

CELL MORPHOLOGY AND ORGANIZATION

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Summary

The cytoplasm of eukaryotic cells contains several membrane bound structures essential for efficient functioning. All the membranes of the cell are organized into an intricate network which connect the nucleus to the cell membrane. The membranes consist of phospholipid bilayers, embedded with proteins involved in receptor signaling, uptake pathways and processing functions. The cell membrane acts as a barrier to the environment and has specialized transport mechanisms to allow substances into and out of the cell. The Golgi apparatus is a membrane structure which gives rise to lysosomes, and protein modifications. Lysosomes contain hydrolytic enzymes which degrade expired cellular contents, or food particles, for digestion. Plant cell carries an extracellular matrix in the form of a cell wall on the outer layer of the cell membrane. This stabilizes and protects the cell. The cytoskeleton is a network of filaments found inside the cell. It plays an important role in maintaining cell shape, supporting organelles within the cytoplasm, and in cell movement. Cytoskeletal filaments can also associate to form cilia or flagella. These are appendages which assist in cell movement. Plant cells are connected to one another by plasmodesmata, which brings the cytoplasm of neighboring cells into contact. Animal cells are linked together by one of three junctions; each with its own function: desmosomes, tight and gap junctions. Vacuoles are important membrane bound structures found mostly in plant cells. Their major function is that of maintaining turgor, but they are also important storage sites. Protein synthesis by ribosomes happens either free in the cytoplasm, or attached to the endoplasmic reticulum, where they are then processed and transported to the Golgi for further processing. The endoplasmic reticulum is also the site of lipid synthesis and protein glycosylation. Proteins are degraded in the cell by proteosomes or lysosomes.

1. Introduction

All living organisms on the planet are made up of cells. They can exist as a single unit as in the unicellular amoeba, or a multicellular organism, like a human being.

Cells can be broadly classified into five major kingdoms: these are the Kingdoms of Animalia, Protista, Plantae, Fungi, and Monera containing the Eubacteria and Archaeobacteria. These Kingdoms can in turn be separated according to their intracellular structure and organization, into prokaryotes and eukaryotes. Eukaryotes fall within the scope of this section, while prokaryote cell structure and function are described in *Microbiology*. Eukaryote cells are further subdivided into the unicellular organisms such as yeast, plant cells and animal cells. Each has specific structural features.

1.1. The cytoplasm

Most of the cell interior consists of cytoplasm, or cytosol. It contains water, salts, organic molecules, organelles and proteins. This well regulated environment is cut-off from the exterior by the selectively permeable cell membrane.

1.2. Membranes

1.2.1 Structure

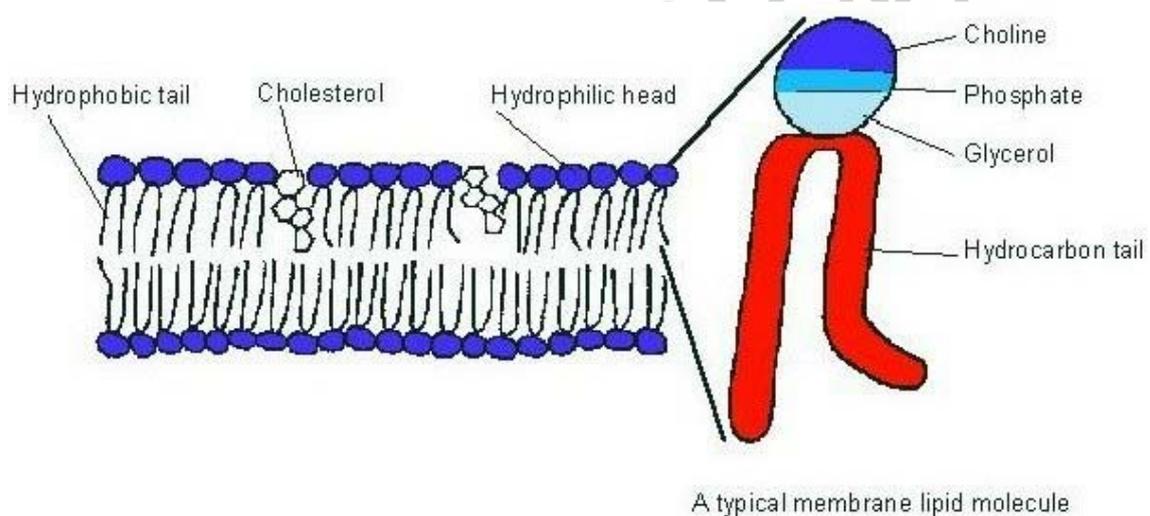


Figure 1: Diagram illustrating the structure of a lipid bilayer

All cell membranes have as their basic structure a lipid bilayer. This consists of two layers of lipid molecules which each consists of a hydrophilic polar head and two hydrophobic tails. The most abundant lipids are phospholipids, which have a phosphate group linking the hydrophilic head to the hydrophobic tail molecules. Phosphatidylcholine is the most common component in the lipid bilayer and consists of choline attached to the phosphate group, which in turn is bound to a glycerol molecule, to make up the polar head. The two hydrophobic carbon chains are attached to the glycerol and extend towards the inner surface of the lipid bilayer. Their composition determines the fluidity of the lipids in the membrane structure. If all the carbon molecules in the chain carry a full complement of hydrogen molecules it is said to be saturated. One of the hydrophobic chains of the phospholipids is always saturated while the second usually carries a couple of carbon double bonds and is said to be unsaturated. The double bonds create bends in the fatty

acid tail and thereby prevent the phospholipids from packaging themselves too tightly. The resultant fluidity is essential for the movement of proteins embedded in the membrane to move to different sites within the membrane structure. This permits receptors and other surface proteins to move to where they are required on the cell surface.

Cholesterol stabilizes the cell membrane in animal cells by filling the gaps caused by the kinks in the hydrocarbon chains. It lessens the fluidity of the membrane and prevents random entry of unwanted compounds across the membrane.

The phospholipids are amphipathic as they carry two charged domains. The hydrophilic domains associate with the aqueous environment, while the hydrophobic domains associate on the inner surface of the membrane bilayer. If a hole appears in the bilayer, the inner surfaces are exposed to the aqueous environment, a situation unfavorable to the hydrophobic tail molecules. The lipid bilayer quickly reforms, or separates, into smaller miscelles to form energetically favorable structures. New components of the cell membrane are added to the interior cell surface. Addition of phospholipids to the inner surface results in the inner surface being larger than the outer surface. The enzyme flipase serves to flip phospholipids, situated on the inner cytosolic surface, to the outer surface, thereby restoring an energetically stable membrane, and allowing the membrane to expand.

1.2.2 The cell cortex

The cell cortex stabilizes the plasma membrane on the cytosolic side. This cortex is a network of proteins which attach transmembrane proteins, thereby stabilizing the membrane structure. Spectrin is the major component of the cell cortex which associates to form a strong meshwork which stabilizes the cell membrane and gives the cell its characteristic shape. Spectrin is a long, thin and flexible protein in a rod shape, about 100 nm long. An additional network of actin filaments extend into the cytoplasm from the cell cortex. This mesh of protein stabilizes the cell structure and strengthens the cell membrane.

1.2.3 Transmembrane proteins

The aqueous solutions on the inside of the cell are separated from the extracellular environment by a membrane, permeable only to small hydrophobic particles or very small uncharged polar molecules, capable of diffusing through the membrane. Charged molecules and all ions are not permitted to pass through the lipid bilayer. The membrane can regulate transport of restricted compounds into, and out, of the interior of the cell by specialized transport mechanisms which require membrane proteins embedded within the cell membrane. These proteins can take on the form of carriers or transporters, linkers, receptors or enzymes. Approximately 50% of the animal cell membrane is made up of protein. Cell types vary in their protein make-up reflecting their function in their cell membrane composition.

Transmembrane proteins have very specific structural requirements in order to embed themselves within the lipid bilayer. They require a transmembrane domain to anchor

them in the lipid bilayer. This domain is usually constructed from hydrophobic proteins arranged in one or more alpha helices. The transmembrane proteins also have hydrophilic regions which interact with the aqueous environments both in- and outside the cell membrane.

Some proteins are bound to the external surface of the cell membrane by a covalent link to a lipid in the outer layer of the membrane. Another means of protein anchorage is to bind to another transmembrane protein. Transmembrane proteins and lipid linked proteins are directly linked to the lipid bilayer and their removal would disrupt the membrane structure. These proteins are referred to as integral membrane proteins. Peripheral membrane proteins can easily be removed from the cell surface without disrupting the cell surface.

1.2.4 Endoplasmic reticulum

The endoplasmic reticulum is a network of membranous channels that connect the nuclear membrane to the outer cell membrane. It can be smooth or studded with ribosomes to form the rough endoplasmic reticulum.

The smooth endoplasmic reticulum serves as the major site of lipid synthesis, including the phospholipids found in all the membranes of the eukaryotic cell. The enzymes necessary for lipid synthesis are found on the non-cytosolic or inner surface of the endoplasmic reticulum. The smooth endoplasmic reticulum also synthesizes certain hormones, such as testosterone and estrogen.

The rough endoplasmic reticulum is responsible for synthesis of membrane bound proteins or proteins for export. The ribosomes on its cytosolic surface translate proteins directly into the lumen of the endoplasmic reticulum. These proteins migrate to the end of the lumen, near the Golgi apparatus, where they bud off into membrane bound vesicles. These vesicles then migrate through the cytoplasm toward the Golgi along the microtubule network.

1.2.5 Golgi apparatus

The Golgi apparatus consists of a stack of membranes resembling those found in the smooth endoplasmic reticulum. It fuses with vesicles derived from the endoplasmic reticulum, with the two membranes joining, and the contents of the vesicle being emptied into the lumen of the Golgi. Here proteins and lipids are separated according to their destination, such as hormones for secretion and digestive enzymes for the lysosome. The Golgi is also responsible for modifying certain molecules, such as adding carbohydrates to proteins in order to make glycoproteins. These various substances are accumulated into new vesicles which bud from the Golgi and move to their final destination within the cell, or to the cell surface.

The membrane systems within the cell combine to form an organized complex. The nuclear membrane is linked to the endoplasmic reticulum, the Golgi, and the cell membrane, in an integrated network. Membrane structures are synthesized within the endoplasmic reticulum and recycled throughout the cell in an orderly fashion. The Golgi

is able to separate proteins destined for the cell surface from those of the internal membrane structures. It sends the surface lipids and proteins off to the cell membrane in a vesicle which eventually fuses with that of the cell membrane, thereby depositing the proteins and lipids on the cell surface in the correct orientation. Empty vesicles containing only internal membrane proteins and lipids, pinch off from the Golgi, and return to the endoplasmic reticulum.

1.2.6 Lysosomes

The digestive enzymes are processed within the Golgi and sent to another membranous structure within the cytoplasm, namely the lysosome. The lysosomes are membrane bound structures which store enzymes for degradation of nutrients and waste products. They prevent these enzymes from being released into the cytoplasm and breaking down cytosolic components. Lysosomes fuse with food vesicles or vesicles containing cell debris, and digest their contents. The broken down products then diffuse through the membrane and into the cytoplasm, for use in normal biochemical synthesis pathways.

1.3. Extracellular matrices

1.3.1 Glycocalyx

Glycolipids serve to protect the cell from external damage. They are phospholipids which carry a carbohydrate chain on the aqueous side of the molecules. They gain their carbohydrate moieties in the Golgi apparatus during transport to the cell surface, and are found on the non-cytosolic side of the plasma membrane. The Golgi deposits it on the outer surface, so no flipase activity is required. These glycolipids serve several functions. They associate with other carbohydrates on the outer cell surface to form the glycocalyx, a protective layer on the cell exterior. They give cells a slime layer which is of special use to white blood cells, as it permits them to move through the small gaps between cells. The glycocalyx also plays an important role in cell-cell recognition and adhesion.

1.3.2 Cell walls

The cells observed by Robert Hooke under his rudimentary microscope were dead. The structure was however being maintained by the rigid outer wall of the cell. Young and actively dividing cells have primary cell walls which are flexible and thinner than their mature counterparts. Cell walls function in osmo-regulation, nutrition, growth, reproduction, communication and defense of plant cells.

Primary cell walls encompass newly formed cells in the meristem. They are semi-rigid and are generally composed of approximately 25% cellulose, whereas a mature cell wall is usually composed of 65% cellulose fibers. The remainder is made up of pectins, hemicelluloses and glycoproteins.

Certain types of cells develop a secondary cell wall beneath the primary cell wall which is primarily composed of cellulose and 25% lignin. This cell wall is stronger and provides a rigid framework to support the plant. The cell walls gain their strength from long fibers of cellulose held in place by a protein and polysaccharide matrix. The matrix consists

mainly of hemicellulose, pectin and glycoproteins

Cellulose chains comprise a linear chain of glucose in a β 1-4 linkage. Hemicellulose consists of cellulose with branched polysaccharides attached non-covalently to its surface. Pectin has a high galacturonic acid content, giving it a high negative charge. If exposed to calcium, it forms a semirigid gel, serving to cross-link cell wall components. The pectic layer, or middle lamella, is the agent used to thicken jams and jelly.

Some cells have developed specialized mechanisms for preventing water loss from the plant. Suberin, found in the bark of cork oaks, is a compound which inhibits water loss at the plant surface.

The glycoproteins found in the cell wall contain many repeat sequences rich in hydroxyproline. Short oligosaccharide chains are attached to the hydroxyproline and serine residues providing half the weight of the glycoproteins. These compounds are thought to strengthen and toughen the cell wall.

The cell wall grows from the inner surface. All the compounds required for cell wall synthesis are manufactured inside the cell, transported to the cell membrane, and exported to the outside of the cell at the site of cell wall synthesis. Structures called dictyosomes, or the Golgi apparatus, transport pectins, hemicelluloses and glycoproteins within the cell. If a cell needs to expand, it requires absorption of water. This expansion requires the cell wall to stretch, something the cellulose fibers cannot do. They need to be separated and new cellulose is then deposited between the relaxed cell wall fibers. This deposition occurs at right angles to the direction of cell growth in stem cells, allowing the cell wall to increase in length and not in width. Deposition of cellulose occurs in a random fashion in storage tissues to allow for expansion in all directions.

The cell wall allows water, small molecules such as sucrose and potassium ions as well as gases to diffuse through with ease. It provides only 10% of the resistance to water entering the cell. All signaling molecules have to be in the order of 15 nm, in diameter or about 20 kilodaltons, in order to enter the cell wall. Plant hormones are all small, in the range of 500 nm.

The cell wall provides the resistance to osmosis of water from the hypotonic environment to the hypertonic cytosol. If the cell wall were absent, water would diffuse into the cells and the cell would expand beyond its ability and burst. The cell wall allows the accumulation of hydrostatic pressure on its inside also known as turgor pressure.

1.4. Cytoskeleton

The cytoskeleton, which comprises a network of protein filaments inside the cell, plays an important role in maintaining cell shape, supporting organelles within the cytosol and in cell movement. The cytoskeleton is an extremely dynamic structure, with sections being built and dismantled continuously. This allows the interior of the cell to be in a constant state of motion, transporting organelles from one site to another, linking enzymes in complex biochemical pathways and dividing the cell into two daughter cells at cell division. The cytoskeleton consists of three major types of protein filaments:

microfilaments, microtubules and intermediate filaments.

1.4.1 Microfilaments or Actin filaments

Microfilaments consist mostly of actin and occasionally myosin. The actin polymers of 7 nm in diameter, form flexible structures inside the cytoplasm. The highest concentration is immediately beneath the surface of the cell membrane, within the cell cortex.

Actin filaments consist of actin monomers which associate in a polar manner to form long filaments. Each monomer has a helical structure, which enables it to associate with another monomer to form a structure resembling a two-stranded helix. Each actin monomer has a GTP bound tightly to it. Hydrolysis of the GTP weakens the interaction between the monomers and allows the cell to disassemble the filaments when required. Only about half of the cellular actin is sequestered into filaments. The remaining actin monomers are associated with thymosin and profilin, blocking them from polymerization until required.

1.4.2 Intermediate filaments

Intermediate filament fibers are eight to ten nanometers in diameter. They are made up of a minimum of five proteins arranged in a solid rope-like structure which provides the tensile strength required to prevent a cell from being pulled apart. They form the nuclear lamina on the inner surface of the nuclear membrane and span the cytoplasm from side to side.

Intermediate filaments are made from protein sub-units which carry two globular regions, one at the amino terminus, the other at the carboxyl terminus, inter-spaced by a rod-like structure. This rod consists of an alpha helix which enables two of the sub-units to inter-link and form a stable dimer. Two dimers associate to form tetramers, which then link together to form the final intermediate filament. The tail regions of the sub-units determine the interaction of the intermediate filament with its surrounding cellular components. Intermediate filaments serve to strengthen the links between adjacent cells and prevent tissues from shearing under severe tension or stress. Keratin filaments are found in epithelial cells. They span the cell from side to side and are linked to the desmosomes, which attach neighboring cells to each other. There are many different types of keratin filaments, depending on the tissue which it supports. Vimentin and related filaments are found in connective tissues, muscles and neuroglial cells. Neurofilaments are found only in nerve cells and stabilize their structure.

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Biographical Sketch

Michelle Gehringer is a visiting scientist at the School of Biotechnology and Biomolecular Sciences of the University of New South Wales in Sydney, Australia. She is continuing her work on the toxic effects of the cyanobacterial toxins, microcystin and cylindrospermopsin, on humans and animals that accidentally ingest them from contaminated drinking water sources. This research has provided insight into the way the body deals with the toxin as well as potential means of offering dietary protection to potential victims.

Dr. Gehringer has several year lecturing experience from the University of Port Elizabeth, South Africa, where she was actively involved in introducing the topics of Biochemistry and Microbiology to the general public and school goers. Her MSc was obtained at the University of Cape Town, South Africa where she worked on means to control Cucumber Mosaic Virus infections of crop plants.