6. **Skeletal Muscle Contraction:** The sarcoplasmic reticulum in skeletal muscle cells release Ca2+ ions to cause contraction and absorbs Ca2+ ions to bring about relaxation.
7. **Fat Oxidation:** The SER membranes carry out the initial reactions in the oxidation of fats.

(B) Functions of rough endoplasmic reticulum:

1. **Surface for Ribosomes:** The RER provides a large surface for the attachment of ribosomes.
2. **Surface for synthesis:** The RER offers extensive surface on which protein synthesis can be conveniently carried on by ribosomes. The newly formed proteins may enter the ER membranes, becoming a part of the membrane structure or pass into the ER lumen. The proteins becoming a part of ER membrane eventually move from the ER via membranes of other cell organelles, namely Golgi apparatus, secretary vesicles to become permanent plasma membrane proteins. The proteins entering ER lumen are packed for export.
3. **Packaging:** The proteins in ER lumen are processed and get enclosed in spherical membrane bound vesicles which get pinch off from the ER. These vesicles have various fates. Some remain in the cytoplasm as storage vesicles while others migrate to the plasma membrane and expel their contents by exocytosis. Some fuse with Golgiapparatus for further processing of their proteins for storage or release from the cell (Figure 20).

4. **Smooth ER Formation:** The RER gives rise to the smooth ER by loss of ribosomes.
5. **Formation of Nuclear Envelope:** The RER forms nuclear envelope around daughter cells in cell division.
6. **Formation of Glycoproteins:** The process of linking sugars to proteins to form glycoproteins starts in the RER and is completed in Golgi apparatus.
1. **Location of Enzymes:** A variety of enzymes is located in the ER membranes tocatalyze the biochemical reactions.

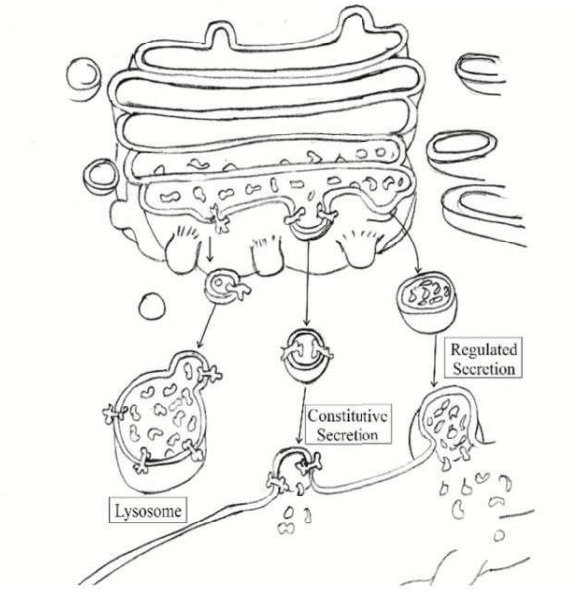

Figure 20: Transport of proteins from Golgi apparatus. Proteins are sorted and transformed in Golginetwork and transported in vesicles to their final destination.

RIBOSOMES

George E. Palade (1953) was the first to observe dense particles or granules in animal cells under electron microscope. These were thus called as Palade's Particles. Later Richard B. Roberts named them "ribosomes" in 1958. Tissieres and J.D. Watson (1958) isolated ribosomes from E. coli for the first time. It was shown that ribosomes contain approximately equal amount of RNA and proteins

Structure of Ribosome:

Ribosomes are of two types **70S and 80S. 'S'** is **Svedberg unit**, a measure of particle size dependent on the speed with which the particles sediment in the ultracentrifuge. The **70S** ribosomes are found in the **prokaryotic cells** and in the **mitochondria and plastids** of eukaryotic cells. The **80S** ribosomes occur in the cytoplasm of the eukaryotic cells. Both the 70S and 80S ribosomes are similar in structure. They are small, spherical structures of which 70S ribosomes are around 200Å in diameter, while 80S are 250 to 300Å in diameter. They are porous and hydrated having two subunits, one is larger (140-160Å in diameter) having dome shaped structure and the other is smaller in size, found over the larger subunit, forming a cap like structure. The two subunits are separated by clefts (Palade and Kuff, 1966). **Membrane is absent around them**. The subunits occur separately in the cytoplasm, and join to form ribosomes only at the time of protein synthesis. Many ribosomes line up and join the mRNA chain. After the synthesis of protein, the ribosomes leave the mRNA chain and dissociate into subunits.

Functions of Ribosome:

1. **Attached Ribosomes:** The ribosomes provide space and enzymes for the synthesis of proteins in the cell. The ribosomes bound to the ER membranes synthesize:
   (i) integral proteins for cellular membranes.
   (ii) lysosomal proteins.
   (iii) secretary proteins for export as secretions.
2. **Free Ribosomes:** The free ribosomes produce structural and enzymatic proteins for use in the cell itself. These proteins include glycolytic enzymes and most extrinsic membrane proteins, such as spectrin.

GOLOGI APPARATUS

History: Camillo Golgi in 1898 discovered the Golgi apparatus in the nerve cells of barn owl and cat by metallic impregnation method. After it's discoverer's name, the Golgi apparatushas been variously named as Golgisome, Golgi material, Golgi membranes, Golgi body, etc.

Structure of Golgi Bodies (Figure 21):

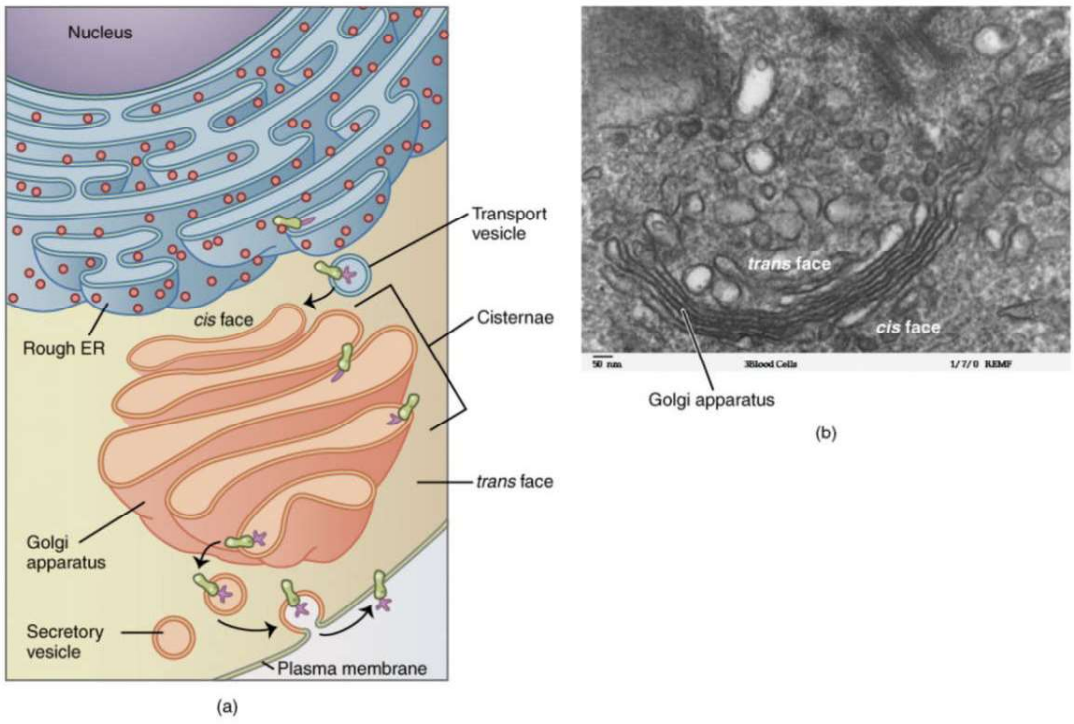

Figure 21: Golgi Apparatus. (a) The Golgi apparatus manipulates products from the rough ER, and produces new organelles called lysosomes. (b) An electron micrograph of the Golgi apparatus.

Golgi bodies varies in size and form in different types of cells, but they have similar organization in all kinds of cells. For example, it is well developed in secretory and nerve cells, but is rather small in muscle cells. Golgi bodies are compiled as a central stack (pile) of flattened sacs or cisternae and many peripheral tubules and vesicles.

1. **Cisternae:** The cisternae vary in number from 3 to 7 in most animal cells and from 10to 24 in plant cells. They are usually equally spaced in pile so that they are nearly parallel to one another, having 200-300Å wide inter-cisternal spaces containing alayer of parallel fibers called inter-cisternal elements. These support the cisternae and maintain regular spacing between them. The cisternae may be flat, but are often curved, having a distinct polarity with a convex face towards the cell membrane and concave face towards the nucleus. They are free of ribosomes and have swollen ends. They look like the smooth endoplasmic reticulum and are continuous with it at certainplaces.
2. **Tubules:** Short tubules arise from the periphery of the cisternae. Some of these enlarge at their ends to form vesicles.
3. **Vesicles:** The vesicles lie near the ends and concave surface of the Golgi complex. They are pinched off from the tubules of the cisternae. They are of three types: transitional, smooth or secretary and coated vesicles
   a. **Transitional Vesicles:** These are the small outgrowths formed from the transitional ER. They migrate to, converge and coalesce to cis face of Golgi, where they form new cisternae.
   b. **Smooth Vesicles:** These have smooth surface and contain secretions of the cell and so they are also called secretary vesicles. They arise from the ends of the cisternae tubules.
   c. **Coated vesicles:** These have rough surface, and they also arise from the cisternae tubules. They play a role in intracellular traffic of secretary protein molecules.

The Golgi complex has 3 functional regions: cis region that lies nearest the ER, medial region in the middle, and Tran's region with trans Golgi reticulum nearest to the plasma membrane. These regions have different enzymes which introduce different modifications to secretary and membrane proteins passing through them. The principal modification is glycosylation, i.e., addition of sugars to proteins, forming glycoproteins. Glycosylation starts in the ER and is completed in the Golgi complex. Modification of proteins in the Golgi apparatus also involves addition of lipids, forming lipoproteins (liposylation), and even the addition of other groups (Figure 22).

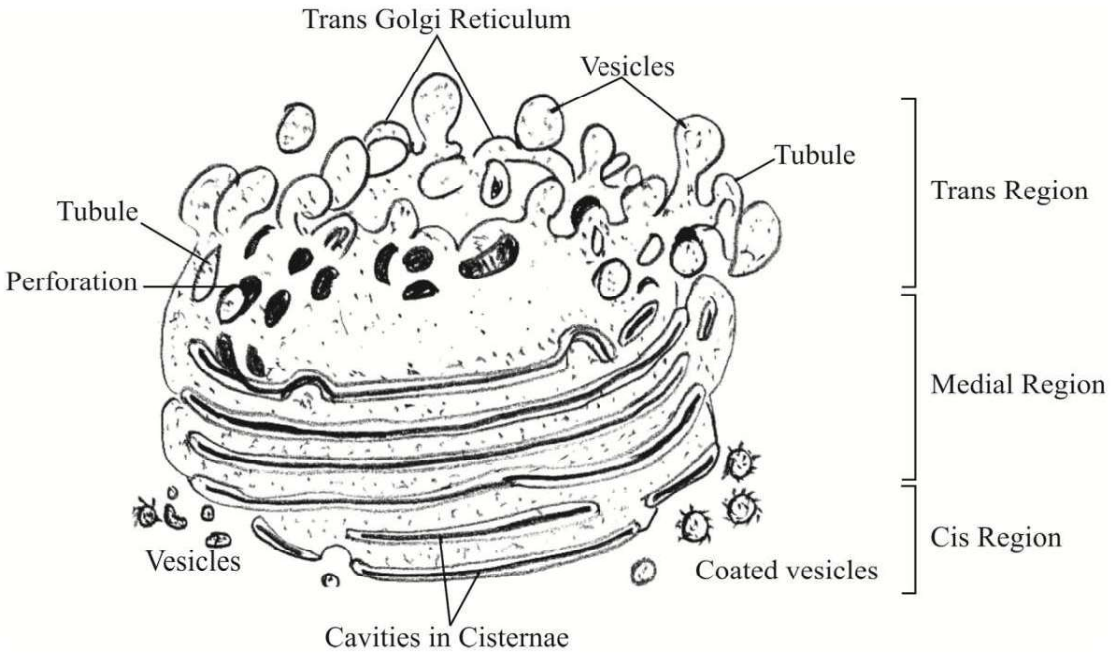

Figure 22: Thee-dimensional view of Golgi apparatus

Functions of Golgi Bodies:

1. **Formation of secretary vesicles:** The Golgi complex processes and packagesproteins and lipids coming from the ER for transport to other parts of the cell or out of the cell. Packaging involves

wrapping the materials by a membrane, forming secretary vesicles. The materials so packed includes zymogen in pancreatic cells, mucus in goblet cells, lactoprotein in mammary gland cells, pigment granules in pigment cells, collagen in connective tissue cells, hormones in endocrine cells, etc.

2. **Synthesis of carbohydrates:** The Golgi apparatus synthesizes certain mucopolysaccharides from simple sugars.
3. **Formation of Glycoproteins:** The Golgi apparatus links the sugars with proteins coming from rough ER to form glycoproteins.
4. **Formation of Lipoproteins**: Lipids and proteins coming from the ER are complexed into lipoproteins in the Golgi apparatus.
5. **Addition to Cell Membrane:** The Golgi apparatus provides membrane material for the plasma membrane in pinocytotic and phagocytotic vesicles and for the formation of cleavage furrow during the division of animal cells. The transfer of membrane from the ER via transition vesicles, Golgi complex and secretary vesicles to the plasma membrane is called membrane flow.
6. **Membrane Transformation:** The Golgi apparatus changes one type of membrane into another type. Membranes are gradually modified from the ER type to one with characteristics of the plasma membrane as they shift through the Golgi complex.
7. **Formation of cell wall:** In some algae, cellulose plates for cell wall is synthesized in Golgi complex. In higher plants the Golgi complex (a) synthesizes pectin and some carbohydrates necessary for the formation of cell wall and (b) produces some secretions such as mucilage, gums, etc.

8. **Formation of lysosomes:** The Golgi complex gives rise to primary lysosomes by budding. The lysosomes may also arise from ER.
9. **Acrosome Formation**: The Golgi complex gives rise to the acrosome in a sperm.
10. **Formation of Yolk and Cortical Granules**: The Golgi complex produces yolk and cortical granules in the eggs. Formation of yolk is called vitellogenesis.
11. **Formation of Nematocysts and Trichocysts**: The Golgi apparatus gives rise to the nematocysts in Hydra and perhaps also in other coelenterates, and trichocysts in ciliates such as Paramecium.
12. **Storage of Secretions:** The Golgi complex stores cell secretions such as proteins and lipids.
13. **Absorption of Materials:** Golgi apparatus absorbs materials from the environment. For example, cells of the intestinal lining use Golgi apparatus to absorb lipids from the intestine.
14. **Location of Enzymes:** A variety of enzymes is localized in the Golgi complex to helpin the cell's biochemical reactions.

LYSOSOMES AND PEROXISOMES

History: Lysosome is an organelle which unlike other organelles, first became known through the biochemical studies and thereafter their morphological identifications were made. Christian de Duve, a Belgian cytologist and biochemist, in 1955 reported the presence of lysosomes in the cells by biochemical studies. Later on, Novikoff in 1956 observed these lysosomes as distinct cell organelles with the help of electron microscope.

Structure of Lysosomes:

Lysosomes (Figure 23) are round tiny bags filled with dense material rich in acid phosphatase (tissue dissolving enzymes) and other hydrolytic enzymes. They consist of two parts: (i) limiting membrane and (ii) inner dense mass.

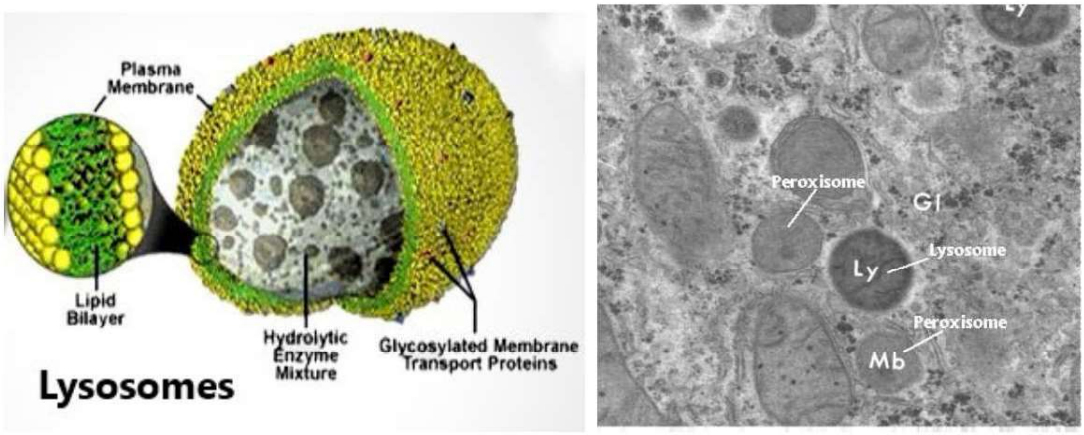

Figure 23: The structure of lysosomes

I- **Limiting membrane:** This membrane is single and is composed of lipoprotein Chemical structure is homologous with unit membrane of plasmalemma, consisting ofbimolecular layer.

II- **Inner dense mass:** This enclosed mass may be solid or of very dense contents. Some lysosomes have a very dense outer zone and a less dense inner zone. Some others have cavities or vacuoles within the inner granular material. Lysosomes are of varioustypes, and they help in intracellular digestion. Their contents vary with the stage of digestion.

Chemical Nature of Lysosomes:

Chemically lysosomes are defined as a body rich in acid hydrolases. Acid phosphatase has been found in many cells of plant roots, fungi, liver, kidney, and endocrine glands. The lysosomal enzymes can break down all major biological macromolecules present in the cells or entering the cells from outside into their building block subunits by adding water. The common enzymes in the lysosomes are proteases, nucleases (deoxyribonuclease and ribonuclease), glycosidase, lipases, sulphatases and phosphatase, which hydrolyses proteins, nucleic acids, polysaccharides, lipids, organic sulphatases and organic phosphates respectively.

Kinds of Lysosomes:

There are four types of lysosomes: primary, secondary, residual bodies and cyto-lysosome or autophagosome.

1. **Primary Lysosome (storage granules):** It is a small sac like body. Its enzymatic contents are synthesized by ribosomes and accumulated in ER. From there, they enter the Golgi region, where acid phosphatase reaction takes place. The GERL region, i.e., acid

phosphatase rich region of Golgi maturing face is thought to be involved in the production of lysosomes. The primary lysosome comprises only one type of enzymeor another.

2. **Secondary Lysosome (digestive vacuole or heterophagosome)**: These are produced either from phagocytosis or pinocytosis of foreign material by the cell. Actually, within the cell, after phagocytosis or pinocytosis, the foreign bodies or extra-cellular substances are enclosed within the membrane and these membranes bound structures are known as **phagosome or pinosomes.** These ultimately fuse with primary lysosomes, thus forming secondary lysosome. This body having engulfed material within membrane has also full complements of acid hydrolases (hydrolytic enzymes). The digested material of these lysosomes passes through the lysosomal membrane and is incorporated into the cell so that they may be reused in metabolic pathways.

3. **Residual bodies:** These are formed in case the digestion is incomplete. In some cells, such as Amoeba and other protozoa, these residual bodies are eliminated by defecation. Hence, lysosomes **having undigested material or debris** are called residual bodies. These bodies are formed due to lack of certain enzymes in lysosomes. These are rejected from the cell by exocytosis and some time in certain cells these bodies remain in cells for long time causing ageing. These residual bodies also cause diseases in man such as **fever, hepatitis, polynephritis, hypertension, congested heart failure** etc. If the debris which is mostly lipid in nature may

accumulate and condense into concentric lamella, it forms myelin (Figure 24).

4. **Autophagic vacuole (cytolysosome or autophagosome):** In this case, the lysosome **digests a part of cell** (e.g., mitochondria or portion of ER) by the process of autophagy. For example, liver cell shows numerous autophagosome during starvation among which remnants of mitochondria occur. This is a mechanism by which the cell can achieve degradation of its own constituents without irreparable damage.

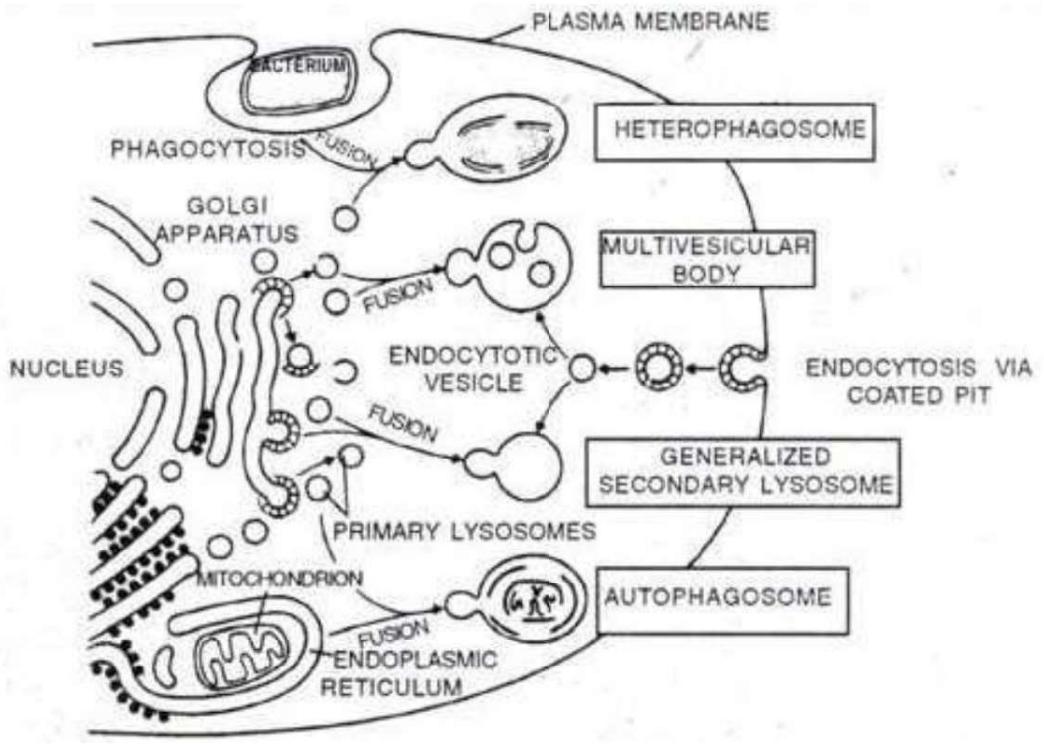

Figure 24: Formation of lysosomes and intracellular digestion in them.

Functions of Lysosomes:

1. **Digestion of useful materials:** Intracellular digestion is a regular feature in protozoans and in lower invertebrates such as sponges and coelenterates. In thisprocess the organic substances (food particles) taken up by the cells in vacuoles (pinosomes or phagosome) from the environment are digested.
2. **Digestion of harmful materials*:*** The foreign particles, such as viruses, bacteria, and toxic molecules, are disposed of by hydrolyzing them in certain leucocytes and macrophages. This is called natural defense of the body. This activity of lysosomes is characteristic of higher animals.
3. **Digestion of unwanted materials:** The dead cells and debris that accumulate at the sites of injury are destroyed in some white blood cells. This is called natural scavenging of the body.
4. **Renewal of cells and organelles:** The old worn-out cells and cell organelles are broken down to make the component molecules available for formation of new cells. and cell organelles. Thus, the lysosomes facilitate the turn-over of cells in normal tissues and of organelles in normal cells.
5. **Feeding of starving animals*:*** Food to a starving animal is provided by digesting the stored food materials (proteins, lipids, and glycogen) and even the cells. This is called autophagy.
6. **Autolysis*:*** Autolysis caused by the lysosomal enzymes plays a role in normal developmental changes in both animals and plants. E.g.,

in the breakdown and absorption of tail during the metamorphosis of frog's tadpole. In autolysis, lysosome membrane ruptures and releases the enzymes into the surrounding cytoplasm. This kills and lyses the cell.

7. **Aid in fertilization:** The lysosome of sperms releases their enzymes to dissolve the egg membranes for the entry of the sperm into the ovum in fertilization. This is called extracellular digestion.

PEROXISOMES

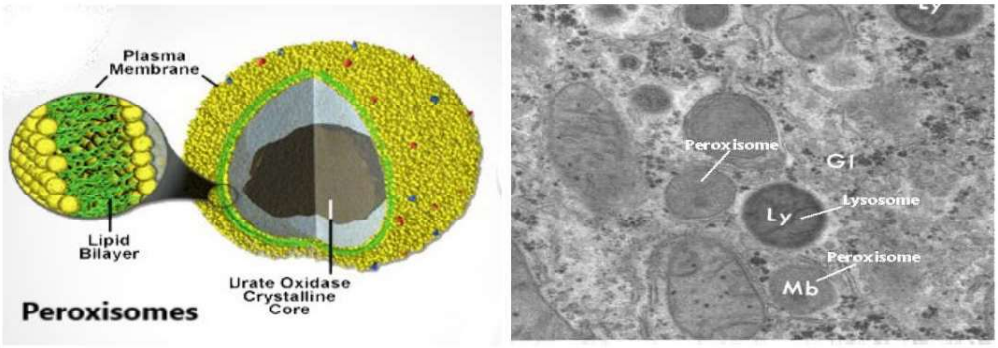

Figure 25: Structure of peroxisomes

Peroxisomes (Figure 25) are among the simplest of the subcellular organelles that are characteristic of all eukaryotic cells. With , 60 known enzymes in the matrix and ,45 documented integral or peripheral membrane proteins, it is a reasonable guess that this organelle has only , 125 proteins, which makes it much less complex than other organelles. The peroxisome derives its name from the fact that many metabolic enzymes that generate hydrogen peroxide as a by-product are sequestered here because peroxides are toxic to cells. Within peroxisomes, hydrogen peroxide is degraded by the enzyme, catalase, to water and oxygen.

Peroxisomes are surrounded by a single membrane, and they range in diameter from 0.1 to 1 mm. They exist either in the form of a network of interconnected tubules (peroxisome reticulum), as in liver cells, or as individual micro peroxisomes in other cells such as tissue culture fibroblasts. Peroxisome-Like Organelles Peroxisomes are related to specialized peroxisomes called glycosomes in parasites such as Trypanosomes, and to plant glyoxysomes, but are unrelated to hydro-genosomes, mitochondria, and chloroplasts. Collectively, peroxisomes, glyoxysomes, and glycosomes are also referred to as microbodies.

Peroxisome Distribution and Origin:

Peroxisomes exist in all eukaryotes from single- and multi- cellular microorganisms, to plants and animals. Unlike mitochondria, nuclei, and chloroplasts, peroxisomes have no DNA. Consequently, all their proteins are encoded by nuclear genes. They are proposed to have originated from endosymbionts that subsequently lost their DNA, but the evidence for an endosymbiont origin is much weaker than it is for mitochondria and chloroplasts.

Functions of Peroxisomes:

The principal function of peroxisomes is to house many metabolic pathways that are involved in various aspects of lipid metabolism. These include the following:

1- enzymes involved in the degradative oxidation (e.g., b-oxidation of very long chain fatty acids, 2-methyl-branched fatty acids, dicarboxylic acids, leuko- trienes, bile acid intermediates and cholesterol side chains, and both a- and b-oxidation of 3-methyl-

branched chain fatty acids).

2- The early steps in the synthesis of ether glycero-lipids.
3- The formation of bile acids, dolichol, and cholesterol.
4- The catabolism of purines, polyamines, and amino acids, and the detoxification of reactive oxygen species such as hydrogen peroxide, superoxide anions, and epoxides. In methylotrophic yeasts, peroxisomes are also involved in the metabolism of methanol and methyl amines.

Difference between Peroxisomes and Lysosomes:

Peroxisome and Lysosome two organelles, filled with enzymes that catalyze different biochemical processes inside the cell. Also, the primary **Difference between Peroxisomes and Lysosomes** may be the enzymes they consist of and their features. Lysosomes contain enzymes, which degrade biopolymers like proteins, lipids, polysaccharides, and nucleic acids. Peroxisomes have enzymes for the oxidation of organic and natural compounds, the era of metabolic based energy. Both lysosomes and peroxisomes will be related structurally. But you can find the Difference between Peroxisomes and Lysosomes in proportions. Lysosomes are often large in comparison to peroxisomes and their dimensions vary together with the materials that are uptake into the organelle. Both organelles are usually enclosed by way of a single membrane.

THE CYTOSKELETON

Much like the bony skeleton structurally supports the human body, the cytoskeleton helps the cells to maintain their structural integrity. The **cytoskeleton** (Figure 26) is a group of fibrous proteins that provide structural support for cells, but this is only one of the functions of the cytoskeleton. Cytoskeletal components are also critical for cell motility, cell reproduction, and transportation of substances within the cell. The cytoskeleton forms a complex thread-like network throughout the cell consisting of three different kinds of protein-based filaments: microfilaments, intermediate filaments, and microtubules (Figure 27).

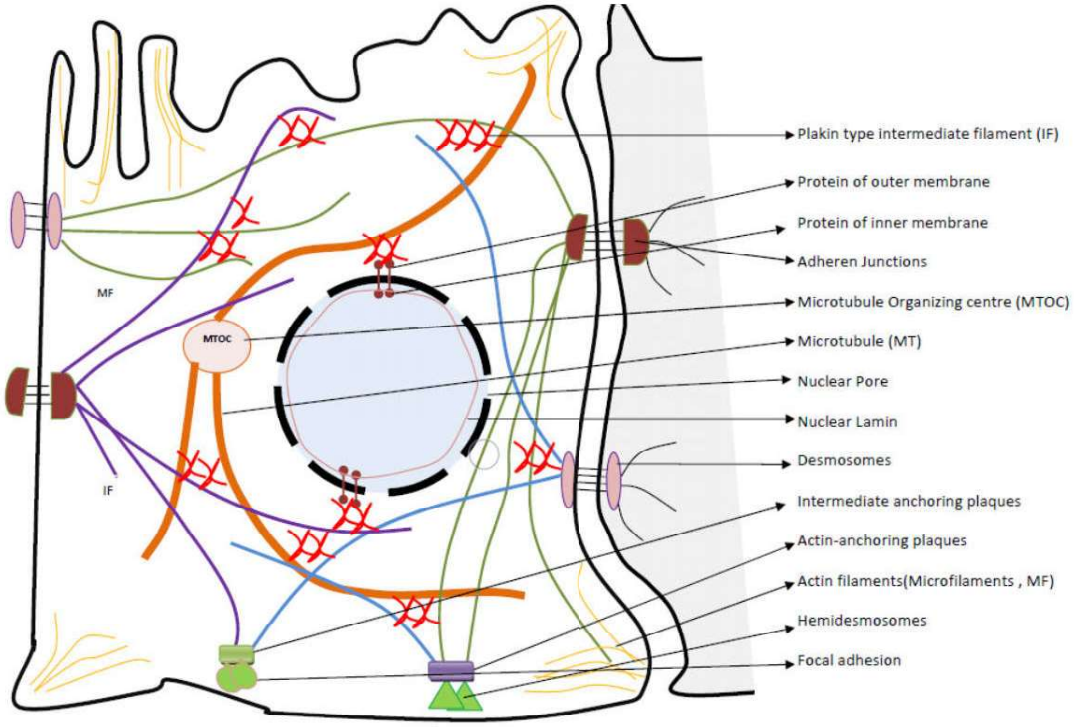

Figure 26: Cytoskeleton structures in cell.

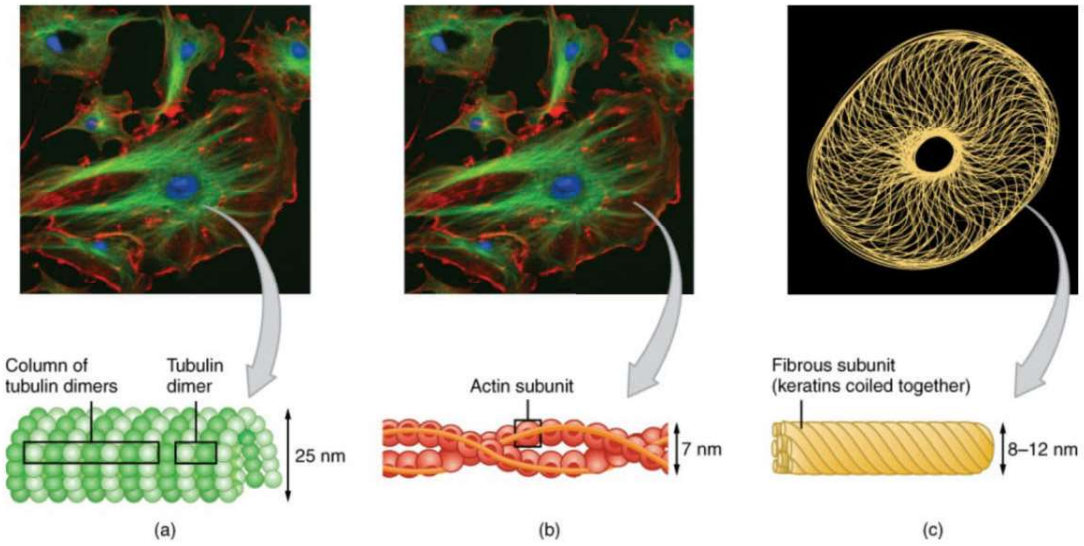

Figure 27: The Three Components of the Cytoskeleton. The cytoskeleton consists of (a) microtubules, (b) microfilaments, and (c) intermediate filaments. The cytoskeleton plays an important role in maintaining cell shape and structure, promoting cellular movement, and aiding cell division.

Cytoskeleton functions:

The cytoskeleton plays an important role in maintaining cell shape and structure, promoting cellular movement, and aiding cell division.

1. To provide structural support in maintaining shape of the cells and resilience to tension and stress.
2. Intracellular transport of vesicle and movement of mRNA (refer to vesicular transport: from ER to Golgi apparatus to Plasma membrane) and translocation of organelles (to position various organelles within the cell).
3. The cytoskeletons also function as apparatus for cell motility by crawling movement (filopodia, lamellipodia) on substratum or swimming in aqueous medium through cilia or flagellar movement (microtubules) in single cell animals.
4. Motility: In multi-cellular organism, the contraction of muscles,

movement of sperms, neurons, WBC and phagocytes are some mentions.

5. It forms the most essential component of cell division machinery. Cytoskeletons are responsible for the alignment and separation of Chromatids and subsequent cytokinesis to form daughter cells.

Structure of cytoskeleton:

1- Microtubules:

Structure of Microtubule:

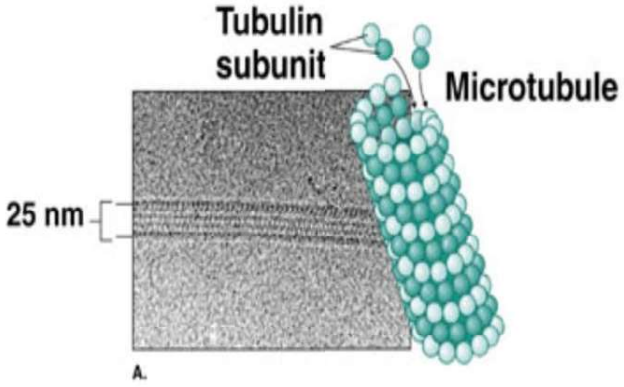

Figure 28: Structure of microtubules.

The microtubules are hollow, unbranched cylinders, generally about 200 to 270 Å thick and several micrometers long (the diameter of the microtubule fiber is 25 nm with GTP-αβ tubulin heterodimers as protein subunits (monomers). They may occur singly or in bundles and radiate from the centriole to the periphery of the cell. The microtubule is composed of 13 parallel proto- filaments that run its entire length and enclose a central lumen about 150 Å wide (Figure 28). Each proto filament is made up of a row of globular subunits that have a diameter of about 40to 50 Å. There may be cross bridges between adjacent microtubules.

Functions of microtubules:

1. **Form and support-** The microtubules form a part of cytoskeleton which (a) maintains the shape of the cell and (b) provides mechanical support to the cell. This role of microtubules is especially evident in cells having long processes such as the axopodia of certain protozoans and axons of nerve cells. Red blood corpuscles of non-mammalian vertebrates are kept flat by peripheral band microtubules.
2. **Movement-** The microtubules form the motile elements of cilia and flagella. These bring about locomotion in protists and cause currents in the environment of animals.
3. **Components of centriole and basal bodies-** The microtubules are components of centriole and basal bodies. The centriole give rise to the mitotic spindle and the basal bodies produce cilia and flagella.

   Cilia are found on many cells of the body, including the epithelial cells that line the airways of the respiratory system. Cilia move rhythmically; they beat constantly, moving waste materials such as dust, mucus, and bacteria upward through the airways, away from the lungs and toward the mouth. Beating cilia on cells in the female fallopian tubes move egg cells from the ovary towards the uterus.

   A **flagellum** (plural = *flagella*) is an appendage larger than a cilium and specialized for cell locomotion. The only flagellated

cell in humans is the sperm cell that must propel itself towards female egg cells.

4. **Formation of mitotic spindle-** The microtubules form the spindle and astral rays in cell division.
5. **Chromosome movement-** The chromosome fibers of spindle bring about movement of the chromosomes to the opposite poles of the cell in the anaphase.
6. **Cell differentiation-** The microtubules play a role in cell differentiation and determination of polarity.
7. **Intracellular transport-** Vesicles and protein molecules in the cell move along the "tracks" of microtubules. The movement is brought about by motor proteins kinesin and MAPIC (cytoplasmic dynin) powered by ATP.

2- Microfilament:

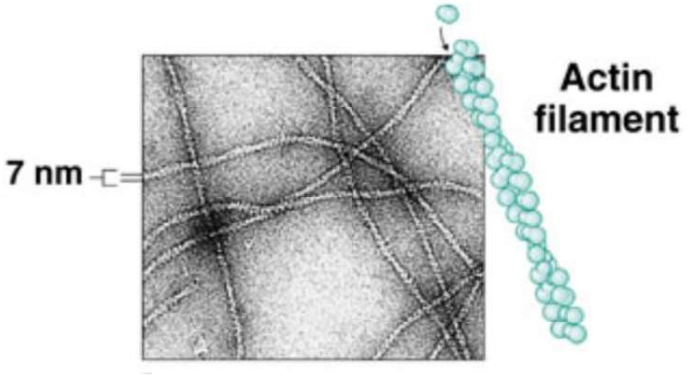

Figure 29: Structure of microfilaments.

In contrast with microtubules, the **microfilament** is a thinner type of cytoskeletal filament. The diameter of the microfilament or actin

filament is 8 nm with ATP Actin molecules as protein subunits (monomers). (Figure 29). Actin, a protein that forms chains, is the primary component of these microfilaments. Actin fibers, twisted chains of actin filaments, constitute a large component of muscle tissue and, along with the protein myosin, are responsible for muscle contraction. Like microtubules, actin filaments are long chains of single subunits (called actin subunits).

Functions of microfilaments (Actin filaments):

1. Membrane endocytosis during phagocytosis.
2. Vesicle transport along ER - GA – PM axis.
3. Locomotion for single cell organism: endoplasmic streaming.
4. Muscle Contraction: filament sliding.
5. Cytokinesis during cell division.

3- Intermediate filament:

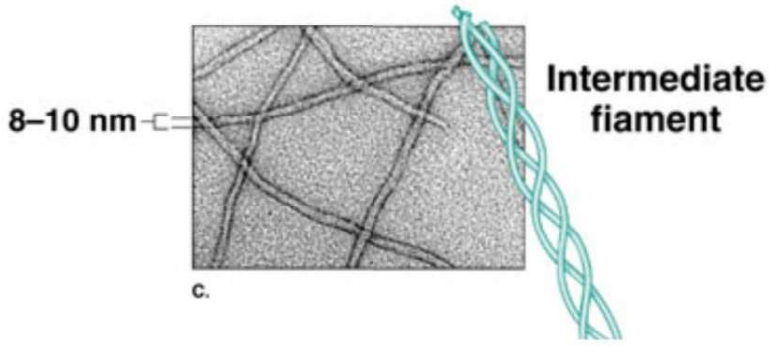

Figure 30: Structure of intermediate filaments.

As its name would suggest, an **intermediate filament** is a filament intermediate in thickness between the microtubules and microfilaments. The diameter of the intermediate filaments is 10-12 nm

(Figure 30). Intermediate filaments are made up of long fibrous subunits of a protein called keratin that are wound together like the threads that compose a rope. Intermediate filaments, in concert with the microtubules, are important for maintaining cell shape and structure. Unlike the microtubules, which resist compression, intermediate filaments resist tension the forces that pull apart cells. There are many cases in which cells are prone to tension, such as when epithelial cells of the skin are compressed, tugging them in different directions. Intermediate filaments help anchor organelles together within a cell and link cells to other cells by forming special cell-to-cell junctions.

Functions of Intermediate filaments:

1- Membrane mechanical support (nucleus inner membrane lined with Lamin A and C) and organizes nuclear content.
2- In cytosol, they form internal framework that supports the cell and add resilience of the cell.
3- They form the connecting network for cell attachment to their extra cellular matrix through hemidesmosomes and cell-cell adhesion through desmosomes.
4- They form the interconnecting link between cytoskeletons.

CENTRIOLES

History: Van Benden in 1880 discovered centrosome in cells of certain parasites of cephalopods. Centrosome is the area of cytoplasm, often a clear zone, around the centriole. It is found lying in the center of the cell, near the nucleus, in the cytoplasm. In Metazoa, centrosome lies outside the nucleus, but in Protozoa it lies within the nucleus. It is lacking in some plant cells. T. Boveri in 1888 described centrosome in detail.

Structure of Centriole:

The centrioles usually occur as paired hollow cylinders which are about 0.2 nm in diameter and 0.3 to 0.5 nm in length. The two centrioles usually lie at right angles to each other.

The centriole is composed of nine sets of microtubules triplets arranged in a ring and embedded in a dense granular or amorphous, electron dense matrix (Figure 31, 32). There are no microtubules at the center of the ring giving the "9+0" pattern for the centriole. Each microtubule in a triplet is about 250Å wide. The triplets are tilted in such a way that each forms an angle of about 30 to 40° to the circumference of the cylinder, with the A sub tubule of each set nearest the center of the ring. Membrane around the centrioles is absent. Sometimes a granular disc, called satellites, appears around centriole.

All the triplets of centriole are similar and indistinguishable from one another. The three microtubules often called sub-tubules, of a triplet are named A, B and C, beginning from the inside of the cylinder.

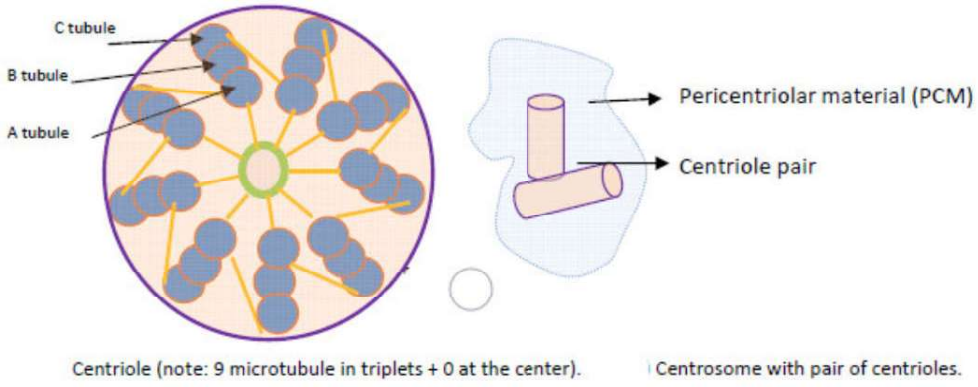

Figure 31: The centriole structure.

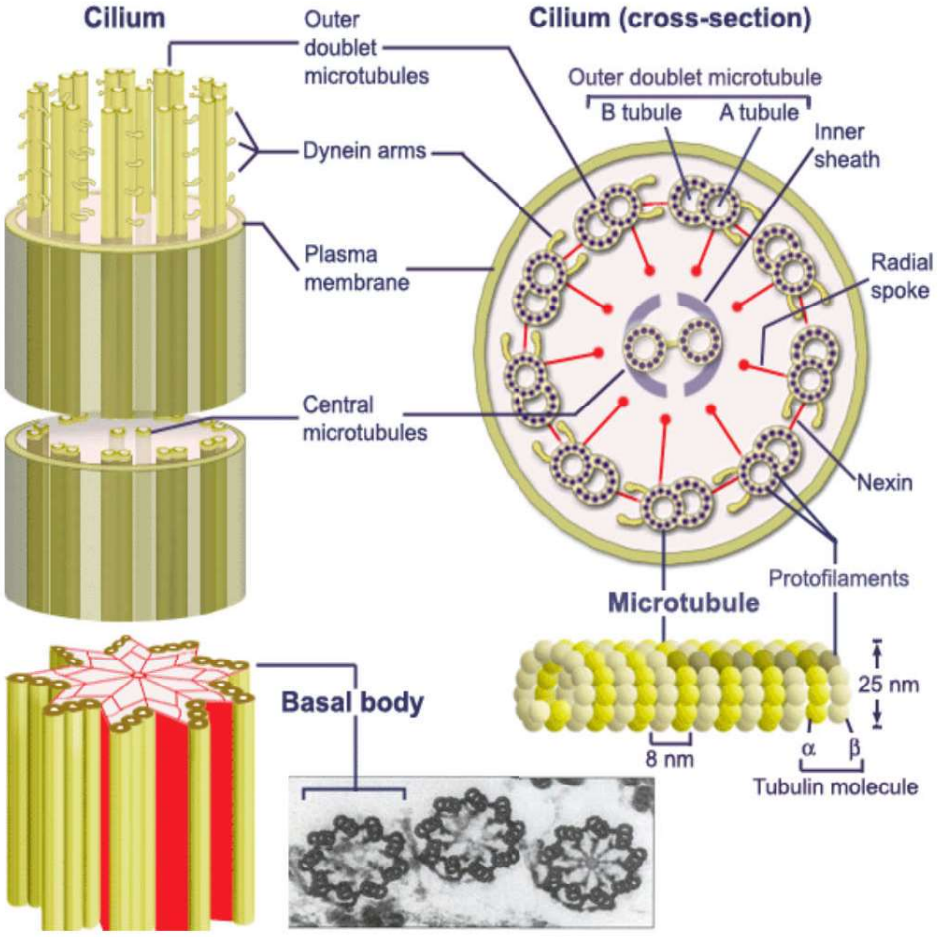

Figure 32: T.S. Centriole, cilium, and microtubule (showing faint 'cartwheel' pattern of fibrils).

Chemical Composition:

The microtubule of the centriole is composed of a protein tubulin and some lipids having a high concentration of ATPase enzymes. They seem to contain RNA and a small DNA molecule. Proteins encoded by this DNA are presumably translated on cytosolic ribosomes and then incorporated into the centriole.

Functions of Centriole:

The centriole serves the following functions:

(i) They help in organizing spindle fibers and astral rays during mitosis and meiosis.

(ii) They provide basal bodies giving rise to cilia and flagella.

(iii) Pericentriolar material acts at the MTOC (microtubule organizing center) for thecytoplasmic microtubules.

NUCLEUS

History: Nucleus was observed by a Dutch Microscopist, Antonie van Leeuwenhoek in 1710,as a centrally placed clear area in the blood cells of amphibians and birds. Fontana (1781) recorded an ovoid structure in each of the isolated epidermal cells of eel's skin. However, Robert Brown (1831) was the first to use the term nucleus for a prominent body present in the orchid cell. He stated that nucleus was the regular feature of the cells and initiated the concept of nucleated cells.

Structure of Nucleus:

The nucleus consists of various parts. It is bounded by a thin but clearly defined covering, the **nuclear envelop** or karyotheca. Within the envelope is a clear fluid substance called **nucleoplasm** or nuclear sap or karyolymph is present in which the solutes of the nucleus are dissolved. Suspended in the nucleoplasm are network of protein-containing fibrils called **nuclear matrix**; fine intermingled nucleoprotein filaments collectively referred to as thechromatin; and one or more spherical bodies known as nucleoli (singular, nucleolus). There are no membranes or microtubules inside the nucleus (Figure 33)

- **Chemical Composition:** The nucleus is composed of about 9-12% DNA, 5% RNA, 3% lipids, 15% simple basic proteins such as histone or protamines, about 65% complex acid or neutral proteins, including enzymes such as polymerases for the synthesis of DNA and RNA, organic phosphates and inorganic salts or ions such as Mg^{++}, Ca^{++} and Fe^{++}.

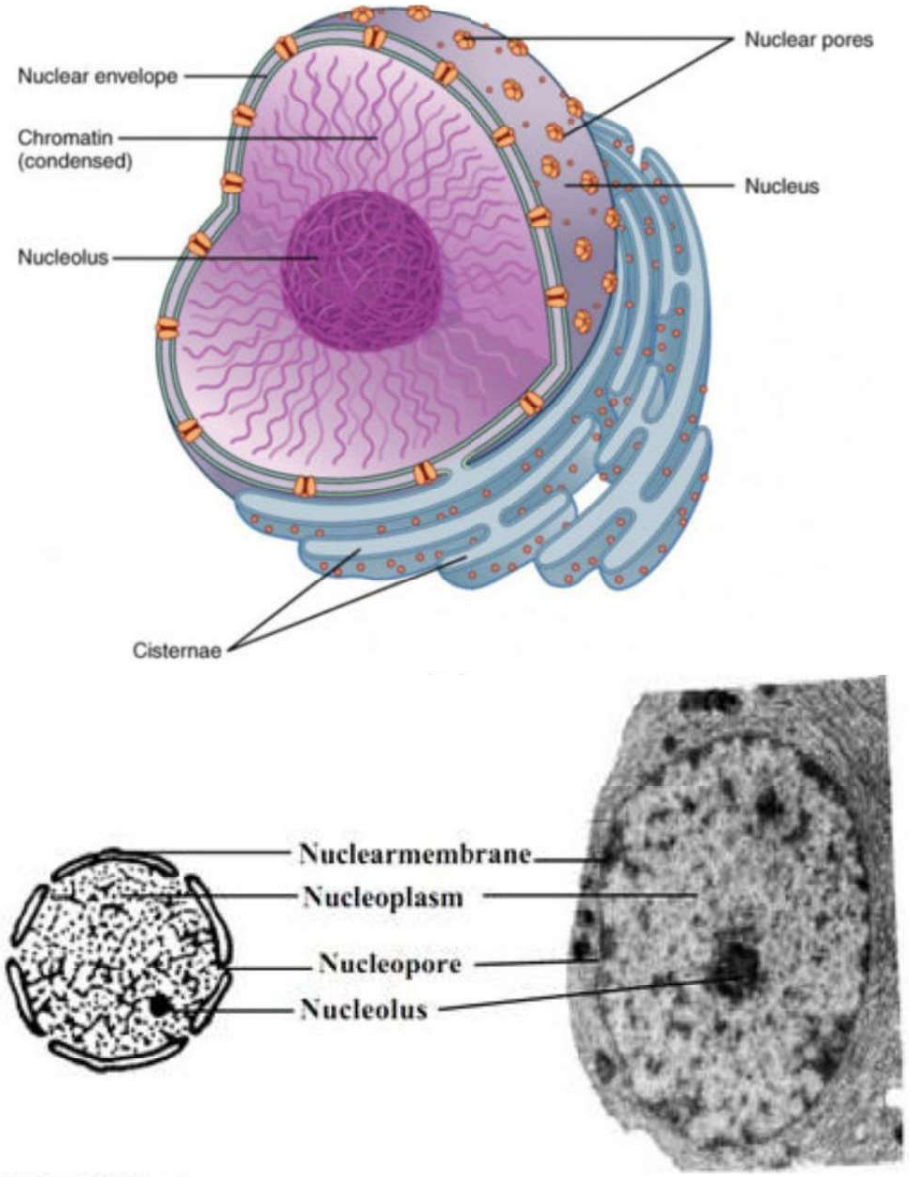

Figure 33: The Nucleus.

- **Functions:** The nucleus acts as a control center of the cell. It serves the following main functions:
  - It maintains the cell by directing the synthesis of structural proteins.
  - It regulates cell metabolism by directing the synthesis of enzymatic proteins.

- It contains genetic information for reproduction, development and behavior of theorganism besides for structure &metabolism.
- It brings about cell replication when needed.
- It is the site for the formation of ribosome subunits.
- It brings about cell differentiation by keeping only certain genes operational.
- It develops genetic variations that result in evolution

I- Nuclear Envelope:

The nuclear envelop separates the nucleoplasm from the cytoplasm. It consists of two-unit membranes: outer and inner. Each unit membrane is about 75Å thick and is a trilaminar lipoprotein like the plasma membrane. The two-unit membranes are separated by a space called the inter membrane or perinuclear space. It is about 250Å wide. The outer or cytoplasmic surface of the outer membrane is studded with ribosomes and polysomes and is rough. These ribosomes carry on protein synthesis. The outer membrane is continuous with RER at certain places. Thus, the perinuclear space is continuous with the channels of theRER. The inner membrane of the nuclear envelope is free of ribosomes, but has a dense layer, the nuclear lamina, closely associated with its inner or nucleoplasm surface.

Nuclear Pores: The nuclear envelope is generally perforated by minute apertures, the nuclear pores that control the passage of some molecules and particles. The pores are formed by fusion of the inner and outer membranes of the nuclear envelope. There may be 1000 to 10,000 pores per nucleus.

Each nuclear pore is fitted with an apparatus called the **pore complex** which fills considerable part of the pore. The pore complex is nearly cylindrical, projects into both cytoplasm and nucleoplasm, and projects beyond the rim of the pore over the nuclear envelope. The pore complex consists of two rings, the annuli, one located at the cytoplasmic rim of the pore and the other at the nucleoplasmic rim. Each annulus comprises eightsymmetrically arranged subunits and sends a spoke into the pore. The spoke encloses a channel about 100 to 200 Å wide. Ions and small molecules of the size of monosaccharide, disaccharides or amino acids pass freely between the nucleus and cytoplasm. The pore complexes do control the passage of larger molecules, such as RNA and proteins, and of ribosomal subunits. The pore complexes also act as a barrier to some molecules such as DNAof chromosomes.

Functions:

- It maintains the shape of the nucleus.
- It keeps the nuclear contents in place and distinct from cytoplasm.
- It regulates the flow of materials into and out of the nucleus by active transport andout pocketing.
- Its pores allow the exit of ribosomal subunits formed in the nucleolus and tRNA andmRNA synthesized on the chromosomes.

II- Nucleoplasm:

Nucleoplasm is a transparent fluid material in the nucleus. The chromatin fibers and nucleoli are suspended in it. It contains raw materials (nucleotides), enzymes (polymerases) and metal ions (Mn^{++},

Mg^{++}) for the synthesis of DNA and RNA. It also contains proteins and lipids. The proteins include basic histones and acidic or neutral non-histones that associate with the DNA molecules. There are proteins for the formation of ribosomal subunits also. The RNAs (rRNAs, tRNAs, mRNAs) and ribosomal subunits synthesized in the nucleoplasm pass into the cytoplasm via nuclear pores (Figure 67).

Functions:

- It is the seat for the synthesis of DNA, RNAs, ribosomal subunits, ATP, and NAD.
- It supports the nuclear matrix, chromatin material and nucleoli.
- It provides turgidity to the nucleus

III- Nuclear Matrix:

The nuclear matrix is a network of thin, criss-crossing, protein-containing fibrils that are connected at their ends to the nuclear envelope. It forms a sort of nuclear skeleton. It remains intact after the chromatin and DNA have been removed.

Functions:

- It maintains the shape of the nucleus.
- Chromatin fibers are anchored to nuclear matrix.
- The machinery for various nuclear activities, such as transcription and replication, isassociated with the matrix.
- It has also been implicated in the processing of newly formed RNA molecules andtheir transport through the nucleus.

IV- Chromatin:

The term chromatin was first coined by Flemming in 1879. The chromatin occurs in an interphase (non-dividing) nucleus as fine filaments, the **chromatin fibers**. The fibers lie criss-cross to give the appearance of a diffuse network often referred to as the nuclear or chromatin reticulum. The chromatin occupies most of the nucleus. The chromatin fibers are simply extremely extended chromosomes. A chromatin fiber is normally about 100Å in diameter. A fiber thicker than 100Å appears to be coiled or folded, a fiber thinner than 100Å seems to have less protein content associated with it. Chromatin fibers typically appear approximately 250Å in diameter. During cell division, the chromatin fibers, by condensing and tight coiling, form short, thick, rod like bodies known as **chromosomes.**

Upon staining, this diffuse network of chromatin material shows light stained and dark stained areas. After cell division, the chromosomes change back into chromatin fibers. Most of the chromatin fibers become uncoiled, extended, and scattered in the nucleoplasm. These represent the **euchromatin** (true chromatin) of the interphase nucleus. They are stainedlightly.

The term **heterochromatin** is applied to those chromosomal regions that stain darker than others. They remain coiled and compacted in the interphase too. Heterochromatin represents relatively inactive parts of the chromosomes. It contains less DNA and more RNA than the euchromatin. Few mutations occur in this region. Little or no mRNA is synthesized here. Most of the DNA in heterochromatin is highly

repeated DNA, which is never, or very seldom, transcribed. Heterochromatin is of two types: **constitutive and facultative**. The DNA of constitutive heterochromatin is permanently always inactivated and remains in the condensed state. It occurs at several places: adjacent to the centromere of the chromosome, at the ends (telomeres) of the chromosomes, at certain portions within the euchromatin, and adjacent to the nuclear envelope. Facultative heterochromatin is partly condensed and inactivated. **One X-chromosome in female mammals is condensed to form the heterochromatic Barr body.**

Nucleosomes: In 1974, Kornberg and Thomas proposed that a chromatin fiber is a chain of similar subunits called nucleosomes (Figure 34). The nucleosome consists of a core particle wrapped by DNA strand. The core particle is an octamer of **8 histone molecules**, two each of the histones H2A, H2B, H3 and H4. The non-histone proteins do not occur in the nucleosome structure of chromatin. Nucleosomes are not formed in prokaryotes.

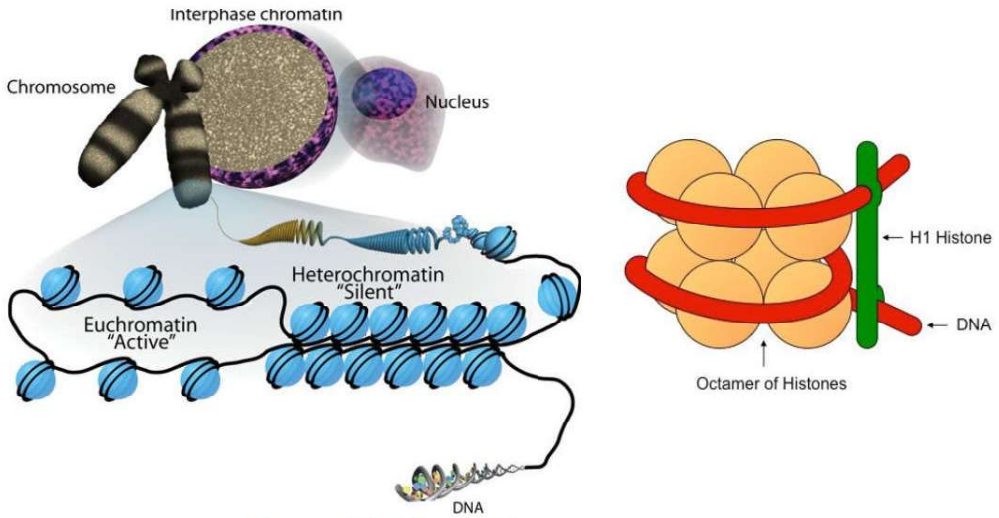

Figure 34: Chromatin and Nucleosome.

V- Nucleolus (Little Nucleus):

The nucleolus was discovered in 1781 by F. Fontana in the slime from the eel skin. It is present in the nucleus of most cells, but is inconspicuous or absent in sperm cells and in muscle cells. It is usually spherical but may have other forms. The number of nucleoli in a nucleus varies in different species. The nucleoli disappear during cell division, and are reformed at specific sites, the nucleolar organizers or nucleolar organizer regions (NORs), of certain chromosomes, the nucleolar chromosomes, at the end of cell division before the chromosomes become diffuse. Position of the nucleolus in the nucleus is often eccentric. However, it occupies a specific position on its chromosome.

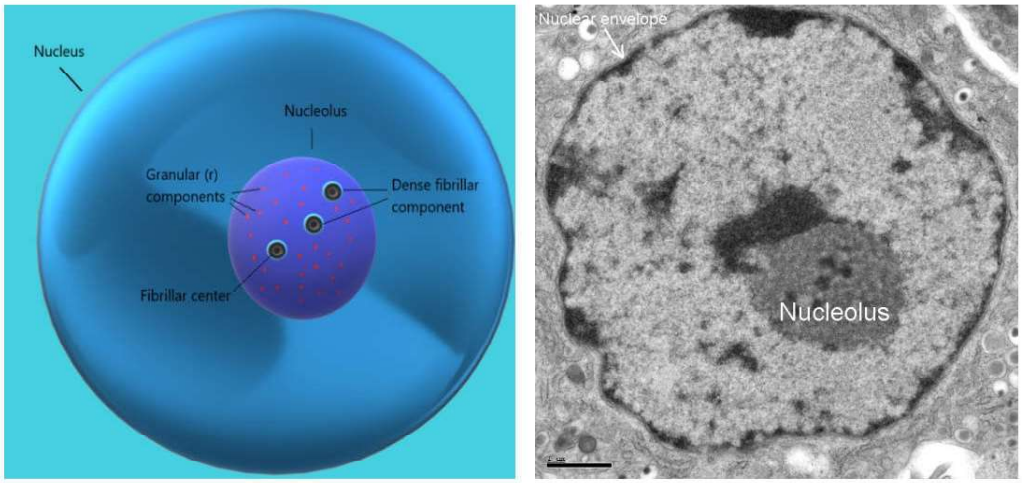

Figure 35: Nucleolus diagram and ultrastructure

The nucleolus (Figure 35) is a dense, somewhat rounded, dark staining organelle. It is without a limiting membrane. Calcium ions keep it intact. It consists of four regions.

1. Fibrillar Region or Nucleolonema- It contains indistinct fibrils about 50-100Å in diameter. The fibrils represent the long rRNA

precursor molecules in early stages of processing before the processing enzymes have cut off segments from them.

2. Granular Region- It contains spherical, electron dense particles, about 150-200 Å in diameter and with fizzy outline. The granules are ribosomal subunits (rRNA + ribosomal proteins) that are nearly ready for transport to the cytoplasm.
3. Amorphous Region or Pars Amorpha- It is a structure-less proteinaceous matrix in which the granular and fibrillar regions are suspended.
4. Nucleolar Chromatin- It consists of 100 Å thick chromatin fibers. The latter are a part of the nucleolar chromosome which follows a tortuous path through the granular and fibrillar components of the nucleolus. This part contains many copies of DNA that directs the synthesis of ribosomal RNA. The rest of the nucleolar chromosome lies in the nucleoplasm.

Functions of Nucleus:

- The nucleolus synthesizes and stores rRNA.
- It also stores ribosomal proteins received from the cytoplasm.
- It forms ribosomal subunits by wrapping the rRNA by ribosomal proteins. The ribosomal subunits pass out through the nuclear pores into the cytoplasm. Here the subunits join to form ribosomes when needed. Thus, it is the nucleolus which provides machinery (ribosomes) for protein synthesis.
- The nucleolus also plays a role in cell division.

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CHROMOSOMES

History: W. Hofmeister in 1848, discovered nuclear filaments in the nuclei of pollen mother cells of *Tradescantia*. First accurate count of chromosomes was made by W. Flemming in 1882, in the nucleus of a cell. In 1884, W. Flemming, Evan Beneden and E. Strasburger demonstrated that the chromosomes double in number by longitudinal division during mitosis. Beneden in 1887 found that the number of chromosomes for each species was constant. The term "Chromosomes" was coined in 1888 by W. Waldeyer for the nuclear filaments. W.S. Sutton and T. Boveri suggested the role of chromosomes in heredity in 1902, which confirmed by Morgan in 1933.

Morphology of Chromosomes:

During the interphase stage, the eukaryotic chromosomes are extended into long and thin chromatin fibers where they lie criss-cross to form the **chromatin reticulum**. They replicate in the S-phase and become double. At this stage they consist of two chromatids that are held together at one point called **centromere** (Figure 36). At the time of cell division, the chromosomes condense and tightly coil up and become distinct at metaphase stage. The eukaryotic chromosomes vary in number, size, shape and position but they have remarkably uniform structure.

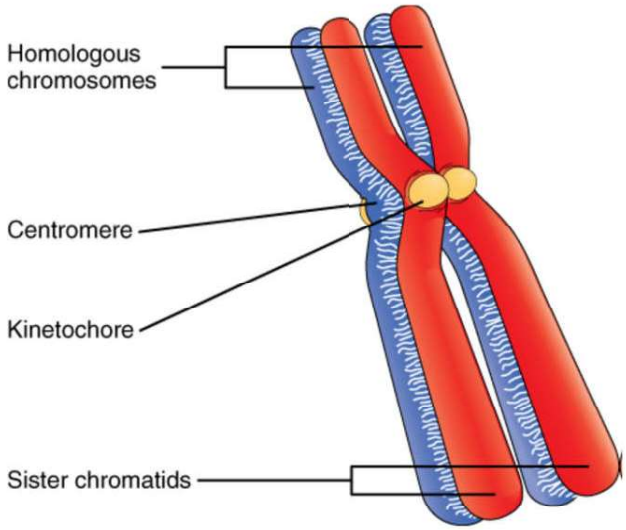

Figure 36: A Homologous Pair of Chromosomes with their Attached Sister Chromatids. The red and blue colors correspond to a homologous pair of chromosomes. Each member of the pair was separately inherited from one parent. Each chromosome in the homologous pair is also bound to an identical sister chromatid, which is produced by DNA replication, and results in the "X" shape.

1. **Number:** Eukaryotic chromosomes vary in number from two to a few hundred in different species. In a species all the individuals have same number of chromosomesin all of their cells, except the gametes. Since the chromosome number is constant for a species, it is helpful in determining and taxonomic position of thespecies.
2. **Size:** In a **species all the chromosomes are not of the same size.** Their size also varies from species to species. The particular chromosome of a species however has more or less a constant size. The organisms having fewer chromosomes have large sized chromosomes than those having many. Generally, plant chromosomes are larger than animal chromosomes and among plants the monocots have larger chromosomes than the dicots.
3. **Shape:** The chromosomes at metaphase stage look like slender

rods that may be straight or curved to form an arc or a letter S. In anaphase stage they may assume J or V shapes, depending upon the position of the centromere.

4. **Position:** In a nucleus each chromosome is independent of all the other chromosomes in its location. Thus, they may occupy any region of the nucleus.
5. **Structure:** At **metaphase stage**, since the chromosome is a highly condensed nucleoprotein filament, it contains two greatly coiled sister chromatids. These chromatids that lie side by side along their length, are held together at a point called centromere, an area of the narrow region also called **primary constriction** of the metaphase chromosome. At the centromere each chromatid has a darkly staining, disc like, fibrous structure, called **kinetochore**, to which spindle microtubules attach during cell division. Kinetochores are the sites where force is exerted to pull the chromatids towards the poles. One or more chromosomes may have additional narrow regions called the **secondary constrictions**. The part of the chromosome separated by secondary constrictions is termed as **satellite**. A chromosome with a satellite is called **sat chromosome**. The size and the shape of the satellite remain constant for a species. Secondary constrictions are associated with the nucleoli and are known as the **nucleolar organizers**. The chromosomes which have nucleolar organizing regions are known as the **nucleolar chromosomes** (Figure 37).

   Ends- The ends of chromosomes are called **telomeres**. The function of telomere varies from the rest of the chromosome. On exposure to

X-rays a chromosome may break and its pieces may rejoin, but no segment connects to the telomere, showing that the telomere has a polarity, and it, somehow "seals" the end.

6. **Ultra-structure:** A chromatid contains a very fine filament called chromonema which is a single, long, double stranded DNA molecule. It is wrapped around histones to form **nucleosomes**. The nucleosome and non-histone proteins together form the chromatin fiber. The chromatin fiber has reactive groups, probably H1 histone molecules, which act as "folders" and crosslink the chromatin fiber changing it into a great coiled, compact metaphase chromatid.
7. **Chemical composition:** The chromatin in the eukaryotic chromosome consists chemically of about 35% DNA, about 60% proteins, about 5% RNA, some metal ions and certain enzymes.

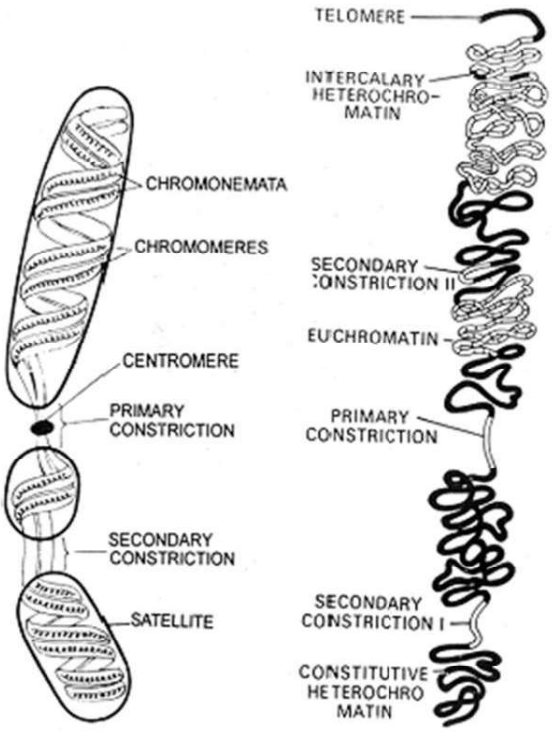

Figure 37: Detailed schematic structure of chromosomes.

8- Types of chromosomes: On the basis of the position and number of centromeres, chromosomes are classified as below (Figure 38):

(i) Metacentric: In metacentric chromosomes the centromere is at the middle of the chromosome, and the arms are equal. In anaphase the chromosome appears V-shaped. For example: human chromosome no. 3

(ii) Submetacentric:. In such chromosome, the centromere is near the center of the chromosome, and the arms are slightly unequal and in anaphase the chromosome appears J or L shaped. For example: Human chromosome No. 1.

(iii) Acrocentric: In this type the centromere is near one end of the chromosome, and the arms are very unequal. For example: Human chromosome No. 4 & 5.

(iv) Telocentric: The centromere is at one end in such chromosomes, and the arms are on one side only. The chromosome remains rod shaped in anaphase also

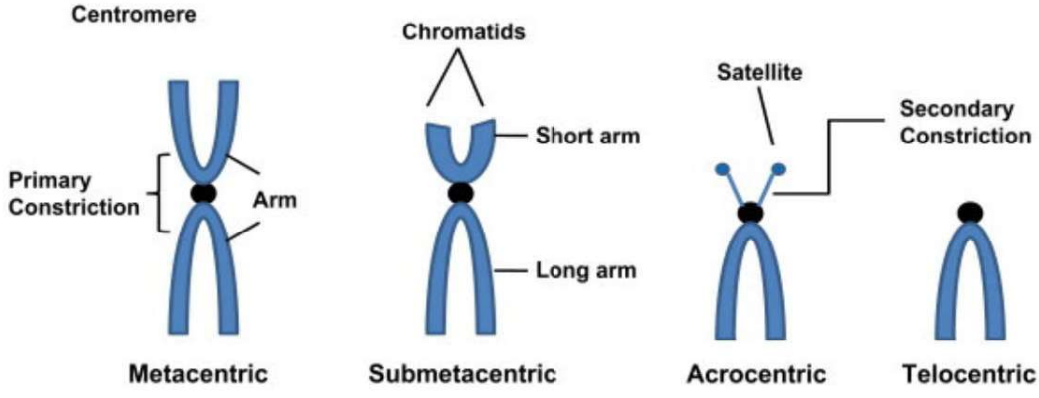

Figure 38: Types of chromosomes based on the position and number of centromeres and normal human karyotype.

Depending upon the number of centromeres there are three types of chromosomes:

(i) **Acentric:** The chromosome is without a centromere, which is formed by breakage of the chromosome. It does not attach to spindle microtubules, so it is lost in the cell division.

(ii) **Monocentric:** It is the chromosome with a single centromere, and it is the most common type.

(iv) **Dicentric:** It is the chromosome with two centromeres and is formed by the fusion of two chromosome segments each having a centromere. It is unstable and may break when the two centromeres are pulled to opposite poles in mitosis.

Functions of Chromosomes:

1- Chromosomes carry hereditary characters from parents to offspring.

2- They direct the synthesis of structural proteins and thus, help the cell grow, and divide.

3- By directing the formation of necessary enzymes, they control metabolism.

4- They guide cell differentiation during development.

5- They form nucleoli at nucleolar organizer sites in daughter cells.

6- They produce variations through changes in their genes and contribute to theevolution of the organisms.

7- They play role in sex determination.

8- They maintain the continuity of life by replication.

CELL DIVISION

A multicellular organism starts its life as a single cell and it undergoes repeated division, thus, the growth and development of every living organism depends on the growth and multiplication of its cells. The cell increases in size due to growth and it is the characteristic feature of all the living organisms. After the cell attains maximum growth, it begins to divide. The vegetative growth of an organism takes place by an increase in the number of cells through cell divisions which follows the geometrical progression. The cell division is a continuous and dynamic process, and it involves the following three stages:

1. DNA or genome replication.
2. Nuclear division or karyokinesis.
3. Cytoplasmic division or cytokinesis.

The cell division is of two types on the basis of number of genomes present in the daughter cells in comparison to the dividing parent cell **mitosis** and **meiosis**.

1. ***Mitosis-*** The term mitosis was coined by W. Flemming in 1882. The multiplicationof a body cell into two daughter cells of equal size and containing the same number of chromosomes as in the parent cell is called mitosis or **somatic division**.
2. ***Meiosis-*** The term meiosis was first coined by J. B. Farmer (1905) with J. E. Moore. Meiosis occurs only in gonads (germ cells) during the formation of gametes like sperm and ovum. It is a process by means of which double number or 2N or diploid chromosomes is reduced to its half number or N or haploid (**reduction process).**

Cell Cycle Stages, Mitosis & Cytokinesis: -

Cell Cycle: Every cell having the capacity to divide passes through a regular cycle of changes known as cell cycle. A cell starts its cycle in diploid condition.

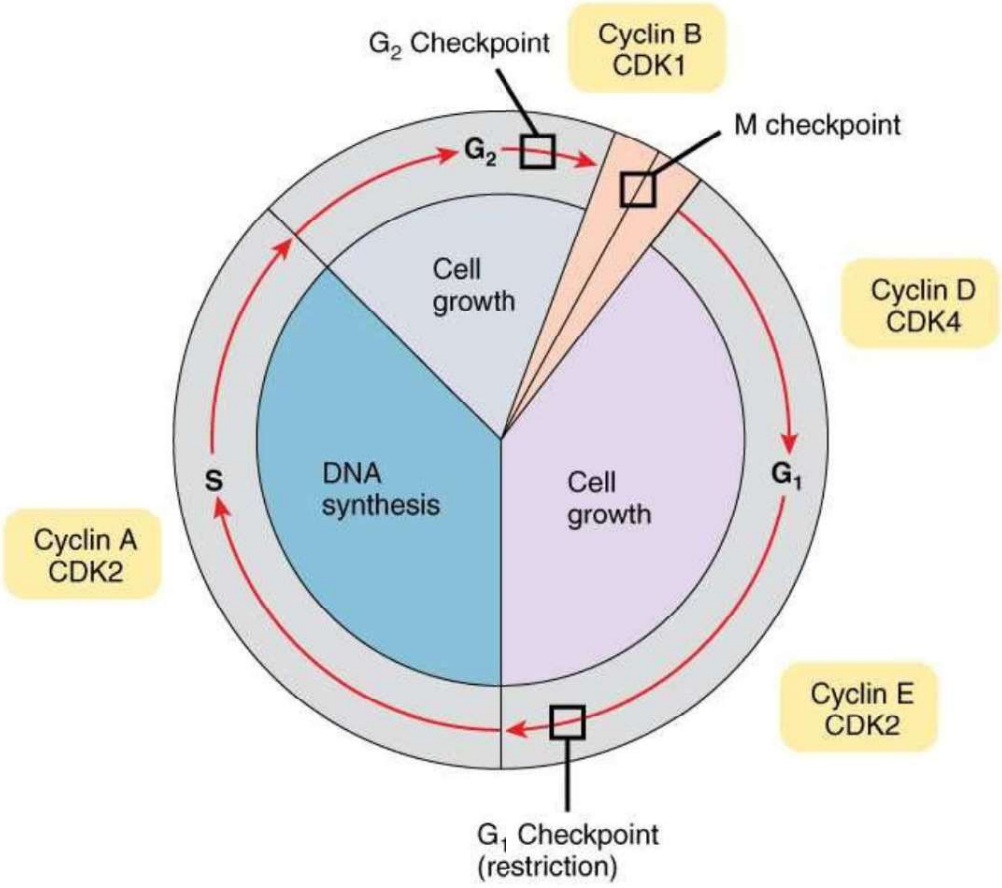

Figure 39: Cell cycle phases.

Phases of cell cycle:

Cell cycle consists of two stages: A long un-dividing stage called **interphase or I-phase** and a short dividing stage **mitotic or M-phase.**

1. ***Interphase-*** The time between the end of telophase and the beginning of the next M- phase is called the interphase. It is a long stage that lasts for 10 to 30 hours. During this phase the cell grows

by synthesizing biological molecules such as lipids, proteins, carbohydrates, nucleic acids. Interphase is further divided into three sub phases or periods: first gap or G1 phase, synthetic or S phase and second gap or G2 phase.

(i) **G_1 phase-** The **gap between previous mitosis and beginning of DNA synthesis** is represented by G_1 phase. In this stage initial growth of a newly formed cell takes place. Various biological molecules (carbohydrates,proteins, lipids, including some non-histones, RNAs) are synthesized in this phase. Normal metabolism is carried out for the preparation for DNA replication that is to take place next to it. DNA synthesis does not occur in thisphase.

(ii) **S Phase-** During this **phase duplication of each chromosome** take place by replication of new DNA molecule on the template of the existing DNA. Synthesis of histone proteins and their mRNA, some non-histone proteins and formation of new nucleosome also occur in S-phase only. In most of the eukaryotes the S-phase lasts for 6 to 8 hours.

(iii)**G_2 Phase-** G_2 phase is the gap between DNA synthesis and nuclear division. RNA transcription and protein synthesis continues during this phase. Further growth of the cell and preparation for its division also takes place in this stage.During this stage the cytoplasmic organelles such as centrioles, mitochondria and Golgi apparatus are doubled, proteins for spindle and asters are synthesized and active metabolism stores energy for the next mitosis. It takes in most cells lasts for 2 to 5h.

2. ***Mitotic Phase-*** Interphase is followed by mitotic phase. During mitotic phase the already **duplicated chromosomes are equally distributed to the daughter cells** which contain exactly the same hereditary information as the parent cell. Though, the other cell components (organelles and molecules) are also divided approximately equally between the daughter cells, but not as precisely as the DNA. After the mitosis is over, the daughter cells enter the G_1 phase of the next cell cycle.

   During mitosis many structural and physiological changes take place in the cell, as the chromatin of the nucleus is packed into visible chromosomes, which are set free by breakdown of nuclear envelope. An extensive reorganization of the membranous components and cytoskeletal elements takes place. Endoplasmic reticulum and Golgi apparatus break down into small vesicles and stops the protein movement. Microtubules dissociate into tubulin dimers and are assembled into the spindle which occupies most of the cell and helps in the distribution of chromosomes into the daughter cells. Actin filaments get reorganized and form a contractile ring for the cytoplasmic division.

MITOSIS DIVISION:

Mitosis (Figure 40) is defined as the division of a parent cell into two identical daughter cells eachwith a nucleus having the same amount of DNA, the same number and kind of chromosomes and the same hereditary instructions as the parent cell. Therefore, it is also known as the equational division. There are two main events involved in mitosis:

Karyokinesis or divisionof the nucleus and cytokinesis or division of cytoplasm.

Karyokinesis:

In eukaryotes, karyokinesis is a complex process due to the presence of many chromosomes. It is a continuous process which may be divided into four stages: prophase, metaphase, anaphase and telophase.

1- **Prophase-** In an interphase cell the chromosomes are greatly extended and spread throughout the space in the nuclear compartment. Approximately 4 meters of DNA is organized into 46 duplicated chromosomes is present in the nucleus of a human G2 cell. The prophase is long and complex that lasts for about 50 minutes. It may be divided into 3 sub stages: early prophase, middle prophase and late prophase.

A) Early prophase- During the early prophase of mitosis the following events take place:

(i) The shape of cell becomes almost rounded and the cytoplasm becomes viscous.

(ii) The centrioles lie close to the nucleus and around them assembles the short radiating microtubules by polymerization of the tubulin dimers. Both pairs of centrioles also called **diplosomes**, start moving to the opposite ends of the cell.The microtubules surrounding each pair of centrioles appear like a star body and are called the **aster**. The microtubules which

are also termed as **astral rays**, are not in contact with the centrioles, but are separated from them by an amorphous zone of cytoplasm known as **pericentriolar cloud**. The microtubules stretching between the diplosomes moving apart increase in number and length by incorporating more tubulin dimers. Thus, asters shift theduplicated centrioles to the opposite ends of the cell from where the centriole pair will pass into separate daughter cells when cytokinesis occurs. Though thecentrioles have no role in the formation of the spindle, but they may be concerned with orienting the spindle.

(iii) Long microtubules assemble on one side of the nucleus to form mitotic spindle. **Microtubules are arranged in bundles called spindle fibers** and at each pole of the spindle lies the mother-daughter centriole pair.

(iv) The chromosomes that appear like threads in the nucleus gradually change into short, thick rods by loss of water and progressive coiling and become visible. Due to the duplication of DNA and chromosomal proteins during the interphase, each chromosome appears longitudinally double, consisting of two identical sister chromatids which are held together at the narrow region called **primary constriction or centromere**. Each chromatid has a disc like structure at centromere, where the spindle microtubules join it. This disc is called as **kinetochore**.

B) Middle prophase- It includes the following events:

(i) The chromosomes further get shorter, thicker and their chromatids become uncoiled and finally they assume their characteristics sizes and become distinguishable individually.

(ii) **Nucleoli** progressively become smaller and **finally disappear.** Nuclear envelope begins to breakdown into small vesicles which disperse into the cytoplasm. The lamina dissociates into its protein subunits.

C) Late Prophase- This phase involves the following events:

(i) The nuclear envelope breaks completely thus, releasing the chromosomes and other nuclear contents into the cytoplasm.

(ii) The spindle gains their proper shape and size.

(iii) The growing spindles push the centriole pairs to the opposite ends of the cell.

2- Metaphase- The metaphase being short and simple lasts for 2 to 10 minutes and itinvolves the following events:

A. The spindle occupies the region of the nucleus.

B. The chromosomes move to the equatorial plane of the spindle.

C. Some spindle microtubules extend to and join the chromosomes. These are called chromosomal or kinetochore microtubules.

D. The chromosomes get aligned at the middle of the spindle in the form of a plate called equatorial or metaphase plate. This plate is formed by the kinetochores, the arms of the chromatids trailing away on the sides. It is at the right angles of the long axis of the spindle. During metaphase the chromosomes have

fully aligned into a plate and await the separation of their chromatids.

3. **Anaphase-** Anaphase lasts only 2 to 3 minutes and it comprises the following events:
   A. The **sister chromatids of each chromosome slightly separate** at the primary constriction so that their kinetochores stretch towards the opposite poles of thespindle. In all the chromosomes separation of chromatids occurs almost simultaneously. The **chromatids are now referred to as chromosomes** because they are no longer held to their duplicates.
   B. After a short time, the chromatids separate completely from their formermates, and start moving to opposite poles of the spindle. As each chromosome is being pulled by its attached microtubules, its kinetochore leads and armstrail behind. As a result, the chromosomes are pulled into V, J and I shapes, depending upon the position of the kinetochore. (Metacentric, sub metacentric or telocentric respectively)
   C. As the chromosomes move toward their respective poles, the two poles move farther apart by elongation of spindle.

   The anaphase ends when all the chromatids reach the opposite poles. Each pole of the spindle receives one chromatid from every metaphase chromosome, the two groups of chromatids have the same hereditary information.

4. **Telophase-** The telophase is long and complex and lasts for an hour or so. In this phase nucleus is reconstructed from each group of