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B. D. Hames & N. M. Hooper

Biochemistry

生物化学

（第二版）
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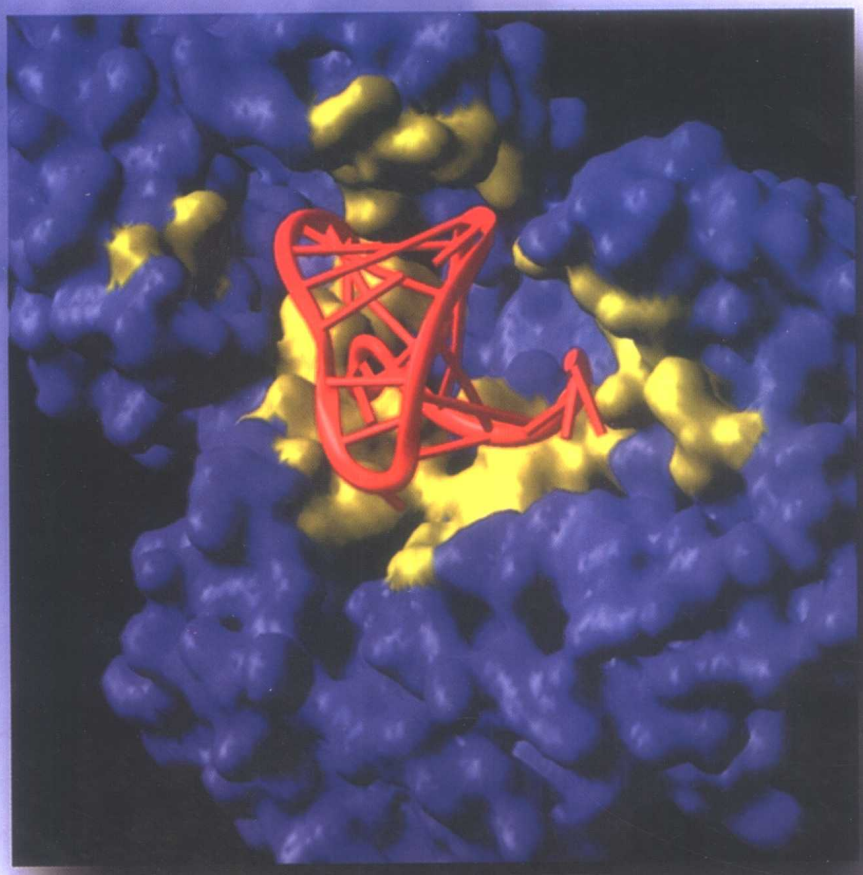

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内 容 简 介

"精要速览系列(*Instant Notes Series*)"是国外教材"Best Seller"榜的上榜教材。该系列结构新颖,视角独特;重点明确,脉络分明;图表简明清晰;英文自然易懂,被国内多所重点院校选用作为双语教材。先锋版是继"现代生物学精要速览"之后推出的跨学科的升级版本。

本书是该系列中的《生物化学(第二版)》分册,全书共 14 章。新版在原版的基础上内容进行了全面地修订和扩充,增加了许多新的章节和阐述,如基因表达、RNA 合成与处理、热动力学等方面。

本书是指导大学生快速掌握生物化学基础知识的优秀教材,也是辅助教师授课的极佳教学参考书,同时可供相关专业的研究生参考。

B. D. Hames & N. M. Hooper
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PREFACE

Three years ago, the sight of first-year students wading through acres of fine print in enormous biochemistry textbooks led us to believe that there must be a better way; a book that presented the core information in a much more accessible format. Hence *Instant Notes in Biochemistry* was born. The tremendous success of this book has proved the concept. However, not surprisingly, we did not get everything right at the first attempt. Student readers and lecturing staff told us about the relatively scant coverage of gene expression, for example, plus a host of other more minor, but significant points. We have addressed all of these issues in this new edition. There is a major expansion of coverage of gene transcription and its regulation in both prokaryotes and eukaryotes, as well as RNA processing and protein synthesis (sections G and H). Many other topics have been added or rewritten in the light of comments, including acids and bases, pH, ionization of amino acids, thermodynamics, protein stability, protein folding, protein structure determination, flow cytometry, and peptide synthesis. Whilst writing the new edition, we have also looked at each illustration again and made modifications as necessary to make these even clearer for the student reader. Many new illustrations have also been included. Naturally, all of this has led to a substantial lengthening of the book. However, in every case, whether considering the text or the illustrations, we have been at pains to include only the information that we believe is essential for a good student understanding of the subject. The key features of this new book therefore remain the same as for the first edition: to present the core information on biochemistry in an easily accessible format that is ideally suited to student understanding – and to revision when the dreaded examinations come! We have been told by students that the first edition did just that. We have great hopes that the same will hold true for this new update.

David Hames
Nigel Hooper

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A1 PROKARYOTES

Key Notes

Prokaryotes

Prokaryotes (bacteria and blue-green algae) are the most abundant organisms on earth. A prokaryotic cell does not contain a membrane-bound nucleus. Bacteria are either cocci, bacilli or spirilla in shape, and fall into two groups, the eubacteria and the archaebacteria.

Cell structure

Each prokaryotic cell is surrounded by a plasma membrane. The cell has no subcellular organelles, only infoldings of the plasma membrane called mesosomes. The deoxyribonucleic acid (DNA) is condensed within the cytosol to form the nucleoid. Some prokaryotes have tail-like flagella.

Bacterial cell walls

The peptidoglycan (protein and oligosaccharide) cell wall protects the prokaryotic cell from mechanical and osmotic pressure. A Gram-positive bacterium has a thick cell wall surrounding the plasma membrane, whereas Gram-negative bacteria have a thinner cell wall and an outer membrane, between which is the periplasmic space.

Related topics

Eukaryotes (A2)
Amino acids (B1)
Membrane lipids (E1)
Chromosomes (F2)
Cilia and flagella (N2)

Prokaryotes

Prokaryotes are the most numerous and widespread organisms on earth, and are so classified because they have no defined membrane-bound nucleus. Prokaryotes range in size from 0.1 to 10 μm, and have one of three basic shapes: spherical (**cocci**), rodlike (**bacilli**) or helically coiled (**spirilla**). They can be divided into two separate groups: the **eubacteria** and the **archaebacteria**. The eubacteria are the commonly encountered bacteria in soil, water and living in or on larger organisms, and include the Gram-positive and Gram-negative bacteria, and cyanobacteria (photosynthetic blue-green algae). The archaebacteria grow in unusual environments such as salt brines, hot acid springs and in the ocean depths, and include the sulfur bacteria and the methanogens.

Cell structure

Like all cells, a prokaryotic cell is bounded by a **plasma membrane** that completely encloses the cytosol and separates the cell from the external environment. The plasma membrane, which is about 8 nm thick, consists of a lipid bilayer containing proteins (see Topic E1). Although prokaryotes lack the membranous subcellular organelles characteristic of eukaryotes (see Topic A2), their plasma membrane may be infolded to form **mesosomes** (*Fig. 1*). The mesosomes may be the sites of deoxyribonucleic acid (DNA) replication and other specialized enzymatic reactions. In photosynthetic bacteria, the mesosomes contain the proteins and pigments that trap light and generate adenosine triphosphate (ATP). The aqueous cytosol contains the macromolecules [enzymes, messenger ribonucleic acid (mRNA), transfer RNA (tRNA) and ribosomes], organic compounds and

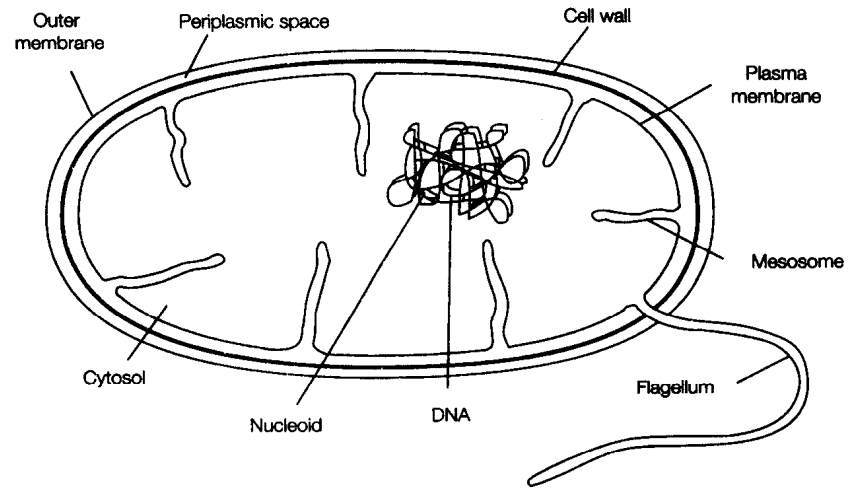

Fig. 1. Prokaryote cell structure.

ions needed for cellular metabolism. Also within the cytosol is the prokaryotic 'chromosome' consisting of a single circular molecule of DNA which is condensed to form a body known as the **nucleoid** (*Fig. 1*) (see Topic F2). Many bacterial cells have one or more tail-like appendages known as **flagella** which are used to move the cell through its environment (see Topic N2).

Bacterial cell walls

To protect the cell from mechanical injury and osmotic pressure, most prokaryotes are surrounded by a rigid 3–25 nm thick **cell wall** (*Fig. 1*). The cell wall is composed of **peptidoglycan**, a complex of **oligosaccharides** and **proteins**. The oligosaccharide component consists of linear chains of alternating *N*-acetylglucosamine (GlcNAc) and *N*-acetylmuramic acid (NAM) linked β(1–4) (see Topic J1). Attached via an amide bond to the lactic acid group on NAM is a **D-amino acid**-containing tetrapeptide. Adjacent parallel peptidoglycan chains are covalently cross-linked through the tetrapeptide side-chains by other short peptides. The extensive cross-linking in the peptidoglycan cell wall gives it its strength and rigidity. The presence of D-amino acids in the peptidoglycan renders the cell wall resistant to the action of **proteases** which act on the more commonly occurring L-amino acids (see Topic B1), but provides a unique target for the action of certain **antibiotics** such as **penicillin**. Penicillin acts by inhibiting the enzyme that forms the covalent cross-links in the peptidoglycan, thereby weakening the cell wall. The β(1–4) glycosidic linkage between NAM and GlcNAc is susceptible to hydrolysis by the enzyme **lysozyme** which is present in tears, mucus and other body secretions.

Bacteria can be classified as either **Gram-positive** or **Gram-negative** depending on whether or not they take up the **Gram stain**. Gram-positive bacteria (e.g. *Bacillus polymyxa*) have a thick (25 nm) cell wall surrounding their plasma membrane, whereas Gram-negative bacteria (e.g. *Escherichia coli*) have a thinner (3 nm) cell wall and a second **outer membrane** (*Fig. 2*). In contrast with the plasma membrane (see Topic E3), this outer membrane is very permeable to the passage of relatively large molecules (molecular weight > 1000 Da) due to **porin proteins** which form pores in the lipid bilayer. Between the outer membrane and the cell wall is the **periplasm**, a space occupied by proteins secreted from the cell.

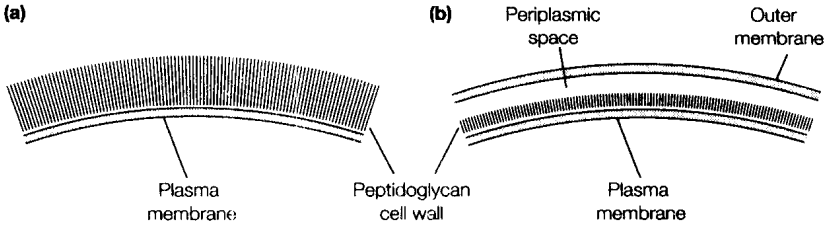

Fig. 2. Cell wall structure of (a) Gram-positive and (b) Gram-negative bacteria.

A2 EUKARYOTES

Key Notes

Eukaryotes

Eukaryotic cells have a membrane-bound nucleus and a number of other membrane-bound subcellular (internal) organelles, each of which has a specific function.

Plasma membrane

The plasma membrane surrounds the cell, separating it from the external environment. The plasma membrane is a selectively permeable barrier due to the presence of specific transport proteins. It is also involved in receiving information when ligands bind to receptor proteins on its surface, and in the processes of exocytosis and endocytosis.

Nucleus

The nucleus stores the cell's genetic information as DNA in chromosomes. It is bounded by a double membrane but pores in this membrane allow molecules to move in and out of the nucleus. The nucleolus within the nucleus is the site of ribosomal ribonucleic acid (rRNA) synthesis.

Endoplasmic reticulum

This interconnected network of membrane vesicles is divided into two distinct parts. The rough endoplasmic reticulum (RER), which is studded with ribosomes, is the site of membrane and secretory protein biosynthesis and their post-translational modification. The smooth endoplasmic reticulum (SER) is involved in phospholipid biosynthesis and in the detoxification of toxic compounds.

Golgi apparatus

The Golgi apparatus, a system of flattened membrane-bound sacs, is the sorting and packaging center of the cell. It receives membrane vesicles from the RER, further modifies the proteins within them, and then packages the modified proteins in other vesicles which eventually fuse with the plasma membrane or other subcellular organelles.

Mitochondria

Mitochondria have an inner and an outer membrane separated by the intermembrane space. The outer membrane is more permeable than the inner membrane due to the presence of porin proteins. The inner membrane, which is folded to form cristae, is the site of oxidative phosphorylation, which produces ATP. The central matrix is the site of fatty acid degradation and the citric acid cycle.

Chloroplasts

Chloroplasts in plant cells are surrounded by a double membrane and have an internal membrane system of thylakoid vesicles that are stacked up to form grana. The thylakoid vesicles contain chlorophyll and are the site of photosynthesis. Carbon dioxide (CO_2) fixation takes place in the stroma, the soluble matter around the thylakoid vesicles.

Lysosomes

Lysosomes in animal cells are bounded by a single membrane. They have an acidic internal pH (pH 4–5), maintained by proteins in the membrane that pump in H^+ ions. Within the lysosomes are acid hydrolases; enzymes involved in the degradation of macromolecules, including those internalized by endocytosis.

Peroxisomes

Peroxisomes contain enzymes involved in the breakdown of amino acids and fatty acids, a byproduct of which is hydrogen peroxide. This toxic compound is rapidly degraded by the enzyme catalase, also found within the peroxisomes.

Cytosol

The cytosol is the soluble part of the cytoplasm where a large number of metabolic reactions take place. Within the cytosol is the cytoskeleton, a network of fibers (microtubules, intermediate filaments and microfilaments) that maintain the shape of the cell.

Cytoskeleton

Eukaryotic cells have an internal scaffold, the cytoskeleton, that controls the shape and movement of the cell. The cytoskeleton is made up of actin microfilaments, intermediate filaments and microtubules.

Microtubules

Microtubule filaments are hollow cylinders made of the protein tubulin. The wall of the microtubule is made up of a helical array of alternating α- and β-tubulin subunits. The mitotic spindle involved in separating the chromosomes during cell division is made of microtubules. Colchicine inhibits microtubule formation, whereas the anticancer agent, taxol, stabilizes microtubules and interferes with mitosis.

Plant cell wall

The cell wall surrounding a plant cell is made up of the polysaccharide cellulose. In woody plants, the phenolic polymer called lignin gives the cell wall additional strength and rigidity.

Plant cell vacuole

The membrane-bound vacuole is used to store nutrients and waste products, has an acidic pH and, due to the influx of water, creates turgor pressure inside the cell as it pushes out against the cell wall.

Related topics

Microscopy (A3)
Membrane transport: macromolecules (E4)
Signal transduction (E5)
Chromosomes (F2)
Protein targeting (H4)
Electron transport and oxidative phosphorylation (L2)
Photosynthesis (L3)
Cilia and flagella (N2)

Eukaryotes

A eukaryotic cell is surrounded by a **plasma membrane**, has a membrane-bound nucleus and contains a number of other distinct **subcellular organelles** (*Fig. 1*). These organelles are membrane-bounded structures, each having a unique role and each containing a specific complement of proteins and other molecules. Animal and plant cells have the same basic structure, although some organelles and structures are found in one and not the other (e.g. chloroplasts, vacuoles and cell wall in plant cells, lysosomes in animal cells).

Plasma membrane

The plasma membrane envelops the cell, separating it from the external environment and maintaining the correct ionic composition and osmotic pressure

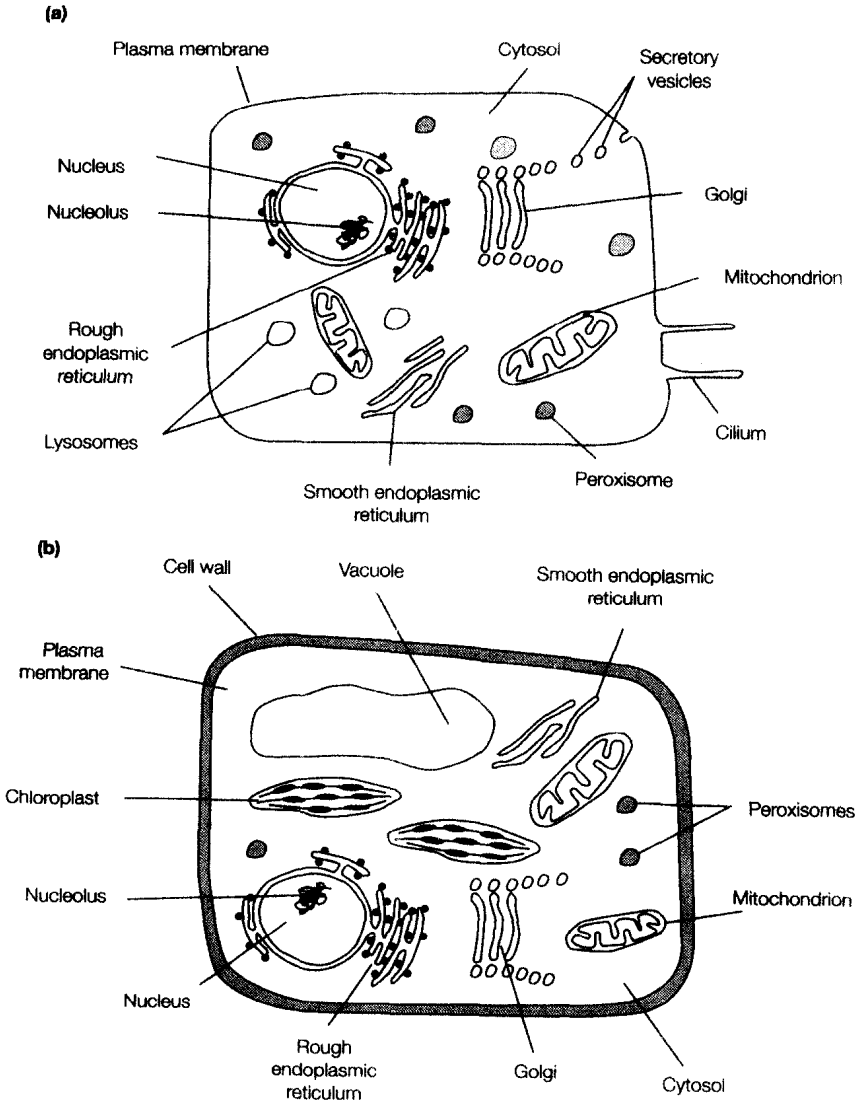

Fig. 1. Eukaryote cell structure. (a) Structure of a typical animal cell, (b) structure of a typical plant cell.

of the cytosol. The plasma membrane, like all membranes, is impermeable to most substances but the presence of specific proteins in the membrane allows certain molecules to pass through, therefore making it **selectively permeable** (see Topic E3). The plasma membrane is also involved in communicating with other cells, in particular through the binding of ligands (small molecules such as hormones, neurotransmitters, etc.) to **receptor proteins** on its surface (see Topic E5). The plasma membrane is also involved in the **exocytosis** (secretion) and **endocytosis** (internalization) of macromolecules (see Topic E4).

Nucleus

The nucleus is bounded by two membranes, the **inner and outer nuclear membranes**. These two membranes fuse together at the **nuclear pores** through

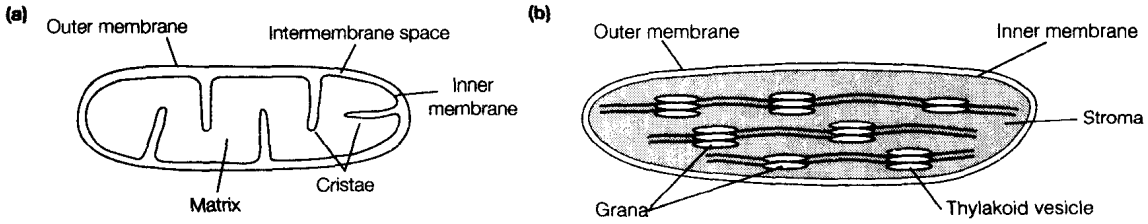

Fig. 2. Structure of (a) a mitochondrion and (b) a chloroplast.

which molecules [messenger ribonucleic acid (mRNA), proteins, ribosomes, etc.] can move between the nucleus and the cytosol. Other proteins, for example those involved in regulating gene expression, can pass through the pores from the cytosol to the nucleus. The outer nuclear membrane is often continuous with the rough endoplasmic reticulum (RER). Within the nucleus the **DNA** is tightly coiled around **histone proteins** and organized into complexes called **chromosomes** (see Topic F2). Visible under the light microscope (see Topic A3) is the **nucleolus**, a subregion of the nucleus which is the site of ribosomal ribonucleic acid (rRNA) synthesis.

Endoplasmic reticulum

The endoplasmic reticulum (ER) is an interconnected network of membrane vesicles. The **rough endoplasmic reticulum (RER)** is studded on the cytosolic face with **ribosomes**, the sites of **membrane and secretory protein biosynthesis** (see Topic H3). Within the lumen of the RER are enzymes involved in the **post-translational modification** (glycosylation, proteolysis, etc.) of membrane and secretory proteins (see Topic H5). The **smooth endoplasmic reticulum (SER)**, which is not studded with ribosomes, is the site of **phospholipid biosynthesis**, and is where a number of **detoxification reactions** take place.

Golgi apparatus

The Golgi apparatus, a system of flattened membrane-bound sacs, is the **sorting center** of the cell. Membrane vesicles from the RER, containing membrane and secretory proteins, fuse with the Golgi apparatus and release their contents into it. On transit through the Golgi apparatus, further **post-translational modifications** to these proteins take place and they are then sorted and packaged into different vesicles (see Topic H5). These vesicles bud off from the Golgi and are transported through the cytosol, eventually fusing either with the plasma membrane to release their contents into the extracellular space (a process known as **exocytosis**; see Topic E4) or with other internal organelles (lysosomes, peroxisomes, etc.).

Mitochondria

A mitochondrion has an **inner and an outer membrane** between which is the **intermembrane space** (*Fig. 2a*). The outer membrane contains **porin proteins** which make it permeable to molecules of up to 10 kDa. The inner membrane, which is considerably less permeable, has large infoldings called **cristae** which protrude into the **central matrix**. The inner membrane is the site of oxidative phosphorylation and electron transport involved in ATP production (see Topic L2). The central matrix is the site of numerous metabolic reactions including the citric acid cycle (see Topic L1) and fatty acid breakdown (see Topic K2). Also within the matrix is found the mitochondrial DNA which encodes some of the mitochondrial proteins.

Chloroplasts

Chloroplasts also have **inner and outer membranes**. In addition, there is an extensive internal membrane system made up of **thylakoid vesicles** (interconnected vesicles flattened to form discs) stacked upon each other to form **grana** (*Fig. 2b*). Within the thylakoid vesicles is the green pigment **chlorophyll** (see Topic M4), along with the enzymes that trap light energy and convert it into chemical energy in the form of ATP (see Topic L3). The **stroma**, the space surrounding the thylakoid vesicles, is the site of carbon dioxide (CO_2) fixation – the conversion of CO_2 into organic compounds. Chloroplasts, like mitochondria, contain DNA which encodes some of the chloroplast proteins.

Lysosomes

Lysosomes, which are found only in animal cells, have a single boundary membrane. The internal pH of these organelles is **mildly acidic** (pH 4–5), and is maintained by integral membrane proteins which pump H^+ ions into them (see Topic E3). The lysosomes contain a range of hydrolases that are optimally active at this acidic pH (and hence are termed **acid hydrolases**) but which are inactive at the neutral pH of the cytosol and extracellular fluid. These enzymes are involved in the degradation of host and foreign macromolecules into their monomeric subunits; **proteases** degrade proteins, **lipases** degrade lipids, **phosphatases** remove phosphate groups from nucleotides and phospholipids, and **nucleases** degrade DNA and RNA. Lysosomes are involved in the degradation of extracellular macromolecules that have been brought into the cell by **endocytosis** (see Topic E4).

Peroxisomes

These organelles have a single boundary membrane and contain enzymes that degrade fatty acids and amino acids. A byproduct of these reactions is **hydrogen peroxide**, which is toxic to the cell. The presence of large amounts of the enzyme **catalase** in the peroxisomes rapidly converts the toxic hydrogen peroxide into harmless H_2O and O_2:

$$2H_2O_2 \xrightarrow{\text{Catalase}} 2H_2O + O_2$$

Cytosol

The cytosol is that part of the **cytoplasm** not included within any of the subcellular organelles, and is a major site of cellular metabolism. It contains a large number of different enzymes and other proteins. The cytosol is not a homogenous 'soup' but has within it the **cytoskeleton**, a network of fibers criss-crossing through the cell that helps to maintain the shape of the cell. The cytoskeletal fibers include **microtubules** (25 nm in diameter), **intermediate filaments** (10 nm in diameter) and **microfilaments** (8 nm in diameter) (see Topic N2). Also found within the cytosol of many cells are **inclusion bodies** (granules of material that are not membrane-bounded) such as glycogen granules in liver and muscle cells, and droplets of triacylglycerol in the fat cells of adipose tissue.

Cytoskeleton

In the cytosol of eukaryotic cells is an **internal scaffold**, the cytoskeleton (see Topic E2). The cytoskeleton is important in maintaining and altering the **shape of the cell**, in enabling the cell to **move** from one place to another, and in **transporting intracellular vesicles**. Three types of **filaments** make up the cytoskeleton: microfilaments, intermediate filaments and microtubules. The **microfilaments**, diameter approximately 7 nm, are made of **actin** and have a mechanically supportive function. Through their interaction with myosin (see Topic N1), the microfilaments form contractile assemblies that are involved

in various intracellular movements such as cytoplasmic streaming and the formation of membrane invaginations (see Topic E4). The **intermediate filaments** (7–11 nm in diameter) are probably involved in a load-bearing function within the cell. For example, the skin in higher animals contains an extensive network of intermediate filaments made up of the protein **keratin** that has a two-stranded α-helical coiled-coil structure.

Microtubules

The third type of cytoskeletal filaments, the **microtubules**, are hollow cylindrical structures with an outer diameter of 30 nm that are built from the protein **tubulin**. The rigid wall of a microtubule is made up of a helical array of alternating α- and β-tubulin subunits, each of 50 kDa. A cross-section through a microtubule reveals that there are 13 tubulin subunits per turn of the filament. Microtubules in cells are formed by the addition of α- and β-tubulin molecules to pre-existing filaments or nucleation centers. The microtubules form a supportive framework that guides the movement of subcellular organelles within the cell. For example, the **mitotic spindle** involved in separating the replicated chromosomes during mitosis is an assembly of microtubules. The drug **colchicine** inhibits the polymerization of microtubules, thus blocking cell processes such as cell division that depend on functioning microtubules. Another compound, **taxol**, stabilizes tubulin in microtubules and promotes polymerization. It is being used as an anticancer drug since it blocks the proliferation of rapidly dividing cells by interfering with the mitotic spindle.

Plant cell wall

Surrounding the plasma membrane of a plant cell is the cell wall, which imparts strength and rigidity to the cell. This is built primarily of **cellulose**, a rod-like **polysaccharide** of repeating glucose units linked β(1–4) (see Topic J1). These cellulose molecules are aggregated together by hydrogen bonding into bundles of fibers, and the fibers in turn are cross-linked together by other polysaccharides. In woody plants another compound, **lignin**, imparts added strength and rigidity to the cell wall. Lignin is a complex water-insoluble phenolic polymer.

Plant cell vacuole

Plant cells usually contain one or more **membrane-bounded vacuoles**. These are used to store nutrients (e.g. sucrose), water, ions and waste products (especially excess nitrogen-containing compounds). Like lysosomes in animal cells, vacuoles have an **acidic pH** maintained by H^+ pumps in the membrane and contain a variety of **degradative enzymes**. Entry of water into the vacuole causes it to expand, creating hydrostatic pressure (**turgor**) inside the cell which is balanced by the mechanical resistance of the cell wall.

A3 MICROSCOPY

Key Notes

Light microscopy

In light microscopy, a beam of light is focused through a microscope using glass lenses to produce an enlarged image of the specimen.

Standard light microscopy

The specimen to be viewed is first fixed with alcohol or formaldehyde, embedded in wax and then cut into thin sections. A section is illuminated from below with the beam of light being focused on to it by the condenser lens. The incident light that passes through the specimen is then focused by the objective lens on to its focal plane, creating a magnified image.

Staining

Subcellular organelles cannot readily be distinguished under the light microscope without first staining the specimen with a chemical. Proteins can be stained with eosin or methylene blue, DNA with fuchsin. The location of an enzyme in a specimen can be revealed by cytochemical staining using a substrate which is converted into a colored product by the enzyme.

Dark-field microscopy

In dark-field microscopy, light from the condenser lens is directed at an angle on to the specimen such that only light which has been refracted or diffracted by the specimen enters the objective lens and forms an image.

Phase-contrast microscopy

In phase-contrast microscopy, the light microscope is adapted to alter the phase of the light waves to produce an image in which the degree of brightness of a region of the specimen depends on its refractive index.

Immunofluorescence microscopy

In immunofluorescence microscopy, fluorescent compounds (which absorb light at the exciting wavelength and then emit it at the emission wavelength) are attached to an antibody specific for the subcellular structure under investigation. The antibody is then added to the specimen and allowed to bind. Unbound antibody is removed and the specimen is illuminated at the exciting wavelength, to visualize where the antibody has bound.

Confocal scanning microscopy

This variation of immunofluorescence microscopy uses a laser to focus light of the exciting wavelength on to the specimen so that only a thin section of it is illuminated. The laser beam is moved through the sample, producing a series of images which are then reassembled by a computer to produce a three-dimensional picture of the specimen.

Electron microscopy

In electron microscopy, a beam of electrons is focused using electromagnetic lenses. The specimen is mounted within a vacuum so that the electrons are not absorbed by atoms in the air.

Transmission electron microscopy

In transmission electron microscopy, the beam of electrons is passed through a thin section of the specimen that has been stained with heavy metals. The electron-dense metals scatter the incident electrons, thereby producing an image of the specimen.