The Cambridge Encyclopedia of Life Sciences

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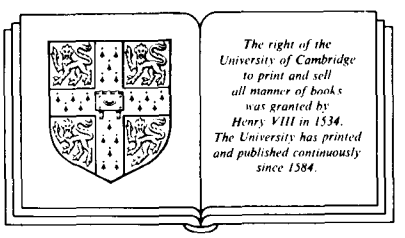

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Contents

Foreword

The human species must always have been interested in the living organisms with which it shares this planet: primarily for strictly practical reasons, as gatherers and hunters, then as cultivators and pastoralists, and subsequently in attempts to understand more completely the world, the origin of the human species, and its fate.

For at least 2000 years attempts have been made to discover the relationships between living things, and in particular to classify the always increasing number of plants and animals known, from the few hundred familiar to Aristotle and Theophrastus, to the thousands known to Ray and von Linné (Linnaeus), and the millions which are currently studied with the sophistication of modern technology. In addition, the question of the origin of life on this planet has taxed the imagination since remote antiquity. Scientific explanations have ranged from Aristotle's hypotheses of spontaneous generation by natural forces, to the not totally dissimilar ideas of some modern scientists based on the production of simple organic compounds by electrical discharge in mixtures of gases, with the more complex organic molecules arising in what J.B.S. Haldane has termed the 'hot dilute soup' of primaeval oceans. This curiosity about the origins and variety of life has led to what is arguably one of the greatest revolutions in human thought, Charles Darwin's theory of organic evolution by natural selection, and the accumulated knowledge concerning the other organisms with which we share this planet has provided insight into our own nature and emphasised the dangers that threaten the human species.

It is a current conceit, and one frequently encountered in forewords of this kind, that we live in the age of 'the revolution in biology'. In one sense this is quite untrue, as some of the biological advances of early ages, such as Pasteur's dismissal of the theory of spontaneous generation of life, or Darwin's demonstration of the existence of organic evolution and his discovery of its mechanism, were in concept truly more revolutionary than any recent advances in biological knowledge. It is the impact of modern technology on the detailed elucidation of living processes that is currently revolutionary. In particular, the ability to study living cells as physicochemical systems has led to the recent spectacular growth of biophysics and molecular genetics. This growth will undoubtedly have an increasing effect on many aspects of human life, ranging from the sophisticated control of our own bodily processes to dramatic changes in our methods of production of food and fuel. Despite its successes, however, the molecular approach can make only limited contributions to the elucidation of the mechanisms by which organisms function as integrated units and interact as communities and populations. The understanding of such complex levels of organisation as the behaviour of animals and the human mind involves concepts of high order which modern biologists are only beginning to attempt to formulate. The final implications of this research cannot yet even be imagined.

To attempt to summarise in a single volume the available information on the living organisms which inhabit, or have inhabited, the earth is, if not impossible, certainly a daunting task. The two very obvious reasons why this should be so are the extreme complexity and the enormous diversity of such organisms. Fortunately the molecular and biochemical approaches to living systems have tended to emphasise the essential similarities of the mechanisms involved in basic cellular processes such as genetic inheritance, metabolism and growth, although even this apparent unity may be illusory and a consequence of the way that we choose to look at these processes. With an appropriate viewpoint, however, it is possible and useful to compare the basic cellular functions of different organisms, such as sea-weeds and orchids, or eels and apes. Such broad comparisons become progressively less useful when applied to tissues and to organs, and at these levels of organisation it may be more profitable to consider specialised aspects of cellular function and, in particular, the transfer of information between cells. The understanding of the integrative functions of such information transfer is now one of the central biological problems, for example in developmental biology, and will undoubtedly become an essential factor in our understanding of the neural basis of animal behaviour and of our own mental processes.

This *Encyclopedia* describes a hierarchy of interactions or, perhaps better, a hierarchy of environments: the various controlled environments within the cell, the immediate extracellular environment provided for the cells within tissues, the environments provided for the tissues by their organisation into organs and then for the organ systems within organisms, and finally the components, both physical and biological, of the external environment of the whole organism. The adaptations of plants and animals to their environments, and their relations with other organisms within these environments, are central features of this book. This emphasis is very much a product of its time; it both reflects the current concern with the accelerating rate at which the environment is being exploited and destroyed, and is a natural stage in the development of the sciences of life.

J.E. Treherne

Mixed tropical riverine forest in the gorge of the Nyamugasani River, Queen Elizabeth National Park, Western Uganda.

Introduction

The most striking feature of any natural assemblage of living things is the great diversity of size and form of the micro-organisms, plants and animals within it. This diversity is perhaps most obvious in the teeming jungles of the rain-forests of the tropical regions of the world, but on closer examination is found to be almost as great in habitats as different as temperate woodlands, the continental deserts, the vast oceans which cover the greater part of the earth's surface and, perhaps surprisingly, many of the altered environments created by agriculture, industry and the building of cities.

Close observation of the natural world has, in many instances, led to major advances in biological thinking. Darwin's theory of evolution by natural selection, for example, which revolutionised biology in the nineteenth century, arose as a result of a lifetime's detailed observation of plants and animals. The observational approach of the naturalist has continued into the present century, and today is perhaps more important than ever as the activities of the human species lead to the modification or destruction of more and more habitats and the extinction of an ever-growing number of species, many of which are, and may remain, unknown to science.

The approach of the naturalist, the observer, is however limited and, although an essential prerequisite for most forms of investigation, is not sufficient to explain all the complexities of biological organisation. In the historical development of the life sciences the descriptive approach has, in most fields, been augmented by a more critical experimental tradition: the recognition that to understand the properties of the living world it is necessary to frame the right questions and to ask them in such a way that answers may be obtained with some conviction.

The experimental tradition in modern biology developed much earlier in studies of animals than in studies of plants. Walters, in *The Shaping of Cambridge Botany* (Cambridge University Press, 1981), suggested that this may have come about because, although modern botany and zoology both had their origins in medicine, the function of the botanists was accurately to describe and identify all plants, or 'herbs', for use as therapeutic agents, whereas zoology developed from comparative studies of both human anatomy **and** physiology. Thus the zoologist was more likely than the botanist to consider **together** both observation and experiment. It was not until the twentieth century, however, that the experimental approach gathered momentum in biology as a whole, and it is important to recognise that even now the enterprise is only trivially complete, despite the fact that as a result of modern developments in molecular biology it is already possible for the human species to modify other organisms genetically in ways quite unconsidered just a few years ago.

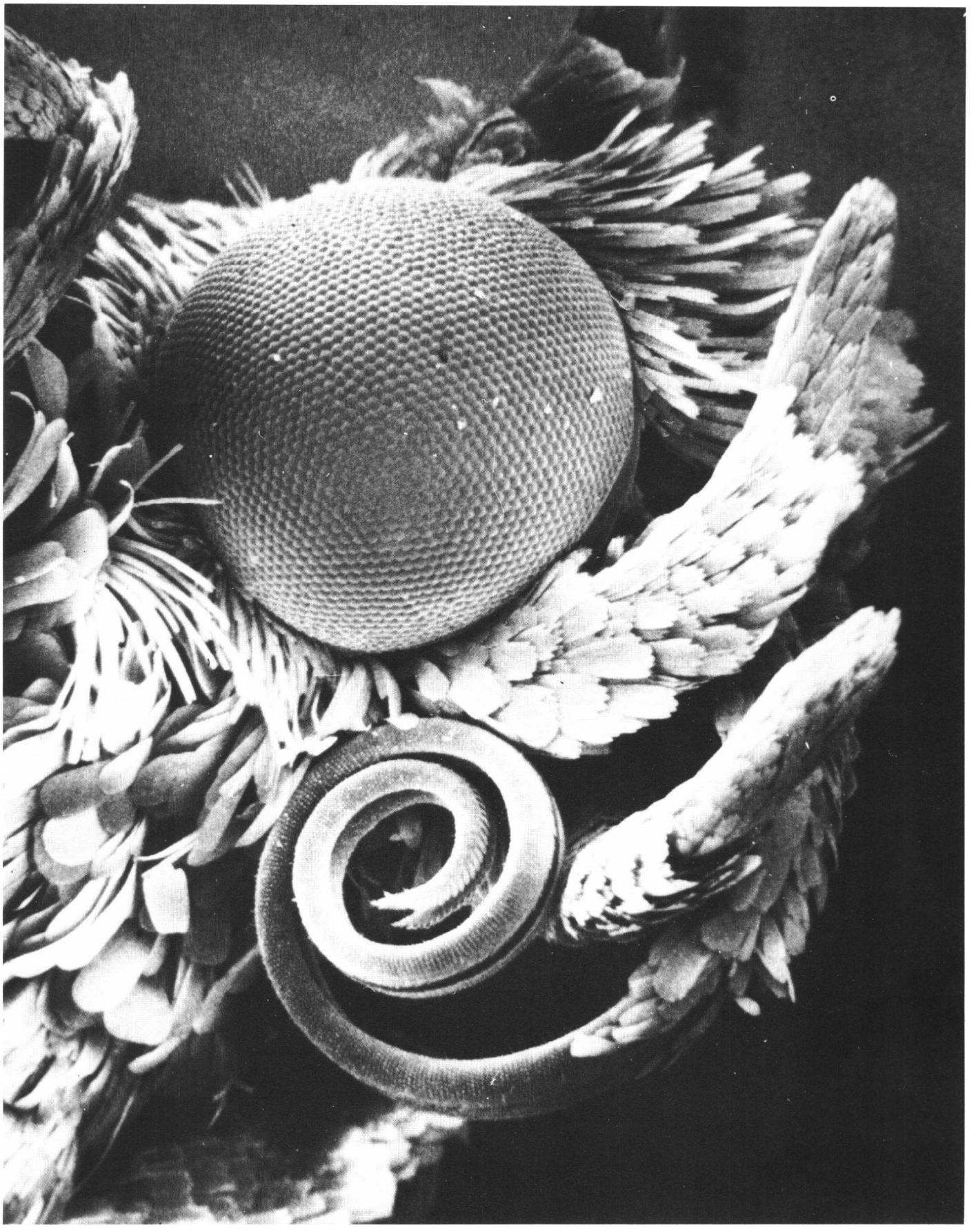
The Cambridge Encyclopedia of Life Sciences surveys the current state of knowledge in biology, thus providing a synthesis which draws both on the observations of the naturalist tradition and on the findings of the experimental approach which has arisen from it. Studies of micro-organisms, plants and animals remained largely as separate strands of research until comparatively recently, when advances in cell biology emphasised the ubiquity of basic cellular structures and metabolic processes in **all** living things. It is at the level of the cell, therefore, that the *Encyclopedia* begins, examining the ways in which cells are constructed, how their biochemistry and biophysics are organised and controlled, how cells reproduce, and how they differentiate to perform specific functions. Some organisms, such as bacteria and many microscopic plants and animals, consist of one cell only. Others are composed of more cells and range in complexity from algae to flowering plants and vertebrate animals containing many millions of cells differentiated in a variety of ways to perform numerous different functions. Consideration is next given, therefore, to the principles underlying the control of growth, development, physiology and reproduction of both unicellular and multicellular organisms. The discussions of behaviour and ecology which follow place organisms, including the human species, in the context of the living world as a whole and show how they interact with one another and with the environment to form assemblies and communities.

This analysis of the principles and processes of biology provides a firm foundation for a survey of the diversity of organisms within the major environments of the earth: marine, coastal, terrestrial and freshwater. The physical and climatic features of these environments are described, and the major assemblages of living organisms within them are presented, with consideration being given to the structural and physiological variations that enable such organisms to succeed in spite of the variety of stresses placed upon them. Also, where appropriate, the impact of the human species on environments is discussed. Finally, cells and multicellular organisms are considered as environments themselves, for parasites and pathogens.

Having dealt with the present-day living world, the *Encyclopedia* turns to evolution, a topic which has been and remains a constant source of debate among scientists and laymen alike. The controversial theories of the origin of life are examined, the forces of selection and extinction which may have led to the present-day flora and fauna are discussed through reference to the fossil record and to modern observation and experiment, and the origin of the human species itself is considered.

The Cambridge Encyclopedia of Life Sciences is not a natural history cataloguing the living world, it does not attempt to argue a case for or against biological conservation, nor does it consider the yet greater ethical problems which arise from the genetic manipulation of cells. Instead, the *Encyclopedia* seeks to present biology as a science, and in addition constitutes a plea for considering all biological phenomena as indissolubly linked, a circumstance which underlies both the frustration and the fascination felt by all life scientists.

Adrian Friday
David S. Ingram



Part one
Processes and organisation

Some of the most difficult problems in biology are those involving levels of organisation. How, for example, is the genetic message encoded in each organism unpacked and interpreted in a disciplined manner during development to give rise to the whole organism? How are changes in the genetic material sometimes incorporated in all members of a descendent population? How do the interactions of individual nerve cells confer upon a nervous system the ability to interpret the messages of the sense organs and to coordinate complex behaviour patterns?

In the first chapters of this volume the basic chemical processes of living organisms are described, together with the principles of genetic inheritance at the molecular level and at the level of the organism. The ways in which the bodies of multicellular plants and animals are constructed can often be understood by analogy with the concepts of engineering: highly sophisticated solutions to problems of engineering design frequently turn out already to have evolved in the natural world. The ways in which the components of living systems interact have parallels in other sciences and it is clear that, whatever peculiar properties living systems might possess, they developed of necessity, in accord with the laws of physics and chemistry.

Animals, being for the most part possessed of nervous systems and being more mobile than plants, exhibit behaviour patterns. A recent field of progress in biology has dealt with the social interactions within and between animal species. This and some of the concepts of behavioural ecology, recognising the ways in which animal behaviour is affected by environmental factors, form the subject of a further chapter in Part One.

A further level of interaction among and between the species of plants and animals is considered in the chapter dealing with the principles of ecology. Again, organisms must work within the constraints of the physical factors in their external as well as their internal environments, but they will often interact also with other organisms.

The basic principles of plant and animal design recur again and again in those succeeding parts of this book dealing with the diversity of organisms in environments worldwide and with the patterns and processes of evolution.

*Scanning electron micrograph of the head of the flour moth (*Ephestia kuhniella*) showing the compound eye and coiled proboscis (x 84).*

1 The Cell

1.1 BASIC THEMES OF LIVING ORGANISMS

By far the greatest number of living organisms on the earth are single cells, micro-organisms invisible to the naked eye. The majority of micro-organisms are bacteria, which have a simple internal structure enclosed within a single limiting cell membrane called a **plasma membrane**. This membrane has the important function of enabling the cell to maintain an internal molecular composition which is completely different from that of the medium in which it lives. The membrane is selective in the types of molecule which it allows to enter and to leave the cell, and indeed some substances may be actively accumulated from the medium. The genetic material of bacterial cells is not contained in a true nucleus bounded by a nuclear membrane, and such organisms are described as **prokaryotic** (Fig. 1.1). The other major group of prokaryotic organisms is the blue-green algae.

In contrast, **eukaryotic** cells are organised in a fundamentally different way; within their bounding plasma membrane they are internally divided into discrete membrane-bounded compartments, and their genetic material is held in a **nucleus** bounded by a nuclear membrane. The nucleus is surrounded by the rest of the cellular contents, the **cytosol** (or cytoplasm) and the **organelles** this contains. Some types of eukaryotes, such as protozoa and yeasts, are free-living micro-organisms (see section 2.1), but eukaryotic cells are also the building blocks from which the familiar multicellular organisms, plants, fungi and animals, are constructed (see sections 2.2 to 2.4 and Fig. 1.1). In a multicellular organism the individual cells are dependent on each other, and have become structurally and functionally differentiated to perform various specialised roles necessary for the whole organism.

The protoplasm of prokaryotes (their internal contents) relies, as far as is known, simply on diffusion for mixing of the molecules it contains. The time needed for transport by diffusion increases, however, in proportion to the square of the distance to be travelled, and this relationship restricts the size of prokaryotic cells; the volume of a typical bacterium is about 1 cubic micrometre. In contrast, eukaryotes have evolved a stirring mechanism called protoplasmic streaming which enables effective communication to be maintained within the cytoplasm of much larger cells: typical volumes are about 2000 to 4000 cubic micrometres for a liver cell or root meristem cell, although plant cells that contain large central vacuoles can be much larger.

Although the structural organisation of prokaryotic and eukaryotic cells is so different, the basic tasks which the cells must perform are the same and are covered by two key themes of cell biology: energy conservation and transfer, and information flow.

Energy conservation and transfer

It is convenient to distinguish two types of process from an energetic point of view: those that occur spontaneously, and those that need the expenditure of energy to drive them. Thus a car freewheels downhill, but needs to be driven uphill; and a waterfall requires no input of energy to the water, while a geyser needs the water to come into contact with hot rocks. Similarly, sugar is readily oxidised and broken down by cells, while photosynthesis to produce sugar from carbon dioxide and water is carried out by green plants using the free energy of sunlight. A thermodynamic quantity called **free energy** (or Gibbs free energy) describes the energy released during spontaneous processes and the use of energy by energy-requiring processes. Free energy is measured in joules; 1 joule will heat 1 gram of water by about 0.25 °C. 'Free' energy means that the energy is available to do work; it is not equivalent to heat: in essence, work stimulates organised motion and heat stimulates random motion. If a process that releases free energy can be coupled mechanistically to another process that will not occur without a supply of free energy, coupled so that one cannot happen without the other, then a proportion of the free energy released by the first, 'downhill', process can be used to do work by driving the second process energetically 'uphill'; except under ideal conditions, however, some of the free energy will be dissipated as heat.

It is this type of coupling of processes that enables living organisms to function. Cells are able to use the free energy available from the metabolic breakdown (**catabolism**) of complex food molecules, such as sugars or fats, to drive energy-requiring processes like the biosynthesis (**anabolism**) of proteins, nucleic acids, polysaccharides and other polymers from their subunits. Highly specific catalysts called enzymes (see section 1.3) are biochemical devices that enable the coupling of energy-yielding and energy-requiring processes to occur. Energy released from catabolic reactions (and, in photosynthetic organisms, energy trapped during the excitation of chlorophyll by light, see section 1.3) is funnelled to drive the 'uphill' formation of the key biochemical intermediate adenosine triphosphate (ATP) from adenosine diphosphate (ADP) and inorganic phosphate. The formation of 1 mole of ATP requires an input of free energy of about 60 kilojoules under prevailing cellular concentrations of reactants and products (a 'mole' of ATP contains 6×10^{23} molecules of ATP, the same number as there are atoms of carbon in 12 grams of the isotope carbon-12), and thus if it is then hydrolysed back to ADP and inorganic phosphate a corresponding amount of free energy will be released. Coupling of the hydrolysis of ATP to a step of an energetically unfavourable synthetic process, by the mechanism of the particular enzyme that catalyses that step, means that some of the free energy from ATP hydrolysis that would have been released is instead used to drive the synthetic process in a direction that would otherwise not occur.

ATP molecules are the common unit of energy exchange in

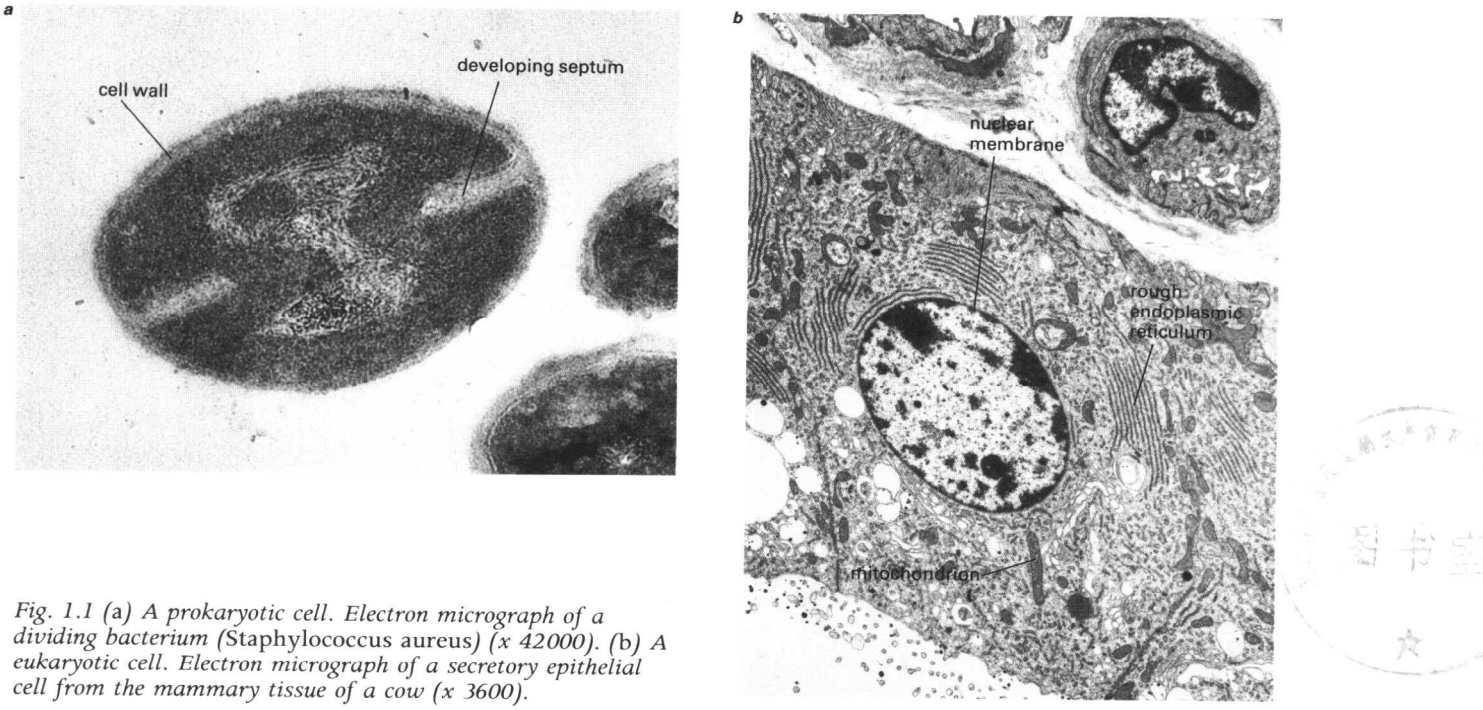


Fig. 1.1 (a) *A prokaryotic cell. Electron micrograph of a dividing bacterium (*Staphylococcus aureus*) (x 42000).* (b) *A eukaryotic cell. Electron micrograph of a secretory epithelial cell from the mammary tissue of a cow (x 3600).*

the cell, able to link diverse biochemical reactions because of the mechanisms of the enzymes that catalyse these reactions, and ATP is often thought of metaphorically as the energy currency of the cell. It enables energetic assets to be transferred from food materials to build the cell's own structure and to power other functions such as cytoplasmic streaming. Gradients of concentration of various ions across membranes, for example of sodium and potassium ions across the plasma membrane (see section 1.4) or of hydrogen ions across the mitochondrial inner membranes, and electric potential gradients across membranes, are also used to store energy and to do useful work. These metabolic interconversions will be described in more detail in section 1.3.

Information flow

A unicellular organism is capable of growth, of changing its activities in response to environmental signals, and of reproduction. In multicellular organisms, the cells become differentiated (see section 1.6) and can receive signals (mechanical, chemical and/or electrical) from other cells in the organism as well as from the external environment (see section 1.4 and pages 89–94); only a few of the individual cells of the organism, the cells constituting the **germ-line**, are carried over to form the members of the next generation when the organism reproduces.

The characteristics that distinguish one type of organism from another are due to differences in the properties of their proteins. Proteins are a versatile class of macromolecule, and can, for example, function as highly specific catalysts (enzymes and membrane-bound carriers), antibodies, intercellular messengers (hormones like insulin), and structural components of cells and tissues; the structure of the other major macromolecular components of tissues, carbohydrates, depends upon the nature of the enzyme proteins synthesising the carbohydrate molecules. The properties of a protein depend ultimately upon the sequence of amino-acids that comprise it, and the information content required to specify a particular organism is that needed to specify the sequence of amino-acids in its proteins. This is stored in coded form in deoxyribonucleic acid (DNA, see section 3.1).

DNA is a polymer of four different types of subunit, called nucleotides, which are assembled one by one during biosynthesis. Each nucleotide contains a particular nitrogenous base, and the sequence in which these bases occur along the DNA molecule constitutes the heritable information of the cell. At the mitotic division of a cell nucleus which precedes cell division, each daughter cell obtains a copy of the DNA identical to that of its parent (see section 1.5). Except for any mutation, a spontaneous change in the sequence of bases in the DNA (see section 3.1), the total nuclear information content of an asexually reproducing population is thus conserved; the process of sexual reproduction, however, includes mechanisms by which a rearrangement of this genetic information occurs (see sections 1.5 and 3.2).

There are two aspects of the actual utilisation of the genetic 'blueprint' encoded in DNA. First, there has to be a mechanism for making the encoded information real in terms of molecular transformations and interactions. Secondly, since DNA contains a variety of pieces of information that a cell can call on throughout its life, there must be control mechanisms to allow the expression of this information to be selective (see section 3.1). For the first aspect, DNA programmes the biosynthesis of proteins, by specifying the order of the 20 different types of amino-acid in each protein from the sequence of bases in particular sections of the DNA molecule. A region of the DNA containing a piece of information that can affect the properties of an organism, by programming the synthesis of a protein, is called a **gene**. The second aspect, the control of gene expression, demands mechanisms for switching particular genes on and off in response to regulatory signals. In prokaryotes these signals are usually provided by the nutritional status of the

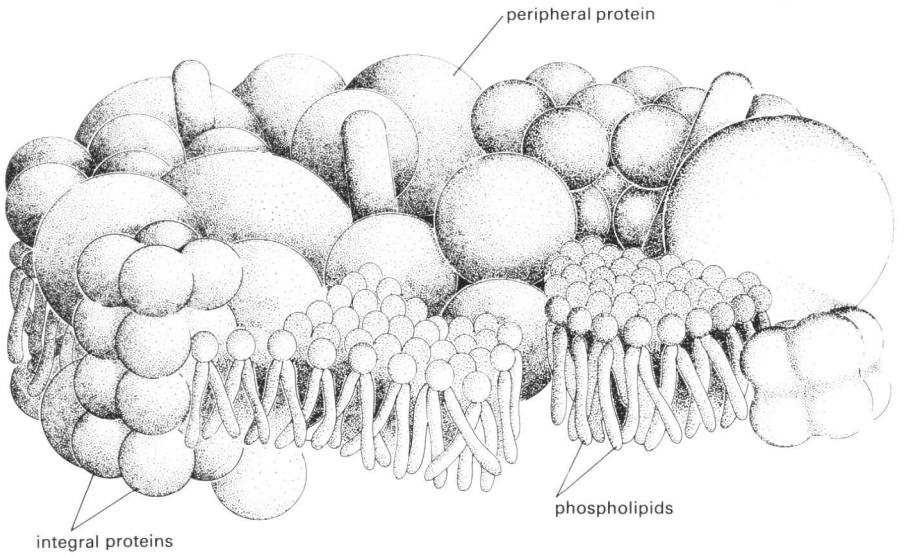


Fig. 1.2. Model of the mitochondrial membrane. Most membranes consist of a phospholipid bilayer with proteins scattered in and on it. The mitochondrial membrane has a very high content of protein and here the lipid bilayer fills the gaps between the proteins.

growth environment of the organism. For example, the presence of a particular type of potential food molecule may switch on the synthesis of enzymes needed to metabolise that nutrient, while the absence of key nutrients may trigger the organism to produce the proteins required to form a cyst and become dormant.

The adaptation of eukaryotes to environmental changes, and the wider issues of cell differentiation in the multicellular eukaryotic organisms (see section 1.6) are much more complicated problems to resolve at the molecular level, largely because the organisation and expression of the genetic material of eukaryotes is formidably complex in comparison with that of prokaryotes (see section 3.1). Nevertheless, the receipt of signals from the environment and from other cells of the multicellular organism, and the implementation of these signals in terms of altered cellular activity including differential gene expression, is taken to be responsible for morphogenesis and differentiation in eukaryotes just as in prokaryotes.

1.2 FINE STRUCTURE OF CELLS

Introduction

The chemical composition and function of subcellular structures are studied in biochemistry, while observations with the electron microscope give information about the shape and arrangement of these structures.

Biochemistry

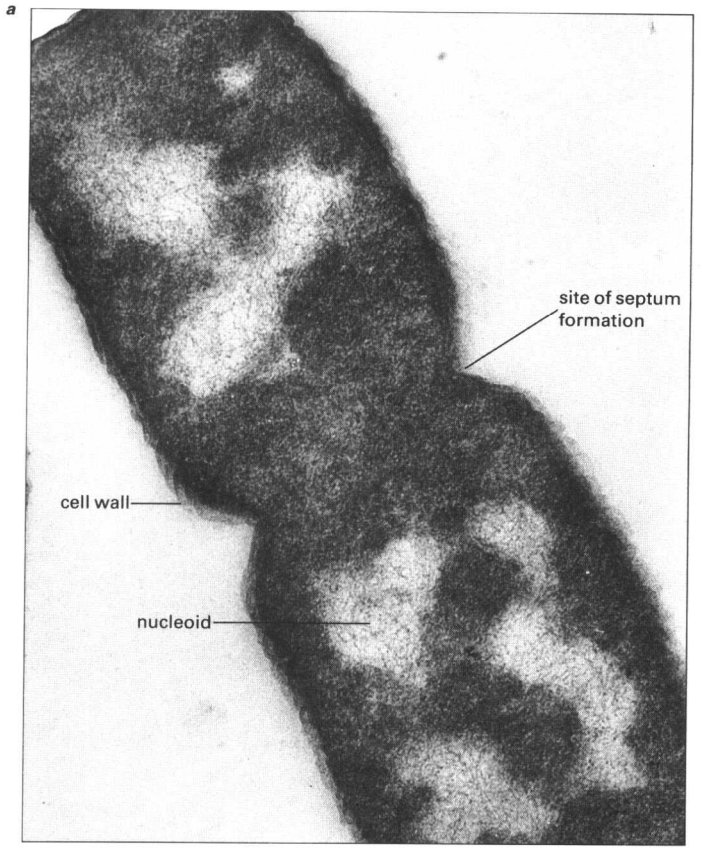
The atoms inside living systems are organised to various extents. Almost all are covalently bonded in extremely precise groups to form molecules, but these molecules vary enormously in size. Large molecules are stable and of precise shapes, but this is achieved at the expense of the speed of chemical reactions. The largest molecules are of deoxyribonucleic acid, DNA (see section 3.1), the function of which is to preserve in a stable form, through many generations, all the precise instructions for building the cell. The metabolism of living cells also needs the chaos of small molecules in solution, and the molecules undergoing frenetic chemical transformation to supply the cell with energy are among the smallest in the cell (see section 1.3).

The structures of the cell are built up of molecules of intermediate sizes: lipids and proteins. They link up with each other via reversible forms of attachment which, though much weaker than covalent bonds, are present in large numbers to compensate for this. The most important of these weak interactions is the tendency for non-polar groups (groups soluble in organic solvents) to be pushed together in water and to be excluded from the aqueous phases of the cell, just as oil spontaneously separates from water; other reversible linkages include attractions between groups with opposite electric charges, and 'hydrogen bonds' similar to the bonds between water molecules.

The structural lipids of the cell, called phospholipids, all consist of a polar, water-soluble head end, covalently linked to two long, parallel-sided, non-polar tails. The tails do not dissolve in water and thus tails of different lipid molecules lie side by side and end to end, but the heads dissolve in the aqueous phase, so that the phospholipid comes to form sheets that are two molecules thick (Fig. 1.2). Each sheet is a **membrane**. Sheets of membrane are unstable at their edges, and these coalesce, converting the sheet to a seamless bag called a vesicle.

Each living cell is contained by such a seamless coat of membrane, the **plasma membrane**. Inside eukaryotic cells (see section 1.1), membranes enclose regions of specialised function, called **organelles** by analogy with organs of specialised function in animals. Many functions are carried out in the region called the **cytosol** (or cytoplasm) that is outside the organelles but enclosed within the plasma membrane.

The complex folding of the chain of covalently linked amino-acids during the synthesis of proteins similarly involves the exclusion of non-polar sections of the protein chain from water into the interior of the molecule, while polar groups are pulled outwards until the chain settles to a stable arrangement.



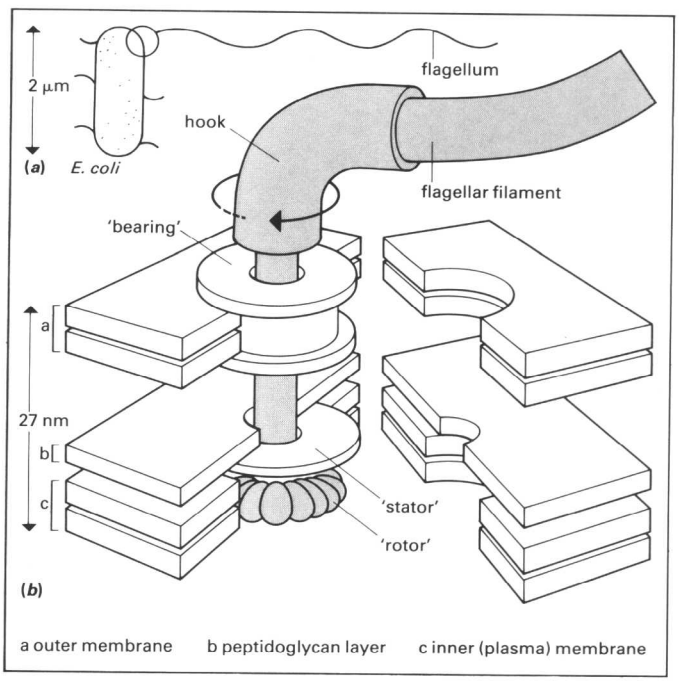


Fig. 1.3. (a) *Transmission electron micrograph of a thin section of the bacterium* Escherichia coli *(x 60000).* (b) *The component parts of the bacterial flagellum, a structure unique in living organisms in that it revolves like the wheel of a car. Driven by a 'motor' inside the cell, the spinning 'drive-shaft' is set in a molecular scale 'sealed bearing'.*

(Proteins found in a non-polar environment, such as the inside of a lipid membrane, have polar interiors and non-polar exteriors.) For some proteins it is not possible to tuck away all the non-polar regions, and hydrophobic patches remain on the surface of the folded protein; when such proteins meet in the polar aqueous environment, they will be pushed against each other, becoming the subunits of 'multimeric' protein complexes. Multisubunit proteins vary tremendously in their size and complexity depending on the numbers and shapes of their subunits, their hydrophobic patches and any other bonding groups. Structures made up of protein molecules can be internally complex in spite of being relatively small, such as ribosomes, or can be composed of just a few types of subunit even though their final structure is huge, such as microtubules. The structures that support the nucleic acid in chromatin and in viruses assemble by these types of protein–protein interactions.

The presence of particular bonding regions on their surface can also result in proteins being pushed into the surface of membranes, which become studded with these **extrinsic** (or **peripheral**) components. Extrinsic proteins diffusing over the membrane surface can associate with each other to form chains or aggregates (Fig. 1.2). Some proteins are inserted into a membrane as they are synthesised, and fold in the non-polar environment. These **intrinsic** (or **integral**) membrane proteins often function to communicate between the two aqueous regions separated by the membrane, for example by transporting polar substances across membranes or by relaying external signals into the cell (see sections 1.3 and 1.4).

Membranes, therefore, are barriers to non-selective movement of polar molecules, and divide the cell into compartments between which any movement of ions, sugars and other polar molecules is strictly controlled by membrane proteins; the water molecule is in fact small enough to slip through the lipid bilayers fairly effectively by itself. Membranes also provide the hydrophobic environment needed for certain reactions, such as in the synthesis of non-polar molecules and in electron transport (see section 1.3).

Electron microscopy

Most intracellular structures are considerably smaller than the wavelength of light, and can only be seen by electron microscopy. This requires the different features of the cell to be loaded with electron-opaque elements to be visible in the beam of electrons. The commonest technique is to view thin slices (some 200 to 300 nanometres thick) of killed preserved cells, stained with heavy elements like osmium, lead or uranium, and embedded in polyester resin to stiffen the material so that it can be sliced thinly.

Such **thin sections** provide a two-dimensional view only. A widely used method which generates pictures also containing information on the third dimension involves breaking rapidly frozen tissue, and then making an accurate picture (called a replica) of the fracture surface in heavy metal by coating it from the side with platinum vaporised in a vacuum. The planes of weakness followed by the fracture run between the lipid layers in each membrane, these being no longer squeezed together by liquid water. The replica is then viewed in the electron microscope. A modification of this **freeze-fracture** technique is to sublime some of the ice from the fracture face before making the replica, thereby revealing features on membrane

surfaces previously submerged under ice. This technique is called **freeze-etch**.

Surface features on, for example, isolated organelles and viruses can be seen in great detail when the interstices between the features are flooded with a solution of phosphotungstic acid, which highlights unstained prominences: this technique is called **negative staining**.

Cell structures

Nuclear structures

Prokaryotes have a central area, the **nucleoid** (Fig. 1.3) containing the compactly folded circular molecule of DNA, but it is not isolated from the rest of the cell by any membrane. The distinguishing feature of eukaryotic cells is the nucleus, the central membrane-bounded organelle containing virtually all the DNA of the cell. The single circle of DNA in a prokaryote is a copy of the complete information for survival of that species, which in eukaryotes is distributed among the chromosomes, a number of linear pieces of DNA only visible as discrete entities during cell division (see section 1.5). Another feature of eukaryotic DNA is that the molecule, which is negatively charged, is wrapped around a series of protein particles each consisting of eight positively charged protein molecules, to form a structure resembling a string of beads. The positively charged proteins are called **histones**, and the individual beads **nucleosomes**. The nucleosomes are drawn closer together by another type of histone molecule to form threads of **chromatin** 10 to 30 nanometres across (see section 3.1). The nucleus is surrounded by two concentric membranes barely separated by a perinuclear space (Fig. 1.4). Part of the chromatin is thickly draped over the inside of the inner nuclear membrane, to which it is attached at intervals by a framework of extrinsic proteins, the nuclear lamina. Different proteins stabilise complex pores through both nuclear membranes. The dinoflagellates, unicellular algae which were the commonest plants in seas in the Palaeozoic era, are intermediate in having a typically eukaryotic nuclear membrane surrounding histone-free nucleoids that are typically prokaryotic.

Nuclei contain one or more large, densely staining bodies not bounded by a membrane, called **nucleoli**; these are the site of synthesis of the RNA backbone of ribosomes and sites of assembly of proteins on to the ribosomal RNA.

Cytoplasmic structures

Ribosomes (Fig. 1.4) are cytoplasmic particles about 30 nanometres across, and are precisely organised, containing over 50 different protein subunits around a core of RNA molecules. Each ribosome can translate faithfully into protein the information in specific RNA copies of portions of the DNA (messenger RNA) (see section 3.1). Ribosomes are electron-dense in thin sections of cells viewed in the electron microscope, but are not seen by freeze-etch techniques. In prokaryotic cells they fill up the space between the nucleoid and the plasma membrane. Eukaryotic ribosomes are slightly larger than prokaryotic ribosomes, and are located outside the nucleus, both free in the cytoplasm and attached to the cytoplasmic face of both the outer nuclear membrane and a system of membranes, called the **endoplasmic reticulum**, that extends through the rest of the cell. The ribosomes may be arranged in groups called polysomes; each polysome consists of a number of ribosomes at various stages of translating one messenger RNA molecule.

The endoplasmic reticulum encloses a narrow space, the lumen, that is connected to the perinuclear space, and the endoplasmic reticulum itself is chemically very similar to nuclear membrane. Ribosomes attached to the endoplasmic reticulum synthesise integral membrane proteins which stay in the membrane, and also synthesise proteins for export which move through this membrane into the lumen. The amount of endoplasmic reticulum is much greater in cells actively exporting proteins, and its shape varies from closely packed concentric sheets to thinly dispersed tubes. Regions that become loaded with newly synthesised protein break up into small vesicles which fuse with the Golgi apparatus, or are linked to it via tubular connections.

Each **Golgi body** is a stack of flattened membranous vesicles, like a pile of hollow pancakes, firmly cemented to one another. Each vesicle, or cisterna, travels through the stack as vesicles from the endoplasmic reticulum fuse to form new cisternae at one face of the stack. As it passes through the Golgi body, the lipid composition of the cisterna membrane is altered, many of the protein and some of the lipid components have sugars linked covalently to them, and, from around its rim each cisterna alternately balloons out and dimples in until opposing dimples fuse, releasing vesicles called Golgi vesicles. In animal cells the Golgi bodies are located together and form a network in which groups of vesicles are interlinked by stacks of cisternae. The network is called the Golgi complex and each component stack a dictyosome.

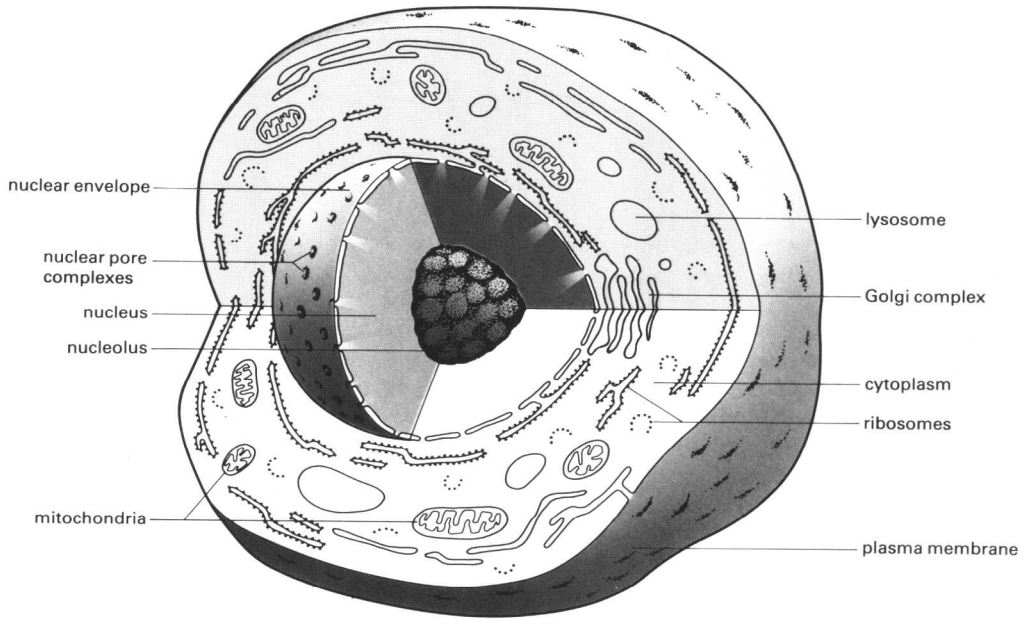
Proteins destined for export are secreted by exocytosis, fusion of the Golgi vesicle with the plasma membrane. Alternatively the contents of the Golgi vesicle can be secreted internally by fusion with lysosomes.

Lysosomes are small vesicles containing hydrolytic enzymes capable of breaking down proteins, lipids and nucleic acids to low-molecular-weight components. They are involved in the autodigestion of cellular structures, and in the digestion of material brought into the cell by phagocytosis, in which the plasma membrane invaginates to capture a small amount of extracellular material.

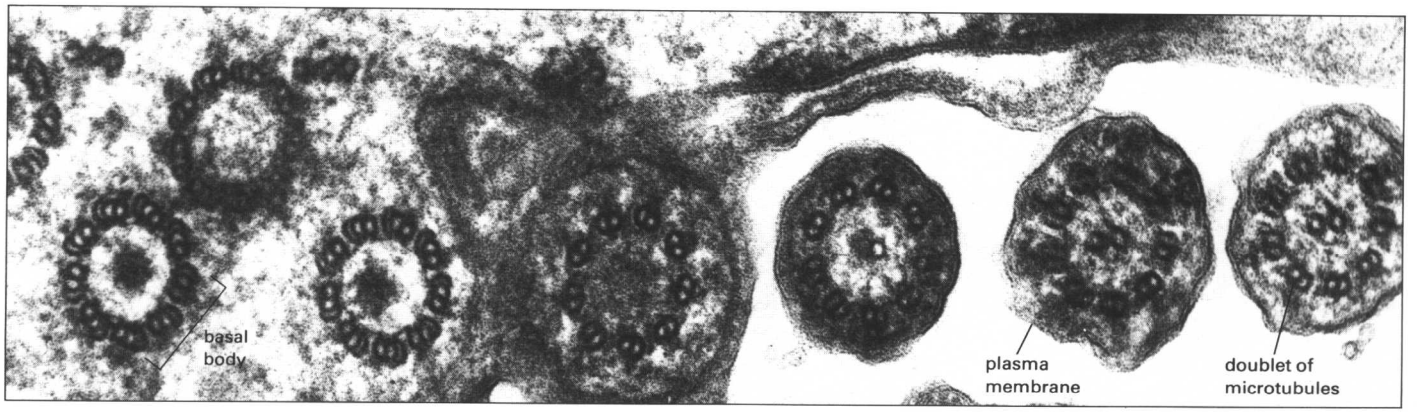
Lysosomes occur in animal cells (Fig. 1.4). If there is an equivalent in plant cells it is the **vacuole** (Fig. 1.5), a very large vesicle which fills most of the cell and contains a dilute, acidic sap, a solution chiefly of potassium malate, with a profuse

Fig. 1.4. (a) *Diagram of a generalised animal cell, showing its component parts and their distribution within the cell.* (b) – (d) *Transmission electron micrographs of thin sections.* (b) *An oblique section through the surface of a protozoon,* Tetrahymena, *showing the structure of cilia at a series of points along this organelle (x 96000).* (c) *From a cell of the intestinal epithelium of a pig, showing microvilli, surface projections supported by an internal framework of actin (x 2240).* (d) *From a cell of rat liver, often thought of as 'typical' animal tissue.*

a



b



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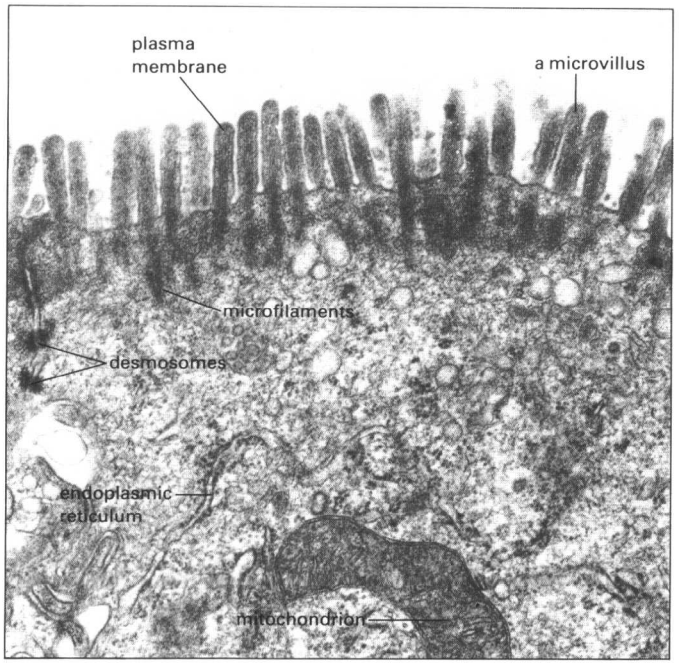

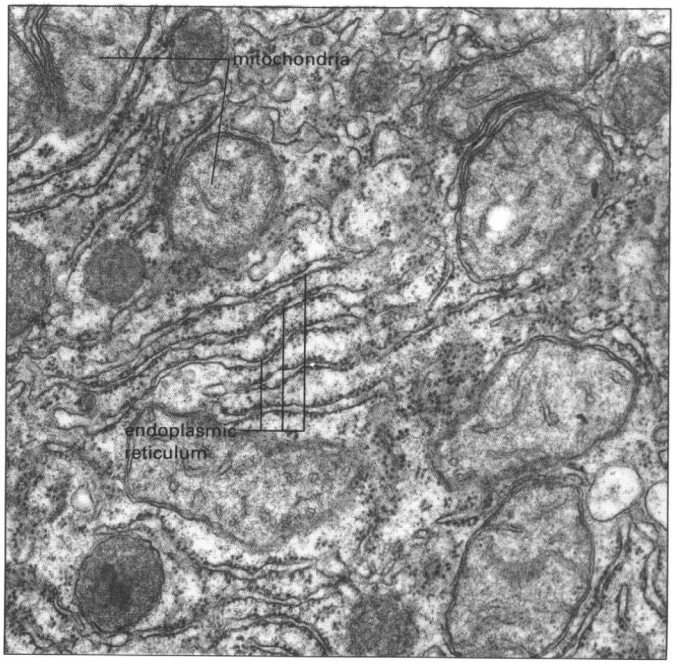

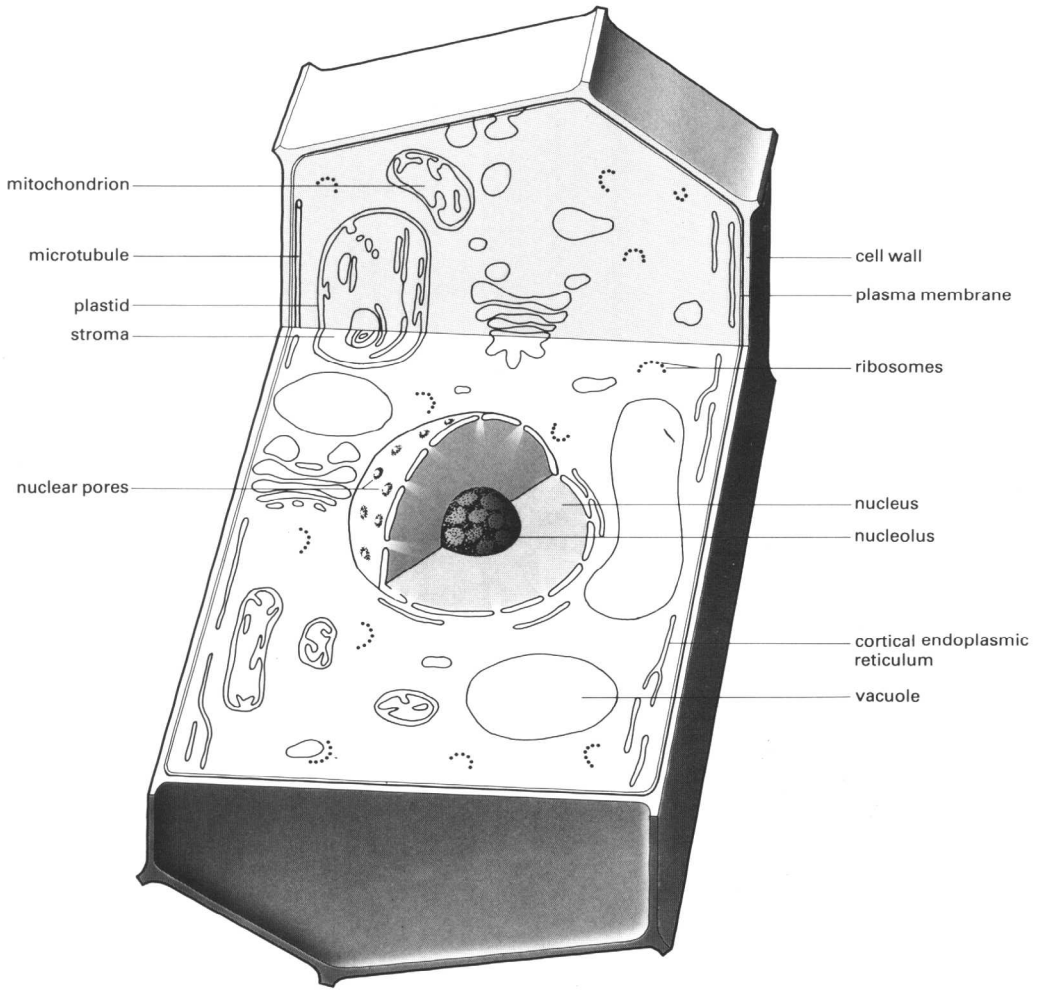

Fig. 1.5. Diagram of a generalised plant cell, showing its component parts and their distribution within the cell.

variety of hydrolytic enzymes, phenolic compounds and other organic substances.

Plastids are unique to plant cells. The most important plastids are **chloroplasts** (Fig. 1.5), the organelles which trap the energy of solar radiation (see section 1.3). Chloroplasts exist within an envelope of two membranes separated only by a narrow space, and contain a complex system of chlorophyll-rich, flattened membrane sacks, the thylakoids, piled like coins into stacks, called grana, and floating in an enzyme-rich solution, the stroma. The grana are interconnected via sheets of paired membranes, called stromal lamellae, which enclose a narrow space continuous with the lumen (internal space) of the thylakoids. As well as metabolic enzymes, the stroma contains circles of histone-free DNA coding for some of the chloroplast proteins; there are also prokaryotic-type ribosomes and all the enzymic machinery for protein synthesis in the chloroplast. The similarity between chloroplasts and the prokaryotic blue-green algae, the chlorophyll of which is associated with single thylakoids derived from the plasma membrane, suggests that chloroplasts originated as free-living prokaryotes which have become modified to live inside another cell.

Under illuminated conditions, chloroplasts are produced by growth and division of other chloroplasts. They can also develop from small simple, double-membrane vesicles, called proplastids which in non-photosynthesising cells fill with stored starch, becoming amyloplasts. During development, chloroplasts can also fill with brightly coloured yellow, orange or red pigments, and so convert to chromoplasts.

Mitochondria (Fig. 1.4) resemble chloroplasts in having a double-membrane envelope enclosing an enzyme-rich matrix, histone-free circles of DNA, ribosomes different from those of the cytoplasm, the capacity to grow and divide, and the ability to make some of their own proteins. The principal function of mitochondria is to generate the energy-rich molecule ATP (see sections 1.1 and 1.3) by the oxidation of pyruvate, itself the end product of oxidation of glucose in the cytoplasm, and by the oxidation of fats, but they also play a major part in the synthesis of lipids, and of amino-acids for proteins.

These functions are carried out by the enzymes of the matrix and by the highly organised and protein-rich inner membrane, which projects into the matrix as folds or fingers called cristae enabling large amounts of mitochondrial inner membrane to be packed into each mitochondrion, and increasing the interface of the membrane with the matrix. The inner membrane provides the insulation required for electron transfer, and a barrier across which the gradient of hydrogen ions is established (see section 1.3). The enzyme complex, called ATPase, which converts the energy of this chemical and electrical gradient into the energy of chemical bonds in ATP can be seen in the electron microscope in negatively stained preparations of the inner membranes, as structures resembling lollipops and projecting into the matrix. While each chloroplast