closed in the fragments of cell membrane are called phagosomes which fuse wit lysosomes and form a single large digestion vacuole where the engulfed materia is digested. Later the digestion vacuole fuses with the cell membrane to expel th residual material.

2. **Autophagy.** During adverse conditions, lysosomes begin to digest the othe cell inclusions such as mitochondria and endoplasmic reticulum. This is calle their cellular autophagy which is supposed to be a process of obtaining the needfu energy by making use of these constituents as a source.

3. **Ageing.** Lysosomes are considered as agents of ageing and three differen roles are assigned to them. *Firstly,* they produce autolytic enzymes, that slowly disrupt the delicate intracellular machines. *Secondly,* they produce some byproducts that clog the gears of metabolic machinery and *thirdly,* they may digest some functional elements and then produce insoluble residues. Thus, these are called **suicidal bags.**

4. **Autolysis.** One of the roles assigned to lysosome is the removing of dead or degenerating cells. During the process, the lysosome membrane ruptures and enzymes are set free to digest the dead cells and to get rid of the cell debris. This digestive process in the dead cells is called autolysis. The digestion of the tail of a tadpole is also carried out by them.

5. **Seedlings.** Allison (1974) found lysosomes in corn seedlings rich in enzymes *protease, carboxypeptidase, DNAse, RNAse,* β-*amylase,* α-*glucosidase* etc. In seedlings, they are involved in the hydrolysis and removal of protein and starch during germination. He proposed that in plants, they may be involved in intra-cellular and extra-cellular digestion and also in the process of development.

LOMASOMES

These structures, referred to as border bodies, were discovered by Moore and Mc Alear (1961). Structurally, these are membraneous or vesicular structures present between the cell wall and cell membrane and are formed by evaginations delimited by cell membrane. Functionally, lomasomes play a role in–(*i*) secretions, (ii) increasing the surface area for the diffusion of substances involved in cell wall formation or breakdown, (iii) in endocytosis and (iv) in membrane proliferation.

MICROTUBULES

The term microtubules was given by Slautterback (1963) to include a class of subcellular filamentous components found in the eukaryotic cells. These are straight cylinders (dia. 240 Å) with a hollow core (150 Å). Microtubule consists of 13 longitudinal protofilaments, each composed of a linear chain of dimers of alpha and beta tubulins. These are capable of being rapidly assembled and disassembled. The assembly is accompanied by the hydrolysis of GTP to GDP. Within the cell, microtubules are in equilibrium with free tubulin. The phosphorylation of tubulin by a *cyclic AMP dependent kinase* favours the polymerisation. The control of assembly and disassembly of tubulin involves Ca-ions and calcium binding protein, the **calmodulin.**

Recent studies have shown that microtubules do not consist of tubulin only but contain about 15 to 20 per cent other proteins. These proteins are known as *microtubular associated proteins.* Of these, small proteins are called **tau.** A tau factor is a **calmodulin binding protein** and plays an important role in the assembly and disassembly of microtubules.

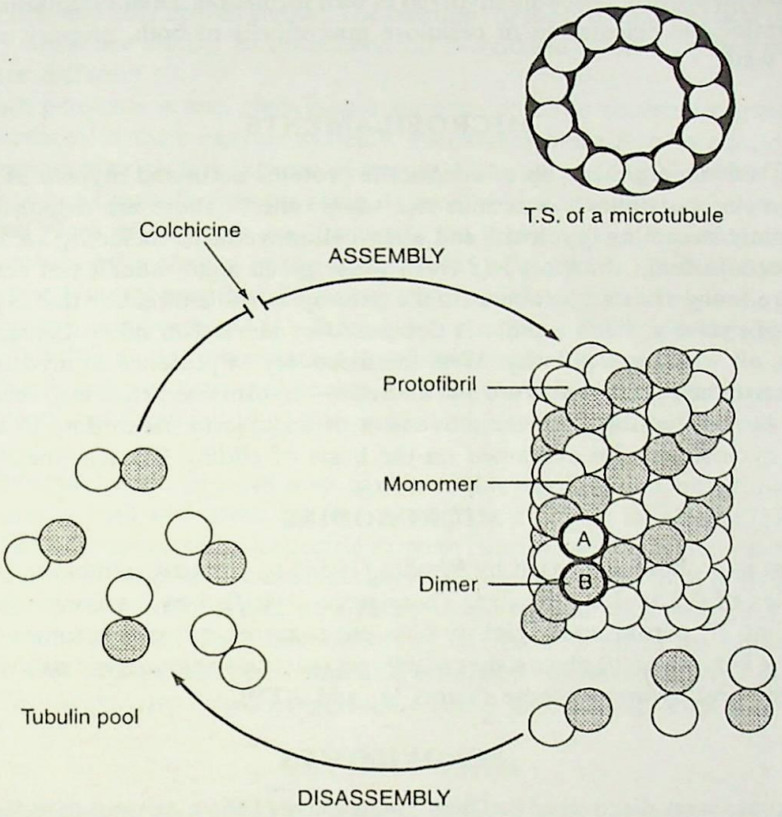

Fig. 1.18. Structure of microtubule showing T.S., helicoidal arrangement of protofibrils made up of tubulin dimers, assembly and disassembly.

Microtubules arise from **microtubule organising centres** (MTOC). One of them is centriole, or poles of mitotic spindle, kinetochores and polar plaques. MTOC contains tubulin, other proteins, steroid hormones, *ATPase* and RNA. RNA is important in maintaining the MTOC activity of centriole during mitotic spindle formation.

Microtubules are self-assembling polymers and are specially observed in the mitotic apparatus, cortex of meristematic plant cells, elongating cells etc.

Functions of Microtubules

These are associated with diverse functions such as:

(*i*) chromosome movement,
(*ii*) intracellular transport of materials and circulation,
(*iii*) cellular polarity and motality,

(*iv*) ciliary and flagellar movements,
(*v*) development and maintenance of cell form (*i.e.* morphogenesis),
(*vi*) movement of organelles within cell, etc.

These are main agents that establish asymmetries, polarities and changes of shape in higher plants.

Microtubules are probably involved in wall formation. Their orientation seems to determine the orientation of cellulose microfibrils of both, primary and secondary walls.

MICROFILAMENTS

Microfilaments are made up of contractile proteins **actin** and **myosin** as well as tropomyosin, troponin-C, α-actinin and some others. These are responsible for cytoplasmic streaming (cyclosis) and other cell movements including amoeboidal movements in fungi. In *Nitella* (a fresh water green alga), bundles of actin filaments are found situated just beneath the chloroplasts in a direction that is parallel to that of cyclosis. Each bundle is composed of about 100 microfilaments of 5 to 6 nm, all with same polarity. With the discovery of presence of myosin in the cytoplasm of the alga, it is believed that the **actin—myosin** interaction in the ectoplasm may be the motive force for the movement of endoplasm. According to a recent theory, cyclosis can be explained on the basis of sliding filament theory.

MICROBODIES

The term microbody was used by Rhodin (1954) to one unit membrane bounded organelles of 0.2 to 1.0 n m size. These were classified by Lazarow and Fujiki (1985) into (*i*) peroxisomes (rich in *catalase* enzyme), (*ii*) glyoxysomes (rich in *isocitrase* enzyme), (*iii*) glycosomes (catalyses reactions of glycolytic pathway upto PGA) and (*iv*) hydrogenosome (forms H_2 and ATP).

PEROXISOMES

Peroxisomes were discovered by Christian de Duve (1965). According to Salisbury and Ross (1986), these are found exclusively in photosynthetic tissues closely appressed with the chloroplast but Lazarow and Fuziki (1985) have reported their presence in animals, plants and fungal cells that carry out respiration (based on H_2O_2 metabolism) and fatty acid oxidation. The recent studies revealed that peroxisomes of a cell are found interconnected with each other through narrow, branched and tortuous tubules called *peroxisomal reticulum*. In yeast, peroxisomes reveal extensive interconnections among different peroxisomes which some times form elaborate compartments and parts of which resemble endoplasmic reticulum. Peroxisome is the third organelle, besides mitochondria and chloroplast, whose bio-genesis is through fission. It has to pass on to the next generation through germ cells which must contain at least one peroxisome. However, it differs from both mitochondria and chloroplast as it is bounded by one unit membrane and lacks DNA.

Peroxisomes are one unit membrane-bounded organelles, the membrane being 6.5 to 7 nm thick. The constitution of membrane protein is different from that

of ER which indicates that these are not formed by ER. Its membrane proteins are mainly synthesised by membrane-bound ribosomes *(ER* + ribosomes) but all enzymatic proteins (including *catalase* and other enzymes) are synthesised on free ribosomes and are inserted post-translationally into pre-existing peroxisome membrane. Peroxisome contains the enzyme system for respiration, based on hydrogen peroxide metabolism and fatty acid oxidation. The reactions of the β-oxidation (beta oxidation) of fatty acids are similar to mitochondrial β-oxidation, but enzymes catalysing them are different.

Both peroxisome and glyoxysome are considered as separate organelles due to differences in their enzyme systems. Peroxisomes are rich in *catalase* while glyoxysomes are rich in *isocitrase.* However, Lazarow and Fujiki (1985) proposed that these two organelles are the same. Immuno-electron microscopy has revealed that both types of enzymes are present in the same organelle during transition, which occurs by a change in the complement of enzymes. Thus, these two organelles are interconvertible. In young stages particularly during seed germination, glyoxysomes are found in a large number within a cell while during the later stages of a life cycle, peroxisomes are found in abundance.

Peroxisomes are now well known for their participation in photo-respiration in C_3 plants and β-oxidation of fatty acids and play an important role in thermogenesis.

Photorespiration process also involves chloroplasts and mitochondria. In peroxisomes, both formation and decomposition of H_2O_2 take place. Hydrogen peroxide is decomposed by a specific enzyme *catalase* which is abundantly found in this organelle. *Catalase* constitutes about 40 per cent of the total proteins found in the organelle. *Catalase* acts as a safety value to deal with peroxides that are dangerous to the cell. The other important enzymes found in the organelle are *glycolic acid oxidase* and peroxisomal β- oxidation enzymes (*acyl-Co A-oxidase, enoyl-CoA-hydrolase, 3-hydroxyacyl-CoA and 3 keto-acyl-CoA-thiolase*).

GLYOXYSOMES

Glyoxysomes were discovered by Breidenbach and Beevers (1967) from the extracts of the endosperm of germinating castor beans. These are 0.5 to 1.0 μm in size and are analogous particles to peroxisomes. Each glyoxysome has a single layered bounding membrane enclosing a fine granular stroma.

The enzymes of glyoxysomes are synthesised on free ribosomes in the cytosol and are then transported to the organelle. These enzymes are used to transform the fat stores of the seed into carbohydrates through the glyoxylate cycle. The overall equation of this cycle is as follows.

$$2 \text{ Acetyl CoA} \longrightarrow \text{Succinate} + 2H^+ + 2\text{CoA}$$

This cycle is a modification of Krebs cycle in which two auxiliary enzymes, *isocitrase lyase* and *malate synthetase* and two molecules of acetyl CoA are required, instead of one. The other three enzymes of the cycle *(citrate synthetase, aconitase* and *malate dehydrogenase)* are similar to those of Krebs cycle. In castor, these are involved in triglyceride metabolism.

Both peroxisome and glyoxysome are considered as separate organelles due to differences in their enzymes systems. Peroxisomes are rich in *catalase* while glyoxysomes are rich in *isocitrase*. Lazarow and Fujiki (1985) proposed that these two organelles are the same. Immuno-electron microsocopy reveals that both types of enzymes are present in the same organelle during transition, and transition occurs by a change in the complement of enzymes. Thus, these two organelles are interconvertible. In young stages, particularly during seed germination, glyoxysomes are found in a large number within a cell, while during later stages of a life cycle, peroxisomes are found in abundance in the cytoplasm. These are bounded by a single lipoproteinaceous unit membrane. They are believed to be formed by the pinching off of small bits of endoplasmic reticulum and contain mostly phospholipids, reserve oil droplets and hydrolytic enzymes.

SPHEROSOMES

Spherosomes were discovered by Dangeard (1919) but were named by Perner (1952). These are minute spherical bodies lying free in the cytoplasm and are thought to be involved in fat synthesis and storage and transport of lipids. They are bounded by a half (one protein and one lipid layer only) unit lipoproteinaceous membrane and are probably formed by the pinching off of small bits of endoplasmic reticulum. These may be involved in certain other activities also. Sorokin (1967) found in them the presence of mostly phospholipids and very little natural lipids and reserve oil droplets of similar nature. Holocomb *et al.* (1967) observed the presence of hydrolytic enzymes in these bodies, *e.g. proteases, nucleases, phosphatases, esterases etc.*

CILIA AND FLAGELLA

These are delicate, protoplasmic extensions of variable sizes and number. Flagella are longer, cylindrical, fewer in number showing independent movement, while cilia are shorter, flat, more in number exhibiting combined action during movement.

A cilium or flagellum arises from a basal body, the blepharoplast granule and consists of a central axial filament, *the axoneme.*

The axoneme consists of nine peripheral duplets of tubulin protein and two protein strands in the centre, *i.e.* 9+2 arrangement of tubulin fibrils.

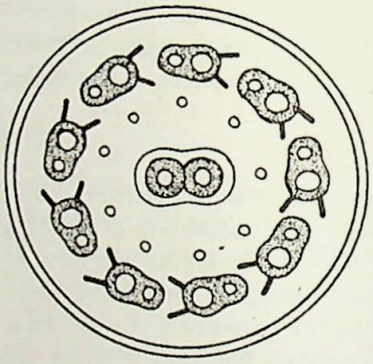

Fig. 1.19. C.S. of a flagellum showing 9+2 arrangement of fibrils.

NUCLEUS

The nucleus as a prominent body within a cell was first discovered by Robert Brown in 1831, in an orchid cell.

Structure and Composition

The nucleus is more or less spherical, lying in the cytoplasm and occupying about two-thirds of the cell space. Normally, a cell contains a single nucleus but multinucleate

cells have been reported in *Cladophora, Pithophora,* laticiferous cells in angiosperms etc. A typical nucleus is composed of a few prominent structures:

(*i*) **Nuclear membrane.** The nucleus remains bounded by two unit membranes of lipoproteinaceous nature, which run parallel to one another with a gap of about 200 to 400 Å. This gap is called perinuclear space and is an electron transport area. Electron microscopy shows that the nuclear envelope has a complex double membrane structure. The outer membrane at places gives out a tubular structure, referred to as endoplasmic reticulum. Small tubules known as microtubules remain attached to the surface of the nucleus. The nuclear envelope possesses openings of 300-600 Å size, called *annuli,* through which nucleoplasm communicates with the cytoplasm. Yoo and Bayley (1967) observed eight spheroid protein particles arranged around the circumstance of each annulus, which regulate the size of the annulus. Next to the inner membrane, an internal dense lamellae region of 200–800 Å size has been recognised.

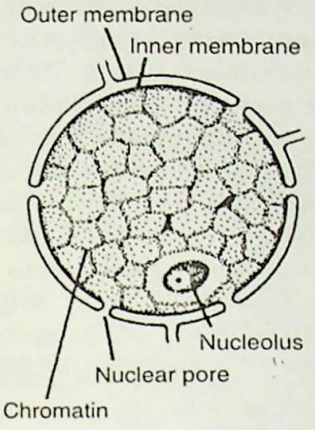

Fig. 1.20. A schematic figure of nucleus.

(*ii*) **Nuclear sap.** Encircled by the nuclear envelope is found the nuclear sap (nuclear matrix) variously termed as *nucleoplasm* or *karyolymph.* It is a semi-fluid substance and consists of proteins which also contains nucleic acids, nucleoproteins (both histones and protamines) etc.

(*iii*) **Nucleolus.** It is found lying in the nucleoplasm closely associated to the nucleolar organiser of one specific chromosome. The position of the nucleolus is a *species specific trait.* The nucleolus is a spherial body made up largely of proteins followed by *r*RNAs and *r*DNAs. Electron microscopic studies reveal that a typical nucleolus exhibits two distinct structural regions–the *core* (central region composed of compact fibrous elements) and the *cortex* (the surrounding granular area).

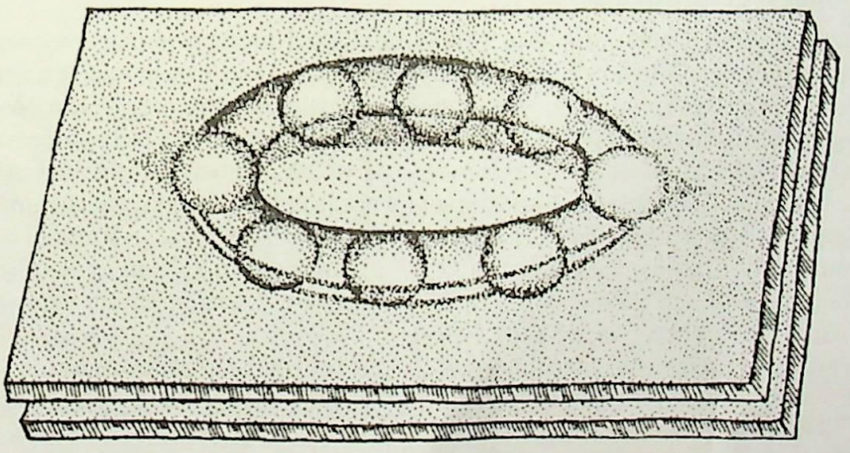

Fig. 1.21. Schematic representation of an annulus of nuclear membrane surrounded by eight spheroids.

Recent studies have shown that DNA of a nucleolus is circular and called *r*DNA (ribosomal DNA) which actively transcribes *r*RNA. Nucleolar DNA is *highly redundant* (highly repetitious type) and is an example of a giant *palindrome* (inverted repeat sequence). There are thousands of copies of *r*RNA genes in it. Each such gene transcribes to form 45 S *r*RNA, which is short-lived and is processed into 5.8 S, 18 S and 28S *r*RNAs. The systematic transcription of rows of genes simultaneously, gives to *r*DNA the appearance of a *christmas tree.* Nucleolus is thus actively involved in the synthesis of different types of ribosomal RNAs.

The assembly of ribosomes takes place on the surface of the nucleolus, from which, the ribosomal RNAs are formed within the nucleolus and ribosomal proteins are synthesized in the cytoplasm. From the cytoplasm, the ribosomal proteins are transported to the surface of the nucleolus where they are assembled with the *r*RNAs to form the ribosomes. These ribosomes are of 80 S type. At the time of cell division, the necleolus is withdrawn within the nucleolar organiser of the chromosome.

(*iv*) **Chromatin network.** This forms the skeleton of the nucleus and is so organised as to give a reticular appearance. Chromatin threads are the sites of main genetic material which controls all activities of the cell, metabolism as well as heredity. During cell division, the chromatids become tightly coiled, get enclosed in a definite proteinaceous matrix and are identified as chromosomes.

Chemically on dry weight basis, a nucleus has 70% proteins, 10–14% lipids, 5–10% DNA, 3–5% phospholipids and a chromatin consisting of DNA, some RNAs, some *RNA polymerases* and 3–5 or even more types of proteins (histones).

CHROMOSOMES

Strasburger (1875) is credited with the discovery of these thread-like structures which appeared during cell division. These structures called chromosomes (Greek word: *chroma* = colour; *soma*=body) became the most significant component of the cell, present in a highly organised fashion within the nucleus and specific in their number, size and shape.

Morphology of Chromosomes

The morphological aspects of a chromosome are studied during metaphase or anaphase. The number of chromosomes in a nucleus varies to a great extent and is a *species-specific trait.* In *Haplopappus gracilis,* a diploid nucleus contains only 4 chromosomes, while in *Ophioglossum regalis* (a pteridophyte) there are 1262 chromosomes in a diploid nucleus. Haploid set of chromosomes which is inherited is called **genome** and the whole collection of chromosome in a nucleus is referred to as chromosome complement. The genome in *Pisum sativum* is 7, *Allium cepa* is 8 etc. The size of chromosome shows a variation from 0.25 μm in fungi to 3.0 μm in some plants.

The shape of the chromosome is decided by the position of the centromere. Accordingly these may be of four types:

(*i*) *Telocentric*–The centromere is at the tip of the chromosome.

(*ii*) *Acrocentric*–The centromere is sub-terminal and chromosomes appear rod-like, having one small arm and the other very long.

(*iii*) *Sub-metacentric*–The centromere is close to the centre and the chromosome has unequal arms resembling a J-shape.

(*iv*) *Metacentric*–Centromere is situated at the centre of the middle part of the chromosome and has two equal arms. It appears V-shaped.

Structure

Chromosome is the most wonderful gift of nature. Structurally, they appear as a rod-shaped structure, bounded by a proteinaceous pellicle which encloses a jelly-like substance called matrix. The presence of matrix has been clearly shown in *Luzula campestris* (woodrush).

During metaphase, a chromosome is seen to consist of two symmetrical structures called chromatids, which become intertwined in the matrix. These chromatids are attached to each other by the centromere. During prophase and sometimes during metaphase, the chromosomal material becomes visible as very thin filaments called *chromonemata.* Several chromonemata coiled together and enclosed in a separate common matrix form a chromatid. The chromonema may be composed of 2, 4 or more fibrils which are coiled with each other. If the coiling is easily separable, it is termed as paranemic coiling and if closely intertwined and inseparable, it is termed as plectonemic coiling. The chromonemata of one chromosome are identical in nature to the chromonemata of other chromosomes in the same cell.

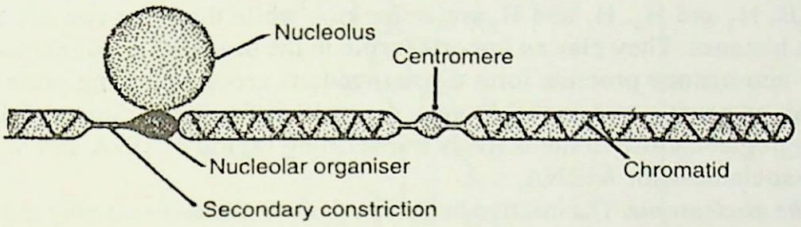

Fig. 1.22. Schematic figure of a chromosome.

The group of chromonemata at places show superimposed coiling, forming a dark band-like structure called *chromomere,* whereas the regions in between two chromomeres are designated as *interchromomeres.* The chromomeres were earlier believed to be the sites of genes, but these dark band structures found on chromosomes are now called heterochromatin segments and are the sites of genetically inactive genes. Euchromatin segments are light in colour and are genetically active.

The chromosome is not uniform throughout, but has a constriction called *centromere.* These have a basic structure consisting of a dense, dark-staining region called spherule or kinosome surrounded by inter-chromomeral fibrillae. Centromere has two important functions:

(*i*) It holds the two sister chromatids together until the end of the metaphase.

(*ii*) It is the site for the attachment of spindle fibres in order to transport the sister chromatids to opposite poles. This is mediated by the kinetochore. Chromosomes are usually monocentric (one centromere) but some are dicentric (two centromeres) or polycentric (many centromeres).

The chromosomes in addition to primary constriction (centromere) may sometimes possess secondary constriction at any point. It is associated with the nucleolus and may take part in the reorganisation of the nucleolus at the end of cell division, as such it may be called nucleolar-organising region. The part of the chromosome,