Indira Gandhi
National Open University
School of Sciences

BBYET-141
CELL AND MOLECULAR BIOLOGY

Block

2

CELL STRUCTURE AND FUNCTION

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BLOCK 2 : Cell Structure and Function

The second block of this course includes a detailed study of structure of cell and its various functions. These units will help you in understanding the structure of cell and cellular processes taking place in it. The study of this Block will also make you aware about the structural differences in prokaryotic and eukaryotic cells and also between plant and animal cells.

You will be studying about the various cell types and their characteristics. The structural details of different components of cell will be provided to you. Information related to structural details of important cell organelles viz. chloroplasts, mitochondria, peoxisomes and nucleus has been included in this block. Ultrastructural details of various organelles has been included to give a realistic picture. The detailed information related to various events taking place in cell cycle and types of cell division has been provided to you. Various stages in the mitotic and meiotic division have also been covered in detail.

The block comprises of five units which provide detailed information about cell structure and function.

Unit 4 provides information about the discovery of cell, cell theory and structural differences between various types of cells. The theory related to origin of eukaryotic cell has also been included in this unit.

Unit 5 describes structure of cell wall and cell membrane. The details related to various models of cell membrane, its chemical composition and characteristics of cell membrane fluidity has also been included.

A lucid account of structure and function of cell organelles viz. mitochondria, chloroplast, endoplasmic reticulum, Golgi body and lysosomes has been provided in Unit 6. An account of origin of organelles such as chloroplast and mitochondria has also been provided to you. The semiautonomous nature of the organelles viz. chloroplast and mitochondria has also been explained in this unit.

The structure and function of other organelles such as peroxisomes, glyoxysomes, nucleus and ribosomes has been covered in the following unit i.e. Unit 7. The information related to main structural components of cytoskeleton, cell inclusions and ribosomes have been included in this section.

Unit 8 provides you an overview of the cell cycle and discusses about major cell division types i.e. mitosis and meiosis in detail. It also provides information about the role of various factors involved in regulation of cell cycle in plants.

The study of these units will be helpful to you as your basic concepts about the cell biology will be clear and it would be much easier for you to understand the units of the Volume 2.

Objectives

After studying this block, you should be able to :

- explain the structure of cell;
- describe the differences between prokaryotic and eukaryotic cells;
- describe the structure and function of major cell organelles;
- describe the parts of cell cycle;
- differentiate between mitosis and meiosis; and
- explain the various factors regulating cell cycle.

UNIT 4

CELL

Structure

4.1 INTRODUCTION

In block 1 of this course you have studied about the various techniques used to study cell and molecular biology such as microscopy, chromatography, and electrophoresis. In this unit 4 of block 2, we are going to discuss about the cell. As you know that cells are the basic building blocks of all living beings. A cell is a membrane bound structure considered as structural and functional unit of life. It is the smallest unit of living organisms that is capable of carrying out all the activities necessary for life. It is considered as a complete metabolic unit because it has all the chemical and physical components required for its growth. We can define cell as the smallest basic biological unit that contains the fundamental molecules of life of which all living beings are made of.

The word cell is derived from Latin word ***cella*** which means “a small room” or ‘a compartment’. Cell contains a jelly like substance called protoplasm bounded by a cell membrane. The cytoplasm has cell organelles. Many cellular inclusions or biomolecules like proteins, nucleic acids and lipids are also present in the cytoplasm. Each cell is a unique molecular factory made up of carbon-based molecules and uses same basic mechanisms for energy metabolism. Many microorganisms like bacteria, some algae and fungi are made up of a single cell (unicellular) and remain as single celled structure throughout their life. In multicellular organisms, different types of cells with specialized functions are present. Cells function in coordination with each

other. All cells are believed to have evolved from a common ancestor. Studies have shown that the first cell originated about 3.8 billion years ago. All living beings including plants, animals and microbes are made up of cells. Most of the plants and animals are multicellular and made up of large number of cells. Our own body itself, is made up of trillions of cells.

This unit introduces you to cell and its components (organelles).

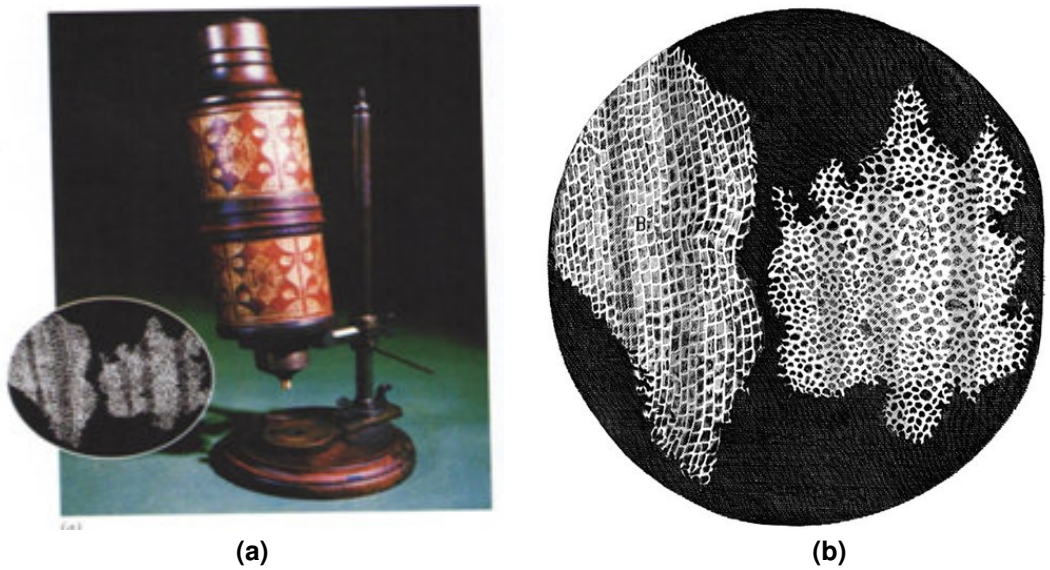
Objectives

After studying this unit, you would be able to:

- appreciate the history of discovery of cell and cell theory;
- describe the structure of prokaryotic and eukaryotic cells and differentiate between them;
- provide details about various cell-shapes, sizes, and their number; and
- explain the endosymbiotic theory of origin of eukaryotic cells.

4.2 DISCOVERY OF CELL AND CELL THEORY

Discovery of cell is one of the most remarkable advancements in the field of science. As we have mentioned above that all the living organisms i.e., plants, animals or microbes are made up of cells. The knowledge of structure and function of cell has helped us to understand life in a better manner. The term 'cell' was proposed by an English scientist, **Robert Hooke** (1635-1702). In 1665, he observed cells of cork of a white oak plant (*Quercus suber*) under a compound microscope (Fig. 4.1a), using three lenses and a stage light by which the specimens got well illuminated and enlarged. He observed tiny pores or honeycomb like compartments in the cork and called them as cell since they reminded him of cells or rooms in a monastery (Fig. 4.1b). He published his observations, though not being aware that the cork cell he had observed were in fact empty cell walls of dead plant tissue and therefore, lacked the internal structures found in living cells.



(a) (b)

Fig 4.1: a) Robert Hooke's compound microscope; b) Hooke's drawings of a thin slice of cork, showing the honeycomb- like structures of cells.

Not long after Hooke discovered cork cell, a Dutch microscope maker, **Anton von Leeuwenhoek** in 1675 detected other hidden miniscule organisms. He used monocular microscope with single lens and perfected the design of this simple microscope so that it could magnify the object up to 200-300 times to its original size. Leeuwenhoek observed living cells of bacteria and protozoa under his microscope (See Fig.1.1 of Block I). He observed unicellular microorganisms in rainwater and called them **'Little animalcules'**. He was the first to observe microscopic single celled protists. Later he also observed free cells found in animal and plant tissues, bacteria, protozoa, RBCs, and sperms. He discovered microscopic animals such as nematodes (round worms) and rotifers too.

Leeuwenhoek' s observations were translated into English and published in the series called ***Philosophical Transactions of the Royal Society***

Despite the earlier description of cells by Hooke and Leeuwenhoek their significance as basic unit of life was not recognized for more than 150 years. In 1838, **Matthias Jakob Schleiden** (1804–1881), a German botanist observed plant tissues under microscope and stated that they were composed of cells. The plant cells were easily seen because they were clearly separated by their thick cell walls. Schleiden believed that cells were the units of structure in plants. They were seeded by the nucleus and grew from there. **Theodor Schwann**, a German Zoologist (1810-1882) also made similar microscopic observations of animal tissue and claimed that like plants, animal cells were also fundamentally composed of different types of cells. He also stated that cells were formed by crystallization from other cells not by cell division. In 1839, after a conversation with **Schleiden**, **Schwann** realized that similarities existed between plant and animal cells. This led to the foundation of cell theory and the idea that cells are the fundamental components of plants and animals. Schleiden and Schwann proposed the unified cell theory and summarized their observations into three tenets about cells.

i) The cell is the fundamental unit of structure and function in living things.

ii) All living beings are composed of one or more cells.

iii) Cells form by free-cell formation, like the formation of crystals (spontaneous generation).

But after more advancement in research now we know that the first two tenets of this theory were correct but the third one was wrong. Later **Robert Remak**, a German neurologist and embryologist, provided evidence that cells are derived from other cells because of cell division. Remak published his observations on cell division in 1852, claiming that Schleiden and Schwann were incorrect about spontaneous generation. **Rudolf Virchow** (1858) a German pathologist, also made similar observations and made important contributions to cell theory. Virchow described that each organism is made up of a sum of vital units (cells) bearing complete characteristics of life. He gave the concept of *"Omnis cellula e cellula*" meaning all cells arise only from other preexisting living cells. Thus, according to him, cell is functional unit comprising protoplasm, limited by a membrane, and containing one or more nuclei.

The concept of Cell Theory formulated in 1839 by Schleiden and Schwann and later revised after Virchow's work formed the foundation of modern biology. The three tenets of classical Cell Theory are as below:

i) All organisms are made up of one or more cells;

ii) The cell is the basic unit of life; and

iii) New cells arise from preexisting cells.

Three more principles have been incorporated in the modern version of Cell Theory. It states that:

1. All known living beings (plants and animals) are made up of one or more cells.
2. The cell forms the structural and functional unit of all living organisms.
3. All living cells arise from division of pre-existing cells.
4. Cells contain genetic information (within the nucleus in DNA), which is transmitted from cell to cell during cell division.
5. Cells of all organisms within a similar species are, by and large the same both in basic chemical composition and functions.
6. The energy flow (metabolism and biochemical reactions) occurs within cells.

These principles are based on observations made over a long period of time and some basic facts.

SAQ 1

a) State whether the following statements are **True** or **False**. Write **T** for True and **F** for False in the given brackets.

i) Protists, fungi, plants, and animals are example of eukaryotes [ ]

ii) Robert Hooke observed cork of an oak plant (*Quercus suber*). [ ]

iii) Anton von Leeuwenhoek observed only bacteria. [ ]

iv) *Omnis Cellula e cellula*" means that cells arise from new cells. [ ]

v) Prokaryotic cells have a rigid cell wall which is made up of only lipid and carbohydrates. [ ]

b) Match the name of scientists in column I with their contribution in column II.

	Column I		Column II
i)	Robert Hooke	1.	Cell theory
ii)	Anton van Leeuwenhoek	2.	Discovered cell in cork
iii)	Schleiden and Schwann	3.	Grouped cells into eukaryotes and prokaryotes
iv)	Rudolf Virchow	4.	Observed bacteria and other living cells by his single lens microscope.
v)	Dougherty	5.	All cells arise from other living cells.

c) Define cell. Who discovered cell? What are the three tenets of classical Cell Theory?

4.3 CELL-SHAPE, SIZE AND NUMBER

Cells occur in various shapes, size, and numbers. In animals, shape of the cells is generally spherical (round), elongated or irregular. In contrast, plant cells are more rigid and usually polyhedral or rectangular. Bacterial cells are typically round, rod, spiral or coma shaped. The cells can also be flattened (e.g., epithelial cells), spindle-shaped (e.g., muscle cells) or spider-shaped (e.g., nerve cells). A typical parenchyma cell in plants can have 14 sides. Some cells like Amoebae, leukocytes, algae like diatoms and desmids occur in various shapes as you can see below in the Fig 4.2.

We use the metric system for measuring the size of the cell. These conversions help us in understanding the measurement of size in biology.

1 metre = 100 cm = 1,000 mm = 1,000,000 µm = 1,000,000,000 nm

1 centimetre (cm) = 1/100 metre = 10 mm

1 millimetre (mm) = 1/1000 metre = 1/10 cm

1 micrometre (μm) = 1/1,000,000 metre = 1/10,000 cm

1 nanometre (nm) = 1/1,000,000,000 metre = 1/10,000,000 cm

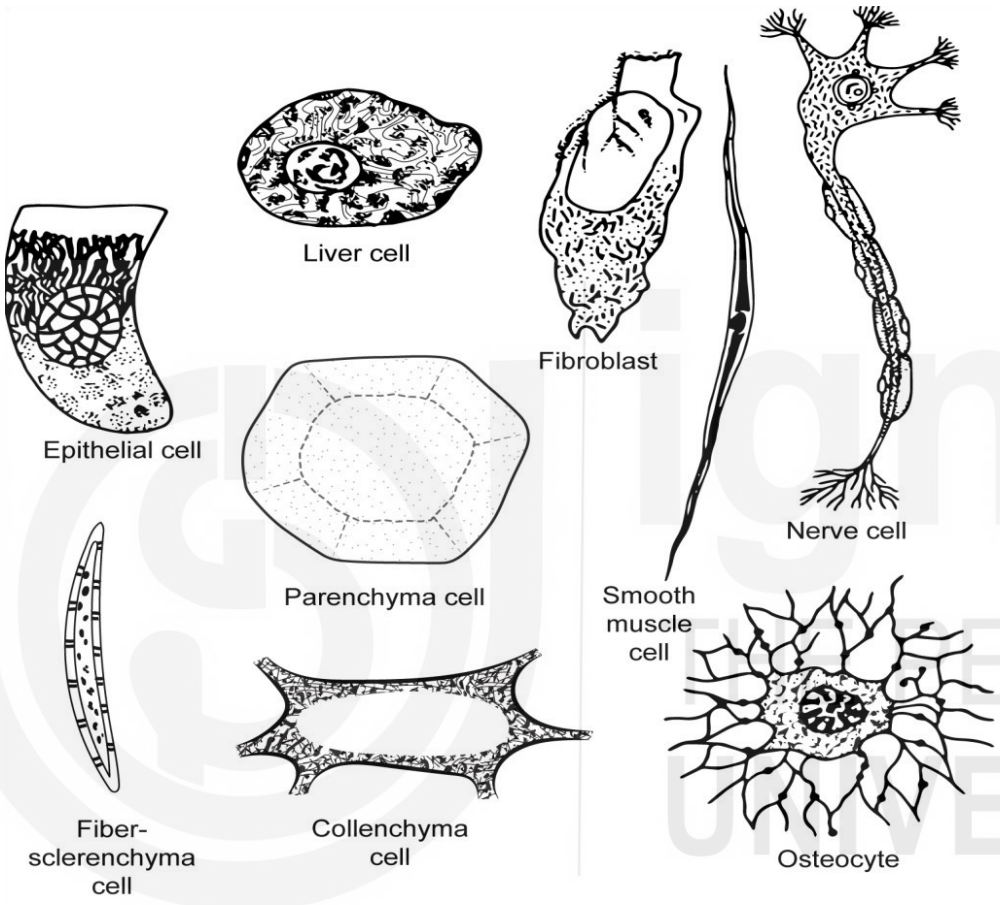


Fig. 4.2: Cells with different shapes.

The size of the cell also varies among living organisms. The prokaryotic cells are generally small (only few micrometers in size) or sometimes a bit larger. The size of eukaryotic cells usually ranges between 1 to 100 micrometers (µm) in diameter. Some multicellular forms (Rotifers) may be even smaller in size than many unicellular forms i.e. *Amoeba, Spirostomum*. Some single cells like the eggs of birds and reptiles are quite large. A nerve cell may attain a length of several meters. Red blood cells are only 5-8 µm in diameter.

An Ostrich egg cell is reported as the largest animal cell which can measure as much as 6 inches (15.2 cm) in diameter with shell around it. It is the largest cell and is about 75000 times bigger than the smallest bacterial cell.

Size of cell also varies greatly in plants and animals. Plant cells can be larger than animal cells. The normal range for an animal cell varies from 10 to 30 µm while that for a plant cell stretches from 10 to 100 µm. Most bacterial cells range from 0.2 to 10 µm in size.

In animals, length of a nerve cell may be up to 90 cm (Fig. 4.2). Egg cells are usually larger in size.

The smallest cell reported in the living world is of *Mycoplasma gallisepticum*. The size of the cell is about 0.1 µm. On the other extreme the cell of single celled alga *Acetabularia* consists of a stalk and a cap making up to 10 cm in height. *Caulerpa taxifolia,* unicellular algae possess a single cell that can grow to a length of six to twelve inches (Fig 4.3). A phloem fiber of ramie (*Boehmeria nivea*) has been reported to attain a length of about 550 mm.

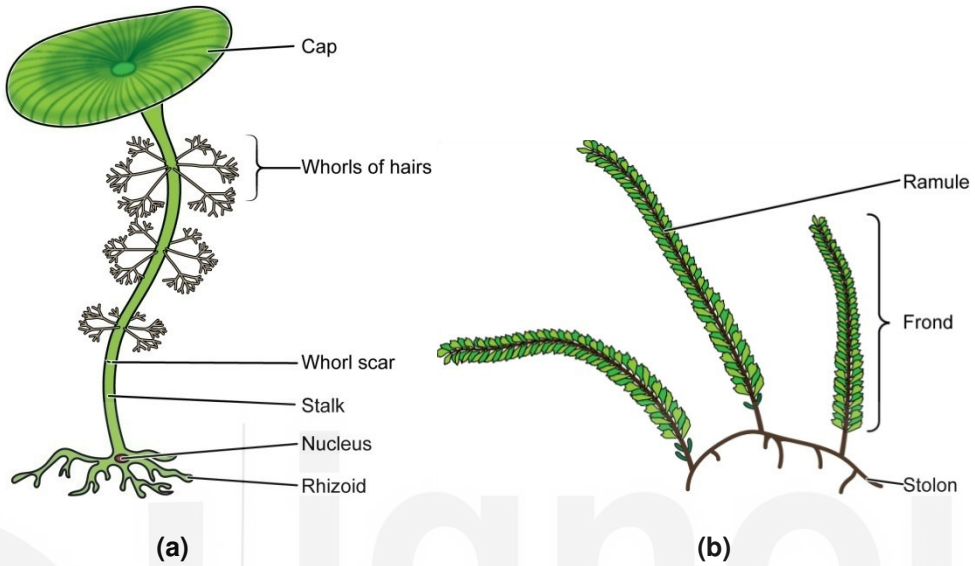


Fig 4.3: Single celled alga a) *Acetabularia;* and b) *Caulerpa*.

The comparative size ranges of biological molecules and different organisms are shown in Figure 4.4.

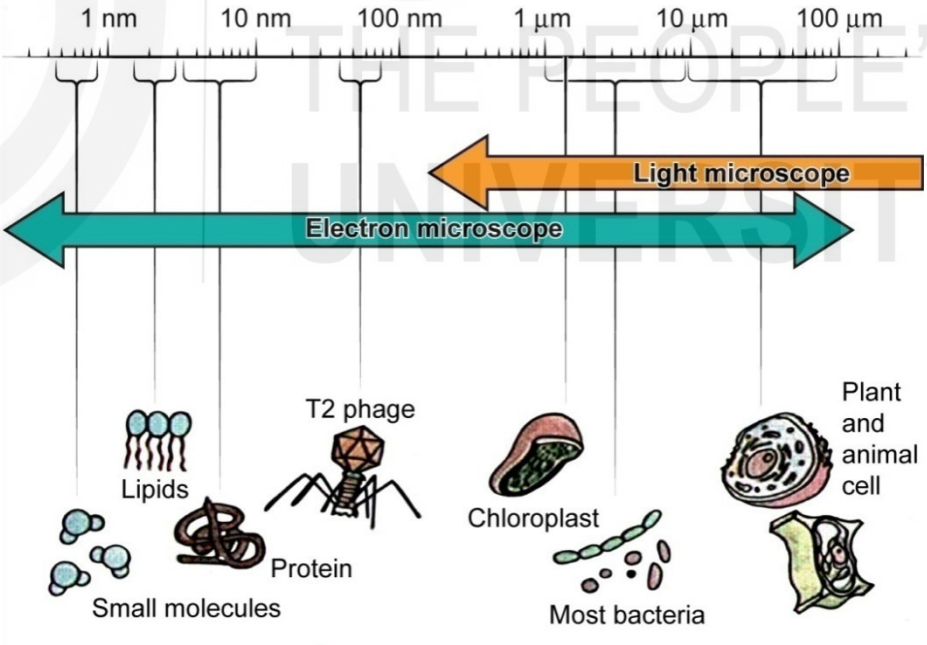


Fig. 4.4: Size chart of viruses, biomolecules, and cells of organisms.

Number of cells also varies greatly from one organism to other. In some organisms, the body is made up of many cells (multicellular) while in others it is made up of single cell only (unicellular). The number of cells in most multicellular organisms is somewhat indefinite and occurs in millions, but in some organisms, it may be fixed, like in the green algae *Pandorina* and *Eudorina* (Fig 4.5). About 60,000 billion cells have been found in human being weighing about 80 kg. Number of cells increases up to a certain period of life

and ceases afterwards. The cells in a multicellular body are of two types, germ cells and somatic cells. The cells which are solely responsible for reproduction are called **germ cells**, whereas the remaining vegetative cells forming structure of an organism are termed as **somatic** cells.

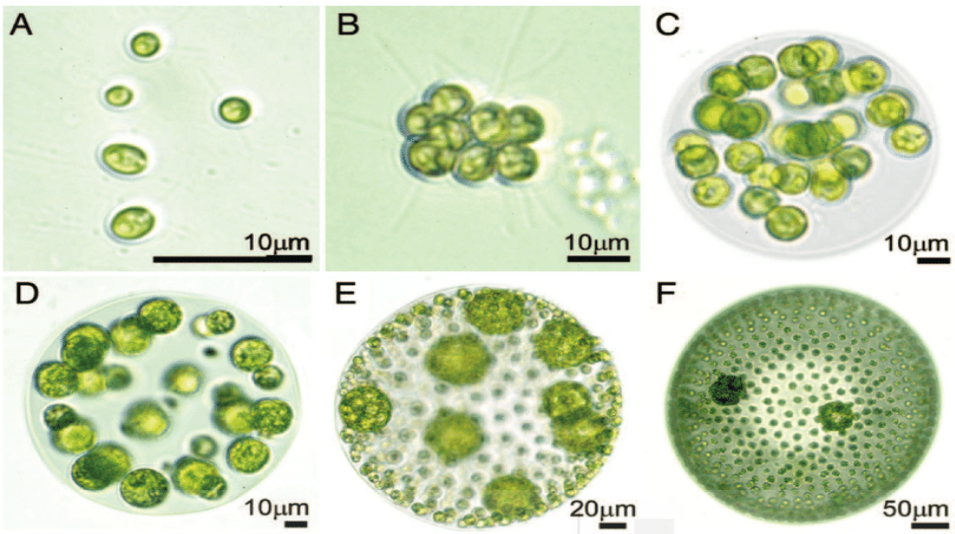
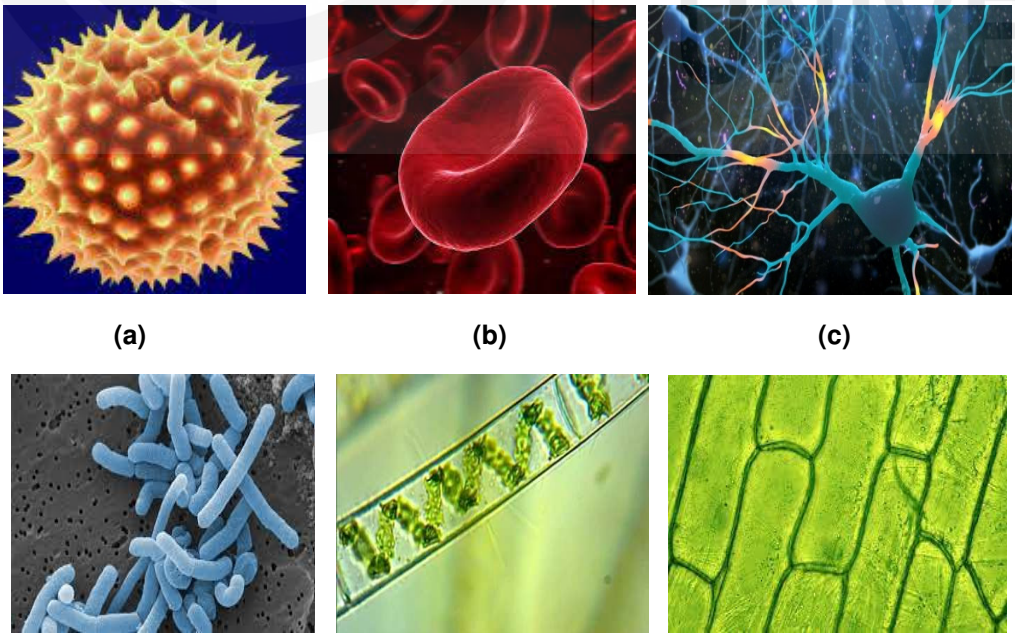


Fig 4.5: Cell size and cell number in some organisms.

The size and shape of a cell are also related to its function. Each cell type has developed a shape that is best suited to its function (Fig. 4.6). You can see examples of neurons that have long, thin extensions that connect to other nerve cells and help in transmitting the chemical and electrical messages quickly within the body. Similarly, RBCs (red blood cells) are biconcave and move easily through capillaries. The spikes or spines on the pollen grain help it in sticking to insects or animals to facilitate pollination. Long whip- like flagella in some aquatic small algae (*Volvox, Chlamydomonas*) and other organisms help them in swimming.



(a) **(b)** **(c)**

(d) **(e)** **(f)**

Fig 4.6: Size and shape of various cells. a) Pollen grain of marigold; b) red blood cell (RBC) in humans; c) nerve cell in humans; d) Lactic acid bacteria; e) *Spirogyra*; f) Plant cells.

The shape of the cells governed by four factors (1) surface area-volume ratio, (2) nucleo-cytoplasmic ratio, (3) rate of cellular activity, and (4) cell associations. The cells are small in volume but maintain a large surface area-to volume ratio. The amount of chemical activity of cells per unit of time is determined by its volume. The surface area determines the amount of absorption of waste products and amount of their release by the cells. The smaller cells have larger surface area- volume ratio and show high metabolic activity.

Some cells are surrounded by a rigid wall, which limits their shape, while others have a flexible cell membrane (and no rigid cell wall). e.g. pollen grains and amoeba.

The total surface area of a cell is just sufficient for its inner content. Any increase in the surface area produces manifold increase of the cell volume which upsets the balance. The shape and size attained by a cell is determined by the ratio of its surface area and inner volume.

Functioning of cell depends on proper coordination of activities between its different parts such as nucleus and cell organelles present in cytoplasm. Certain substances are produced by nucleus that move to cytoplasm and control its activity which you will be studying in Unit 10 DNA of Volume 2. If the cytoplasmic area is very large, it will not be possible for the nucleus to control its activity. Hence for proper functioning of cell, nucleo-cytoplasmic ratio of the cell is important. In a large cell, this difficulty can be overcome by the presence of more than one nucleus.

Some cells are metabolically more active than the others. The more active cells are usually smaller. In such cells, the surface area- volume ratio and nucleocytoplasmic ratios are properly balanced so they can function more actively than the larger cells.

In multicellular organisms the cell-to-cell association is important as it accounts for rigidity, which in turn determines the shape of the cell and its functional capacity. The above given four factors play an important role in determining the size, shape and characteristics of a cell.

SAQ 2

a) State whether the following statements are **True** or **False.** Write **T** for True and **F** for False in the given brackets.

i) *Acetabularia* is a single cell alga which consists of a stalk and a cap.

ii) Cell shape also depends upon the function.

iii) Some cells like amoebae and leukocytes change their shape.

iv) The number of cells in most multicellular organisms is somewhat definite.

v) *Caulerpa* (an alga) may have cells as long as 6 to 12 inches.

b) Fill in the blanks;

i) In *Volvox*, long……..like flagella are found which help in swimming.

ii) …….. is reported as the smallest cell of the living world.

iii) In some green algae like …… and ……. the number of cells is usually fixed.

iv) The cells responsible for reproduction are called as …… .

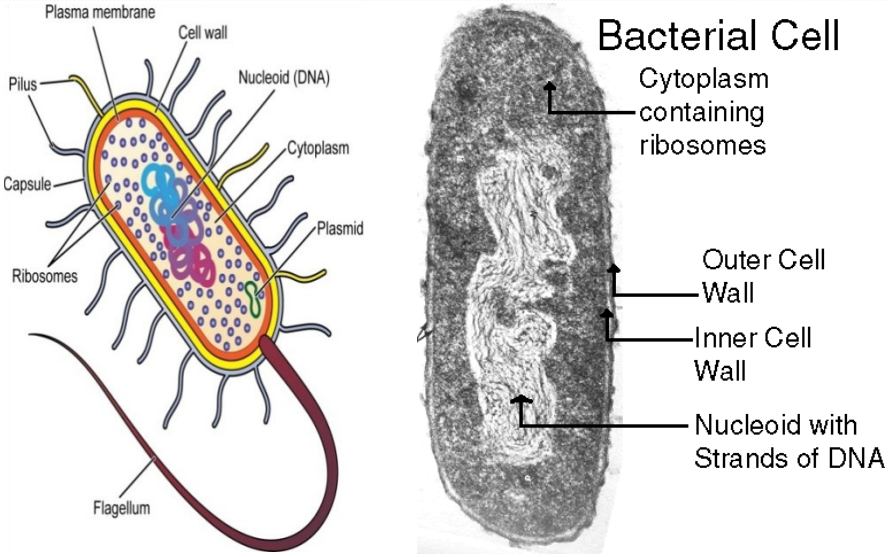
v) Some multicellular forms like …….. may be smaller in size than many unicellular organisms like *Amoeba.*

4.4 PROKARYOTIC AND EUKARYOTIC CELLS

With the invention of electron microscope, biologists were able to observe the internal structure of different types of cells. You have already studied the details of working of Electron microscope in Unit 1 Microscopy of this course. During 1950s, scientists put forward the concept that all organisms may be classified on the basis of their cell structure**.** Cells were grouped into two main classes- prokaryotic and eukaryotic by **Dougherty** in 1957. This division is based on the nuclear organization and types of cell organelles present. The cells of both prokaryotes and eukaryotes possess basic features such as plasma membrane (also called cell membrane), cytoplasm, genetic material i.e. DNA, RNA, and ribosomes. The cells of prokaryotes are simpler than those of eukaryotes and lacks internal compartmentalization and complexity. Prokaryotic cells also lack a distinct nucleus, and the chromatin bodies are scattered inside the cytoplasm. Internal membrane bound cellular bodies (organelles) are also absent. Prokaryotes are bacteria and archaea which are very small while eukaryotic cells are much larger, and complex structures compared to their prokaryotic counterparts. They possess distinct nucleus and membrane bound organelles. Examples of eukaryotes are protists, fungi, plants, and animals.

4.4.1 Prokaryotic Cell Structure

The term prokaryote is derived from the Greek word ***pro*** meaning before and ***karyon*** meaning kernel i.e., nucleus. It translates to *before nuclei* .Prokaryotes are one of the most ancient groups of living organisms on earth. They do not possess true nucleus and membrane bound organelles. Examples of prokaryotes are bacteria, cyanobacteria, Mycoplasma, Ricketssiae and Spirochaetes. Prokaryotes are mostly single celled organisms, but can also associate together in clusters and chains to form multicellular structures. Cells are generally smaller and much simpler than eukaryotic cells. Prokaryotes have a rigid cell wall made up of lipid, carbohydrates, and proteins but no cellulose. Inside the cell wall is the plasma membrane which encloses the cell (Fig. 4.7). The genetic material is present on a single chromosomal, circular, double stranded DNA molecule in a region called **nucleoid**. You have studied in detail about Prokaryotic cell in unit 3 of course BBYCT-131. Here we are discussing in brief about various cell structures found in a prokaryotic cell.



(a) **(b)**

Fig. 4.7: a) Diagrammatic representation depicting structure of a prokaryotic cell; b) Electron micrograph of a bacterial (prokaryotic) cell.

These include:

i) **Capsule** - Bacterial cells have an outer protective covering, in addition to cell wall. It is composed of polysaccharides. Proteins may or may not be present. The capsule protects the cell when it is engulfed .It also retains moisture within the cell to prevent from desiccation. It also helps in the attachment of cells to nutrients and the surfaces.

ii) **Cell wall** - It is the outermost layer of the cell made up of lipids, carbohydrates, and amino acids. It gives shape to the cell and prevents a bacterial wall from bursting when present in a hypotonic solution. Cell wall of Gram-positive bacteria is single layered and uniform in thickness (10-80 nm) whereas in Gram-negative bacterial cell wall is double layered but thinner (7.5-12 nm).

iii) **Cell membrane** - Beneath the cell wall and surrounding the cytoplasm is a semipermeable, fluid dynamic layer called cell membrane that regulates the entry and exit of substances in a cell. It invaginates to form mesosomes and thylakoids in cyanobacteria.

iv) **Cytoplasm** - It is a granular, crystallo-colloidal complex comprising of enzymes and salts that fills the whole cell. Various cell structures like ribosomes, mesosomes, chromatophores, inclusion bodies and plasmids lie in it.

v) **Ribosomes** - These are the spherical structures embedded in the cytoplasm. Prokaryotic ribosomes are 70S type which is made up of larger 50S and smaller 30S subunits. About 4-8 ribosomes attach to a single RNA during protein synthesis.

vi) **Mesosome** - Mesosomes (chondrioids) are convoluted membranous infoldings of the cell membrane. They can be considered as analogous to mitochondria of eukaryotic cells as they are the sites of respiratory enzymes. They also help in cell wall formation and bacterial replication. Mesosomes also increase the surface area of cell membrane.

vii) **Chromatophores** - These form the internal membrane system of prokaryotic cells. In photosynthetic bacteria they are very extensive and complex and called as thylakoids or photosynthetic lamallae. In nitrifying bacteria, the chromatophores increase the surface area for metabolism.

viii) **Inclusion bodies** - The nonliving structures present freely in the cytoplasm are called as inclusion bodies. They may be organic or inorganic and include food reserves, gas vacuoles, carboxysomes and magnetosomes. All inclusion bodies except food reserves are surrounded by a single layered 2-5 nm thick membrane.

a) **Food reserves -** These are storage granules not bounded by any membrane. Usually, a bacterial species stores only one type of reserve food material. For example, volutin granules store phosphate while sulphur gets stored in sulphur granules. The organic food reserves include glycogen granules, protein granules, cyanophycean granules (starch granules) and poly beta hydroxybutyrate (PHB) granules.

b) **Gas vacuoles -** Gas vacuoles are common in most aquatic free-floating bacteria. Each vacuole is made up of many hollow cylindrical gas vesicles. Gas vacuoles help in floating, buoyancy and proper positioning of photosynthetic bacteria and phytoplankton in water for trapping sunlight for photosynthesis. These gas vacuoles are better called pseudovacuoles as they are not limited by any membrane. (Eukaryotes have a tonoplast).

c) **Carboxysomes** - These bodies serve as main sites of carbon dioxide concentration around the enzyme Rubisco for CO_2 fixation (refer to BBYCT -137 Unit 6 Photosynthesis Mechanism of Volume 1) in autotrophic prokaryotes like cyanobacteria, nitrifying bacteria, and purple sulphur bacteria.

d) **Magnetosomes** - Magnetosomes are the vesicles filled with magnetite and help the aquatic bacteria to orient themselves in magnetic field and determine the direction of swimming.

e) **Plasmids** - These are the ring like, self-replicating, extra chromosomal double stranded DNA particles found in cytoplasm of prokaryotes. The term plasmid for these inclusions was introduced by **Lederberg and Hays** (1952). Their size varies from 1-300 kilobase pairs and carries 5-100 genes, they are also called as minichromosomes.

ix) **Flagella** - They are present on the bacterial surface. These are long, fine locomotory appendages for swimming. Flagellation i.e., the number and arrangement of flagella is characteristic feature of different genera of bacteria.

x) **Pili and fimbriae** - Pili (singular pilus) are tubular outgrowths about 18-20 nm long and made up of pilin protein. They are found in Gram negative bacteria and help in conjugation.1-4 pili are present per cell. Fimbriae are bristle- like surface appendages, 6.1-7.5 nm long and 3-10 nm in diameter. They help in adhesion.

4.4.2 Eukaryotic Cell Structure

The term eukaryotic is derived from the Greek word ***eu*** meaning good/true and ***karyon*** meaning kernel i.e., nucleus. These cells possess a true nucleus. Detailed study of cell, its nucleus and other organelles became possible only after the invention of electron microscope. Cytologists usually divide a eukaryotic cell in two parts- nucleus and cytoplasm. A eukaryotic cell has a true nucleus surrounded by nuclear membrane and many membrane bound organelles (including endoplasmic reticulum, Golgi apparatus, chloroplasts, and mitochondria) that divide the cell into many compartments. The presence of cell organelles is one of the most important features of eukaryotic cell. These cells can maintain different environments within a same cell so that various metabolic reactions occur simultaneously. All the reactions proceed without any difficulty because they occur in separate organelles. The compartmentation in eukaryotic cell increases its functional efficiency by isolating specific processes and permitting a division of labour within the cell.

The detailed account of various organelles present in a eukaryotic cell are given separately in coming units of this block. Therefore, we are discussing briefly about the structure of a typical eukaryotic cell here.

The eukaryotic cell contains:

Cell membrane - Cell membrane or plasma membrane surrounds the cell and separates the internal contents of cell from outside environment. It is a thin, flexible phospholipid bilayer with proteins and cholesterol embedded in it. Phospholipid is a lipid molecule with two fatty acid chains and a phosphate containing group. Cell membrane controls the movement of materials like organic molecules, ions, water, oxygen and waste products like carbon dioxide and ammonia in and out of cell. The detailed structure of cell membrane will be discussed in next unit.

Cell wall - It is a thick or thin layer present outside the cell membrane and surrounds it. It gives strength and rigidity to a cell. Cell wall is absent in animal cells, but most of them have a layer made up of carbohydrate called glycocalyx or cell coat. The plant cell wall is made up of cellulose. It may also contain hemicellulose, pectin, lignin, and other polysaccharides. Cell wall is three layered i.e., the primary and secondary cell walls and the middle lamella. Plant cell walls usually contain plasmodesmata. Plasmodesmata are the channels that connect to the cytoplasm of neighboring cells. In fungi cell walls are made up of chitin.

Cytoplasm - It is the region between the cell membrane and nuclear envelope. It is composed of the organelles suspended in a gel like semisolid cytosol, the cytoskeleton and various enzymes and chemicals. Though cytoplasm contains 70-80 percent water, it occurs in semisolid form due to presence of proteins. Besides proteins, carbohydrates like glucose and other simple sugars, amino acids, polysaccharides, nucleic acids, fatty acids, and ions are also present in cytoplasm. Many metabolic reactions occur in cytoplasm.

Nucleus - The nucleus separates the genetic material of cell from rest of the cell components. It is the most prominent organelle of a eukaryotic cell. Interestingly, red blood cells in humans lack nucleus at maturity. The nucleoplasm present within the nucleus contains hereditary material DNA and proteins. A double-membrane structure that constitutes the outermost portion of the nucleus is called nuclear envelope (Fig. 4.8). It is continuous with the endoplasmic reticulum. The nuclear envelope possesses pores which allow the entry and exit of substances such as ions, molecules, and RNA between the nucleoplasm and cytoplasm. The nucleoplasm is a semisolid gel like fluid within the nucleus containing chromatin (a DNA /proteins complex) and nucleolus. During cell division the chromatin gets condensed and isolates as clearly visible chromosomes. Chromosomes are made up of DNA which is the genetic or hereditary material of a cell. They are linear or rod-shaped structures. The nucleolus is a dark-coloured region of chromatin. It is a site of ribosome synthesis.

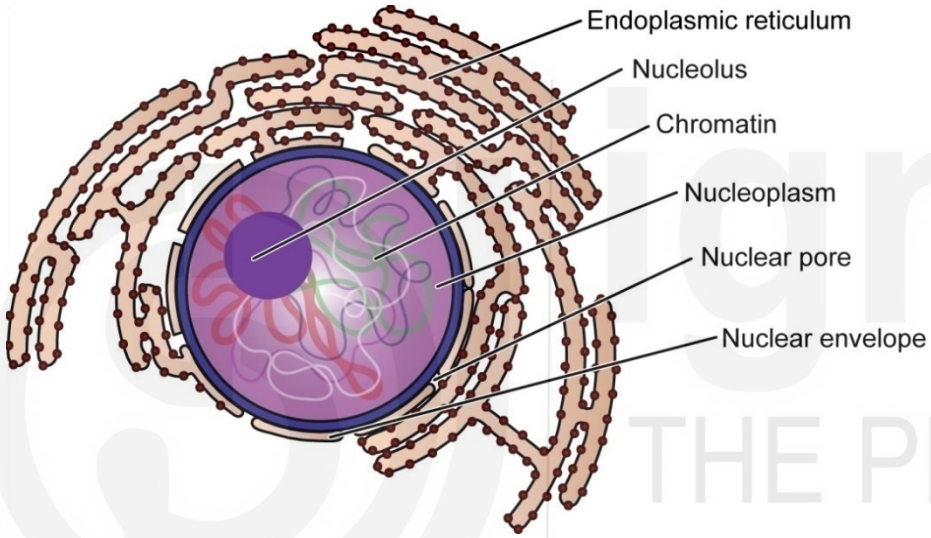


Fig.4.8: Diagrammatic representation of the nucleus found in eukaryotes.

Mitochondria - These oval or sausage shaped organelles (about 8 µm long), are often called as powerhouses or energy factories of cell as they synthesize energy carrying molecule of cells i.e. ATP (adenosine triphosphate) through cellular respiration. Respiration is a process by which glucose is broken down to liberate energy in the presence of oxygen. This you have already read in the Unit 10 Respiration of BBYC-137 course. Mitochondria (singular mitochondrion) are surrounded by double membrane; the outer membrane is permeable and simple but inner membrane is folded to form cristae. ATP synthesis is carried out in the cristae of inner membrane. Folding increases the surface area. The region surrounded by inner membrane is called mitochondrial matrix. It contains small circular strands of DNA and 70S ribosomes (mitoribosomes).

Endoplasmic reticulum (ER) - It is a network of short tubular interconnected structures scattered in the cytoplasm. ER divides the inner region of cell into luminal (inside ER) and extra-luminal (cytoplasm) parts. ER is of two types- rough endoplasmic reticulum (RER) and smooth endoplasmic reticulum (SER). RER has a rough surface due to the presence of ribosomes. It is the site of protein synthesis .It also transports proteins to Golgi apparatus. SER lacks ribosomes and is involved in synthesis of lipids.

Golgi apparatus - Golgi apparatus is made up of many smooth membranous flat, disc shaped cisternae. They are arranged near the nucleus in concentric, parallel discs. It has two faces- *cis* face and *trans*-face. Golgi apparatus helps in sorting, tagging, packaging, and distribution of lipids and proteins. All secretory processes in a cell involve Golgi apparatus.

Ribosome - they are the small non-membranous particles measuring about 20-30 nm. Ribosomes are basophilic and can be stained by any basic dye. These are made up of rRNA (ribosomal RNA) and almost 80 different proteins. Ribosomes are found floating singly in cytoplasm or appear in clusters (polyribosomes). They are involved in protein synthesis and are found in abundance in cells that synthesize large number of proteins.

Plastids - these are the double membrane bound structures present in plant cells only. Plastids are of three types:

i) Chloroplasts are the green-coloured plastids containing chlorophyll which capture the light energy that drives the reactions of photosynthesis the process by which plant synthesize their food.

ii) Chromoplasts are coloured plastids containing pigment carotene. They impart yellow, orange, or red colour to plant parts such as flowers and fruits which you have seen in your daily life.

iii) Leucoplasts are colourless plastids and act as sites for storage of fats, oils, carbohydrates, and proteins.

Peroxisomes-are small, round organelles. They are surrounded by single membrane and their main function is to break down fatty acids and amino acids and detoxify poisons by carrying out oxidation reactions. In plants, specialized peroxisomes called glyoxysomes are found that convert stored fats into sugars. Plant cells possess different types of peroxisomes that are involved in metabolism, pathogen defense, stress response and other activities.

Vacuoles and vesicles- are membrane-bound sacs which contain water or dilute salt solutions. Plant cells usually contain one large vacuole occupying most of the cell. These vacuoles are filled with cell sap and help in maintaining the rigidity and turgidity of cell by regulating the water balance. Vesicles are small vacuoles and function in storage and transport of materials. The membranes of vesicles can fuse with either the plasma membrane or other membrane systems within the cell.

Cytoskeleton-all the organelles get physical support and stability by the cytoskeleton. It is composed of a complex of microtubules, microfilaments or actin filaments and intermediate filaments.

i) Microtubules- are made up of tubulin protein subunits. They are widely distributed in cytoplasm and actively involved in transport of materials in a cell. Besides the cytoplasmic microtubules, nuclear microtubules are present in the form of centrioles and mitotic spindles. Cilia and flagella, the structures that help in cellular motion are also made up of microtubules.

ii) Microfilaments/actin filaments- these are double stranded, helical structures made up of globular protein subunits and maintain the structural integrity of cell. They are widely distributed in body cells and help in movement of organelles in cell. Actin filaments are involved in cleavage of cell during cell division. They are of two types- free globular **G-actin** and polymerized form **F-actin.** These along with myosin filaments helps in muscular contraction.

iii) Intermediate filaments- they are smaller than microtubules but bigger than microfilaments. Their size ranges from 10-12 nm in diameter. Structurally these filaments are more stable than the other two types of filaments. Their chemical composition varies as per their function and place of occurrence. e.g. examples include keratin, desmin and lamin.

Centriole- it is made up of two cylindrical microtubular structures oriented at right angles to each other. Each cylinder is composed of nine triplets of parallel microtubules. They are involved in organization of microtubules in mitotic spindle formation. Basal bodies of cilia and flagella are also formed by centrioles.

Inclusion bodies-these are the transient bodies found in cytoplasm like accumulated metabolites, lipid droplets, glycogen granules, minerals, and pigments. Inclusion bodies do not participate directly in cell metabolism and are sporadically distributed in body cells.

4.4.3 Plant Cell Versus Animal Cell

Structurally plant and animal cells are very similar because both are eukaryotes. Both possess a true nucleus that is enclosed and separated from other organelles by a nuclear envelope. Both types of cells contain membrane-bound organelles such as the nucleus, mitochondria, endoplasmic reticulum, Golgi apparatus, lysosomes, and peroxisomes. Both also contain similar membranes, cytoplasm, and cytoskeletal elements. The functions of these organelles are also similar.

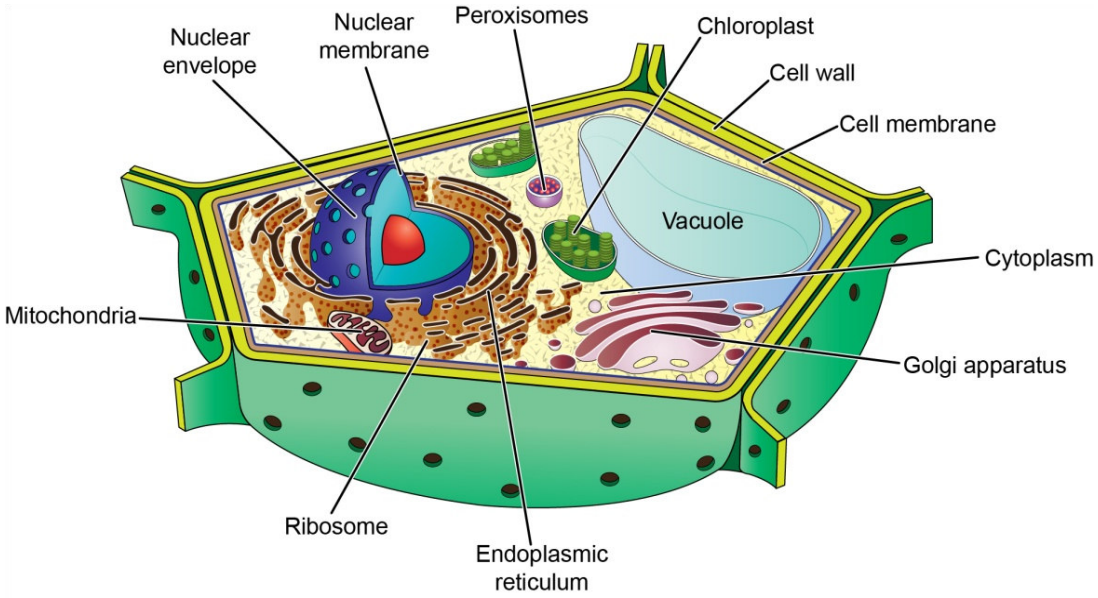


Fig 4.9: A three dimensional representation of structure of a Plant cell.

Growth and reproduction occurs in both plants and animals via cell division processes such as mitosis and meiosis. They also undergo cellular respiration for synthesizing energy required to perform growth processes and maintain normal functions.

Although plant and animal cells possess many fundamental similarities, a few striking differences are also found between the two. e.g. plant cells possess cell wall, chloroplasts, and vacuoles while these are absent in animal cells (Fig 4.9). Vacuoles regulate storage of water and other molecules in plant cells.

Animal cells have lysosomes, which assist in the digestive processes in the cell. In plant cells the vacuoles are sites for digestive enzymes and may function as lysosome. Both animal and plant cells have microtubule organizing centers (MTOCs). Animal cells have centrioles associated with the MTOC complex, called the centrosome which is found near the nuclei (Fig.4.10).

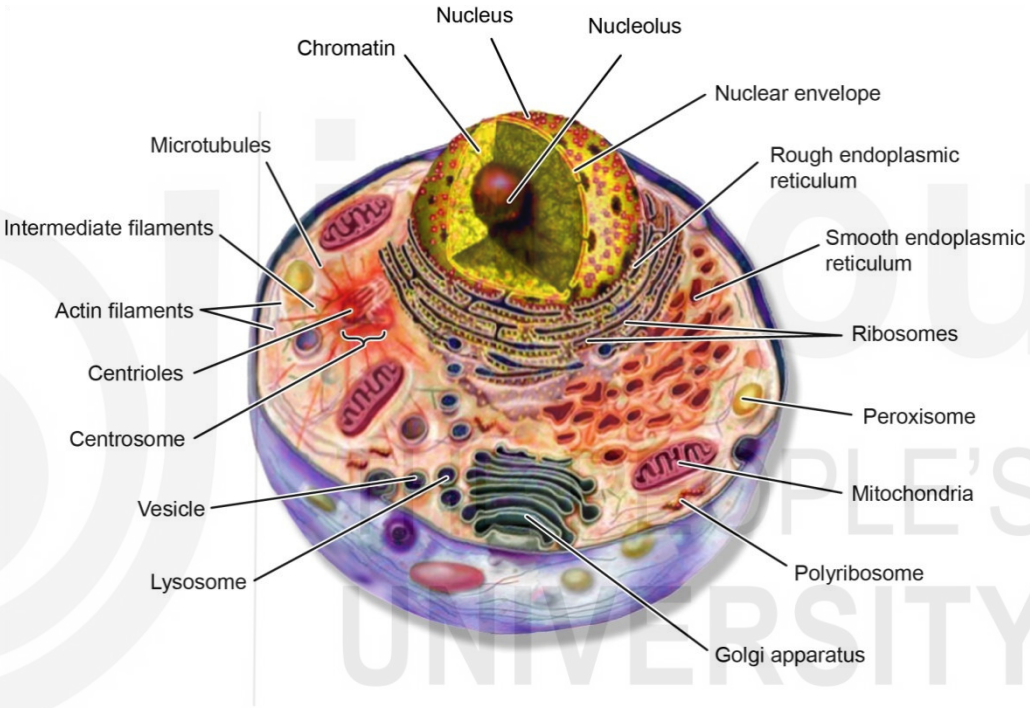


Fig. 4.10: A three dimensional representation of structure of an animal cell.

A brief description of various organelles of a eukaryotic cell and their functions are given below in table 4.1.

Table 4.1: Eukaryotic cell organelles and their functions

S. No.	Organelle	Description	Functions
1.	Cell membrane	It has lipid bilayer in which different proteins are distributed in mosaic patterns.	• maintains the shape of the cell • protects the cell • control of movement of substances in and out of the cell • helps in communication with other cells

2.	Endoplasmic reticulum (ER) Smooth and Rough	Network of intricate tubular membranes that extends in the cytoplasm. Forms system of tubes and vesicles Smooth ER lacks ribosomes on outer surface In rough ER ribosomes are present on the outer surface	• helps in intracellular transport of materials • produce steroids in certain cells • help in synthesis and transport of proteins
3.	Ribosomes	small and globular, non-membranous structures made up of RNA and proteins	• synthesize protein
4.	Mitochondria	Double membrane, sac like structures; inner membrane is folded to form cristae	• known as powerhouse of the cell • act as main site of cellular respiration
5.	Plastids	Double membrane, discoid structures found in plant cell, the three forms are chloroplasts, chromoplasts and leucoplasts	• chlorophyll present in the chloroplast trap light energy and participate in photosynthesis.
6.	Golgi apparatus	stacks of flattened membranous sacs	• help in sorting, packaging, and distribution of lipids and proteins
7.	Lysosomes	membranous sacs filled with hydrolytic enzymes	• release enzymes to hydrolyze proteins and other materials • involved in process of apoptosis or cell death
8.	Vacuoles	Membrane bound sacs in plants	• storage of ingested materials or cellular secretions or wastes
9.	Microtubules	non-membranous, hollow, spirally arranged tubular structures	• provide structural support to cell • involved in cell movement • component of flagella, cilia, and centrioles.
10.	Peroxisomes	membranous sacs containing oxidative enzymes	• help in splitting of H_2O_2 • glyoxysomes are the site of the glyoxylate cycle and participate in the process of photorespiration

11.	Microfilaments	non-membranous, rod like structures made up of contractile proteins	• give structural support to cell • helps in movement of cell
12.	Centriole	a pair of hollow cylindrical tubules located in centrosome region	• play a role in organizing microtubules that form an important part of cell's skeletal system
13.	Cilia	non-membranous, hollow tubes made of nine peripheral microtubules; extended outside of cell	• help in movement of cells in cellular fluids • also play a role in clearance of mucus, circulation of fluid and chemosensation
14.	Flagella	membrane- bounded, hollow tubes made up of two central and nine peripheral microtubules; extended outside of cell and are longer than cilia	• locomotion of cell • found in sperm cells of humans
15.	Nucleus	double membrane-bounded large spherical structure containing nucleolus and chromosomes	• contain genetic material • site of RNA synthesis • helps in regulating cell metabolism by generating various enzymes
16	Chromosomes	long thread like structures made up of DNA and proteins	• contain the genes that determine the structure and activity of the cell

After going through the above table, you have become familiar with the description and function of each of the cell organelles. In the coming units you will study in detail about various cell organelles.

It is interesting to note that cell organelles like mitochondria and plastid have their own self-replicating machinery like the nucleus and thus are independent in nature.

SAQ 3

a) Fill in the blanks with appropriate words:

i) Cytologists had divided a eukaryotic cell into two important compartments ……..and ……..

ii) Nucleus is a ……. of the cell.

iii) Mitochondria are also called as the ……..of the cell.

iv) Chloroplasts contain chlorophyll, which…….in photosynthesis.

v) Both mitochondria and chloroplasts are thought to have evolved from…….living in larger cells.

vi) Major function of cell membrane is the ……of cell.

b) Match the cell organelles in column A with their correct function in column B.

Column A		Column B	
i)	Vacuoles	1.	release enzyme to hydrolyze protein.
ii)	Lysosome	2.	intracellular transport of material.
iii)	Mitochondria	3.	contain ingested material and waste.
iv)	Golgi bodies	4.	protein synthesis.
v)	Endoplasmic reticulum	5.	sorting, packaging and distribution of protein and lipids.
vi)	Ribosome	6.	powerhouse of cell.

c) Differentiate between plant and animal cell.

4.5 EUKARYOTIC CELL ORIGIN (THE ENDOSYMBIOTIC THEORY)

In this section we will discuss about the origin of eukaryotic cells. It is thought that life arose on earth around 3.8 billion years ago. Fossil records show that prokaryotes appeared at least 2 billion years before the first eukaryote, which appeared some 1.8 billion years ago. The prokaryotic cells are simpler and more primitive in their organization. A theory has been developed by researchers to explain the origin of eukaryotic cell. This is referred to as the **Endosymbiotic Theory.** This seems to be consistent with general evolutionary theory that all organisms arose from a single common ancestor which probably resembled a bacterium or a prokaryote. During the course of time, these bacteria diverged in form and function. Some acquired the ability to process energy from environment through photosynthesis by production of sugar from sunlight (photosynthetic bacteria), while others developed the novel ways to use this sugar through oxidative phosphorylation, which produced ATP (energy) from the breakdown of sugars with oxygen. According to this view, eukaryotic cells are thought to have evolved from endosymbiotic association of prokaryotes. An endosymbiont is an organism that lives inside another organism. A summary of the events leading to the origin of eukaryotic cell has been diagrammatically represented in Fig. 4.11.

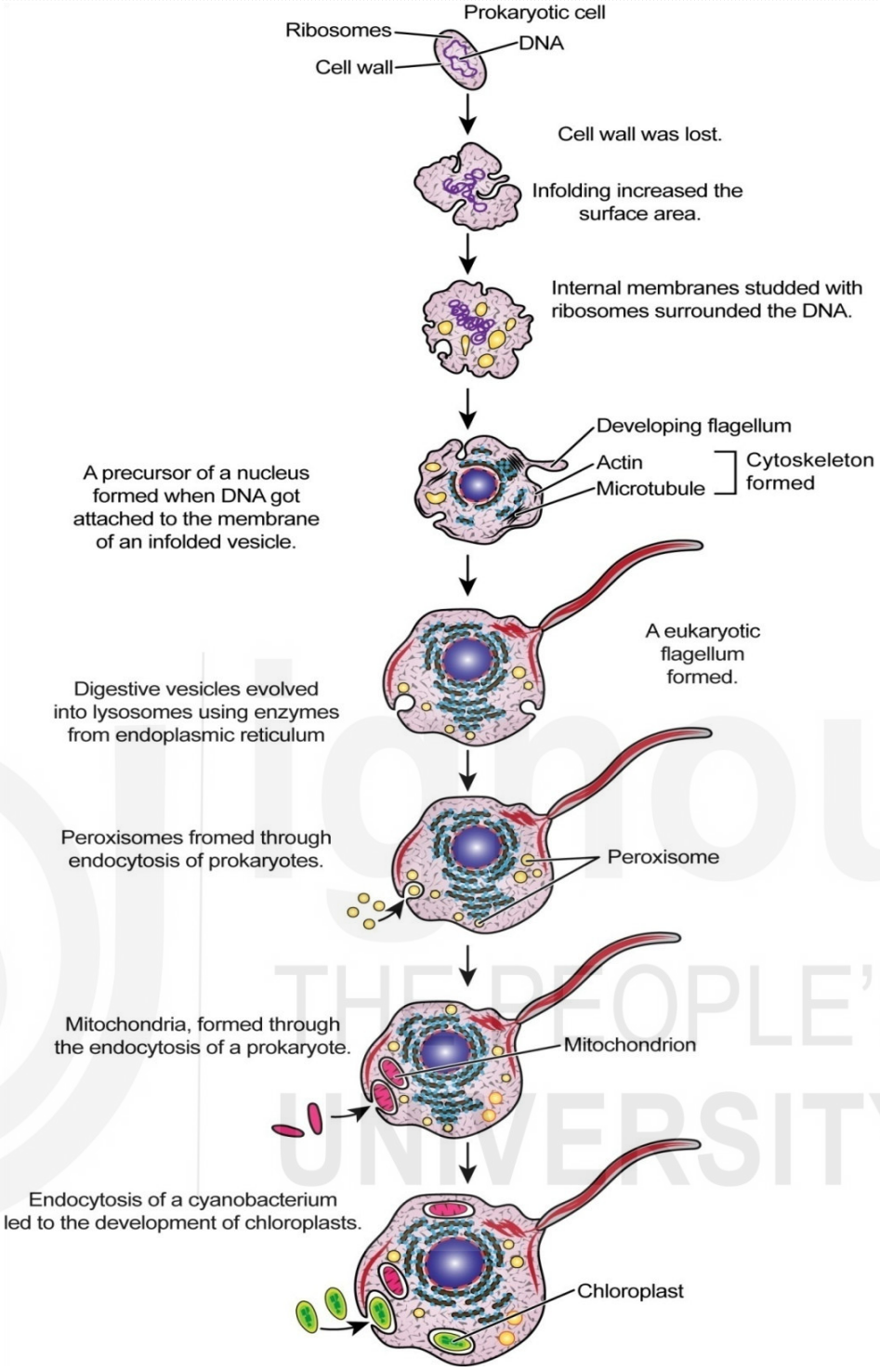


Fig. 4.11: Diagrammatic representation of various steps involved in the origin of a eukaryotic cell, mitochondria, and chloroplasts.

This theory has provided us the probable explanation about the origin of eukaryotic cell. Endosymbiotic theory states that some of the organelles in present day eukaryotic cells like mitochondria and chloroplast were once free-living cells. They were prokaryotic microbes that ended up inside of other cells (host cells). The theory was first proposed by former Boston University Biologist **Lynn Margulis** in the 1960's and officially in her 1981 book "Symbiosis in Cell Evolution ".

The formation of membrane bound subcellular organelles in eukaryotic cells is presumed to have arisen by endosymbiosis where one cell living inside another and both are benefitted by this association.

The studies of mitochondria and chloroplasts have supported the endosymbiotic theory. Both mitochondria and chloroplasts are thought to have evolved from eubacteria living in larger cells. Mitochondria would have originated as free-living aerobic bacteria – 'aerobic' because unlike the host cell, they could use oxygen in the air to oxidize their food to carbon dioxide and water. Chloroplasts would have originated as cyanobacteria (photosynthetic prokaryotes known as blue green algae).You will also study about the endosymbiotic origin of mitochondria and chloroplasts in Unit 6 of this Block.

4.6 SUMMARY

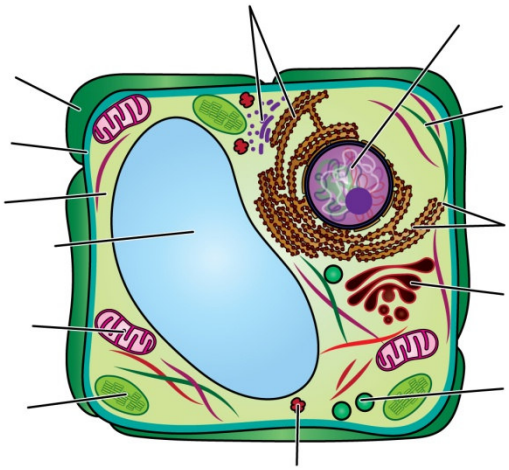
In this Unit you have studied that:

- The cell is the basic unit of structure and function in all living organisms.
- The cell theory proposed that each cell can carry out all the functions independently, cells arise from pre-existing cells.
- The cells of all prokaryotes and eukaryotes show basic differences in their structure such as presence of nucleus, internal cellular bodies (organelles). In eukaryotes, the membrane bound organelles are present but they are absent in eukaryotes. e.g. Prokaryotes are bacteria and archaea, while fungi, plants, and animals are examples of eukaryotes.
- The structure of plant and animal cell is different though they also have some similarities.
- Cells occur in variety of shape and sizes. The numbers of cells also vary in each organism.
- Endosymbiotic theory explains the formation of membrane bound subcellular organelles in eukaryotic cells and proposed that eukaryotic cells have evolved from symbiotic associations of prokaryotes by endosymbiosis.
- Eukaryotic cells possess nucleus and cell organelles like mitochondria, chloroplast, endoplasmic reticulum, vacuoles, Golgi complex, ribosomes, lysosomes, and peroxisomes. Each organelle carries out a specific function and work in coordination with each other.

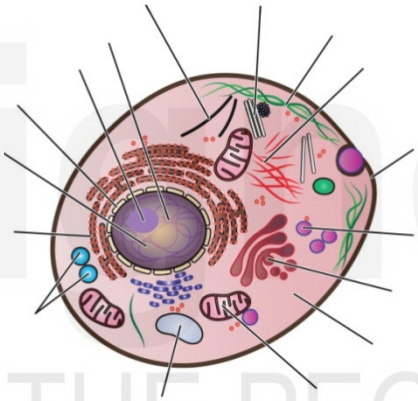
4.7 TERMINAL QUESTIONS

1. Describe the modern version of cell theory.
2. Differentiate between prokaryotic and eukaryotic cell.
3. Discuss endosymbiotic theory of origin of eukaryotic cell with well labelled diagram.
4. Make a chart of eukaryotic cell showing description and functions of its various organelles.

5. Label the various organelles found in a plant cell in the diagram given below.



6. Label the diagram given below.



4.8 ANSWERS

Self-Assessment Questions

1. a) i) True; ii) True; iii) False; iv) False; v) False

   b) i) discovered cell in cork

   ii) observed bacteria and other living cells by his single lens microscope

   iii) cell theory

   iv) all cells arise from other living cells

   v) grouped cells into eukaryotes and prokaryotes

   c) Refer to Section 4.2.

2. a) i) True; ii) True; iii) True; iv) False; v) True

   b) i) whiplike

   ii) *Mycoplasma gallisepticum*

   iii) *Eudorina, Pandorina*

iv) germ cells

v) rotifers

3. a) i) nucleus, cytoplasm

ii) control centre

iii) powerhouse

iv) traps energy

v) eubacteria

vi) protection

b) i) contain ingested material and waste

ii) release enzyme to hydrolyze protein

iii) powerhouse of cell

iv) sorting, packaging and distribution of protein and lipids

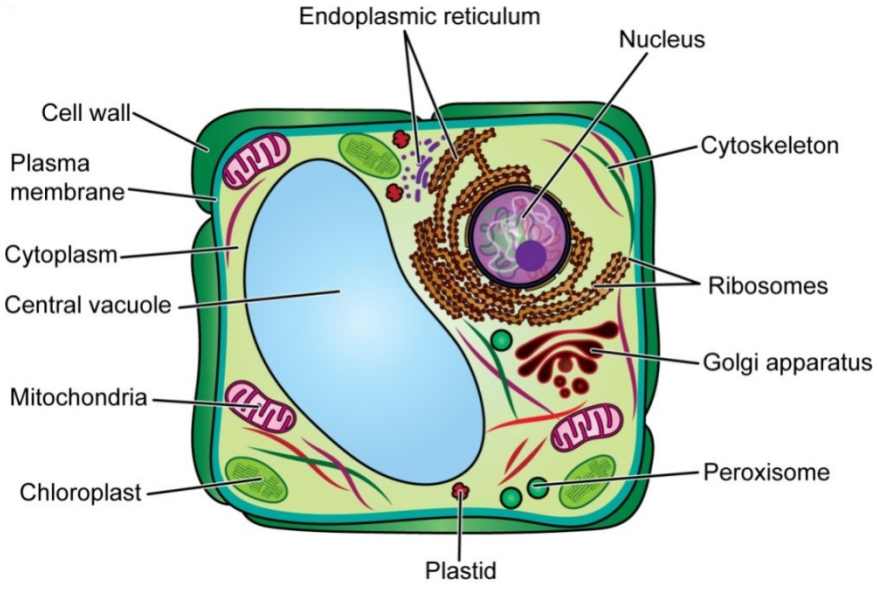
v) intracellular transport of material

vi) protein synthesis

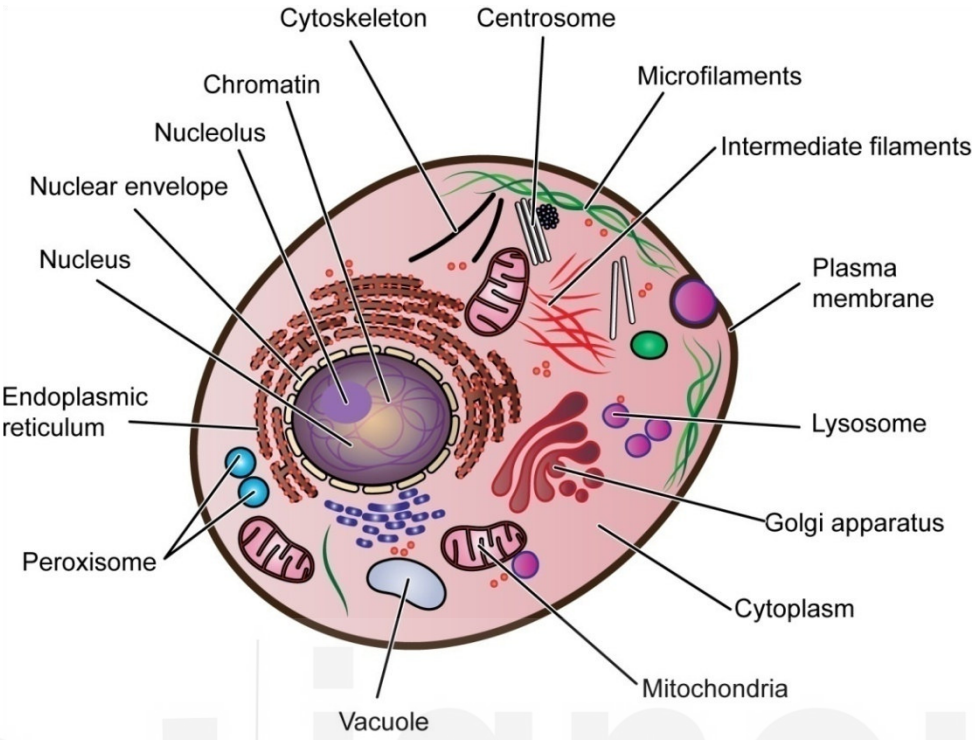
c) Refer to Section 4.4.3

Terminal Questions

1. Refer to Section 4.2
2. Refer to Section 4.4
3. Refer to Section 4.5
4. Refer to Table 4.1
5.



6.



Acknowledgements

Fig. 4.1 : Source: https://www.google.im/imgres?imgurl=https%3A%2F%2Fc8.alamy.com%2Fcomp%2FE59GYH%2Fmicroscope-used-by-robert-hooke-in-1664-to-make-his-early-observations-E59GYH.jpg

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Fig. 4.4 : https://www.google.im/imgres?imgurl=http%3A%2F%2Fwww2.estrellamountain.edu%2Ffaculty%2Ffarabee%2FBIOBK%2Fcellsize_1.gif&imgrefurl=http%3A%2F%2Fwww2.estrellamountain.edu%2Ffaculty%2Ffarabee%2FBIOBK%2Fbiobookcell2.html&tbnid=D12Cn_oqXTIr2M&vet=12ah

Fig. 4.5 : https://www.google.im/imgres?imgurl=https%3A%2F%2Fwww.pnas.org%2Fcontent%2F103%2F5%2F1353%2FF1.large.jpg

Fig. 4.6 : https://www.google.im/search

Youtube videos

https://www.youtube.com/watch?v=rm7ujEFWWbE

https://www.youtube.com/watch?v=URUJD5NEXC8

https://www.youtube.com/watch?v=ApvxVtBJxd0

https://www.youtube.com/watch?v=RKmaq7jPnYM

UNIT 5

CELL WALL AND CELL MEMBRANE

Structure

5.1 INTRODUCTION

In the previous unit you have studied about the cell. Now in this unit you will study in detail about the structure and functions of the plant cell wall and cell membrane. Both prokaryotic and eukaryotic cells possess a cell membrane. Cell membrane forms an integral part of the cell and defines its boundary. It separates its internal contents from the outer environment. Cells of bacteria, fungi, algae, and higher plants are also surrounded by rigid cell walls apart from cell membrane. Cell wall is absent in animal cells. Cell membrane is also known as plasma membrane. It provides structural support to the cell and serves as a selective permeability barrier which allows the passage of specific molecules.

Objectives

After studying this unit, you would be able to :

- describe the structure and composition of cell wall;

- list various functions of cell wall;
- illustrate structure and composition of cell membrane;
- distinguish between various models proposed to explain the structure of cell membrane; and
- be acquainted with the various functions performed by cell membrane.

5.2 CELL WALL

Agar agar is a jelly like substance obtained from the red algae *Graciliaria* and *Gelidium*. It is composed of agarose (a polysaccharide) and agaropectin.

Cell wall is a rigid semi-permeable layer that surrounds cells of bacteria, algae, plants, and fungi. It is present outside the cell membrane. It mainly provides structural support and shape to cell. Cell walls are present both in prokaryotic and eukaryotic plant cells. The chief components of plant cell wall are cellulose, hemicellulose and pectins, while the prokaryotic cell wall is made up of peptidoglycans. The chemical composition of cell walls of fungi and protists is different from that of plant cell walls. Fungal cell wall is composed of a chitin polymer, **N-acetylglucosamine**, algal cell walls are made up of polysaccharides and glycoproteins like agar and carrageenin. In this section you will study the structure and functions of plant cell wall.

5.2.1 Chemical Nature of Cell Wall

The cell wall in plants is mainly composed of cellulose. Cellulose is a carbohydrate (polysaccharide) made up of long chains of glucose molecules linked together. These chains lie parallel to each other to form the bundles (Fig. 5.1).

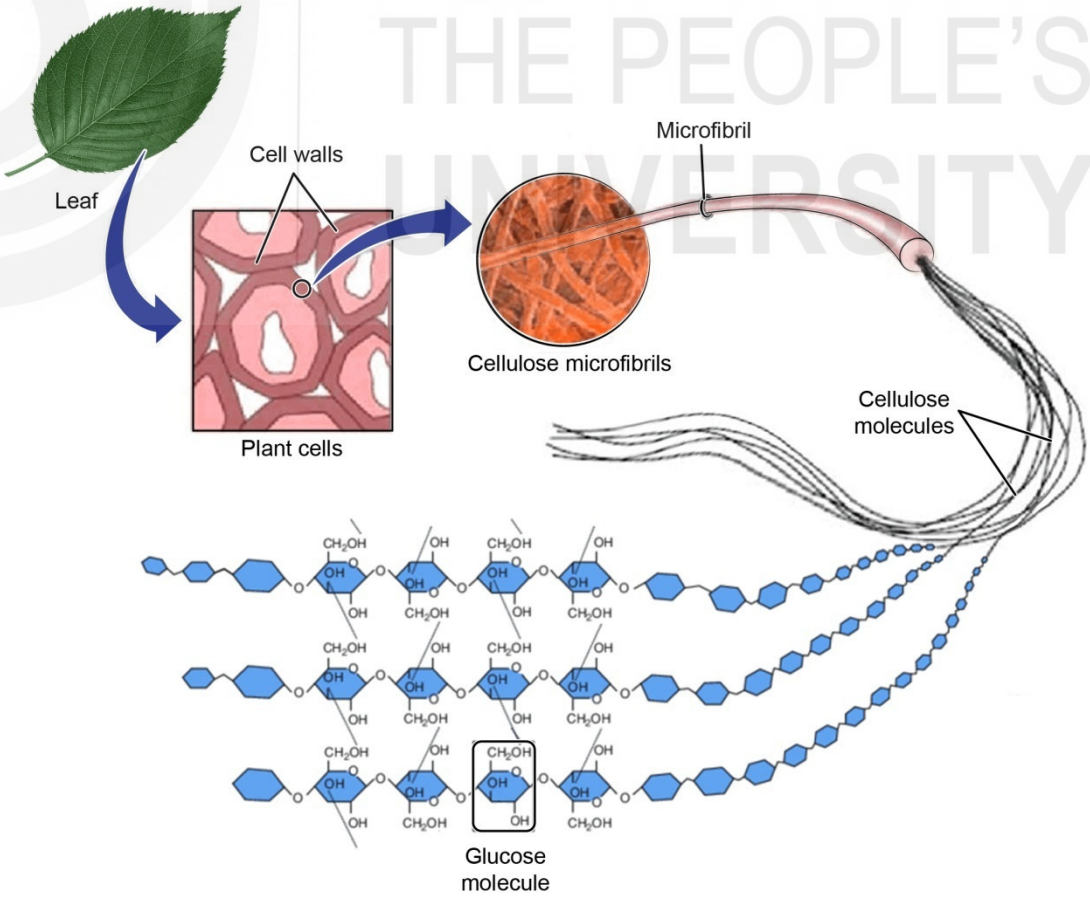


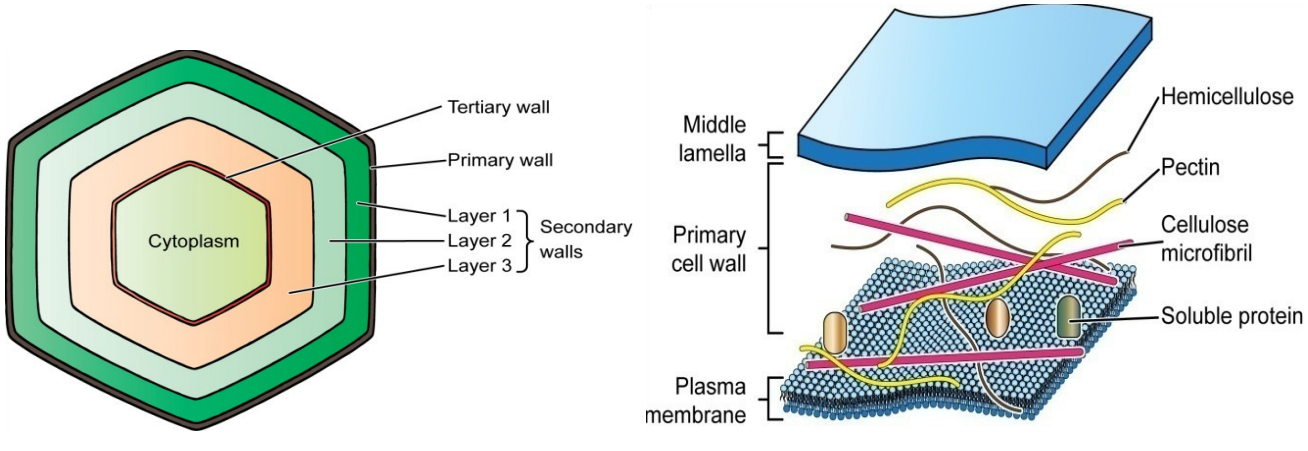
Fig. 5.1: Structure of cell wall showing the presence of cellulose microfibrils and further composition of cellulose.

A bundle of 100 chains of cellulose molecules forms the elementary fibril known as the **micelle**. About 20 micelles get arranged in a parallel manner to form **micro-fibrils** which are about 25 nm thick and 2-7 µm long. The microfibrils form large sized bundles (0.5 µm thick) of cellulose fibers known as **macro-fibrils.** Together these fibrils form the main framework of the cell wall.

Besides cellulose, various other chemical substances such as hemicellulose, pectin, lignin, cutin and chitin are also found in cell wall. The cell wall also contains certain minerals such as calcium and magnesium. The hemicelluloses are made up of monosaccharide units arranged together (like in cellulose) with short side chains of xylose and other uncharged sugars like arabinose and galactose. Pectin is composed of the pectic polysaccharides, glucuronic and galacturonic acids. Galacturonic acid and rhamnose sugar residues form the linear backbone of pectins. Lignin, along with suberin and cutin are known as cell wall plastics. They contain many organic compounds cross-linked to form a three-dimensional network. Lignins are diverse group of phenolic polymers of aromatic alcohols**.** They are mainly deposited in secondary cell walls and provide rigidity to plants. Cross linking between different polymers results in rigidity of cell wall, making it an effective barrier against penetration by microbes. Chitin is a polymer formed of glucosamine units. Cellulose, hemicellulose, and lignin are entangled with each other to form a complex matrix. The physico-chemical properties of plant cell walls are determined by the spatial organization and interactions of these cell wall polymers.

5.2.2 Structure of Cell Wall

Cell wall is made up of three layers which mainly include the primary and secondary cell walls, and the tertiary cell wall. Tertiary cell wall is present in some plants (Fig. 5.2a). The middle lamella forms a cementing layer formed between the primary walls of adjacent cells. It is composed of pectin (calcium and magnesium pectates), cellulose, and different polymers. It is a viscous, jelly like substance and acts as an adhesive material which binds/cements the primary cell walls of neighbouring cells. The primary cell wall layer is formed between middle lamella and cell membrane. It is primarily composed of cellulose microfibrils present in a gel like matrix having pectic substances and hemicellulose fibers (Fig. 5.2 b). This layer is generally 1-3 µm thick. The primary cell wall is thin and elastic but becomes thick and rigid in older cells. It provides strength and flexibility to the cell required during cell growth.



(a) **(b)**

Fig.5.2: a) The structure of cell wall showing three layers; b) Diagrammatic representation of structure of cell wall.

In some mature and specialized cells, the secondary cell wall is formed between the primary cell wall and the cell membrane. It is about 5 to 10 µm thick. After the formation of the secondary cell wall, contents of the protoplasm degenerate. Secondary walls are generally made up of three layers, which differ in the orientation of their cellulose microfibrils (Fig. 5.3). These are the outer layer (layer 1), the middle layer (layer 2), and the inner layer (layer 3). The successive layers are laid down at different angles to one another. In most plants, the microfibrils contain cellulose, but sometimes they may also have other polysaccharides like lignin that strengthen the wall and help in water transport to vascular tissues. In some algae, the microfibrils are made up of polysaccharides like xylans and mannans.

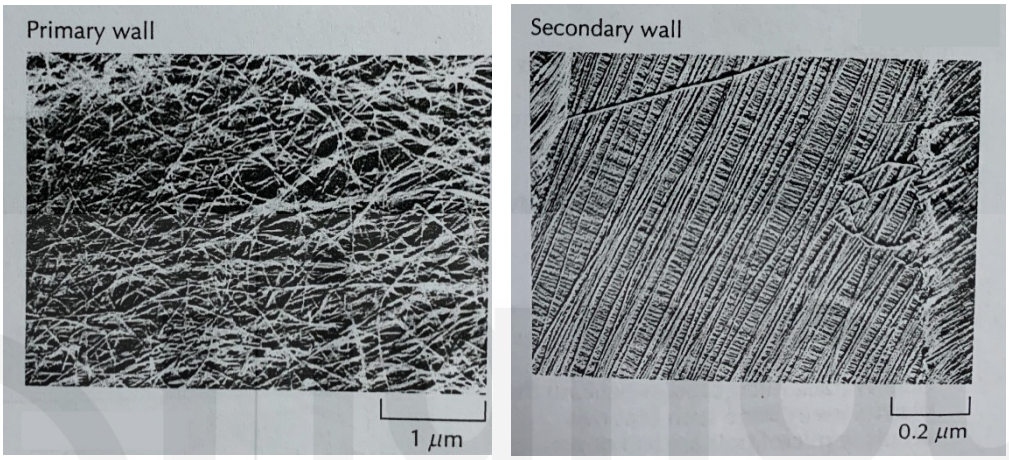


Fig. 5.3: Primary and secondary wall of plants as observed in Scanning electron microscope.

In certain plant cells, even a tertiary cell wall is laid down beneath the secondary cell wall. It differs from the primary and secondary cell walls in its morphology, chemical nature, and staining properties. Tertiary wall is made up of cellulose and xylan. This layer is very thin, and it is usually found in the xylem tracheids of gymnosperms.

Electron microscopic studies have shown that cell wall in most plants, is composed of two main parts (i) the microfibrils made of cellulose, and (ii) the ground substance or matrix in which fibrils are embedded. The ultrastructural organization of plant cell wall varies from species to species. In most plants, the crystalline cellulose microfibrils are embedded in an amorphous matrix of non-crystalline cellulose, hemicellulose, and pectin. The amount and orientation of microfibrils may vary in cell wall of different cells. In primary cell wall the microfibrils constitute loose framework as they run in all planes of cell wall; while in secondary wall, the densely packed thicker microfibrils are arranged in a parallel fashion (Fig. 5.3).

The cell walls and middle lamella of plant cells are not found as continuous layers, but are perforated by minute apertures to maintain cytoplasmic connections with each other. Such cytoplasmic junctions or bridges between the adjacent cells are known as **plasmodesmata** (Fig.5.4). The plasmodesmata of meristematic cells have been found to be continuous with those of adjacent cells. The intercellular transfer of solutions containing nutritional products, dissolved gases, ions, and other substances takes place through these plasmodesmata.

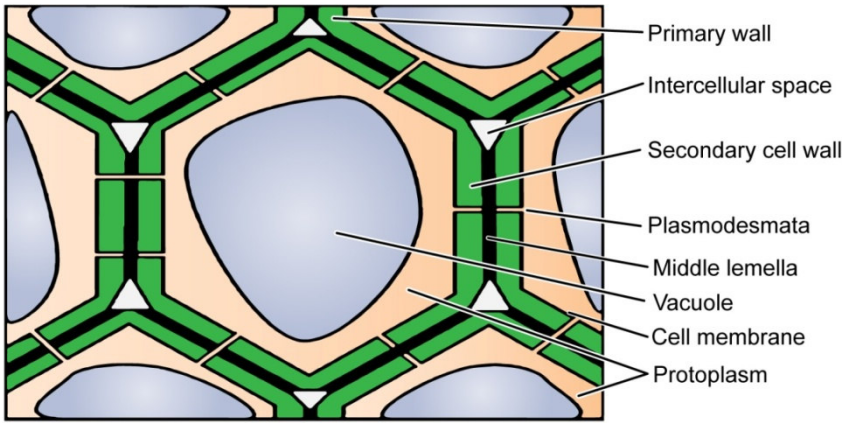


Fig. 5.4: Cell wall showing plasmodesmata connections to adjacent cells.

5.2.3 Functions of Cell Wall

- The main function of cell wall in vascular plants it to provide mechanical strength to the cell.
- Cell wall acts like a supporting skeletal framework in plants.
- The cell wall maintains the shape of the cell. Cells develop **turgor pressure** which is the pressure that contents of the cell exert against the cell wall.
- Cell wall plays a role in metabolic processes such as **absorption, secretion** of substances and **regulation of growth** and development.
- In some plants, cell wall also functions as storage unit for carbohydrates especially in seeds. It also acts a storage site of regulatory molecules that sense the presence of pathogenic microbes.
- Movement of water, nutrients, and minerals in and out of the cells is also regulated by cell wall.

SAQ 1

a) Answer in one word:

i) It is the main component that forms the cell wall.

ii) Cellulose is formed of long chains of these molecules.

iii) Chains of cellulose molecules lie parallel to each other to form the bundles.

iv) This cell wall layer may also be present in cell wall of some plants.

v) In most plants, the crystalline cellulose microfibrils are embedded in it.

vi) Cytoplasmic junctions or bridges between the adjacent cells.

b) Fill in the blanks:

i) In …….. cells, cell wall is absent.

ii) Loose framework of ……. is found in primary cell wall.

iii) In plant cell wall and middle lamella …….. form cytoplasmic connections with the adjacent cells.

iv) ……is a viscous jelly like outer layer of cell wall.

v) In some algae microfibrils are made up of ……. and mannans.

c) Enlist the important functions of cell wall in plants.

5.2.4 Bacterial Cell Wall

The cell wall gives rigid and characteristic shape to the bacteria. e.g., some bacteria such as *E. coli* are rod-shaped, whereas others like *Pneumococcus* and *Staphylococcus* are spherical. Depending upon the staining properties of their cell walls (known as the Gram staining), bacteria are broadly classified into two types- Gram positive (Gram +ve) and Gram negative (Gram -ve). Gram -ve bacteria such as *E. coli* show presence of a dual membrane system. In contrast, Gram +ve bacteria such as *Staphylococcus aureus* show the presence of only a single plasma membrane surrounded by a thick cell wall. The principal component of the cell walls of both Gram +ve and Gram -ve bacteria is a peptidoglycan layer which consists of linear polysaccharide chain, cross linked by short peptides (Fig. 5.5).The thickness of the peptidoglycan layer and presence or absence of the outer lipid membrane differentiates Gram +ve and Gram -ve bacteria.

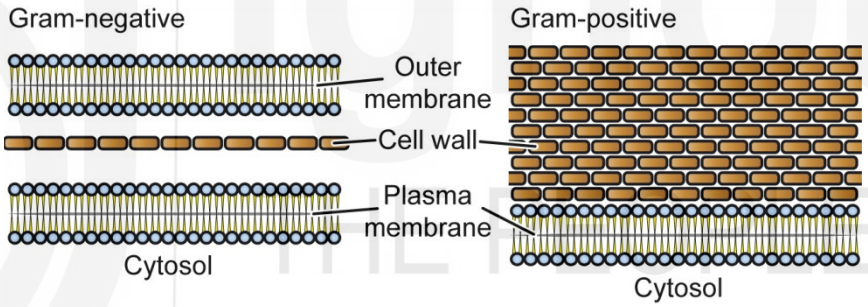


Fig. 5.5: Difference in structure of cell wall of a) Gram –ve; and b) Gram +ve bacteria.

Gram +ve bacteria have a distinctive purple appearance when observed under a light microscope following Gram staining. This is due to retention of the purple crystal violet stain in the thick peptidoglycan layer of their cell wall (Fig. 5.6).

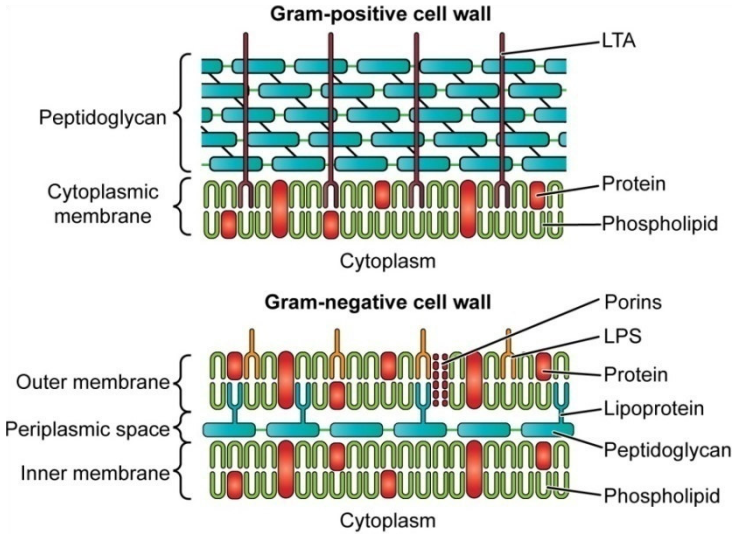


Fig. 5.6: Dye binding by Gram positive and Gram negative bacteria. LTA-Lipoteichoic acid, LPS-Lipopolysaccharide.

Staphylococci and some *Istria* species are Gram -ve bacteria. On the other hand, Gram –ve bacteria appear pale reddish in colour. This is because their cell wall is not able to retain the crystal violet stain and gets stained only by the safranin stain e.g., *Enterococcus sp., Salmonella sp.*, and *Pseudomonas sp*.

SAQ 2

a) How do Gram +ve and Gram -ve bacteria differ from each other in terms of their cell wall and membranes?

b) Define

i) cellulose

ii) micelle

iii) plasmodesmata

5.3 CELL MEMBRANE

Both prokaryotic and eukaryotic cells are surrounded by a cell membrane (plasma membrane, cytoplasmic membrane or plasmalemma). Cell membrane separates the inner cell contents from the outside environment. The cell membrane was first recognized by Swiss botanist **Karl Nageli** and **C. Cramer** in 1885. **Karl Wilhelm Nägeli** coined the term 'cell membrane'. They found that the cell surface was not continuous, and was more viscous, and denser in comparison to the cytoplasm. The framework of membrane consists of a lipid bilayer and proteins distributed at the outer surfaces as peripheral proteins or traverse the basic two layered structure and serve as membrane transporters.

Cell membrane is selectively permeable and therefore, acts as a selective barrier which regulates the movement of substances in and out of the cells. The protein molecules of a membrane are responsible for many of its functions because of their specific properties. The membrane proteins catalyze reactions occurring at the membrane and help in the transport of specific substances and chemical information in and out of cell.

5.3.1 Various Models for the Structure of Cell Membrane

Various models have been proposed by scientists to explain the structural organization of cell membrane. We are discussing here some of the important models:

i) Overton's Lipid Layer Model

Charles Earnest Overton in1900 proposed this model. According to this model, cell membrane was made up of thin layer of lipids. He proposed that compounds soluble in organic solvents entered the cells more rapidly in comparison to those soluble in water. The differences were attributed to the selective permeability of the membrane. Lipid-soluble materials pass into the cell because they get dissolved in the corresponding lipid elements present in the membrane. According to Overton, cholesterol and lecithin were the main lipid constituents of the cell membrane.

ii) Lipid Bilayer Model

Lipid bilayer or bimolecular lipid model of the structure of the cell membrane was given by **E. Gorter** and **F. Grendel** in 1925. According to this model, the cell membrane was made up of two layers of lipids. They further suggested that the heads of the lipid molecules formed a layer directed toward the water (hydrophilic) and the polar ends were directed inwards (hydrophobic). Although, this model could not explain the exact structure of cell membrane, it certainly laid down the foundation for future models of membrane structure.

In 1935, **J.F. Danielli** and **E.N. Harvey** proposed that oil droplets and other lipid inclusions in cells were bounded at their surface by an organized layer of the lipid and a layer of protein. It was postulated that the proteins, which consisted of a monomolecular layer of hydrated molecules faced the aqueous cytoplasm and simultaneously interacted with the polar portions of the lipid layer.

iii) Sandwich Model or Lipid Protein Model

In 1935 **J.F. Danielli** and **H. Davson** proposed a sandwich or lipid-protein model of cell membrane. It is also called the Davson-Danielli model. The model suggested that the membrane was composed of lipid bilayer and there was a lining of globular proteins on both outer and inner surfaces of this lipid bilayer (Fig. 5.7). In 1950, both the workers further explained that the selective permeability of membrane was due to the presence of pores lined with proteins within the lipid bilayer that allowed the entry and exit of polar solutes and ions. Based on the speed of penetration of membrane by different molecules, they predicted that lipid bilayer was 6.0 nm thick and each of the two protein layers about 1.0 nm thick. Hence the thickness of membrane was presumed to be about 8.0 nm. The electrostatic interactions occur between the surface proteins and bimolecular lipid molecules. This type of membrane exhibits selective permeability. This model was capable of distinguishing between molecules of different size, solubility and also between ions of different charges. The model was also supported by electron microscopic studies. High magnification electron micrographs revealed that the membrane in fact appeared to have two dark-coloured parallel bands (of protein coating) along with a light coloured region (phospholipids) in between. However, the major drawback of the model was that it assumed that all the membranes to be of uniform thickness with symmetrical inner and outer surfaces. It also could not explain about the selective permeability of certain substances along the membrane.

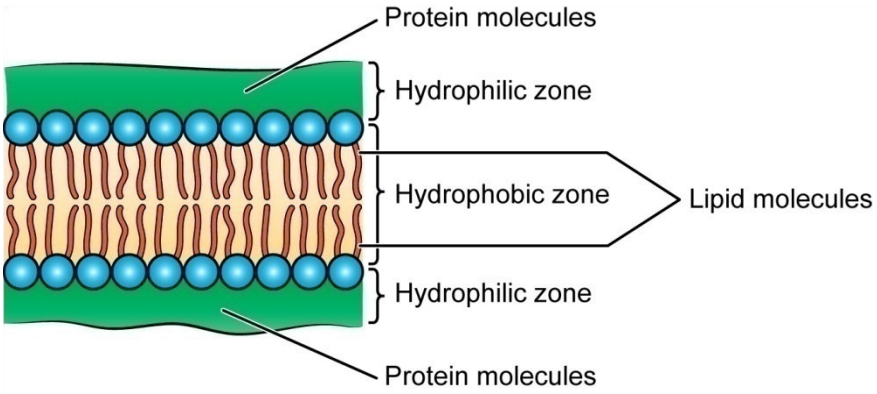


Fig. 5.7: Diagrammatic representaton of sandwich model of cell membrane as proposed by Davson and Danielli.

iv) Robertson's Unit Membrane Model

J.D. Robertson, in late 1950s proposed the Unit membrane model in which he showed that the membrane fixed with osmium tetroxide depicted a **trilaminar appearance,** consisting of two parallel outer dark layers (osmiophilic) and a central light layer (osmiophobic). The model was referred to as trilaminar as in this model a bimolecular lipid layer was present between two protein layers. The cell membrane appears like two dense osmiophilic bands separated by a clear zone when observed under the electron microscope. According to Robertson's model, the cell membrane is made up of bimolecular lipid layer sandwiched between outer and inner layers of protein, organized in the pleated sheet configuration (Fig. 5.8). Each band is made up of protein (20 Å) and polar group of lipids (5 Å). The clear zone is 25 Å thick and consists of the bimolecular lipid layer without the polar groups. Thus, the unit membrane is 75 Å thick with a 35 Å lipid layer between the protein layers of 20 Å each.

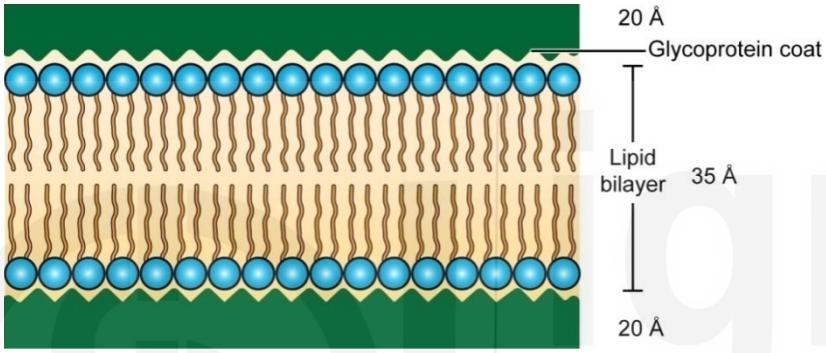


Fig. 5.8: Unit membrane model.

v) Fluid Mosaic Membrane Model

Fluid Mosaic Membrane Model was given by **S.J. Singer and Garth L. Nicolson** in1972 to explain the structure of cell membrane. According to this model the lipid bilayer exists in a relatively fluid state. Substances such as phospholipids, cholesterol, proteins, and carbohydrates present in the cell membrane give it a fluid character. The proportion of these components varies in different types of cells. The lipids present in each monolayer are capable of moving laterally within the plane of the membrane. The proteins commonly associated with the cell membrane include integral proteins and peripheral proteins (Fig. 5.9).

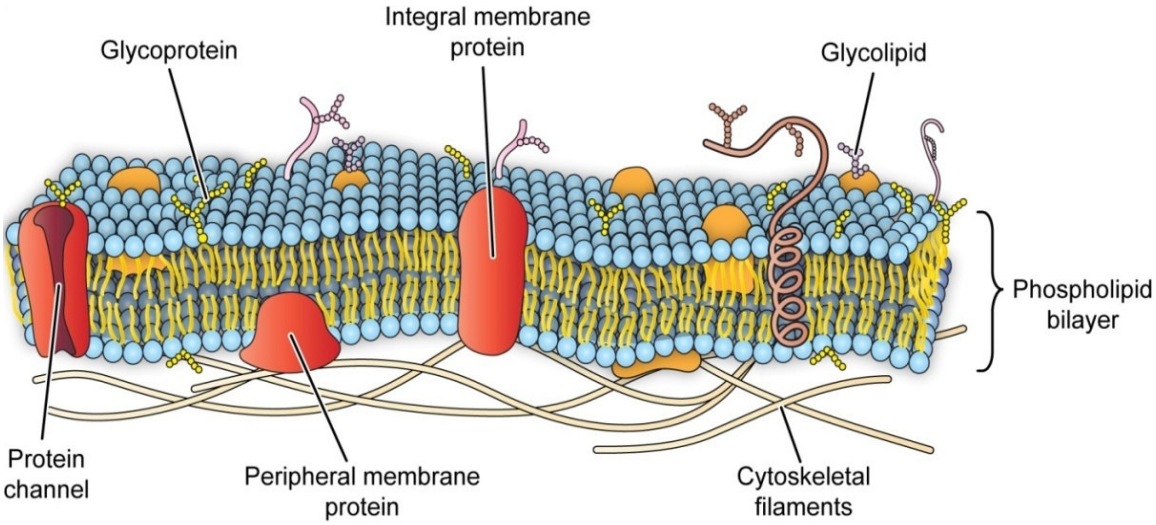


Fig. 5.9: 3-D representation of the Fluid Mosaic Membrane Model.

Angstrom (A^o) is not a part of SI system of unit, yet is an important unit used for measuring wavelengths of light and cellular components.

1 Å (angstrom) $=10^{-10}$ m= 10^{-4} µm = 0.1 nm

Proteins present on the surface are **peripheral (extrinsic)** and the proteins that extend into or through the bilayer or found embedded in the membrane are **integral (intrinsic)** proteins (Fig. 5.10). A **channel (transmembrane) protein** is an example of an integral protein. This protein selectively allows movement of particular materials such as ions to pass into or out of the cell. The protein molecules present on surface of the lipid bilayer acts as channels and pumps. Protein molecules can move laterally within the plane of the lipid bilayer. They rarely "flip-flop" from one surface to the other surface across the bilayer. Some of the lipids at the outer surface form complexes with carbohydrates to form glycolipids. Studies suggest that hydrophobic interactions along with hydrophilic interactions help to determine the three dimensional shape of molecules present in the cell membrane and also regulate the membrane fluidity (Fig. 5.10). Hydrophobic interactions in particular determine the spatial position of mainly the peripheral proteins in the membrane.

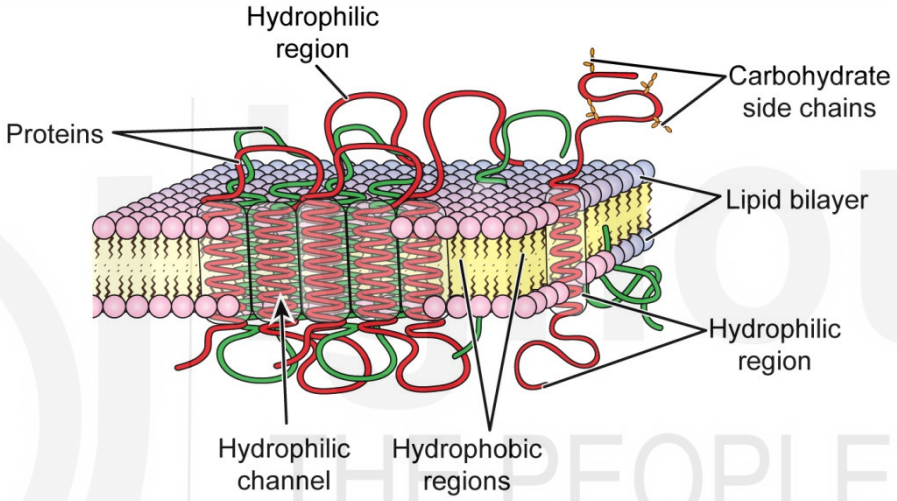


Fig. 5.10: Structure of cell membrane according to Fluid Mosaic Model.

Cell recognition proteins are another important group of integral proteins. These proteins get easily recognized by other cells. A protein that selectively binds to a specific molecule outside the cell is called a receptor. It is a type of recognition protein and its binding induces a chemical reaction within the cell. A specific molecule that binds to a receptor and activates it is called a **ligand**.

Later in the 1970s, Unwin and Henderson revealed that most membrane proteins contain alpha helical (α-helix) transmembrane segments. The transmembrane segments anchor the protein to the membrane and hold it in proper alignment within the lipid bilayer. Successive transmembrane segments are linked to each other by short loops of hydrophilic proteins that extend into or protrude from the polar surfaces of the membrane. Transmembrane segments hold the proteins within the lipid bilayer (Fig. 5.11). Interaction between a membrane protein and a particular lipid is highly specific and critical for membrane protein structure and function. Lipid bilayer provides the matrix in which membrane proteins are partially or fully embedded and plays an important role in vertical positioning and tight integration of proteins in the membrane. Lipid binding also helps in assembly and stabilization of oligomeric and multisubunit complexes. Interactions between membrane proteins and the lipid bilayer maintain the diffusion barrier and allow structural rearrangements. Protein–lipid interactions thus are required for the assembly, stability and functioning of membrane proteins.

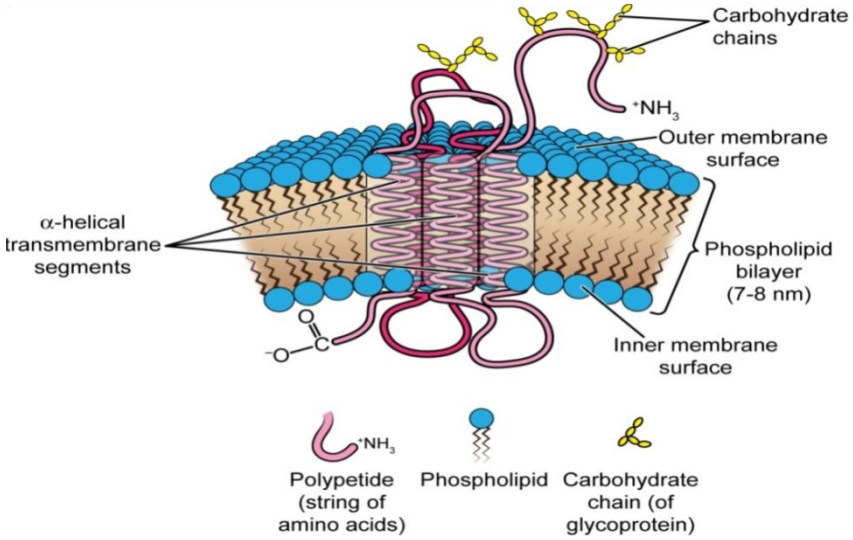


Fig. 5.11: Diagrammatic representation of the cell membrane showing transmembrane segments.

A chronological series of events leading to the development of present day Model of cell membrane (suggested by Unwin and Henderson) is depicted in Fig. 5.12.

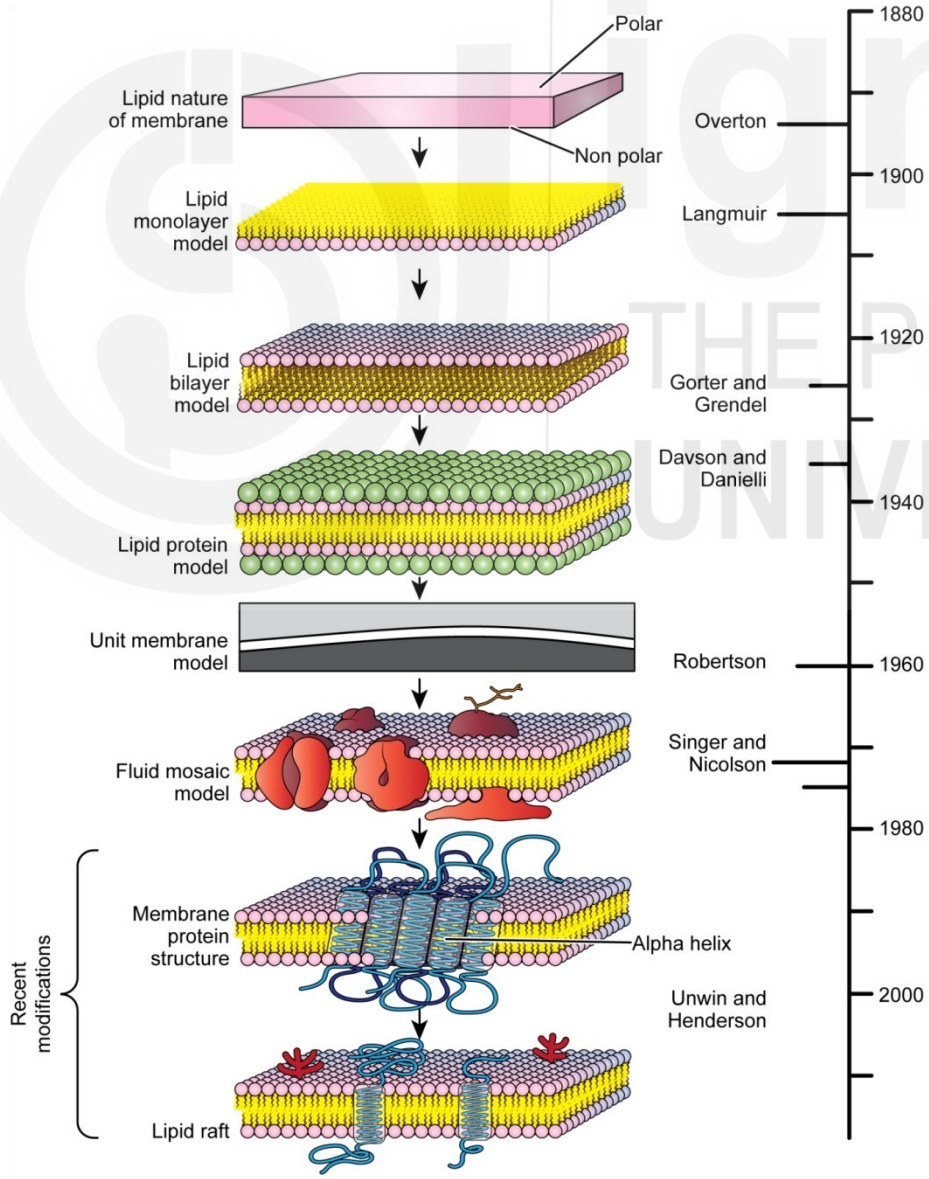


Fig. 5.12: A time bound series of events leading to the development of present day Fluid mosaic model of cell membrane (modified from Karp 8th edition).

Overton proposed lipid nature of membrane. A transition from a single lipid layer to lipid bilayer was noted in Gorter and Grendel's lipid bilayer model. Later the presence of protein molecules in cell membrane was reported in Davson and Danielli's lipid protein model. As the techniques developed, the presence of integral (intrinsic) and peripheral (extrinsic) proteins were noted (Fluid Mosaic Model). Thereafter the presence of transmembrane segments in membrane proteins was reported. Later Unwin and Handerson suggested that transmembrane segments hold the proteins within the lipid bilayer. According to the latest model, membrane associated proteins form lipid rafts on the membrane surface. These rafts act as the membrane organizing centers, and thus influence the fluidity of membrane and transport of proteins.

5.3.2 Chemical Composition of Cell Membrane

The cell membrane is mainly composed of proteins, lipids and small amount of oligosaccharides that are attached to lipids (glycolipids) or the proteins (glycoproteins). There is wide variation in the lipid – protein ratio in cell membrane (1:4 to 4:1).

Membrane Lipids- Cell membranes contain lipids which are amphipathic in nature i.e. they contain both hydrophilic and hydrophobic groups. Three types of lipids are present in the membranes which are phospholipids, cholesterol and galactolipids. The composition of lipids varies in each type of membrane. In lipid membrane, a phospholipid molecule and two fatty acid molecules are attached to first and second carbon of three-carbon glycerol backbone and form two hydrophobic tails containing saturated or unsaturated fatty acids, while a phosphate-containing group is attached to the third carbon forming a hydrophilic head. The phospholipid molecule thus possesses one hydrophilic head and two hydrophobic tails (Fig 5.13). The phosphate hydrophilic "head" is polar in nature while the lipid hydrophobic "tail" is non-polar. Unsaturated fatty acids form the curves in the hydrophobic tails. The phospholipids with a glycerol backbone are called **phosphoglycerides**, while those having an additional phosphate group linked to it are the **phosphodiglycerides**. The phospholipids possess an additional group which is commonly a choline (forming phosphatidylcholine) or ethanolamine (forming phosphatidylethanolamine) or serine (forming phosphatidylinositol). The fatty acids in phospholipid tails get saturated by binding to hydrogen atoms. The hydrophilic heads of phospholipids form hydrogen bonds with water present within the cytosol. The hydrophilic regions of the membrane interact with the hydrophobic region of the phospholipid bilayer.

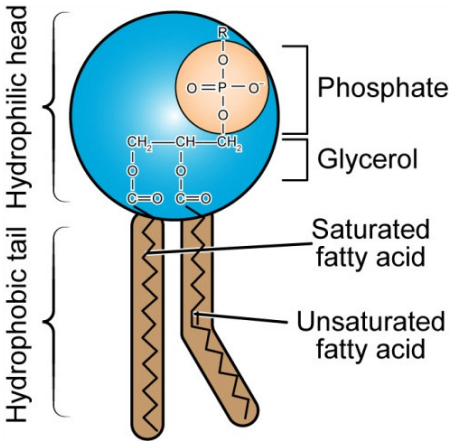


Fig. 5.13: Structure of a phospholipid molecule.

About 5-20% of phospholipids such as phosphatidylinositol, phosphatidylserine, cardiolipin, phosphatidyl glycerol and sulpholipids are acidic. These acidic phospholipids are negatively charged but other phospholipids which have neutral pH have no charge.

The distribution of proteins and phospholipids make the cell membrane asymmetrical. Choline, phospholipids, and glycolipids are found in the external half of the bilayer and the amino phospholipids are localized in the inner or cytoplasmic half of the bilayer. Another class of lipids are the Sphingolipids which consists of sphingosine linked to a fatty acid by its amino group. These lipids can associate with cholesterol and some membrane-associated proteins forms characteristic lipid subdomains on the membrane surface called **rafts**. Lipid rafts are believed to function as specific organizing centers in a membrane and are also known to influence membrane fluidity and transport of proteins.

Membrane Carbohydrates- In the cell membrane, carbohydrates are present as short, branched chains of sugar attached either to exterior peripheral proteins (forming glycoproteins) or to the polar ends of phospholipid molecules in the outer lipid layer (forming glycolipids). The carbohydrates are not found on the inner surface. The oligosaccharide chains, glycoproteins and glycolipids present in the membranes are formed by combination of six sugars viz. D-galactose, D-mannose, L-Fucose, N-acetyl neuraminic acid (also called sialic acid), N-acetyl D-glucosamine, and N-acetyl – D-galactosamine.

Membrane Proteins-Proteins represent the main component of most biological membranes. They play an important role not only in the mechanical structure of the membrane but also act as carriers or channels for transport. They may also be involved in regulatory or ligand–recognition. Many enzymes, antigens and various kinds of receptor molecules are present on cell membrane. The outer and inner regions of the cell membrane contain different types of peripheral proteins in variable amounts. This irregular distribution of membrane protein is known as membrane asymmetry.

Enzymatic Properties of Membrane proteins-Membrane proteins also possess enzymatic activity. Enzymes present in cell membrane of various cells include *acetyl phosphatase*, *acetylcholine esterase*, *acid phosphatase*, *adenosine triphosphatase*, *adenylate cyclase*, *alkaline phosphatase*, *alkaline phosphodiesterase*, *amino peptidase, lactase*, *maltase, and* NADH *oxidizing* enzymes among others. The membrane enzymes are of two types-

i) Ectoenzymes – their catalytic activity is associated with the exterior surface of the cell membrane.

ii) Endoenzymes – their catalytic activity is associated with the inner surface of cell membrane.

SAQ 3

a) Fill in the blanks.

i) The Fluid Mosaic Membrane model states that …….. exists in fluid state in cell membrane.

ii) J.F. Danielli and H. Davson proposed …….. model for cell membrane which showed that …….. molecules were associated with lipid bilayer.

iii) J.D. Robertson showed that membrane fixed with osmium tetroxide revealed a characteristic ……. appearance consisting of two parallel outer dark (osmiophilic layers) and a central light (osmiophobic layer) layer.

iv) Membrane lipids contain both hydrophilic and hydrophobic regions which are …….. in nature.

v) The phospholipid molecule has one …… head and …… hydrophobic tails.

b) Match the name of scientists given in column A to the model proposed by them in column B.

Column A		Column B	
i)	C.E. Overton	a)	unit membrane model
ii)	Gorter and Grendel	b)	fluid mosaic model
iii)	Danielli and Davson	c)	lipid layer model
iv)	Singer and Nicholson	d)	lipid protein model
v)	J. D. Robertson	e)	lipid bilayer model

5.4 CELL MEMBRANE FLUIDITY

You can find out yourselves that water being less viscous flows easily while honey being more viscous does not flow easily.

Cell membrane fluidity (CMF) is a parameter that describes the movement of lipids, proteins, and other biomolecules within the cell membrane. It is related to the viscosity of lipid bilayer of cell membrane whereas fluidity determines how easily lipids and proteins can flow or diffuse within the membrane, viscosity gives a measure of the resistance to flow. Fluidity and viscosity are inversely related. Lipids can exist in a crystalline solid phase or liquid phase depending on temperature. Unsaturated fatty acids are present in artificial bilayer made of phosphatidylcholine and phosphatidylethanolamine. Lipids exist in a relatively fluid or liquid like state if the temperature of the bilayer is about 37^{o}C. The lipid bilayer appears as a two-dimensional liquid crystal. The molecules also retain their specific orientation at this temperature. If the temperature is lowered, the nature of the bilayer changes. The lipid gets converted from normal liquid like state to a “frozen” crystalline gel. This restricts the movement of the phospholipids. The temperature at which this change occurs is called the **transition temperature**.

The molecular dynamics and mosaic organization of the cell membrane contribute to membrane fluidity and play an important role in the functions of membrane.

5.4.1 Importance of Membrane Fluidity

The fluidity allows the membrane proteins to assemble at a particular site and form specialized structures called **intersection junctions**, **light capturing complexes** and **synapses**. Membrane fluidity provides balance between a rigid, organized structure with no mobility and a completely fluid, non-viscous liquid with no orientation of membrane components and mechanical support. Fluidity allows interactions to take place within the membrane and plays a role in assembly of membrane by the insertion of lipid and protein components into the fluid matrix of the membranous sheet. The basic cellular processes such as movement, growth, division, formation of **intercellular junctions**, **secretions**, and **endocytosis** depend on the movement of membrane components i.e. fluidity of the membrane.

For signal transfer across the cell membrane, the interaction of trans-membrane receptors helps in binding of ligands on the outer surface of membrane and stimulates the activity of enzymes present on the inner surface of membrane. Membrane fluidity allows the interacting molecules to come together and carry out the necessary reaction and later move apart.

5.4.2 Maintaining Membrane Fluidity

The regulation of fluidity of the membrane is essential in the changing conditions. This is done mainly by controlling the phospholipids. Maintenance of membrane fluidity shows homoeostasis at the cellular level. If the temperature of culture of cells is lowered, the cells respond metabolically. The response is mediated by enzymes that can “remodel” the membrane. Re-modelling is accomplished by de-saturating single bonds in fatty acyl chains to form double bonds and by reshuffling the chains between different molecules to form phospholipids, containing two unsaturated fatty acids. The cell changes the types of phospholipids being synthesized by promoting the synthesis of unsaturated fatty acids.

Brownian motion, diffusion and membrane organization are the fundamental aspects of cell membrane dynamics. According to the Brownian motion principle, molecules are constantly in a moving state, colliding with each other, bouncing back and forth as the result of thermal agitation processes. The collision with other molecules slows down the diffusion of biomolecules. Molecular density of the medium affects the rate of diffusion. If density is high, the rate of diffusion is low.

Live cell membrane domains are not homogeneous in terms of their length due to the variations in composition, asymmetric organization, and thickness of membrane. Enzyme activities, membrane recycling, and signaling events constantly disturb the equilibrium of cell membrane. These events increase the concentration of subset of molecules, thus creating heterogeneity via generation of small domains. In fluid mosaic model, membrane proteins are supposed to be dispersed as monomers when present in low concentrations in a homogeneous lipid bilayer. A more mosaic and highly dynamic picture of membrane organization occurs when the proteins form preferential associations in a crowded environment. Lipid and protein diversity and organization affect the level of heterogeneity in cell membranes.

SAQ 4

a) State whether these statements are 'True' or 'False'.

i) Fluidity and viscosity are directly related to each other.

ii) The molecular dynamics and mosaic organization contribute to fluidity of the cell membrane.

iii) Fluidity plays a role in assembly of membrane by the insertion of lipid and protein components into the fluid matrix.

iv) At transition temperature, the lipid is converted from its normal liquid like state to a "frozen" crystalline gel.

v) Membrane fluidity does not allow interacting molecules to come together and carry out the necessary reaction.

b) Write a short note on importance of membrane fluidity.

5.5 FUNCTIONS OF CELL MEMBRANE

- The main function of cell membrane is protection of cell from environmental changes and external damage.
- It retains cytoskeleton, thus providing shape to the cell. It encloses cell and organelles and gives them stability and support**.**
- It maintains the cell potential by regulating the differences in the concentration of substances between the intracellular and extracellular compartments.
- It shows a characteristic feature of selective permeability. This means that only certain molecules can pass through it and the entry of others is restricted within the cell. Water, oxygen, and carbon dioxide easily pass through it. Cell membrane thus, acts as a barrier that maintains essential constituents (nutrients) within the cell and removes unwanted substances out of the cell.
- The proteins mediate the passage of ions and other biological molecules across the cell membrane. They are responsible for the selective movement of molecules into and out of the cell. Intrinsic proteins act as transport systems which allow ions to diffuse directly into the cell or solutes directly diffuse out of the cell through the membrane.
- It helps in communication and signaling between cells. Proteins of the cell membrane control the interactions between cells and serve as source, through which the cell receives signals from its environment.
- The proteins/enzymes located at the interface between the lipid and aqueous phases of membranes help in carrying out various cellular processes. Specific membrane proteins called transport proteins allow solutes to move across membrane by passive transport which you have

studied in Unit 2 of BBYCT-137. Some of the transport proteins called **channel proteins** form aqueous channels that traverse membranes and permit solutes of appropriate size and charge to move across the bilayer by simple free diffusion. Other transport proteins, called **carrier** proteins bind to a specific molecule and transfer it across the bilayer by the process of facilitated diffusion. Carrier proteins are highly specific and transport only one type of chemical compound such as ions or sugars, or only a certain molecule.

Certain transport proteins present in the form of protein complexes open only in response to a particular stimulus. Such temporarily opening passageways are called gated pores or gated channels. Gated pores open in response to a ligand binding to cell surface receptors, or due to change in the extracellular or intracellular concentration of specific ions or changes in the membrane potential.

- Substances can move across the membrane by passive transport (without the use of energy by simple or facilitated diffusion), active transport (by use of energy against the concentration gradient) or by enclosure of substances in membrane vesicles (pinocytosis, exocytosis, endocytosis) (Box 5.1). You have already studied about these processes in detail in unit 2 and 4 of Block I of Physiology course (BBYCT-137).
- Outer surface of the cell membrane contains hormone receptors which recognize specific hormones and convey the information to the interior of the cell.

Box 5.1 : Active transport

Active transport involves movement of ions and metabolites against their electro-chemical gradients by use of energy. Sugar and ions bind to different sites of a common transmembrane carrier protein, which helps sugar to move into the cell by active transport while Na^+ moves by passive transport. Active transport of solutes, macro molecules and particles across the membrane also occurs by the formation of membrane-bounded vesicles or the fusion of vesicles with the cell membrane. Substances enter the cell after being enclosed in a small portion of the cell membrane, which first invaginates and then pinches off to form an intra-cellular vesicle containing the material (endocytosis).

SAQ 5

a) Define the terms:

i) Brownian movement

ii) Viscosity

iii) Hormone receptors

iv) Endocytosis

b) Fill in the blanks:

i) ……. is the property of cell membrane by which there is free movement of lipids, proteins, and other biomolecules within the membrane.

ii) Passage of ions and other biomolecules across the membrane is mediated by …… .

iii) Cell membrane helps in …… and …….. between the cells.

iv) ……. are the transport proteins which open only in response to a particular stimulus.

v) …….. located on the outer surface of the cell membrane recognize specific hormones and convey the information to the interior of the cell.

5.6 SUMMARY

- The cell wall of higher plants is composed of cellulose and hemicellulose embedded in a gel like matrix of polysaccharides and proteins. The fungal cell wall is made up of chitin and that of algae of polysaccharides and glycoproteins. The uptake of water through cell wall allows plant cells to expand.
- The principal component of bacterial cell wall is a peptidoglycan consisting of polysaccharide chains cross-linked by short peptides.
- Three layers distinguished in the cell wall of plants are – primary cell wall, middle lamella, and secondary cell wall. Occasionally a tertiary cell wall may be present.
- Cytoplasmic junctions or bridges between the adjacent cells are known as plasmodesmata. The main function of cell wall in plant cells is to provide mechanical strength to plants. It also provides protection from pathogens and prevents swelling of cell due to variations in osmotic pressure.
- The fundamental structure of the cell membrane is composed of phospholipid bilayer which contains glycolipids and cholesterol.
- Various models have been proposed to explain the structure of cell membrane. These include Overton's lipid layer model, lipid bilayer model, Sandwich Model or Lipid Protein Model, Robertson's Unit Membrane Model and Fluid Mosaic Model.
- The most accepted model is the fluid mosaic model proposed by Singer and Nicolson. This model suggests that peripheral and integral proteins are inserted into phospholipids. Membrane proteins, carbohydrates, lipids, and small percentage of oligosaccharides may be attached to either the lipids (glycolipids) or the proteins (glycoproteins). Lipids exist in a relatively fluid, liquid like state.
- Transport of biomolecules and ions across the membranes may occur either passively by free diffusion or facilitated diffusion or through active transport that requires energy to move a substance against its concentration gradient. The cell membrane acts as a dynamic, regulatory barrier for the entry and exit of molecules and particles.

5.7 TERMINAL QUESTIONS

1. Describe the structure and chemical composition of cell wall of higher plants.
2. Discuss the role of microfibrils and lignin in structural organization and functions of cell wall.
3. Draw neat and labelled diagram of structure of plant cell wall.
4. Write the differences between primary and secondary cell wall.
5. Enumerate the difference between Gram –ve and Gram +ve bacteria with well labelled diagram.
6. Describe the chemical composition of cell membrane and discuss the role of phospholipids and glycolipids in the maintenance of structure and functions of cell membrane.
7. The fluid mosaic model of cell membrane is the best suited model. Explain.
8. What are the main functions of cell membrane?
9. Briefly describe the unit membrane model of cell membrane.
10. What is membrane fluidity? How is it maintained?
11. Differentiate between:
    i) peripheral proteins and integral proteins
    ii) carrier proteins and channel proteins
    iii) passive transport and active transport

5.8 ANSWERS

Self-Assessment Questions

1. a) i) cellulose
   ii) glucose
   iii) micelle
   iv) tertiary
   v) amorphous matrix
   vi) plasmodesmata

   b) i) animal
   ii) microfibrils
   iii) plasmodesmata
   iv) middle lamella
   v) xylan

   c) Refer to Subsection 5.2.3

2. a) Refer to Subsection 5.2.4

   b) i) Cellulose is a carbohydrate (polysaccharide) made up of long chains of glucose molecules linked together.

   ii) A bundle of about 100 chains of cellulose molecules forms the elementary fibril known as the micelle.

   iii) The cytoplasmic junctions or bridges between the adjacent cells are known as plasmodesmata.

3. a) i) lipid bilayer

   ii) sandwich, protein

   iii) trilaminar;

   iv) amphipathic

   v) hydrophilic, two

   b) i) lipid layer model

   ii) lipid bilayer model

   iii) lipid protein model

   iv) fluid mosaic model

   vi) unit membrane model

4. a) i) False; ii) True; iii) True; iv) True; v) False

   b) Refer to Subsection 5.4.1

5. a) i) Brownian motion is the constant movement of molecules colliding with each other and bouncing back and forth as the result of thermal agitation processes.

   ii) Viscosity is a measure of the resistance to flow. Fluidity and viscosity are inversely related.

   iii) The cell membrane contains receptors which recognize specific hormones and convey the information to the interior of the cell. The hormone receptors are located on the outer surface of the cell membrane.

   iv) Endocytosis is the process through which substances enter the cell after being enclosed in a small portion of the cell membrane, which first invaginates and then pinches off to form an intra-cellular vesicle containing the material to be entered.

   b) i) fluidity

   ii) proteins

   iii) communication, signalling

   iv) gated pores or gated channels

   v) hormone receptors

Terminal Questions

1. Refer to Subsection 5.2.1 and 5.2.2
2. Refer to Section 5.2
3. Refer to Fig. 5.2
4. Refer to Subsection 5.2.2
5. Refer to Subsection 5.2.4
6. Refer to Subsection 5.3.2
7. Refer to Subsection 5.3.1
8. Refer to Section 5.5
9. Refer to Subsection 5.3.1
10. Refer to Subsections 5.4.1 and 5.4.2
11. i) Refer to Subsection 5.3.1
    ii) Refer to Section 5.5
    iii) Refer to Section 5.5

Acknowledgements

Fig.5.3 : Source: https://www.google.com/imgres?imgurl=https%3A%2F%2Fi.pinimg.com%2F

Videos suggested for watching

https://www.youtube.com/watch?v=re4kAtxViiQ

https://www.youtube.com/watch?v=78cjL-o2aoc

https://www.youtube.com/watch?v=fotU_yxJkrk

UNIT 6

CELL ORGANELLES (I)

Structure

6.1 INTRODUCTION

Cells carry out all the functions necessary for the survival of living beings and represent a closed system, capable of self replication and are the building blocks of our body. In this unit we will study about the internal organization of a cell and find out how the cell functions. Eukaryotic cells possess a true nucleus and specialized structures called organelles which carry out specific functions. We will also study about some membrane-bounded organelles of a plant cell like mitochondria, chloroplasts, endoplasmic reticulum (ER), Golgi apparatus and lysosomes/vesicles. Organelles are small structures present within the cytoplasm that carry out functions necessary to maintain homeostasis in the cell. Cell organelles are either membrane- bounded or non-membranous. Membrane-bounded organelles have their own plasma membrane to create a space separate from the cytoplasm. Non-membranous organelles are not surrounded by a cell membrane. Membrane-less organelles mostly form major part of the cytoskeleton (the support structure) of the cell.

These include microfilaments, microtubules, and centrioles. The chloroplasts present in the plant cell help in carrying out essential metabolic processes such as photosynthesis. They store chlorophyll pigments that capture light energy. Mitochondrion is the organelle that performs the important function of providing energy to the cell for carrying out various functions. Other organelles such as endoplasmic reticulum, Golgi apparatus, and lysosomes participate in other essential activities of the cell which mainly include synthesis and transport of proteins, and removal of wastes.

In the previous units of this block, you have been given an introduction about the basic structure of the plant cell. The present unit will provide you with detailed information about some membrane-bounded organelles which play an important role in various essential metabolic activities in plants.

Objectives

After studying this unit, you would be able to :

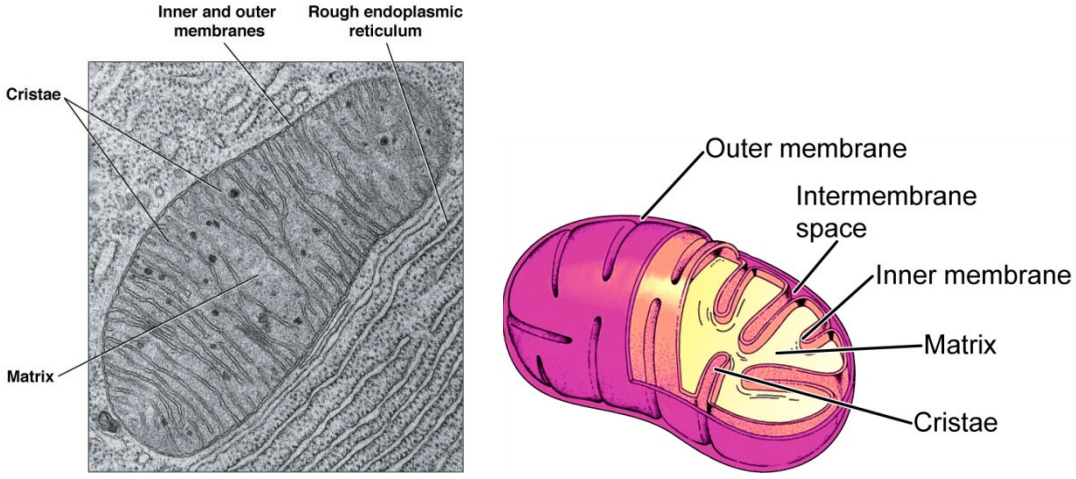
- describe the structure and functions of mitochondria and chloroplasts;
- discuss the endosymbiotic origin of mitochondria and chloroplasts;
- enumerate the reasons why mitochondria and chloroplasts are considered as semiautonomous organelles; and
- describe the structure and functions of other cell organelles such as endoplasmic reticulum (ER), Golgi bodies and lysosomes.

6.2 MITOCHONDRIA

Mitochondria (singular- mitochondrion) are important cell organelles present in the cell. They are referred to as the 'powerhouse of the cell'. This is because they are the main sites of synthesis of energy molecules such as adenosine triphosphate (ATP) in plants and animals by oxidation of various respiratory substrates. You have already read about the respiratory cycle in detail in Units 10 and 11 of your Plant Physiology course BBYCT-137. The number of mitochondria found in a cell is considered as a good indicator of its metabolic activity. More the number of mitochondria, more metabolically active is the cell.

6.2.1 Structure and Composition

Mitochondria are double membrane-bounded organelles. Mitochondria are round to oval in shape with size ranging between 0.5 to 10 µm. They have an outer and inner membrane with an intermembrane space between them. The inner membrane surrounds a liquid filled compartment called m**atrix**. The inner membrane forms invaginations that extend deeply into the matrix. These are called as **cristae**. The cristae are finger like, disk-like, lamellar, tubular or bag-like extensions. Various enzymes, proteins or protein complexes are present in the inner and outer membrane of mitochondria. They play a role in creating an electrochemical gradient required for ATP synthesis (Fig.6.1).



(a) (b)

Fig. 6.1: a) Electron micrograph (EM) showing internal structure of a mitochondrion; b) Structure of a mitochondrion.

The cristae increase the surface area available for generation of energy via oxidative phosphorylation. The membranes of cristae contain an enzyme *ATP synthase* along with protein complexes that take part in the electron transport chain (Fig. 6.2). The cristae form a compartment called the cristae lumen. This compartment contains large amounts of a soluble electron carrier protein such as cytochrome *c*. The protein lined pores known as **porins** present on the outer membrane allow movement of ions into and out of the mitochondrion.

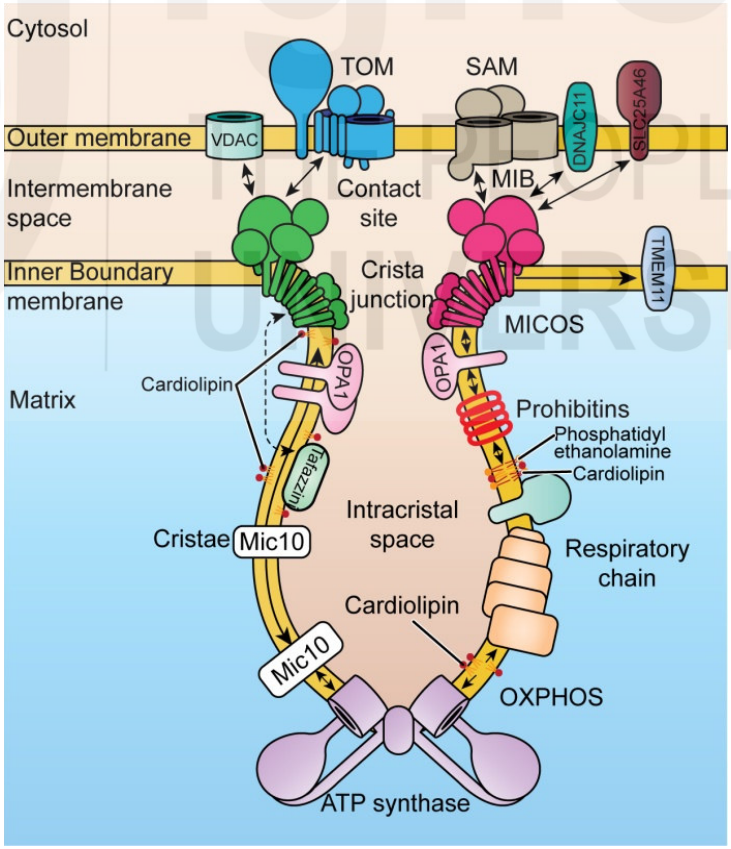


Fig 6.2: Cristae showing the presence of various enzymes, proteins or protein complexes that play an important role in ATP synthesis and oxidative phosphorylation. TOM- Protein *translocases* of the outer membrane, MICOS- the mitochondrial contact site and cristae organizing system, SAM- Sorting and Assembly Machinery, MIB- inter-membrane space bridging complex, OXPHOS- Oxidative phosphorylation

Mitochondrial matrix is the site where DNA replication, transcription, protein biosynthesis and numerous enzymatic reactions take place. The mitochondrial matrix is distinguished by a pH of 7.9 to 8. The high pH of the mitochondrial matrix creates the trans-membrane electrochemical gradient that drives ATP synthesis. Enzymes present in the matrix take part in Krebs (TCA) cycle and fatty acid cycle.

Functions

- The mitochondrion is the site of synthesis of energy-rich molecule ATP. It helps in carrying out metabolic functions in plants. ATP is generated from ADP and inorganic phosphate ions via enzyme *ATP synthase*. The major functions of ATP include cell division, biosynthesis of intermediary compounds, folding and degradation of proteins and generation and maintenance of membrane potential.
- It plays a very important role in cellular respiration. The protein complexes located on the inner membrane of mitochondria take part in respiratory chain. These mainly include electron transport complexes comprising of enzymes viz. complex I (*NADH/ubiquinone oxidoreductase*), II (*succinate dehydrogenase*), III (*cytochrome c reductase*), IV (*cytochrome c oxidase*) and the *ATP synthase* (also known as complex V). The protein complexes I, III and IV pump protons from the matrix across the cristae membrane out to the intermembrane space creating the proton gradient that drives ATP synthesis. It is the site where oxidative phosphorylation takes place. You have already studied the details of cellular respiration in units 10 and 11 of BBYCT-137.
- It also play a role in production of NADH and GTP, used in the citric acid cycle.
- The membrane proteins play a role in passage of ions/molecules, stress responses and cell signaling.

Box 6.1 : Mitochondria and Apoptosis

In mammalian cells, mitochondria usually activate many signals that induce apoptosis i.e. the process of programmed cell death. The multidomain BcL-2 family proteins present on the outer membrane of mitochondria which initiate the mitochondrial pathway to form proapoptic molecules. Capsases (proteases) initiators are activated which mask the beginning of cell death.

The process of apoptosis seems to be blocked in cancer cells. This is due to loss of apoptotic control by mitochondria due to alteration in functions of anti or pro-apoptotic proteins through post translational modifications by cancer cells. Hence this mitochondrial dysfunction inhibits cell death but allows cancer cells to survive longer.

6.2.2 Semi Autonomous Nature

The organelles having their own genetic material and are capable of synthesizing proteins required for their functioning are called **semi-autonomous organelles**. Chloroplasts and mitochondria are two genetically semi- autonomous organelles found in plants. They can perform many functions independent of the nucleus. A mitochondrion is considered as a semi-autonomous organelle because:

1. It possesses its own circular DNA (called mtDNA) and RNA (mRNA, tRNA and rRNA). It can replicate by itself within a cell from preexisting mitochondria. However, the mitochondria do not arise *de novo* (meaning from the new).

2. It possesses ribosomes called as mitoribosomes.

3. It can synthesize some of its own structural proteins.

4. It can synthesize some of the enzymes required for its functioning e.g. *succinate dehydrogenase.*

5. It can generate ATP by itself. ATP is synthesized with the help of enzyme *ATPase,* present in F_1 particle or head region.

6. It can show hypertrophy i.e. excessive growth.

6.2.3 Proteins Synthesized within Mitochondria, Mitochondrial DNA, and Marker Enzymes

Only a small fraction of proteins are synthesized inside the mitochondria whereas most mitochondrial proteins (about 99%) are synthesized outside the mitochondria i.e. in the cytoplasm of the cell. Mitochondrial proteins synthesized in the cytoplasm enter the organelle by a complex process. The proteins produced in the cytoplasm are transferred to mitochondria through special set of carrier proteins called ***translocases*** located on the outer membrane of mitochondria. These proteins contain specific amino acids known as leader sequences that get recognized by receptors present on the outer membranes of mitochondria. The membrane channels guide these proteins. These proteins function in the biosynthesis, folding/degradation of proteins and also in generation and maintenance of membrane potentials.

Genome represents the entire genetic material of an organism. It includes all the nuclear genes (coding and non-coding) along with mtDNA and chloroplast DNA. Genomics is the study of genome.

New insights into the structural and functional arrangement of protein complexes present in the in the membrane has been obtained through the technique of electron cryomicroscopy which you have acquainted with in Unit 1 of this course. The matrix proteins get transferred from the cytoplasm into the mitochondrion through the outer as well as inner membrane and also through intermembrane space. The carrier proteins present on the inner membrane help in shuttle of ions, ATP, ADP and small metabolites between the cytoplasm and the matrix. The matrix proteins perform critical functions inside mitochondria. The protein complexes of the respiratory chain and *ATP synthase* present in the inner membrane of cristae play an important role in energy metabolism. *ATP synthase,* an important protein complex found within the mitochondrion helps in the synthesis of ATP. The enzyme uses electrochemical proton gradient to produce ATP. The ATP production occurs with the help of pH gradient between cytosol and matrix. The basic assembly of *ATP synthase* complexes is conserved. The proteins get transported into the mitochondria from the cytoplasm via specific systems. We would suggest to read Unit 11 of BBYCT-137 before reading this section.

The cristae of mitochondria contain F_1-F_o *ATP synthase* protein complex. The proton pumps are located in the membrane regions of the cristae which guide protons from their source to the proton sink. The proton pumps of the electron transport chain assemble into supercomplexes or **'respirasomes'**. The mitochondrial contact site and cristae organizing (MICOS) system, an

assembly of one soluble and five membrane proteins is found attached to the cristae. It anchors to the outer membrane of mitochondria (see Fig. 6.2).

Mitochondrial DNA

In most organisms mitochondria contain a small, circular DNA. This genetic material is known as mitochondrial DNA or mtDNA. It is organized as mitochondrial nucleoids comprising DNA-protein complexes which are distributed in the matrix. Plant mtDNA represents genetic information encoded in the mitochondrion.

Plant mitochondrial genomes are larger and more complex as compared to animals. The plant mitochondrial genomes range between 200-2,000 kbp. The increased size of mitochondrial DNA is due to the presence of repeated sequences, AT-rich non-coding regions, and large introns and non-coding sequences. Plant mtDNA exists as a collection of linear DNA with combinations of smaller circular and branched molecules. The mitochondrial DNA is important for many pathways that produce energy within the mitochondria.

Genome of both mitochondrial and nuclear DNA works in coordination to regulate production of energy. Mitochondrial DNA is transcriptionally different from the nuclear DNA of any eukaryotic cell. Nuclear DNA produces messenger RNA that codes for only one protein (monocistronic). On the other hand, the mitochondrial DNA is polycistronic, and codes for three proteins.

Lynn Margulis suggested that mitochondrial genome has been derived via process of endosymbiosis from a eubacterial ancestor. It means that genome of plant mtDNA is a remnant of its prokaryotic symbiotic ancestor. Earlier this genome must have been much larger but evolved rapidly in structure because of its extensive recombination activities.

Box 6.2 : Human mitochondrial DNA

Mitochondrial DNA is about 16,569 bp (base pairs) long. It contains 37 genes and a “non-coding” region that does not code for any gene product (either proteins or various forms of RNA). All the 37 genes are essential for normal functioning of mitochondria. These genes encode different proteins that are specific for mitochondria. Out of these 37 genes, 22 codes for transfer RNA, two genes code for ribosomal RNA and the remaining13 code for proteins/enzymes involved in oxidative phosphorylation. About 13 proteins encoded by mtDNA play a role in formation of ATP via the process of oxidative phosphorylation.

Mitochondrial marker enzymes

Enzymes confined to a specific type of organelle or a cell are called as marker enzymes. These enzymes characterize a cell type. In mitochondria, the marker enzymes are specifically present in the matrix (mt-matrix), inner mitochondrial membrane (inner mt-membrane), inter-membrane space or the outer membrane. *Succinate dehydrogenase* has been considered as the main marker enzyme for mitochondria**.** It acts as a link between oxidative phosphorylation and electron transport. The enzyme catalyses the oxidation of succinate into fumarate in the Krebs cycle. The electrons derived in the process are used in the respiratory chain complex III to reduce oxygen and form water. Some other marker enzymes of mitochondria are:

- *Citrate synthase* (mt-matrix)
- *NAD^+ malate dehydrogenase* (mt-matrix).
- *NAD^+ glutamate dehydrogenase* (mt-matrix).
- *Succinate cytochrome c reductase* (inner mt-membrane).
- Rotenone-sensitive *NADH cytochrome C reductase* (inner mt-membrane).
- *Adenylate kinase* (inter membrane space).

6.2.4 Symbiont Hypothesis (The Endosymbiotic Theory)

We have already introduced the endosymbiotic theory in unit 4 of this course. Here we are giving the key points of this theory along with the phylogenetic analysis of mitochondrial genes and the striking similarities between mitochondria and some modern prokaryotes. The endosymbiotic theory or the symbiont hypothesis suggests that the origin of organelles such as mitochondria and chloroplasts in the eukaryotic cells has been from some primitive prokaryotes (Fig. 6.3). This theory was proposed by **Lynn Margulis** in 1967.

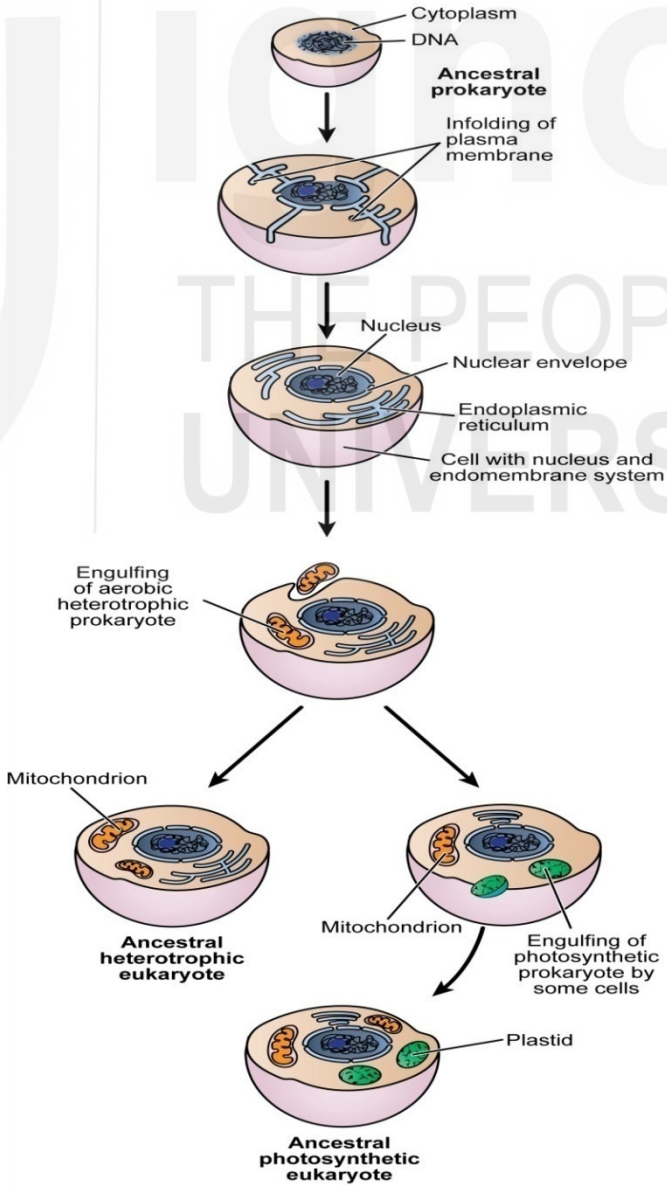


Fig. 6.3: The events of endosymbiosis theory as proposed by Lynn Margulis (diagrammatic).

The theory states that some of the organelles found in today's eukaryotic cells were once prokaryotic microbes. The first eukaryotic cell was probably an *Amoeba*-like cell that got nutrients through phagocytosis. These *Amoeba*-like organisms ingested prokaryotic cells which survived within the organism and developed a symbiotic relationship with their host. The host provided Amoeba with a stable osmotic environment and an access to nutrients. In turn, the endosymbiont provided the host with an oxidative ATP-producing system or a photosynthetic energy-producing reaction.

Archaezoa, termed as 'the proto-eukaryote', represent the descendants of a hypothetical lineage. A bacterial species, probably an archaebacteria merged with another host microbe giving rise to eukaryotes. A diagrammatic representation of set of events of endosymbiosis for development of some organelles in eukaryotic cells is given in Figs.6.3 and 6.4.

The key points of the hypothesis are:

- mitochondria are the result of endocytosis of aerobic bacteria;
- aerobic bacteria got ingested by anaerobic bacteria;
- both performed mutually benefiting functions i.e. they developed a symbiotic relationship. The aerobic bacteria provided oxygen for the anaerobic bacteria, while in turn, the anaerobic bacteria supplied food. This arrangement became a mutually beneficial relationship (symbiotic) for both.
- the inner lipid bilayer might have been the bacterial cell's own plasma membrane and the outer lipid bilayer came from the cell that engulfed it.

The concept that mitochondria are descendants of endosymbiotic bacteria was given by **Ivan Wallin** in 1926. In 1985 **Carl Woese** et al. performed phylogenetic analysis and found that ***Alphaproteobacteria*** (*α-proteobacteria*) like Rickettsiales, the oceanic SAR11 and Rhodospirillales were the precursors or ancestral forms of mitochondria. They proposed that mitochondria might have originated from endosymbiosis when a nucleated cell engulfed an aerobic prokaryote. The mitochondria eventually lost their cell wall, DNA and genes that were present in the prokaryotic ancestor. About 99 % of the genes got transferred to the nucleus.

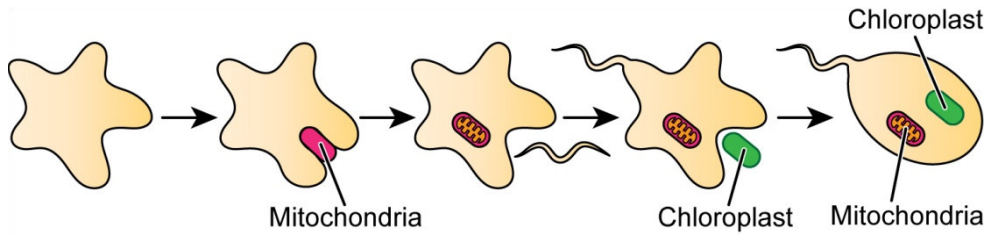


Fig. 6.4: Endosymbiosis through engulfment of bacterium by a host cell membrane.

The DNA of mitochondria differs from that of bacterial ancestor and their eukaryotic hosts. Mitochondria possess its own protein translation machinery with ribosomes, tRNAs, and associated protein factors that resemble those of their bacterial ancestors. Synthesis of some proteins occurs in mitochondria though majority of them are encoded in the nuclear genome. Mitochondrial proteins are produced mostly in the cytoplasm and imported into the organelle by an elaborate set of *protein translocases*.

Mitochondria have the following striking similarities with some modern prokaryotes:

- The mitochondria are of the same size as prokaryotic cells, and are self-replicating.
- They contain their own DNA and protein-synthesizing machinery as in prokaryotes.
- They have their own prokaryote-like circular genome.
- They show independent DNA replication and division. The genes found in mitochondria are homologous to bacterial genes.
- The DNA in mitochondria is not associated with histones whereas in eukaryotes a strong association exists between DNA and histones.
- Mitochondria have their own ribosomes containing 30S and 50S subunits like those found in prokaryote.

The respiratory chain complexes of mitochondria show close homology to bacteria. Inner membrane of mitochondria contains electron transport proteins similar to that found in plasma membrane of prokaryote

SAQ 1

a) Fill in the blanks:

i) Mitochondria are the main site of synthesis of …… .

ii) The mitochondrial matrix is distinguished by a pH of …… ..

iii) The inner membrane of mitochondria forms invaginations that extend deeply into the matrix and called …….. .

iv) The proteins produced in the cytoplasm are transferred to mitochondria through special set of proteins called …….. .

v) The mitochondrial DNA itself encodes about …… proteins.

vi) …….. is an important protein complex made within the mitochondrion which helps in the synthesis of ATP.

b) State whether these statements of true or false:

i) Modern mitochondria have same size as prokaryotic cells and they are self replicating.

ii) The cristae increase the surface area available for production of ATP via oxidative phosphorylation.

iii) Most mitochondrial proteins (about 99%) are synthesized inside the mitochondrion.

iv) Mitochondrial DNA contains 200 genes.

v) According to phylogenetic analysis, alpha proteobacteria is the precursor or an ancestral form of mitochondria.

vi) According to endosymbiotic theory, mitochondria found in today's eukaryotic cells were once prokaryotic microbes.

6.3 CHLOROPLASTS

Chloroplasts are organelles found exclusively in plants and algae. They are spherical, ovoid, discoid, biconvex or planoconvex in shape. The shape and size of the chloroplasts varies from one plant to another. In algae chloroplasts appear as a network, a spiral band, or a stellate plate. Chloroplasts possess a diameter of about 5-7 µm. In some plants, chloroplasts are relatively larger (upto 10 µm) in diameter. Chloroplasts are always found in the mesophyll cells of plant leaves and algae.

In normal developing plants the youngest plastids have few concave and perforated internal membranous structures called proplastids. The proplastids later develop into mature chloroplasts. Chloroplasts function as site of photosynthesis. As you have already studied in the Units 5 and 6 of BBYCT-137, photosynthesis is the process by which plants (primary producers) are able to convert solar energy to chemical energy using water, carbon dioxide and minerals to produce oxygen and energy-rich carbohydrates (glucose).

6.3.1 Structure and Composition

Chloroplast is a double membrane-bounded organelle. The outer and the inner membranes of the chloroplast are separated by a thin space (intermembrane) (10-20nm). Outer membrane of chloroplast is permeable and allows movement of small organic molecules while the inner membrane is less permeable. The inner membrane is folded to form stacks of flattened disks like structures called the **thylakoids**. The thylakoid membrane vesicles are organized into stacks called **grana** (singular-granum). Each granum contains around 10-20 thylakoids. Grana are connected by stroma lamellae which are the membranous extensions that connect one granum to the other neighbouring granum (Fig. 6.5). An aqueous region found inner to thylakoid membrane is known as thylakoid lumen. Metabolites such as fatty acids, lipids and carotenoids are synthesized in the inner membrane of chloroplast. The proteins located in the membrane regulate the transport across the inner membrane.

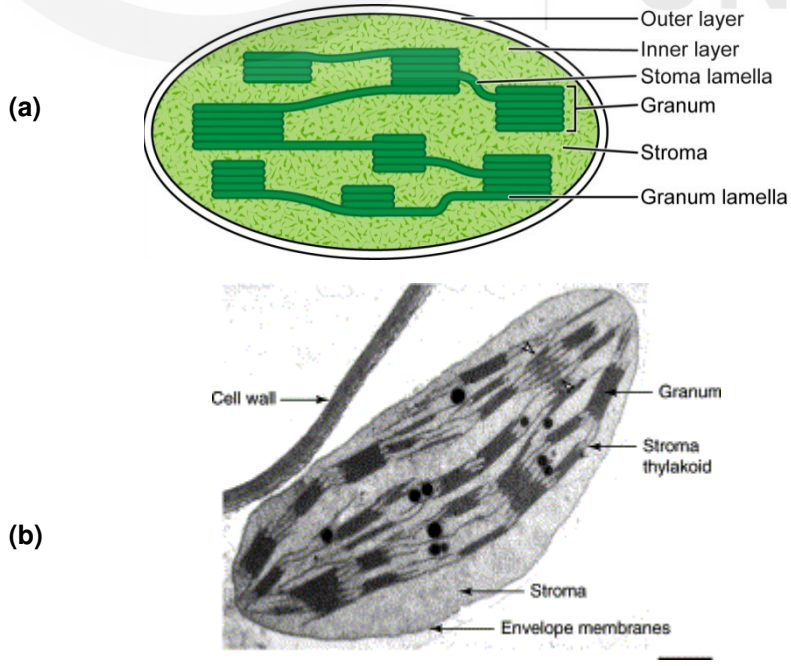


Fig. 6.5: a) Diagrammatic representation of a chloroplast; b) An electron micrograph showing chloroplast structure.

The stroma forms the innermost matrix of chloroplasts and contains dissolved enzymes and starch granules. Stroma is an alkaline, aqueous region present within the inner membrane of the chloroplast. It is rich in proteins. Thylakoids play an important role in photosynthesis. The thylakoids have the light-harvesting complex which contains pigments such as chlorophyll. The photosynthetic pigments are present in the membranes of the vesicles embedded in the thylakoid membrane (Fig. 6.6). Transmembrane protein complexes viz. Photosystems I and II (PSII and PSI) contain chlorophyll pigments that absorb photons.

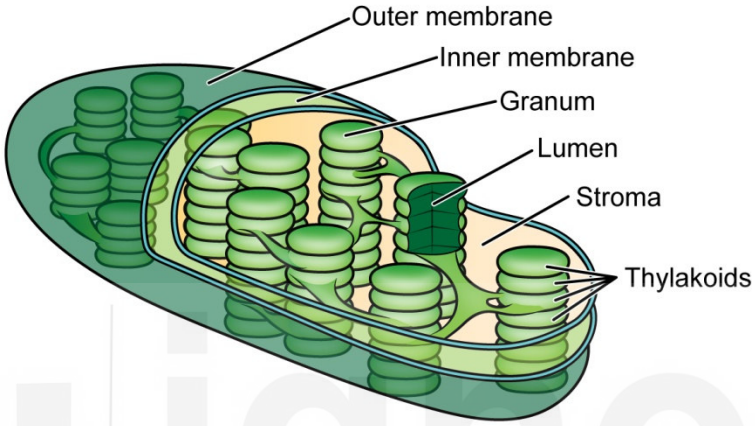


Fig. 6.6: Interconnected stacks of grana lamellae inside the chloroplast.

You have studied about the two main phases of photosynthesis in Unit 6 of your Physiology course BBYCT-137. You can revise those before studying this section. Light phase (light reactions) occurs in the thylakoid membrane while the dark phase (dark reactions) takes place in the stroma.

Functions

- It is the main site for photosynthesis. The chlorophyll pigment captures the light energy from sun, stores it in the form of ATP and NADPH molecules and later converts it into chemical energy in the form of organic compounds such as carbohydrates, along with release of oxygen.
- The components of chloroplast participate in several regulatory functions of the cell as well as in photorespiration.
- It also provides a site for various metabolic activities such as synthesis of fatty acids, membrane lipids, isoprenoids, tetrapyrroles, starch, and hormones.
- The chloroplasts along with the nucleus, cell membrane and ER play a role in defense against pathogens.
- It also acts as cellular sensor.

6.3.2 Semiautonomous Nature

Like mitochondria, chloroplast also shows semi-autonomous nature. These organelles show the presence of their own DNA, RNA, and ribosomes. DNA present in chloroplast is circular, as seen in prokaryotes. The chloroplast

shows the presence of 70S ribosomes, which is characteristic feature of prokaryotes. In addition, they can synthesize their own proteins.

Origin of chloroplast

The hypothesis of the endosymbiotic origin of chloroplasts was given by the Russian botanist **K. Mereschkowsky**. He observed similarities between cyanobacteria and chloroplasts of plants and algae. This hypothesis was then reaffirmed by Margulis. The theory suggests that chloroplasts have descended from photosynthetic cyanobacteria-like organisms which are close relatives of chloroplasts. The chloroplast originated by an endosymbiosis event where an eukaryotic cell engulfed a photosynthetic bacterium. It is suggested that photosynthetic eukaryotic cells arose more than a billion years ago through the engulfment of a cyanobacterium that later transformed into a chloroplast (Fig. 6.7). Thus, chloroplasts are the result of endocytosis of photosynthetic bacteria.

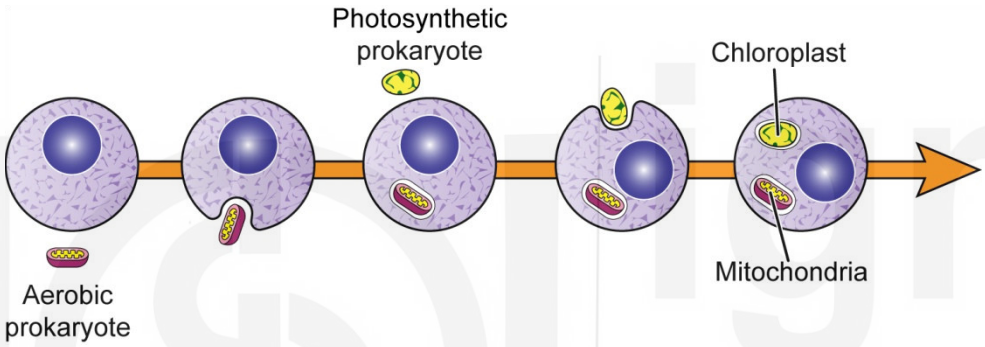


Fig. 6.7: The suggested sequence of events leading to the origin of the chloroplasts via endosymbiosis in which a eukaryotic cell took in a photosynthetic bacterium (prokaryote).

Following evidence supports the idea of origin of chloroplasts from prokaryotic photosynthetic bacteria:

1. Chloroplasts divide by binary fission. They are self-dividing, contain their own circular (not linear) DNA, and protein-synthesizing machinery like that seen in prokaryotes.
2. Like in prokaryotes, the DNA is not associated with histones.
3. It produces ATP and trap photons by mechanisms that are similar to those found in prokaryotes. 70S ribosomes are present, a feature which resembles prokaryotic ribosomes. Also, the 30S and 50S subunits of ribosomes in chloroplasts as like those found in prokaryotes.
4. They synthesize several proteins and lipids necessary for their structure and activity.

These similarities led to assumption that chloroplasts are direct descendants of prokaryotes. Following endosymbiosis, transition from a symbiont to an organelle took place. It involved steps such as loss of the bacterial cell wall, the acquisition of protein importing machinery for transfer of nuclear-encoded proteins from the cytosol to the chloroplast, and finally relocation of most chloroplast genes to the nucleus.

The presence of a similar protein importing machinery has been noted in the different Archaeplastid lineages which suggest the single origin of chloroplasts. This supports the hypothesis that chloroplasts have their own genome and transcription machinery and specific genetic code which is not linked to the nuclear genome. Only small number of proteins is synthesized within the chloroplast. Most of the chloroplast proteins are synthesized in the cytoplasm and enter the organelle by a complex process via outer and inner membranes. Chloroplast genomes are known to be highly conserved.

Cyanobacterial genomes encode about 2000 proteins whereas the current plant plastomes encode only 80–200 proteins. It is believed that during endosymbiosis, thousands of genes would have relocated within the nuclear genome. The massive reduction of plastome size and gene content occurred with time. Most of the chloroplast genes have been functionally relocated to the nucleus with their proteins targeted back to the organelle. Chloroplasts retain small, circular genomes that resemble those of cyanobacteria. Coding sequences for most chloroplast proteins have been lost, and most of the proteins are now encoded by the nuclear genome, synthesized in the cytoplasm and transported from the cytoplasm into the chloroplast. The chloroplast genome reveals that chloroplast DNA (cpDNA) contains a limited number of genes that descended from primary endosymbiosis while majority of endosymbiotic genes were transferred to the nuclear genome during evolution. Transcription/translation machineries of chloroplasts resemble those of prokaryotes.

6.3.3 Chloroplast DNA

Chloroplast DNA (cpDNA) is the DNA present in the chloroplast*s* (Box 6.2). It is sometimes called the **plastidome,** which is the genome of the chloroplasts and plastids. Chloroplast DNA (cpDNA) is responsible for the energy metabolism in eukaryotic cells (green plants and algae). The presence of DNA in chloroplasts was reported first by **Ris *et al.*** in 1962.

About 120 genes are present in the chloroplast of higher plants. Each chloroplast contains several copies of cpDNA molecules. Most cp DNAs contains inverted repeats that are about 4,000 to 25,000 bp long. The cpDNAs encode for rRNAs, tRNAs, ribosomal proteins, and *RNA polymerase* subunits, which are all essential for protein synthesis. Chloroplast DNA codes for proteins and RNAs that play an important role in essential metabolic functions. The rRNAs, tRNAs, ribosomal proteins, *RNA polymerase* subunits, photosystem I, photosystem II, cytochrome *bf* complex, *ATP synthase*, and the large subunit of *ribulose bisphosphate carboxylase* (*Rubisco*) are encoded by chloroplast DNA. The current genome of chloroplast in most plants encodes more than 2000 proteins, suggesting the functional gene transfer and relocation of most chloroplast genes to the nucleus. The chloroplast genes are of prokaryotic origin. After the functional transfer of a chloroplast gene to the nucleus, two genes present in two different cellular compartments encode for the same chloroplast protein. Some part of the chloroplast genome must have got transferred to the nuclear genome by the process of endosymbiotic gene

transfer. This transfer results in reduction of chloroplast genome that is comparable in size to that of cyanobacteria. The chloroplast genome of highly evolved plants is reduced in size. This is because more number of chloroplast genes has been transferred to the genome in the cell nucleus.

The size of chloroplast DNA ranges between 120-155 kb. It is usually 140 kb in higher plants and less than 190 kb in lower eukaryotic plants. In higher plants, the cpDNA exists as double-stranded circular molecule which is about 120–200 kb in length. This DNA has a mass of about 80-130 kDa. Recent studies have confirmed that chloroplast DNA contains 45 genes coding for RNA, and 27 genes coding for proteins. These proteins are mainly involved in chloroplast gene expression. The genes coding for proteins of the thylakoid membrane and another 10 gene products are committed for the electron transport process. The first chloroplast genome study was reported in 1986 from tobacco (*Nicotiana tabacum*). Chloroplast genome include four genes for rRNA, 20 genes for ribosomal proteins, 30 genes for tRNAs, many of the photosynthetic proteins, six to nine genes for *ATPase*, and chloroplast *RNA polymerase*. The DNA of chloroplast regulates its functioning.

Box 6.2 : Mitochondrial and Chloroplast DNA

Both cpDNA and mtDNA are extranuclear DNAs. They are *semi-autonomous*, self-reproducing cytoplasmic structures, possessing their own genetic system. Both are believed to be maternally inherited and have endosymbiotic origins. In most cells, both cpDNA and mtDNA are organized as a circular DNA, like the prokaryotic DNA, thereby supporting the theory of endosymbiosis. In fact, cpDNA is larger and more complex than mtDNA. The cpDNA has about 120 genes whereas mtDNA has about 37 genes. Both encode for proteins and RNAs vital to their functions. Whereas, mtDNA encodes for proteins of electron transport chain involved in aerobic respiration (ATP synthesis), the cpDNA encodes for proteins essential to photosynthesis.

Both cpDNA and mtDNA occur in multiple copies, since there are several chloroplasts and mitochondria occurring inside a cell. Thus, a cell often contains thousands of copies of mtDNA and cpDNA.

Marker enzymes in chloroplast

Like mitochondria, the chloroplasts also possess some marker enzymes. *NADP reductase* is the marker enzyme present in the grana thylakoid of chloroplast. This enzyme plays a role in light reaction of photosynthesis and is responsible for creating energy gradient in the chloroplast. *Phosphoenol pyruvate carboxylase (PEPcase)* is the enzyme present in the mesophyll cells of C_4 plants, while the *Ribulose-1,5-bisphosphate carboxylase/oxygenase* (*Rubisco)* is present in C_3 plants. *Phosphoenol pyruvate* functions as a primary CO_2 acceptor in C_4-plants. Enzymes present on the thylakoid membrane play a major role in non-cyclic photophosphorylation and are responsible for splitting of water to form two hydrogen ions (H^+), oxygen and electrons. *Rubisco* is one of the major marker enzymes in chloroplasts.

SAQ 2

a) Answer in one word

i) Chloroplasts are found in this region of plant leaves.

ii) These structures develop into plastids.

iii) In most plants, the thylakoids are arranged in these stack-like structures**.**

iv) The chlorophyll is contained in the vesicles embedded in this membrane**.**

v) Dark reactions (Calvin cycle) take place in this part of chloroplast.

b) Match the following

	Column A		**Column B**
i)	thylakoids	1.	between 120 and 155 kb
ii)	stroma	2.	major marker enzymes in chloroplasts.
iii)	chloroplast genome	3.	about 120 genes
iv)	size of chloroplast DNA	4.	stacks of flattened disks like structures
v)	*Rubisco*	5.	alkaline, aqueous region

c) Enlist the important functions of the chloroplast.

6.4 OTHER ORGANELLES

In addition to mitochondria and chloroplast, other membrane-bounded organelles are also found in eukaryotic plant cell. You will be studying some of these organelles in this section.

6.4.1 Endoplasmic Reticulum

Endoplasmic reticulum (ER) is a continuous membrane system found within the cytoplasm of the eukaryotic cells. It appears as flattened sac like structures extending from the cell membrane through the cytoplasm and forming a continuous connection with the nuclear envelope. ER is composed of membranous sheets and tubules that arise from the nucleus and extend across the cell.

Endoplasmic reticulum is of two types- rough endoplasmic reticulum (**RER**) and smooth endoplasmic reticulum (**SER**). These two differ in morphology and function. Rough ER has ribosomes attached to its outer (cytoplasmic) surface where protein synthesis occurs. The membrane of rough ER is usually continuous with the outer membrane of the nuclear envelope and lies adjacent to the nucleus. The proteins synthesized at the site get enclosed within the ER membrane followed by their transfer to Golgi apparatus and translocation to

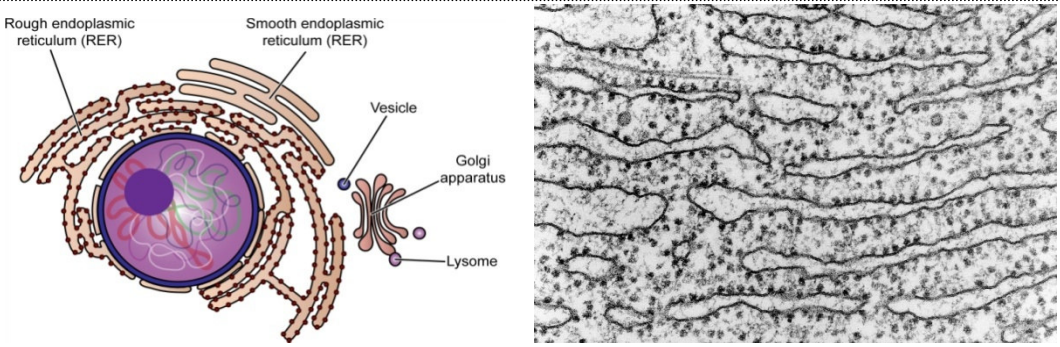
other organelles such as lysosomes or cell membrane. The proximity of the rough ER to the cell nucleus helps in processing of proteins. On the other hand, smooth ER is not associated with ribosomes (Fig. 6.8). It is involved in the synthesis of lipids such as cholesterol and phospholipids. These metabolites are used in the production of phospholipid molecules necessary for biosynthesis of membranes such as plasma membrane.

Structure

The endoplasmic reticulum may occur as lamellae, cisternae or vesicles. Cisternae are long, flattened, sac-like, unbranched tubules having a diameter of 40 to 50 µm. They remain arranged parallel in bundles or stacks. The tubules are branched structures forming the reticular system along with the cisternae and vesicles. They usually have a diameter from 50 to 190 µm and occur in almost all the cells. Tubular form of ER is often found in smooth ER. The vesicles are oval, membrane-bounded vacuolar structures having a diameter of 25 to 500 µm. ER sheets are membrane-enclosed, two-dimensional flattened sacs extending across the entire cytoplasm. These sheets are associated with ribosomes and special proteins called **translocons** which play a vital role in protein translocation.

Function

- Endoplasmic reticulum plays multiple roles in plants ranging from protein synthesis, folding, modification, transport of proteins and lipid metabolism to detoxification of the cell.
- Rough ER serves the main function of protein synthesis. Ribosomes present on RER serve as the site of protein assembly, folding, and modification.
- Cisternae are small folds of the smooth ER and are commonly associated with lipid metabolism**.**
- The ER provides an ultrastructural skeletal framework to the cell and gives mechanical support to the colloidal cytoplasmic matrix.
- The membranes of ER possess many kinds of enzymes required for various important synthetic and metabolic activities. These include enzymes such as esterases, *NADH-cytochrome C reductase, NADH diaphorase, glucose-6-phosphatase*, and Mg++ activated *ATPase.*
- The lumen (cavity) of ER is well developed and acts as a passage for the secretory products. The transport of proteins and carbohydrates to other organelles such as lysosomes, Golgi apparatus and plasma membrane is assisted by ER. It acts as an intracellular circulatory or transporting system.
- ER provides an increased surface area for cellular reactions.
- The synthesis of proteins, lipids, glycogen, and other steroids is facilitated by ER. Smooth ER plays a role in lipid metabolism (synthesis of a variety of phospholipids, cholesterol, and steroids).



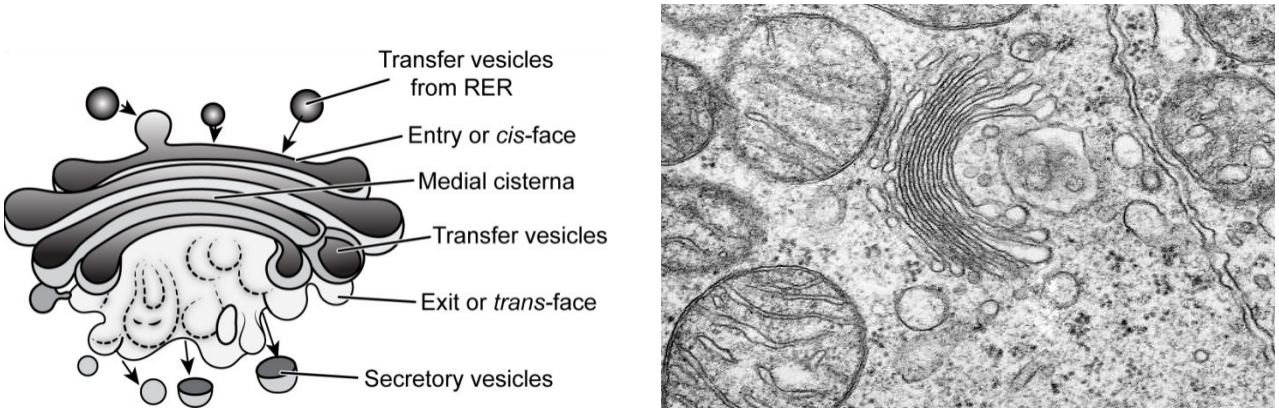
(a) (b)

Fig. 6.8: a) Diagrammatic representation of Endoplasmic reticulum associated with nucleus; b) Electron micrograph showing Rough ER.

6.4.2 Golgi Apparatus

Golgi apparatus is a membrane-bounded organelle found in eukaryotic cells. It appears as a assembly of interconnecting tubules, vesicles and cisternae. It is located in the cytoplasm next to the ER present near the nucleus. It is also called as Golgi complex or Golgi body. It appears as an extension of the endoplasmic reticulum and is slightly smaller and smoother in appearance. Their number can vary from one to several in the plant cells. The Golgi apparatus was observed in 1897 by Italian cytologist **Camillo Golgi**.

The whole apparatus is composed of stacks of flattened sac like structures called cisternae. They contain numerous vesicles containing secretory granules (Fig. 6.9) Cisternae are about 1 µm in diameter. They are present as bundles or stacking one above the other. Each cisternae is surrounded by a 7.5 nm thick smooth membrane. The lumen width varies from 500 to1000 nm. The cisternae are separated from each other by a space which is about 20 to 30 nm and may contain rod-like elements or fibers. Stack of 20 or more cisternae forms a dictyosome. Each cisterna is curved at margins to give dictyosome a bow-like appearance. The cisternae are held together by matrix proteins. The ***cis*- face** of the organelle is closest to the endoplasmic reticulum. The ***trans*-face** is the side farthest from the nucleus, which secretes vesicles to various parts of the cell (Fig. 6.9, 6.10). The sacs tend to move from the *cis* face to the *trans* face of the Golgi apparatus over a period of time. New sacs are formed close to ER. These sacs “age” as they move towards the *trans* face of the Golgi apparatus and their product becomes fully mature.



(a) (b)

Fig. 6.9: a) Golgi apparatus; b) an electron micrograph showing Golgi apparatus.

Vesicles are small membranous structures which protrude out of transitional ER. They migrate and join *cis* face of Golgi. At this site they coalesce (to come together to form one larger group) to form new cisternae. They are generally 60 nm in diameter. Vesicles bud off, fuse with cisternae membranes and transport molecules back to ER. The fusion of vesicle cluster with the *cis* membrane delivers the contents into the lumen of the *cis* face cisterna. The migration of proteins and lipids from the *cis* to *trans* face modifies these functional molecules and ensures their delivery to specific intracellular or extracellular locations. Some molecules such as soluble proteins and secretory proteins are carried in vesicles to the cell membrane for exocytosis (release into the extracellular environment).

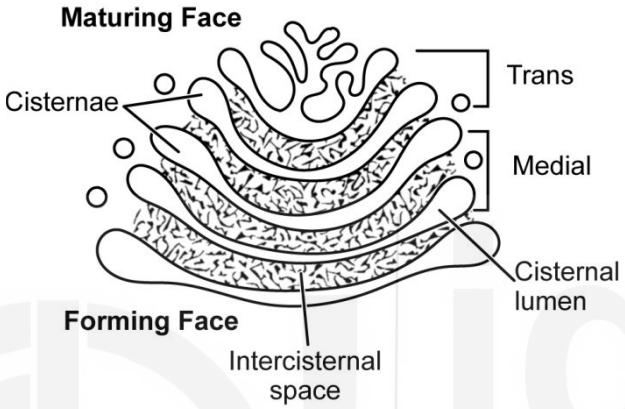


Fig. 6.10: Diagram showing *cis* and *trans* faces of Golgi apparatus.

Functions

- The Golgi apparatus is an assembly from where the raw materials are directed to the other organelles before being passed out from the cell.
- It helps in the transport, modification and packaging of proteins and lipids into vesicles to be delivered to targeted destinations. The proteins get packaged into vesicles prior to their secretion. Hence Golgi bodies also play a role in the secretory pathway.
- The vesicles of Golgi apparatus play a role in sorting proteins and membrane constituents present in the cell and direct them to their respective destinations. The enzymes present in the vesicles react with secretory proteins, and modify them while they pass through the Golgi lumen.
- It also performs the function of synthesizing the polysaccharide molecules for the cell wall formation in plant cells. It also helps in the secretion of primary and secondary cell wall materials (e.g. glycoproteins, lipids, pectins and monomers for hemicellulose, cellulose, and lignin).

Thus, the Golgi apparatus helps in secretion and transport of molecules from the ER to their final destination and modifying products to their final form by additions to their structure. After modifications, the products are packaged in vesicles and tagged with markers followed by their delivery to different locations throughout the cell.

SAQ 3

a) Fill in the blanks with appropriate words:

i) …… are attached to the outer surface of rough endoplasmic reticulum.

ii) Lipids are synthesized in …….. .

iii) Protein synthesis occurs in …….. endoplasmic reticulum.

iv) An Italian scientist …… observed Golgi apparatus in cell.

v) Cell organelle …… is responsible for packaging and transport of …… and lipids to vesicles for their delivery to targeted destination.

b) Distinguish between smooth and rough ER.

6.4.3 Lysosomes

Lysosomes (derived from Greek words-lysis=loosen/breakdown, and soma=body) are subcellular organelles found in nearly all the eukaryotic cells. In plants, the vacuoles generally carry out the lysosomal function. Lysosomes are single membrane-bounded organelles. Lysosomes look like dense spherical bodies having variation in size and shape because of differences in the materials that they take up for digestion. These are small organelles with size of 0.1-0.5 µm. These organelles have a simple spherical structure made up of a lipid bilayer formed of phospholipids.

Lysosomes were discovered by the Belgian cytologist **Christian René de Duve** in 1950s. Lysosomes originate by budding off from the membrane of the trans-Golgi network (Box 6.2). These membrane-bounded organelles have an acidic pH. Lysosomes contain numerous hydrolytic enzymes. These enzymes specifically break down large molecules through hydrolysis. The enzymes found in lysosomes include proteases, amylases, nucleases, lipases, and acid phosphatases, among many others. These enzymes are named on the basis of their function. Enzyme proteases break down proteins, nucleases break down nucleic acids while amylases break down starches into sugars. The products obtained after hydrolysis can be recycled back to the cell for use in the synthesis of new cellular components.

The enzymes present in the lysosomes are mainly acid hydrolases, which are active at the acidic pH (about 5.0) maintained within lysosomes. To maintain their acidic pH, lysosomes concentrate H^+ ions (protons) via a proton pump. The proton pump maintains approximately a hundred-fold higher H^+ concentration inside the lysosome. The acidic environment is responsible for the digestion of macromolecules and old cells.

Molecules of mannose-6-phosphate get tagged with hydrolytic enzymes (acid hydrolases) followed by their transport to vesicles in Golgi apparatus, and subsequent packaging into lysosomes. The fusion of lysosomes with membrane vesicles occurs via three pathways: endocytosis, auto phagocytosis, and phagocytosis. In endocytosis, extracellular macromolecules are taken up into the cell to form membrane-bound vesicles called **endosomes** that fuse with lysosomes. In auto phagocytosis (a process where old organelles and malfunctioning cellular parts are removed from a cell) the molecules are enveloped by internal membranes that subsequently fuse with lysosomes. In phagocytosis, large particles (such as bacteria) are taken up into phagocytic vacuoles or phagosomes which then fuse with lysosomes, resulting in digestion of their contents (Fig. 6.11). Phagocytosis is carried out by specialized cells called macrophages. Macrophages take up and degrade large particles; cell debris, aged cells and bacteria that need to be eliminated from the body. Lysosomes are responsible for autophagy i.e., destruction of the cell's own non-functional organelles. The first step in autophagy appears to be the enclosure of an organelle (e.g., a mitochondrion) within a membrane derived from the ER. The resulting vesicle called **autophagosome** then fuses with a lysosome, and its contents are digested. Many of the products of lysosomal digestion are recycled back to the cell for use in the synthesis of new cellular components.

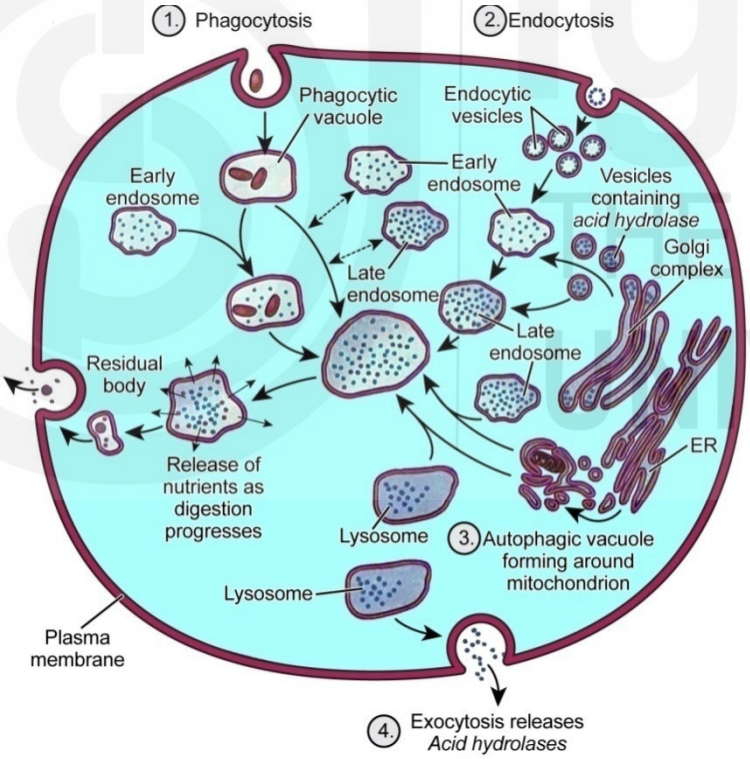


Fig. 6.11: Phagocytosis in lysosomes.

Box 6.2 : Plant Lysosomes: Myth or Reality?

The presence of lysosomes in plants has long been debated. Many cytologists claim that plant cells do not have lysosomes because they are not required. Plant cells have cell walls that are strong enough to keep the large/foreign substances out of the cell that are usually digested by lysosomes. However, there is emerging evidence that plant cells contain lysosomes. Techniques such as isolation of vacuoles have proved that plant vacuoles contain enzymes found in animal lysosomes, suggesting their presence in the plant cell.

Functions

- Lysosomes function as the digestive system of the cell as they break down molecules using hydrolytic enzymes. They function in degrading intracellular material and digestion of complex molecules such as carbohydrates, lipids, proteins, nucleic acids and obsolete components of the cell itself.
- Lysosomes are involved in the dismantling and re-cycling of various substrates received through endocytosis, phagocytosis, and auto phagocytosis. In phagocytosis, a cell engulfs a molecule that needs to be broken. The process is also known as “cell eating”. The process is supported by enzymes. The hydrolytic enzymes contained within the lysosome disintegrate the foreign particles.

SAQ 4

Fill in the blanks.

i) Lysosomes were discovered by the Belgian cytologist …… .

ii) Lysosomes originate by budding off from the membrane of ……..... .

iii) Lysosomes contain many hydrolytic enzymes which catalyze …….. .

iv) Phagocytosis is carried out by specialized structures called …….. .

v) The enzymes *acid hydrolases* present in the lysosomes are active at ……. maintained within lysosome

6.5 SUMMARY

- Mitochondria are double membrane-bounded cell organelles present in the plant cell. They are the main sites of ATP synthesis in plants.
- Most mitochondrial proteins (about 99%) are synthesized outside the mitochondrion i.e. in the cytoplasm of the cell. The proteins produced in the cytoplasm are transferred to mitochondria through special set of protein called *translocase*.
- Mitochondria contain a small, circular DNA (mitochondrial DNA or mtDNA). Mitochondrial DNA has about 16,569 bp and 37 genes. All the 37 genes encode different proteins that are specific for the mitochondria.
- Chloroplasts are organelles restricted to plants and algae. They are spherical, ovoid, discoid, biconvex or planoconvex double membraned structures. Internal membrane is folded and appears as stacks of flattened disks called the thylakoids. The thylakoid vesicles are organized into stacks called grana. An aqueous region present inside the thylakoid membrane is known as thylakoid lumen.

- The chloroplast is the main site for carrying out the process of photosynthesis. Light reaction takes place in the thylakoid membranes while stroma of chloroplast acts the main site of dark reactions (Calvin Cycle).
- Both chloroplast and mitochondria show semi autonomous nature as they have their own DNA, RNA, and ribosomes. DNA present in these organelles is circular as seen in prokaryotes and the ribosomes are of 70S type. They can synthesize their own proteins. Both the organelles are believed to have once been independent prokaryotes that were internalized by eukaryotes via endosymbiosis during evolution.
- Chloroplast DNA is a double-stranded circular molecule which is about 120-155 kb long. The first chloroplast genome study was reported in 1986 from tobacco (*Nicotiana tabacum*) chloroplast genome among higher plants. About 120 genes are known to be present in the chloroplast. The chloroplast DNA regulates its functioning.
- Endoplasmic reticulum (ER) is a continuous membrane system found within the cytoplasm of eukaryotic cells. It looks like flattened sacs arising from the cell membrane. It plays multiple roles in plants ranging from protein synthesis, folding, modification, transport of proteins and lipid metabolism to detoxification of the cell. Rough ER serves main function of protein synthesis.
- Golgi apparatus is a membrane-bound organelle found in eukaryotic cells. It helps in transporting materials within and out of the cell. It plays a role in packaging proteins and lipids into vesicles for transport and delivery to targeted destinations. The vesicles contain enzymes and proteins. The materials get transported from Golgi lumen to their final destination.
- Lysosome is a single membrane bound structure that looks like dense spherical bodies. They are made up of a lipid bilayer that encloses fluid that contains a variety of hydrolytic enzymes which catalyze hydrolysis reactions. The enzymes found in lysosomes include proteases, amylases, nucleases, lipases, and acid phosphatases.

6.6 TERMINAL QUESTIONS

1. Describe the main features of the ‘The Endosymbiotic Theory’ of origin of mitochondria.
2. Why mitochondria and chloroplast are considered as ‘semi autonomous’ organelles?
3. Enlist the differences between mitochondrial and chloroplast DNA.
4. Lysosomes function as the digestive system of the cell. Justify the statement.
5. List the major marker enzymes of chloroplast and mitochondria.
6. Describe the structure and functions of endoplasmic reticulum.

6.7 ANSWERS

Self-Assessment Questions

1. a) i) adenosine triphosphate (ATP)
   ii) 7.9 to 8
   iii) cristae
   iv) translocase
   v) 13
   vi) *ATP synthase*
   b) i) True; ii) True; iii) False;
   iv) False; v) True; vi) True
2. a) i) mesophyll cells
   ii) proplastids
   iii) grana
   iv) thylakoid
   v) stroma
   b) i) stacks of flattened disks like structures
   ii) alkaline, aqueous region
   iii) about 120 genes
   iv) between 120 and 155 kb
   v) marker enzymes in chloroplasts
   c) Refer to Subsection 6.3.1
3. a) i) ribosomes
   ii) smooth endoplasmic reticulum
   iii) rough
   iv) Camillo Golgi
   v) Golgi apparatus, proteins
   b) Refer to Section 6.4.1
4. i) Christian René de Duve
   ii) trans-Golgi network
   iii) hydrolysis reactions
   iv) macrophages
   v) acidic pH (about 5.0)

Terminal Questions

1. Refer to Subsection 6.2.4.
2. Refer to Subsections 6.2.2 and 6.3.2.
3. Refer to Subsections 6.2.3 and 6.3.3.
4. Refer to Subsection 6.4.3.
5. Refer to Subsections 6.2.3 and 6.3.3.
6. Refer to Subsection 6.4.1.

Acknowledgements

Fig.6.1 a : Source: https://www.google.com/imgres?imgurl=https%3A%2F%2Fwww.biology-pages.info%2FM%2Fmitochondrion.jpg

Fig 6.5 b: : Source: https://www.google.com/imgres?imgurl=https%3A%2F%2Fels-jbs-prod-cdn.jbs.elsevierhealth.com%2Fcms%2Fattachment%2F565094%2F4093134%2Fgr1.gif&imgrefurl

Fig. 6.8 b : Source: https://www.google.com/imgres?imgurl=https%3A%2F%2Fuseruploads.socratic.org%2FyNFXjnHuSqG7xT0Ndi7l_37237.jpg&imgrefurl=https%3A%2F%2Fsocratic.org%2Fquestions%2Fhow-does-rough-endoplasmic-reticulum-differ-from-smooth-endoplasmic-reticulum&tbnid=

Fig.6.9 b : https://www.google.com/imgres?imgurl=http%3A%2F%2Fmedcell.med.yale.edu%2Fhistology%2Fcell_lab%2Fimages%2Fgolgi_em.jpg&imgrefurl=http%3A%2F%2Fmedcell.med.yale.edu%2Fhistology%2Fcell_lab%2Fgolgi_em.php&tbnid=0ZfJV_qYhB9nRM&vet

Suggested videos for watching

https://www.youtube.com/watch?v=39HTpUG1MwQ

https://www.youtube.com/watch?v=eOPEn2qYff4

https://www.youtube.com/watch?v=RKmaq7jPnYM&t=77s

https://www.youtube.com/watch?v=6cCjAWnb-Wc

https://www.youtube.com/watch?v=xRTymrPUGqw

UNIT 7

CELL ORGANELLES (II)

Structure

7.1 INTRODUCTION

The previous units have provided you with an overview of structure of prokaryotic and eukaryotic cells. A detailed account of structure of plant cell membrane, major cell organelles such as chloroplasts, mitochondria, endoplasmic reticulum (ER), Golgi bodies has been presented along with their functions. In this unit you will be studying about the master organelle nucleus in detail along with small organelles such as peroxisomes, glyoxysomes and ribosomes that also play an essentially important role in cellular processes taking place in plants. These membrane-bounded or membrane less spherical bodies possess a size in the range of 0.2 to 1.5 µm and are found closely associated with organelles such as ER, mitochondria or chloroplasts. These organelles have a central granular or crystalloid core containing some specific enzymes and are called **microbodies**. Microbodies are globular organelles present in the cytoplasm of the cell. They mainly include peroxisomes, glyoxysomes, and glycosomes. Microbodies have characteristic morphological features i.e., they are bounded by a single membrane and have no internal membranes and may contain amorphous or paracrystalline inclusions. They contain various enzymes that play an important role in different metabolic activities of the cell.

Christian Rene de Duve did pioneering work in the discovery and isolation of these sub cellular organelles. The organelles were separated on the basis of their sedimentation coefficient and density. Ribosomes are usually considered as the smallest organelles. They are membrane less and are often called the protein factories.

Objectives

After studying this unit, you would be able to :

- explain the structure, and functions of peroxisomes, glyoxysomes and ribosomes;
- know about other various cell inclusions;
- describe the structure of nucleus, nuclear pore complex, and chromatin material; and
- describe the structural components and functions of cytoskeketon.

7.2 PEROXISOMES

Peroxisomes are small, single membrane-enclosed ubiquitous organelles. They are found closely associated with cell organelles such as ER, mitochondria or chloroplast. They are morphologically similar to lysosomes. They are present in all eukaryotic cells including both animal and plant cells. In plants, they are also found in all the photosynthetic cells. They are prominently present in etiolated leaf tissue, coleoptiles and hypocotyls, while in mammals, they are found in abundance in liver cells and adipocytes.

Structure

Peroxisomes are spherical (0.2 – 1.5 µm diameter) in appearance but may also exist in variable sizes and shapes. The single lipoprotein membrane encloses the granular or fibrillar matrix (Fig. 7.1). The contents may be in the form of threads/fibrils or crystalloids.

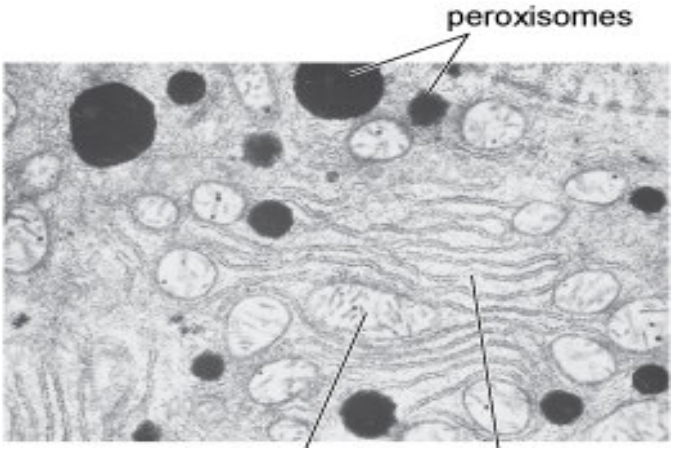


Fig. 7.1: Electron micrograph showing the structure of peroxisome.

Peroxisomes were first discovered by Rhodin (1954) with the help of electron microscopic studies in mouse kidney. This single membrane bounded organelle was earlier known as microbody. De Duve and Bandhuin (1966)

reported similar structures in plant cells (Fig. 7.2). Peroxisomes are considered to be highly dynamic organelles exhibiting varying morphology and diverse metabolic activities. They exist either in the form of a network of interconnected tubules called peroxisome reticulum or as individual microperoxisomes. A cell contains few to numerous peroxisomes depending on the organism. In mammals, a single hepatocyte (liver cell) usually consists of about 400 to 600 peroxisomes. They occupy about 2% of the cell volume.

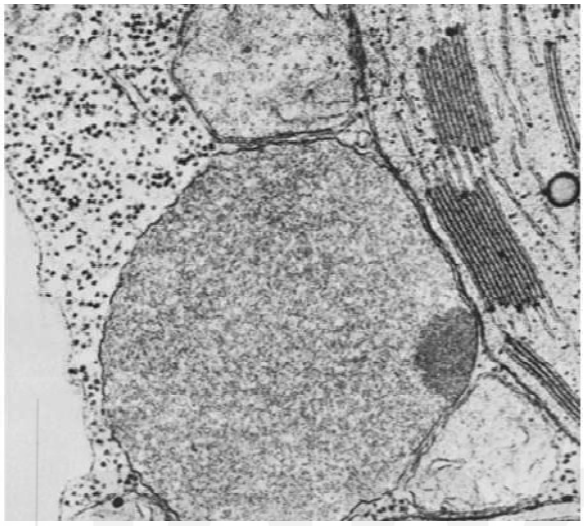


Fig. 7.2: Electron micrograph showing peroxisome in tobacco leaf cell (40,000 X).

7.2.1 Biogenesis/Origin of Peroxisomes

Three models have been proposed for the origin or biogenesis of peroxisomes in plants. We will describe them one by one.

According to **ER vesiculation model**, peroxisomes originated from endoplasmic reticulum (ER) (Fig. 7.3). The similarity noted between some of the proteins of this organelle and those found in the endoplasmic reticulum provided evidence in support of the hypothesis.

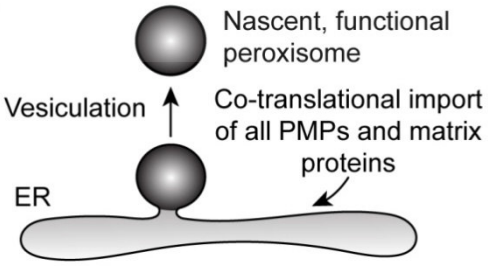


Fig. 7.3: ER vesiculation model for the Biogenesis of Peroxisomes in plants.

Another model is the **Gowth and division model.** According to this model all peroxisomes are autonomous organelles that arise from division of pre-existing peroxisomes (Fig. 7.4). A pre-existing peroxisome grows and divides. The division process may be symmetrical or asymmetrical. The symmetrical division produces peroxisomes of the same size, while asymmetrical division results in the production of peroxisomes of varying sizes. Following division and multiplication, peroxisomes move to different locations of the cell. This movement is facilitated by microtubules.

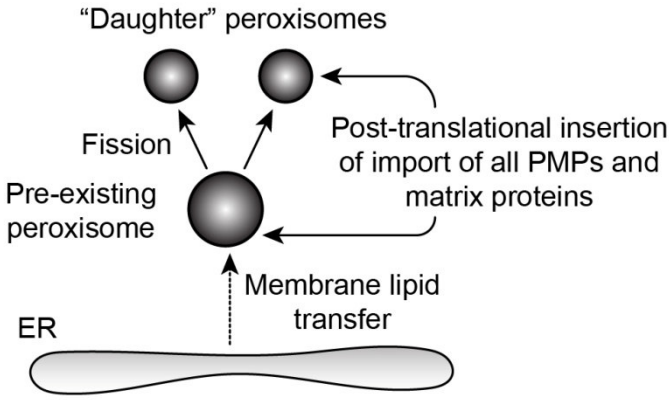


Fig. 7.4: Growth and division model for the Biogenesis of Peroxisomes in plants.

Recently, a model called as **ER semi–autonomous model** has been proposed to suggest the biogenesis of peroxisomes. This model incorporates various aspects of earlier models. This model suggests that synthesis of peroxisomes starts from specific regions of the ER. The ER-derived preperoxisomes (i.e., vesicles or membrane fragments/lamellae) form the peroxisomes. The preperoxisomes or vesicles either deliver phospholipids and some peroxisomal membrane proteins (PMPs) to preexisting peroxisomes or fuse together to form a new peroxisome (Fig. 7.5). The PMPs are produced in the free polyribosomes present in the cytosol.

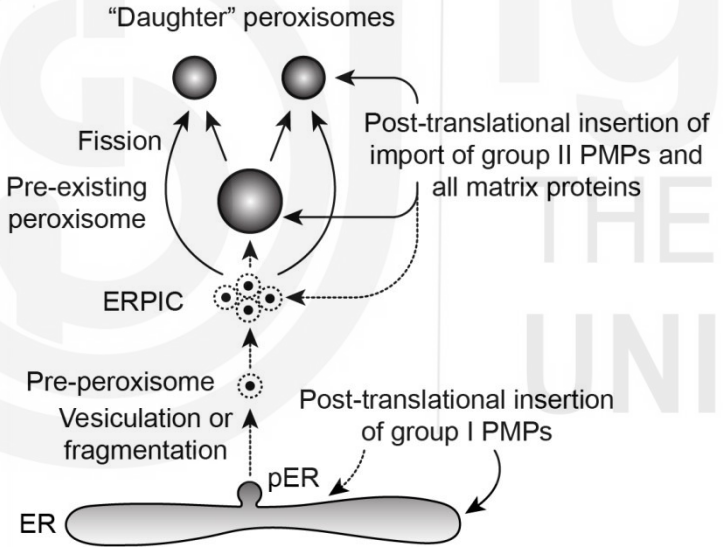


Fig. 7.5: ER semi-autonomous model for the Biogenesis of Peroxisomes in plants. ER-peroxisome intermediate compartment (ERPIC).

So, it can be concluded that biogenesis of peroxisomes is a relatively complex process that involves several phases such as formation of peroxisome membrane, import of matrix proteins, transfer of lipids obtained from the ER. The PMPs and matrix proteins get arranged in preexisting and new (daughter) peroxisomes after translation resulting in their growth. The proteins participating in peroxisomal protein targeting and peroxisome division have been identified and characterized in *Arabidopsis*. Recent studies have tried to fill gaps in our understanding of how peroxisomal proteins are imported, regulated, and degraded.

Thus the current ideas of peroxisome biogenesis reflect a combined view of their *de novo* biogenesis from fragments of ER and also by fission of pre - existing peroxisome.

7.2.2 Functions

Peroxisomes play a vital role in plant growth processes of primary and secondary metabolism, development, and environmental stress response. Their role in plant metabolism is now well established. They help in oxidation of fatty acids, during glyoxylate cycle in seedlings, photorespiration in leaves, and biosynthesis of phytohormones such as indole-3-acetic acid, jasmonic acid, and salicylic acid. The oxidative enzymes present in peroxisomes play a role in metabolic reactions. The peroxisomes take part in metabolism, scavenging of reactive oxygen species generated during stress and signaling pathways (via synthesis of molecules such as jasmonic acid, auxin, and salicylic acid).

- In plant cells peroxisomes occur as the main site of β- oxidation of fatty acids. The fatty acids are first transported to the peroxisomes where they get transformed into the CoA-esters before entering the β-oxidation cycle. In the process the long fatty acid chains (with 20 or more carbon atoms) get converted into acetyl CoA, which is a source of metabolic energy. In animal cells, the process of β-oxidation takes place in mitochondria and peroxisomes. In contrast, the plant cells involve only peroxisomes in the process.
- During photorespiration, peroxisomal enzymes oxidize molecules like fatty acid and amino acids. The *catalase* enzyme present in the peroxisomes breaks down the harmful hydrogen peroxide (H_2O_2) into harmless products (water and oxygen). It increases the efficiency of photosynthesis. Hence the process of photorespiration helps in protecting the cellular organelles from the toxic effect of H_2O_2. *Catalase* also utilizes H_2O_2 to oxidize various substances.
- Photorespiration is one of the main processes that take place in peroxisomes in plants. Peroxisomes are one of the three organelles which take part in photorespiration, the other two being chloroplasts and mitochondria.
- Peroxisomes present in seeds convert stored fatty acids to carbohydrates, thus providing energy and raw materials for the growth of germinating seeds.
- Peroxisomes help in the biosynthesis of jasmonate hormone that is involved in growth, development as well as defense mechanism of plants.
- The number and morphology of peroxisomes is dynamically regulated to maintain homeostasis in cells exposed to environmental stresses. Damaged peroxisomes are removed by autophagy to ensure the normal functioning of the cell. Reactive oxygen species (ROS) produced in peroxisomes under stress conditions activate signal transduction pathways (retrograde signaling), which regulates defense systems in plants.
- Antioxidant enzymes are essential components present in peroxisomes and help in maintaining redox homeostasis in a cell.
- Peroxisomes play a vital role in metabolism of Indole-3-butyric Acid and polyamines.

SAQ 1

a) Fill in the blanks

i) In hepatocyte (liver cell) of mammals usually 400 to 600 of …….. are present.

ii) According to the concept of vesiculation, peroxisome originated from …….. .

iii) The symmetrical division produces peroxisomes of the …….. size.

iv) …… model incorporates aspects of earlier models and has been considered as the current model for peroxisome biogenesis.

v) During the process of ……, enzyme present in peroxisome assist in the elimination of hydrogen peroxide.

vi) …… process in seeds converts long chain fatty acids to two acetyl co A. C_2 fragments.

b) Describe the role of peroxisomes in response to environmental stress.

7.3 GLYOXYSOMES

Glyoxysomes are specialized peroxisomes found in plants, predominantly in the fat storage tissues of germinating seeds. Glyoxysomes were discovered by **R. W. Breidenbach** and **H. Beevers** in 1961.These organelles are found mainly in the cells of lipid storing endosperm and cotyledons. They are also present in cells of yeast, *Neurospora* and oil rich seeds of many higher plants.

Glyoxysomes occur temporarily during seed germination in fatty seeds. They are present in the endosperm cells of fatty seeds and participate in fatty acid oxidation. Glyoxysomes of higher plants are the sites of β-oxidation of fatty acids and contain enzymes for glyoxylate cycle.

Structure

Glyoxysomes resemble peroxisomes and other microbodies found in plants in their structural features and morphology. They are single membrane bounded organelles usually spherical in shape (Fig. 7.6). In germinating seeds they show the presence of crystalloid core made up of dense rods.

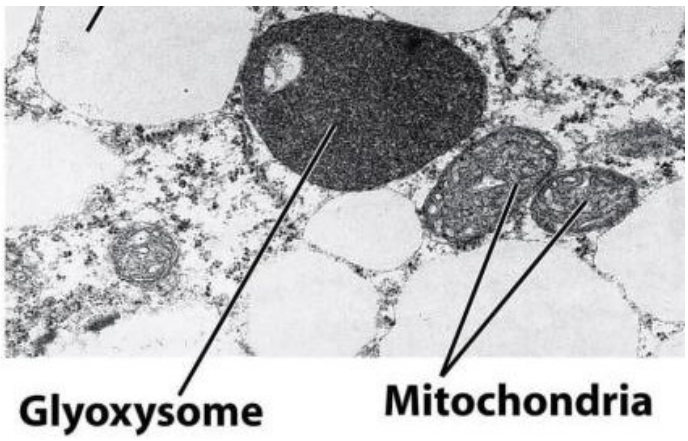


Fig. 7.6: Electron micrograph showing structure of gloxysome.

7.3.1 Biogenesis of Glyoxysomes

The glyoxysome has been considered as a type of plant peroxisome because it is also rich in *catalase*. It has been proposed that glyoxysomes might be derived from microbodies or peroxisomes. They appear to be formed by a process similar to that of peroxisomes i.e., by fission or budding of preexisting glyoxysomes. According to one hypothesis, glyoxysomal enzymes are synthesized by free ribosomes present in the cytosol and get translocated into the membranes of glyoxysomes present in the cell.

Beevers et al. proposed that the glyoxysomal membrane is derived directly from a specific region of the rough endoplasmic reticulum (RER) by a process of vesiculation and excision. The current concept of their biogenesis in endosperm suggests that glyoxysomes are formed by vesiculation from endoplasmic reticulum (ER). ER is the main site of phospholipid synthesis. Phospholipids then gets sorted in ER and further transported to glyoxysomes. The matrix and peripheral membrane proteins are added posttranslationally, during formation and/or following detachment from ER. The mode of transfer of these proteins can be either direct from ER and/or by budding of vesicle or fusion. Glycosylation of proteins occurs exclusively in endosperm ER .This has been referred to as **modified ER-vesiculation model**.

7.3.2 Functions

1. Glyoxysomes are the site for fatty acid metabolism (β-Oxidation). During the germination of oily seeds, the stored lipid molecules get hydrolyzed by the enzyme *lipase* (*glycerol ester hydrolase*) to form glycerol and fatty acids. The phospholipid molecules are hydrolyzed by the enzyme *phospholipase*. The long chain fatty acids get hydrolysed to form two carbon or C_2 fragments. The process is known as β-oxidation. Acetyl-CoA produced by β-oxidation chain does not get oxidized by the Krebs cycle but undergoes the glyoxylate cycle to be converted into succinate. Succinate is the end product of fatty acid metabolism in glyoxysomes. Succinate diffuses out into mitochondria for further metabolic reactions ultimately leading to the formation of sugars in the cytoplasm (gluconeogenesis). Glyoxysomes contain all the enzymes for β-oxidation and glyxoylate cycle viz. *citrate synthase*, *aconitase*, *isocitrate lyase*, *malate synthase,* and *malate dehydrogenase*.

In Krebs cycle, isocitrate is successively decarboxylated, producing two molecules of carbon dioxide and succinate. In the glyoxylate cycle, isocitrate is converted to succinate and glyoxylate. The glyoxylate cycle is especially significant for cells growing exclusively on acetate or fatty acids.

SAQ 2

a) Complete the sentence

i) Glyoxysomes are the organelles found mainly in the cells of lipid storing …….. .

ii) Glyoxysomes also appear to be formed from preexisting glyoxysomes by a process of …….. .

iii) Since glyoxysomes are rich in *catalase*, it has been proposed that they might be derived from …… .

iv) Acetyl-CoA produced by β-oxidation undergoes the glyoxylate cycle to get converted into …… .

b) Enumerate the major roles of gloxysomes in cell.

7.4 THE CYTOSKELETON

A complex network of interconnected filaments and tubules that extend throughout the cytosol from the nucleus to the inner surface of the cell membrane forms the cytoskeleton. The fibrous proteinaceous matrix present in the cytoskeleton helps in providing an architectural framework and structural support to cells. Cytoskeleton provides stability to cell shape. Cytoskeletal components play an important role in cell motility, cell reproduction, and transportation of substances within the cell. The complex thread-like network present in the cytoskeleton is composed of three protein-based components- (i) microtubules, (ii) microfilaments and (iii) intermediate filaments (Fig. 7.7).

Structural Components of Cytoskeleton

The existence of three components of cytoskeleton was revealed through electron microscopy and images obtained by immunofluorescence microscopy. Each structural element has a characteristic size, shape, and intracellular distribution (Fig.7.7). Each component is formed by the polymerization of different kind of protein monomers. Microtubules are composed of protein tubulin and are about 25 nm in diameter. Microfilaments possess an average diameter of 7nm and are polymers of protein actin. On the other hand, intermediate filaments possess a diameter of 8-10 nm on an average. Each type of filament present in the cytoskeleton has a number of additional proteins associated with it. These proteins are called as accessory proteins and account for the structural and functional diversity of cytoskeletal elements. Both microfilaments and microtubules (MTs) play a role in cell motility. Microfilaments form the essential component of muscle fibers while microtubules are structural elements of cilia and flagella.

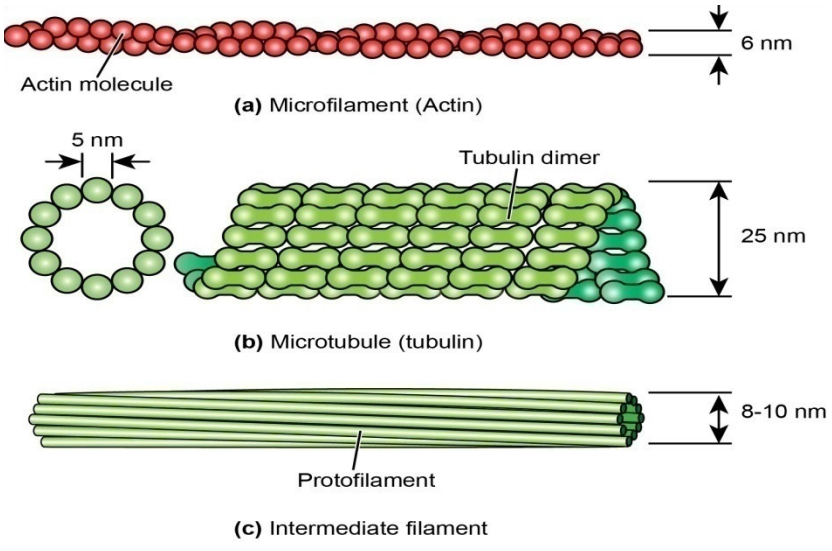


Fig. 7.7: Components of cytoskeleton.

Microtubule is a structural filament composed of subunits of a protein called **tubulin.** It is the thickest of all three. Microtubules maintain cell shape and structure, help resist compression of the cell, and play an important role in positioning the organelles within the cell. Microtubules also form two important cellular appendages that help in cell motility viz., cilia and flagella.

Cilia are cellular appendages found in microorganisms and animals. They are not found in higher plants. In multicellular organisms, cilia function to move a cell or group of cells or to help transport fluid or materials past them. Cilia are found on surface of epithelial cells that line the airways of the respiratory system. Cilia move rhythmically and beat constantly, moving waste materials such as dust, mucus, and bacteria upward through the airways, away from the lungs and toward the mouth. A flagellum (plural= flagella) is a hair like structure or appendage found on the surfaces of cells and used for movement by microorganisms and some specialized cells such as the gametes of certain plants. Flagellum is generally larger than a cilium.

7.4.1 Microtubules

They are the largest cytoskeletal elements found in eukaryotic cells. Microtubules (MTs) are filamentous/thread like hollow cylindrical structures with an outer diameter of about 25nm and inner diameter of about 15nm. Their length varies from a few nanometers to several micrometers. The wall of MTs consists of circular array of globular subunits of tubulin called protofilaments (Fig.7.8).

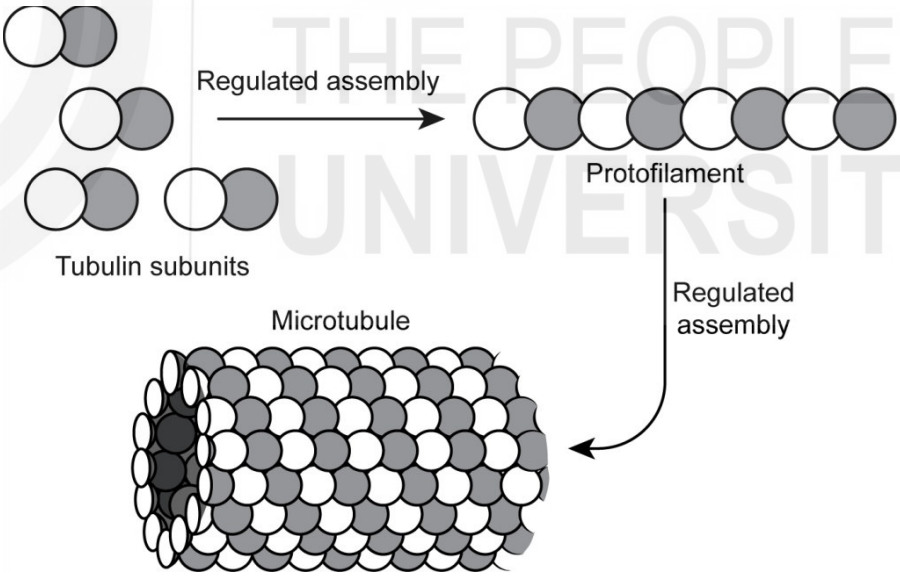


Fig. 7.8: Diagram showing assembly of tubulin subunits to form microtubule.

Thirteen protofilaments (each 5-7 nm in diameter) are arranged helically around the central axis, hollow lumen or center. The basic unit of a protofilament is a heterodimer of the protein tubulin. The heterodimer is composed of one molecule of α and β tubulin molecule. Both the molecules tightly bind together to produce α-β heterodimer. In addition several proteins are also associated with tubulins. They help in polymerization–depolymerization of microtubules. These are called microtubule-associated proteins (MAPs).

Microtubules are formed by the reversible polymerization of the tubulin dimers. Tubulin dimers aggregate to form clusters called oligomers. From these oligomers, new MTs are formed and the process is called as nucleation. After nucleation, the MT grows by addition of subunits at both the ends. The process is known as elongation. MTs elongate preferentially from one end known as plus end.

Origin of MTs

The microtubules originate from a structure in cell called microtubule organizing center (MTOC). At this site the MT assembly is initiated. In addition MTOC, may act as an anchor for the microtubules (Fig.7.9). Some cells at the interphase have a MTOC called the centrosome which is present near the nucleus. Within the centrosome, is embedded a pair of small cylindrical structures called centrioles. Centrioles occur in most of the animal cells. The walls of centrioles are formed by nine pairs of triplet microtubules. The centrioles are oriented at right angles to each other. The centrioles are known to be involved in the formation of basal bodies which are important for formation of cilia and flagella. Microtubule associated proteins (MAPs) modulate structure, assembly and function of MTs and increase their stability.

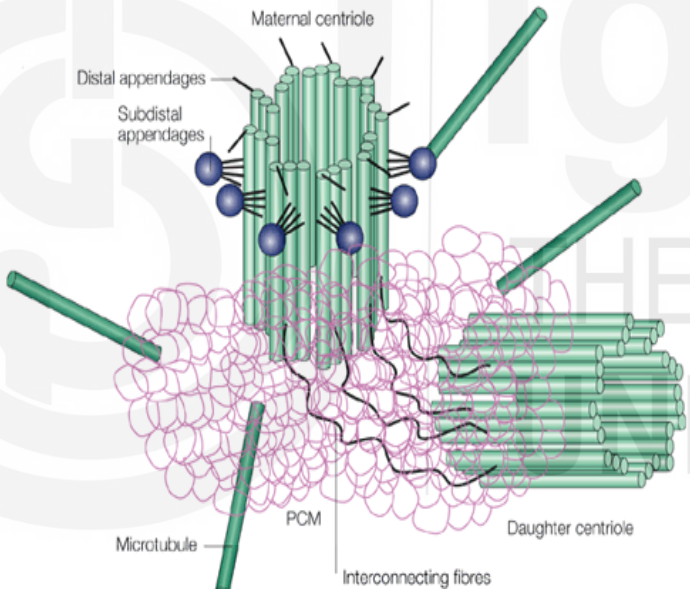


Fig. 7.9: Arrangement of microtubules at the centriole.

Types of MTs

Generally two types of MTs viz. **axonemal** and **cytoplasmic** microtubules occur in eukaryotes. Both the microtubules differ in their organization and structural stability. Axonemal microtubules are highly organized, stable and found in specific subcellular structures associated with cellular movement i.e. cilia and flagella. The central shaft or the axoneme of a cilia or flagellum consists of a highly ordered bundle of axonemal MTs and associated proteins. Cytoplasmic microtubules are loosely organized and form dynamic network of MTs. These MTs carry out various functions in a plant cell such as directing the orientation and deposition of cellulose microfibrils during growth of cell walls along with directional movement of vesicles and other organelles. They form the spindles essential for the movement of chromosomes during mitosis and meiosis.

7.4.2 Microfilaments

These are the small cytoskeletal filaments about 7nm in diameter. They occur in all eukaryoytic cells and are known to be involved in movement. In animal cells, these help in contraction of muscle cells. They are formed of actin, a protein which is abundantly found in plants, algae and fungi. Individual actin molecules are referred to as G-actin (globular actin). These G-actin molecules polymerize to form microfilaments and this form of actin is referred to as F-actin (filamentous actin). Both G and F forms of actin bind to proteins called actin-binding proteins (Fig. 7.10). Amoeboid movement of cells occurs due to microfilaments (MFs). Cytolplasmic streaming is another example of role of microfilaments in locomotion. MFs also play an important role in development and maintenance of cell shape.

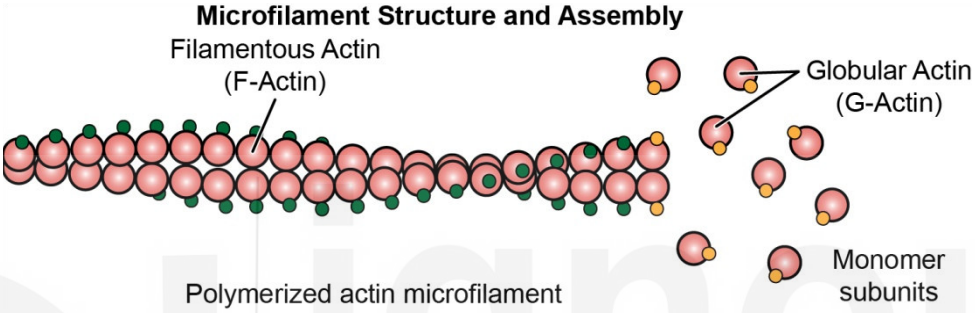


Fig. 7.10: Structural assembly of microfilaments.

7.4.3 Intermediate Filaments

They have a size intermediate between MTs and MFs. They have of a diameter of 8-12 nm. Although, these filaments are not directly involved in cell movements, they play a structural role of providing mechanical strength to cells and tissues. They are composed of a variety of proteins that are expressed in different types of cells. More than 50 different intermediate filament proteins have been identified and classified into six groups based on similarities between their amino acid sequences.

7.4.4 Functions

- They take part in the process of cell division, growth, and differentiation.
- They maintain the cell's overall shape and is responsible for the movement of various organelles within it. In single-celled organisms such as *Amoeba,* the cytoskeleton is responsible for the locomotion of the individual itself.
- They are associated with cytoplasmic streaming or cyclosis. During this process, the organelles and other substances travel in between the microfilaments and the tonoplast with the help of moving currents. Such moving currents of cytoplasm are believed to facilitate transport of nutrients, enzymes, and other substances between the cell and its surroundings, and within the cell itself.
- They mediate the movement of the cell nucleus before and after cell division. It also facilitates specific activities such as cell division including cell cleavage during mitosis. They also play a role in cell plate formation in dividing cells.

- Microtubules are crucial for the movement of motile appendages (locomotory organs) such as cilia and flagella.

7.4.5 Structure of Cilia and Flagella

Cilia (singular-cilium) are thread like structures present in both unicellular and multicellular organisms (Fig. 7.11). They are about 2-10 µm long and about 0.25µm in diameter. Each cilium is bounded by a single cell membrane. Unicellular organisms use cilia for locomotion and collection of food particles, while multicellular organisms may use them for specialized functions, e.g. epithelial lining of respiratory tract of humans possesses several hundred cilia and beating of these structures carries dust, mucus, dead cells and foreign matter out of the lungs.

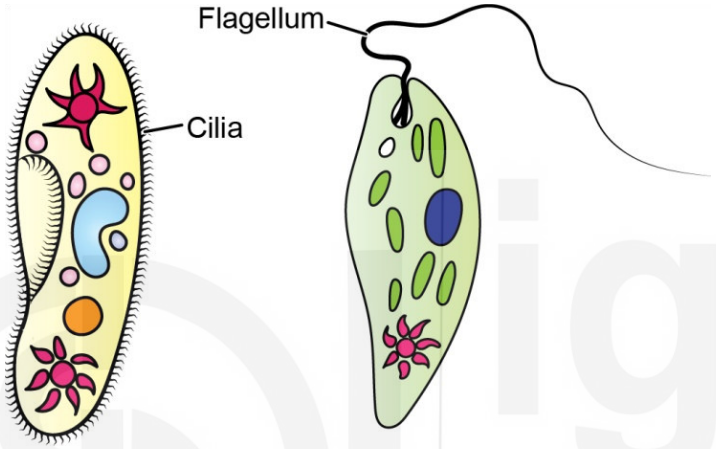


Fig. 7.11: Cells showing cilia and flagella.

Both cilia and flagella share a common structural basis but differ in terms of relative length, number per cell and type of movement. Cilia show a particular rhythmic pattern of beating movements. The cilia beat in a coordinated manner to facilitate the movement on the fluid surface. Each cycle requires 0.1-0.2 s. and involves an active power stroke followed by a recovery stroke. The pattern of beating generates a force parallel to the surface.

Flagella (singular- flagellum) are also thread like structures but are much longer than cilia. Their length ranges from 10 to 200 µm. Flagella are also bounded by a single cell membrane. The beating of flagella propagates a bending motion that is symmetrical. The beating generates a force parallel to the axis of the flagellum. The locomotion by flagella involves propulsion.

The ciliary apparatus of the cilia or flagella consists of i) shaft or cilium projecting out of the cell, ii) the basal body from which the cilium originates, iii) ciliary rootlets. The shaft consists of a basic framework called **axial complex** or **axoneme** (Fig. 7.12). It is a cylinder formed by tubules having a diameter of about 0.25 µm. The length of this part ranges from few micrometers to 1mm with a diameter of about 0.2 to 10µm. It is thicker at the base and becomes thinner along the length. The axoneme is surrounded by an outer ciliary membrane which is trilamellar protein structure continuous with the protoplasm. The components of axoneme are embedded in the ciliary ground substance or matrix. The axoneme is connected to the basal body and is surrounded by an extension of cell membrane. A transition zone present

between the axoneme and the basal body shows a similar pattern of nine microtubules as seen in axoneme. Also, the basal body has a structure similar to the centriole. It consists of nine sets of tubular structures arranged around its periphery. Each set is called as a triplet as it contains three tubules sharing common walls. The centriole acts as a nucleation site for MT assembly, initiating polymerization of nine outer doublets of the axoneme.

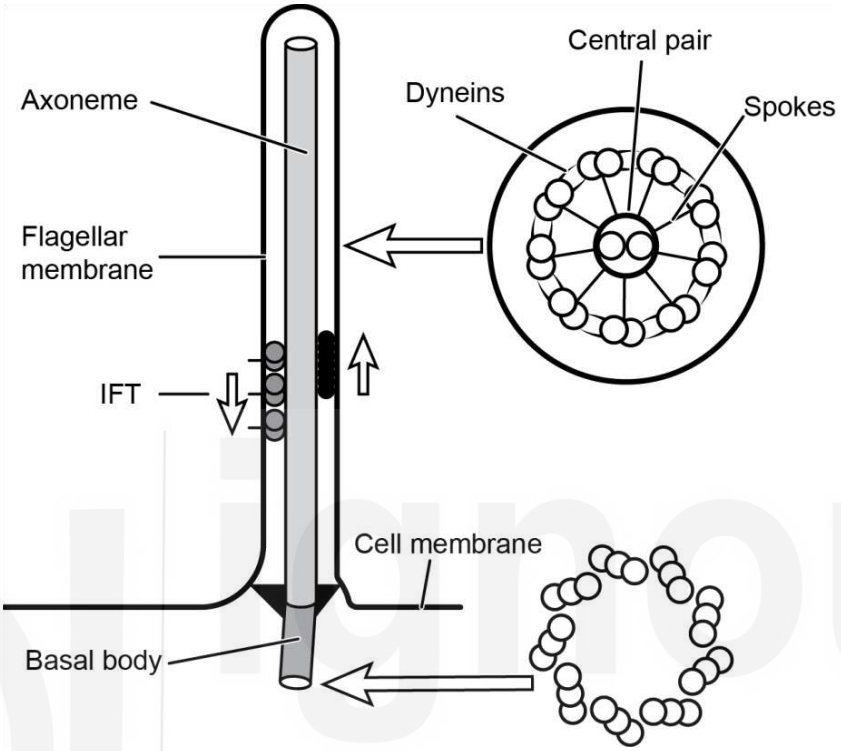


Fig. 7.12: Diagrammatic representation of internal organization of flagella.

Each axoneme possesses a characteristic 11 fibrils running longitudinally and arranged in 9+2 pattern (Fig. 7.13a, b). Two fibrils are centrally located and the remaining nine are arranged around them. The central fibril (25 nm) consists of single microtubule singletwhile each of the peripheral fibrils (36 nm) is made up of a pair of ellipsoidal microtubules (18-25nm). The peripheral doublets remain separated from each other by a distance of 20 nm and from a ciliary membrane by a distance of 25nm. The doublets consists of two microtubules or subfibers of which one is smaller (A) but complete (13 protofilaments) and lies closer to axis. The other one is bigger (B) but incomplete (11 protofilaments) and is skewed at about 10^{o} away from the axis. Each subfiber has a claw like dynein arms (Fig. 7.13c). The central pair of singlets has a complete set of 13 protofilaments each. In addition to tubulin, another protein tektin is also present.

The nine outer doublets of axoneme are thought to be extensions of two of three sub fibers from each of the nine triplets of the basal body. Each central fibril has a wall which is 6 nm thick and is located 35nm away from each other. It remains enclosed in a common central sheath. Each peripheral doublet remains connected through its smaller subunit A to the central sheath by cross links with a head or knob. The smaller arms are peripheral microtubule A and radial linkage between peripheral doublet and central sheath consist of a protein dynein.

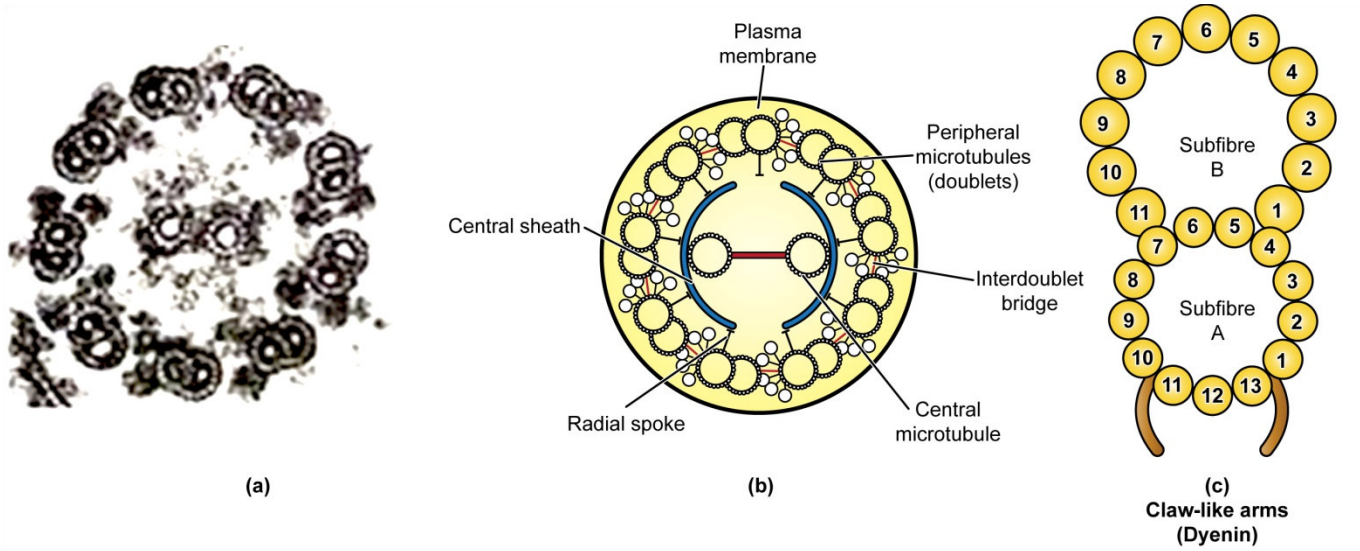


Fig.7.13: a) Ultrastructure of an axoneme; b) Internal structure of axoneme showing 9+2 arrangement of microtubules; c) Structure of the subfibers of the peripheral 9 doublets.

7.5 CELL INCLUSIONS

Cell inclusions or ergastic substances are the products of cell metabolism present inside a cell at various stages of its life-cycle. These include various nutrients and/or pigments. Ergastic substances may be present either in the cell walls or vacuoles or within different organelles. They may be present in a soluble or insoluble state and organic or inorganic in nature. Cell inclusions include a variety of reserve foods, inorganic materials, secretory and excretory products.

i) Reserve foods

These occur in the form of starch, glycogen, fat droplets and aleurone grains. Starch grains are found in plant storage organs such as seeds, fruits, tubers and rhizome. Fats are abundant in the seeds in endosperm or cotyledons. Aleurone grains are insoluble storage proteins that occur in special leucoplasts called aleuroplasts. They occur in the outer endosperm cells of cereals such as wheat, rice, and maize grains (Fig. 7.14).

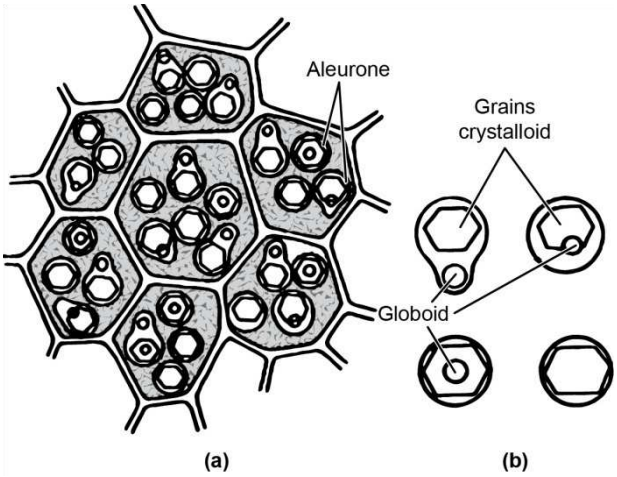


Fig. 7.14: a) Aleurone the grains in endosperm of castor seed; and b) grains containing crystalloids and globoids.

ii) Inorganic Materials (Mineral Matter)

The inorganic materials found within plants include calcium salts or anhydrous silicate salts. The deposits of calcium oxalate of prismatic, needle-shaped, rhomboidal (diamond-shaped) shapes have also been reported in plants of many families. **Raphides** occur in the form of bundles. Raphides are needle-shaped structures containing crystals of calcium oxalate. They are found in more than 200 families of plants. Crystals of calcium carbonate occur in some plants in the form of **cystoliths**. A cystolith is an outgrowth of the epidermal cell wall formed in a cellulose matrix in special cells called lithocysts. These are found in leaves of plants. Cystoliths have been reported in the families Acanthaceae, Urticaceae, and Moraceae which you have already studied in BBYCT-133.

iii) Secretory Products

The substances secreted by glands and other organs of plants are also included in the category of cell inclusions or ergastic substances. These mainly include green pigments such as chlorophyll a, chlorophyll b, orange and yellow pigments like carotene, xanthophylls and anthocyanin pigments. Anthocyanins are found in vacuolar sap of fruits, petals of flowers and young leaves of some plants. Other products include nectar, secreted by nectaries in plants and enzymatic proteins present in the protoplasm.

iv) Excretory Products

The chemical substances produced during metabolism but not used in plants are called excretory products. These include alkaloids which are nitrogenous compounds made up of carbon, hydrogen, oxygen and nitrogen. These are found in storage organs of plants like seeds, bark and leaves. They are soluble in alcohol. The plants do not have any special mechanism to remove alkaloids like substances, e.g. quinine, reserpine, nicotine, caffeine, strychnine, morphine, and atropine. Besides alkaloids, the glucosides which are degradation products of carbohydrates are also excretory products. e.g. digitoxin. Some other important examples of excretory products include tannins that occur in vacuolar sap, cell wall, bark and leaves of some plants and latex, a milky substance secreted by latex glands of *Hevea brasiliensis* (rubber). Volatile oils produced by cells, resins produced by the oxidation of essential oils, gums produced by the disintegration of cellulose cell wall and organic acids found in leaves and fruits are some other examples of excretory products.

SAQ 3

a) State whether the statements are ‘True’ or ‘False’.

i) Microtubules assist in maintaining cell shape and structure along with positioning of organelles within the cell.

ii) Cilia are cellular appendages that help in mobility of the cell in higher plants.

iii) The basal body from which the cilia originate look similar to centriole.

iv) Microfilaments are cytoskeletal elements that occur in all eukaryoytic cells and are believed to be involved in contraction of muscle cells, and locomotion.

v) Cytoplasmic microtubules form a part of cilia and flagella.

vi) Cell inclusions are mainly present in the cell walls or vacuoles or in the organelles of protoplasm.

b) With the help of a well labelled diagram, explain the structure of flagella.

c) Answer in one word.

i) These filaments are a part of cytoskeleton and mainly involved in providing mechanical strength to cells and tissues.

ii) A hair like structure or appendage found on the surfaces of cells and used for movement by microorganisms and some specialized cells in plants.

iii) An outgrowth of the epidermal cell wall containing calcium carbonate.

iv) Microtubules which are highly organized, stable and found in cilia and flagella associated with cellular movement.

v) The compounds produced during metabolism but are not of use to plants.

vi) These structural elements help in amoeboid movement of cells.

7.6 RIBOSOMES

Ribosomes are membrane-less organelles present as dense granules of about 150-200A^0 diameter. Ribosomes are considered to be the smallest organelle in a cell. These can be found free floating in the cytoplasm or attached to the ER. In 1955 **Palade** named these organelles as ribosomes. Ribosomes serve as the site of protein synthesis. Each ribosome is composed of two RNA subunits. The two subunits align with mRNA to initiate the process of translation (protein synthesis), which you will study in the unit 13 of this course. Magnesium ions play an important role in holding the two subunits together and maintaining their structure. Below a certain level of Mg^{2+} concentration, the two subunits of the ribosomes separate. Lowering of Mg^{2+} content below a critical level results in breaking of the subunits themselves.

Ribosomes are of 2 types-70S and 80S (S-refers to Svedberg units). 80S ribosomes are found in eukaryotes. These consist of a large 60S subunit and a small 40S subunit. The 70S ribosomes are relatively smaller and are found in prokaryotes. These consist of a large 50S subunit and a small 30S subunit (see Fig. 7.15 and Table 7.1).

Svedberg unit is a sedimentation coefficient which shows how fast cell organelle sediments in a $CsCl_2$ gradient in an ultracentrifuge.

Ribosomes may occur in the free form in prokaryotes and are known as monosomes or may be associated with mRNA to form polysomes or polyribosome. In eukaryotes, ribosomes are usually associated with the membrane of ER, thereby giving the latter a rough appearance (RER).

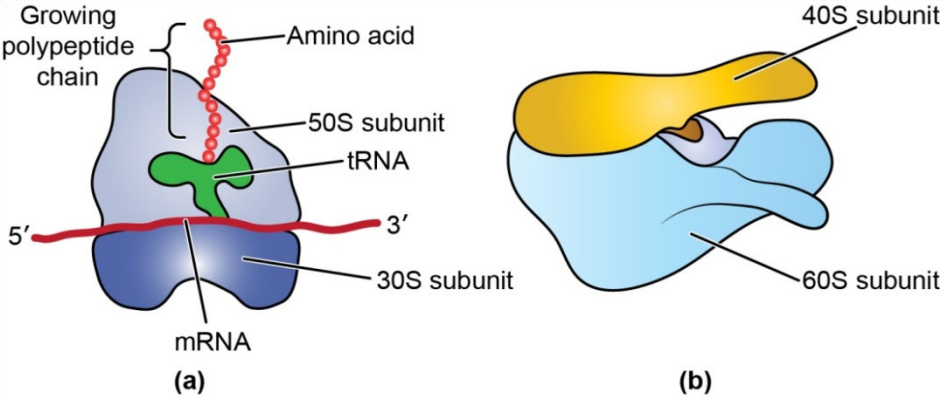


Fig. 7.15: Structure of a) prokaryotic; and b) eukaryotic ribosome.

Table 7.1 : Difference between ribosomes found in prokaryotes and eukaryotes.

	Prokaryotic ribosome	**Eukaryotic ribosome**
1	70S ribosomes, made of a 30S and a 50S subunits	80S ribosomes, made of a 40S and 60S subunits
2	Small in size	Large in size
3	Svedberg coefficient 70S	Svedberg coefficient 80S
4	30S subunit (small subunit) with 16S RNA, comprises of 1540 nucleotides bound to 21 proteins.	40S subunit (small subunit) with 18S RNA comprises of 33 proteins and 1900 nucleotides.
5	Molecular weight 3x 10^6 Da	Molecular weight 4-5x 10^6 Da
6	Large subunit (50S) contains 23S RNA with 2900 nucleotides, 5 S RNA with 120 nucleotides and 31 proteins	Large subunit (60S) contains 5S RNA with120 nucleotides, 28S RNA with 4700 nucleotides and 5.8S RNA with 160 nucleotide subunits and 46 proteins

7.7 Nucleus

The nucleus is one of the largest and prominent membrane-bounded cell organelle occupying about 10 percent of the cell's volume. It contains the hereditary information and controls the growth and reproduction of cell. The nucleus is considered as the control center of the cell as it stores all of the genetic information related to the synthesis of proteins, regulation of gene integrity, gene expression and directs metabolic activities taking place in a cell. It also sends "commands" to the cell which translates information from DNA via molecular messengers. The nucleus is enclosed by a double nuclear membrane which separates it from rest of the cell or cytoplasm . Nucleus was discovered by **Robert Brown** in 1831. In 1869 **Friedrich Miescher** suggested that DNA was the component of the nucleus. **Waldeyer** in 1888 observed rod-like structures in the nucleus and designated them as **chromosomes**.

In prokaryotes, a well defined nucleus organization is not observed. Instead, a nucleoid is present which is devoid of a nuclear membrane and shows the presence of single circular chromosome made up of DNA alone (no associated histones). A well defined nucleus is present in all eukaryotic cells except mature mammalian erythrocytes. Cells that have a single nucleus are

called mononucleate, and those having two nuclei are called binucleate. Multinucleate cells possess many nuclei. e.g. muscle cells.

Nucleus is characterized by the presence of hereditary material i.e. DNA. DNA duplication takes place within the nucleus. mRNAs are also synthesized (transcription) in the nucleus. The genetic information stored in DNA eventually gets translated to proteins in the cytoplasm via mRNA.

Structural components of Nucleus

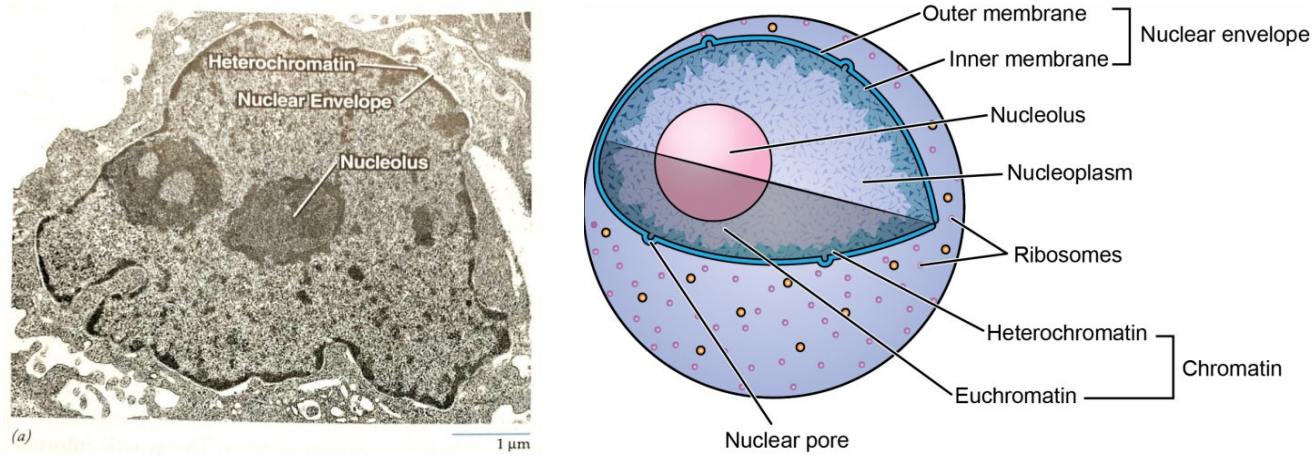
The components of nucleus are:

- Nuclear membrane/envelope
- Nuclear matrix and nuclear lamina
- Nucleoplasm
- Nucleolus
- Nuclear pore complex
- Chromosomes

Nuclear Membrane/Envelope

It is a double-layered structure that encloses the nucleus. A fluid-filled space or perinuclear space is present between the two layers of a nuclear membrane which about 10 to 15 nm in width. The outer layer of the membrane is continuous with the endoplasmic reticulum. The nuclear envelope helps in maintaining shape of the nucleus. Nuclear pores are the small openings or pore like structures present on the nuclear membrane that help nucleus to communicate with the cell or the cytoplasm (Fig. 7.16). These pores are around 100nm in diameter. The nuclear pores regulate flow of molecules into and out of the nucleus.

The thickness of both outer and inner nuclear membrane is similar (about 7-8nm). However, outer membrane differs from the inner nuclear envelope in its chemical composition and function. While ribosomes are attached only with the outer nuclear envelope, the inner nuclear envelope is closely associated with the chromatin.



(a) **(b)**

Fig. 7.16: a) Electron micrograph; and b) diagrammatic representation of Nucleus.

Nuclear matrix and nuclear lamina

The shape of the nucleus is maintained by fibrous network of proteins. This network is called nuclear matrix (or nuclear skeleton). It is a protein mesh present on the inner surface of the nucleus, and provides skeletal support and anchors the chromatin during DNA or RNA synthesis. The fibrous network present beneath the inner nuclear membrane is called fibrous lamina or **nuclear lamina**, which is 10 to 40 nm thick. It consists of 60-80 kDa proteins called **lamins**. Lamins help in dissolution, disorganization of nuclear envelope at the time of cell division and its reorganization after the cell division is over. The phosphorylation of lamins results in their depolymerization leading to nuclear envelope dissolution. The phosphorylation and dephosphorylation of lamins is triggered by a specific protein kinase. When phosphate groups are not attached to lamins, they get assembled to form an ordered structure, which helps in reorganizing nuclear envelope at the time of cell division.

Nucleoplasm

Nucleoplasm (karyoplasm) is the gelatinous substance present in the nuclear envelope. It is a semi-aqueous material composed mainly of water with dissolved salts, enzymes, and suspended organic molecules. The nucleolus and chromosomes are surrounded by nucleoplasm. Nucleoplasm functions as a cushion and protects the contents of the nucleus. It helps in maintaining its shape of the nucleus and also act as the medium in enzymes and nucleotides (DNA and RNA subunits) get transported throughout the nucleus. Substances get exchanged between the cytoplasm and nucleoplasm through nuclear pores.

Nucleolus

Nucleoli (single-nucleolus) are dense, membrane-less globular structures present within the nucleus. A nucleolus is composed of RNA and proteins. It was first described by **Fontana** in 1781. Generally a single nucleolus is present in a cell but upto four nuclei have also been reported. The phosphoproteins form the main component of nucleolus. Nucleolus contains nucleolar organizers which are part of chromosomes and contain genes for ribosome synthesis. The nucleolus is one of the most active sites of RNA synthesis and ribosome formation. It produces 70-90% of cellular RNA. It is the site of ribosomal RNA production, synthesis and assembly of ribosomal subunits. These subunits later join together to form a ribosome during protein synthesis. The nucleolus disappears (disorganizes) during cell division but reappears (reorganizes) after the completion of cell division.

The nucleolus consists of a continuous coiled filament called **nucleonema** embedded in a homogenous matrix, the **pars amorpha**. Four distinct zones are present in the nucleolus: (i) granular zone (ii) fibrillar zone (iii) nucleolus associated chromatin (iv) matrix or amorphous zone (Fig. 7.17).

i) Granular zone consists of electron dense granules (15-20nm diameter). They are equal in size. These granules are precursors of ribosomes. The granules appear as vesicles with a light central core and a dense peripheral structure. They are connected together by a thin filament, forming a structure (the primary-nucleonema) resembling a string of beads. The primary-nucleonema undergoes folding to from the

secondary-nucleonema. The nucleonema may also have fibrills. The granular areas represent ribosome precursor particles at various stages of assembly and processing. Once the ribosomal subunits are mature, they are released from the nucleolus through the nuclear pores into the cytoplasm.

ii) Fibrillar zone consists of fine fibers of 5-10nm in diameter. It generally occupies the central region of the nucleolus. It contains RNA and probably acts as the precursor of the granular zone. The granular and fibrillar components may either be separate in the nucleolus or may be mixed together forming fibrillo-granular areas.

iii) Nucleolar associated chromatin is composed of fibers 10nm in thickness situated around the nucleolus and even extending into it. The fibers may occupy special areas within the nucleolus.

iv) Matrix is an amorphous background in which the granular and fibrillar components are suspended. Matrix is proteinaceous in nature.

The ribonucleoproteins are synthesized in cytoplasm and are imported from the cytoplasm to the nucleus through the nuclear pore. These proteins get associated with the rRNA to from ribosomes.

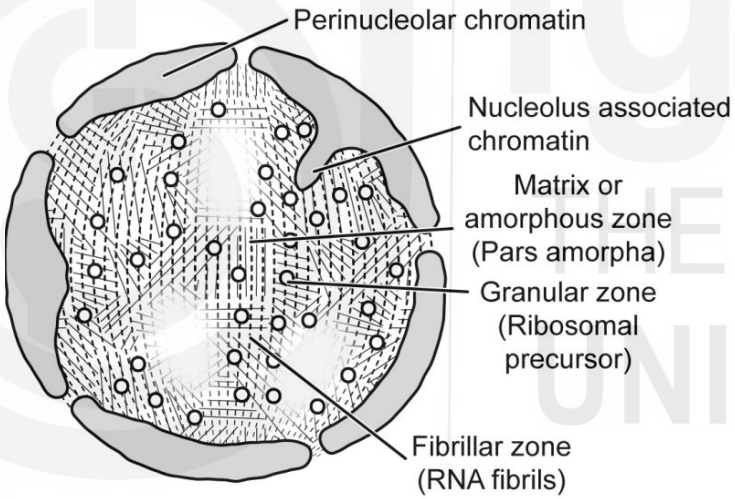


Fig. 7.17: Diagrammatic representation of various zones in nucleolus.

SAQ 4

a) Differentiate between prokaryotic and eukaryotic ribosomes.

b) Draw a well labelled diagram of nucleolus.

Chromosomes

The chromosomes are the carriers of hereditary material present in the nucleus. The chromosomes are present in the form of long intertwined structures made up of DNA and proteins (mostly histones) called chromatin. The chromatin is classified into **heterochromatin** and **euchromatin.** Heterochromatin is a highly condensed, transcriptionally inactive form of DNA. It is found present adjacent to the nuclear membrane. It is densely packed.

On the other hand, euchromatin is a delicate, less condensed organization of chromatin. It is found abundantly in an actively transcribing cell. Euchromatin is present during gene expression. Euchromatin stains lighter than heterochromatin which reflects its relative less density in electron micrographs (Fig. 7.18).

Heterochromatin can either be **constitutive** or **facultative**. Constitutive heterochromatin is permanently condensed. This is also called junk DNA. This does not have any specific function. It appears as dark irregular layer around the nuclear periphery in electron micrographs. This part of chromatin is bound to inner surface of nuclear envelope and remains condensed. It is also found distributed in centromeric and telomeric regions of chromosomes. DNA of constitutive heterochromatin consists of short sequences that are called tandem repeats. Facultative heterochromatin undergoes periodic dispersal and becomes transcriptionally active. It differs from cell to cell of an organism or in different organisms of a species.

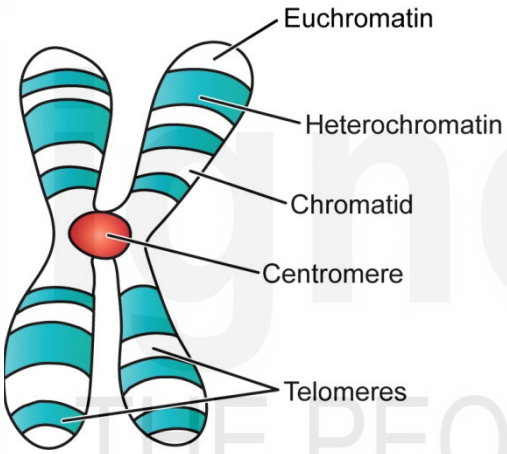


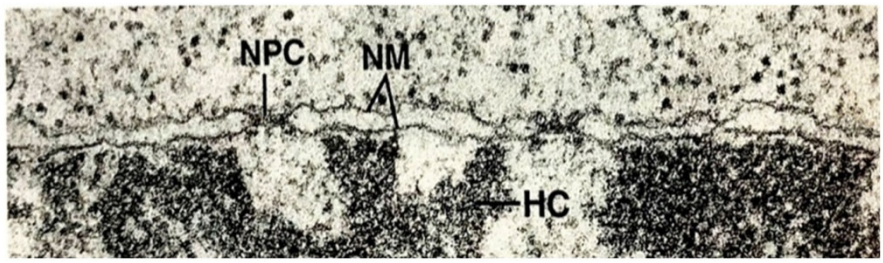
Fig. 7.18: A chromosome showing euchromatin and heterochromatin region.

Nuclear pore and Nuclear pore complex

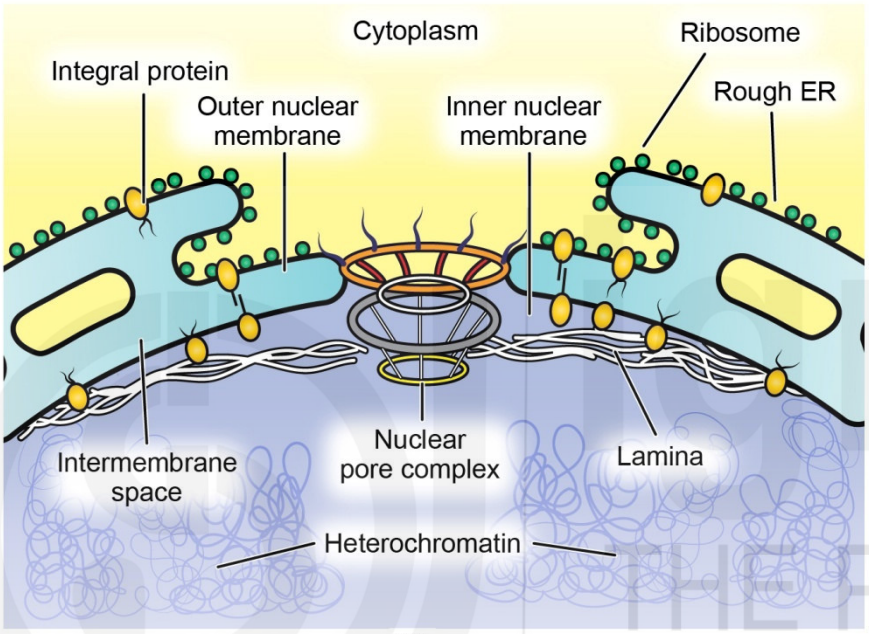
The nuclear envelope is not continuous and consists of number of pores through which nucleoplasm is connected to cytoplasm. These pores are called nuclear pores. A nuclear pore is a tiny way for the passage of proteins, RNA, and solutes between the nucleus and the cytoplasm. Number of nuclear pores varies greatly with the cell type. There are about 10-20 pores per square micrometer in typical mammalian cell.

Nuclear pores are complex in structure. The structure is called **nuclear pore complex (NPC)** which has a diameter of 120 nm. Recent electron microscopic studies revealed have that structure of NPC is like a basket. It is present towards nucleoplasm and is suspended by means of spokes. It consists of two rings: cytoplasmic ring (which is present towards cytoplasm) and nucleoplasmic ring (present towards nucleoplasm). Both the rings are connected to each other by means of spokes. There is one central channel through which proteins and RNA are thought to pass through, while low molecular weight solutes are believed to pass through the slots between the spokes (Fig. 7.19). These cytoplasmic filaments help in movement of proteins through the pores. NPC contains 30 different proteins called nucleoporins. Many proteins and ions shuttle continuously between the nucleus and the cytoplasm via NPC. The mobility of molecules depends on their size. Small

molecules and proteins (molecular mass less than 20-40 kDa) pass freely (diffuse) through the pore in either direction i.e. cytoplasm to nucleus and in reverse direction.



(a)



(b)

Fig. 7.19: a) Electron micrograph of Nuclear pore complex (NPC); b) Diagrammatic representation Nuclear pore complex (HC- heterochromatin; NM= nuclear membrane)

Functions

- The nucleus stores genetic information in the form of DNA. The main function of the nucleus is to control gene expression and mediate the replication of DNA during the cell cycle. It controls the heredity of an organism.
- The nucleus is also the site for transcription where messenger RNA (mRNA) is produced.
- DNA is duplicated (replication) before it can be distributed equally into daughter cells during the cell division. When a cell divides, the DNA must be duplicated so that each new cell receives a full complement of DNA.
- Ribosome subunits are synthesized within the nucleus, which are then transported to the cytoplasm.
- Selective transportation of ions, proteins and other molecules occurs through nuclear pores present on the nuclear envelope.

SAQ 5

a) Define the following terms:

i) Nuclear lamina

ii) Nucleoplasm

iii) Lamins

iv) Chromatin

b) Enumerate the functions of nucleus.

7.7 SUMMARY

- Peroxisomes are small, round structures bounded by single membrane. They contain enzymes that play a role in a number of metabolic reactions including fatty acid oxidation, glyoxylate cycle and photorespiration. They are found in both animal and plant cells. New peroxisomes arise from pre existing ones and grow by importing lipids, membrane proteins and matrix proteins from cytosol. Recent studies also give some indication of their ER- mediated *de novo* synthesis.
- Glyoxysomes are found in germinating seeds. In addition to other enzymes, these organelles contain enzymes of the glyoxylate cycle.
- Microtubules are fine, unbranched hollow tubes made up of subunits consisting of the protein tubulin. These structural elements may be arranged singly or as a network or parallel bundles. These provide tensile strength and rigidity to cellular regions. Microfilaments are linear, unbranched fibers made up of the protein actin. They are also called as actin filaments. Microfilaments are smaller than microtubules and occur singly, as networks or as parallel bundles in the cytoskeleton.
- Cell inclusions or ergastic substances are the products of cell metabolism. These substances are present in the cell walls or vacuoles and in the organelles of cytoplasm. They include various nutrients, reserve foods, inorganic materials, pigments, secretory and excretory products.
- Ribosomes are the smallest organelles present in a cell and are present as dense granules in the cytoplasm. It can be found free floating in the cytoplasm or attached to the ER. It serves as the site of protein synthesis. Each ribosome is composed of two ribosomal RNA subunits.
- Nucleus is a master organelle present in the eukaryotic cells. It is the site where the duplication of DNA takes place and the genetic information gets transcribed to form mRNA. The mRNA carries the information from nucleus to cytoplasm which gets translated during protein synthesis. The nuclear envelope is a well organized structure in eukaryotes with nuclear pores. Through these nuclear pores, exchange of molecules occurs in regulated way in between nucleoplasm and cytoplasm.

- Nucleolus is a structure present within the nucleus. It is responsible for the organization of ribosomes. Ribosomal proteins are synthesized in cytoplasm and are imported from to nucleolus. Nuclear lamina is a proteinaceous structure present just below the nuclear envelope. It provides skeletal support to nuclear envelope and provides site for the attachment to chromatin fibers. It consists of proteins known as lamins.

7.8 TERMINAL QUESTIONS

1. What are microbodies?
2. Distinguish between –
   a) peroxisome and glyoxysomes
   b) euchromatin and heterochromatin
3. In what ways are peroxisomes similar to mitochondria and how they are unique?
4. Discuss the role of *catalase* in peroxisomal activities.
5. Discuss the structure and functions of glyoxysomes.
6. Describe in brief the major components of cytoskeleton of cell.
7. Enlist the major functions of cytoskeleton in cell.
8. Describe the structure of nucleus and its role in eukaryotic cell.
9. Write a short note on cell inclusions.

7.9 ANSWERS

Self-Assessment Questions

1. a) i) peroxisomes
      ii) endoplasmic reticulum (ER)
      iii) same
      iv) ER semi–autonomous
      v) photorespiration
      vi) β-oxidation
   b) Refer to Subsection 7.2.2
2. a) i) endosperm and cotyledons
      ii) fission or budding process
      iii) microbodies or peroxisomes
      iv) succinate
   b) Refer to Subsection 7.3.2

3. a) i) True; ii) False; iii) True

   iv) True; v) False; vi) True

   b) Refer Section 7.4.5

   c) i) intermediate filaments

   ii) flagellum

   ii) cystolith

   iii) axonemal

   iv) excretory products

   v) microfilaments

4. a) Refer to Section 7.6 and Table 7.1

   b) See Figure 7.17

5. a) i) The fibrous network present beneath the inner nuclear membrane is called fibrous lamina or nuclear lamina.

   ii) The gelatinous substance present in the nuclear envelope is called nucleoplasm. It is mainly composed of water with dissolved salts, enzymes, and suspended organic molecules. Nucleoplasm functions as cushion and protects the contents of the nucleus. It supports nucleus by maintaining its shape.

   iii) Lamins are a class of intermediary filament proteins. They provide the site for attachment to chromatin fibers and also help in the dissolution of nuclear envelope at the time of cell division and its reorganization after the division is over.

   iv) The chromosomes are organized into long entangled structures called chromatin. Chromatin is a complex of DNA and proteins that forms chromosomes.

   b) Refer to Section 7.7

Terminal Questions

1. Refer to Section 7.1

2. a) Refer to Sections 7.2 and 7.3.

   b) Refer to Section 7.7

3. Mitochondria and peroxisomes are organelles present in cell. They occur in the size range of 0.1 to 1 μm. They both play major roles in cell metabolism, especially fatty acid metabolism, reactive oxygen species (ROS) production, and ROS scavenging. Both mitochondria and peroxisomes share some properties but differ in terms of origin, structure, and physiological roles. The mitochondrion is surrounded by a double membrane, while peroxisomes are enclosed by a single membrane.

4. Refer to Subsection 7.2.2

5. Refer to Section 7.3
6. Refer to Section 7.4
7. Refer to Subsection 7.4.4
8. Refer to Section 7.7
9. Refer to Section 7.5

Acknowledgements for Figures

Fig. 7.1 : Source: https://www.google.co.in/imgres?imgurl=https%3A%2F%2Fwww.open.edu%2Fopenlearn%2Focw%2Fpluginfile.php%2F313588%2Fmod_oucontent%2Foucontent%

Fig. 7.2 : Source: The Journal of Cell Biology, 91, 272s, 1981.

Fig. 7.6 : Source: Sunderland (MA): Sinauer Associates; 2000. The Cell: A Molecular Approach. 2nd edition. Cooper GM.

Fig.7.9 : https://www.google.co.in/imgres?imgurl=https%3A%2F%2Fmedia.springernature.com%2Ffull%2Fspringer-static%.

Doxsey, S. Re-evaluating centrosome function. Nat Rev Mol Cell Biol 2, 688–698 (2001).

Fig. 7.13 a : https://www.google.co.in/imgres?imgurl=https%3A%2F%2Fars.els-cdn.com%2Fcontent%2Fimage%2F3-s2.0-B9780123708731000435-gr1.jpg&imgrefurl=https%3A%2F%2Fwww.sciencedirect.com%

Fig 7.16 a : https://www.google.co.in/imgres?imgurl=http%3A%2F%2Ffaculty.ccbcmd.edu%2Fcourses%2Fbio141%2Flecguide%2Funit1%2Fproeu%2Fimages_CC_new%2520figs%2Fnucleus_label_50.jpg&imgrefurl=

Fig. 7.19 a : Source: https://www.google.co.in/imgres?imgurl=https%3A%2F%2Fmmegias.webs.uvigo.es%2F02-english%2F5-celulas%2Fimagenes-e%2Fporos-p.png&imgrefurl=https%3A%2F%2Fmmegias.webs.uvigo.es%2F02-english%2F5-celulas%2F4-poros.php

Suggested videos for watching

https://www.youtube.com/watch?v=tO-W8mvBa78

https://www.youtube.com/watch?v=5rqbmLiSkpk

https://www.youtube.com/watch?v=kGzg7Nea6_o

https://www.youtube.com/watch?v=URUJD5NEXC8&t=50s

https://www.youtube.com/watch?v=v_xlBmFYu5Y

https://www.youtube.com/watch?v=gG7uCskUOrA

UNIT 8

CELL CYCLE

Structure

8.1 INTRODUCTION

Cells are the basic unit of life. By now you know its structure and various theories related to the origin of cells have also been explained to you. In this unit you will be studying one of the important process of cell division. The process of cell division may be different for unicellular and multicellular organisms. In some simple unicellular organisms, one cell division may be enough to reproduce a new organism, while other multicellular organisms large numbers of cell divisions are required to produce an organism with cellular complexity in the form of various tissues and organs.

The cell cycle in eukaryotes includes two distinct types of cell divisions (i) mitosis (ii) meiosis. **Mitosis** or equational division ensures the production of cells genetically identical to their parent. In this division, the daughter cells maintain their original genome. This cell division helps in the continuous construction and repair of the organism and replacing the ageing or dead cells. **Meiosis** or reduction cell division occurs in reproductive cells where the number of chromosomes in the daughter cells is reduced by half to produce haploid gametes. In this type of division, four haploid daughter cells are produced which are genetically different from their parents. These cell division cycles are used in the process of sexual reproduction at some point in the life cycle of plants and animals. There exists great variation in the relative dominance of haploid and diploid phases in different plant groups. e.g. Fungi with haplontic life cycle shows sporic meiosis where the reduction division occurs immediately after gametic fusion. In both mosses and ferns which

exhibit alteration of generation, gametes develop from haploid cells, fuse and it is only the sporophyte that undergoes meiosis to form haploid spores (intermediate meiosis). Higher plants and animals are predominantly diploid and haploid generation is limited to only gametes (gametic meiosis). In *Chlamydomonas*, the zygote undergoes meiosis to produce haploid zoospores leading to the formation of haploid plants (zygotic meiosis). The present unit will provide you information about various events of the cell cycle and various factors responsible for its regulation.

Objectives

After studying this unit, you will be able to :

- ❖ appreciate the different stages of cell cycle;
- ❖ explain the various factors responsible for the regulation of cell cycle;
- ❖ differentiate between various stages of during mitosis and meiosis;
- ❖ describe the role of kinetochore during cell division; and
- ❖ enumerate the differences between mitotic and meiotic cell division.

8.2 OVERVIEW OF CELL CYCLE

One of the important properties of all the living cells, prokaryotic or eukaryotic cell is the ability to duplicate their genomic DNA and to pass the copy of the replicated chromosomes to the daughter cells during cell division. Cell cycle is the series of events occurring between one stages of cell division and the same stage of the next division. The cell cycle comprises two phases/periods:

1. cell division (mitosis) and separation of daughter cells,
2. interphase- the period of cell growth.

Modern scientists divide cell cycle into 4 phases viz.

i) **Gap 1 (G_1),**

ii) **Synthesis (S),**

iii) **Gap 2 (G_2)** and

iv) **Mitotic (M)** phase (Fig.8.1).

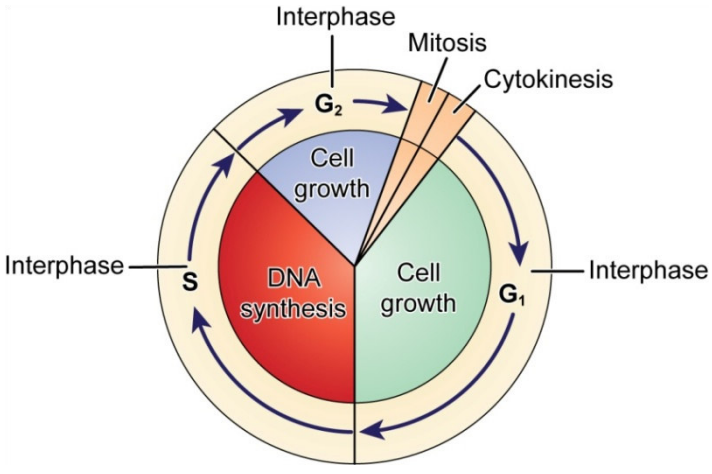


Fig. 8.1: Various phases of Cell cycle.

The initial three phases viz. G_1, S and G_2 constitute the interphase. Interphase is considered as the **resting stage** because it appears that there is no activity in a cell during this time. On the contrary, it is the metabolically most active phase where the cell prepares itself for division. Most of the vital cellular functions take place during interphase. It is infact, the longest phase in the cell cycle that takes place in the cytoplasm and the cell nucleus. In typical human cell proliferating in cultures, interphase occupies 23 h (G_1 -11h, S-8h, G_2-4h) out of a 24 hour cycle, with just one hour for M phase.

Gap 0 or G_0 phase – It is that period of time of the cell cycle where the cell is present in a **quiescent stage** or resting phase. It does not divide or grow. Cells remain metabolically active but do not proliferate.

Gap 1 or G_1 Phase-This is the first phase of interphase. During G_1, many genes become active, RNA and proteins are synthesized. The most important event in this phase is the transcription of three types of RNAs which undergo translation to form proteins and enzymes necessary for other events in the cell cycle. During this phase, cell increases in size and volume. The cellular contents get duplicated within 8-12 h. This is the metabolically active phase in which materials required for next cell division are produced. It is considered as the most variable period which can be as short as 2 to 3 h and as long as many days, depending on external conditions and extracellular signals from other cells.

The cells at G_1 phase are diploid. Cells in the G_0 phase get stimulated to enter G_1 stage after addition of hormones to the growth medium and/or onset of favorable conditions. Favorable conditions make the resting cells to progress and reach a point near the end of G_1 known as **Start** (in yeast) or the **restriction point R** (in mammalian cells). After passing through this point, cells start replicating DNA even if the extracellular signals get removed.

Some cells exit the cell cycle and undergo terminal differentiation. They never divide again. Most of the nerve cells are in this state. Cells that divide very rapidly have a short G_1 phase or do not have G_1 phase at all. The embryonic cells of insects, amphibians and non-mammalian animals have very short cell cycles with no G_1 phase and/or a short S phase.

Synthesis Phase (S) - A cell leaves G_1 phase, and enters the **S phase** or the synthesis phase. This phase may occupy 35-45% of the entire cell cycle in a rapidly growing cell. This phase is a part of interphase where important events like DNA replication and formation of histone proteins take place. The entry into the S phase is regulated by the G_1/S checkpoint which allows cells with enough nutrients and healthy DNA to enter the next phase.

DNA synthesis occurs during S phase and each chromosome carries two sister chromatids that remain attached at the centromere. The cell synthesizes and doubles its DNA contents. Each chromosome gets duplicated and nucleus synthesizes histones and proteins within 6-8 h. Histone proteins that help in chromosome condensation and form the integral part of nucleosome are also synthesized during this phase.

BOX 8.1 : Determining the duration of S-phase

The cells in the S phase incorporate newly synthesized DNA such as the thymidine analog bromodeoxyuridine (BrdU) and are identified by observing the molecule under the microscope. The nuclei of the cell containing Brd U are seen by staining with anti BrdU antibodies. The duration of S phase can be determined by exposing cells to radioactively labelled DNA precursor (^{3}H-thymidine) for a short period of time. The DNA content of cell can be determined by incubation of the cells with a DNA specific fluorescent dye followed by analysis of intensity of fluorescence of cell in a **flow cytometer** or **fluorescence activated cell sorter**.

Gap 2 or G_2 Phase - This is the second phase following the S phase. Generally G_2 phase is shorter in duration (lasts for 4-6 h). Several biochemical events necessary for cell division take place in this phase. The cell collects nutrients and releases proteins in order to prepare the cell for the M phase. This phase is also important as it checks for DNA damage (during replication) to ensure that the cell undergoes division. The entry of the cell from the G_2 phase to the M phase is regulated by the G_2 checkpoint in which various proteins and protein complexes are involved. The cell remains in the G_2 phase and does not divide if the DNA gets damaged or conditions show insufficient nutrient supply.

Mitotic Phase (M) - The M phase or Mitotic phase of the cell cycle is the most crucial phase of the entire cycle. It is shortest of all the phases. In this phase, the cell divides to form identical daughter cells. Karyokinesis (nuclear division) is the important event of this phase. The chromosomes separate into sister chromatids. The separation of sister chromatids results in formation of a cell with complete set of genetic information. A cell entering the M phase has four times more the concentration of genetic material which gets reduced to two times at the end. Hence each of the cells formed contains 2N concentration of DNA. Mitotic cell division or M phase includes five stages viz. prophase, prometaphase, metaphase, anaphase, and telophase.

Cytokinesis - It is the division of cytoplasm resulting in formation of two halves. This phase indicates end of cell division. Cytokinesis occurs immediately after the M phase. The nucleus, cell membrane and cytoplasm get separated into two halves to form two distinct and complete cells. The constriction of cell membrane formed during anaphase continues to grow deeper to finally cause cleavage. A distinct cell plate is formed at the middle of the dividing cell which separates the cytoplasm and cell organelles into equal halves. The ell plate is initiated in the middle and grows towards the periphery.

SAQ 1

a) Fill in the blank with the appropriate word.

i) …… is also referred to as reductional division.

ii) Mitosis is also called …….. division.

iii) According to current concept, the cell can be divided into …… phases.

iv) Interphase includes ……. phases of division.

v) …….. is the most metabolically active period in the cell cycle.

b) Describe in brief the following phases of cell cycle

i) S phase

ii) M phase

iii) G_0 phase

8.3 REGULATION OF CELL CYCLE

Cell division in a cell is regulated by various signals and events external to the cell. A series of events within the cell allow it to proceed into interphase. Regulator molecules promote the progression of cell cycle or stop it. The daughter cells produced after cell division are generally identical to the parent cell (duplicate). Errors during the duplication or distribution of the chromosomes lead to mutations that may be passed on to every new cell produced. Internal control mechanisms operate at three points in cell cycle to check and prevent a compromised cell from continuing to divide. A **checkpoint** is that point at which the progression of a cell to the next stage in the cell cycle is halted until conditions are favorable. These checkpoints are noted mainly in the eukaryotic cells. These checkpoints occur near the end of G_1, at the G_2/M transition, and also during metaphase (Fig. 8.2).

A regulatory network ensures that all events required for duplication of cellular contents and their subsequent segregation occur in the correct order, at specific intervals; and with the highest possible fidelity. Change in the state of phosphorylation and component levels of the cell cycle regulates the transitions between various stages of cell cycle. Entry into S-phase and M-phase are mediated by *cyclin-dependent kinases* (Cdks), and *serine-threonine kinases*. They require a regulatory cyclin subunit for their activity. The transition to the interphase state is mediated by *protein phosphatases* (PPs). This happens by counteracting Cdks by dephosphorylating their substrates.

8.3.1 Cell Cycle Checkpoints

The transition of cell through different phases of the cell cycle requires the role of specific chemical signals and accordingly, a response to these signals. If the signals are incorrectly sensed or the cell fails to respond, the cell can become cancerous. The transition from one phase to another is regulated at check points**.** Hence, checkpoints act as surveillance mechanisms that halt the progression of cell cycle if any of the chromosomal DNA is damaged, or processes like DNA synthesis during S phase or chromosome alignment during M phase have not been completed. Checkpoints ensure that each of the events that make up the cell cycle occurs accurately and in proper order. Many proteins are a part of checkpoint machinery but they do not have a role in any of the cell cycle events.

Various checkpoints recognized have been labelled as **G_1/S checkpoint**, **G_2/M checkpoint** and the **spindle assembly checkpoint in M phase** (Fig.8.2).

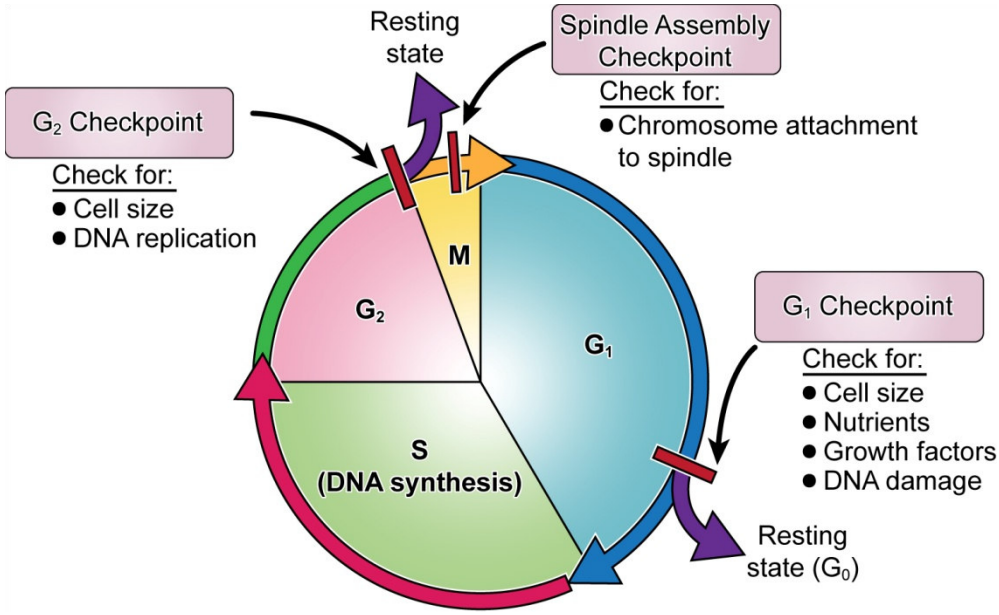


Fig. 8.2: Cell Cycle depicting various checkpoints.

The G_1 Checkpoint

It is commonly called as **START** (or **restriction point**) checkpoint. This checkpoint holds the cell in G_1 phase until the cell has availability of all the enzymes/nutrients necessary for the replication of DNA and has attained a certain size. This checkpoint ensures that conditions are favourable for cell division to proceed. Once the cell progresses through this point, it enters the cell cycle and undergoes chromosome duplication. The passage of cell through this point is influenced by the presence of extracellular growth factors, which play an important role. The genomic DNA damage is checked at the G_1 checkpoint. If a cell does not meet all the requirements the division cannot progress into the S phase. The cell cycle can halt at this stage or can advance into G_0 and the further progress will be resumed only after the signals are received. The cells enter and reside in G_0 phase for variable period of time and wait for the signal that will allow them to re-enter G_1 phase and pass through restriction point.

The G_2 Checkpoint

The checkpoint G_2/M occurs near the end of G_2 phase. The cell is destined to enter the mitosis phase. The events that initiate the alignment of chromosome through spindle as in metaphase of mitosis get triggered. This checkpoint ensures that all of the chromosomes get replicated and that the replicated DNA is not damaged (see Fig. 8.2). If any problems with DNA are detected at this checkpoint, the cell cycle is halted. Repair of damaged DNA is followed by DNA replication, If DNA replication is not complete, cell restricts itself from G_2/M transition. The cell crosses this regulatory checkpoint only when the DNA replication is complete. In certain cells, the halt in cell cycle at G_2 phase makes the cells enter a non-dividing state i.e. G_0 phase.

The M Checkpoint

The M checkpoint occurs near the end of the metaphase stage of karyokinesis. This regulatory checkpoint is also known as **spindle assembly**

checkpoint. This checkpoint occurs at the junction of metaphase and anaphase. The two sets of chromosomes are set to get transferred to daughter cells. This checkpoint determines whether sister chromatids are correctly attached to the spindle microtubules and the distribution of the chromatids to the daughter cells takes place correctly. The separation of the sister chromatids during anaphase is an irreversible step, The kinetochores of each pair of sister chromatids get firmly anchored to spindle fibers arising from opposite poles of the cell. This ensures proper attachment of chromatids to the spindle present at opposite poles and distribution of chromosomes to the two daughter cells**.**

8.3.2 Role of Regulator Molecules of the Cell Cycle

In addition to the internally controlled checkpoints, two groups of intracellular molecules also regulate the cell cycle. These regulatory molecules either promote progress of the cell to the next phase (positive regulation) or halt the cycle (negative regulation). Regulator molecules may act directly or influence the activity or production of other regulatory proteins. Where more than one mechanism controls the same event, non-functionality of a single regulator does not affect the cell cycle. Conversely, the effect of a non-functioning regulator (deficient) can be wide-ranging and fatal to the cell if multiple processes are affected.

Positive Regulation of the Cell Cycle

Two groups of proteins, called **cyclins** and **Cyclin-dependent kinases** (Cdks), regulate progress of the cell division through various checkpoints.

The level of cyclins (proteins) fluctuates throughout the cell cycle. The cyclins are expressed between G_1 and S phases, during the S phase, and between G_2 and M phases. Accordingly these are known as G_1/S-phase cyclin, S-phase cyclin, and G_2/M-phase cyclin, respectively. Each cyclin is synthesized during a specific phase of the cell cycle. It gets degraded after its function is over. The breakdown of cyclin is essential for the cell cycle to make a transition to the next step.

The concentration of cyclin proteins increases under the influence of external and internal signals. When the cell moves to the next stage of the cell cycle, cyclins that were active in the previous stage get degraded. Hence, cyclin acts as control switch which regulates the movement of cell cycle from G_1 to S or from G_2 to M.

Cyclin-Cdk (cyclin-dependent protein kinase) complexes play an important role in progression of cell cycle (Fig. 8.3). Since these complexes help in smooth running of cell cycle, these are called as “cell cycle engines.” The binding of cyclins and Cdks at specific points in the cell cycle regulates different checkpoints and hence the cell cycle. The phosphorylation of Cdk/cyclin complex in specific locations is necessary so that it can remain fully active. Studies have shown that active Cyclin/Cdk complex triggers several events such as:

- breakdown of nuclear envelope,
- chromosome condensation,

- spindle formation, and
- protein degradation.

The transition from G_2 to M phase is thought to be triggered by a Cdk /cyclin complex or the maturation promoting factor (MPF). Recent studies have established that Cyclin/Cdk complexes are a type of protein kinases that serve as a regulator of transition from M-phase. The structure and function of MPF (Cdk/cyclin B) provides an understanding of molecular basis for entry and exit from M phase.

Cyclin/Cdk complex regulates phosphorylation of several structural proteins involved in cellular reorganization. It plays a role in chromatin condensation, organization of nuclear pore complexes, phosphorylating lamins fragmentation of the Golgi apparatus by phosphorylating Golgi matrix proteins, and spindle formation by phosphorylating centrosome-associated proteins and microtubule associated proteins (MAPs). Without a specific concentration of fully activated cyclin/Cdk complexes, the cell cycle cannot proceed through the checkpoints.

Different Cdks bind with various cyclins thereby promoting cell cycle transition. In mammals nine Cdks have been found, out of which four Cdks viz. Cdk1, Cdk2, Cdk4 and Cdk6 regulate progression of cell cycle, when activated by cyclin A, cyclin B, cyclin D and cyclin E in various associations (Fig. 8.3). Cdk/cyclin complexes function at different stages of cell cycle. In the absence of other Cdks, Cdk1 binds to all of the cyclins and drives the progression of cell cycle through different stages.

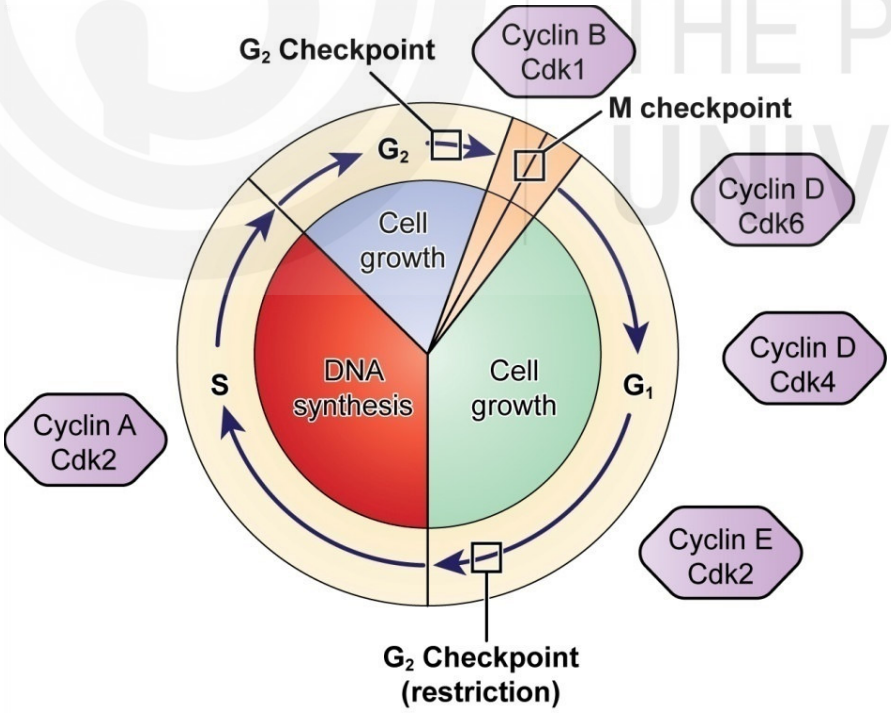


Fig. 8.3: Various Cdks involved in regulation of cell cycle.

Some molecules prevent activation of Cdks. These are called Cdk inhibitors. Many of these inhibitor molecules regulate events of cell cycle directly or indirectly. They block the progress of the cell cycle until the problems get resolved.

8.3.3 Regulation of Cell Cycle by *Protein kinase*

Investigations by **Hartwell et al.** on *Saccharomyces cerevisiae* and **Paul Nurse** on *Schizosaccharomyces pombe* have lead to the discovery of genes that drive the cell through various phases of cell cycle accomplishing several activities. One such gene identified has been named as cdc 2 i.e. cell division cycle 2. This gene has been found responsible for initiating mitosis and moving cell from G_2 to M phase. Further studies revealed that cdc is a protein kinase, an enzyme that catalyze the transfer of phosphate group from ATP to other target proteins. A series of protein kinases particularly that produced by cdc 2 controls the progression of cell cycle.

The activated Cdc 2 kinase phosphorylates numerous proteins and results in initiation of mitosis. Phosphorylation induces the reorganization of microtubules which result in the formation of spindle. The phosphorylation of lamins (filamentous proteins in nuclear lamina) leads to the breakdown of nuclear envelope, while that of histone H1 causes condensation of chromatin. The enzyme Cdc2 kinase turns off its own activity by activating an enzyme that degrades cyclin.

Box 8.1 : Negative Regulation of the Cell Cycle

The negative regulators form second group of cell cycle regulatory molecules. These regulators stop the progress of the cell cycle. These regulatory molecules include protein retinoblastoma (Rb), p53, and p21. The numbers 53 and 21 designate the functional molecular masses of the proteins (p) in kilodaltons. Retinoblastoma proteins are a group of tumor-suppressor proteins found in many cells. All three of these regulatory proteins were found to be damaged or non-functional in cells that had begun to replicate uncontrollably (became cancerous).

Rb, p53, and p21 act primarily at the G_1 checkpoint. p53 is a multi-functional protein and blocks the cell cycle if the DNA is damaged. In case damaged DNA is detected, p53 stops the cell cycle from progressing and involves enzymes that repair DNA. If the DNA cannot be repaired, then p53 can trigger apoptosis, or cell suicide to prevent the duplication of damaged chromosomes. Also p53 levels are increased in damaged cells. A mutation in p53 leads to cancer. A genetic defect in p53 leads to a high frequency of cancer in affected individuals known as Li Fraumeni syndrome.

With an increase in levels of p53, the production of p21 is triggered. p21 stops the cell cycle. This happens because p53 binds to Cdk/cyclin complex and inhibits its activity. Accumulation of high levels of p53 and p21 prevent the cell from going to S phase. Another protein, p27 binds to cyclin and Cdk blocking the entry of cell into S phase. Recent studies suggest that breast cancer prognosis is determined by p27 levels.

8.3.4 Mechanism of Cdk Regulation

Cyclin-dependent kinases **(Cdks)** regulate cell division cycle in eukaryotes. Cdks are enzymes (kinases) that phosphorylate proteins. They add phosphate to a protein along with cyclins. Phosphorylation activates the protein by changing its shape (Fig. 8.4). The phosphorylated proteins play a role in transfer of cell to the next phase. The levels of Cdk proteins are relatively stable throughout the cell cycle.

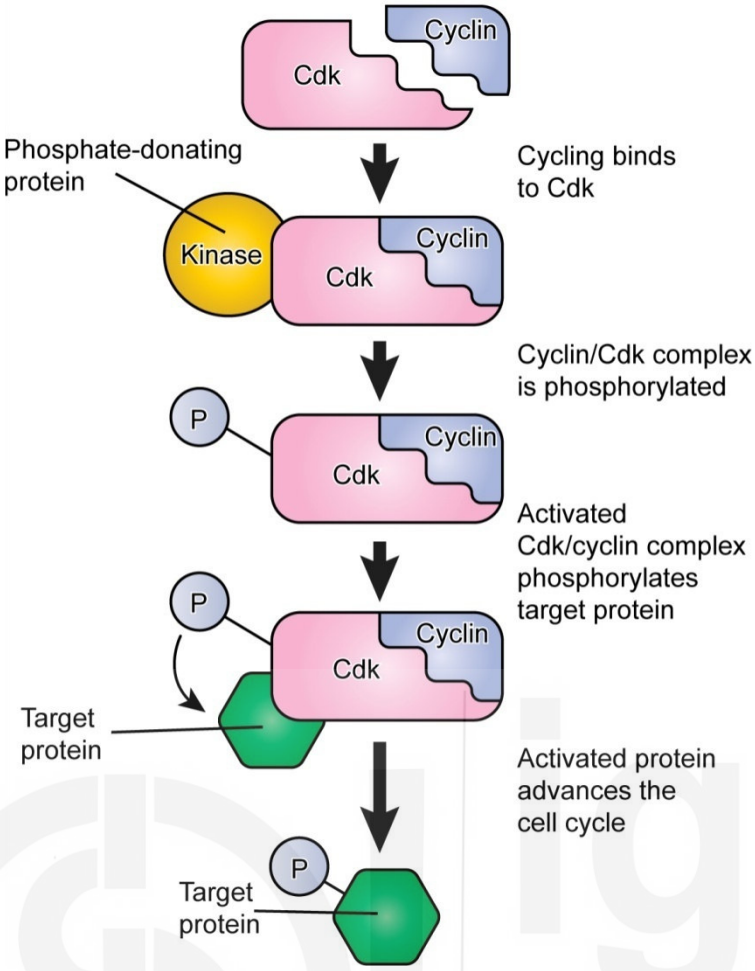


Fig. 8.4: Cyclin-dependent kinases (Cdks) are protein kinases, when fully activated, can phosphorylate and thus activate other proteins that advance the cell cycle past a checkpoint. A Cdk must bind to a cyclin protein and then be phosphorylated by another kinase to become fully activated.

Cyclin-dependent kinases modulate transcription in response to several extra- and intracellular signals. Their role is to phosphorylate proteins on either S or T amino acids and thereby regulate the activity of those proteins. Cdks are controlled through several different processes involving the binding of activating cyclin subunits, of inhibitory Cip or INK4 subunits, and phosphorylation. The activity of Cdks during cell cycle progression is regulated by four molecular mechanisms viz. cyclin binding, CAK phosphorylation, regulatory inhibitory phosphorylation, and binding of Cdk inhibitory subunits (CKIs) (Fig. 8.5)

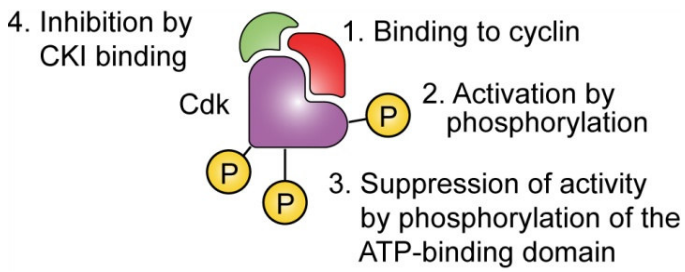


Fig. 8.5: Factors regulating Cdk activation.

The **first level** of regulation involves the association of Cdks with their cyclin partner. The catalytic activity of active Cdks is dependent on association with a regulatory cyclin subunit. Accumulation and proteolytic degradation of different

cyclin subunits regulates their association with Cdks to control different stages of cell division. Cdks have a modified ATP-binding site that can be regulated by cyclin binding. Without cyclin, a flexible loop called the activation loop (T-loop) blocks the cleft and ATP-binding is restricted. ATP binding occurs in presence of cyclin. The binding of cyclin with Cdk is specific. Cyclin binding determines the specificity of the cyclin-Cdk complex for specific substrates. Phosphorylation increases the activity of the complex (Fig. 8.6).

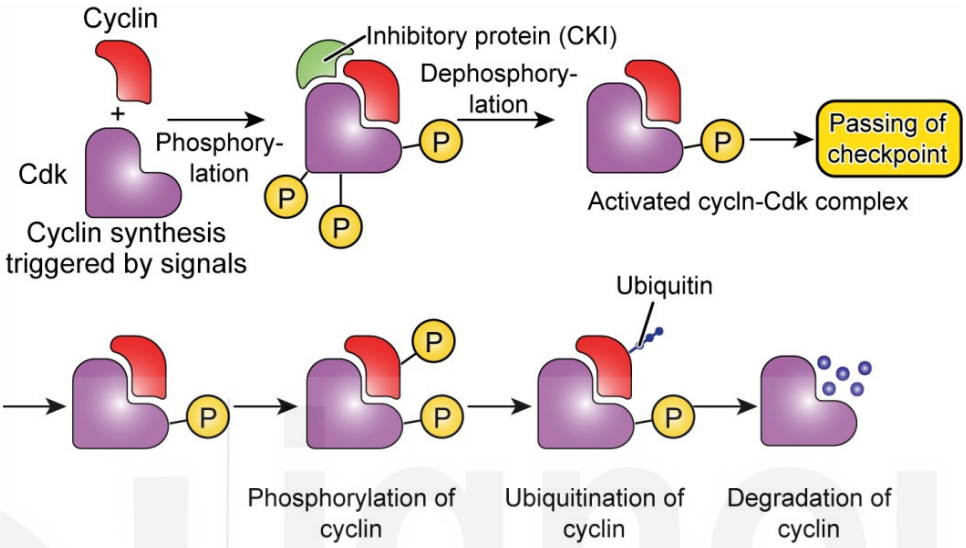


Fig. 8.6: Mechanism of formation of cyclin-CDK complex and regulation of cyclin-CDK activity.

In the **second level,** Cdks promote progression of cell cycle by phosphorylating substrates. Cyclin binding causes partial activation of Cdks, but complete activation also requires phosphorylation. The process of phosphorylation is catalyzed by an enzyme called *Cdk activating kinase* (CAK). CAK phosphorylates the Cdk subunit only after cyclin binding.

Third level of regulation involves inhibition of phosphorylation of tyrosine residue near the Cdk amino terminus. The reaction is catalyzed by enzyme *Wee1 protein kinase*. Phosphorylation of tyrosine 15 and threonine 14 inhibits Cdk1 and Cdk2. The inhibited Cdk's can be activated by dephosphorylation of these residues by protein *phosphatase* (Fig. 8.6).

Activities of Cdks are also controlled by the binding of inhibitory proteins called *cyclin dependent kinase* inhibitors (**CKIs**). Cyclin dependent kinase inhibitor is a protein that interacts with a cyclin-Cdk complex to block kinase activity, usually during G_1 or in response to signals from the environment or from damaged DNA. Two major CKI families of CKIs viz. INK4 and the CIP/KIP family have been identified in animal cells. During G_1, high levels of CKIs prevent cell cycle events from going out of order by letting transition to the Start checkpoint.

Box 8.2 : Important components of Cdk regulation

Cyclin-Dependent Protein Kinase (Cdks) - it is an enzyme that adds negatively charged phosphate groups to other molecules through the process of phosphorylation. The phosphorylation of Cdks signals the cell to enter the next stage of the cell cycle. These enzymes are dependent on cyclins (class of regulatory proteins). Binding of cyclins to Cdks phosphorylate other molecules activating them.

Cyclins - These are regulatory proteins that undergo a constant cycle of synthesis and degradation during cell division. They act as activating proteins. They bind to Cdks forming a cyclin-Cdk complex. This complex signals the cell to pass to the next cell cycle phase. Eventually, the cyclin degrades, deactivating the Cdk. Cyclins are of two types: mitotic cyclins and G_1 cyclins.

G_1 cyclins - G_1 cyclins bind to Cdk proteins during G_1. The binding leads to activation causing the signals of the cell to exit from G_1 and entry into S phase. Eventual degradation of cyclins deactivates the Cdk and leads to entry into S phase**.**

Mitotic Cyclins - Mitotic cyclins accumulate gradually during G_2. High concentratons of cyclins bind to Cdks. The resulting complex is known as Mitosis-promoting factor (MPF). This complex acts as the signal for the G_2 cell to enter mitosis. The degradation of cyclin activates the MPF.

Cyclin B - It is a member of the cyclin family. It is a mitotic cyclin. Cyclin B is necessary for the progression of the cells into and out of M phase of the cell cycle. Cyclin B binds to Cdk1 and the activity of the cyclin B-Cdk complex increases through the cell cycle until mitosis. Later concentration of cyclin falls abruptly due to degradation of cyclin B. The complex of Cdk and cyclin B is called maturation promoting factor or mitosis promoting factor (MPF).

You should remember the following important points before proceeding further

i) **START** is the check point in cell cycle after which once crossed, the cells are irreversibly committed to undergo a cell cycle.

ii) Cells do not proliferate in G_0 phase.

iii) G_1 is the longest and the most variable phase in cell cycle. It is the decision making phase

iv) In early G_1 no cyclin-Cdk's are active. They appear only in mid G_1, G_1/S phase where they activate gene transcription required for replication.

v) G_1 Cdk and G_1/S phase Cdk prepare cells for S phase

vi) S phase Cdk activates replication. Histone proteins are synthesized in S phase

vii) Bud in budding yeast emerges at the end of G_1 phase. G_2 is not well defined in yeast.

viii) Mitotic Cdk's induce mitosis.

SAQ 2

a) What is the role of check points in cell cycle regulation?

b) Give the full forms of the following abbreviations.

i) Cdc

ii) Cdk

iii) CKIs

SAQ 3

State whether these statements are 'True' or 'False'.

i) A point at which the progression of a cell to the next stage in the cell cycle goes smoothly is called as **checkpoint**.

ii) The checkpoints occur near the end of G_1, at the G_2/M transition, and during metaphase

iii) In the G_2/M checkpoint, cells in the G_1 phase ensure that cell has all the enzymes/nutrients necessary for the replication of DNA.

iv) Active Cyclin/Cdk complex stimulates build up of nuclear envelope.

v) Cyclin/Cdk complexes are *protein kinases* that act as a regulator of transition from M-phase.

8.4 MITOSIS

Mitosis is a cellular process in which chromosomal replication is followed by the equal division of the cell nuclei and other cell contents into two daughter cells. Mitosis is the step in the cell cycle in which newly duplicated DNA is separated and two new cells are formed with equal genetic material in them. Mitosis follows the G_2-phase of the interphase in the cell cycle. At the beginning of mitosis the nuclear envelope disorganizes and the chromosomes strongly condense by folding in a spiral manner around protein molecules. Mitosis has several distinct stages, or phases. These include prophase, metaphase, anaphase, and telophase.

Prophase

Prophase is the first stage of mitosis. Chromosomes are visible as thin threads accomplished by progressive coiling and folding. Each chromosome is composed of two **chromatids,** formed as a result of replication during the S phase of cell cycle. Chromatids are joined at the centromere. The two chromatids are usually twisted around each other. During prophase, the nucleolus breaks down and its components disperse throughout the nucleus. The mitotic spindle is formed which is an organized array of microtubules that move the chromosomes. In animal cells, the spindle grows out from a pair of centrosomes present at the opposite end of the cell. Each centrosome has a pair of centrioles composed of microtubules. In animals centriole is present, hence the cell division in animals is said to be **astral** or **amphiastral.** In contrast, in plants cell division is **anastral** (without centriole). At the end of prophase, the nuclear envelope breaks into fragments allowing the chromosomes to spread over the greater part of the cell.

Prometaphase (Metakinesis)

The disintegration of nuclear envelope marks the start of prometaphase. The chromosomes are freely floating in the cell. Spindle microtubules, which until now were outside the nucleus, enter the nuclear region. Microtubules are

made of tubulin protein. Tubulin is added and removed from the microtubule causing them to undergo a repeated cycle of growth and shrinkage respectively. When the microtubules encounter a kinetochore, they become stabilized. Each chromosome within the cell get attached to the microtubules arising from the opposite poles at the kinetochore of each sister chromatid. This arrangement is known as chromosome bi-orientation.

Kinetochore is a protein structure formed on a chromatid during cell division and allows attachment on a chromosome via spindle fiber. The pulls the chromatids apart and helps in cell division by making sure that each new cell has one chromatid from each pair. During the replication process, the two chromatids unite by way of a centromere (Fig. 8.7).

Kinetochores consist of three regions: an inner and outer region, as well as a fibrous corona (Fig. 8.7b).

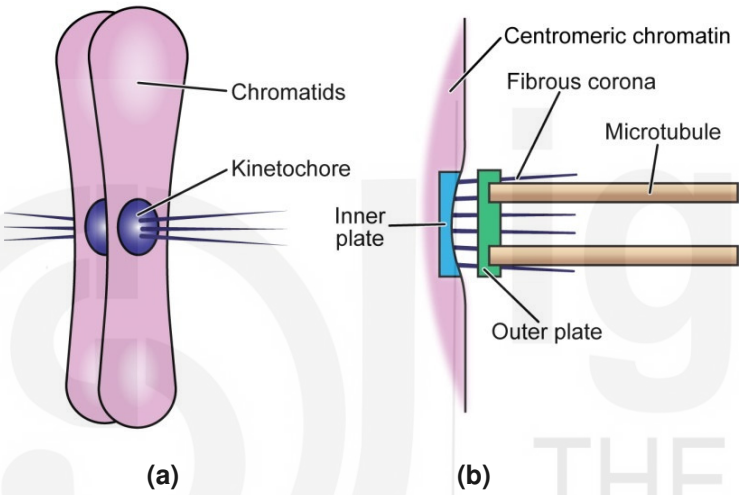


Fig. 8.7: a) Structure of a kinetochore; b) Structural details of kineochore.

Each region helps in the separation of the sister chromatids. Each chromatid receives its own kinetochore. The inner plate of the kinetochore is connected with the centromere, where it works closely with centromeric DNA. The centromere is where the sister chromatids connect and form a **chromosome.**

Metaphase

At metaphase the chromosomes are at their highest level of coiling and therefore, appear much shorter and thicker. Their morphology is unique at this stage which makes them ideal for cytotaxanomic studies. The chromatids are no longer twisted about each other but lie side by side attached at the undivided centromere (Fig. 8.8). In colchicines treated cells the chromatids are clearly visible as cross-shaped structures joined at centromere and are called as **c-pairs.** At metaphase, the chromosomes become arranged in a single plane on the equatorial/metaphase plate between the two centrosomes. Spindle assembly checkpoint ensures that each chromosome is aligned on the metaphase plate and attached to spindle fibers from opposite poles. When the spindle fibers get attached to the kinetochore plates on both sides of the chromosomes it creates a tension which is required to pass through the spindle assembly check point. If this tension is not generated in the chromosomes due to failure of spindle/microtubule, the cell does not progress to the next stage of cell cycle.

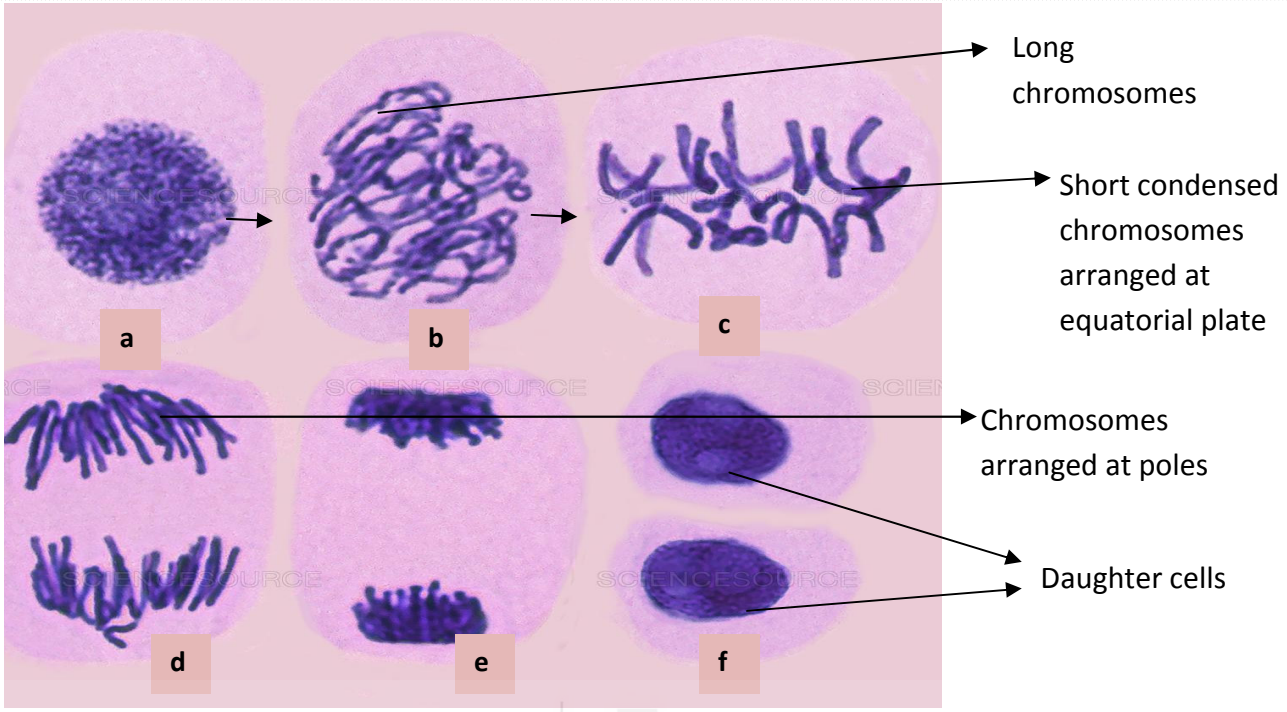


Fig. 8.8: Different stages of mitosis a) prophase, b) prometaphase, c) metaphase, d) anaphase, e) telophase, f) cytokinesis.

Anaphase

Anaphase is a stage of active and rapid movement and is the shortest of all mitotic stages. During this stage the spindle elongates and moves closer to the cell periphery. The anaphase movement of chromosomes is observed as a shortening of chromosomal spindle fibers. This results due to disassembly of tubulin molecules at kinetochore end (called + end) and the spindle end (called – end) of spindle fiber. The connection between the sister chromatids breaks down and the chromatids are pulled to the opposite poles (Fig. 8.9).

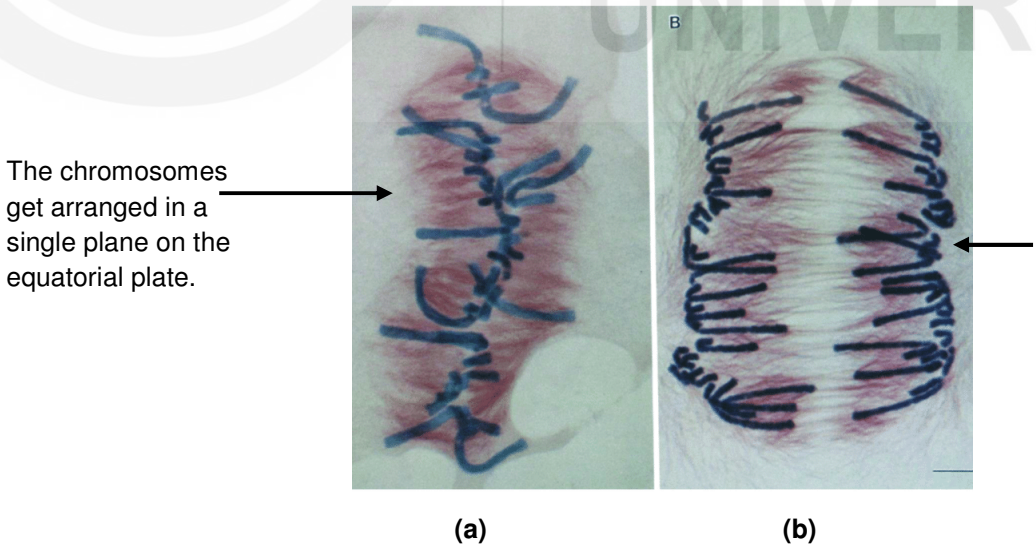


Fig. 8.9: An enlarged view of cell showing chromosomal arrangement during a) metaphase; and b) anaphase of mitosis.

This chromatid separation marks the beginning of anaphase. Special proteins called **molecular motors** disassemble tubulin molecules from the spindle and generate forces that pull the chromosomes toward the pole. Depending on the

position of centromere, the chromatids appear **V** shaped, **J** shaped, **L** shaped or **rod** shaped (Box 3). If a chromosome has two centromeres, it is called **dicentric**. The two centromeres move towards opposite poles forming a **dicentric anaphase bridge** that eventually tears apart somewhere between the two centromeres.

Telophase

Telophase usually begins when the chromosomes reach the opposite poles. The nuclear membrane reconstitutes around each set of chromosomes at the two poles forming two separate nuclei within the cell. The nucleolus reorganizes at the distinct site of nucleolus organizer chromosomes called **Nucleolus organizing region (NOR).** Chromosomes relax and lengthen. Hydration and uncoiling of the chromatin threads aid in the process of reforming an interphase nucleus where the chromosomes lose their density and stainability. In many cells, division of cytoplasm (cytokinesis) is simultaneous with telophase.

Importance of Mitosis

- Mitosis helps in vegetative growth in plants. It helps in increasing the cell number.
- Mitosis is also important in organisms which reproduce asexually: this is the only way that these cells can reproduce.
- One of the important functions of mitosis is repair. When an organism gets injured, its cells are damaged and these cells need to be replaced. Mitosis helps in renewal of cells.

SAQ 4

Enumerate the importance of mitosis.

Box 8.3 : Shapes of chromosomes

Each chromosome has a definite shape and size. The chromosomes are attached to the spindle by means of centromere. The position of the centromere in the chromosome determines its shape during the movement towards the poles. This is because the centromeres attached to the spindle fibres and moves while the arms are passively dragged.

Based on the position of centromere, the chromosomes are of different shapes:

Metacentric: Centromeres lies in the centre of the chromosome. The chromosomes appear V-shaped and two arms are equal in length.

Sub-metacentric: Chromosomes have arms of unequal length as the centromere lies a little far from the center. They appear J-shaped or L-shaped.

Acrocentric: Centromeres lie near one end and have a small arm beyond centromere.

Telocentric: The centromeres are located on one end on a rod like chromosomes.

In metaphase, each chromosome consists of two symmetrical, identical threads called chromatids, hence the chromosome appears V shaped while during anaphase chromosomes appear sub-metacentric i.e. 'L' shaped chromosomes (Fig. 8.10)**.**

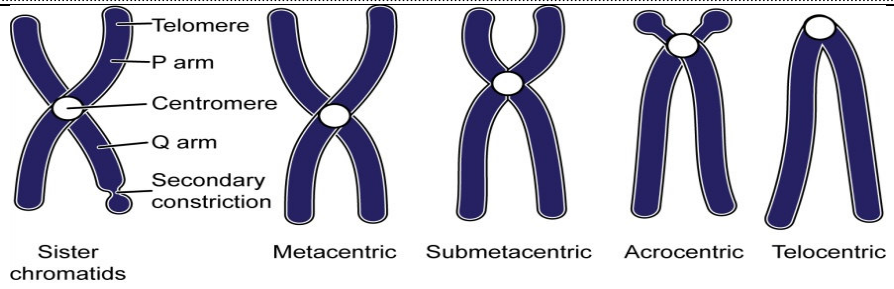


Fig. 8.10: Different shapes of chromosomes on the basis of position of centromere.

8.5 MEIOSIS (REDUCTION DIVISION)

Meiosis is the division that takes place in those organisms which have at least a diploid set of chromosome. It is not seen in haploids. During meiosis, several unique events take place that have important genetic consequences. It plays a key role in reproduction among eukaryotes. Without meiosis, organism would double their chromosome number every generation which would jeopardize the very existence of the organism.

Like mitosis, meiosis is also preceded by an interphase stage that includes G_1, S and G_2 phase. It is divided into two phases: meiosis I and meiosis II. The first division i.e. meiosis I is the reduction division, as the number of chromosomes at the two poles is reduced to half. The second division i.e. meiosis II is an equational division, very much similar to mitotic division.

8.5.1 Meiosis I

The first meiotic division is complicated and protracted. Each chromosome has two chromatids at the beginning of meiosis. The first stage of meiosis i.e. **prophase I** is the longest phase divided into five stages. Each stage is denoted by a Greek term which reflects the key features about the appearance or behavior of the chromosomes. These are: **leptotene or leptonema, zygotene/zygonema, pachytene/pachynema, diplotene/diplonema** and **diakinesis** (Fig. 8.11).

Leptotene

At leptonema stage the cell shows an increase in the volume of nucleus partly due to increased hydration level. Chromosomes appear as long thin threads. Individual chromosomes can barely be seen. Bead like structures called chromomeres are visible along the entire length of thin long chromosome. Each chromosome has two chromatids which are visible only with electron microscope. In some animals certain type of polarization has been observed in which the ends of the chromosome seem to be attached to the nuclear envelope at the site of centrosome. This has been referred to as the **bouquet stage**. It is believed that bouquet stage helps in homologue pairing of chromosomes. In plants similar kind of arrangement has been observed with chromosomes clumped into a dense knot called as **synizesis or synizetic knot.**

Zygotene

As condensation continues, the chromosomes become shorter and thicker and appeared darkly stained. Zygotene is primarily the stage of pairing of homologues. This pairing is envisioned as being in a zipper like fashion starting at any or even at several “contact points” along the chromosomes. Meiotic pairing of homologous chromosomes is remarkably precise. The phenomenon of chromosome pairing is called **synapsis** and is required for orderly separation of homologous chromosomes at later stage. A proteinaceous structure appearing as a tripartite ribbon found at site of synapsis called as **Synaptonemal Complex (SC).** It is composed of three parallel, electron dense elements that are separated by less dense areas. The two **lateral elements** seem to be composed of fibers that are slightly wider than 10nm (**synaptomeres**) (Fig. 8.11). These elements vary in structure between different stages of meiotic prophase I within a species. The **central element** is a ladder- like configuration in the center of SC. The **transverse elements** are electron-dense filaments that interconnect the central element with the lateral elements. Cytochemical studies have revealed lateral elements to be rich in DNA, RNA, and proteins, while the central element contains mainly RNA and proteins. Certain SC modifications have been observed at the cross over sites called as **recombination nodules (RN).** These structures are believed to play a key role during crossing over.

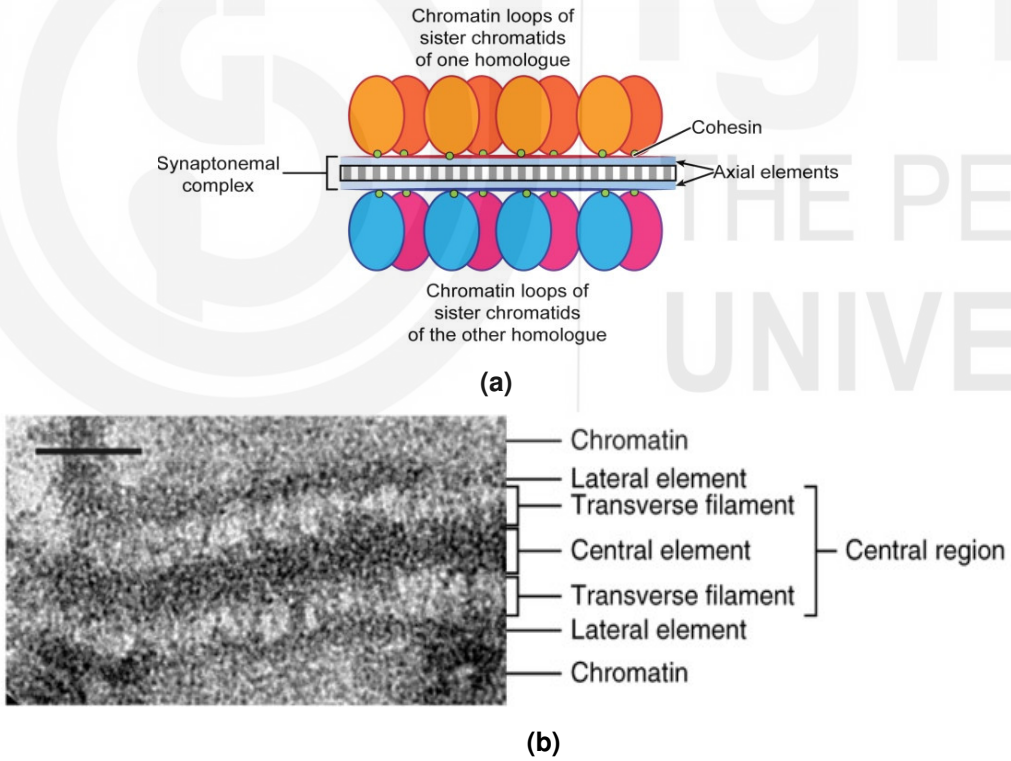


Fig. 8.11: a) Different zones of synaptonemal complex; b) Electron micrograph showing synaptonemal complex.

Pachytene

As synapsis progresses, the duplicated chromosomes continue to condense into smaller volumes. The thickened chromosomes are the characteristic feature of **pachynema**. At this stage paired chromosomes, also called **bivalents**, can easily be seen with a light microscope. In this stage, pairing of homologues is complete. Each chromosome in the bivalent has two sister

chromatids and hence also referred to as a **tetrad** of chromatids (Fig.8.12). During pachynema the chromosomes seem to exchange genetic material. Individual sister chromatids undergo breakage at certain sites followed by the exchange of broken fragments between chromatids within a tetrad. The breakage and reunion leads to recombination of genetic material which becomes clearly visible when cell enters the diplotene stage.

Diplotene

At this stage, the paired chromosomes begin to separate. However, they remain in close contact at the sites where crossing over has taken place. These contact points are called **chiasmata** (singular chiasma) which involve only two non sister of the four chromatids in the tetrad. This stage may last a very long time. The longer the chromosome the more chiasmata are present. As diplotene progresses, the chiasmata seems to move away from the centromere and diminish in number. This process is called **chiasma terminalization.** If terminalization is absent the chiasmata are called **localized**. During diplotene the bivalents are generally observed more distinctly because of a widening gap between them, which suggest a repulsion force, this is even more evident in the next substage diakinesis.

Diakinesis

The bivalents show the greatest degree of terminalization and contraction at this stage (Fig. 8.12). Bivalents may appear as rods, open rings or ring structures depending on the position and number of chiasmata formed. The nuclear membrane ruptures and the nucleoli, which generally fuse towards the end of prophase I forming one large nucleolus, disappear at this stage. The spindle fiber apparatus is not yet attached to the kinetochore. As a result bivalents appear scattered in the cell.

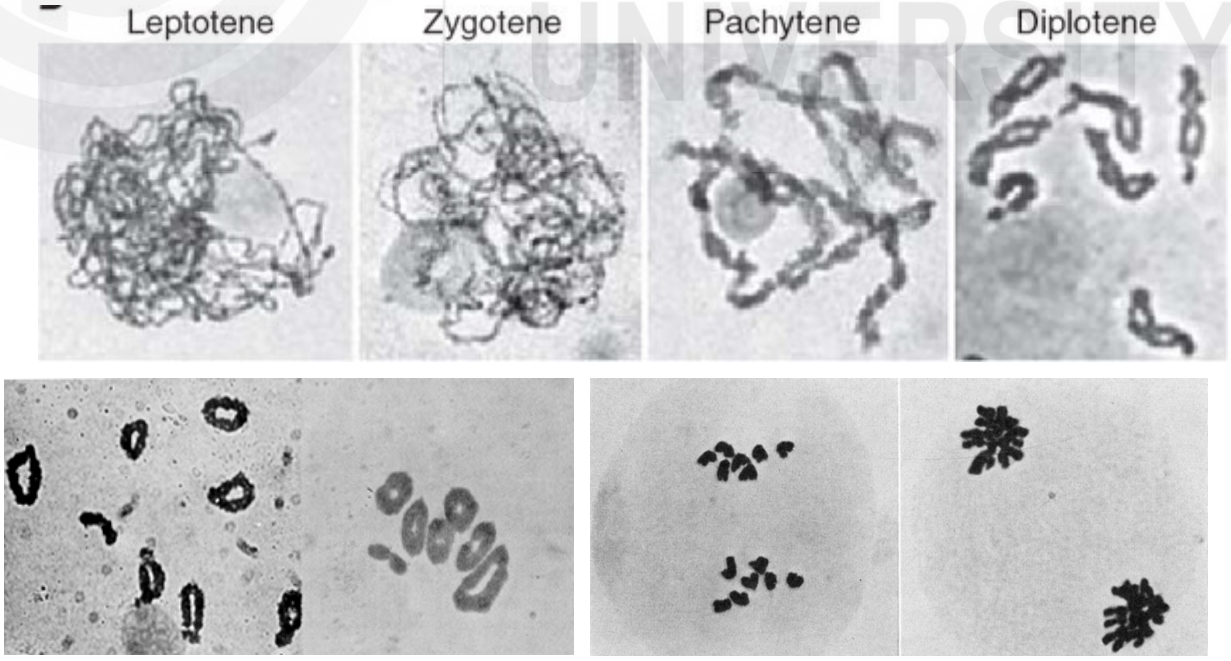


Fig. 8.12: Different stages of meiosis I. Leptotene, Zygotene, Pachytene, Diplotene, Diakinesis, Metaphase I, Anaphase I, Late Anaphase I.

Metaphase I

In this stage, the bivalents assemble at the equatorial plate with spindle fibers arising from the two poles attached to the kinetochore plate of each centromere facing the opposite poles. This orientation on the equatorial plate determines the meiotic segregation and distribution of the paternal and maternal chromosomes to the daughter cells of the first meiotic division. The chiasmata, that generally holds the two chromosomes together, slips towards the end. This terminalization of chiasmata is due to the growing repulsion between the members of each chromosome pair.

Anaphase I

During anaphase I, the tetrad chromosomes separate into dyad chromosomes as the co-oriented centromeres move toward the opposite poles. This separation called **chromosome disjunction** is mediated by the spindle apparatus acting on each of the bivalent in the cell. Each anaphase I dyad has two chromatids that remain joined at the centromere until anaphase II (Fig. 8.13).

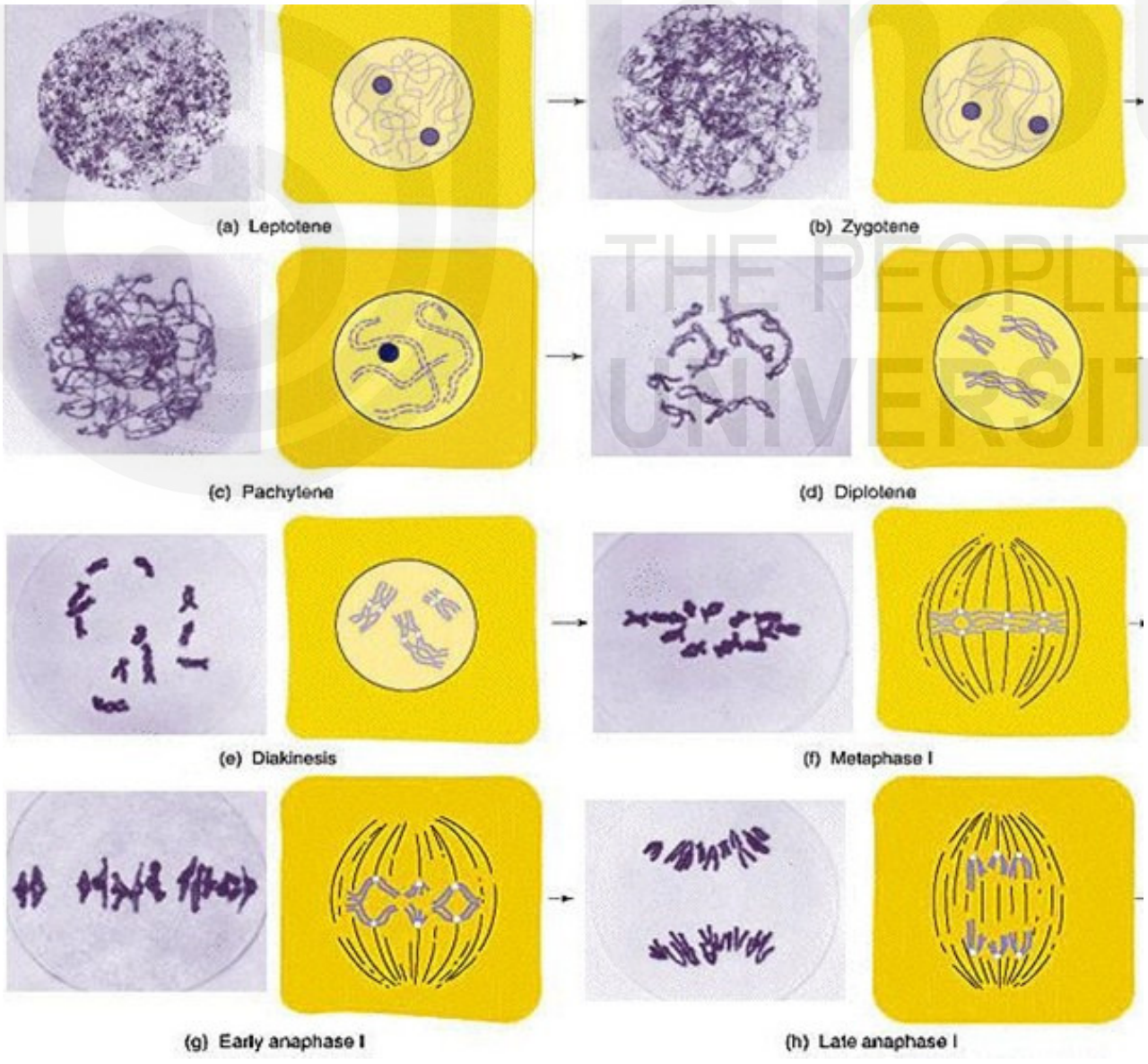


Fig 8.13: Various stages of meiosis I.

Telophase I

During telophase I, the chromosomes at the two poles decondense and a nuclear membrane reorganizes around them. The daughter cells get separated from each other by a membrane. The two daughter cells produced contain the haploid number of chromosomes. Each chromosome still has two chromatids which may not be genetically identical owing to the gene reshuffling that occurred due to crossing over during prophase I.

Telophase I is followed by interphase or **interkinesis** during which the chromosomes do not synthesize new DNA consequently there is no reduplication. The chromosomes are already prepared for the second division in which two chromatids only held together by a centromere. Therefore, despiralization, uncoiling, and hydration of chromosome are not necessary**.** In *Trillium* the chromosomes orient themselves at the poles and pass directly to the equatorial plate of second division (M II).

8.5.2 Meiosis II

Meiosis II is similar to a mitotic division. At **Prophase II** the chromosome condensation begins and the spindle is formed. At **prometaphase** II the nuclear envelope, which was formed during the telophase I stage, breaks down and the spindle organizes across the cell. Spindle fibers arising from the two poles get attached to the kinetochore plates of the centromeres facing each pole. At **metaphase II** the movement of the spindle microtubules aligns the chromosomes at the metaphase plate which is at right angle to the metaphase plate formed during meiosis I. During **Anaphase II** the centromeres split and the two sister chromatids separate and move to the opposite poles. Each separated chromatid is considered a full chromosome. The last stage is **telophase II** where chromosomes start decondensing and a nuclear envelope forms around each set of chromosomes and cytokinesis take place. After telophase II chromosomes continue decondensing, eventually becoming invisible under the light microscope (Fig. 8.14).

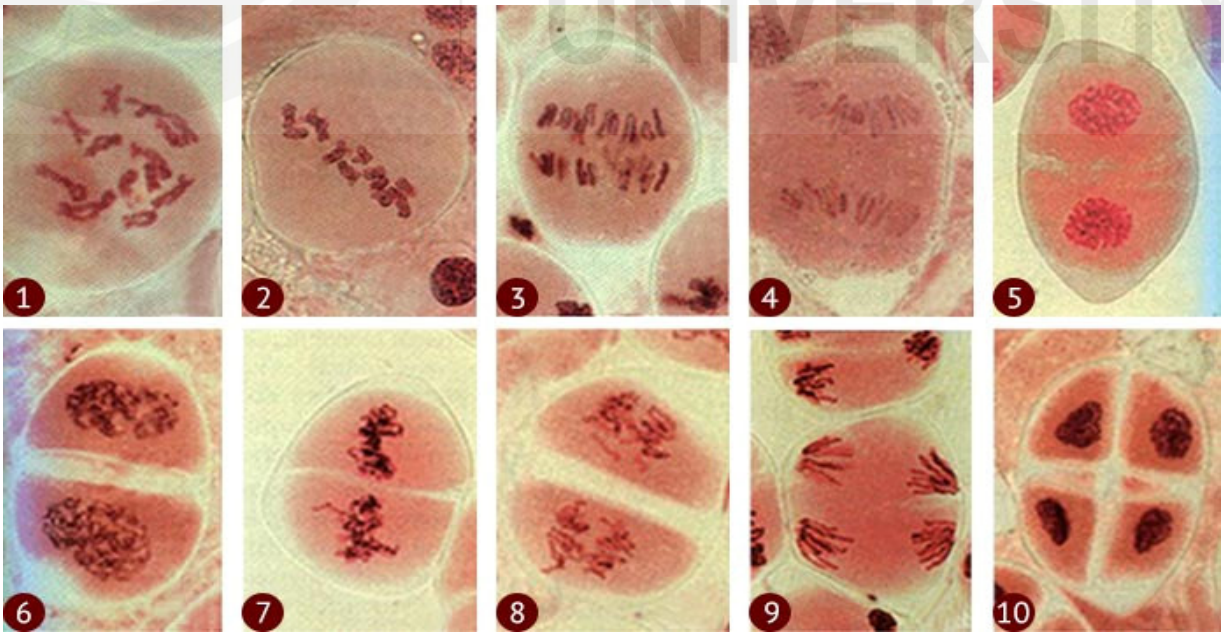


Fig. 8.14: Squash preparation of onion showing various stages of meiosis. 1. Prophase I, 2. Metaphase I, 3.Anaphase I, 4.Telophase I, 5. Cytokinesis I, 6. Prophase II, 7. Metaphase II, 8. Anaphase II, 9. Telophase II, 10. Cytokinesis II.

The end product of two meiotic divisions is four haploid cells arising from one diploid cell. The chromosomes in each cell/gamete are not the exact copy of the original/ parent chromosome due to crossing over.

Biological significance of meiosis

1. Meiosis helps to maintain a constant number of chromosomes by reducing the chromosome number in the gametes that is essential for sexual reproduction.
2. Meiosis helps in the formation of haploid gametes and spores for sexual reproduction.
3. Number of chromosome remains fixed in a species from generation to generation.
4. Crossing over brings genetic variations in offspring. Meiosis generates genetic diversity by shuffling genes across chromosomes followed by their random separation into gametes. Genetic variation is one of the key factors in evolutionary fitness and biological diversity. Meiosis generates genetic diversity when homologous chromosomes exchange parts by crossing over.
5. Failure of disjunction in meiosis leads mutation to the formation of polypoid forms.
6. The random distribution of maternal and paternal chromosomes takes place into daughter cells during meiosis and it is a sort of independent assortment which leads to variation.

SAQ 5

a) Answer in brief

i) Various stages of mitosis.

ii) What is synaptonemal complex (SC)?

iii) What is the role of nucleolus organizing region (NOR)?

iv) What are chiasmata?

v) What is metakinesis?

b) Answer in one word

i) Each chromosome is made of two units.

ii) A pair of centrioles in each centrosome is made up of

iii) The protein that forms the microtubules.

iv) At this stage of meiosis, chromosomes appear as long thin threads.

v) Meiosis II is similar to this type of division.

SAQ 6

Complete the statements

i) The chromosomes are attached to the spindle by means of …… .

ii) Homologous pairing of chromosomes is known as …….. .

iii) During anaphase, the spindle elongates and the centrioles/centrosomes …….. .

iv) The chromatids appear V shaped, J shaped, L shaped or rod shaped depending on the …… .

v) The stage at which the paired chromosomes remain in close contact at chiasmata and show crossing over is …….. .

8.6 SUMMARY

- The cell cycle represents various stages through which a cell passes from one cell division to the next. Every dividing cell passes through four phases which are a part of both mitotic as well as meiotic cell cycle.
- First three of these phases viz., G_1, S and G_2 are grouped under a broader phase, the interphase. The G_1 phase is the post-mitotic or pre-DNA synthesis phase (the phase following mitosis and preceding DNA replication). A cell would proceed to division once it has entered the S-phase or the DNA replication as it has already crossed the checkpoint in the G_1 phase. The G_2 or the post-DNA synthesis phase is characterized by the preparation for cell division, where the replication of organelles like mitochondria and plastids takes place. So calling the interphase as a resting phase is a misnomer, as in fact it is the most metabolically active phase.
- The M-phase or mitotic phase (meiotic phase in meiosis) involves the actual division of the cell. M-phase comprises mitosis and cytokinesis. Different phases of cell cycle vary in their time duration in different organism, and even different tissues within the same organism.
- There is a series of regulatory proteins and factors which function as checkpoints during the cell cycle. These signals determine whether the division should proceed or stop. Cyclins and *Cyclin-dependent kinases* (Cdks) are considered to act as key molecules along with some cytoplasmic signals in the regulation machinery of cell cycle.
- Mitosis is meant for multiplication of cells and is necessary for their maintenance, growth, and repair. This ensures the continuity of life. Mitosis also ensures that two daughter nuclei receive a complete and equivalent complement of genetic material. The two daughter cells are quantitatively and qualitatively identical to each other as well as to their parent cell. Mitosis is divided into prophase, prometaphase, metaphase, anaphase, and telophase.

- Interestingly the pattern of cytokinesis is different in plant and animal cells. In animals, the division of the cytoplasm into two daughter cells occurs by constriction or a cleavage furrow, plant cells divide by the formation of cell plate.
- Meiosis or reduction division is a process that results in reduction in the number of chromosomes by half in the gametes or sex cells. Meiosis comprises two sequential nuclear divisions, producing haploid daughter nuclei that contain only one member of each pair of homologous chromosomes. The reduction division can take place at different stages in the life cycle, depending on the type of organism, viz., during formation of gametes (gametic), in the zygote (zygotic), or at the time of spore formation (intermediate or sporogenic). To ensure that each daughter nucleus has only one set of homologues, an elaborate process of chromosome pairing occurs during meiotic prophase I that is accompanied by the formation of a proteinaceous, ladder like structure called the synaptonemal complex (SC). This helps in the genetic recombination between the homologous chromosomes to form chromosomes with new combinations of maternal and paternal alleles.

8.7 TERMINAL QUESTIONS

1. What are the different checkpoints recognized by cell during its division cycle?
2. Discuss the role of Cdk's during cell cycle progression.
3. Why is Meiosis II similar to a mitotic division? Explain.
4. Explain the various stages of Meiosis I with the help of well labelled diagram.
5. Why is meiosis considered as reductional division?

8.8 ANSWERS

Self-Assessment Questions

1. a) i) meiosis
   ii) equational division
   iii) four
   iv) G_1, S, and G_2
   v) Interphase

   b) i) Synthetic phase – This phase occupies about 35-45% of the entire cell cycle. In this phase important events like DNA replication and formation of histone proteins take place.

   ii) Mitotic phase – This is the most crucial phase of the entire cycle. In this phase, the cell divides to form identical daughter cells.

iii) Quiescent stage – In this stage, cell is in its quiescent or resting phase. It does not divide or grow. Cells remain metabolically active but do not proliferate.

2. a) Checkpoints are surveillance mechanisms that stop the progress of cycle if 1) any of the chromosomal DNA is damaged, and 2) critical process like DNA synthesis during S phase or chromosome alignment during M phase have not been properly completed. The checkpoints ensure that each of the various events that make up the cell cycle occurs accurately and in proper order.

   b) i) cell division cycle

   ii) Cyclin dependent protein kinase

   iii) cyclin dependent kinase inhibitors.

3. i) False; ii) True; iii) False; iv) False; v) True

4. Refer to Section 8.4

5. a) i) prophase, prometaphase, metaphase, anaphase and telophase.

   ii) A proteinaceous structure, appearing as a tripartite ribbon has been observed at the site of synapsis during zygotene stage of called as synaptonemal complex (SC).

   iii) Refer to section 8.4.

   iv) Refer to section 8.5.1.

   v) Refer to section 8.4.

   b) i) chromatids

   ii) microtubules

   iii) tubulin

   iv) leptotene

   v) mitotic division

6. i) centromere.

   ii) synapsis

   iii) move closer to the cell periphery.

   iv) position of centromere,

   v) diplotene

Terminal Questions

1. Refer to Subsection 8.3.1
2. Refer to Subsection 8.3.3
3. Refer to Subsection 8.5.2

4. Refer to Subsection 8.5.1

5. Refer to Section 8.5

Acknowledgements for Figures

Fig. 8.8 : Source: https://www.google.co.in/imgres?imgurl=https%3A%2F%2Fmedia.sciencephoto.com%2Fimage%2Fc0225100%2F800wm&imgrefurl=https%3A%2F%2Fwww.sciencephoto.com%2Fmedia%2F623749%2Fview%2Fplant-cell-mitosis-light-micrograph

Fig. 8.9 : Source: https://www.google.co.in/imgres?imgurl=https%3A%2F%2Fwww.researchgate.net%2Fpublication%2F313834705%2Ffigure%2Ffig2%2FAS%3A620084141764610%40152485098898 2%2FLight-micrographs-of-metaphase-a-and-late-anaphase-b-plant-endosperm-Haemanthus.png&imgrefurl

Fig. 8.11b : Source: https://www.google.co.in/imgres?imgurl=https%3A%2F%2Fmedia.springernature.com%2Fm685%2Fspringer-static%2Fimage%2Fart%253A10.1038%252Fnsmb.3208%2FMediaObjects%2F41594_2016_Article_BFnsmb3208_Fig1_HTML.jpg&imgrefurl=http

Fig. 8.12 : Source: https://www.google.co.in/imgres?imgurl=https%3A%2F%2Fmedia.springernature.com%2Ffull%2Fspringer-static%2Fimage%2Fart%253A10.1007%

Fig.8.13 : Source: https://www.google.co.in/imgres?imgurl=http%3A%2F%2Fwww.cas.muohio.edu%2F~wilsonkg%2Fold%2Fgene2005%2Fimages%2Ffig3p2.jpg&imgrefurl

Fig.8.14 : Source: https://www.google.co.in/imgres?imgurl=https%3A%2F%2Fopenoregon.pressbooks.pub%2Fapp%2Fuploads%2Fsites%2F12%2F2016%2F06%2F08.mitosisinonionmicroscope

Suggested videos for watching

https://www.youtube.com/watch?v=DwAFZb8juMQ

https://www.youtube.com/watch?v=7NM-UWFHG18

https://www.youtube.com/watch?v=ofjyw7ARP1c

https://www.youtube.com/watch?v=VLJF8Pf8spw

https://www.youtube.com/watch?v=Jmqd9Qj_PTA

GLOSSARY

Aberrations : Deviation from the normal type

Acceleration : The rate at which something moves more quickly or faster

Achromatic : Transmit light without separating it into constituent colours

Analyte : Substance that is separated by chromatography

Apochromatic : Free from chromatic aberration

***ATP synthase* dimer** : A structure of mitochondrial enzyme *ATP synthase* in which edges of the inner membrane cristae is folded to form rows of V-shaped *dimers*

Birefringent : Structure having two different refractive indices

Chromatogram : A visual record showing various components of a compound separated by chromatography

Cuvette : A clear container for holding liquid samples in a spectrophotometer

Detector : A device or instrument used to detect the presence of a particular substance.

Diagnostics : Act of identifying a disease from its signs and symptoms

Diffracted : Bending and spreading of a wave around the edge of an object

Discrete : Individually separate and distinct.

Electrolyte : A liquid which contains ions

Eluate : Solution having solvent and dissolved matter resulting from elution

Eluent : Solvent used for eluting a substance

Endocytosis : The process of taking in of matter by a living cell by invagination of its membrane to form a vacuole

Endosymbiosis : Symbiosis where one of the symbiotic organisms lives inside the other

Extrinsic : Coming from outside

Fidelity : The degree of exactness with which something is copied or reproduced

Fluoresce : Shine or glow due to fluorescence

Forensic : Test or technique used in detection of crime

Freon : A group of chlorofluorocarbons used as aerosol propellants, refrigerants

Genome : Complete set of genes or genetic material present in a cell or organism

Homoeostasis : Tendency of a system to remain in equilibrium or maintain internal stability and resist change

Homogenize : The act of making something uniform in composition

Immersed : Dipped or submerged in a liquid

Inert : Chemically inactive

Intrinsic : Present within a structure

Isoelectric focusing : A technique for separating different molecules on the basis of differences in their isoelectric point

Isoelectric point : The pH at which a molecule carries no net electrical charge

Ligand : An ion or molecule that binds to a central atom to form a coordination complex

Miniscule : Very small

Monastery : A house or place occupied by a community of persons, especially monks

Osmiophilic : Having an affinity for or staining readily with osmic acid or osmium tetroxide

Osmiophobic : Having no affinity for or staining with osmic acid or osmium tetroxide

Pulse field electrophoresis : A technique used for the separation of large molecules by applying to a gel matrix an electric field that periodically changes direction

Replica : An exact copy or model of something

***Sieving* effect** : Movement of molecules (DNA or protein) through the gel matrix based mostly on the molecular weight and shape

Spokes : A set of radial handles projecting from a wheel.

Synapses : Points in the nervous system at which a signal passes from one nerve cell to another

Synchrotron : An apparatus for imparting very high speeds to charged particles by means of a combination of a high-frequency electric field and a low-frequency magnetic field

Transient : Lasting only for a short time (short duration)

Vesiculation : Formation of vesicles or making a structure vesicular

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