THE EUKARYOTIC CELL

Structure and Function

M. R. INGLE

STUDIES IN ADVANCED BIOLOGY 1

THE EUKARYOTIC CELL

Structure and Function

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PREFACE

Most students have access to a general text which provides the framework on which their course is constructed. This series builds on that framework by examining defined areas of the syllabus more closely. It looks especially at those parts of the subject which have recently undergone the most change, and brings together new concepts which are presently widely scattered amongst the available literature. New and powerful techniques in microscopy and molecular biology have enabled questions about eukaryotic cells to be answered, which previously could not even have been asked. Throughout the book I have tried to avoid simply substituting new dogmatic assertions for old, and to show how today's concepts have evolved from previous ones.

In keeping with the direction the subject has taken, a quantitative and biochemical treatment is used where appropriate.

Key words are highlighted in bold type and a glossary is provided to avoid interrupting the text with too many asides.

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Units, abbreviations and constants

Units of length

1m = 10^3mm = 10^6μm = 10^9nm

1nm = 10^{-3}μm = 10^{-6}mm = 10^{-9}m

C2, C3, etc. = compounds containing 2 or 3, etc., number of carbon atoms

C-2, C-3, etc. = the *second* or the *third*, etc., carbon atom in a compound

Abbreviations

- μm = micrometre (unit of length)
- N = Newton (unit of force)
- Pa = Pascal (unit of pressure; Nm^{-2} is an alternative)
- J = Joule (unit of energy)
- M = mole (6.02×10^{23} molecules, ions, etc. A molar solution contains the mass of this number of particles dissolved in $1dm^3$ of water)
- S = Svedberg (unit of sedimentation in a centrifuge)

Constants

Avogadro's constant (Na)	$= 6.02 \times 10^{23}$
Faraday's constant (F)	= 96500 coulombs mol^{-1}
Universal Gas constant (R)	= 8.31 JK^{-1} mol^{-1}
Absolute zero (T_0)	= −273K

Contents

1

The Concept of the Cell

SUMMARY

The basic functional unit of life is the cell.
There are striking similarities between cells even of the most diverse origins.
The following terms are used:
colloid glycolysis nucleic acid

In 1665 Robert Hooke, using a primitive microscope first described how cork was composed of 'chambers' or 'cells'. Ten years later, Anton van Leeuwenhoek made his historical observations of micro-organisms, including what we now call *Protozoa* and bacteria. The use of stains to enhance the contrast between microscopic structures and their background, the improved sectioning of material, and advances in optics, made possible the description of many plant and animal tissues in the early nineteenth century. This work culminated in the **cell theory** (Schleiden and Schwann, 1838–9).

1.1 THE CELL THEORY

(i) *All living organisms are composed of one or more units called cells*

A working definition of a cell is that it is a unit of **protoplasm** surrounded by a thin **plasma membrane**. Some examples are shown in Fig.1.1 overleaf.

The protoplasm of both animal and plant cells usually contains an approximately spherical object, the **nucleus**. Such cells are described as eukaryotic (true nucleus) to distinguish them from the **prokaryotic** (non-nucleate) bacteria and blue-green algae. Some of the other important differences which exist between eukaryotes and prokaryotes are indicated in Table 1.1. (See also *Microbes and Biotechnology* in this series.)

The rest of the protoplasm is called the **cytoplasm**. Using appropriate staining and microscopic techniques, the cytoplasm is seen to contain many subcellular structures called **organelles** (Figs.1.2 and 1.3). Some of these are **membrane bound** (see Chapter 4), others are **fibrillar** (see Chapter 5). The **cytosol** (syn. ground matrix, hyaloplasm) in which the structures are embedded is rather gelatinous, mainly on account of the proteins present, a proportion of which exist as **colloids**. Amongst the proteins of the cytosol are several important enzyme systems, for example those of **glycolysis**. Many organic substances and mineral ions are also present. Some of these greatly affect the solubility of proteins. Raising the Ca^{2+} level, for example, can convert cytosol from a semi-contracted **gel** to a more liquid, relaxed **sol**. The edge of the cell (**ectoplasm**) is often in the former state, and may appear almost transparent due to the exclusion of larger organelles by the fibrillar system. The interior of the cell is usually a granular sol (**endoplasm**).

Whilst organelles may vary from one cell to another, one structure which defines the cell absolutely is the **plasma membrane**. The existence of a living cell without one is inconceivable: we shall see why in Chapters 2 and 3.

No generalisation is universally true, and there are important exceptions to the description of a cell given above. For example, in plant cells the plasma membrane is surrounded by a **cell wall** (Fig.1.1b). By common agreement a plant cell is therefore defined as protoplasm plus cell wall. Again, some cells lack a nucleus altogether, whereas others have more than one (Chapter 6). Finally, in some mature plant cells such as xylem vessels, the protoplasm disappears completely, and the term 'cell' is applied to the cell wall only (Fig.1.1c).

The term 'living jelly' as a synonym for protoplasm is best avoided. It suggests that there is some 'vital' force in a cell giving it life. This view (vitalism) lacks the support of experimental evidence and is only of historical interest. Experimental evidence suggests that the activities in a cell which we call 'life' are best explained in terms of the collective physical and chemical properties of the various parts.

(ii) *Cells are the basic functional units of tissues, organs and organisms*

Cells are the essential working components of every structure in an organism. Parts of organisms which are not composed of cells are difficult to find, although parts of bone and the exoskeleton of insects are two examples. In both cases, however, the material is secreted by cells, so it is of cellular origin.

Whilst cells are the fundamental building blocks of tissues and organs, they do not work in isolation. Recent technical developments have considerably advanced our understanding of how cells communicate with each other to produce a unified and coordinated organism (see Section 2.2.2).

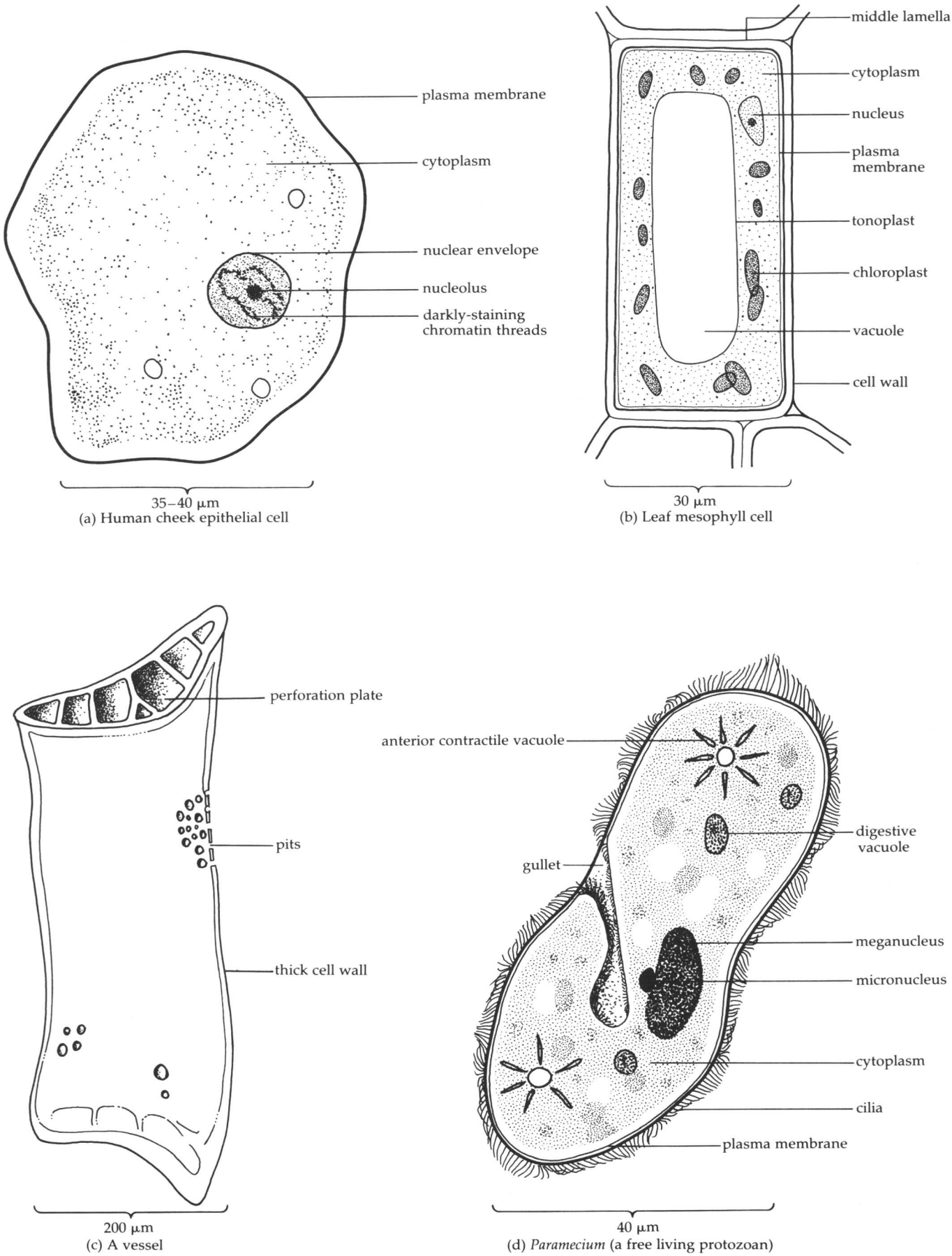


Fig. 1.1 *A variety of eukaryotic cells.* The cells are drawn as they might appear using an optical (light) microscope.

Table 1.1 *Comparison of eukaryotic and prokaryotic cells*

	Eukaryotes (animal/plant cells) (*Eu: true; karyon: nucleus*)	Prokaryotes (bacteria/blue-green algae) (*Pro: without; karyon: nucleus*)
1 Nucleus	Present	Absent
2 Nucleolus	Present	Absent
3 DNA	Confined mostly to several linear nuclear organelles (chromosomes)	Confined mostly to a single circular loop (chromoneme) attached to the plasma membrane
4 DNA packaging	Histones (proteins) help package DNA into chromosomes	Histones absent
5 Cell wall (plants only)	Mostly cellulose, hemicellulose, pectate	Never cellulose, several unique polymers (mureins/techoic acid)
6 Plasma membrane	Phospholipids, sterols, proteins	Phospholipids and proteins, no sterols
7 Membrane-bound systems	Chloroplasts (plants), mitochondria, E.R, Golgi bodies, lysosomes, etc.	None. Photosynthetic pigments (if present) in infoldings of plasma membrane
8 Cilia/flagella	9+2 system of microtubules	If present, superficially resemble single microtubule, but made of a unique protein
9 Internal cytoskeletal components	Extensive microtubules, microfilaments, 10nm filaments	None
10 Ribosomes	80S (larger)	70S (smaller)
11 Storage compounds	Often glycogen (animals) or starch (plants)	Varied. Often a polymerised fatty acid derivative, β hydroxybutyrate (bacteria); sometimes glycogen (blue-green algae). Not starch (except *Clostridium*)
12 Organisation	Cells mostly components of organs and tissues in a complex multicellular organism	Unicells, or short chains of similar cells
13 Size	Varied, typically $10^4\mu m^3$ to $10^5\mu m^3$	Varied, typically $1\mu m^3$ to $10\mu m^3$

(iii) *Cells only come from pre-existing cells*

A cell may divide to produce two or, occasionally, more daughter cells (Chapter 6). Alternatively a cell such as a zygote may arise from a fusion of two cells. In any event, cells never arise *de novo*.

1.2 THE STATUS OF THE CELL CONCEPT

Scientific theories are inventions of the human mind and Nature is under no obligation whatever to obey them. If she chooses not to, we dismiss it as an 'exception'. However, the cell theory is remarkably comprehensive, and about the nearest we get to an exception are the viruses. Elsewhere in this series it is argued that viruses are best regarded as non-living, self-replicating particles, not living organisms. If this view is correct, then there are no exceptions to the cell theory.

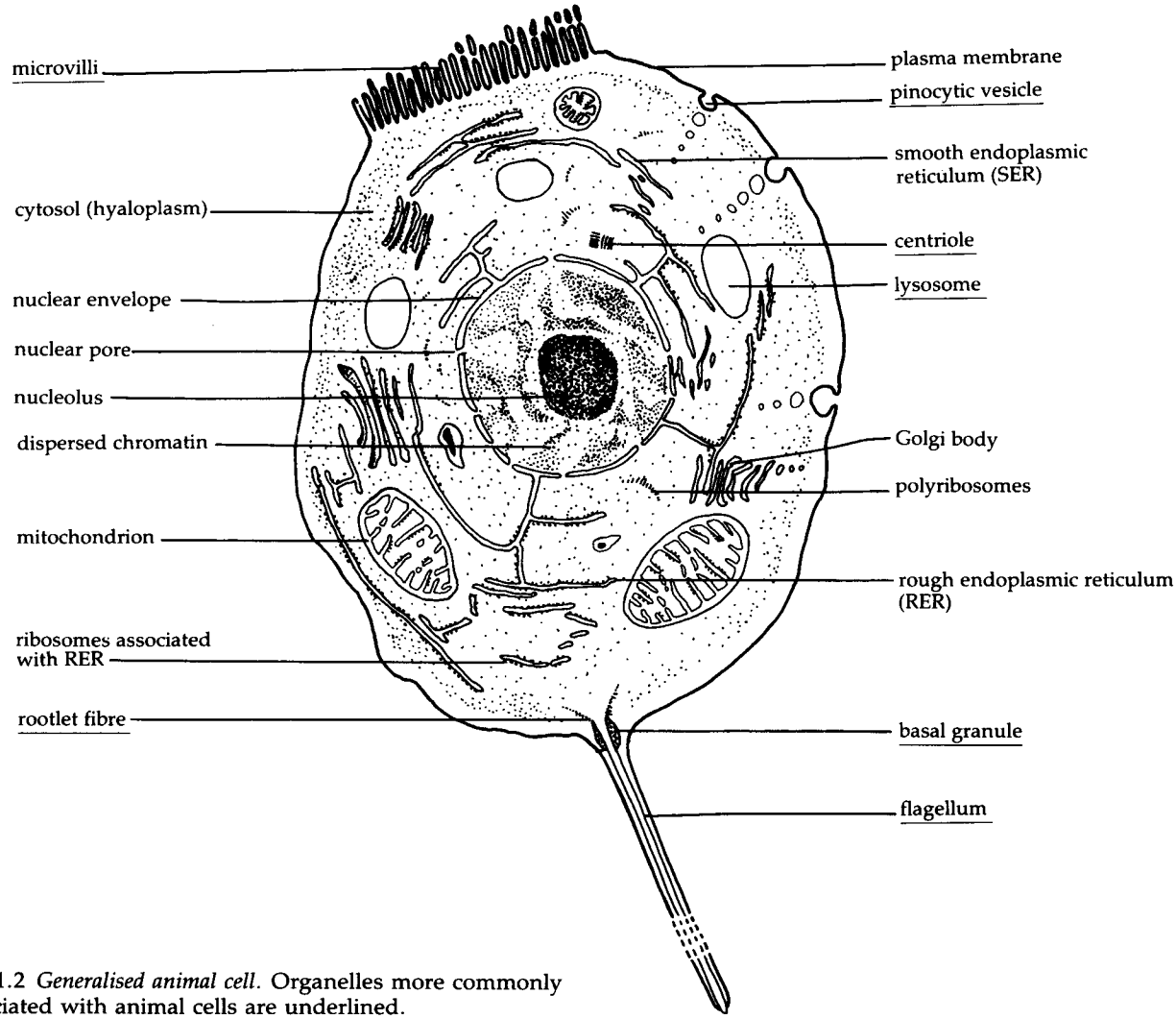


Fig. 1.2 *Generalised animal cell.* Organelles more commonly associated with animal cells are underlined.

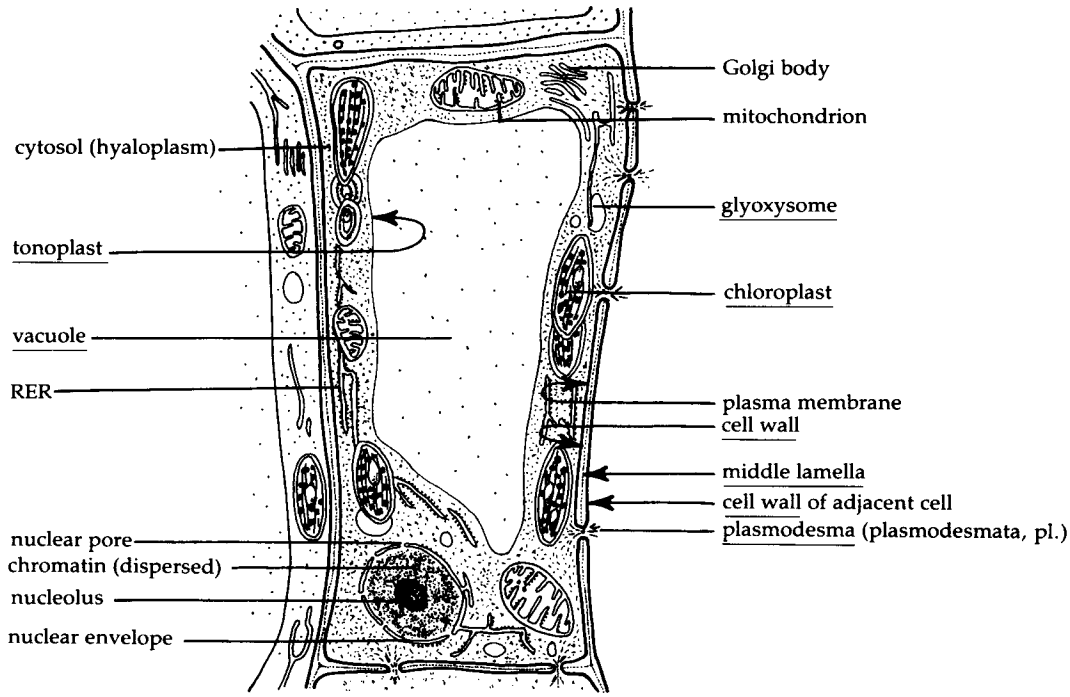


Fig. 1.3 *Generalised plant cell.* Organelles more characteristic of plant cells are underlined.

Study guide

Vocabulary

Explain the meaning of the following terms:

cytoplasm	protoplasm	organelle
eukaryotic	prokaryotic	

Review Questions

1 What are the essential features of the cell theory? Comment briefly on each feature.

2 How many bacteria (0.001mm diameter) does it take to equal the volume of a white blood cell (0.01mm diameter)? Assume for simplicity that both cells are perfect spheres for which the volume = $4/3\ \pi\ r^3$.

3 List the structures found:
(a) in all typical eukaryotic cells
(b) in plant cells only
(c) in animal cells only.
Give one or more functions, as appropriate for each of the structures you have listed.

Extension Question

How do the following differ from typical eukaryotic cells?
a fungal hypha an erythrocyte
a sieve-tube element a striated muscle cell
a tracheid

2

The Plasma Membrane and the Cell Wall

SUMMARY

A phospholipid membrane, 7×10^{-6}mm wide, separates the protoplasm from a hostile environment. It regulates transport in and out of the cell, acts as an identity card, recognises hormonal signals, assists in cell mobility, and binds adjacent animal cells together.

The following terms are used:

α-helix	differentially permeable	phospholipids
β-pleated sheets	glycoproteins	polar molecule
cytosol	hydrophobic	non-polar molecule
globular proteins	impermeable	
saturation of fatty acids	permeable	

Fig.1.1(a/b and d) contains an outrageous lie. The dark line around the edge, easily visible by optical microscopy, is not the plasma membrane (syn. cell membrane, plasmalemma). The membrane is only 7.5nm wide, so at 400× magnification the image, even if the microscope could resolve it, would be only 0.003mm thick. To be visible at all by optical microscopy, it would need to be some 300× thicker. The dark line around the cell is merely a shadow of the edge itself, and to label it 'cell membrane' is a tribute to one's imagination rather than to any skill in observation. If the membrane can only be seen by electronmicroscopy, how did biologists know it existed prior to 1957, when Robertson took the first **electronmicrograph**? Two reasons: firstly, if a cell is ruptured the contents spill out, suggesting that a membrane normally separates the protoplasm from its surroundings. Secondly, the observation that different substances enter or leave cells at different rates, often regardless of their relative concentrations, suggests the existence of a plasma membrane which, moreover, is **differentially permeable** in character.

2.1 STRUCTURE

The differentially-permeable nature of the plasma membrane not only provided circumstantial evidence for its existence, but also the first clue to its structure. Overton (1895) observed that fat-soluble substances passed through plasma membranes most easily, and concluded that **lipids** were an important constituent. Chemical analysis of the membrane subsequently confirmed that it contains **glycoprotein and protein** (60%) and **various lipids** (40%) (Fig.2.1).

Gorter and Grendel (1925) calculated that there was enough lipid in the membrane to form a layer two molecules thick: a **lipid bilayer**. With this knowledge Danielli and Davson (1935) suggested a membrane model in which:

(i) The **phospholipids** (the major lipid constituents) form a bilayer with their polar ends next to the aqueous surroundings, and the non-polar ends pointing inwards to the non-aqueous centre. The latter would thus form a hydrophobic lipid barrier and prevent random mixing of the cell contents with the surroundings. Such a barrier would go a long way towards explaining the differential permeability of the membrane.

(ii) The polar proteins form a layer each side of the phospholipid bilayer.

From a theoretical knowledge of molecular size, Danielli and Davson predicted that the membrane would be about 7.5nm thick, in a 2nm + 3.5nm + 2nm sandwich. This was later supported by thin section electronmicrographs (Fig.2.2).

However, new cytological techniques in the 1960s and 1970s produced results which were incompatible with the Danielli-Davson model:

(i) According to the Danielli-Davson model, membrane proteins should be smooth, β-pleated sheets. In practice the protein is **globular**.

(ii) Branton (1966) froze plasma membranes, then cracked them so that they split down the middle. The effect is rather like opening a sandwich to see inside. The Danielli-Davson model predicts smooth interiors. What is actually seen is shown in Fig.2.3. The 10nm 'cobbles' are the globular proteins and glycoproteins described in (i).

(iii) 10% of the weight of an animal plasma membrane is **carbohydrate** (in the form of **glycoprotein**), which staining techniques show to be on the exterior surface of the membrane (Fig.2.4). This carbohydrate coat, called the **glycocalyx**, is unaccounted for on the Danielli-Davson model.

(iv) The Danielli-Davson model predicts that the proteins are fixed in position. However, if the proteins of two cells are labelled with different

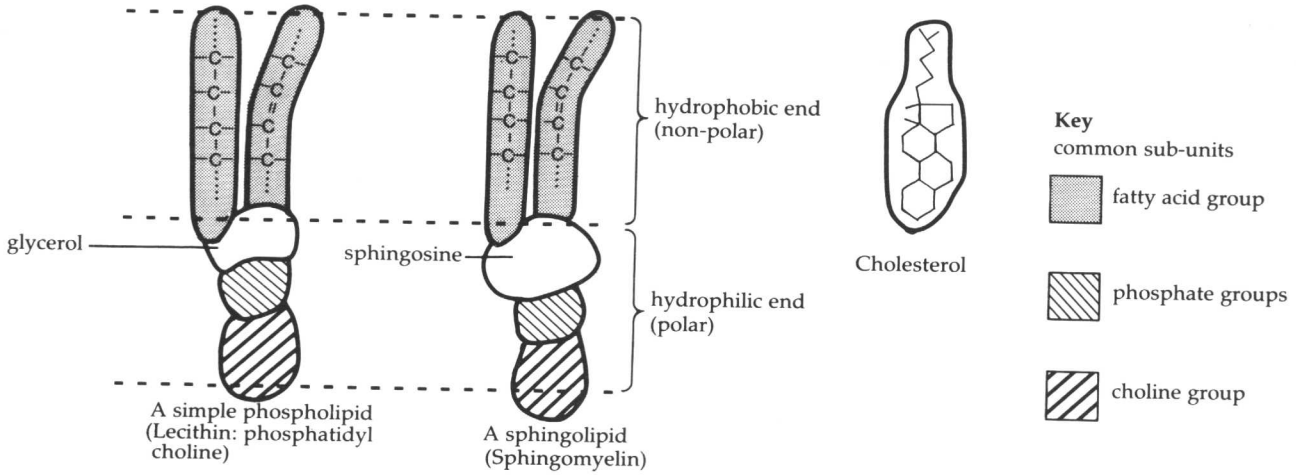


Fig. 2.1 *Membrane components*. Only the main lipid components are shown (a protein molecule on the same scale would occupy the entire page). Phospholipids (glycerol based) are usually the most common followed by sphingolipids (sphingosine based). Note how the the fatty acid side chains can be straight (no double bonds, i.e. saturated) or kinked (at least one double bond, i.e. unsaturated). This is an important feature which affects fluidity (Section 2.2.3.) Cholesterol is not a phospholipid at all but a steroid. It sits between the fatty acid side chains in the membrane and helps to stabilise them.

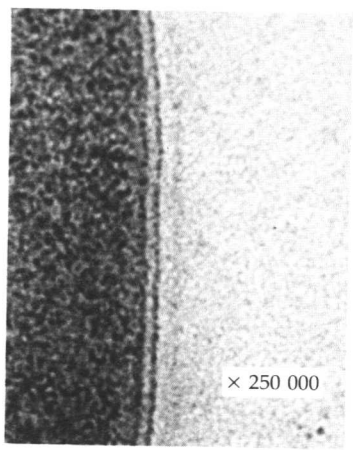


Fig. 2.2 *A thin-section electronmicrograph of a plasma membrane*. The 'tramline' effect was taken as support for Danielli-Davson's model, each dark line being assumed to correspond to a lipid layer coated on the outer surfaces by protein.

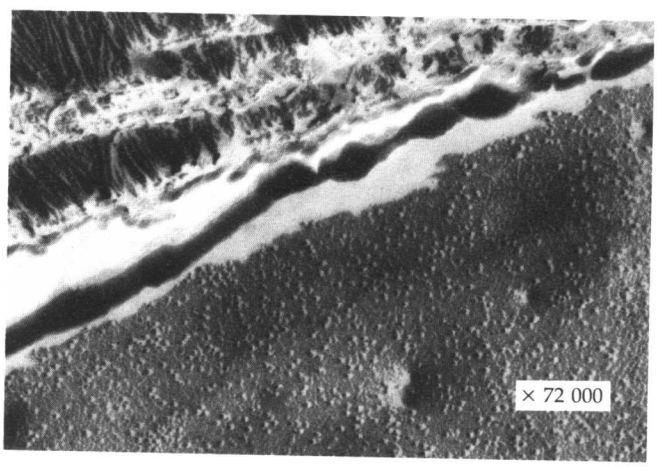
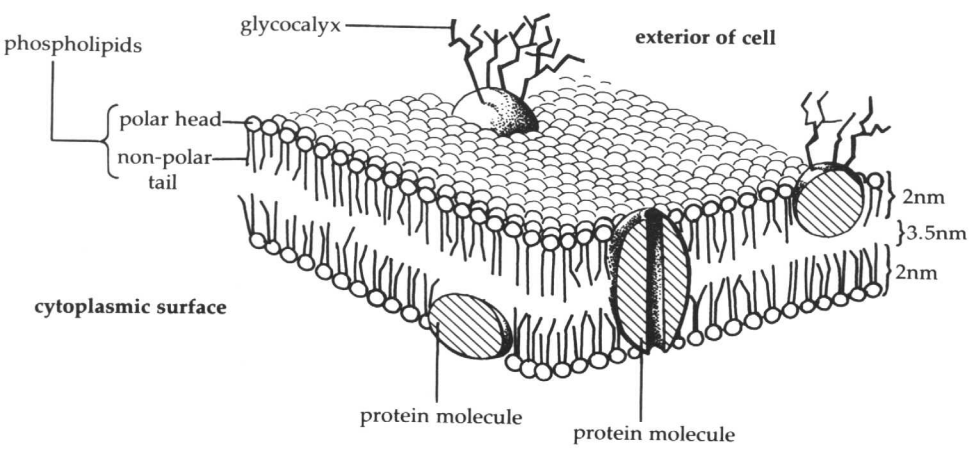


Fig. 2.3 *Freeze-fracture preparation of a plasma membrane*. Heavy-metal shadowed preparations may be viewed either by TEM or SEM.



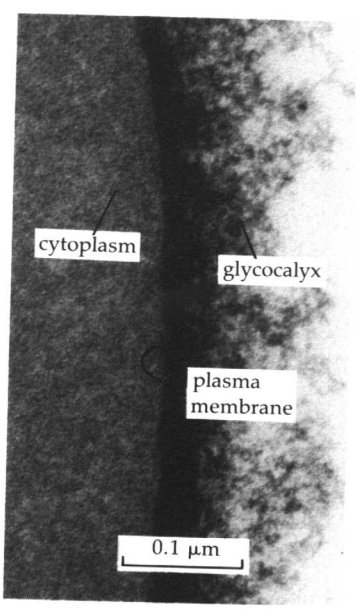


Fig. 2.4 *The Singer and Nicolson Fluid Mosaic Model of a Plasma Membrane*. (Inset: photomicrograph of the glycocalyx).

fluorescent dyes attached to antibodies (see Table A1.1), and the cells are then fused together, the dyes merge. This suggests that the proteins move about.

As a result of such evidence, Singer and Nicolson (1972) proposed the **fluid mosaic model** (Fig.2.4). Its principal features are:

(i) The phospholipids form a bilayer, as in the Danielli–Davson model.

(ii) The globular proteins and glycoproteins float about in a 'lipid sea', with the polar (water soluble) carbohydrate portions forming the glycocalyx on the external surface.

The fluid mosaic model has been enthusiastically received for two reasons. Firstly, it is the most convincing explanation of experimental observations on membrane structure. Secondly, it suggests how membranes can carry out their many and varied functions. This, perhaps, is the crucial test of any model (hypothesis). Ultimately a model has to explain how things work, not simply what they look like.

2.2 FUNCTIONS

Plasma membranes play important roles in:

(i) regulating the transport of substances in and out of the cell
(ii) communication
(iii) cellular movement
(iv) cell recognition
(v) cellular adhesion

2.2.1 Regulation of transport

Preventing the loss of important molecules from cells, or the entry of toxic substances is a precondition for life. Both the phospholipid and protein components contribute to the membrane's differentially permeable character. The phospholipid bilayer effectively prevents water-soluble substances inside the cytoplasm from mixing with those outside, or merely diffusing away. This is due to the fact that lipid and water-soluble substances do not mix. Only in the case of relatively few substances can the distribution either side of the membrane be explained simply by **diffusion.** In most cases transport is regulated by processes in which the membrane proteins play a key role. Such proteins may act as **receptors** to which substances first bind before being transported, or they may act as **pores** through which hydrophilic molecules can pass. As explained in the next chapter, transport proteins are frequently enzymes, and energy (**ATP**) may be needed to drive the transport machinery. Whatever the mechanism involved when a substance crosses a plasma membrane, the larger the surface area of a cell, the faster the rate of transport.

A perfect sphere has the smallest surface area in relation to its volume. A spherical cell will thus have the least favourable surface/volume (s/v) ratio for the transport of substances. Not surprisingly, therefore, very few cells are spherical, and most are elongated or flattened. In addition, many absorptive and secretory cells further increase their surface area by finger-like projections called **microvilli**. The microvilli are so numerous in Fig.2.5 that they create a **brush border** on the edge of the cell.

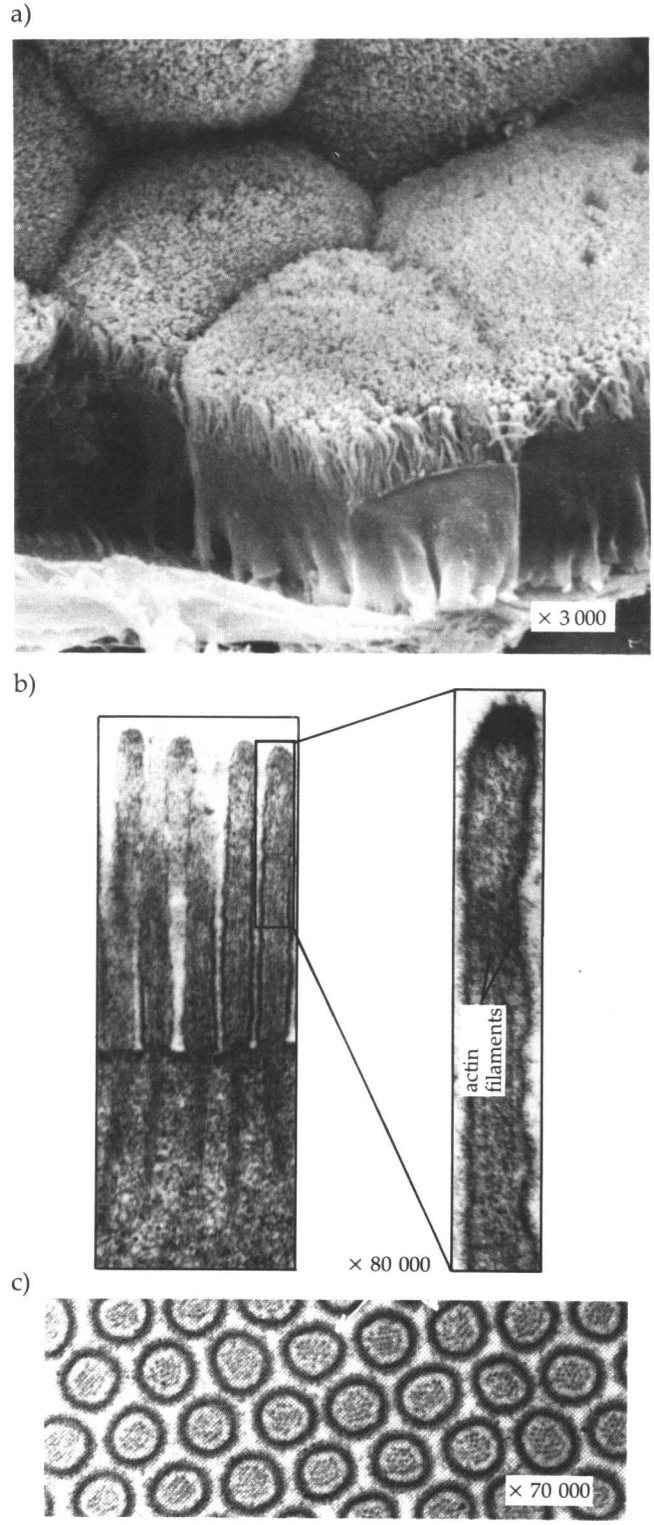


Fig. 2.5 *Microvilli.* (a) SEM of microvilli on simple cuboidal epithelial cells from the proximal tubule of a nephron (× 3000); (b) thin section TEM through intestinal epithelial cells (×50 000); (c) transverse thin section through brush border (right angles to (b)) (× 70 000).

Q1 The extent to which microvilli increase the absorptive surface can be estimated. In Fig. 2.5a, assume the nearest cell approximates to a square.

(i) From the scale given, estimate its absorptive surface, assuming no microvilli.

(ii) Estimate the number of microvilli (to the nearest 50). Each is about 2μm long × 0.1μm diameter. Calculate the absorptive area in the presence of microvilli, assuming that each is a cylinder of surface area $2\pi rh$ (sides) and πr^2 (one end).

(iii) How many times greater is the surface area in the presence of the microvilli?

The bulk import of materials into the cell from the surroundings (**endocytosis**) is principally achieved by **phagocytic** and **pinocytic** vesicles. Both are membrane-lined spheres, originating as infoldings of the plasma membrane. Using an optical microscope the former are just visible in various animal cells, e.g. blood phagocytes, and *Amoeba*, and are associated with the capture of large particles such as bacteria. Pinocytic vesicles (0.1μm diameter or less) are also more commonly seen in animal cells (Fig.1.2). They take into the cell substances adsorbed onto the glycocalyx, such as hormones, plus a drop of the surrounding fluid. This is now thought to be their primary function, not the absorption of water or fluid. Plasma membrane lost during pinocytosis or phagocytosis is thought to be replaced by membrane originating from Golgi body vesicles during **exocytosis** (cellular secretion). As a result of the latter the cell volume stays approximately constant, whilst as a result of phagocytosis and pinocytosis the total membrane area is increased. As we shall see in Chapter 3, the contribution such vesicles make to the absorption of substances into the cytosol is effectively through this increased area.

2.2.2 Cellular communication

Cells of multicellular organisms are not independent entities. Communication between cells, tissues and organs is vital if the integrity of the whole organism is to be maintained.

Communication between adjacent cells

Adjacent plant cells communicate by large, permanent strands of cytoplasm (**plasmodesmata**) passing through holes in the cell walls so that the plasmalemma is continuous between them (Figs.1.3 and 2.11). Large holes (**pits**) are clearly visible in vessels (Fig.1.1c) and tracheids long after the cytoplasm has disappeared. Adjacent animal cells normally communicate by **gap junctions**, 0.1μm pores lined by membrane-bound protein (Fig.2.6). Unlike plasmodesmata they are neither large nor permanent. Only molecules with a molecular mass <1000 can pass through, and if a cell is damaged its altered ionic composition causes them to close. This is a useful feature, since it prevents the damage from spreading.

Neurons are exceptional. A few transmit their impulses directly at modified gap junctions called **electronic synapses**. The vast majority, however, use a molecular signal at special junctions called **chemical synapses** (see below).

Distance communication

Hormones are essentially chemical signals released by one part of the body which have an effect on a different part. However, except in the case of steroid hormones (for example, sex hormones), and some plant hormones (for example, gibberellic acid), these primary chemical messages never pass into the cytoplasm of their target cells. Thus, while the effect of the hormone adrenalin is to convert glycogen to glucose in skeletal muscle cells, the link between the hormone and its effect is the plasma membrane. It is

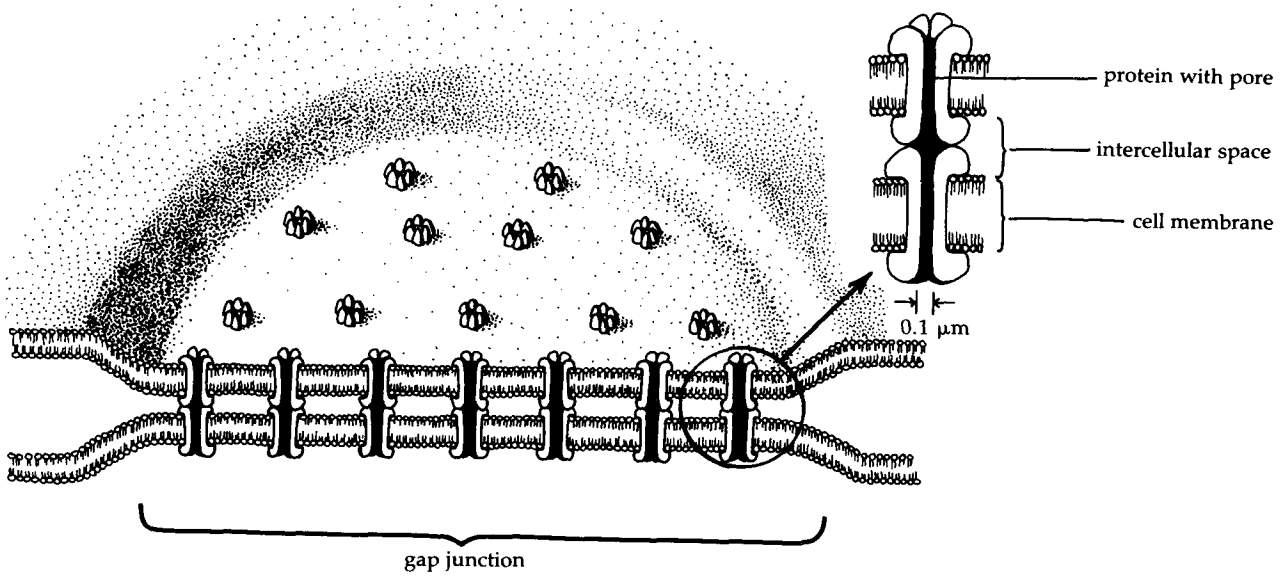


Fig. 2.6 *Gap junctions allow communication between adjacent cells.*

this which reacts with the hormone and translates the message into cytoplasmic activity.

As Fig.2.7 shows, the hormone binds to **membrane-bound receptors** (glycoproteins) on the *outer* surface of the membrane. Binding activates the receptors, and in doing so triggers a sequence of enzymic events on the *inner* (cytoplasmic) surface. Some cells respond in opposite ways to different hormones, suggesting different receptors coupled to opposing systems. Other cells do not respond to a particular hormone at all, suggesting that receptors for that hormone are missing. This range of possibilities has enormous biological significance, since it enables different tissues of the body to be regulated with great precision.

Neurone-to-neurone and neurone-to-muscle communication is also principally by chemicals (**neurotransmitters**) such as acetylcholine. Arrival of a neurotransmitter causes changes in the permeability of the membrane to ions. This results in electrochemical changes, and brings about a new impulse. Only some membrane proteins involved in nervous transmission are receptors. Others act as ion pumps to restore ions to their normal values after they have been disturbed by an impulse. The phospholipids in the membrane also play a key role. As they are good insulators and impermeable to ions, they help to maintain a **potential difference** (p.d.) of some 60–100mV between the inside (negative) and outside (positive) of the cell. Without this potential difference, no impulse would be possible. Its origin is described in Chapter 3.

2.2.3 Cell mobility

Many cells are mobile, for example, *Protozoa*, embryonic cells and phagocytes. Mobility depends in part on the almost fluid nature of the plasma membrane, which in its functional state is an example of a **liquid crystal**. If the temperature drops, phospholipids lose their mobility and the membrane becomes a non-functional solid. The critical temperature at which this happens is called the **transition temperature**. Cell membranes in cold-water animals and plants generally have a low transition temperature. This is achieved by building membrane phospholipids from **fatty acids** which are short and unsaturated. Shorter fatty acids are more mobile, and unsaturated ones cannot be stacked together so easily due to the kink in the side chain (Fig.2.1). Both these features help to prevent the membrane solidifying.

2.2.4 Cell recognition

When a bacterium enters a body it will be attacked by the defence system because it will be recognised as 'foreign'. It is obviously important for a body's defences to distinguish clearly between intruders (**non-self**) and the cells of the body (**self**).

The **glycocalyx** on the plasma membrane provides the body with a kind of 'molecular identity card' which the lymphocytes and phagocytes are able to interpret. The sugar coating on red blood cells, for example, determines the blood groups. Although it works well, the system does have drawbacks. Trans-

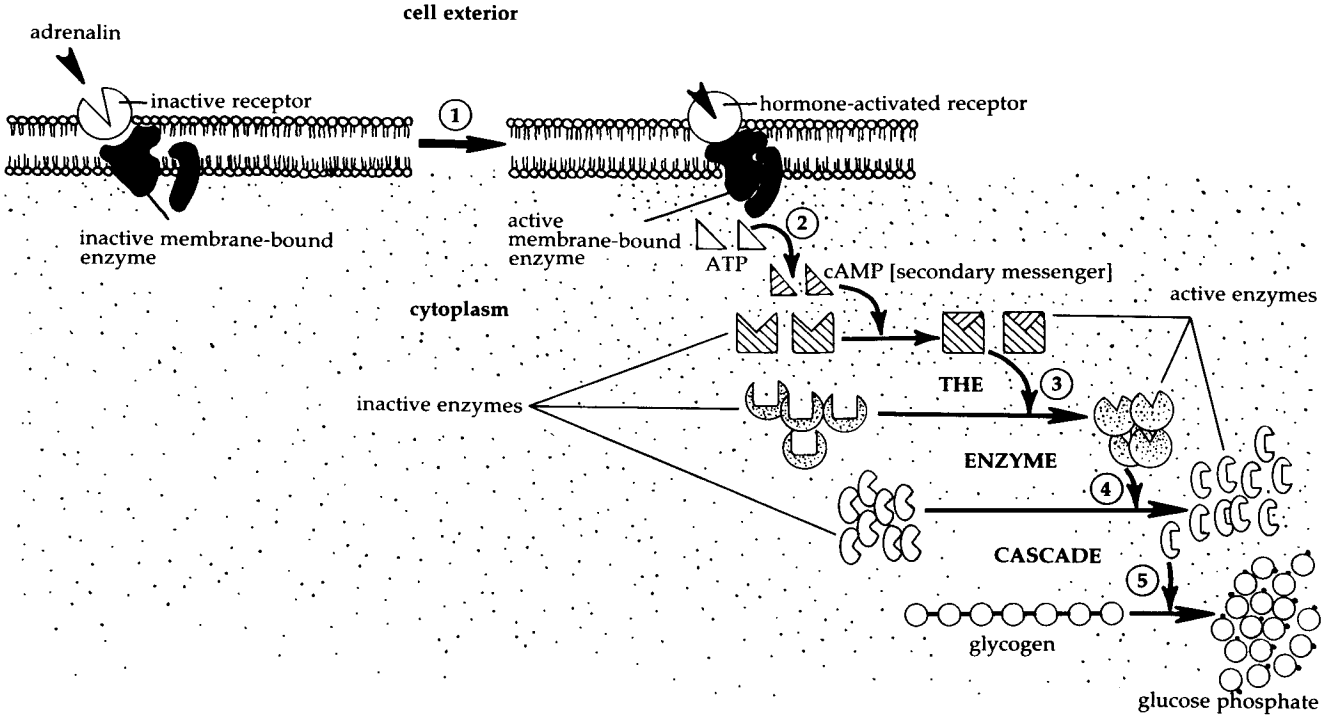


Fig. 2.7 *The role of the plasma membrane in triggering hormonal responses.* The essence of the system is to produce as big a response as possible to a single adrenalin molecule. This is achieved by amplifying the original signal millions of times. At **1**, an adrenalin molecule activates a membrane-bound protein. At **2**, each of these produces many 'secondary messengers' (cAMP) per second. cAMP then activates an enzyme, each molecule of which activates thousands of other enzyme molecules, (**3**). This is repeated, (**4**), until finally an enzyme is activated which breaks down stored food into glucose phosphate, (**5**). The illustration applies to animals only. There is no evidence for the existence of equivalent systems in plants.

planted organs and transfused blood, for example, will be attacked (rejected) if they are regarded as non-self. The system is also open to abuse. Parasitic platyhelminthes (flatworms) such as schistosomes, 'steal' the glycocalyx from their hosts' cells, envelop themselves in it, and so avoid detection by phagocytes. A worm in self's clothing?

2.2.5 Cellular adhesion

Cellular adhesion is essential in multicellular organisms, but the mechanisms employed by animals and plants differ. In animals the main mechanisms are:

(i) *Aggregation factors* (Fig.2.8a)

These are membrane-bound glycoproteins which lock into complementary proteins in adjacent cells or into intercellular glycoproteins. Tissues may have unique and specific aggregation factors; mixtures of isolated cells tend to separate into groups of cells of the same type.

(ii) *Desmosomes* (Fig.2.8b)

Desmosomes are organelles, composed of 10nm protein filaments called **tonofilaments** which appear to 'weld' adjacent cells together on a plate of carbohydrate-rich material. In skin and gut epithelial cells the tonofilaments are made of **keratin** which makes the desmosomes particularly strong.

(iii) *Tight junctions* (Fig.2.8c)

A **tight junction** is formed from huge proteins which span the membrane of adjacent cells rather like a row of tight stitches holding together two pieces of cloth. Their contribution to cellular adhesion is estimated to be quite small, and their main function is probably to prevent leakage of fluid between cells: an undesirable event if it occurs in, for example, bladder epithelial tissue.

(iv) *The extracellular matrix* (Fig.2.8d)

This consists of fibrous proteins like **collagen** embedded in a watery gel of modified carbohydrates like **hyaluronic acid**. The composition, however, is variable, and so therefore are its properties. In cartilage the extracellular matrix is relatively solid, whereas at the synovial joints it is very fluid. Frequently, the matrix acts as a kind of biological superglue, helping to stabilise and bind together the cells of a particular tissue or organ. Additionally it is known to influence an organ's growth and development.

The mechanism binding plant cells together is quite different, and involves the cell wall components.

2.3 THE CELL WALL

It is convenient to conclude this chapter with some mention of cell walls, although they are very different from plasma membranes. Found only in plants and several hundred times thicker than the membranes they enclose, they are made almost entirely of carbohydrate and are fully permeable to a very wide range of substances. The last feature is especially important, since the membrane itself remains the surface for the exchange of metabolites and cell recognition. As mentioned in Section 2.2.2, adjacent cells may communicate by **plasmodesmata** through small perforations in the wall. In transport cells such as vessel elements, tracheids, and sieve-tube cells, these perforations are enormous. At maturity, vessel elements resemble open-ended tubes, devoid of protoplasm, and stacked one on top of the other. Perhaps the most obvious characteristic of cell walls is their strength. The rigidity of wood, for example, is due entirely to the strong, **lignified** walls of its constituent cells (mostly vessels, tracheids and fibres). In contrast parenchyma cells of leaves and young shoots are supported by the **hydrostatic pressure** of the vacuole against the more elastic wall, so here the cell is supported rather like a well-inflated car tyre.

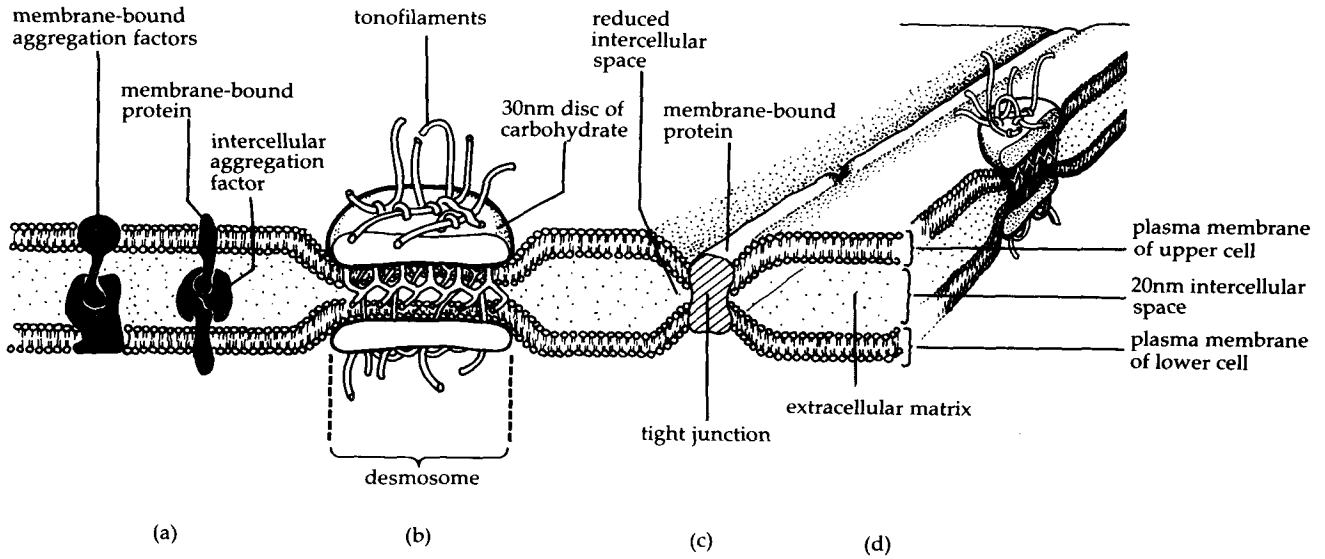


Fig. 2.8 *Factors contributing to cell-to-cell adhesion.*

2.3.1 Composition

The most common component of a cell wall is **water** (60% f.wt.). The main organic constituent is **cellulose**, followed by a variety of other substances depending on the size and type of cell (Table 2.1). If one had to invent a molecule from which to make a cell wall, it would be hard to improve on cellulose. It has great tensile strength, bonds with other substances to produce a rigid, permeable structure, does not dissolve in rain, and is made from **glucose**, a chemical abundantly available as a result of photosynthesis.

Table 2.1 *Cell wall components*

Component	Comments
Water	Up to 60% (f.wt.). Maintains configuration of other components
Cellulose	30%–50% (dry wt.). β1:4 glucose polymer (see text)
Hemicellulose	A mixture of polysaccharides based on xylose/mannose. Very common in young walls. Less rigid than cellulose
Pectate (pectins)	Mostly calcium pectate: salt of β1:4 galacturonic acid (a polysaccharide). Main component of middle lamella. Probably acts as a glue, binding the wall(s) together.
Lignin	Up to 30% (dry wt.) of wall in sclerenchyma, vessels and tracheids. Strongly hydrophobic and helps cross link other components, thus making wall rigid. Completely absent in some cells, e.g., parenchyma, collenchyma
Protein	Up to 3%. Possibly enzymic or structural functions
Chitin and other mucopolysaccharides (in *Fungi* only)	Replaces cellulose, except in a few primitive fungi e.g. *Oomycetes*, and has similar properties. Made from an acetylglucosamine polymer (glucose with a $-CONH_2$ group)

The chemistry of cellulose helps to explain its properties. It is a β1:4 glucose polymer, a single molecule of which can be 5μm long and contain some 10^4 glucose units (Fig.2.9). 'β' means that the –OH on C-1 sticks *upwards*, and '1:4' means that there is a **covalent** (oxygen) **bond** between C-1 of one glucose and C-4 of the next. The geometry of the –OH group on C-1 produces a straight molecule when linked to C-4, and because the bonds are covalent, the molecule is immensely strong. Each glucose unit has additional –OH groups on C-2, C-3, and C-6 which form covalent bonds with adjacent molecules. Parallel chains of several hundred cellulose molecules form, these are called **microfibrils**. Groups of several hundred microfibrils themselves bond together to form **macrofibrils**. Cellulose is insoluble because the hydrophilic –OH groups are used up during fibril formation, and because the macrofibrils are very large.

2.3.2 Formation

The assembly of cell walls begins at the time of cell division between the divided nuclei. The first observable structure is the cell plate (**phragmoplast**) (Fig.2.10). Vesicles containing cell wall materials and enzymes are released from the Golgi bodies and carried to the cell plate by microtubules (Chapters 4 and 5). The contents of the vesicles are deposited, and the cell plate grows towards the existing boundaries of the cell, eventually forming the **middle lamella**.

The daughter cells thus become separated except at pores penetrated by plasmodesmata. Each cell now

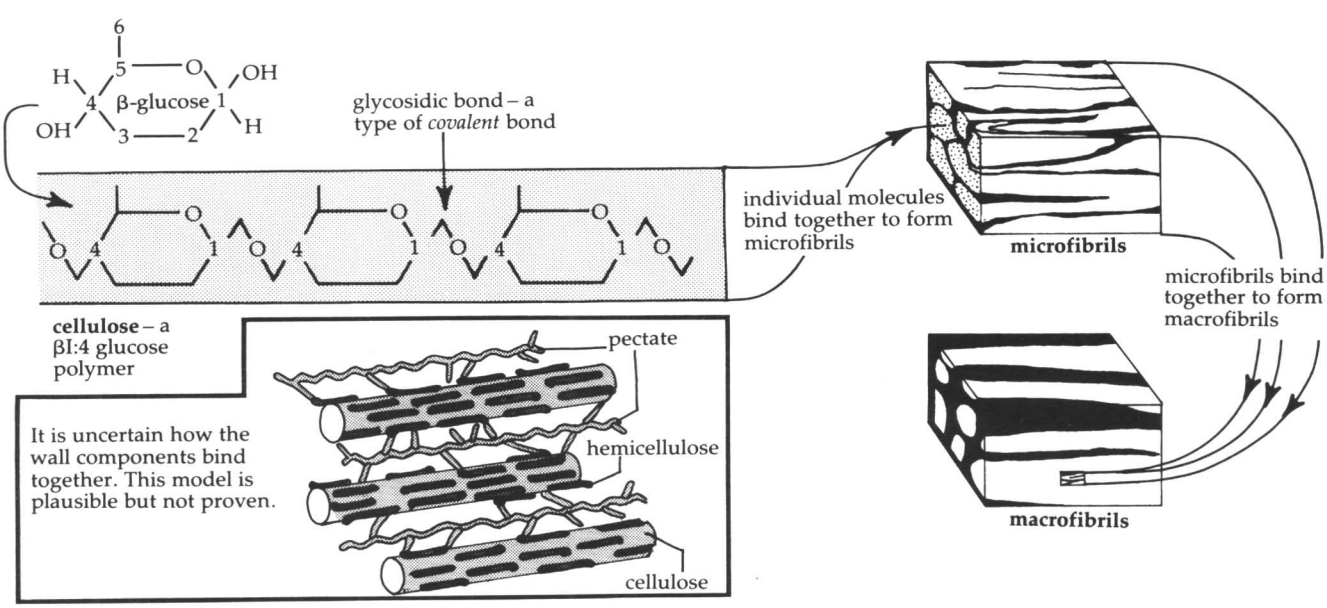


Fig. 2.9 *Cellulose and the molecular biology of cell walls.*