

B1 THE PLANT CELL

Key Notes

Cell structure

The plant cell has a cell wall and plasma membrane enclosing the cytoplasm. Organelles, bounded by membranes, occur within the cytoplasm and are supported and moved by the cytoskeleton. The nucleus contains DNA and nucleoli. Many plant cells have a large vacuole.

Cell membranes

The endomembrane system of the cell is involved in synthesis and transport. The nucleus is surrounded by a nuclear envelope. The endoplasmic reticulum (ER) is divided into perinuclear ER and cortical ER, and may be smooth or rough (coated with ribosomes). Material from the ER is modified and sorted in the Golgi apparatus (GA) from which it travels in vesicles to the plasma membrane or the vacuole.

Organelles of metabolism

Mitochondria generate adenosine triphosphate (ATP) from stored food reserves. Chloroplasts carry out photosynthesis. Microbodies include peroxisomes containing catalase and glyoxysomes containing enzymes of lipid biosynthesis.

The cell wall

The cell wall is a dynamic, metabolic structure made up predominantly of carbohydrate. Adjoining cells are inter-connected by plasmodesmata, in which membranes bridge the wall. Everything within the plasma membrane is the symplast; outside it is the apoplast, which is a water-permeated space, in which hydrophilic molecules are dissolved.

Related topics

The cell wall (B2)	Cell division (B6)
Plastids and mitochondria (B3)	Nucleus and genome (B5)
Membranes (B4)	

Cell structure

Plant cells show a wide range of shapes and internal structures, depending on their function. *Figure 1* illustrates the key features of a typical plant cell. Other cells, such as reproductive cells and conducting cells may be very different in appearance. It consists of a **cell wall** in close contact with a **plasma membrane** surrounding the **cytoplasm**, which is made up of aqueous fluid **cytosol** and many **organelles**. These organelles are supported and moved by a meshwork of fine protein filaments, the **cytoskeleton**, which includes **microtubules** made up of the protein **tubulin** and **microfibrils** made up of the protein **actin**. The nucleus contains genetic information in **chromosomes** and **nucleoli** that contain machinery for the production of **ribosomes**.

In most plant cells, there is a **vacuole** that may occupy up to 90% of the cell volume, surrounded by a membrane, the **tonoplast**. It contains solutes dissolved in water. It is important in storage and osmotic regulation (Topic B4).

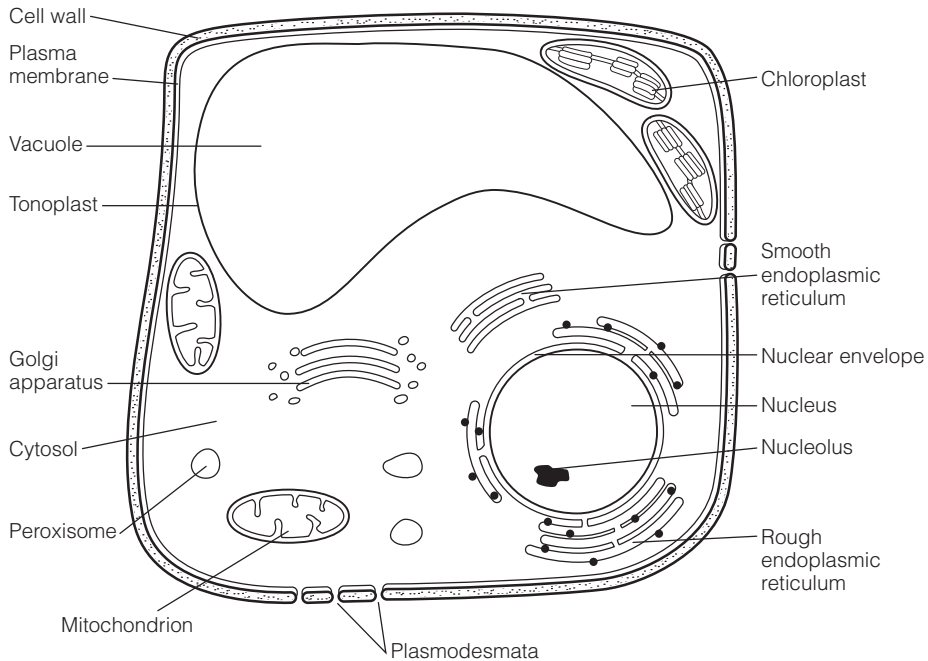


Fig. 1. Features of a typical plant cell.

Cell membranes

The cell contains a system of membranes termed the **endomembrane system** involved in the synthesis and transport of materials. The nucleus is bounded by two membranes, the **inner** and **outer nuclear envelope**, with **nuclear pores** to permit traffic of material. The outer nuclear envelope may be joined to a membrane system, the **endoplasmic reticulum (ER)** which may be **smooth** (site of lipid synthesis) or **rough** (coated with **ribosomes**; site of protein synthesis). In plant cells, the ER is often divided into **perinuclear ER** (ER around the nucleus) and **cortical ER** (ER at the cell periphery). Material from the ER is trafficked to the **Golgi apparatus (GA)**, a series of stacked membrane compartments (**cisternae**) in which modifications are carried out by enzymes. Material leaving the GA travels in **vesicles** to its destination, either the **plasma membrane** or the **tonoplast** (vacuolar membrane).

Organelles of metabolism

Plant cells have two major organelles of energy metabolism, one, the **chloroplast**, not being found in animal cells. **Mitochondria** (Topic B3) are bounded by a double membrane and generate adenosine triphosphate (ATP) from stored food reserves (carbohydrate, lipid; Topic J4). **Chloroplasts** (Topic B3) belong to a group of organelles known as **plastids**. Chloroplasts photosynthesize (Topics J1 and J2), using the energy of sunlight and carbon from carbon dioxide to produce carbohydrate. **Amyloplasts** are plastids modified to store starch. Plant cells also contain **microbodies** that are small membrane-bounded organelles. **Peroxisomes** contain catalase to remove toxic hydrogen peroxide produced in metabolism and **glyoxysomes** contain some enzymes of lipid biosynthesis.

The cell wall

Surrounding the cell is a **cell wall** that is a metabolically active and constantly modified structure made up predominantly of structurally strong complex poly-

saccharides (Topic B2). Adjoining cells may be inter-connected by **plasmodesmata**, pores through the wall where plasma membrane and ER connect. Everything within the plasma membrane is termed the **symplast**; everything outside it is the **apoplast**, which is a water-permeated space, in which hydrophilic molecules are present in solution. Cell walls function to adhere adjacent cells together in the formation of tissues and organs.

B2 THE CELL WALL

Key Notes

Cell wall structure	Primary cell walls are made up of cellulose microfibrils surrounded by a matrix of polysaccharides including hemicelluloses and pectins. Secondary cell walls contain cellulose microfibrils surrounded by polysaccharides and lignin.
Cell wall synthesis	Cellulose microfibrils are synthesized from uridine diphosphoglucose (UDP glucose) by cellulose synthase, an enzyme complex forming rosettes in the plasma membrane. Matrix materials are synthesized in the Golgi apparatus and deposited into the wall by secretory vesicles that fuse with the plasma membrane.
Cell wall function	Cell walls are essential for adhesion and the growth and formation of the plant body. Primary cell walls have high tensile strength and oppose turgor. Lignified secondary walls give greater strength. Cell walls act as a barrier to pathogens and deter herbivory. Primary cell walls are generally permeable to water and small molecules. The dynamic nature of primary cell walls permits cell expansion and plant growth.
Plasmodesmata	Plasmodesmata are structures in which membranes from adjacent cells connect through a pore in the cell wall. They link adjacent plasma membranes and cytoplasm. The desmotubule is a tube of endoplasmic reticulum in the center of the pore surrounded by globular proteins. The structure permits regulated transport between the cells.
Related topics	The plant cell (B1) Roots (C2) Herbaceous stems and primary growth (C3) Woody stems and secondary growth (C4)

Cell wall structure

Almost all plant cells have a **primary cell wall**. It is made of a long-chain polysaccharide, **cellulose**, aggregated into bundles to form fibers, **microfibrils** 10–25 nm in diameter. The orientation of the microfibrils is governed by the **cytoskeleton** (see cell wall synthesis, below) and the fibers are laid down in a coordinated fashion so that the plasma membrane is covered in layers (*Fig. 1*). The orientation of the fibers changes as the cell develops. Microfibrils have a great tensile strength; their strength is further enhanced by interlinking between the fibrils by a **matrix** composed of **hemicelluloses** and **pectins**. Between cells, there is a **middle lamella**, an adhesive region rich in **pectic polysaccharides** where adjacent cell walls adhere to one another.

Some cells of strengthening and vascular tissues develop a **secondary cell wall**, between the primary wall and the plasma membrane. Secondary cell walls also contain cellulose **microfibrils**, infilled with polymerized phenolic

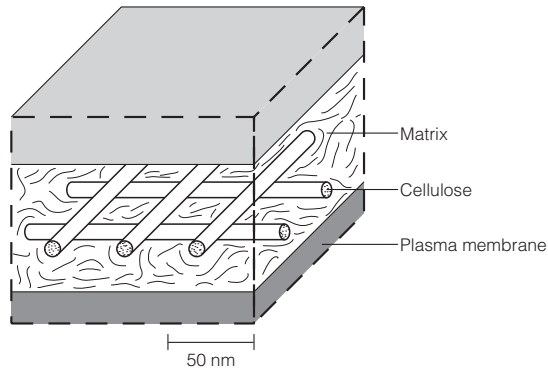


Fig. 1. The primary cell wall consists of cellulose microfibrils deposited in layers surrounded by a matrix of hemicelluloses and pectins.

compounds, **lignins**, that strengthen the wall. This is evident in **wood** (Topic C4). Lignin protects against digestion of the wall by fungal enzymes and against mechanical penetration by fungal hyphae and other pathogens (Topic M4). Secondary walls are produced in layers, with the cellulose fibrils orientated in different directions; this ‘lamination’ gives considerable strength to the structure.

Cell wall synthesis

The **primary cell wall** is deposited while the cell is increasing in size. Cellulose is deposited by an enzyme complex, **cellulose synthase** that appears as a rosette in the membrane (Fig. 2). Cellulose is synthesized from **uridine diphosphoglucose** (UDP glucose) which is added simultaneously to the end of several strands, forming a **cellulose fiber** (or **microfibril**) at the cytoplasmic face of the membrane. As the strand elongates, the rosette moves in the membrane, extruding the strand to lie along the outer face of the membrane. The rosettes move parallel to fibers within the cell, the **cortical microtubules**. **Matrix materials** (hemicelluloses, lignin, pectic substances) are synthesized in the **Golgi apparatus** and transported to the plasma membrane in **secretory vesicles** that discharge their contents into the wall. New wall material is deposited at its inner face – that is the face adjacent to the plasma membrane.

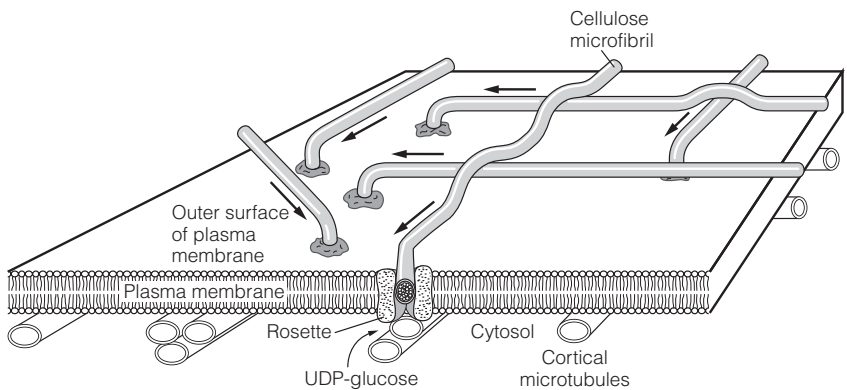


Fig. 2. The deposition of cellulose microfibrils by rosettes of cellulose synthase follows the underlying pattern of cortical microtubules, part of the cytoskeleton. (Redrawn from Raven, P.H. et al. (1992) Biology of Plants, 6th Edn, W.H. Freeman.)

Cell wall function

Primary cell walls have high **tensile strength**. They give strength to stems, leaves and roots, particularly by opposing turgor pressure from cell contents. They show **plasticity** and **elasticity**; as the cell grows, the dynamic structure of the wall means that it is able to adjust its structure to permit that growth. A new cell wall is rapidly formed after cell division. Cell walls prevent plasma membranes from contact except at pores, the plasmodesmata (see below). Primary cell walls are permeable to water and low molecular weight molecules (ions, organic compounds and small proteins) which reach the plasma membrane. This movement is restricted if the wall is lignified or contains suberin as at the endodermis (Topic C2). Adjacent cell walls adhere at the **middle lamella**, giving **cell adhesion** and allowing formation of tissues and organs. **Lignification** in secondary cell walls (Topic C4) greatly enhances **compressive strength**, permitting woody structures more than 100 m tall. Cell walls also provide resistance to pathogens and herbivory.

Plasmodesmata

Plasmodesmata (singular **plasmodesma**) are structures in which membranes from adjacent cells connect through a pore in the cell wall (Fig. 3). The plasma membranes of the two adjacent cells join around the pore and a **desmotubule**, a tube of endoplasmic reticulum (ER), is present in the center of the pore, surrounded by **globular proteins**. This means that the plasma membrane, ER and cytoplasm of two adjacent cells adjoin. The structure permits regulated transport between the cells. Careful study of plant tissues reveal that many cells connect through plasmodesmata forming what could be considered to be colonies of cells all interconnected with their neighbors.

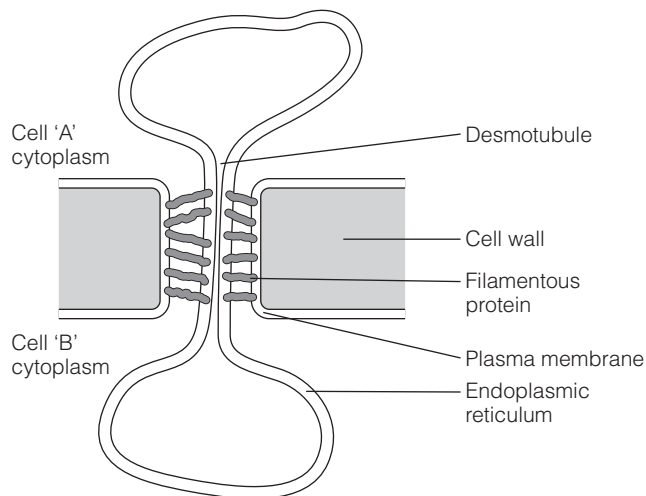


Fig. 3. The structure of a single plasmodesma in transverse section. Note the connecting membranes (endoplasmic reticulum via the desmotubule and plasma membrane) and cytoplasm penetrating the cell wall of two adjoining cells.

B3 PLASTIDS AND MITOCHONDRIA

Key Notes

Plastids

Plastids are a family of organelles bounded by two external membranes. Family members include: photosynthetic chloroplasts; chromoplasts containing pigments; leucoplasts involved in lipid biosynthesis; amyloplasts that store starch; and etioplasts, an intermediate stage in production of chloroplasts.

Chloroplast structure and origins

Plastids contain a small genome encoding some plastid proteins. Many other chloroplast proteins are encoded by nuclear genes. The endosymbiont theory suggests that they arose as primitive photosynthetic organisms that colonized cells. Stacks of thylakoid membranes (grana) containing chlorophyll are present in the matrix space (stroma).

Mitochondria

Mitochondria are the site of synthesis of adenosine triphosphate (ATP) using lipids, carbohydrates and other high energy compounds as fuel.

Mitochondrial structure

Mitochondria are bounded by an outer membrane with an inner fluid-filled stroma (matrix). An inner, selectively permeable membrane, folded into cristae, contains the components necessary for ATP-synthesis. Mitochondria contain a small genome that encodes some, but not all, mitochondrial proteins.

Related topics

The plant cell (B1)
Photosynthetic pigments and the nature of light (J1)

Major reactions of photosynthesis (J2)

Plastids

Plastids are characteristic of plant cells and otherwise only occur in plant-like protists. They are organelles bounded by a double membrane. There are several types of plastid in plant cells. **Chloroplasts** are photosynthetic plastids found in the mesophyll cells of leaves, the cortex of herbaceous stems and in small numbers elsewhere in the plant. The green coloration is due to the presence of the pigment chlorophyll (Topic J1). **Chromoplasts** contain pigments other than chlorophyll and are associated with brightly colored structures like ripe fruit. **Leucoplasts** are colorless and are found in many cell types. They include **amyloplasts** that store starch and **elaioplasts** that synthesize lipid. **Etioplasts** are an intermediate stage in the production of photosynthetic chloroplasts in tissue exposed to light for the first time.

Chloroplast structure and origins

The two membranes of plastids surround a central fluid-filled **stroma** (Fig. 1). Plastids contain their own DNA in a small ‘plastid genome’ containing genes for some chloroplast proteins. This, together with the presence of the double outer

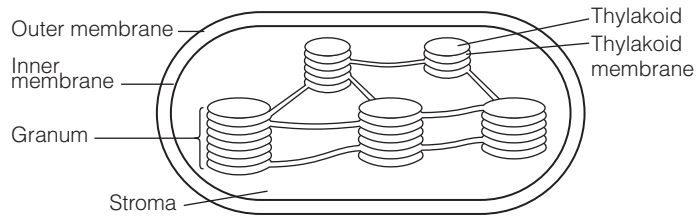


Fig. 1. Chloroplast structure.

membrane, has led to suggestions that they arose as **endosymbionts** – primitive photosynthetic organisms that colonized a non-photosynthetic cell. However, while some chloroplast proteins are synthesized on **plastid ribosomes**, from genes in the chloroplast genome, many others are encoded by nuclear genes and imported. Chloroplasts are highly organized for photosynthesis. Suspended in the stroma are **thylakoids**, membrane discs that form stacks or **grana**. Individual stacks are interconnected by tubes of **thylakoid membrane**. The photosynthetic pigments are arranged in the stacks so that they can be orientated to capture as much light energy as possible. For details of the mechanism of photosynthesis see Topics J1 and J2.

Mitochondria

Mitochondria convert the energy in storage reserves, like lipid, starch and other carbohydrates, into the high energy compound **adenosine triphosphate (ATP)**. The mitochondrion (Fig. 2) provides an isolated environment in which high energy intermediates can be formed without reactions with other cell constituents. Mitochondria contain a small **mitochondrial genome**, a circular piece of DNA encoding some (but not all) mitochondrial proteins, which are synthesized on mitochondrial ribosomes. Other proteins are encoded by nuclear DNA and synthesized on cytoplasmic ribosomes. Mitochondria can divide to give further mitochondria and can fuse to form an interconnected tubular mesh. Mitochondria are present in all cells and are abundant in those with high energy demands like phloem companion cells (Topic C3).

Mitochondrial structure

Mitochondria are bounded by two outer membranes. The inner of these membranes is invaginated (folded) to form **cristae** (singular **crista**) which project into the inner space, the **stroma** or matrix. This inner mitochondrial membrane therefore separates two compartments: the **intermembrane space** and the **matrix space**. It is selectively permeable and contains the transport proteins involved in ATP production (Topic J4).

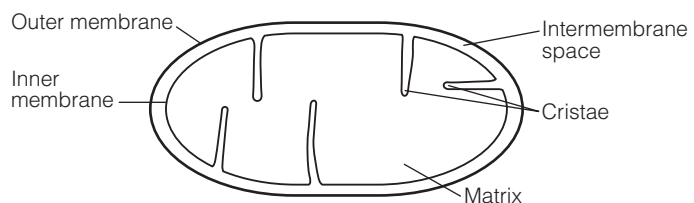


Fig. 2. The structure of a mitochondrion.

B4 MEMBRANES

Key Notes

Membranes

Membranes are made up of a lipid bilayer with membrane proteins. The membrane is a hydrophobic region through which charged or large polar solutes cannot pass unless via a membrane protein. They separate compartments of different composition. Cells contain membrane-bounded organelles such as mitochondria and chloroplasts and membrane systems such as the endoplasmic reticulum (ER) and Golgi apparatus.

Endoplasmic reticulum

The endoplasmic reticulum (ER) is a system of flattened sacs or tubes of membrane. Smooth ER is the site of lipid synthesis and rough ER of protein synthesis. ER may be associated with the nuclear envelope, but may also be at the cell periphery. Proteins targeted for the ER lumen or membrane bear a signal sequence and are synthesized on ER ribosomes. Subsequently, modification of the proteins may occur before they are exported to other locations by vesicles.

The Golgi apparatus

The Golgi apparatus is a system of stacked membrane cisternae. It is a site of protein modification and polysaccharide biosynthesis. Proteins are delivered to the *cis* face by vesicles and move through the *medial* cisternae to the *trans* face for export by the vesicles of the *trans* Golgi network (TGN). Enzymes within the cisternae synthesize polysaccharides or modify proteins by glycosylation.

The plasma membrane

The plasma membrane is a single membrane bounding the cytosol. It generates a *trans*-membrane electrochemical gradient by pumping protons. It maintains ionic homeostasis of the cytoplasm and transports nutrients and other products. Other plasma membrane functions include: sensing and signaling (receptor proteins); secretion, turgor and communicating with adjacent cells through plasmodesmata.

The tonoplast

The tonoplast is a single membrane surrounding the vacuole. It maintains ionic homeostasis of the cytoplasm and transports nutrients and other products by maintaining an electrochemical gradient driven by proton pumping. Vacuoles form from pro-vacuoles formed in the Golgi apparatus. A mature vacuole contains inorganic ions, sugars, enzymes and organic acids. Some contain secondary products.

Related topics

The plant cell (B1) Movement of nutrient ions across membranes (I3)

Membranes

Biological membranes are made up of a **lipid bilayer** in which membrane proteins are embedded, either deeply as integral membrane proteins or at the edge as peripheral membrane proteins (*Fig. 1*). Membrane lipids have **hydrophilic head groups** and **hydrophobic tails** that are buried within the

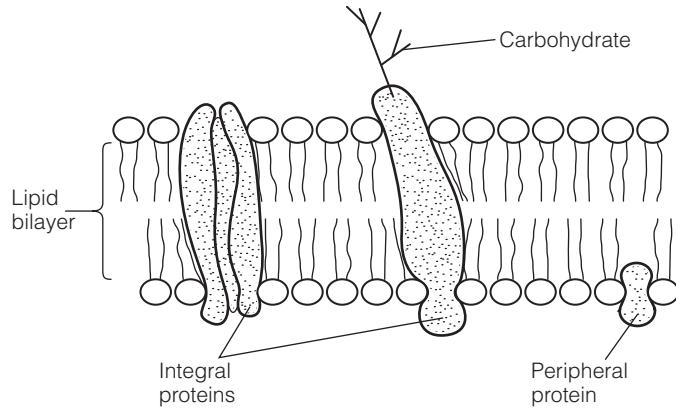


Fig. 1. The membrane consists of proteins and a lipid bilayer. Proteins in a simple biological membrane exist suspended in a surrounding 'sea' of lipid within which they may move laterally and rotate.

membrane, making a hydrophobic domain not readily crossed by charged hydrophilic (polar) substances. This barrier means that the membranes can separate two compartments of different composition. The proteins within the membranes govern the composition of those compartments by **selective transport**. This may be **active** (using ATP) or **passive** (allowing a substance to move from one compartment to another driven by an electrochemical gradient). As well as **transport proteins**, membranes also contain **receptor proteins** that transduce signals such as phytohormones, gravity or light; anchor proteins that attach the membrane to the cytoskeleton and cell wall; and enzymes involved in the synthesis or degradation of cellular constituents.

Some organelles are **membrane-bounded** (e.g. mitochondria and chloroplasts). In other instances, the functional entity is the membrane itself, which may enclose a separate compartment or **lumen** (e.g. the endoplasmic reticulum and Golgi apparatus). The membranes of the cell may be considered as a more or less complete continuum from the sites of synthesis of new membrane to mature, functioning membranes. Old membrane components are constantly being recycled – removed from the membrane and reprocessed or hydrolyzed. Much of this flow of membrane through the cell occurs in **vesicles**, small sacs of membrane.

Endoplasmic reticulum

The **endoplasmic reticulum (ER)** is a network of membranes in the cytoplasm that form either tubules (**tubular ER**) or flattened sacs (**cisternal ER**). The ER may be divided into two types. **Smooth ER** is the site of membrane lipid synthesis and new membrane assembly. **Rough ER** appears rough due to the presence of **ribosomes** and is the site of the synthesis of membrane proteins and proteins destined for secretion or insertion into vacuoles. Free ribosomes, not bound to membrane, are the site of synthesis of proteins not associated with membranes. ER may be closely associated with the outer **nuclear envelope (NE; Topic B5)**. The ER lumen and the lumen between inner and outer NE are a continuum. ER may also be separate from the NE; **cortical ER**, for instance, is located just beneath the plasma membrane. Proteins destined for insertion into the ER membrane or to the lumen bear a **signal peptide**, a short amino acid sequence targeting the protein synthetic apparatus to its destination. Some

simple modifications of protein may occur in the ER – for instance, simple **glycosylation** reactions in which carbohydrate residues are added to the protein. Further modifications require the protein to be transported to the Golgi apparatus (GA), the next stage in the pathway.

The Golgi apparatus

The **Golgi apparatus (GA)** is made up of a stack of flattened membrane sacs called **cisternae**, of which there may be only a few or many. Material enters the GA in vesicles, which fuse with the Golgi membranes. The stacks (**dictyosome**) are polar; new material is added at one face (the **cis face**) and transported through the **medial cisternae** to the **trans face**, from which a network of secretory vesicles, the **trans Golgi network (TGN)**, exports the product (Fig. 2). Two models exist to explain how materials move through the GA; the **cisternal maturation** model suggests new cisternae are constantly being added to the *cis* face, which then gradually mature until released as vesicles at the TGN. The **vesicle traffic model** suggests that the cisternae remain for the lifetime of a GA with material being moved from cisterna to cisterna by vesicles.

The GA prepares proteins and polysaccharides for secretion. Depending on cell type, it may be more or less dedicated to one or other activity. Enzymes in the GA either synthesize complex carbohydrates, or add carbohydrate groups to proteins (**glycosylation**). The *cis*, *medial* and *trans* GA contain different enzymes which progressively modify the material passing through. At the end of the process, material for export is sorted and packaged in **secretory vesicles**, which move to their membrane destination before fusing with it and discharging their contents. Contents in the lumen of the vesicle are either secreted or enter the lumen of the membrane compartment they fuse to; proteins in the vesicle membrane are incorporated into the membrane itself.

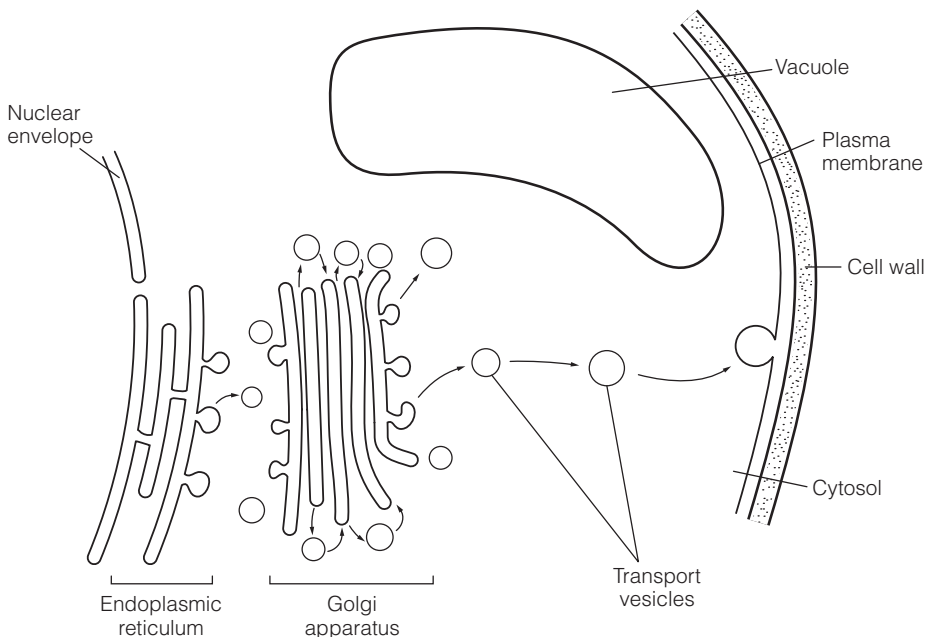


Fig. 2. The secretory pathway and insertion of new material into cell membranes. Membrane vesicles carry new membrane and material for export from the GA to the vacuole or plasma membrane. Membrane material is also returned by vesicles.

The plasma membrane

The **plasma membrane** is a single membrane bounding the cytoplasm. New material is added to it and old material removed by vesicles (*Fig. 2*). The plasma membrane has a number of functions:

- (i) maintaining ionic homeostasis of the cytoplasm and transporting nutrients and other products. To do this, a ***trans*-membrane electrochemical gradient** is maintained, driven by a **proton-pumping ATPase** (which uses the energy of ATP to transport protons across the membrane; Topic I3). Many other proteins located in the membrane transport ions and other molecules;
- (ii) sensing and signaling the cells environment. **Receptor proteins** at the plasma membrane respond to the presence of signals (e.g. hormones) and cause changes in intracellular signaling molecules which result in altered cell functions;
- (iii) **secreting materials** (e.g. the constituents of the cell wall; Topic B2);
- (iv) **regulating turgidity** by osmotic effects resulting in the cytoplasm exerting force against the cell wall;
- (v) **communicating** with other adjacent cells through **plasmodesmata** (Topic B1).

The tonoplast

The **tonoplast** is a single membrane surrounding the vacuole (Topic B1). Like the plasma membrane, the tonoplast has a role in maintaining ionic homeostasis of the cytoplasm and in transporting nutrients and other products. A ***trans*-membrane electrochemical gradient** is maintained, driven by a **proton-pumping ATPase** (Topic I3). The tonoplast also contains other **transport proteins** which regulate the ionic homeostasis of the cytoplasm and vacuole. A mature vacuole contains inorganic ions, sugars, enzymes and organic acids. Specialized vacuoles may contain complex organic compounds (secondary products; Topic J5), long-term storage products such as proteins or organic acids involved in carbohydrate metabolism.

B5 NUCLEUS AND GENOME

Key Notes

Structure of the nucleus

The nucleus is bounded by a double membrane, the nuclear envelope, which is perforated by nuclear pores that permit the movement of materials from the interior of the nucleus (nucleoplasm) to the cytoplasm. The genetic material (DNA) is present as a DNA–protein complex known as chromatin. The nucleolus is the site of synthesis of the ribosome subunits.

Structure and function of chromatin

The DNA double helix is entwined around histone proteins in units called nucleosomes, packed together to give a 30-nm fiber of chromatin. Genetic information is contained within the DNA as codons. Genes are made up of a structural region encoding the protein to be synthesized and promoter regions that control gene activity. In transcription, the DNA untwines and RNA polymerase II copies it as an RNA strand. Non-transcribed introns are removed giving messenger RNA (mRNA) which is translated into protein on ribosomes.

Plant chromosomes

Chromosomes are made up of tightly packed chromatin. Chromosomes in dividing cells have two chromatids joined at a centromere. Endoreduplication results in many copies of each chromosome, while gene amplification results in multiple copies of a few highly used genes. Polyploid cells have more than the usual number of chromosomes; normally only polyploids with an even number of chromosome copies are fertile as they can undergo chromosome pairing in meiosis.

Related topics

Membranes (B4)
Cell division (B6)

Features of growth and development (F1)

Structure of the nucleus

Each living plant cell contains a nucleus separated from the cytoplasm and other organelles by a double membrane, the **nuclear envelope** (Topic B4). The size and prominence of the nucleus varies depending on the major functions of the cell. Cells in meristems (Topic C1), which are to undergo cell division, have a large nucleus. Other cells, such as those of the parenchyma (Topic C3), have a smaller nucleus, with most of the cell occupied by the vacuole (Topic B4). The nuclear envelope surrounds the fluid **nucleoplasm**. Movement from nucleoplasm to cytoplasm is possible through complex protein structures, the **nuclear pores**, which span both membranes. Nuclear pores are complex multi-protein structures that regulate movement into and out of the nucleus; their most important function is to permit messenger RNA (mRNA) molecules and ribosomes to leave the nucleus. Within the nucleus, the DNA is entwined with proteins, the DNA–protein complex being termed **chromatin**. In interphase, the chromatin appears to be spread throughout the nucleoplasm; in mitosis, however, it condenses to form distinct chromosomes (Topic B6).

The **nucleolus** is often seen as a densely stained region in micrographs of the nucleus. It is the center for the synthesis and assembly of components of **ribosomes**, structures involved in protein synthesis. Ribosomes are exported from the nucleus where they function to synthesize proteins either free in the cytoplasm or attached to membranes like the outside of the nuclear envelope or the rough endoplasmic reticulum (Topic B4).

Structure and function of chromatin

DNA in the nucleus is associated with protein in a complex known as chromatin. The basis of chromatin is a double helix of DNA; this entwines around proteins called **histones**. Stretched out, the structure resembles beads on a necklace. Each 'bead' of DNA and histone is known as a **nucleosome**. An additional histone protein binds to the DNA, and causes an additional level of coiling. This results in the DNA-histone 'beads' packing closely together to give a 30-nm fiber of chromatin. This fiber then forms loops along a protein scaffolding. In metaphase (Topic B6), additional coiling and close-packing gives rise to highly condensed chromosomes.

The genetic information of the cell is contained within the DNA in the form of **codons**: triplets of nucleotides which encode an amino acid or indicate the start or finish point of each gene. Each gene is made up of two regions: a **structural region** which contains the information for the amino acid sequence of the protein and which is copied (**transcribed**) to mRNA when the gene is active and a **promoter region** which controls whether the gene is transcribed (*Fig. 1*). A single gene may be regulated by a number of factors, such as hormones and factors specific to where the cell is, for instance the root or shoot. Between the structural and promoter regions lies a sequence rich in adenosine and thymidine (A and T) known as the **TATA box** which is important in binding the enzyme that synthesizes mRNA. Genes contain regions which will be transcribed to mRNA (**exons**) and regions which will not (**introns**). Several (or many) introns may be found within one gene.

In order for a gene to be transcribed, the DNA double helix must unwind over a short region. **RNA polymerase II** commences copying a short distance from the promoter region, then moves along the gene and copies the DNA template as an RNA strand. The RNA strand contains a transcription of both introns and exons. Introns are then removed to form the mRNA which migrates out of the nucleus via the nuclear pores to be translated into protein at ribosomes.

Plant chromosomes

Plant **chromosomes**, which become clearly visible under the microscope in mitosis, are made up of tightly packed chromatin. When visible in this way, the chromosomes have passed through the S-phase of the cell cycle (Topic B6) and so a copy of the DNA has been synthesized by **DNA polymerase**. This remains attached so that the chromosomes have two **chromatids** joined at a **centromere** (*Fig. 2*).

Normally during cell division, each daughter cell receives a copy of the entire genetic information of its parent. At this point, the cell could cease synthesizing DNA and go on to differentiate; however, most plant cells go on to generate further copies of their genes in a process known as **endoreduplication** (Topic B6). In some instances, **gene amplification** results in multiple copies of a few highly used genes being made. If a gamete is formed by cells which have not undergone **meiosis** (Topic B6), the resultant cell has two sets of genes present (it is **diploid**). If it is then fertilized by a normal (**haploid**) gamete, the resulting

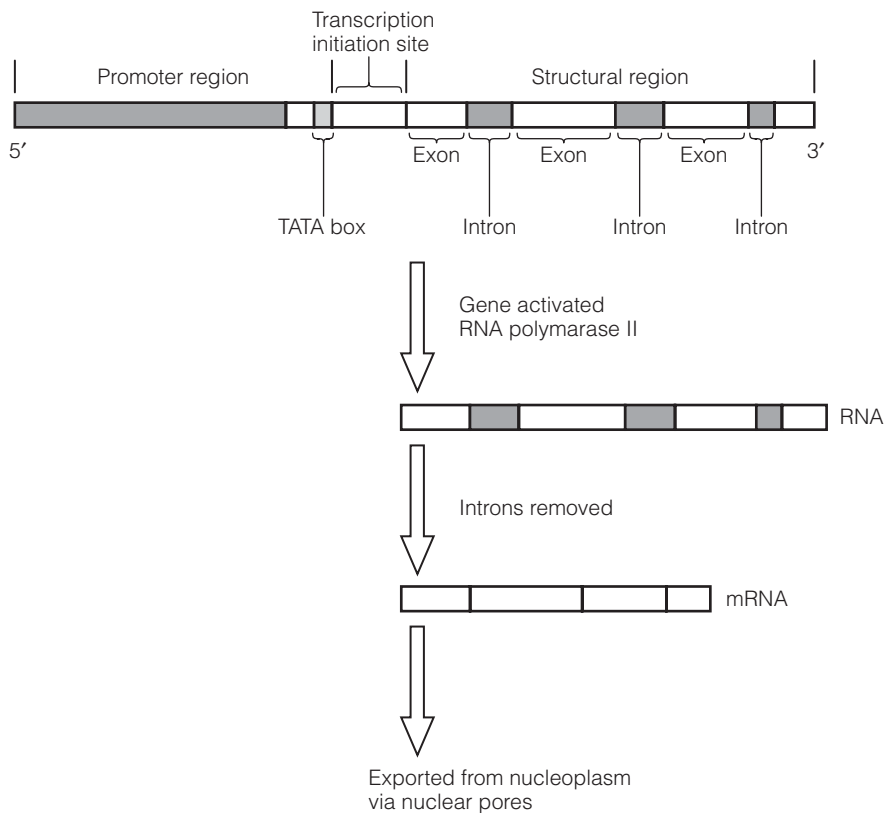


Fig. 1. The structure of a plant gene. The promoter region is adjacent to the structural region that contains the code for the final protein, made up of exons and introns. The TATA box is important in RNA polymerase II binding; DNA copying begins 20–30 base pairs away at the transcription start site.

offspring is **triploid** (has three sets of genes). In plants, this is frequently non-lethal and plants may show **polyploidy**, that is more than one copy of each chromosome. Plants with an even number of copies are fertile, such as **hexaploid** wheat (six copies), while those with an odd number are normally sterile as they cannot undergo pairing of homologous chromosomes during meiosis.

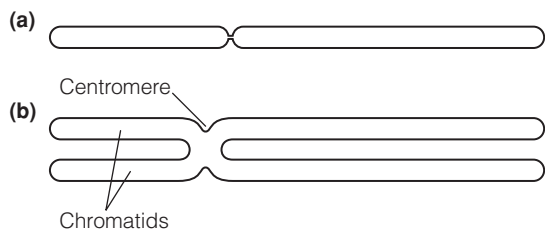


Fig. 2. A chromosome before (a) and after (b) duplication of the single chromatid during S-phase. Note that the two chromatids are joined at the centromere. They later separate to donate one chromatid to each of the daughter cells formed.

B6 CELL DIVISION

Key Notes

The cell cycle

Cell division occurs in stages: interphase G_1 – cell enlarges, nucleus migrates to center, protein synthesis; interphase S – DNA replication occurs; interphase G_2 – preprophase band and structures of mitosis form, chromosomes condense. In M-phase mitosis, chromosomes replicate and divide to form two daughter nuclei. In M-phase cytokinesis, the cytoplasm divides and a cell plate and new cell walls form.

Cell cycle control

The cell cycle has two check-points: G_2/M and G_1/S . Progression through the cycle is controlled by cyclins that are synthesized and degraded through the cycle and activate cyclin-dependent protein kinases (CDPKs).

Meiosis

Meiosis occurs to produce haploid cells. It involves an extra round of cell division. The first phase, prophase to anaphase I, results in exchange of DNA between the pairs of chromosomes followed by their separation with both chromatids present. The second phase (metaphase II to telophase II) is a mitosis resulting in separation of the chromatids and the formation of four haploid cells.

Related topics

- The plant cell (B1)
Nucleus and genome (B5)
Meristems and primary tissues (C1)
- Pollen and ovules (D2)
Features of growth and development (F1)

The cell cycle

Cell division in plants occurs in meristems (Topic C1) and involves two parts: **mitosis** in which the chromosomes are replicated and sorted into two nuclei, and **cytokinesis** in which the cell wall, cytoplasm and organelles divide. In dormant meristems, the cells rest in **G_0 phase**. When conditions are correct, the cell begins the processes leading to division. The entire cycle may be considered as four phases, **G_1 , S , G_2 and M** (Fig. 1).

In **G_1 phase** the cell doubles in size and new organelles and materials needed for two cells are formed. During this phase, the nucleus migrates to the center of the cell and is surrounded by a sheet of cytoplasmic strands called the **phragmosome** that bisects the center of the cell at the plane across which it will divide. The phase ends with the **G_1/S checkpoint**. The process can stop at this point (see Cell cycle control, below), or proceed to **S phase** in which DNA and associated nuclear proteins are replicated. At the end of S phase the cell contains two full copies of its genetic information. It proceeds to **G_2 phase** when the chromosomes begin to condense and structures required for division form. A distinct band of microtubules (Topic B1), the **pre-prophase band**, forms around the cytoplasm in a ring where the edge of the phragmosome lay, again predicting the plane of cell division. At the end of G_2 , the cell has to pass another checkpoint (**G_2/M**) at which stage, if conditions are suitable, it enters **M phase** in which the cell divides.

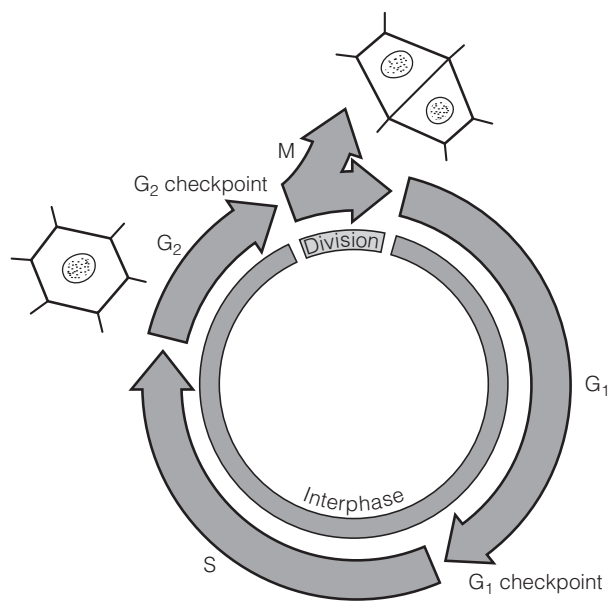


Fig. 1. Key phases of the cell cycle.

Stages G_1 to G_2 are known as **interphase**. M phase, when division occurs, can be divided into a series of stages that can be recognized by microscopy (Fig. 2 and Table 1).

Cell cycle control

In **meristems** (Topic C1), a population of cells characterized by thin cell walls and the lack of large vacuoles are constantly dividing. The daughter cells may undergo a few further divisions, but then lose the capacity to divide and after a phase of cell enlargement generally develop large vacuoles. **Plant hormones**,

Table 1. Events in mitosis

Stage	Events
Early prophase	Chromosomes visible in nucleus
Mid prophase	Chromosomes shorten and thicken; the two parts (chromatids) making up each chromosome become visible with a join (centromere)
Late prophase	Kinetochores (specialized structures attached to microtubules) attach at the centromeres. Nuclear envelope breaks down
Metaphase	Chromosomes align at the center of the cell; chromosomes aligned by microtubules which run from the centromeres to the pole ends of the cell
Anaphase	Begins with coordinated movement of chromatids, drawn by the kinetochore microtubules. The two sets of chromatids (now called daughter chromosomes) are now separated to opposite ends of the cell
Telophase	Daughter chromosomes now visible at ends of cell; nuclear envelopes develop around chromosomes and a cell plate forms which will develop into the cell wall

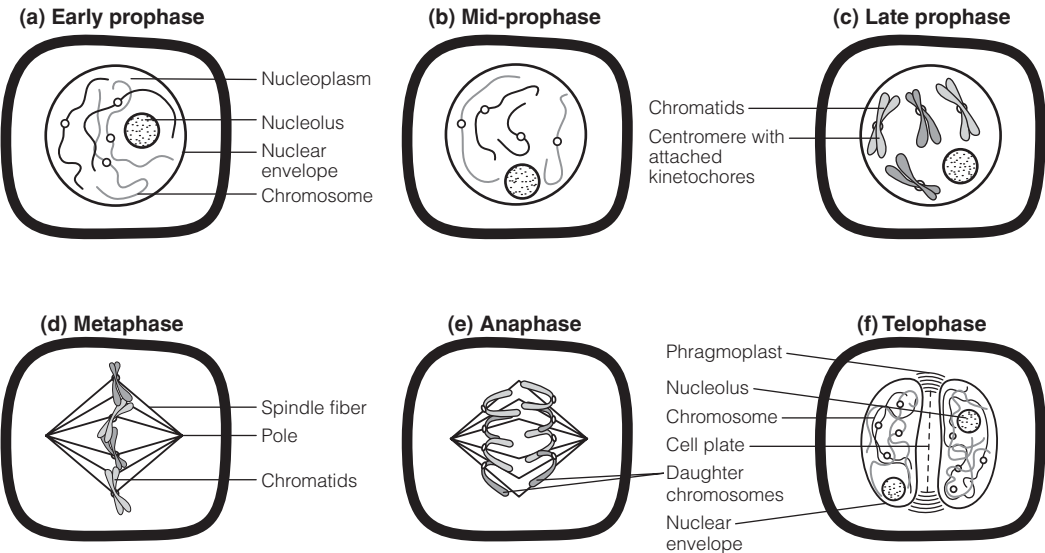


Fig. 2. Stages of mitosis (see also Table 1).

auxin and cytokinin (Topic F2), are known to initiate the cell cycle. Auxin stimulates DNA replication, while cytokinin initiates the events of mitosis. The cell cycle is also controlled by the activity of cell proteins called **cyclins** and **cyclin-dependent protein kinases** (CDPKs; a kinase is an enzyme which will phosphorylate another protein). One group of cyclins, the **G₁ cyclins**, are manufactured by the cell in G₁ and activate CDPKs which stimulate DNA synthesis at the G₁/S control point. If sufficient G₁ cyclins are not formed, the cell will not progress to S. Having passed this point, the G₁ cyclins are degraded and a new family of cyclins, the mitotic or **M cyclins** are produced. These activate a second set of CDPKs which permit the cell to pass the G₂/M control point into mitosis (Fig. 3). Whereas animal cells which pass G₁/S are committed to undergo division, plant cells are not. This means that many plant cells continue to replicate DNA without dividing. This is known as **endoreduplication**, which is shown by more

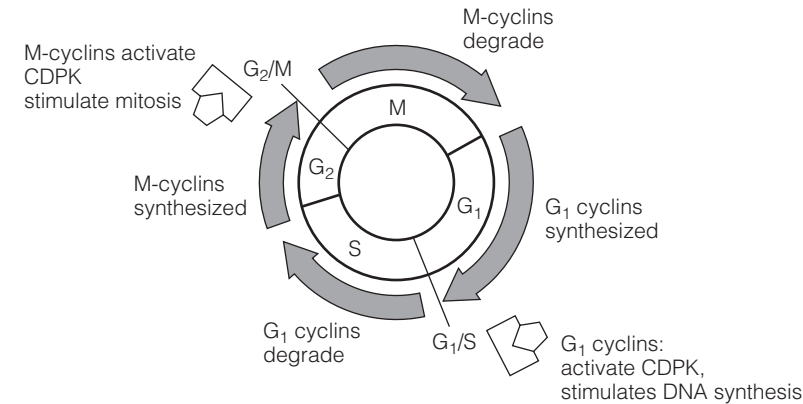


Fig. 3. Cell cycle control by the synthesis and breakdown of cyclins and their binding to cyclin-dependent protein kinases (CDPK).

than 80% of all plant cells and particularly cells with a high metabolic activity and requirement for protein synthesis.

Meiosis

Meiosis occurs in the reproductive tissues of the plant. To do so, it must result in a halving of the number of chromosomes, so that each cell has only one set (**haploid**, rather than the usual two sets, **diploid**) of chromosomes. The full complement of chromosomes is restored after fertilization, when the two sets (one from each gamete) combine. In **interphase**, DNA synthesis occurs and each chromosome exists as a pair of sister chromatids joined by a centromere. In **prophase I**, the homologous chromosomes (originally from the maternal and paternal generative cells) pair up to give a **synaptonemal complex**. Each chromosome can be seen to be composed of two **chromatids**. The chromatids join at points called **chiasmata**, at which genetic material can cross over from one chromatid to another. This can be between homologous chromatids or between sister chromatids. In **metaphase I**, the paired chromosomes move together at the **metaphase plate**. In **anaphase I**, homologous chromosomes, each with its two chromatids, separate to the spindle poles, drawn by microtubules (Topic B1). The daughter nuclei now have a haploid set of chromosomes. Each chromosome has two chromatids (compare mitosis, where at this stage the chromatids separate so each chromosome has only one). Instead of forming new nuclei and stopping division, the cells go on to another phase of division.

In **metaphase II**, a new metaphase plate forms in daughter cells and the chromosomes line up at the equator of the cell. In **anaphase II**, chromatids separate and move to the poles. By **telophase II**, the chromosomes have completed movement and four new nuclei, each having half the original number of single chromosomes, have been formed.

As only one period of chromosome duplication has occurred, the result is four haploid cells. In pollen formation, all four cells survive; in ovule formation, three normally abort leaving one to form the ovule. The stages are shown diagrammatically in Fig. 4.

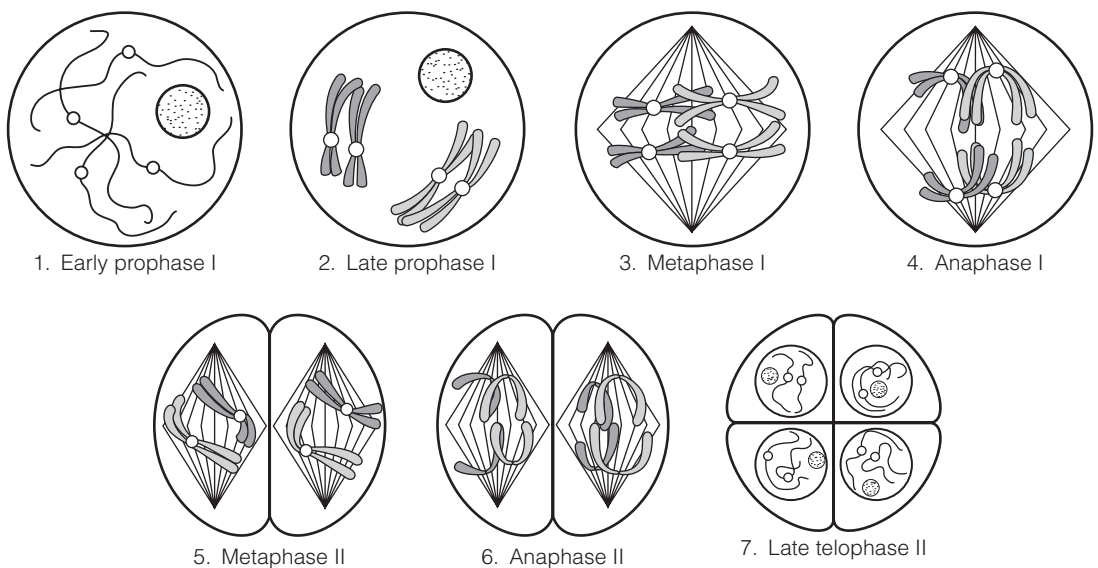


Fig. 4. Key stages of meiosis.

