Metaphase I

Homologous pairs of chromosomes (bivalents) arranged as a double row along the metaphase plate. The arrangement of the paired chromosomes with respect to the poles of the spindle apparatus is random along the metaphase plate.

Anaphase I

The homologous chromosomes in each bivalent are separated and move to the opposite poles of the cell

Telophase I

The chromosomes become diffuse and the nuclear membrane reforms.

Cytokinesis

The final cellular division to form two new cells, followed by Meiosis II. Meiosis I is a reduction division: the original diploid cell had two copies of each chromosome; the newly formed haploid cells have one copy of each chromosome.

Meiosis II

Meiosis II separates each chromosome into two chromatids.

Prophase II, chromosomes condense and the nuclear envelope breaks down, if needed. The centrosomes move apart, the spindle forms between them, and the spindle microtubules begin to capture chromosomes. The two sister chromatids of each chromosome are captured by microtubules from opposite spindle poles.

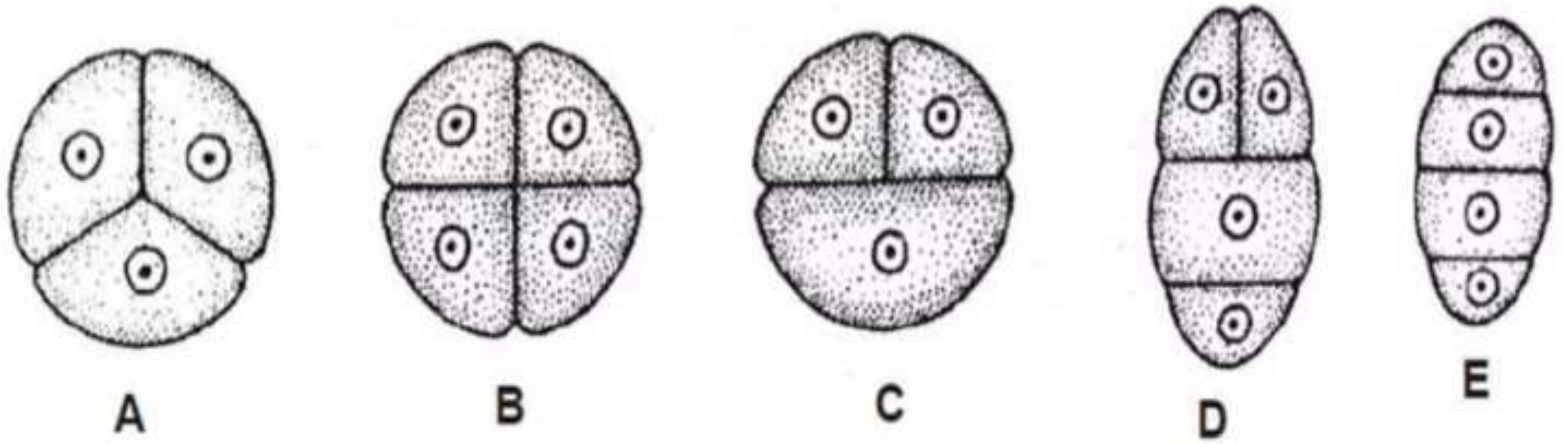
Metaphase II, the chromosomes line up individually along the metaphase plate.

Anaphase II, the sister chromatids separate and are pulled towards opposite poles of the cell.

Telophase II, nuclear membranes form around each set of chromosomes, and the chromosomes decondense.

Cytokinesis splits the chromosome sets into new cells, forming the final products of meiosis: four haploid cells in which each chromosome has just one chromatid.

TYPES OF POLLEN TETRADS



Different types of microspores
A. Tetrahedral, B. Isobilateral, C. Decussate, D. T-shaped, E. Linear

1. Tetrahedral: Only three microspores are observed when we view from one side and the fourth microspore is at the backside.
Example: Most dicotyledonous plants.

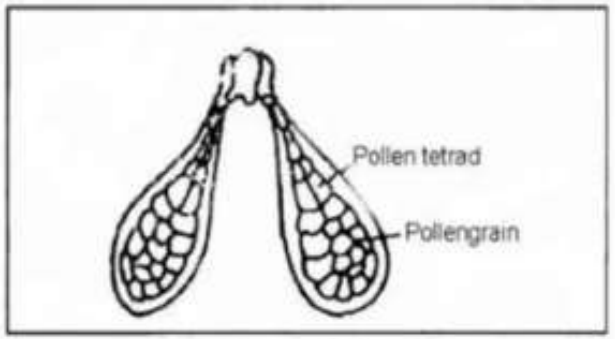
2. Isobilateral: In this, all four microspores are arranged in one plane of the tetrad.
Example: Monocot plants.

3. Decussate: In this two + two microspores are arranged perpendicular in such a way that upper two microspores are visible and only one from lower tier is visible.
Example: *Magnolia.*

4. T-shaped: In this microspores are arranged in a tetrad in such a way that two microspores are arranged in transverse and two in a longitudinal plane.
Example: *Aristolochia.*

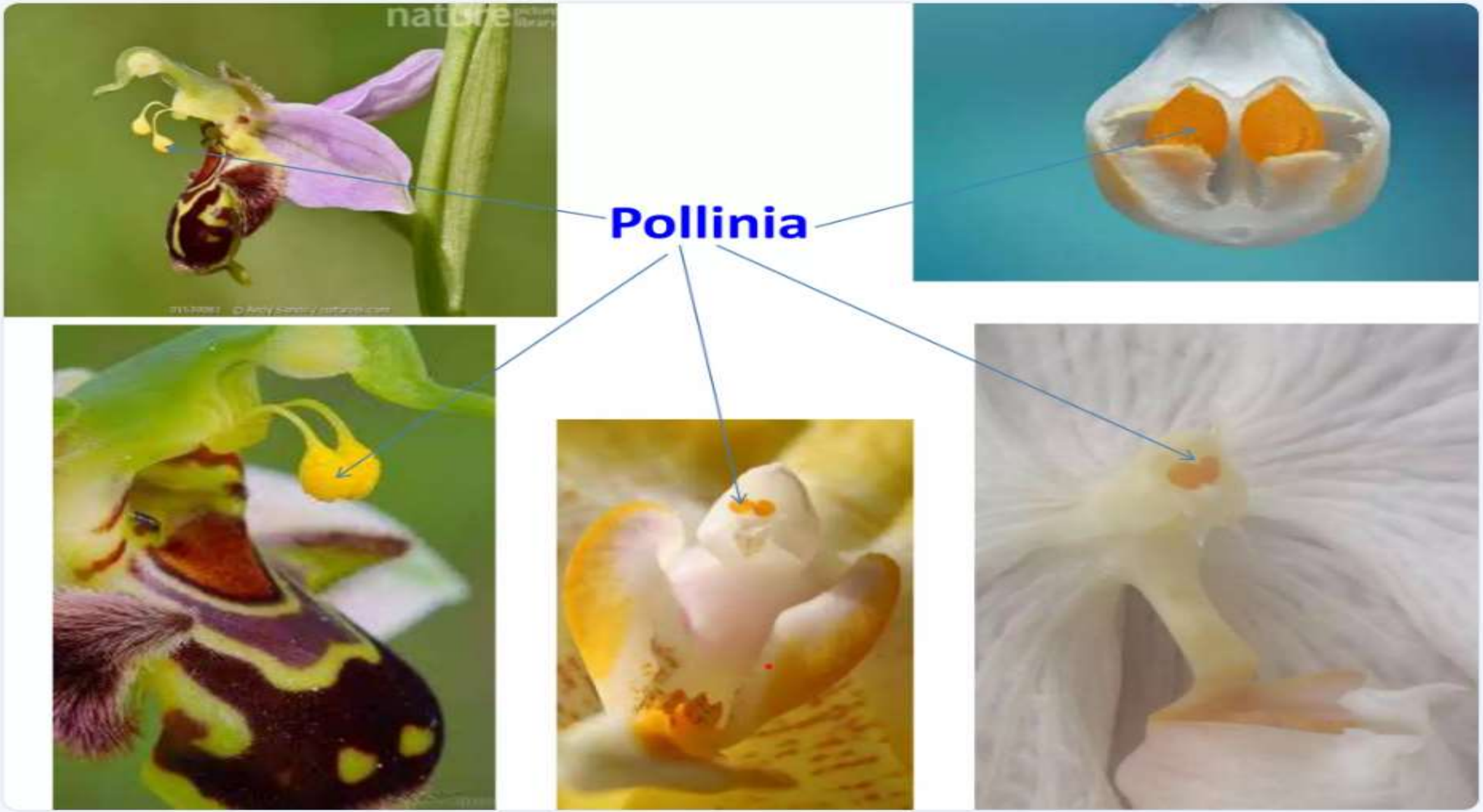
5. Linear: All microspores are arranged in a single linear fashion.

In some plants, pollen grains or microspores of a sporangium cohere (stick) in a single mass called pollinium.
Example: *Calotropis* and in some orchids.



Pollinia in *Calotropis*

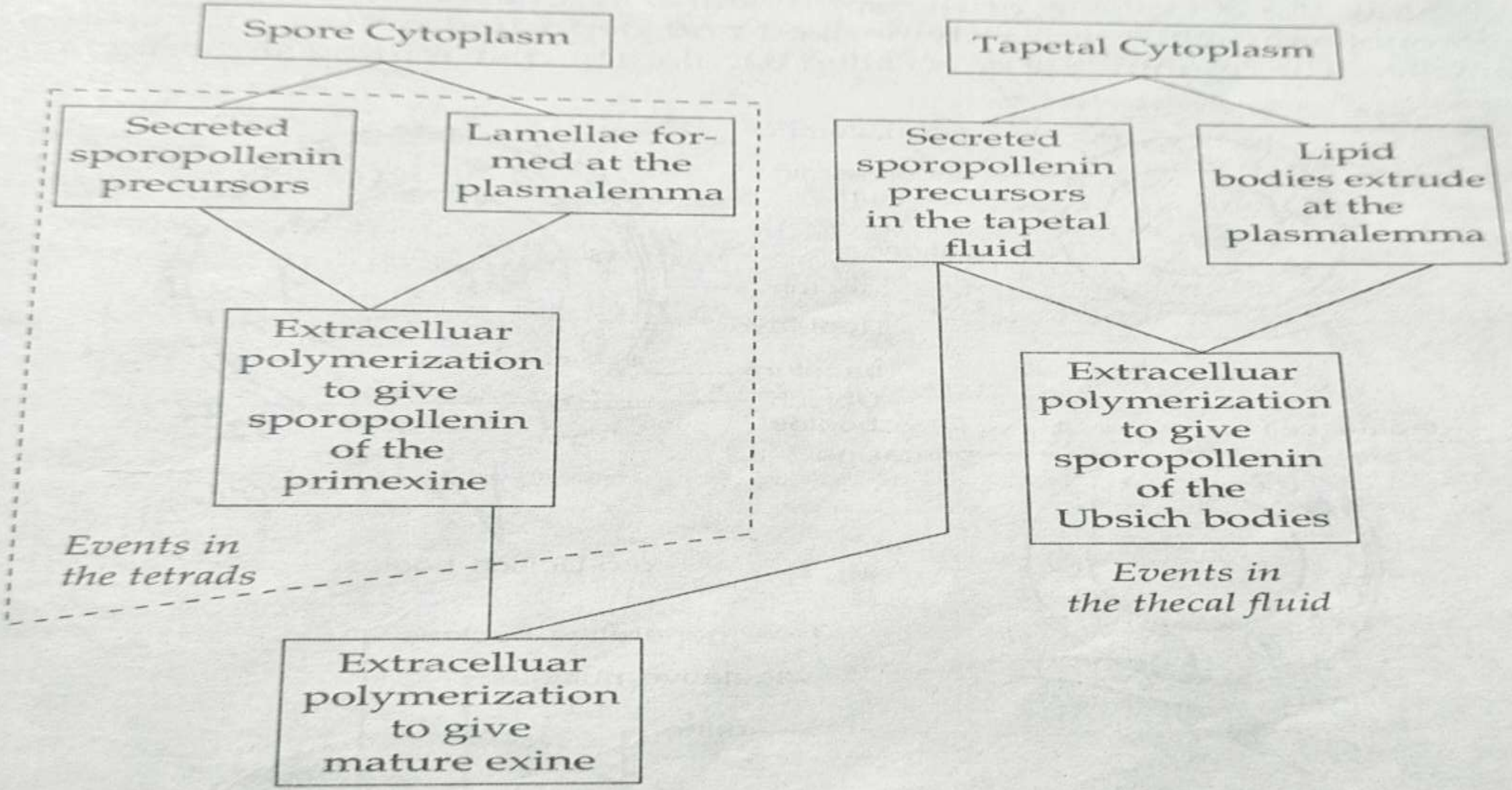
Most commonly the microspores soon separate from one another but sometimes they adhere in tetrads to from compound pollen grains.
Example: *Drimys, Anona, Drosera, Elodea, Typha*.


Pollinia

POLLEN GRAIN

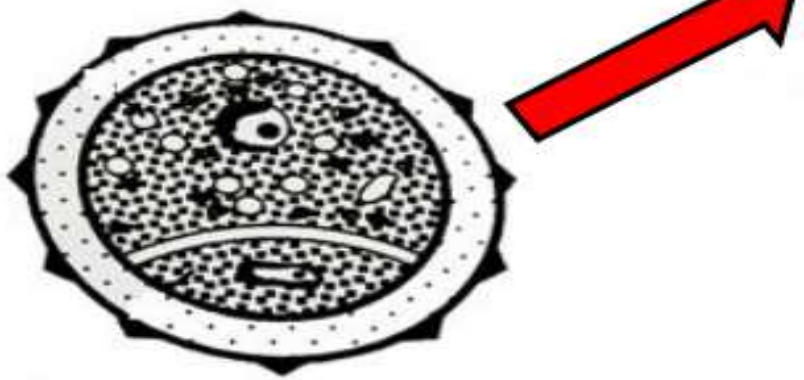
- Pollen grain represent male gametophyte.
- They possess two layered wall.
- The outer wall is called exine and inner wall is called intine.
- The exine is composed of sporopollenin.
- The intine is composed of cellulose and pectin.

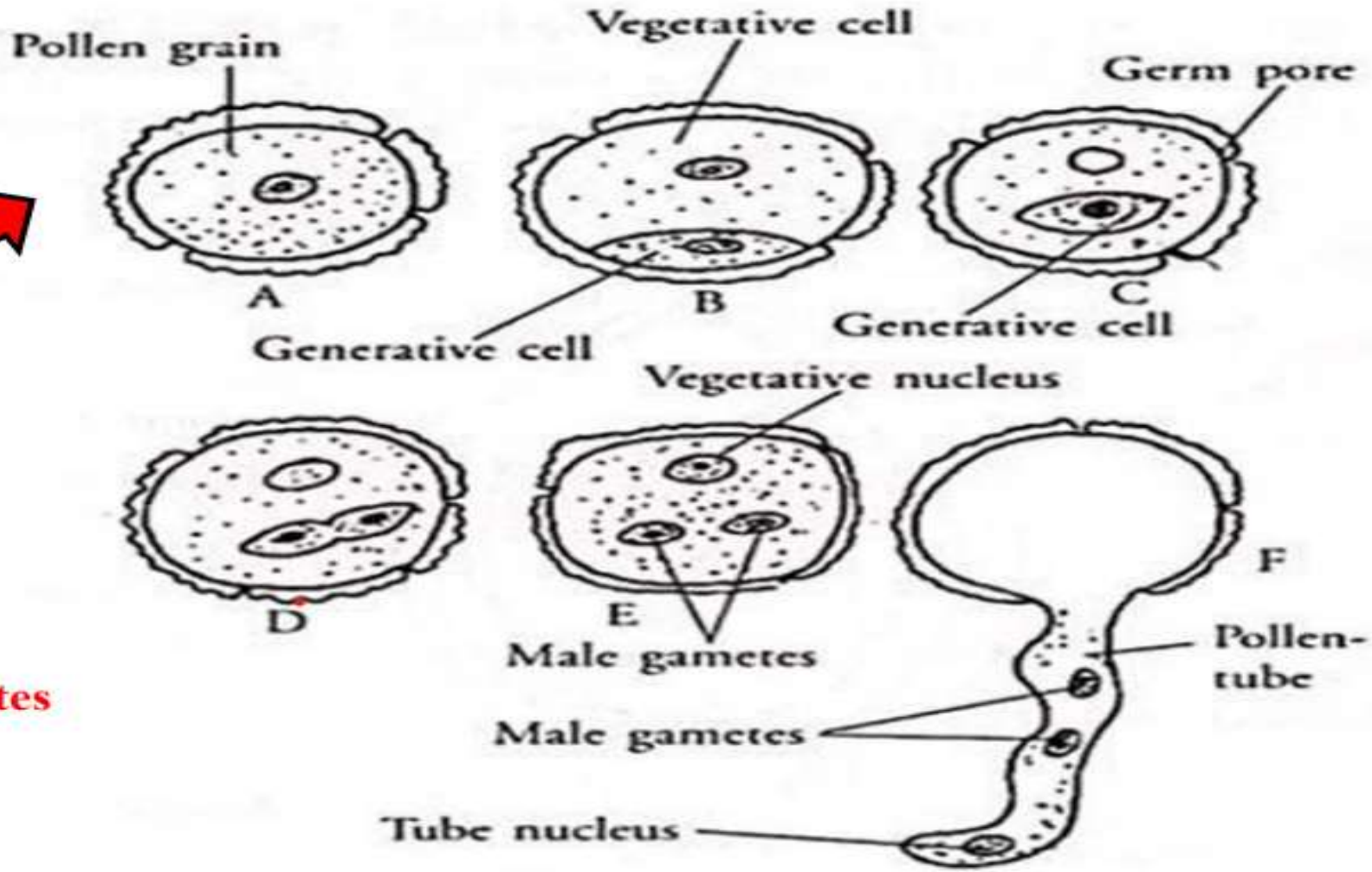
TABLE 4.2 Schematic representation of the formation of Ubisch bodies and exine development in *Lilium*. (*after* Heslop-Harrison, 1972)



Microgametogenesis

- **Microgametogenesis refers to development of male gamete**





- **Vegetative cell- Pollen tube**
- **Generative cell- Two male gametes**

Microgametogenesis

- Unicellular microspores into mature microgametophytes containing the gametes.
- Nucleus undergoes mitosis I leads to two unequal cells, a large vegetative cell and a small generative cell each containing a haploid nucleus.
- The generative cell subsequently detaches from the pollen grain wall and is engulfed by the vegetative cell forming a unique 'cell within a cell' structure.
- The engulfed generative cell divides once more by mitosis II to form two sperm cells completely enclosed within the vegetative cell cytoplasm either before it is shed (tricellular) or within the tube (bicellular).

TABLE I

Chemicals Identified in Volatiles from Pollen and Pollenkitt of *Rosa rugosa* and *R. canina*[a]

Compound	*R. rugosa* pollen	Pollenkitt[b]	*R. canina* pollen[b]
Terpenoids			
6-Methyl-5-hepten-2-one	xx		x
Geranyl acetone	xxx	x	xx
Neral	xx		
Geranial	xxx	x	
Nerol	t		
Geraniol	xx		
Citronellyl acetate	xx	x	
Neryl acetate	xx		
Geranyl acetate	xxx	x	
Aliphatics			
Pentadecane	xx	x	x
2-Undecanone	xxx		
2-Tridecanone	xxx	xx	
2-Pentadecanone	xx		
Tetradecanal	xxx	xx	xxx
Hexadecanal	x		xx
Acetic acid	t		
Tetradecyl acetate	xxx	xxx	
Hexadecyl acetate	t	xxx	
Aromatics			
β-Phenylethanol	xxx		
Methyleugenol	xxx	x	
Eugenol	xx		
β-Phenylethyl acetate	xx	x	

[a] Data from Dobson *et al.* (1987). Dobson *et al.* (1987).

[b] Includes only compounds detected also in *R. rugosa* pollen volatiles. t, trace quantities, identification tentative; x, ≤4%; xx, ≥4% and ≤20%; xxx, ≥20% of largest peak.

Flavonolglycosides Isolated from Pollen

[a]*Fagus sylvatica*
Kaempferol-3-*p*-coumaroylglucoside

[b,c]*Corylus avellana*
Quercetin-3-glucosylgalactoside
[a]Quercetin-3-sophoroside
[a]As a major constituent in pollen from *Juglans cordiformis*, *Juglans siboldiana*, *Alnus cordata*, *Alnus incana*, *Betula medwediewii*, *Carpinus carpinizza*, *Ostrya carpinifolia*, and *Fraxinus sogdiana*

[d]*Populus yunnanesis*
Kaempferol-3-rhamnodiglucoside

[e]*Prunus amygdalus*
8-Methoxykaempferol-3-diglucoside
in trace amount:
Kaempferol-3-diglucoside
Quercetin-3-diglucoside
Kaempferol-3-*p*-coumaroylglycoside

[f]*Cucurbita maxima*
Isorhamnetin-3-rutinoide

Cucurbita moschata
Kaempferol-3-rutinoside
Kaempferol-3-robinobioside
Other flavonoids in minor quantities

Cucurbita ficifolia
Isorhamnetin-3-rutinoside
Quercetin-3-rutinoside
Other flavonoids in minor quantities

Other flavonoids in minor quantities

Cucurbita pepo

Isorhamnetin-3-rutinoside

Other flavonoids in minor quantities

[g] *Petunia hybrida*

Kaempferol-3-glucosylgalactoside

Quercetin-3-glucosylgalactoside

Dihydroquercetin

Other flavonoids in minor quantities

[h] *Tulipa* cultivar Apeldoorn

Quercetin-3-rhamnosylglucoside

Isorhamnetin-3-rhamnosylglucoside

Quercetin-3-glucosylrhamnosylglucoside,

as major compounds:

Kaempferol-3-rhamnosylglucoside

Kaempferol-3-xylosylrhamnosylglucoside

Isorhamnetin-3-xylosylrhamnosylglucoside,

as minor compounds:

Delphinidin-3-rutinoside

[i] *Zea Mays*

Kaempferol-3-glucoside
Quercetin-3-glucoside
Quercetin-3,3′-diglucoside
Quercetin-3,7-diglucoside
Quercetin-3-neohesperidoside
Quercetin-3-glucoside 3′-diglucoside
Isorhamnetin-3-glucoside
Isorhamnetin-3,4′-diglucoside
Isorhamnetin-3-neohesperidoside
Isorhamentin-3-glucoside-4′-diglucoside

[a] Data from Pratviel-Sosa and Percheron (1972).
[b] Data from Strack *et al.* (1984).
[c] Data from Meurer *et al.* (1988).
[d] Data from Sosa and Percheron (1970).
[e] Data from Ferreres *et al.* (1989).
[f] Data from Imperato (1979).
[g] Data from Zerback *et al.* (1989a).
[h] Data from Strack *et al.* (1981a).
[i] Data from Ceska and Styles (1984).