10.1.1 CELLS—UNITS OF LIFE[M17]

At first glance, the petal of a flower or the skin on the back of a human hand may seem smooth and seamless, as if they were composed of a single, indistinct substance. In reality, however, many tiny individual units called cells make up these objects and almost all other components of plants and animals. The average human body contains over 75 trillion cells, but many life forms exist as single cells that perform all the functions necessary for independent existence. Most cells are far too small to be seen with the naked eye and require the use of high-power optical and electron microscopes for careful examination.

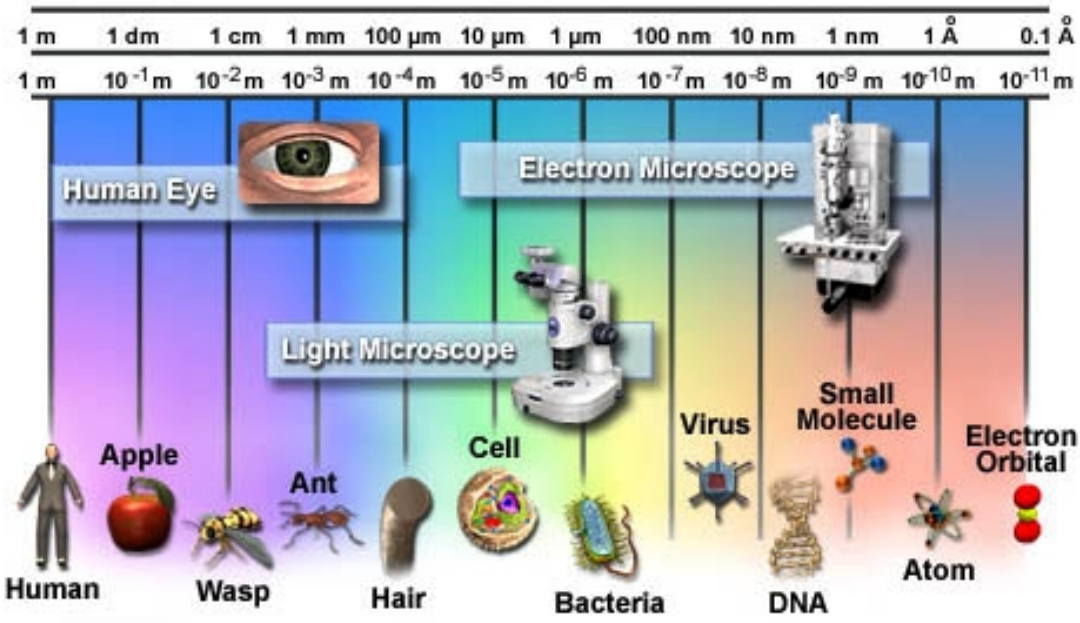

Figure 10.1.1.1 Relative Sizes and Detection Devices[1]

The relative scale of biological organisms as well as the useful range of several different detection devices are illustrated in Figure 10.1.1.1. The most basic image sensor, the eye, was the only means humans had of visually observing the world around them for thousands of years. Though excellent for viewing a wide variety of objects, the power of the eye has its limits, anything smaller than the width of a single human hair being able to pass unnoticed by the organ. Therefore, when light microscopes of sufficient magnifying capability were developed in the late 1600s, a whole new world of tiny wonders was discovered. Electron microscopes, invented in the mid-twentieth century, made it possible to detect even tinier objects than light microscopes, including smaller molecules, viruses, and DNA. The detection power of most electron microscopes used today, however, stops just short of being able to visualize such incredibly small structures as the electron orbital systems of individual atoms. Atoms are considered the smallest units of an element that have the characteristics of that element, but cells are the smallest structural units of an organism capable of functioning independently.

Yet, until the mid-seventeenth century, scientists were unaware that cells even existed. It wasn't until 1665 that English biologist Robert Hooke (1635–1703) observed through his microscope that plant tissues were divided into tiny compartments, which he termed *cellulae* or cells. It took another 175 years, however, before scientists began to understand the true importance of cells. In their studies of plant and animal cells

[1] http://www.molecularexpressions.com/cells/index.html

during the early nineteenth century, German botanist Matthias Jakob Schleiden (1804–1881) and German zoologist Theodor Schwann (1810–1882) recognized the fundamental similarities between the two cell types. In 1839, they proposed that all living things were made up of cells, the theory that gave rise to modern biology.

Nonetheless, most subcellular structures, or **organelles**, are too small to be resolved by a light microscope. Cell biology advanced rapidly in the 1950s with the introduction of the electron microscope. Instead of using light, the electron microscope focuses a beam of electrons through the specimen or onto its surface.

The cell is as fundamental to biology as the atom is to chemistry: All organisms are made of cells. In the hierarchy of biological organization, the cell is the simplest collection of matter that can live. Indeed, there are diverse forms of life existing as **unicellular** organisms. More complex organisms, including plants and animals, are **multicellular**—their bodies are cooperatives of many kinds of specialised cells that could not survive for long on their own. However, even when they are arranged into higher levels of organization, such as tissues and organs, cells can be singled out as the organism's basic units of structure and function. The contraction of muscle cells moves your eyes as you read this sentence; when you decide to turn the next page, nerve cells will transmit that decision from your brain to the muscle cells of your hand. Everything an organism does occurs fundamentally at the cellular level.

10.1.1.1 Cell Structure

10.1.1.1.1 Cell Types

The basic structural and functional unit of every organism is one of two types of cells—a **eukaryote** (from the Greek *eu*, true, and *karyon*, kernel) or a **prokaryote** (from the Greek *pro*, before, and *karyon*, kernel). The major difference between prokaryotic and eukaryotic cells is that the chromosomes of a eukaryotic cell are located in a membrane-enclosed organelle called the **nucleus**. In a prokaryotic cell, the DNA is concentrated in a region called the **nucleoid**, but no membrane separates this region from the rest of the cell.

Bacteria (Figure 10.1.1.2) are a typical example of prokaryotic cells.

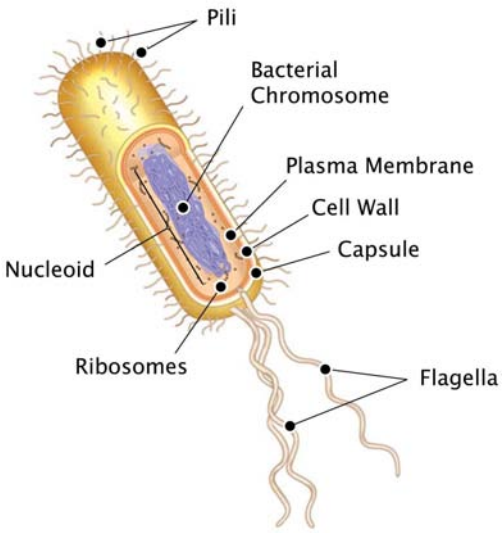

Figure 10.1.1.2 Typical Rod-Shaped Bacterium (Prokaryote)

The cells of both plants (Figure 10.1.1.3) and animals (Figure 10.1.1.4) are examples of eukaryotic cells.

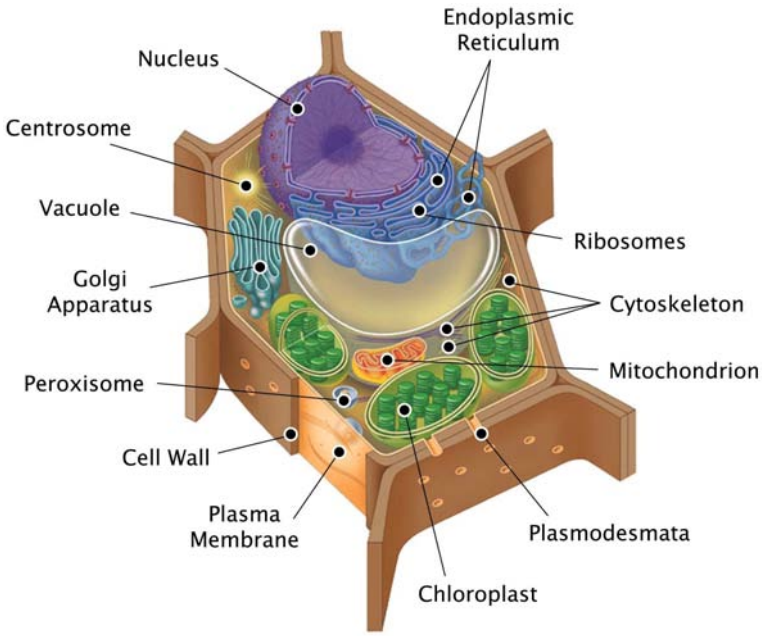

Figure 10.1.1.3 Plant Cell (Eukaryote)

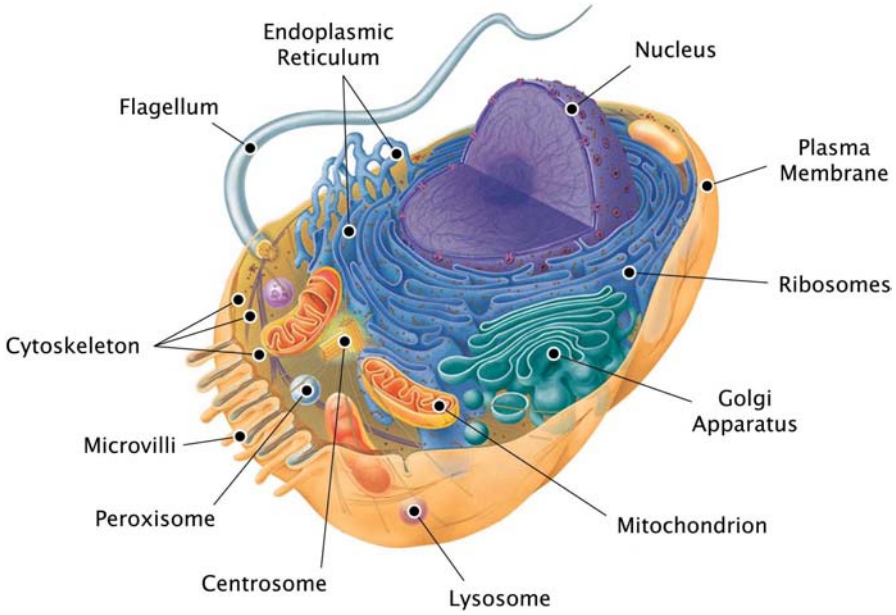

Figure 10.1.1.4 Animal Cell (Eukaryote)

All cells, nonetheless, have several basic features in common:

- They are bounded by a membrane, called a **plasma membrane**;
- Within the membrane is a semi-fluid substance, **cytosol**, in which **organelles** (the structures within a cell) are found;
- They contain **chromosomes**, the cell's 'manufacturing blueprints'; and
- They contain **ribosomes**, within which **proteins** are synthesised.

The entire region between the nucleus and the plasma membrane of a eukaryotic cell is called the **cytoplasm**, a term also used for the interior of a prokaryotic cell. Within the cytoplasm of a eukaryotic cell, suspended in **cytosol**, are a variety of membrane-bound organelles of specialised form and function. These are largely absent in prokaryotic

cells. The one exception is **ribosomes,** the organelles responsible for protein synthesis within cells.

The cytoplasm and the nucleus together are known as **protoplasm**, the living matter of a cell.

Eukaryotic cells are generally quite a bit bigger than prokaryotic cells. Size is a general aspect of cell structure that relates to function. The logistics of carrying out cellular metabolism sets limits on cell size. First of all, a cell must be big enough to accommodate the organelles it needs to survive. However, as an object of a particular shape increases in size, its volume grows proportionately more than its surface area. Thus, the smaller the object, the greater its ratio of surface area to volume and a high surface-to-volume ratio facilitates the exchange of materials between a cell and its environment.

At the boundary of every cell, the plasma membrane functions as a selective barrier that allows sufficient passage of oxygen, nutrients, and wastes to service the entire volume of the cell. The plasma membrane and the membranes of organelles consist of a **lipid bilayer**, a double layer of phospholipids with various proteins attached to or embedded in it (Figure 10.1.1.5).

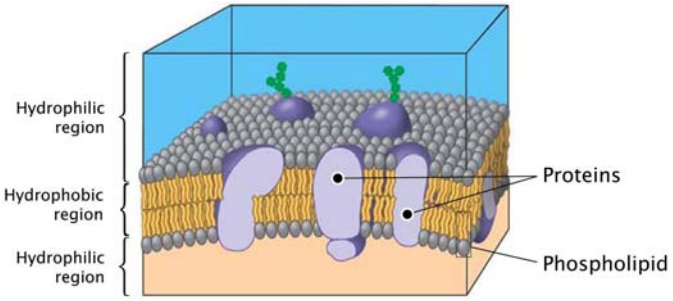

Figure 10.1.1.5 The Structure of the Plasma Membrane

The cells of all organisms perform the same basic functions and thus have the same basic structural requirements. Thus, larger organisms do not generally have larger cells than smaller organisms—simply more cells.

10.1.1.1.2 Eukaryotic Cell Structures

As noted above, eukaryotic cells contain a number of specialised organelles that carry out specific functions within the cell.

Genetic Material

The **nucleus** contains most of the genes in a eukaryotic cell (some genes are located in mitochondria and chloroplasts). It is generally the most conspicuous organelle in a eukaryotic cell (Figure 10.1.1.6).

The **nuclear envelope** encloses the nucleus, separating its contents from the cytoplasm.

Within the nucleus, the DNA is organised into discrete units called **chromosomes**. Each eukaryotic species has a characteristic

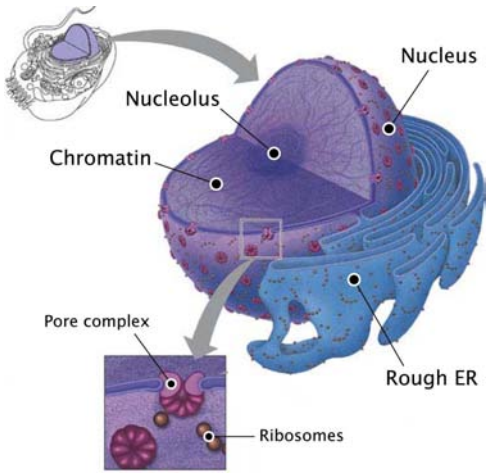

Figure 10.1.1.6 The Nucleus

number of chromosomes. A typical human cell, for example, has 46 chromosomes in its nucleus while a typical fruit fly cell has only 8.

Each chromosome is made up of a material called **chromatin**, a complex of proteins and deoxyribonucleic acid (DNA).

The **nucleolus** is the site within the nucleus where a special type of ribonucleic acid (RNA), ribosomal RNA (rRNA) is synthesised from instructions in the DNA. Proteins imported from the cytoplasm are also assembled with rRNA into large and small ribosomal subunits. These subunits then exit the nucleus through the **nuclear pores** to the cytoplasm, where a large and a small subunit can assemble into a **ribosome**.

Ribosomes (Figure 10.1.1.7) are the organelles that carry out protein synthesis within a cell. Cells that have high rates of protein synthesis have a particularly large number of ribosomes. For example, a typical human pancreas cell (responsible for the production of digestive enzymes such as insulin) contains a few million ribosomes.

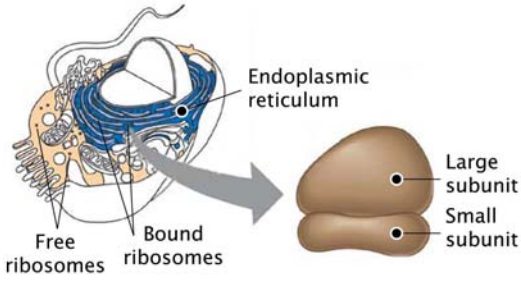

Figure 10.1.1.7 Ribosomes

Endomembrane System

Many of the different membranes within a eukaryotic cell are part of an endomembrane system that carries out a range of tasks, including synthesis of proteins and their transport into membranes and organelles or out of the cell, metabolism and movement of lipids, and detoxification of poisons. The membranes of this system are related either through direct physical continuity or by the transfer of membrane segments as tiny **vesicles** (sacs made of membrane).

The **endoplasmic reticulum** (ER) accounts for more than half the total membrane in many eukaryotic cells. The ER consists of a network of membranous tubules and sacs called **cisternae** (from the Latin *cisterna*, a reservoir for a liquid). The ER membrane separates the internal compartment of the ER, called the **lumen** (cavity) or cisternal space, from the cystol (of the cytoplasm) (Figure 10.1.1.8).

The ER performs a range of metabolic functions within a cell, including the synthesis of lipids, metabolism of carbohydrates and detoxification of drugs and poisons. Proteins generated within the ER are transported to other parts of a cell wrapped in the membranes of vesicles that bud like bubbles from a specialised region called transitional ER. Vesicles in transit from one part of a cell to another are called **transport vesicles**.

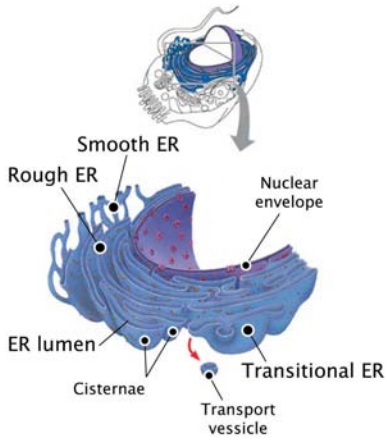

Figure 10.1.1.8
The Endoplasmic reticulum

After leaving the ER, many transport vesicles travel to the **Golgi apparatus**. The Golgi can be likened to a centre for manufacturing, warehousing, sorting, and shipping. Here, products of the ER are modified and stored and then sent to other destinations. Not surprisingly, the Golgi apparatus is especially extensive in cells specialised for secretion.

The Golgi apparatus (Figure 10.1.1.9) consists of stacks of flattened sacs, or cisternae, which, unlike ER cisternae, are not physically connected. (The illustration is a cutaway view.) A Golgi stack receives and dispatches transport vesicles and the products they contain. It has a structural and functional polarity, with a *cis* face that receives vesicles containing ER products and a *trans* face that dispatches vesicles. The *cis* face is usually located near the ER. Transport vesicles move material from the ER to the Golgi apparatus. A vesicle that buds from the ER can add its membrane and the contents of its lumen to the *cis* face by fusing with a Golgi membrane. The *trans* face gives rise to vesicles, which pinch off and travel to other sites. Products of the ER are usually modified during their transit from the *cis* region to the *trans* region of the Golgi.

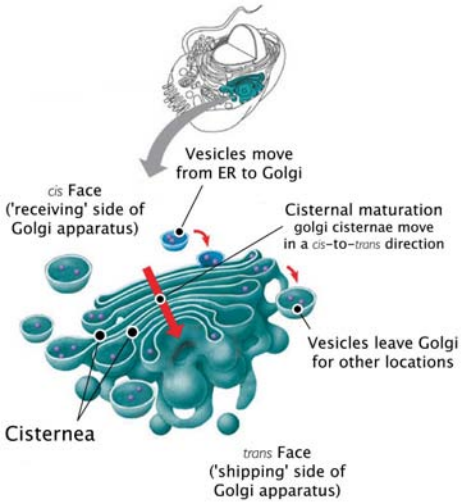

Figure 10.1.1.9
The Golgi apparatus

The Golgi manufactures and refines its products in stages, with different cisternae between the *cis* and *trans* regions containing unique teams of enzymes. Before a Golgi stack dispatches its products by budding vesicles from the *trans* face, it sorts these products and targets them for various parts of the cell. Molecular identification tags, such as phosphate groups that have been added to the Golgi products, aid in sorting by acting like postcodes on mailing labels. Finally, transport vesicles budded from the Golgi may have external molecules on their membranes that recognize 'docking sites' on the surface of specific organelles or on the plasma membrane, thus targeting them specifically.

Also part of the endomembrane system, a **lysosome** is a membranous sac of hydrolytic enzymes that an animal cell uses to break down or digest all kinds of macromolecules. Hydrolytic enzymes and lysosomal membrane are made by the ER and then transferred to the Golgi apparatus for further processing. At least some lysosomes probably arise by budding from the trans face of the Golgi apparatus.

Lysosomes carry out intracellular digestion in a variety of circumstances. Amoebas and many other protists eat by engulfing smaller organisms or other food particles, a process called **phagocytosis** (from the Greek *phagein*, to eat, and *kytos*, vessel, referring here to the cell). The **food vacuole** formed in this way then fuses with a lysosome, whose enzymes digest the food (Figure 10.1.1.10).

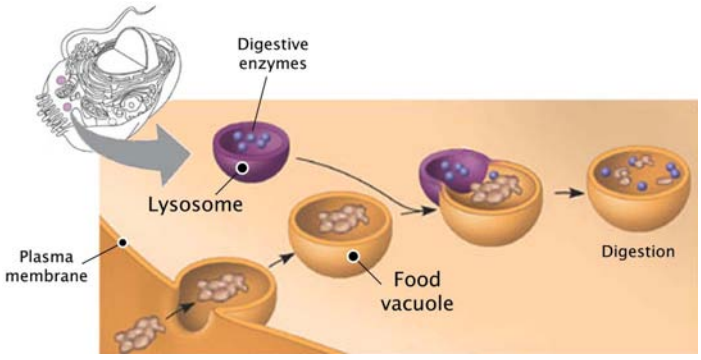

Figure 10.1.1.10 Lysosome Digestion Process

Digestion products, including simple sugars, amino acids, and other monomers, pass into the cytosol and become nutrients for the cell. Among the human cells that carry

out phagocytosis are **macrophages**, a type of white blood cell that helps defend the body by engulfing and destroying bacteria and other invaders.

Lysosomes also use their hydrolytic enzymes to recycle the cell's own organic material, a process called **autophagy**. During autophagy, a damaged organelle or small amount of cytosol becomes surrounded by a membrane, and a lysosome fuses with this vesicle. The lysosomal enzymes dismantle the enclosed material, and the organic monomers are returned to the cytosol for reuse. With the help of lysosomes, the cell continually renews itself. A human liver cell, for example, recycles half of its macromolecules each week.

Plant and fungi cells may also contain **vacuoles** (Figure 10.1.1.11). While these vacuoles carry out hydrolysis and are thus similar to lysosomes, they carry out other functions as well. **Food vacuoles**, formed by phagocytosis, have already been mentioned. Many freshwater protists have **contractile vacuoles** that pump excess water out of the cell, thereby maintaining the appropriate concentration of salts and other molecules. Mature plant cells generally contain a large central vacuole enclosed by a membrane called the **tonoplast**.

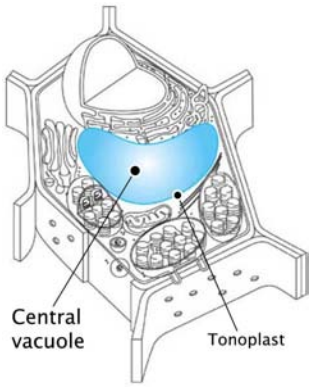

Figure 10.1.1.11
Plant cell vacuole

The central vacuole develops by the coalescence of smaller vacuoles, themselves derived from the endoplasmic reticulum and Golgi apparatus. The vacuole is in this way an integral part of a plant cell's endomembrane system. Like all cellular membranes, the tonoplast is selective in transporting solutes, and as a result, the solution inside the vacuole, called **cell sap**, differs in composition from the cytosol.

The plant cell's central vacuole is a versatile compartment. It can hold reserves of important organic compounds, such as the proteins stockpiled in the vacuoles of storage cells in seeds. It is also the plant cell's main repository of inorganic ions, such as potassium and chloride. Many plant cells use their vacuoles as disposal sites for metabolic by-products that would endanger the cell if they accumulated in the cytosol. Some vacuoles contain pigments that colour the cells, such as the red and blue pigments of petals that help attract pollinating insects to flowers. Vacuoles may also help protect the plant against predators by containing compounds that are poisonous or unpalatable to animals.

Energy Sources

Organisms transform energy they acquire from their surroundings. In eukaryotic cells, mitochondria and chloroplasts are the organelles that convert energy to forms that cells can use for work. **Mitochondria** (singular, *mitochondrion*) are the sites of cellular respiration, the metabolic process that generates adenosine triphosphate (ATP) by extracting energy from sugars, fats, and other fuels with the help of oxygen. **Chloroplasts**, found only in plants and algae, are the sites of photosynthesis. They convert solar energy to chemical energy by absorbing sunlight and using it to drive the synthesis of organic compounds such as sugars from carbon dioxide and water.

Mitochondria are found in nearly all eukaryotic cells, including those of plants, animals, fungi, and protists (Figure 10.1.1.12). Some cells have a single large mitochondrion, but more often a cell has hundreds or even thousands of mitochondria—the number is correlated with the cell's level of metabolic activity. For example, motile or contractile cells have proportionally more mitochondria per volume than less active cells.

The mitochondrion is enclosed by two membranes. The outer membrane is smooth, but the inner membrane is convoluted, with infoldings called **cristae**. This highly folded surface gives the inner mitochondrial membrane a large surface area, enhancing the productivity of cellular respiration. The illustration shows the two compartments bounded by the membranes: the intermembrane space and the mitochondrial matrix. Free ribosomes are seen in the matrix, along with one to several copies of the mitochondrial genome (DNA). The DNA molecules are usually circular and are attached to the inner mitochondrial membrane.

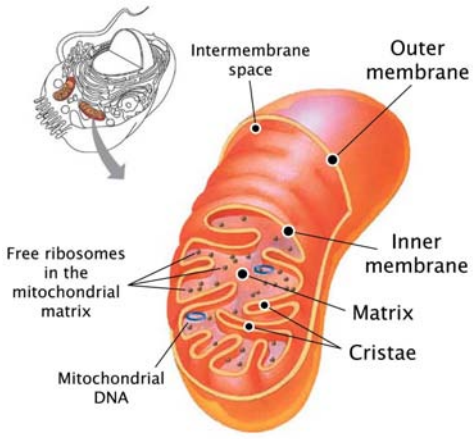

Figure 10.1.1.12 Mitochondrion

The **chloroplast** is a specialised member of a family of closely related plant organelles called **plastids**. Amyloplasts are colourless plastids that store starch (amylose), particularly in roots and tubers. Chromoplasts have pigments that give fruit and flowers their orange and yellow hues. Chloroplasts contain the green pigment **chlorophyll**, along with enzymes and other molecules that function in the photosynthetic production of sugar. These lens-shaped organelles are found in leaves and other green organs of plants and in algae.

The contents of a chloroplast are partitioned from the cytosol by an envelope consisting of two membranes separated by a very narrow intermembrane space. Inside the chloroplast is another membranous system in the form of flattened, interconnected sacs called **thylakoids**. In some regions, thylakoids are stacked like poker chips—each stack is called a **granum** (plural, *grana*). The fluid outside the thylakoids is the **stroma**, which contains the chloroplast DNA and ribosomes as well as many enzymes. The membranes of the chloroplast divide the chloroplast space into three compartments: the intermembrane space, the stroma, and the thylakoid space (Figure 10.1.1.13).

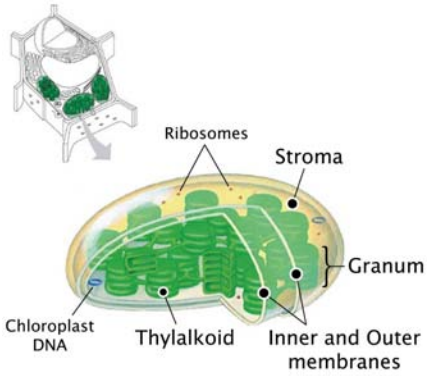

Figure 10.1.1.13 Chloroplast

As with mitochondria, the static and rigid appearance of chloroplasts in micrographs or schematic diagrams is not true to their dynamic behaviour in the living cell. Their shapes are changeable, and they grow and occasionally pinch in two, reproducing themselves. They are mobile and move around the cell with mitochondria and other organelles along tracks of the cytoskeleton, a structural network discussed below.

There is another organelle that works closely with mitochondria. **Peroxisomes** contain enzymes that transfer hydrogen from various substrates to oxygen, producing hydrogen peroxide (H_2O_2) as a by-product (and from which the organelle derives its name). Some peroxisomes use oxygen to break down fatty acids into smaller molecules that can then be transported to mitochondria, where they are used as fuel for cellular respiration. Peroxisomes in the liver detoxify alcohol and other harmful compounds. The H_2O_2 formed by peroxisome metabolism is itself toxic, but the organelle contains an enzyme that converts the H_2O_2 to water. Enclosing in the same space both the

enzymes that produce hydrogen peroxide and those that dispose of this toxic compound is an example of how the cell's compartmental structure is crucial to its functions.

Structural Framework

In the early days of electron microscopy, biologists thought that the organelles of a eukaryotic cell floated freely in the cytosol. Improvements in both light microscopy and electron microscopy, however, have revealed the **cytoskeleton**, a network of fibres extending throughout the cytoplasm of these cells (Figure 10.1.1.14).

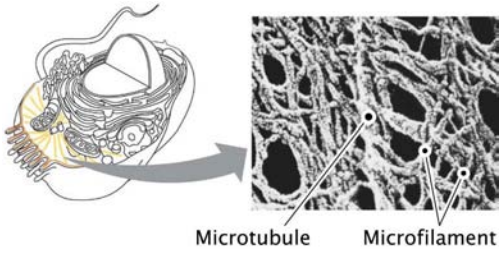

Figure 10.1.1.14 Cytoskeleton

The most obvious function of the cytoskeleton is to give mechanical support to the cell and maintain its shape. This is especially important for animal cells, which lack walls. The remarkable strength and resilience of the cytoskeleton as a whole is based on its architecture. Like a geodesic dome, the cytoskeleton is stabilised by a balance between opposing forces exerted by its elements. The cytoskeleton is also involved in several types of cell motility (movement)—both changes in cell location and more limited movements of parts of the cell.

The cytoskeleton is also involved in several types of cell motility (movement). Cell motility generally requires the interaction of the cytoskeleton with proteins called **motor proteins**. The vesicles that bud off from the ER, for example, travel to the Golgi along 'tracks' built of cytoskeletal elements (Figure 10.1.1.15).

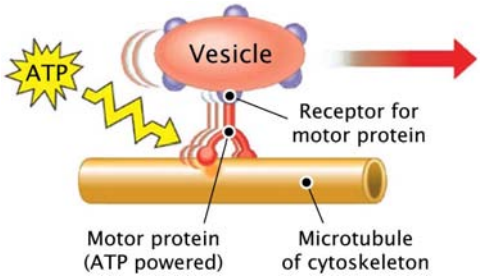

Figure 10.1.1.15
Motor proteins and the cytoskeleton

In some eukaryotes, the cytoskeleton extends into **cilia** (singular, *cilium*) and **flagella** (singular, *flagellum*), tail-like locomotor appendages that protrude from these cells. Cilia are smaller appendages that usually occur in large numbers on the cell surface. Flagella are longer than cilia and are usually limited to just one or a few per cell. Many unicellular eukaryotic organisms are propelled through water by cilia or flagella, and the sperm of animals, algae, and some plants have flagella. When cilia or flagella extend from cells that are held in place as part of a tissue layer, they can move fluid over the surface of the tissue. For example, the ciliated lining of the windpipe sweeps mucus containing trapped debris out of the lungs. In a woman's reproductive tract, the cilia lining

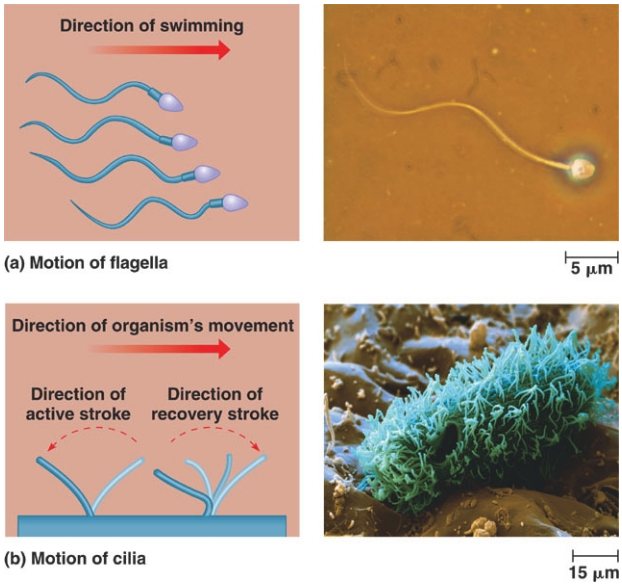

Figure 10.1.1.16 Flagella and cilia

the oviducts (fallopian tubes) help move an egg toward the uterus.

Microvilli, also projections from the cell surface, differ from cilia in that their primary role is one of increasing the surface area of the cell, while cilia are designed primarily for motility (Figure 10.1.1.17).

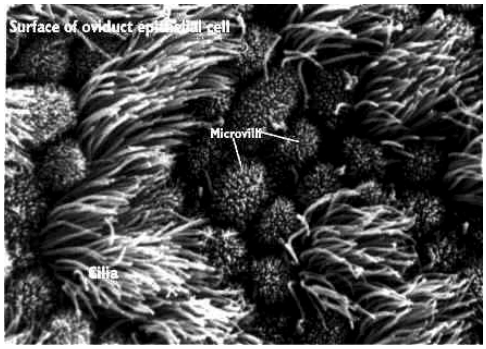

Figure 10.1.1.17 Cilia & microvilli on the surface of an oviduct cell

In many cells, elements of the cytoskeleton grow out from a **centrosome**, a region often located near the nucleus (Figure 10.1.1.18). The centrosome of animal cells also contains a pair of **centrioles**, which play an important role in cell replication.

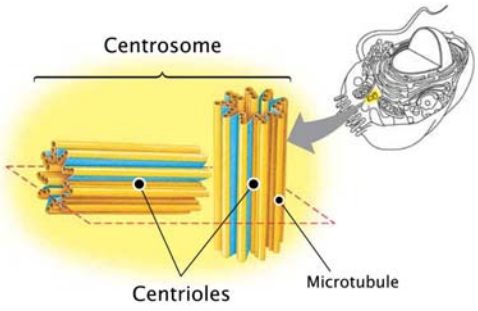

Figure 10.1.1.18 Centrosome

Summary of Structural Differences

In Animal Cells, but not Plant Cells	In Plant Cells, but not Animal Cells
Lysosomes Centrioles Flagella (in some plant sperm)	Chloroplasts Central vacuole and tonoplast Cell wall Plasmodesmata

Extracellular Components

The **plasma membrane** is usually regarded as the boundary of the living cell, but most cells synthesise and secrete materials of one kind or another that are external to the plasma membrane. The **cell wall** is an extracellular structure of plant cells that distinguishes them from animal cells. The wall protects the plant cell, maintains its shape, and prevents excessive uptake of water. On the level of the whole plant, the strong walls of specialised cells hold the plant up against the force of gravity. Prokaryotes, fungi, and some protists also have cell walls.

Plant cell walls are much thicker than the plasma membrane. Microfibrils made of cellulose are embedded in a matrix of other polysaccharides and protein. This combination of materials, strong fibres in a 'ground substance' (matrix), is the same basic architectural design found in steel-reinforced concrete and in fibreglass.
The many cells of an animal or plant are organized into tissues, organs, and organ systems. Neighbouring cells often adhere, interact, and communicate through special patches of direct physical contact. Plant cell walls, for example, are perforated with channels called **plasmodesmata** (singular, plasmodesma—from the Greek *desmos*, to bind). Cytosol passes through the plasmodesmata and connects the chemical environments of adjacent cells. These connections unify most of the plant into one

living continuum. The plasma membranes of adjacent cells line the channel of each plasmodesma and thus are continuous. Water, small solutes and even specific proteins and RNA molecules can pass freely from cell to cell.

In animals, there are three main types of intercellular junctions: tight junctions, desmosomes, and gap junctions. All three types are especially common in epithelial tissue, which lines the internal surfaces of the body. Epithelial cells of the intestinal lining are used to illustrate these junctions in Figure 10.1.1.19.

At **tight junctions**, the membranes of neighbouring cells are very tightly pressed against each other, bound together by specific proteins. Forming continuous seals around the cells, tight junctions prevent leakage of extracellular fluid across a layer of epithelial cells.

Desmosomes (also called *anchoring junctions*) function like rivets, fastening cells together into strong sheets. Intermediate filaments made of sturdy keratin proteins anchor desmosomes in the cytoplasm.

Gap junctions (which are most like the plasmodesmata of plants, and also called *communicating junctions*) provide cytoplasmic channels from one cell to an adjacent cell. Gap junctions consist of special membrane proteins that surround a pore through which inos sugars, proteins, amino acids, and other small molecules may pass. Gap junctions are necessary for communication between cells in many types of tissues, including heart muscle, and in animal embryos.

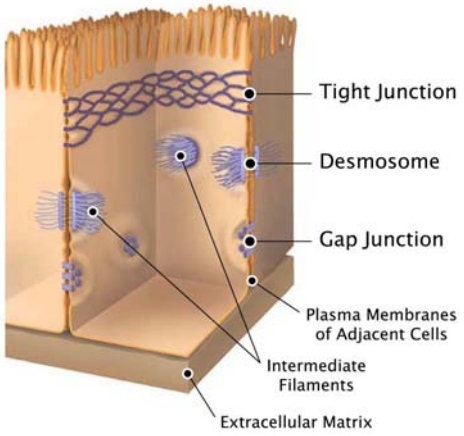

Figure 10.1.1.19
Intercellular Junctions in Animal Tissues

Even as we dissect the cell, however, to examine all of its components, remember that none of its organelles works alone. As an example of cellular integration, consider the microscopic scene in Figure 10.1.1.20. The large orange cell is a macrophage (a type of white blood cell). It helps defend the body against infections by ingesting bacteria (the smaller, yellow cells) into phagocytic vesicles. The macrophage crawls along a surface and reaches out to the bacteria with thin pseudopodia (called filopodia). Actin filaments interact with other elements of the cytoskeleton in these movements. After the macrophage engulfs the bacteria, they are destroyed by lysosomes. The elaborate endomembrane system produces the lysosomes. The digestive enzymes of the lysosomes and the proteins of the cytoskeleton are all made on ribosomes. And the synthesis of these proteins is programmed by genetic messages dispatched from the DNA in the nucleus. All these processes require energy, which mitochondria supply in the form of ATP. Cellular functions arise from cellular order—**the cell is a living unit greater than the sum of its parts**.

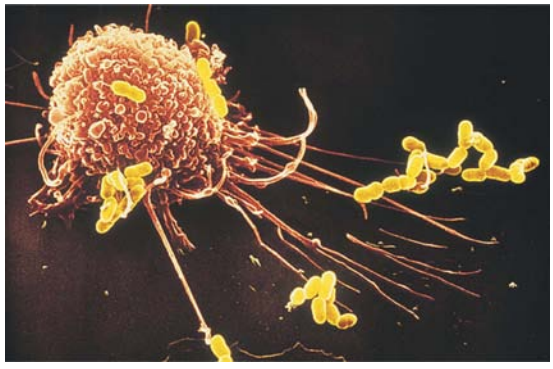

Figure 10.1.1.20 Macrophage in Action

10.1.1.2 Cell Function

10.1.1.2.1 Membrane Structure

Cellular membranes are fluid mosaics of lipids and proteins

A **phospholipid**, as illustrated in Figure 10.1.1.21, characteristically has a **hydrophilic** (polar, attracted to water) **head** and two **hydrophobic** (nonpolar, repelled by water) **tails**. The two fatty acid chains and the groups attached to the phosphate group of the head may vary, and further characterise a specific phospholipid. In the space-filling model, black = carbon, grey = hydrogen, red = oxygen, yellow = phosphorus, and blue = nitrogen.

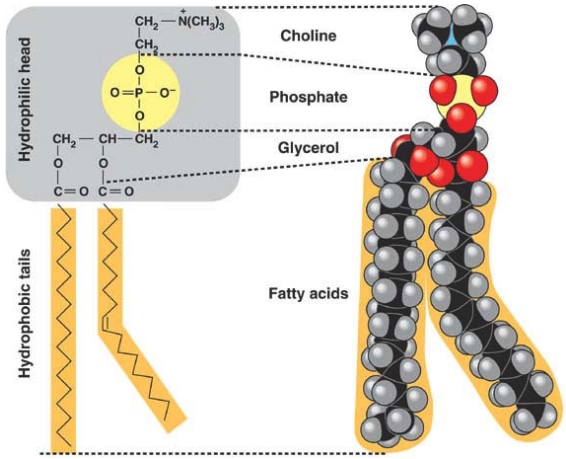

Figure 10.1.1.21 Phospholipid Structure

Due to their bipolar nature, when phospholipids are added to water they self-assemble into double-layered aggregates—bilayers—that shield their hydrophobic portions from water (Figure 10.1.1.22).

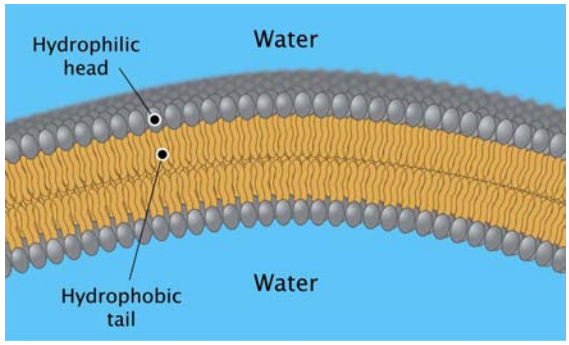

Figure 10.1.1.22 Lipid Bilayer

At the surface of a cell, phospholipids are arranged in a similar bilayer. The phospholipid bilayer forms a boundary between the cell and its external environment—phospholipids are, indeed, major components of all cell membranes.

Proteins are large organic compounds made of amino acids arranged in a linear chain. Most proteins, however, fold into a unique 3-dimensional structure the shape of which is known as its native state.

In 1972, American cell biologists Seymour J. Singer and Garth L. Nicolson proposed that membrane proteins are dispersed and individually inserted into the phospholipid bilayer, with only their hydrophilic regions protruding far enough from the bilayer to be exposed to water (Figure 10.1.1.23).

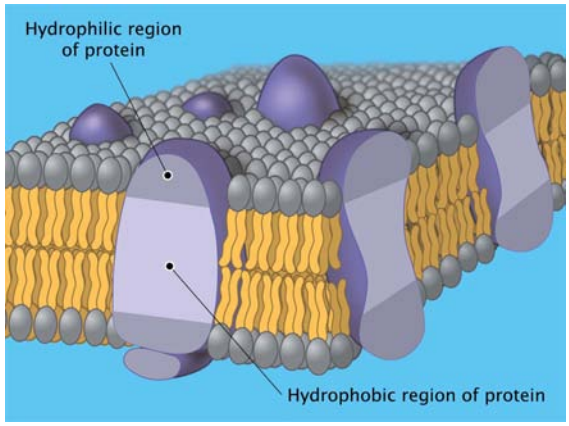

Figure 10.1.1.23 Fluid Mosaic Model

This molecular arrangement would maximise contact of hydrophilic regions of proteins and phospholipids with water while providing their hydrophobic parts with a nonaqueous environment. According to this model, the membrane is a mosaic of protein molecules bobbing in a fluid bilayer of phospholipids.

Membranes are not static sheets of molecules locked rigidly in place. A membrane is held together primarily by hydrophobic interactions, which are much weaker than covalent bonds (the most common type of bonding in organic molecules).

Membrane structure results in selective permeability

A membrane is a collage of different proteins embedded in the fluid matrix of the lipid bilayer. More than 50 kinds of proteins have been found so far in the plasma membrane of red blood cells, for example. Phospholipids form the main fabric of the membrane, but proteins determine most of the membrane's specific functions. Different types of cells contain different sets of membrane proteins, and the various membranes within a cell each have a unique collection of proteins.

Hydrophobic (nonpolar) molecules, such as hydrocarbons, carbon dioxide, and oxygen, can dissolve in the lipid bilayer of the membrane and cross it with ease, without the aid of membrane proteins. However, the hydrophobic core of the membrane impedes the direct passage of ions and polar molecules, which are hydrophilic, through the membrane. Polar molecules such as glucose and other sugars pass only slowly through a lipid bilayer, and even water, an extremely small polar molecule, does not cross very rapidly.

Cell membranes are nonetheless permeable to specific ions and a variety of polar molecules. These hydrophilic substances can avoid contact with the lipid bilayer by passing through **transport proteins** that span the membrane. Some transport proteins, called **channel proteins**, function by having a hydrophilic channel that certain molecules or atomic ions use as a tunnel through the membrane Other transport proteins, called **carrier proteins**, hold onto their passengers and change shape in a way that shuttles them across the membrane. In both cases, the transport protein is specific for the substance it moves, allowing only a certain substance (or substances) to cross the membrane. For example, glucose carried in blood and needed by red blood cells for cellular activities enters these cells rapidly through specific transport proteins in the plasma membrane. This *glucose transporter* is so selective as a carrier protein that it even rejects fructose, a structural isomer of glucose.

Thus, the selective permeability of a membrane depends on both the discriminating barrier of the lipid bilayer and the specific transport proteins built into the membrane.

10.1.1.2.2 Membrane Function

Diffusion across a membrane is governed by a simple rule: In the absence of other forces, a substance will diffuse from where it is more concentrated to where it is less concentrated. Put another way, any substance will diffuse down its **concentration gradient**. No work need be done to make this happen—diffusion is a spontaneous process. Note that each substance diffuses down its own concentration gradient, unaffected by the concentration differences of other substances.

Much of the traffic across cell membranes occurs by diffusion. When a substance is more concentrated on one side of a membrane than on the other, there is a tendency for the substance to diffuse across the membrane down its concentration gradient (assuming that the membrane is permeable to that substance). One important example is the uptake of oxygen by a cell performing cellular respiration. Dissolved oxygen diffuses into the cell across the plasma membrane. As long as cellular respiration consumes the O_2 as it enters, diffusion into the cell will continue, because the concentration gradient favours movement in that direction.

The diffusion of water across a selectively permeable membrane is called **osmosis** and is illustrated in Figure 10.1.1.24. Sugar solutions of different concentrations are

separated by a selectively permeable membrane, which the solvent (water) can pass through but the solute (sugar) cannot. Water molecules move randomly and may cross through the pores in either direction, but overall, water diffuses from the solution with less concentrated solute to that with more concentrated solute. This transport of water eventually equalises the sugar concentrations on each side of the membrane.

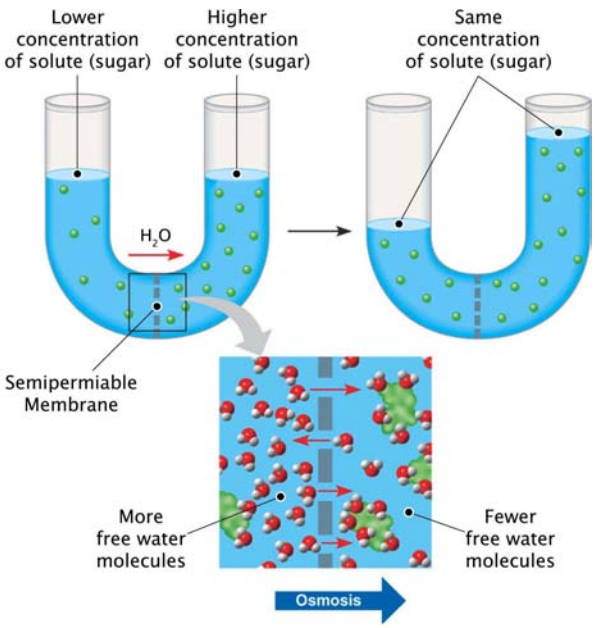

Figure 10.1.1.24 Osmosis

When considering the behaviour of a cell in a solution, both solute concentration and membrane permeability must be considered. Both factors are taken into account in the concept of **tonicity**, the ability of a solution to cause a cell to gain or lose water. If a cell without a wall, such as an animal cell, is immersed in an environment that is **isotonic** to the cell (iso means *same*), there will be no net movement of water across the plasma membrane. Water flows across the membrane, but at the same rate in both directions.

In an environment that is **hypertonic** (hyper means *more*, in this case more nonpenetrating solutes), however, the cell will lose water to its environment, shrivel, and probably die. This is one reason why an increase in the salinity of a lake can kill the animals there—if the lake water becomes hypertonic to the animals' cells, the cells can shrivel and die. Taking up too much water can be just as hazardous to an animal cell as losing water. In an environment that is **hypotonic** to the cell (hypo means *less*), water will enter the cell faster than it leaves, and the cell will swell and lyse (burst) like an overfilled water balloon.

A cell without rigid walls can tolerate neither excessive uptake nor excessive loss of water. This problem of water balance is automatically solved if such a cell lives in isotonic surroundings. Seawater is isotonic to many marine invertebrates. The cells of most terrestrial (land-dwelling) animals are bathed in an extracellular fluid that is isotonic to the cells. Animals and other organisms without rigid cell walls living in hypertonic or hypotonic environments must have special adaptations for **osmoregulation**, the control of water balance.

The cells of plants, prokaryotes, fungi, and some protists have walls. When such a cell is immersed in a hypotonic solution—bathed in rainwater, for example—the wall helps maintain the cell's water balance. Like an animal cell, the plant cell swells as water enters by osmosis. However, the elastic wall will expand only so much before it exerts a back pressure on the cell that opposes further water uptake. At this point, the cell is **turgid** (very firm), which is the healthy state for most plant cells. Plants that are not woody, such as most house plants, depend for mechanical support on cells kept turgid by a surrounding hypotonic solution. If a plant's cells and their surroundings are isotonic, there is no net tendency for water to enter, and the cells become **flaccid** (limp).

However, a wall is of no advantage if the cell is immersed in a hypertonic environment. In this case, a plant cell, like an animal cell, will lose water to its surroundings and shrink. As the plant cell shrivels, its plasma membrane pulls away from the wall. This phenomenon, called **plasmolysis**, causes the plant to wilt and can be lethal.

Bulk transport across the plasma membrane occurs by exocytosis and endocytosis

Water and small solutes enter and leave the cell by passing through the lipid bilayer of the plasma membrane or by being pumped or carried across the membrane by transport proteins. However, large molecules, such as proteins and polysaccharides, as well as larger particles, generally cross the membrane by a different mechanism—one involving vesicles.

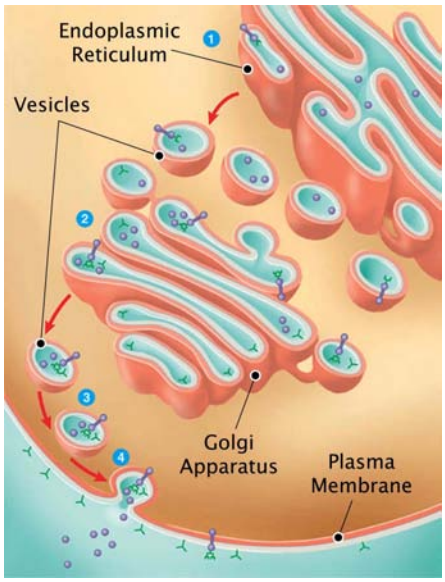

Figure 10.1.1.25 Exocytosis

Exocytosis is the process by which a cell secretes macromolecules by the fusion of vesicles with the plasma membrane (Figure 10.1.1.25). A transport vesicle that has budded from the Golgi apparatus (2) moves along microtubules of the cytoskeleton to the plasma membrane (3). When the vesicle membrane and plasma membrane come into contact, the lipid molecules of the two bilayers rearrange themselves so that the two membranes fuse. The contents of the vesicle then spill to the outside of the cell, and the vesicle membrane becomes part of the plasma membrane (4).

In **endocytosis**, the cell takes in macromolecules and particulate matter by forming new vesicles from the plasma membrane. Although the proteins involved in the processes are different, the events of endocytosis look like the reverse of exocytosis. A small area of the plasma membrane sinks inward to form a pocket. As the pocket deepens, it pinches in, forming a vesicle containing material that had been outside the cell. There are three types of endocytosis: **phagocytosis** (*cellular eating*—see Figure 10.1.1.10), **pinocytosis** (*cellular drinking*—Figure 10.1.1.26), and **receptor-mediated endocytosis**.

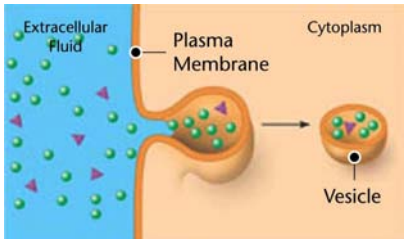

Figure 10.1.1.26 Pinocytosis

Vesicles not only transport substances between the cell and its surroundings but also provide a mechanism for rejuvenating or remodelling the plasma membrane. Endocytosis and exocytosis occur continually to some extent in most eukaryotic cells, and yet the amount of plasma membrane in a nongrowing cell remains fairly constant over the long run. Apparently, the addition of membrane by one process offsets the loss of membrane by the other.

10.1.1.2.3 Cell Metabolism

The living cell is a chemical factory in miniature, where thousands of reactions occur within a microscopic space. The totality of an organism's chemical reactions is called **metabolism** (from the Greek metabole, meaning *change*), and we can picture a cell's metabolism as an elaborate road map of the thousands of chemical reactions that occur in a cell, arranged as intersecting metabolic pathways. A **metabolic pathway** begins with a specific molecule, which is then altered in a series of defined steps, resulting in a

certain product. Each step of the pathway is catalysed by a specific enzyme, as illustrated in Figure 10.1.1.27.

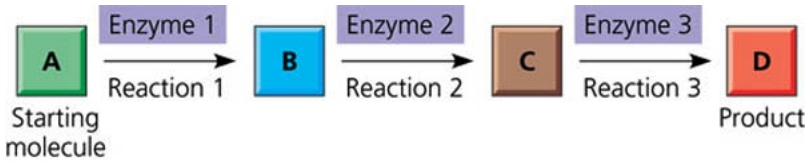

Figure 10.1.1.27 Metabolic Pathway

Metabolism as a whole manages the material and energy resources of the cell. Some metabolic pathways release energy by breaking down complex molecules to simpler compounds. These degradative processes are called **catabolic pathways**—thus catabolic pathways **release energy**. A major pathway of catabolism is cellular respiration, in which the sugar glucose and other organic fuels are broken down in the presence of oxygen to carbon dioxide and water. **Anabolic pathways**, in contrast, **consume energy** to build complicated molecules from simpler ones—they are sometimes called biosynthetic pathways. An example of anabolism is the synthesis of a protein from amino acids. Energy released through catabolic reactions can be stored and used to drive anabolic reactions.

Gibbs Free Energy

Thermodynamics is the study of energy transformations. The Gibbs free energy, named after the American physical chemist J. Willard Gibbs (1839–1903) who developed the mathematics that underpins the study of thermodynamics, is a measure of the useful energy available within a system, and represented by the letter *G*.

The change in free energy, ΔG, can be calculated for any specific chemical reaction using the formula:

$$\Delta G = \Delta H - T\Delta S$$

where ΔH is the change in the system's **enthalpy** (in biological systems, equivalent to total energy), ΔS is the change in the system's **entropy** (a measure of order, or *internal* energy in a system), and T is the absolute temperature in Kelvin (K). Thus, if the energy associated with entropy change within a system ($T\Delta S$) is greater than the total system energy (ΔH), the free energy (ΔG) will be negative and the process in question will be **spontaneous**[2]. For a process to occur spontaneously, therefore, the system must either give up enthalpy (H must decrease), give up order (TS must increase), or both. This means that every spontaneous process decreases the system's free energy. Processes that have a positive or zero values for ΔG are never spontaneous.

Free Energy, Stability, and Equilibrium

We can think of free energy as a measure of a system's instability—its tendency to change to a more stable state. Unstable systems (higher *G*) tend to change in such a way that they become more stable (lower *G*).

Another term for a state of maximum stability is **equilibrium**. There is an important relationship between free energy and equilibrium, including chemical equilibrium. Recall that most chemical reactions are reversible and proceed to a point at which the forward and backward reactions occur at the same rate. The reaction is then said to be at chemical equilibrium, and there is no further net change in the relative concentration of products and reactants. For a system at equilibrium, *G* is at its lowest

[2] A spontaneous reaction will occur by itself, without any outside influence. The fact that a reaction is spontaneous, however has nothing to do with its speed.

possible value in that system. We can think of the equilibrium state as an energy valley. Any small change from the equilibrium position will have a positive ΔG and will not be spontaneous. For this reason, systems never spontaneously move away from equilibrium.

Exergonic and Endergonic Reactions in Metabolism

Based on their free-energy changes, chemical reactions can be classified as either **exergonic** (*energy outward*) or **endergonic** (*energy inward*). An exergonic reaction proceeds with a net release of free energy (Figure 10.1.1.28 (a)).

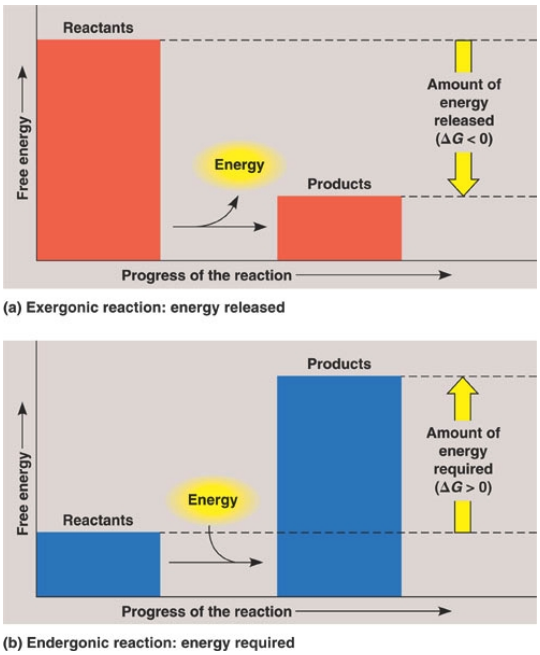

Figure 10.1.1.28
Exergonic and Endergonic Reactions

Because the chemical mixture loses free energy (*G* decreases), **ΔG is negative for an exergonic reaction**. Using ΔG as a standard for spontaneity, exergonic reactions are those that occur spontaneously. The magnitude of ΔG for an exergonic reaction represents the maximum amount of work the reaction can perform. ΔG thus represents a theoretical upper limit of available energy. The greater the decrease in free energy, the greater the amount of work that can be done.

An endergonic reaction is one that absorbs free energy from its surroundings (Figure 10.1.1.28 (b)). Because this kind of reaction essentially stores free energy in molecules (*G* increases), **ΔG is positive for an endergonic reaction**. Such reactions are not spontaneous, and the magnitude of ΔG is the quantity of energy required to drive the reaction.

Equilibrium and Metabolism

Reactions in a closed system eventually reach equilibrium and can then do no work. The chemical reactions of metabolism are reversible, and they, too, would reach equilibrium if they occurred in the isolation of a test tube. Because systems at equilibrium are at a minimum of *G* and can do no work, a cell that has reached metabolic equilibrium is dead! The fact that metabolism as a whole is never at equilibrium is one of the defining features of life.

Like most systems, a cell in our body is not in equilibrium. The constant flow of materials in and out of the cell keeps the metabolic pathways from ever reaching equilibrium, and the cell continues to do work throughout its life.

ATP powers cellular work by coupling exergonic reactions to endergonic reactions

A cell does three main kinds of work:

- **Mechanical** work, such as the contraction of muscle cells, and the movement of chromosomes during cellular reproduction;
- **Transport** work, the pumping of substances across membranes against the direction of spontaneous movement;

- **Chemical** work, the pushing of endergonic reactions, which would not occur spontaneously, such as the synthesis of polymers from monomers.

A key feature in the way cells manage their energy resources to do this work is energy coupling, the use of an exergonic process to drive an endergonic one. **ATP** (**adenosine triphosphate**) is responsible for mediating most energy coupling in cells, and in most cases it acts as the immediate source of energy that powers cellular work.

The ATP molecule contains the sugar ribose, bonded to the nitrogenous base adenine, and a chain of three phosphate groups, as illustrated in Figure 10.1.1.29.

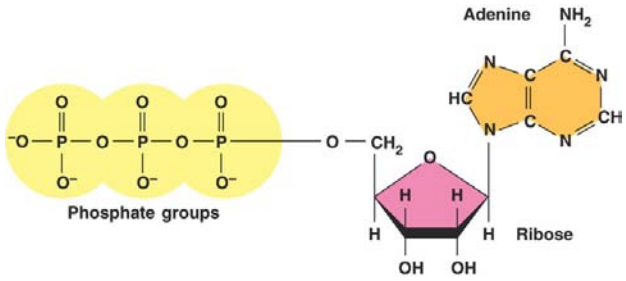

Figure 10.1.1.29 Adenosine Triphosphate (ATP)

The bonds between the phosphate groups of ATP's tail can be broken by hydrolysis. When the terminal phosphate bond is broken, a molecule of inorganic phosphate (abbreviated Pi throughout this document) is split off from ATP, leaving **adenosine diphosphate**, or **ADP** (Figure 10.1.1.30).

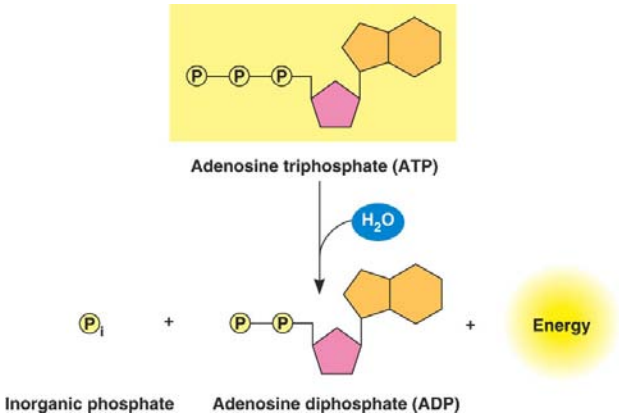

Figure 10.1.1.30 The Hydrolysis of ATP

Thus, if the ΔG of an endergonic reaction is less than the amount of energy released by ATP hydrolysis, then the two reactions can be coupled so that, overall, the coupled reactions are exergonic , as illustrated in Figure 10.1.1.31.

When ATP is hydrolysed in a test tube, the release of free energy merely heats the surrounding water. In an organism, this same generation of heat can sometimes be beneficial. For instance, the process of shivering uses ATP hydrolysis during muscle contraction to generate heat and warm the body. In most cases in the cell, however, the generation of heat alone would be an inefficient (and potentially dangerous) use of a valuable energy resource.

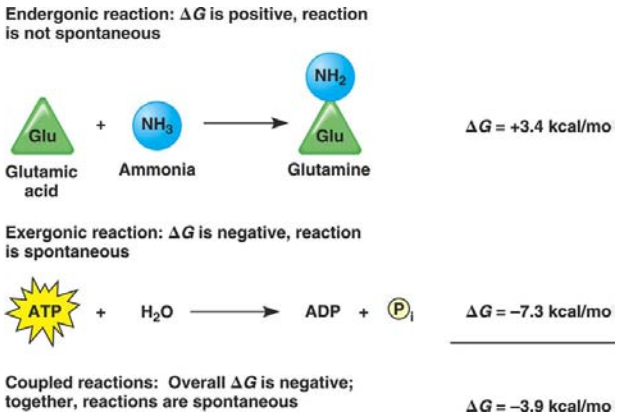

Figure 10.1.1.31 Energy Coupling

The Regeneration of ATP

An organism at work uses ATP continuously, but ATP is a renewable resource that can be regenerated by the addition of Pi to ADP. The free energy required to phosphorylate ADP comes from exergonic breakdown reactions (catabolism), especially

cellular respiration although plants also use ligt energy to produce ATP. This shuttling of Pi and energy is called the **ATP cycle**, and it couples the cell's energy-yielding (exergonic) processes to its energy-consuming (endergonic) ones.

The ATP cycle is thus like a turnstile, through which energy passes during its transfer from catabolic to anabolic pathways.

Enzymes speed up metabolic reactions by lowering energy barriers

A spontaneous chemical reaction occurs without any requirement for outside energy, but it may occur so slowly that it is imperceptible. For example, even though the hydrolysis of sucrose (table sugar) to glucose and fructose is exergonic, a solution of sucrose dissolved in sterile water will sit for years at room temperature with no appreciable hydrolysis. However, if we add a small amount of a **catalyst**, such as the **enzyme** sucrase, to the solution, all the sucrose may be hydrolysed within seconds.

A catalyst is a chemical agent that speeds up a reaction without being consumed by the reaction. **An enzyme is a catalytic protein**.

Every chemical reaction between molecules involves both bond breaking and bond making. Changing one molecule into another generally involves contorting the starting molecule into an unstable state from which the new bonds can be formed. To reach the contorted state where bonds can change, reactant molecules must absorb energy from their surroundings—they must overcome the energy barrier associated with the contorted state. When the new bonds of the product molecules form, energy is released, and the molecules return to stable shapes with lower energy.

The initial investment of energy required to start a reaction—the energy required to contort the reactant molecules so the bonds can change—is known as the free energy of activation, or **activation energy** (EA).

Graphically, the energising, or activation, of reactants is represented by the uphill portion of the curve, with the free-energy content of the reactant molecules increasing. At the summit, the reactants are in an unstable condition known as the transition state—they are activated, and the breaking and making of bonds can occur. The bond-forming phase of the reaction corresponds to the downhill part of the curve, which shows the loss of free energy by the molecules.

An enzyme catalyses a particular reaction by lowering the EA barrier, as illustrated in Figure 10.1.1.32. It will do this by helping the specific reactant molecule(s) contort into a configuration from which the reaction can proceed. An enzyme cannot change the ΔG for a reaction—it cannot make an endergonic reaction exergonic. Enzymes can only speed up reactions that would occur eventually anyway. Because enzymes are very selective in the reactions they catalyse, however, their presence or absence will determine which chemical processes will be active in the cell at any particular time.

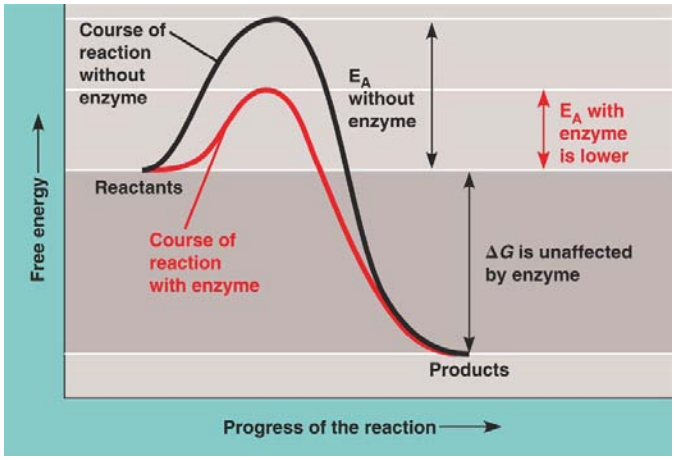

Figure 10.1.1.32 Enzyme effect on Reaction Rate

The reactant an enzyme acts on is referred to as the enzyme's **substrate**. The enzyme binds to its substrate (or substrates, when there are two or more reactants), forming an enzyme-substrate complex that facilitates the conversion of reactant(s) to product(s). The reaction catalysed by any particular enzyme is very specific—an enzyme can 'recognize' its specific substrate even among closely related compounds.

10.1.1.2.4 Cellular Respiration

Living cells require transfusions of energy from outside sources to perform their many tasks-for example, assembling polymers, pumping substances across membranes, moving, and reproducing. Animals obtain energy for their cells by eating plants, and some animals feed on other organisms that eat plants. The energy stored in the organic molecules of food ultimately comes from the sun. Energy flows into an ecosystem as sunlight and leaves as heat, as illustrated in Figure 10.1.1.33.

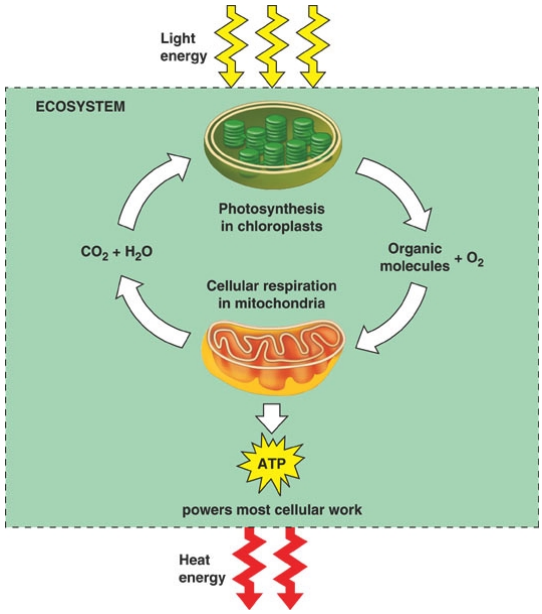

Figure 10.1.1.33
Energy Flow within an Ecosystem

With the help of enzymes, a cell systematically degrades complex organic molecules that are rich in potential energy to simpler waste products that have less energy. Some of the energy taken out of chemical storage can be used to do work, the rest is dissipated as heat. Catabolic processes are the metabolic pathways that release stored energy and the most prevalent and efficient catabolic pathway in a cell is **respiration**, in which oxygen and organic fuel are consumed, generating energy in the form of ATP, and producing carbon dioxide, water and other waste products. In eukaryotic cells, mitochondria house most of the metabolic equipment used for cellular respiration.

Respiration is a cumulative function of three metabolic stages:

1. **Glycolysis**;
2. The **citric acid cycle**, or Krebs Cycle, after the German/British biochemist Hans Krebs (1900–1981); and
3. **Oxidative phosphorylation**—electron transport and **chemiosis**.

Technically, cellular respiration is defined as including only the processes that require O_2—the citric acid cycle and oxidative phosphorylation. Glycolysis is included here, even though it doesn't require O_2, because most respiring cells deriving energy from glucose use this process to produce starting material for the citric acid cycle.

As illustrated in Figure 10.1.1.34,the first two stages of cellular respiration, glycolysis and the citric acid cycle, are the catabolic pathways that decompose glucose and other organic fuels. Glycolysis, which occurs in the cytosol, begins the degradation process by breaking glucose into two molecules of a compound called pyruvate. The citric acid cycle, which takes place within the mitochondrial matrix, completes the breakdown of glucose by oxidising a derivative of pyruvate to carbon dioxide.

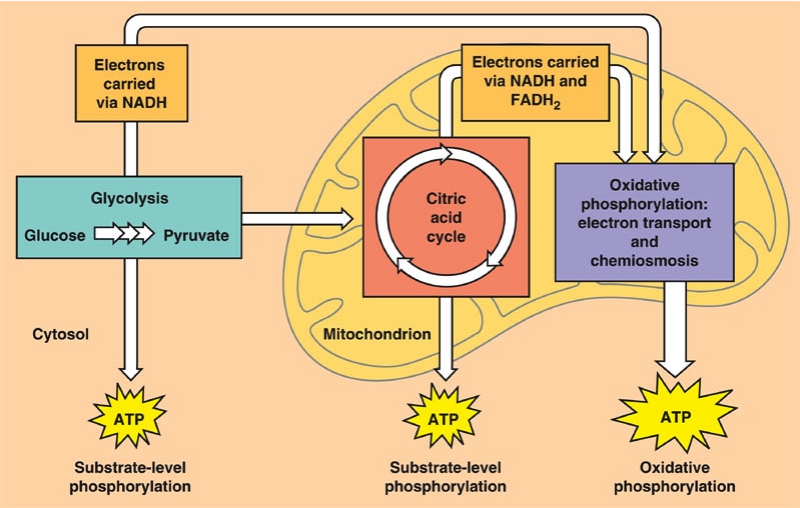

Figure 10.1.1.34 An Overview of Cellular Respiration

Some of the steps of glycolysis and the citric acid cycle are redox reactions in which dehydrogenase enzymes transfer electrons from substrates to a coenzyme[3] called NAD^+ (nicotinamide adenine dinucleotide), and a closely related coenzyme FAD (flavin adenine dinucleotide), forming NADH and $FADH_2$ respectively. As electron acceptors, NAD^+ and FAD function as an oxidising agents during respiration. In the third stage of respiration, the electron transport chain accepts electrons from the breakdown products of the first two stages (most often via NADH) and passes these electrons from one molecule to another. At the end of the chain, the electrons are combined with molecular oxygen and hydrogen ions (H^+), forming water. The energy released at each step of the chain is stored in a form the mitochondrion can use to make ATP. This mode of ATP synthesis is called oxidative phosphorylation because it is powered by the redox reactions of the electron transport chain.

The inner membrane of the mitochondrion is the site of electron transport and chemiosmosis (the transport of hydrogen ions across the internal membranes of mitochondria), the processes that together constitute oxidative phosphorylation. Oxidative phosphorylation accounts for almost 90% of the ATP generated by respiration. A smaller amount of ATP is formed directly in a few reactions of glycolysis and the citric acid cycle by a mechanism called substrate-level phosphorylation.

For each molecule of glucose degraded to carbon dioxide and water by respiration, the cell makes up to around 38 molecules of ATP.

Glycolysis and the citric acid cycle connect to many other metabolic pathways

Although glucose has been used in the above discussion as the fuel for cellular respiration, free glucose molecules are not common in the diets of humans and other animals. Most of our energy is derived from fats, proteins, sucrose and other disaccharides, and starch, a polysaccharide. All these organic molecules in food can be used in the process of cellular respiration to make ATP (Figure 10.1.1.35).

In the digestive tract, starch is hydrolysed to glucose, which can then be broken down in the cells by glycolysis and the citric acid cycle. Similarly, glycogen, the polysaccharide that humans and many other animals store in their liver and muscle cells, can be hydrolysed to glucose between meals as fuel for respiration.

[3] Sometimes referred to a *cosubstrates*, coenzymes are molecules that carry chemical groups between enzymes. ATP is also a coenzyme.

Proteins can also be used for fuel, but first they must be digested to their constituent amino acids. Many of the amino acids, of course, are used by the organism to build new proteins. Amino acids present in excess are converted by enzymes to intermediates of glycolysis and the citric acid cycle. Before amino acids can feed into glycolysis or the citric acid cycle, their amino groups must be removed, a process called deamination. The nitrogenous refuse is excreted from the animal in the form of ammonia, urea, or other waste products.

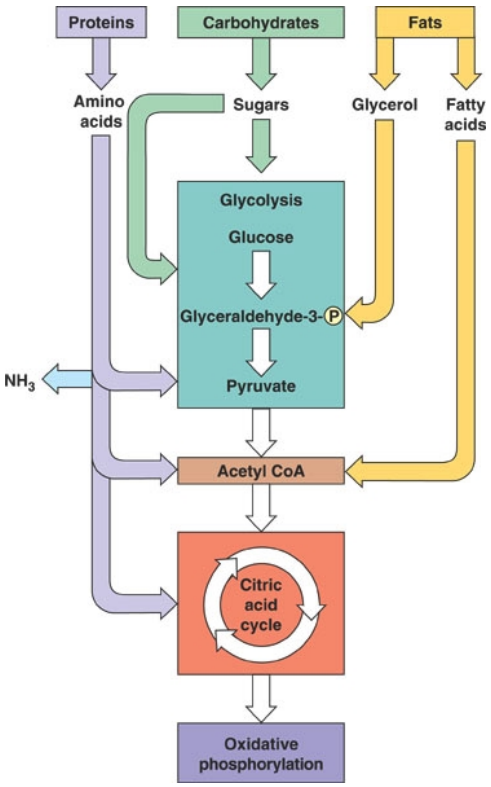

Figure 10.1.1.35 The Catabolism of Different Food Types

Catabolism can also harvest energy stored in fats obtained either from food or from storage cells in the body.

Cells need substance as well as energy. Food must also provide the carbon skeletons that cells require to make their own molecules. Some organic monomers obtained from digestion can be used directly—*e.g.* amino acids from the hydrolysis of proteins in food can be incorporated into the organism's own proteins. Often, however, the body needs specific molecules that are not present as such in food. Compounds formed as intermediates of glycolysis and the citric acid cycle can also be diverted into anabolic pathways as precursors from which the cell can synthesise the molecules it requires. Of course, these anabolic, or biosynthetic, pathways do not generate ATP, but instead consume it.

10.1.1.2.5 Photosynthesis

Life on Earth is solar powered. The chloroplasts of plants capture light energy from the sun and convert it to chemical energy stored in sugar and other organic molecules. This conversion process is called **photosynthesis**.

Photosynthesis nourishes almost the entire living world, either directly or indirectly. An organism acquires the organic compounds it uses for energy and carbon skeletons by one of two major modes: autotrophic nutrition or heterotrophic nutrition. **Autotrophs** are 'self-feeders' (from the Greek autos, meaning *self*, and trophe meaning *nutrition*)—they sustain themselves without eating anything derived from other organisms. Autotrophs produce their organic molecules from CO_2 and other inorganic raw materials obtained from the environment. They are the ultimate sources of organic compounds for all nonautotrophic organisms, and for this reason, biologists refer to autotrophs as the producers of the biosphere.

Almost all plants are autotrophs—the only nutrients they require are water and minerals from the soil and carbon dioxide from the air. Specifically, plants are photo autotrophs, organisms that use light as a source of energy to synthesise organic substances.

Heterotrophs (from the Greek hetero meaning *other*, and trophe meaning *nutrition*) are unable to make their own food, and live on compounds produced by other

organisms. Heterotrophs are the biosphere's consumers. The most obvious form of this 'other-feeding' occurs when an animal eats plants or other animals. But heterotrophic nutrition may be more subtle. Some heterotrophs consume the remains of dead organisms by decomposing and feeding on organic litter such as carcasses, feces, and fallen leaves—they are known as decomposers. Most fungi and many types of prokaryotes derive their nourishment this way. Almost all heterotrophs, including humans, are completely dependent on photoautotrophs for food, and also for oxygen, a by-product of photosynthesis.

Photosynthesis converts light energy to the chemical energy of food

The equation for photosynthesis is a deceptively simple summary of a very complex process. Actually, photosynthesis is not a single process, but two processes, each with multiple steps. These **two stages of photosynthesis** are known as the **light reactions** (the photo part of photosynthesis) and the **Calvin cycle** (the synthesis part)

The **light reactions** are the steps of photosynthesis that convert solar energy to chemical energy. Light absorbed by **chlorophyll** drives a transfer of electrons and hydrogen from water to an acceptor called $NADP^+$ (nicotinamide adenine dinucleotide phosphate), which temporarily stores the energised electrons. Water is split in the process, and thus it is the light reactions of photosynthesis that give off O_2 as a by-product. The electron acceptor of the light reactions, $NADP^+$, is first cousin to NAD^+, which functions as an electron carrier in cellular respiration—the two molecules differ only by the presence of an extra phosphate group in the $NADP^+$ molecule. The light reactions use solar power to reduce $NADP^+$ to NADPH by adding a pair of electrons along with a hydrogen nucleus, or H^+. The light reactions also generate ATP, using **chemiosmosis** to power the addition of a phosphate group to ADP, a process called **photophosphorylation**. Thus, light energy is initially converted to chemical energy in the form of two compounds—NADPH, a source of energised electrons ('reducing power'), and ATP, the versatile energy currency of cells.

The **Calvin cycle** is named after the American chemist Melvin Calvin (1911–1997), who, along with Andrew Benson (1917–) and James Bassham (1922–), began to elucidate its steps in the late 1940s. The cycle begins by incorporating CO_2 from the air into organic molecules already present in the chloroplast. This initial incorporation of carbon into organic compounds is known as **carbon fixation**. The Calvin cycle then reduces the fixed carbon to carbohydrate by the addition of electrons. The reducing power is provided by NADPH, which acquired energised electrons in the light reactions. To convert CO_2 to carbohydrate, the Calvin cycle requires chemical energy in the form of ATP, which is also generated by the light reactions. Thus, it is the Calvin cycle that makes sugar, but it can do so only with the help of the NADPH and ATP produced by the light reactions. The metabolic steps of the Calvin cycle are sometimes referred to as the *dark reactions*, or light-independent reactions, because none of the steps requires light directly. Nevertheless, the Calvin cycle in most plants occurs during daylight, since only then can the light reactions provide the NADPH and ATP that the Calvin cycle requires. In essence, the chloroplast uses light energy to make sugar by coordinating the two stages of photosynthesis.

As illustrated in Figure 10.1.1.36, the **thylakoids** of the chloroplast are the sites of the light reactions, while the Calvin cycle occurs in the **stroma**. In the thylakoids, molecules of $NADP^+$ and ADP pick up electrons and phosphate, respectively, and then are released to the stroma, where they transfer their high-energy cargo to the Calvin cycle.

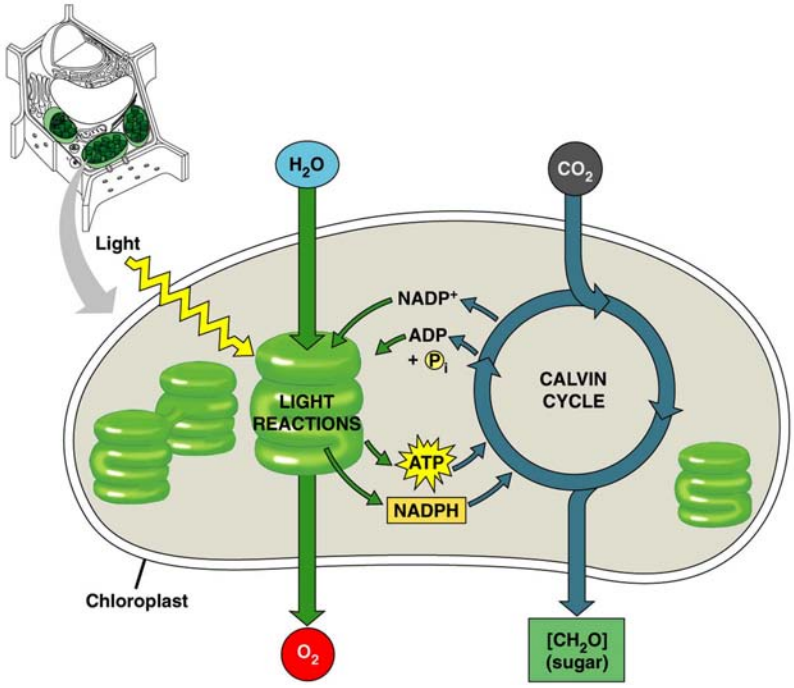

Figure 10.1.1.36 Photosynthesis: The Light Reactions and the Calvin Cycle

A Comparison of Chemiosmosis in Mitochondria and Chloroplasts

Mitochondria and chloroplasts generate ATP by the same basic mechanism: chemiosmosis. But there is a significant difference between oxidative phosphorylation in mitochondria and photophosphorylation in chloroplasts. Mitochondria transfer chemical energy from food molecules to ATP (and NADH), whereas chloroplasts transform light energy into chemical energy in ATP (and NADPH) (Figure 10.1.1.37).

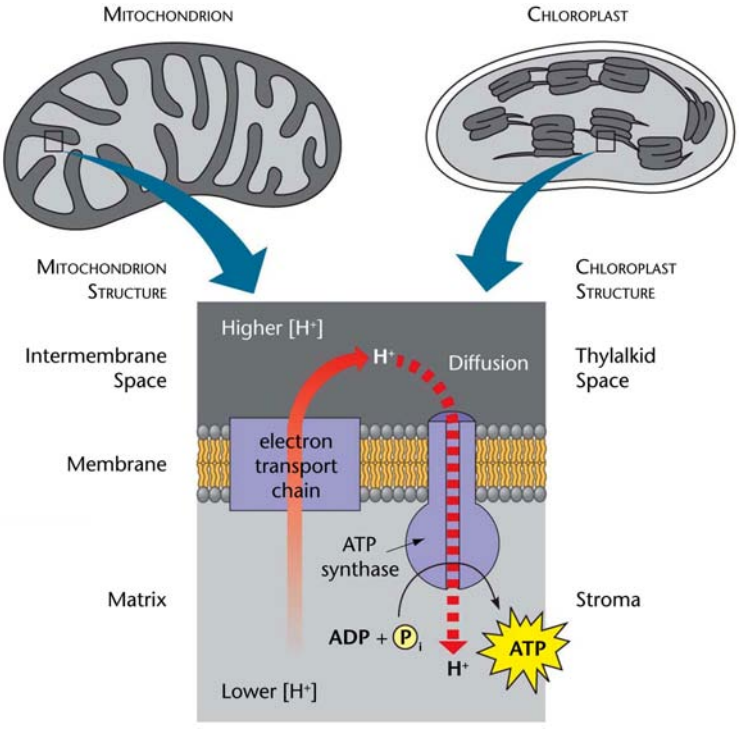

Figure 10.1.1.37 Chemiosmosis in Mitochondria and Chloroplasts

10.1.1.3 The Cell Cycle

The ability of organisms to reproduce their own kind is the most significant characteristic that distinguishes living things from nonliving matter. This unique capacity to procreate, like all biological functions, has a cellular basis.

Cell division plays several important roles in the life of an organism. When a unicellular organism, such as an amoeba, divides and forms duplicate offspring, the division of one cell reproduces an entire organism. On a larger scale, cell division can also produce progeny from some multicellular organisms (such as plants that grow from cuttings), and is the mechanism by which sexually reproducing organisms develop from a single cell—the fertilised egg, or zygote. And after an organism is fully grown, cell division continues to function in renewal and repair, replacing cells that die from normal wear and tear or accidents.

The cell division process is a fundamental part of the cell cycle, the life of a cell from the time it is first formed from a dividing parent cell until its own division into two cells.

10.1.1.3.1 Chromosome Replication

The reproduction of an ensemble as complex as a cell cannot occur by a mere pinching in half—a cell is not like a soap bubble that simply enlarges and splits in two. Cell division involves the distribution of identical genetic material—**DNA**—to two daughter cells. A dividing cell duplicates its DNA, allocates the two copies to opposite ends of the cell, and only then splits into daughter cells.

The complement of DNA within a cell, its genetic information, is called its **genome**. Although a prokaryotic genome is often a single long DNA molecule, eukaryotic genomes usually comprise a number of DNA molecules. These DNA molecules are packaged into **chromosomes**, so named because they take up certain dyes used in microscopy (from the Greek chroma, meaning *colour*, and soma, meaning *body*). Every eukaryotic species has a characteristic number of chromosomes in each cell nucleus. The nuclei of human **somatic cells** (all body cells except the reproductive cells), for example, each contain 46 chromosomes made up of two sets of 23, one set inherited from each parent. Reproductive cells, or **gametes**—sperm cells and egg cells—have half as many chromosomes as somatic cells, or one set of 23 chromosomes in humans.

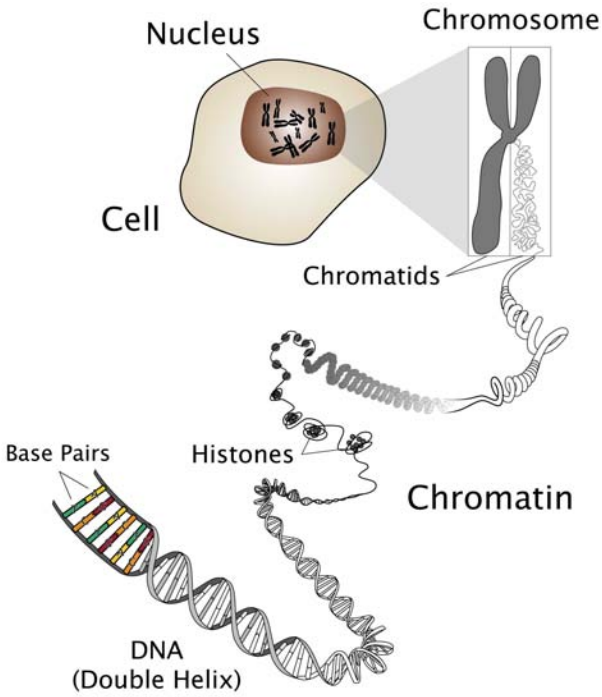

Figure 10.1.1.38
Chromosome Structure

Eukaryotic chromosomes (Figure 10.1.1.38) are made of **chromatin**, a complex of DNA and associated protein molecules (**histones**). Each single chromosome contains one

very long, linear DNA molecule that carries several hundred to a few thousand **genes**, the units that specify an organism's inherited traits. The associated proteins maintain the structure of the chromosome and help control the activity of the genes.

When a cell is not dividing, and even as it duplicates its DNA in preparation for cell division, each chromosome is in the form of a long, thin chromatin fibre. After DNA duplication, however, the chromosomes condense: each chromatin fibre becomes densely coiled and folded, making the chromosomes much shorter and so thick that we can see them with a light microscope.

Each duplicated chromosome has two sister **chromatids**. The two chromatids, each containing an identical DNA molecule, are initially attached by adhesive proteins all along their lengths. In its condensed form, the duplicated chromosome has a narrow 'waist' at a specialised region called the **centromere** where the two chromatids are most closely attached (Figure 10.1.1.39).

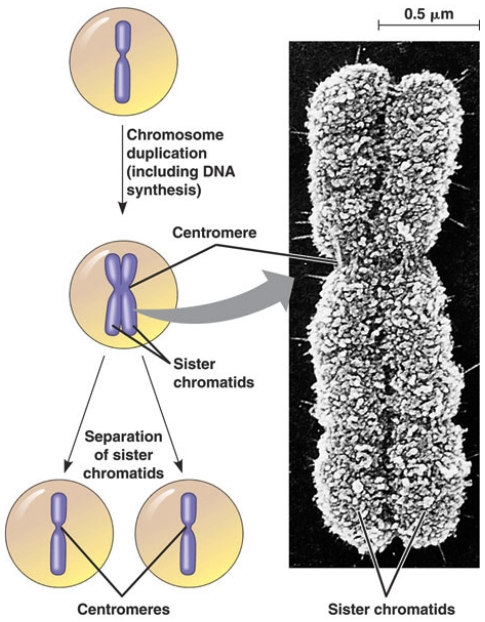

Figure 10.1.1.39
Chromosome Duplication

Later in the cell division process, the two sister chromatids of each duplicated chromosome separate and move into two new nuclei, one at each end of the cell. Once the sister chromatids separate, they are considered individual chromosomes. Thus, each new nucleus receives a group of chromosomes identical to the original group in the parent cell. **Mitosis**, the division of the nucleus, is usually followed immediately by **cytokinesis**, the division of the cytoplasm. Where there was one cell, there are now two, each the genetic equivalent of the parent cell.

What happens to chromosome number as we follow the human life cycle through the generations? You inherited 46 chromosomes, one set of 23 from each parent. They were combined in the nucleus of a single cell when a sperm cell from your father united with an egg cell from your mother, forming a fertilised egg, or **zygote**. Mitosis and cytokinesis produced the 200 trillion somatic cells that now make up your body, and the same processes continue to generate new cells to replace dead and damaged ones. In contrast, you produce gametes—eggs or sperm cells—by a variation of cell division called **meiosis**, which yields nonidentical daughter cells that have only one set of chromosomes, half as many chromosomes as the parent cell. Meiosis occurs only in the gonads (ovaries or testes). In each generation of humans, meiosis reduces the chromosome number from 46 (two sets of chromosomes) to 23 (one set). Fertilisation fuses two gametes together and returns the chromosome number to 46, and mitosis conserves that number in every somatic cell nucleus of the new individual.

10.1.1.3.2 Phases of the Cell Cycle

Mitosis is just one part of the cell cycle (Figure 10.1.1.40). In fact, the mitotic (M) phase, which includes both mitosis and cytokinesis, is usually the shortest part of the cell cycle. Mitotic cell division alternates with a much longer stage called **interphase**, which often accounts for about 90% of the cycle. It is during interphase that the cell grows and copies its chromosomes in preparation for cell division. Interphase can be divided into subphases: the G_1 phase ('first gap'), the S phase ('synthesis'), and the G_2 phase ('second gap'). During all three subphases, the cell grows by producing proteins and cytoplasmic organelles such as mitochondria and endoplasmic reticulum. Chromosomes, however, are duplicated only during the S phase. Thus, a cell grows for a time (G_1), during which it 'decides' whether or not it is going to replicate its DNA or to exit the cell cycle and enter a quiescent state (G_0). If continuing in the cell cycle, it continues to grow as it copies its chromosomes (S), grows more as it completes preparations for cell division (G_2), and then divides (M)—the cycle time is divided in a manner roughly proportional to that illustrated. The daughter cells may then repeat the cycle.

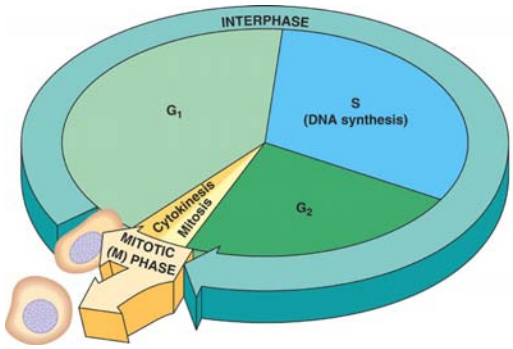

Figure 10.1.1.40 The Cell Cycle

The time required for completion of a eukaryotic cell cycle varies enormously from cell to cell. Embryonic cells that do not need to grow between divisions can complete a cell cycle in as little as eight minutes, whereas cycling times of 10–24 hours are typical of the most rapidly dividing somatic cells. Many somatic cells divide much less frequently—liver cells divide about once a year, and mature neurons never divide. Such cells may be thought of as temporarily or permanently withdrawing from the cell cycle. Most cells of the human body are actually in the G_0 phase. Nonetheless, some cells can be 'called back' from the G_0 phase to the cell cycle by certain external cues, such as growth factors released when the body is injured.

The M phase, mitosis, is by far the most complex phase in the cell cycle. By convention, it is broken down into five stages:

1 Prophase
2 Prometaphase
3 Metaphase
4 Anaphase
5 Telophase

Overlapping with the latter stages of mitosis, cytokinesis completes the mitotic phase (Figure 10.1.1.41).

Many of the events of mitosis depend on the **mitotic spindle**, which begins to form in the cytoplasm during prophase. This structure consists of fibres made of microtubules and associated proteins. While the mitotic spindle assembles, the other microtubules of the cytoskeleton partially disassemble, probably providing the material used to construct the spindle. The assembly of spindle microtubules starts at the centrosome , a nonmembranous organelle that functions throughout the cell cycle to organize the cell's microtubules.

During interphase, the single centrosome replicates, forming two centrosomes, which remain together near the nucleus. The two centrosomes move apart from each other during prophase and prometaphase of mitosis, as spindle microtubules grow out from them. By the end of microtubules grow out from them. By the end of prometaphase, the two centrosomes, one at each pole of the spindle, are at opposite ends of the cell. An **aster**, a radial array of short microtubules, extends from each centrosome.

Each of the two sister chromatids of a chromosome has a **kinetochore**, a structure of proteins associated with specific sections of chromosomal DNA at the centromere. The chromosome's two kinetochores face in opposite directions. During prometaphase, some of the spindle microtubules attach to the kinetochores—called **kinetochore microtubules**. A chromosome's kinetochore is ultimately 'captured' by microtubules and at metaphase, the centromeres of all the duplicated chromosomes have settled on a plane midway between the spindle's two poles.

Meanwhile, microtubules that do not attach to kinetochores have been growing, and by metaphase they overlap and interact with other nonkinetochore microtubules from the opposite pole of the spindle. By metaphase, the microtubules of the asters have also grown and are in contact with the plasma membrane. The spindle is now complete.

Anaphase commences suddenly when proteins holding together the sister chromatids of each chromosome are deactivated. The chromatids separate, into individual chromosomes, and move toward opposite ends of the cell.

At the end of anaphase, duplicate groups of chromosomes have arrived at opposite ends of the elongated parent cell and nuclei re-form during telophase. Cytokinesis generally begins during these later stages of mitosis, and the spindle eventually disassembles.

In animal cells, cytokinesis occurs by a process known as cleavage . The first sign of cleavage is the appearance of a cleavage furrow , a shallow groove in the cell surface near the old metaphase plate.

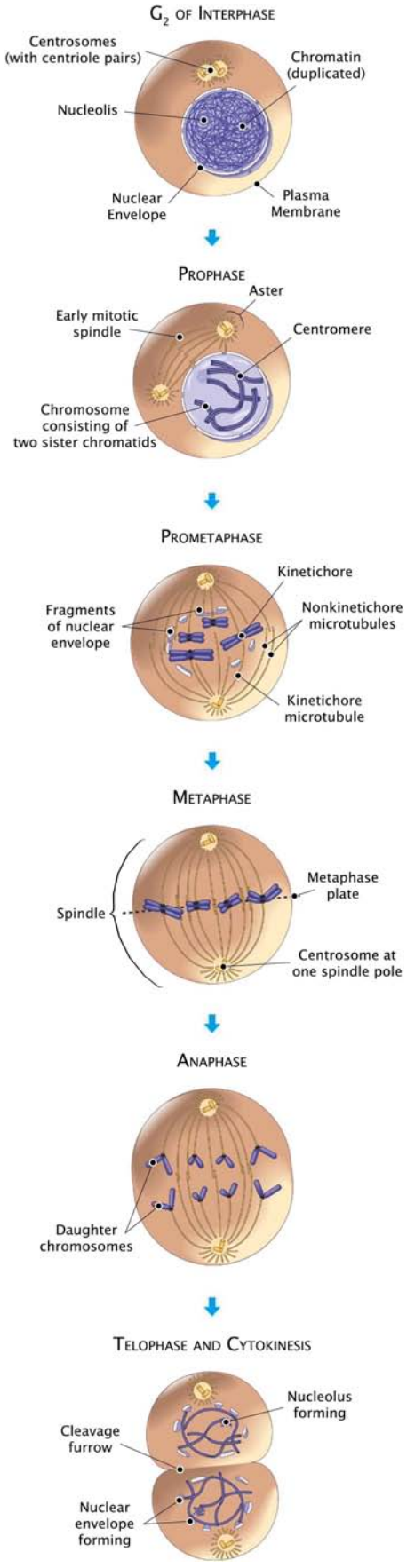

Figure 10.1.1.41 Stages of Mitosis

Cytokinesis in plant cells, which have cell walls, is markedly different. There is no cleavage furrow. Instead, during telophase, vesicles derived from the Golgi apparatus move along microtubules to the middle of the cell, where they coalesce, producing a cell plate. Cell wall materials carried in the vesicles collect in the cell plate as it grows. The cell plate enlarges until its surrounding membrane fuses with the plasma membrane along the perimeter of the cell.

10.1.1.3.3 The Cell Cycle Control System

The timing and rate of cell division in different parts of a plant or animal are crucial to normal growth, development, and maintenance. The frequency of cell division varies with the type of cell. For example, human skin cells divide frequently throughout life, whereas liver cells maintain the ability to divide but keep it in reserve until an appropriate need arises—say, to repair a wound. Some of the most specialised cells, such as mature, fully formed nerve cells and muscle cells, do not divide at all in a mature human. These cell cycle differences result from regulation at the molecular level. The mechanisms of this regulation are of intense interest, not only for understanding the life cycles of normal cells but also for understanding how cancer cells manage to escape the usual controls.

Loss of Cell Cycle Controls in Cancer Cells

Cancer cells do not respond normally to the body's control mechanisms. They divide excessively and invade other tissues. There are, however, other important differences between normal cells and cancer cells that reflect derangements of the cell cycle. If and when they stop dividing, cancer cells do so at random points in the cycle, rather than at the normal checkpoints. Moreover, in culture, cancer cells can go on dividing indefinitely if they are given a continual supply of nutrients—they are said to be 'immortal'. By contrast, nearly all normal mammalian cells growing in culture divide only about 20 to 50 times before they stop dividing, age, and die.

The abnormal behaviour of cancer cells can be catastrophic when it occurs in the body. The problem begins when a single cell in a tissue undergoes **transformation**, the process that converts a normal cell to a cancer cell. The body's immune system normally recognizes a transformed cell as an insurgent and destroys it. However, if the cell evades destruction, it may proliferate and form a **tumour**, a mass of abnormal cells within otherwise normal tissue. If the abnormal cells remain at the original site, the lump is called a **benign** tumour . Most benign tumours do not cause serious problems and can be completely removed by surgery. In contrast, a **malignant** tumour becomes invasive enough to impair the functions of one or more organs.

Tumour cells often have unusual numbers of chromosomes. Their metabolism may be disabled, and they may cease to function in any constructive way. Also, owing to abnormal changes on the cells' surfaces, they lose or destroy their attachments to neighbouring cells and the extracellular matrix and are thus able to spread into nearby tissues. Cancer cells may also secrete signal molecules that cause blood vessels to grow toward the tumour. Thereafter, cells may separate from the original tumour, enter blood vessels and lymph vessels, and travel to other parts of the body. There, they may proliferate and form a new tumour. This spread of cancer cells to locations distant from their original site is called **metastasis**.

A tumour that appears to be localised may be treated with high-energy radiation, which damages DNA in cancer cells much more than it does in normal cells, apparently because cancer cells have lost the ability to repair such damage. To treat known or suspected metastatic tumours, chemotherapy is used, in which drugs that are toxic to actively dividing cells are administered through the circulatory system.

Chemotherapeutic drugs interfere with specific steps in the cell cycle. The drug Taxol, for example, freezes the mitotic spindle by preventing microtubule depolymerisation, which stops actively dividing cells from proceeding past metaphase. The side effects of chemotherapy are due to the drugs' effects on normal cells. Nausea, for example, results from chemotherapy's effects on intestinal cells, hair loss from effects on hair follicle cells, and susceptibility to infection from effects on immune system cells.

10.1.1.3.4 Growth and Differentiation

Although all cells in a multicellular organism contain identical copies of the genetic material for that organism, the same genome, the cells in different parts of the organism (*e.g.* brain, muscle, kidney) are often quite distinct in character. Each specialised cell type in an organism expresses a subset of all the genes that constitute the genome of that species. Cellular **differentiation** is the process by which a less specialised cell becomes a more specialised cell type. Differentiation occurs numerous times during the development of a multicellular organism as the organism changes from a single zygote to a complex system of tissues and cell types.

A cell that is able to differentiate into different cell types is known as **pluripotent**. These cells are called **stem cells** in animals and **meristematic cells** in higher plants. A cell that is able to differentiate into all cell types is known as **totipotent**. In mammals, only the zygote and early embryonic cells are totipotent. In cytopathology (the study and diagnosis of diseases at a cellular level) the level of cellular differentiation is used as a measure of cancer progression. The 'Grade' of a tumour is a measure of how differentiated its cells have become.

Nonetheless, differentiation is a common process in adults as well—adult stem cells divide and create fully-differentiated daughter cells during tissue repair and during normal cell turnover.

Mammalian cell types

Three basic categories of cells make up the mammalian body:

- Germ cells,
- Somatic cells, and
- Stem cells.

Each of the approximately 100,000,000,000,000 (10^{14}) cells in an adult human has its own copy or copies of the genome except certain cell types, such as red blood cells, that lack nuclei in their fully differentiated state. Most cells are **diploid**—they have two copies of each chromosome. Such cells, called **somatic cells**, make up most of the human body, such as skin and muscle cells.

Germ line cells are any line of cells that give rise to gametes—eggs and sperm. Gametes are **haploid**, having only one copy of each chromosome.

Stem cells are cells that have the ability to divide for indefinite periods and to give rise to specialised cells. They are best described in the context of normal human development, which begins when a sperm fertilises an egg and creates a single cell, a zygote, with the potential to form an entire organism. In the first hours after fertilisation, this cell divides into identical cells. In humans, approximately four days after fertilisation and after several cycles of cell division, these cells begin to specialise, forming a hollow sphere of cells, called a **blastocyst**. The blastocyst has an outer layer of cells, and inside this hollow sphere, there is a cluster of cells called the **inner cell mass**. The cells of the inner cell mass, known as pluripotent stem cells, undergo further specialisation into multipotent progenitor cells that then give rise to functional cells in various parts of the body.

Three of the early steps in the development of a mammal are illustrated in the centre of Figure 10.1.1.42. Above and below that are some of the fully-differentiated cell types that will eventually form in the adult.

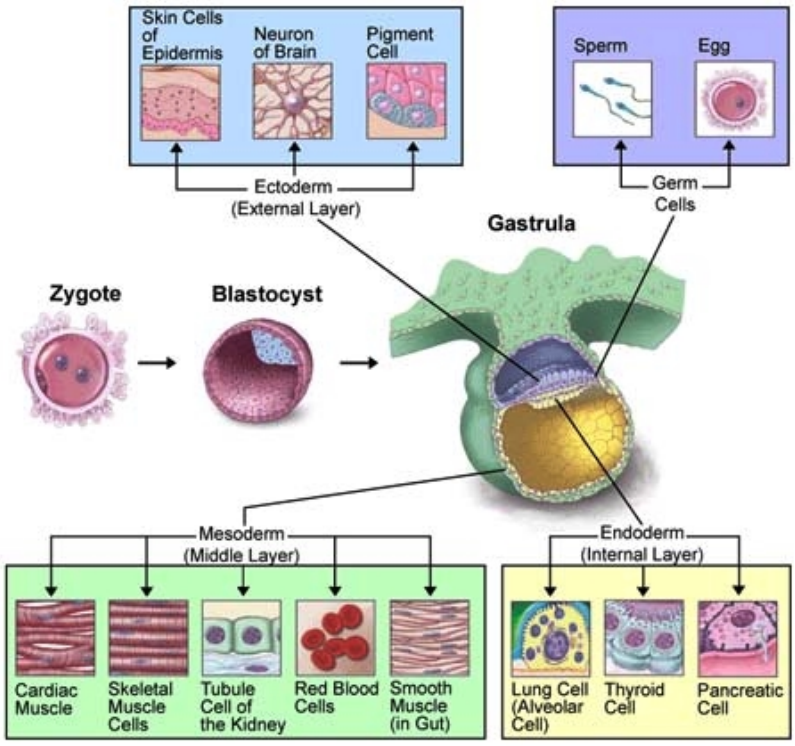

Figure 10.1.1.42 Cell Differentiation

Dedifferentiation is a cellular process, often seen in lower life forms such as worms and amphibians, in which a partially or terminally differentiated cell reverts to an earlier developmental stage, usually as part of a regenerative process. Dedifferentiation also occurs in plants. Some scientists believe that dedifferentiation is an aberration of the normal development cycle that results in cancer, whereas others believe it to be a natural part of the immune response lost by humans at some point in their evolutionary path.

10.1.1.4 Organism Classification

Taxonomy (from the Greek *taxis*, meaning *order*, and *nomos*, meaning *law* or *science*) is the practice and science of classification. Mathematically, a hierarchical taxonomy is a tree structure of classifications for a given set of objects.

Charles Darwin (1809–1882) believed that phylogeny, the ascent of all species through time, was expressible as a metaphor he termed the Tree of Life or an evolutionary tree (Figure 10.1.1.43). The modern development of this idea is a classification scheme called the Phylogenetic Tree or cladogram. Cladistics (from the Greek *klados*, meaning *branch*) is the hierarchical classification of species based on evolutionary ancestry. It is distinguished from other taxonomic systems by its heavy emphasis on quantitative analysis using methodologies such as DNA and RNA sequencing.

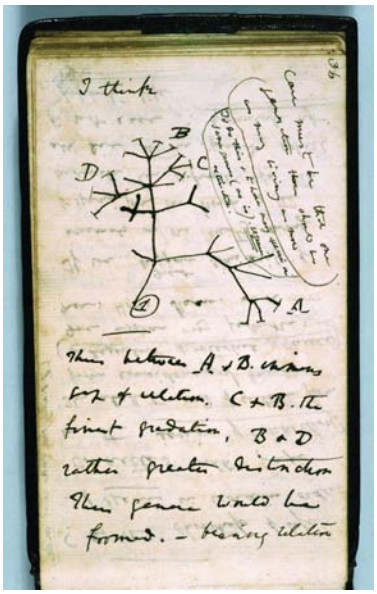

Figure 10.1.1.43
A reproduction of the first-known sketch by Charles Darwin of an evolutionary tree describing relationships among groups of organisms.

10.1.1.4.1 Previous Taxonomic Systems

In the early days of biology (up until ~40 years ago!), all organisms were classified as either plants or animals, because we see a macroscopic, terrestrial realm and rarely notice those organisms that do not fit neatly into a plant-animal dichotomy. The two-**Kingdom** scheme also had a long tradition in formal taxonomy—Swedish botanist Carl Linnaeus (1707–1778), the father of modern taxonomy, had divided all known forms of life between the plant and animal kingdoms in the 18th Century.

Even with the discovery of the diverse microbial world, the two-kingdom system persisted. Taxonomists placed bacteria in the plant kingdom, citing the rigid cell walls of bacteria as justification. Eukaryotic unicellular organisms with chloroplasts were also considered plants. Fungi, too, were classified as plants, partly because most fungi, like most plants, are unable to move about, even though fungi are not photosynthetic and have little in common structurally with plants. In the two-kingdom system, unicellular organisms that move and ingest food—protozoans—were called animals. Microbes such as Euglena that move and are photosynthetic were claimed by both botanists and zoologists and showed up in both kingdoms.

Taxonomic schemes with more than two kingdoms did not become popular with the majority of biologists until 1969, when American ecologist Robert H. Whittaker (1920–1980) argued effectively for a system consisting of five kingdoms: Monera, Protista, Plantae, Fungi, and Animalia (Figure 10.1.1.44). Whittaker's system recognized the two fundamentally different types of cells, prokaryoticand eukaryotic, and set the prokaryotes apart from all eukaryotes by placing them in their own kingdom, **Monera**.

Whittaker distinguished three kingdoms of multicellular eukaryotes—**Plantae**, **Fungi**, and **Animalia**—partly on the criterion of nutrition. Plants are autotrophs (from the Greek *autos*, self, and *trophe*, nutrition), making their food by photosynthesis. Fungi and animals are heterotrophs (from the Greek *heterone*, other, and *trophe*, nutrition),

deriving their nutrition from autotrophes or other heterotrophes. Most fungi are decomposers that invade their food source, secreting digestive enzymes and absorbing the small organic molecules produced by digestion. Most animals ingest (eat) food and digest it within a specialised body cavity.

The kingdom **Protista** was not as clearly defined in Whittaker's five-kingdom system. Protista consisted of all eukaryotes that did not fit the definitions of plants, fungi, or animals. Most protists are unicellular, but the boundaries of Protista were expanded to include some multicellular organisms, such as seaweeds, because of their relationships to certain unicellular protists. With such refinements, the five-kingdom system prevailed in biology for more than 20 years.

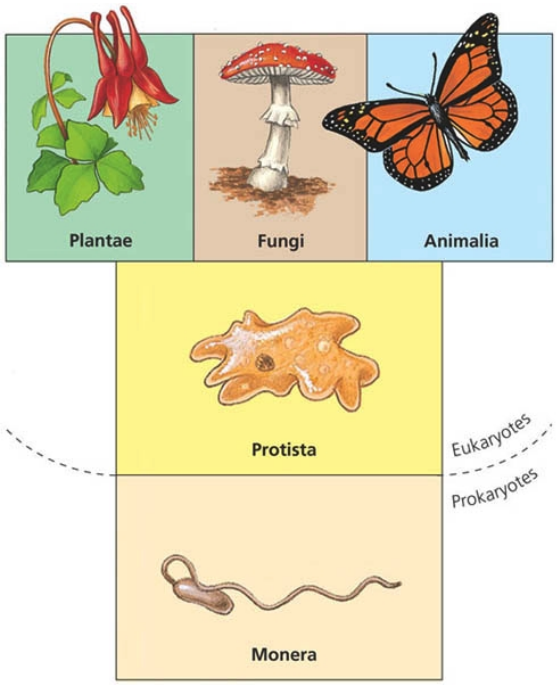

Figure 10.1.1.44
Whittaker's five-kingdom system

10.1.1.4.2 The Three Domains of Life

In 1977, Carl Woese (1928-) developed a new, evolutionary model of classification based on differences in the sequences of nucleotides in a cell's ribosomal RNA (rRNA), as well as a cell's membrane structure. Comparing rRNA structure is especially useful because rRNA molecules throughout nature carry out the same function and, as a consequence, their structure changes very little over time. Accordingly, similarities and dissimilarities in rRNA nucleotide sequence are a good indication of how related or unrelated different cells and organisms are.

This system proposed that a common ancestor cell gave rise to three different cell types, each representing a **Domain**. The three Domains are the **Archaea** (archaebacteria), the **Bacteria** (eubacteria), and the **Eukaryota** (eukaryotes) (Figure 10.1.1.45). The Eukarya are then divided into 4 kingdoms: Protists, Fungi, Anamalia, and Plantae.

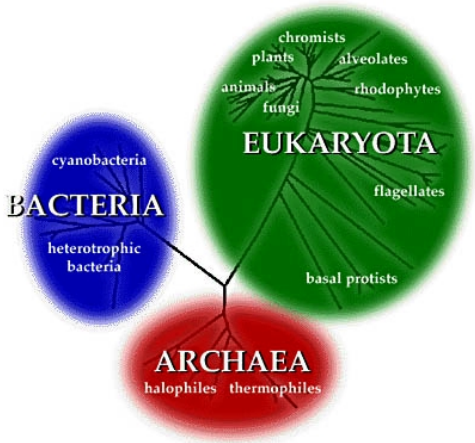

Figure 10.1.1.45 Three Domains

The first two domains, Bacteria and Archaea , both consist of prokaryotes (organisms with prokaryotic cells). Most prokaryotes are unicellular and microscopic. In the five-kingdom system, Bacteria and Archaea were combined in a single kingdom, Monera, because they shared the prokaryotic form of cell structure. But evidence now supports the view that Bacteria and Archaea represent two very distinct branches of prokaryotic life. There is also molecular evidence that Archaea are at least as closely related to eukaryotic organisms as they are to Bacteria.

All the eukaryotes (organisms with eukaryotic cells) are now grouped into the various kingdoms of domain Eukaryota.

In the era of the five-kingdom scheme, most of the single-celled eukaryotes, including the microorganisms known as protozoans, were placed in a single kingdom, the kingdom Protista. Many biologists extended the boundaries of the kingdom Protista to include some multicellular forms, such as seaweeds, that are closely related to certain unicellular protists. The recent taxonomic trend has been to split the protists into several kingdoms. In addition to these protistan kingdoms, the domain Eukarya includes three kingdoms of multicellular eukaryotes: the kingdoms Plantae, Fungi, and Animalia. These three kingdoms are distinguished partly by their modes of nutrition. Plants produce their own sugars and other foods by photosynthesis. Fungi are mostly decomposers that absorb nutrients by breaking down dead organisms and organic wastes, such as leaf litter and animal faeces. Animals obtain food by ingestion, which is the eating and digesting of other organisms. It is, of course, the kingdom to which we belong.

10.1.1.4.3 Reconstructing the Tree of Life: A Work in Progress

Taxonomic systems are human constructs—attempts to order the diversity of life in a scheme that is useful and that reflects phylogenetic (evolutionary) relationships. During the past three decades, systematists have applied cladistic analysis to taxonomy, including the construction of cladograms based on molecular data. We noted above that these data have led biologists to adopt a three-domain system . The domains Bacteria, Archaea, and Eukarya are essentially superkingdoms, a taxonomic level higher than the kingdom level. Bacteria differ from archaea in many key structural, biochemical, and physiological characteristics. These differences justify placing bacteria and archaea in separate domains. Note that the three-domain system makes the kingdom Monera obsolete because it would have members in two different domains. In fact, many microbiologists now divide each of the two prokaryotic domains into multiple kingdoms based on phylogenetic analysis of molecular data (Figure 10.1.1.46).

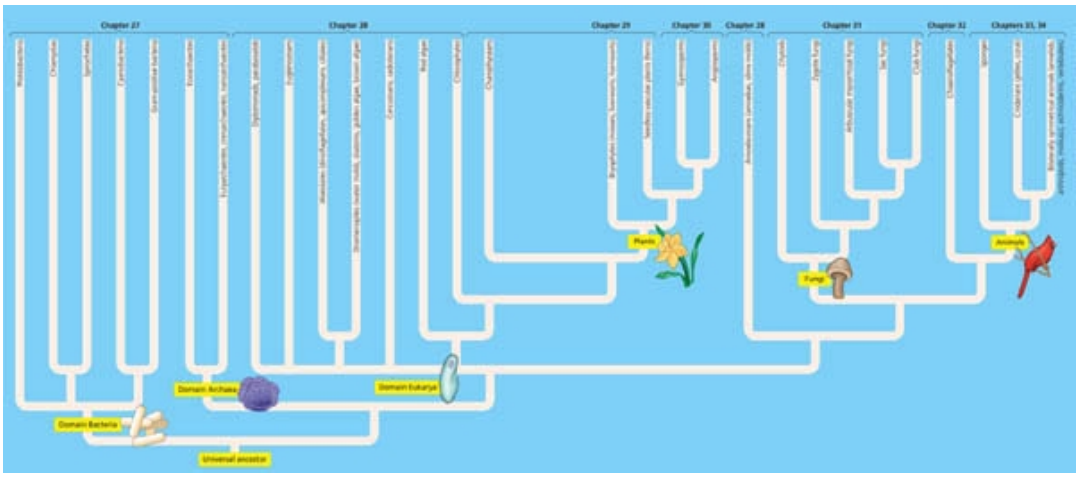

Figure 10.1.1.46 One current view of biological diversity. This tree summarises the diversification of life over evolutionary time.

Another major challenge to the five-kingdom system is being mounted by systematists who are sorting out the phylogeny of the diverse eukaryotes formerly grouped in the kingdom Protista. Biologists who study these organisms now split most of them into five or more newly designated kingdoms, which have a common ancestor near the base of the eukaryotic branch of the tree. Debate continues over whether some single-celled protists should be transferred to Plantae, Fungi, or Animalia.

Much more research is needed before we can arrive at a consensus about how the three domains of life are related and about how many kingdoms each domain should include. As we explore newly discovered microbial communities, such as those that live deep underground, and as we learn how to culture more of the organisms in those communities, we will no doubt discover new groups that will lead to further taxonomic remodelling. Keep in mind that phylogenetic trees and taxonomic groupings are hypotheses that fit the best available data. It is the continuing scrutiny of testable hypotheses that validates evolutionary biology as a natural science.

References

Biology (7th Ed., Australian Version), Campbell, N. A., Reece, J. B. and Myers, N.. (Pearson Education Australia, 2006) [ISBN 1-74103-386-1] (Large portions of the text in this Section, and all illustrations not otherwise credited, are extracts from this book.)

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