Composition and Principles of Organization

The unity and diversity of organisms become apparent even at the cellular level. The smallest organisms consist of single cells and are microscopic. Larger, multicellular organisms contain many different types of cells, which vary in size, shape, and specialized function. Despite these obvious differences, all cells of the simplest and most complex organisms share certain fundamental properties, which can be seen at the biochemical level.

Structural and Functional Units of All Living Organisms

Cells of all kinds share certain structural features (Fig. 1). The plasma membrane defines the periphery of the cell, separating its contents from the surroundings. It is composed of lipid and protein molecules that form a thin, tough, pliable, hydrophobic barrier around the cell. The membrane is a barrier to the free passage of inorganic ions and most other charged or polar compounds. Transport proteins in the plasma membrane allow the passage of certain ions and molecules; receptor proteins transmit signals into the cell; and membrane enzymes participate in some reaction pathways. Because the individual lipids and proteins of the plasma membrane are not covalently linked, the entire structure is remarkably flexible, allowing changes in the shape and size of the cell. As a cell grows, newly made lipid and protein molecules are inserted into its plasma membrane; cell division produces two cells, each with its own membrane. This growth and cell division (fission) occurs without loss of membrane integrity.

The internal volume enclosed by the plasma membrane, the cytoplasm (Fig. 1), is composed of an aqueous solution, the cytosol, and a variety of suspended particles with specific functions. These particulate components (membranous organelles such as mitochondria and chloroplasts; supramolecular structures such as ribosomes and proteasomes, the sites of protein synthesis and degradation) sediment when cytoplasm is centrifuged at 150,000*g* (g is the gravitational force of Earth). What remains as the supernatant fluid is the cytosol, a highly concentrated solution containing enzymes and the

RNA molecules that encode them; the components (amino acids and nucleotides) from which these macromolecules are assembled; hundreds of small organic molecules called metabolites, intermediates in biosynthetic and degradative pathways; coenzymes, compounds essential to many enzyme-catalyzed reactions; and inorganic ions.

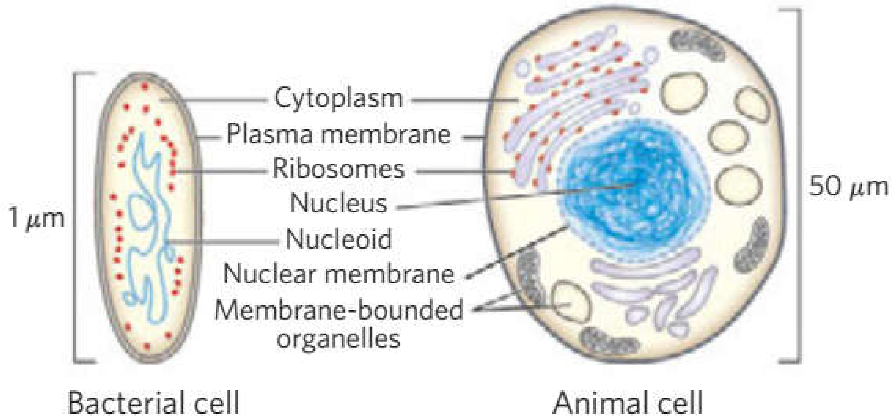

Fig 1. The universal features of living cells.

All cells have, for at least some part of their life, either a nucleoid or a nucleus, in which the genome—the complete set of genes, composed of DNA—is replicated and stored, with its associated proteins. The nucleoid, in bacteria and archaea, is not separated from the cytoplasm by a membrane; the nucleus, in eukaryotes, is enclosed within a double membrane, the nuclear envelope. Cells with nuclear envelopes make up the large domain Eukarya (Greek *eu*, "***true***" and *karyon*, "***nucleus***"). Microorganisms without nuclear membranes, formerly grouped together as prokaryotes (Greek *pro*, "***before***"), are now recognized as comprising two very distinct groups: the domains Bacteria and Archaea.

Cellular Dimensions

Most cells are microscopic, invisible to the unaided eye. Animal and plant cells are typically 5 to 100 μm in diameter, and many unicellular microorganisms are only 1 to 2 μm long (see the inside back cover for information on units and their abbreviations). What limits the dimensions of a cell? The lower limit is probably set by the minimum number of each type of biomolecule required by the cell. The smallest cells, certain bacteria known as mycoplasmas, are 300 nm in diameter and have a volume of about 10^{-14} mL. A single bacterial ribosome is about 20 nm in its longest dimension, so a few ribosomes take up a substantial fraction of the volume in a mycoplasmal cell. The upper limit of cell size is probably set by the rate of diffusion of solute molecules in aqueous systems.

For example, a bacterial cell that depends on oxygen consuming reactions for energy extraction must obtain molecular oxygen by diffusion from the surrounding medium through its plasma membrane. The cell is so small, and the ratio of its surface area to its volume is so large, that every part of its cytoplasm is easily reached by O_2 diffusing into the cell. With increasing cell size, however, surface-to-volume ratio decreases, until metabolism consumes O_2 faster than diffusion can supply it. Metabolism that requires O_2 thus becomes impossible as cell size increases beyond a certain point, placing a theoretical upper limit on the size of cells. Oxygen is only one of many low molecular weight species that must diffuse from outside the cell to various regions of its interior, and the same surface-to-volume argument applies to each of them as well.

Domains of Life

All living organisms fall into one of three large groups (domains) that define three branches of the evolutionary tree of life originating from a common progenitor (Fig. 2). Two large groups of single-celled microorganisms can be distinguished on genetic and biochemical grounds: Bacteria and Archaea. Bacteria inhabit soils, surface waters, and the tissues of other living or decaying organisms. Many of the Archaea, recognized as a distinct domain by ***Carl Woese*** in the 1980s, inhabit extreme environments—salt lakes, hot springs, highly acidic bogs, and the ocean depths. The available evidence suggests that the Archaea and Bacteria diverged early in evolution. All eukaryotic organisms, which make up the third domain, Eukarya, evolved from the same branch that gave rise to the Archaea; eukaryotes are therefore more closely related to archaea than to bacteria.

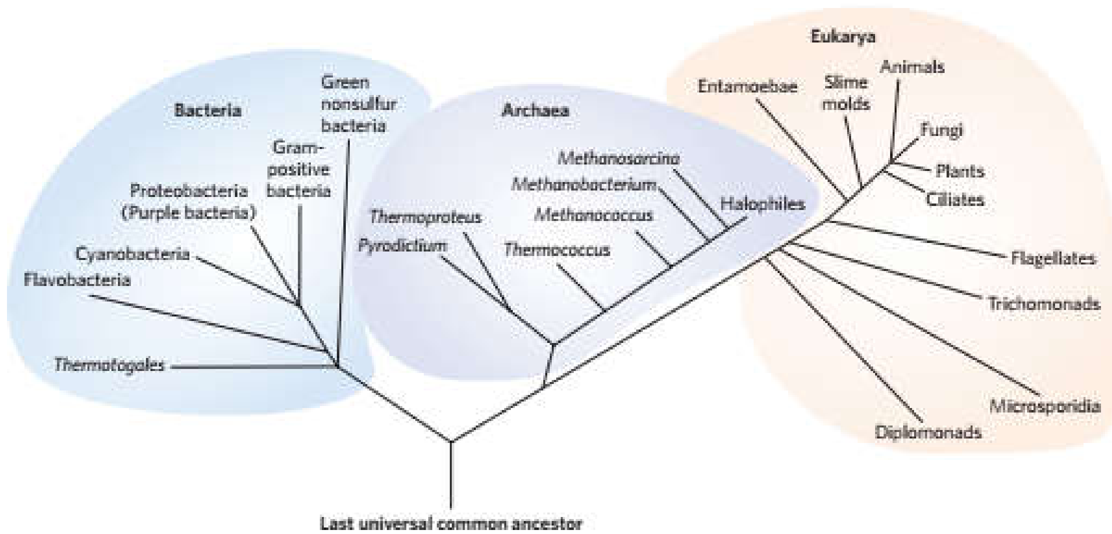

Fig 2. Phylogeny of the three domains of life.

Within the domains of Archaea and Bacteria are subgroups distinguished by their habitats. In aerobic habitats with a plentiful supply of oxygen, some resident organisms derive energy from the transfer of electrons from fuel molecules to oxygen within the cell. Other environments are anaerobic, virtually devoid of oxygen, and microorganisms adapted to these environments obtain energy by transferring electrons to nitrate (forming N_2), sulfate (forming H_2S), or CO_2 (forming CH_4). Many organisms that have evolved in anaerobic environments are obligate anaerobes: they die when exposed to oxygen. Others are facultative anaerobes, able to live with or without oxygen.

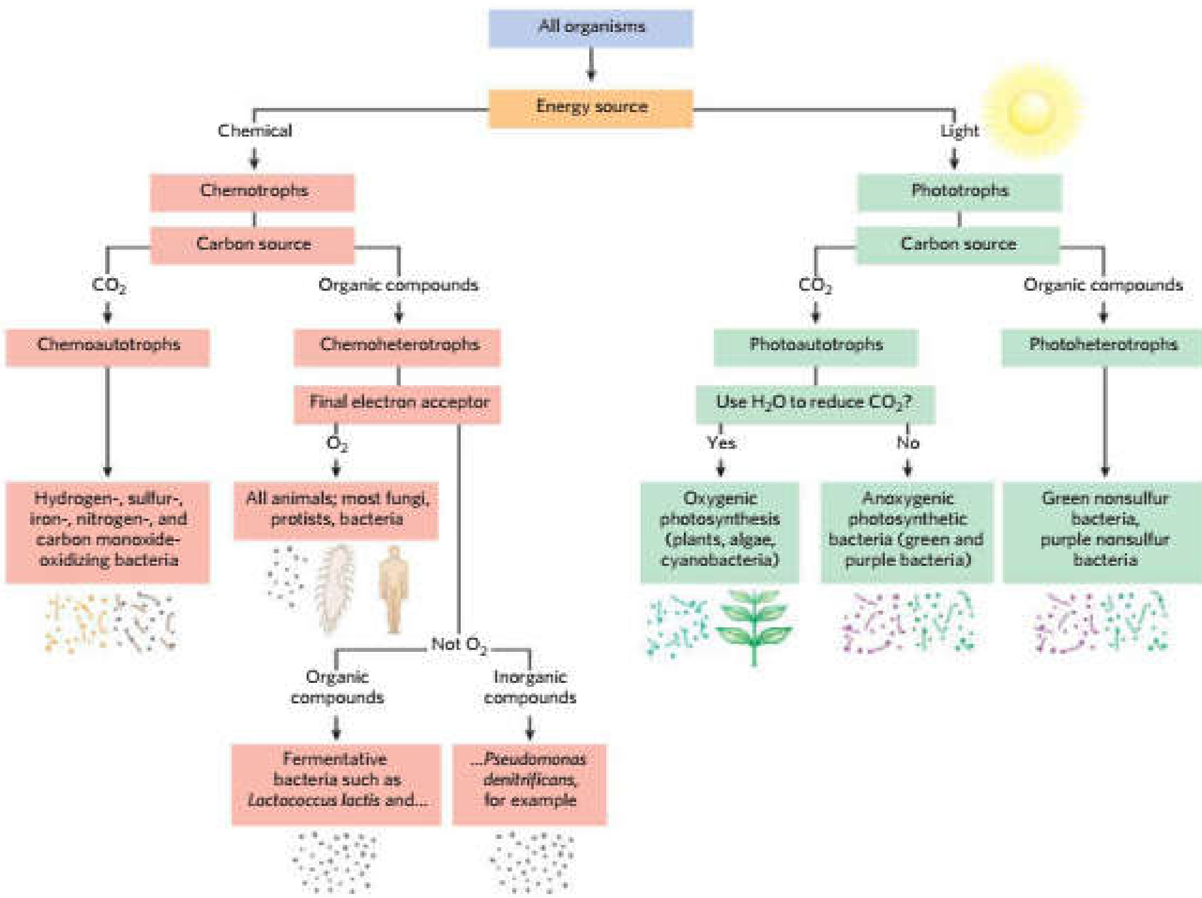

Fig 3. All organisms can be classified according to their source of energy (sunlight or oxidizable chemical compounds) and their source of carbon for the synthesis of cellular material.

Biosynthetic Precursors

We can classify organisms according to how they obtain the energy and carbon they need for synthesizing cellular material (as summarized in Fig. 3). There are two broad categories based on energy sources;

- ***Phototrophs:*** (Greek *trophe* "nourishment") trap and use sunlight &
- ***Chemotrophs:*** derive their energy from oxidation of a chemical fuel

Some chemotrophs oxidize inorganic fuels—HS^- to S^0 (elemental sulfur). For example, Phototrophs and chemotrophs may be further divided into those that can synthesize all of their biomolecules directly from CO_2 (autotrophs) and those that require some preformed organic nutrients made by other organisms (heterotrophs). We can describe an organism's mode of nutrition by combining these terms. ***For example,*** cyanobacteria are photoautotrophs; humans are chemoheterotrophs. Even finer distinctions can be made, and many organisms can obtain energy and carbon from more than one source under different environmental or developmental conditions.

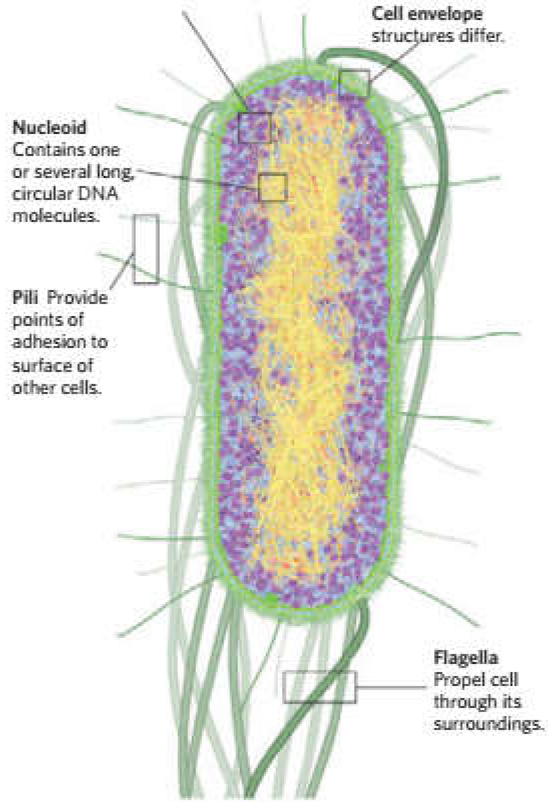

Fig 4a. Some common structural features of bacterial and archaeal cells. This correct-scale drawing of *E. coli* serves to illustrate some common features.

Common Features of Bacterial and Archaeal Cells

The best-studied bacterium, *Escherichia coli*, is a usually harmless inhabitant of the human intestinal tract. The *E. coli* cell (Fig. 4a) is an ovoid about 2 µm long and a little less than 1 mm in diameter, but other bacteria may be spherical or rod-shaped. It has a protective outer membrane and an inner plasma membrane that encloses the cytoplasm and the nucleoid. Between the inner and outer membranes is a thin but strong layer of a high molecular weight polymer (peptidoglycan) that gives the cell its shape and rigidity. The plasma membrane and the layers outside it constitute the cell envelope. The plasma membranes of bacteria consist of a thin bilayer of lipid molecules penetrated by proteins. Archaeal plasma membranes have a similar architecture, but the lipids can be strikingly different from those of bacteria.

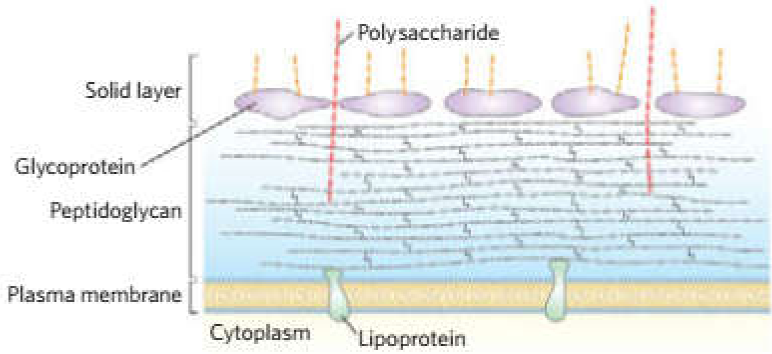

Fig 1–6. (b) The cell envelope of gram-positive bacteria is a single membrane with a thick, rigid layer of peptidoglycan on its outside surface.

Bacteria and archaea have group-specific specializations of their cell envelopes (Fig. 4b-d). Some bacteria, called gram-positive because they are colored by ***Gram's stain*** (introduced by ***Hans Peter Gram*** in 1882), have a thick layer of peptidoglycan outside their plasma membrane but lack an outer membrane. Gram-negative bacteria have an outer membrane composed of a lipid bilayer into which are inserted complex lipopolysaccharides and proteins called porins that provide transmembrane channels for low molecular weight compounds and ions to diffuse across this outer membrane. The structures outside the plasma membrane of archaea differ from organism to organism, but they, too, have a layer of peptidoglycan or protein that confers rigidity on their cell envelopes. The cytoplasm of *E. coli* contains about 15,000 ribosomes, various numbers (10 to thousands) of copies of each of 1,000 or so different enzymes, perhaps 1,000 organic compounds of molecular weight less than 1,000 (metabolites and cofactors), and a variety of inorganic ions. The nucleoid contains a single, circular molecule of DNA, and the cytoplasm (like that of most bacteria) contains one or more smaller, circular segments of DNA called plasmids. In nature, some plasmids confer resistance to toxins and antibiotics in the environment. In the laboratory, these DNA segments are especially amenable to experimental manipulation and are powerful tools for genetic engineering.

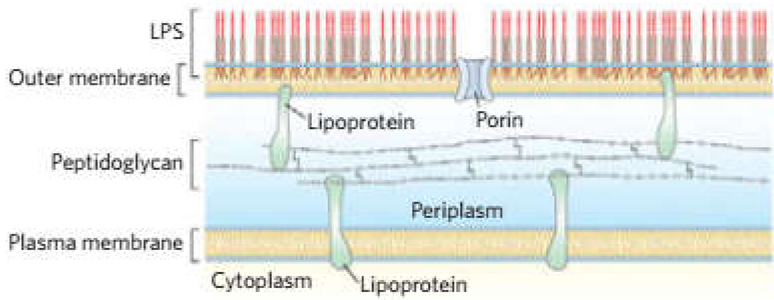

Fig 4c. *E. coli* is gram-negative and has a double membrane. Its outer membrane has a lipopolysaccharide (LPS) on the outer surface and phospholipids on the inner surface.

Other species of bacteria, as well as archaea, contain a similar collection of biomolecules, but each species has physical and metabolic specializations related to its environmental niche and nutritional sources. Cyanobacteria, for example, have internal membranes specialized to trap energy from light. Many archaea live in extreme environments and have biochemical adaptations to survive in extremes of temperature, pressure, or salt concentration. Differences in ribosomal structure gave the first hints that Bacteria and Archaea constituted separate domains. Most bacteria (including *E. coli*) exist as individual cells, but often associate in biofilms or mats, in which large numbers of cells adhere to each other and to some solid substrate beneath or at an aqueous surface. Cells of some bacterial species (the *myxobacteria*, for example) show simple social behavior, forming many-celled aggregates in response to signals between neighboring cells.

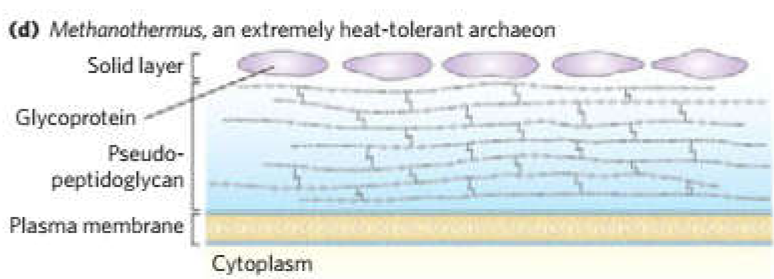

Fig 4d. Archaeal membranes vary in structure and composition, but all have a single membrane surrounded by an outer layer that includes either a peptidoglycan like structure, a porous protein shell (solid layer), or both.

Eukaryotic Cells Membranous Organelles

Typical eukaryotic cells are much larger than bacteria—commonly 5 to 100 μm in diameter, with cell volumes a thousand to a million times larger than those of bacteria. The distinguishing characteristics of eukaryotes are the nucleus and a variety of membrane-enclosed organelles with specific functions.

These organelles include mitochondria, the site of most of the energy extracting reactions of the cell; the endoplasmic reticulum and ***Golgi complexes****, which play central roles in the synthesis and processing of lipids and membrane proteins*; ***peroxisomes***, in which *very long-chain fatty acids are oxidized*; and ***lysosomes***, filled with *digestive enzymes to degrade unneeded cellular debris.* In addition to these, plant cells also contain ***vacuoles*** (which *store large quantities of organic acids*) and ***chloroplasts*** (*in which sunlight drives the synthesis of ATP in the process of photosynthesis*). Also present in the cytoplasm of many cells are granules or droplets containing stored nutrients such as starch and fat.

In a major advance in biochemistry, Albert Claude, Christian de Duve, and George Palade developed methods for separating organelles from the cytosol and from each other—an essential step in investigating their structures and functions. In a typical cell fractionation, cells or tissues in solution are gently disrupted by physical shear. This treatment ruptures the plasma membrane but leaves most of the organelles intact. The homogenate is then centrifuged; organelles such as nuclei, mitochondria, and lysosomes differ in size and therefore sediment at different rates. These methods were used to establish, for example, that lysosomes contain degradative enzymes, mitochondria contain oxidative enzymes, and chloroplasts contain photosynthetic pigments. The isolation of an organelle enriched in a certain enzyme is often the first step in the purification of that enzyme.