**Eukaryotic Cell Structure and Function:**

The science or study of cells is sometimes called **cytology**, and deals with cell structure, function and chemistry. Like other branches of biology, cytology has undergone extensive change over time, and many courses dealing with the topic are currently entitled cell and molecular biology (or something similar).

The term **cell** (cella = a small room or hollow) was first used by **Robert Hooke** (1665) with reference to an empty space or chamber. Hooke (sometimes called the father of cytology) was observing dead cells from the bark of cork oak trees, and saw only cell walls (dead layers found outside certain types of cells) rather than living protoplasm. We now know cells are living, dynamic entities, and not empty chambers. Their internal structures are variable, but typically quite complex.

According to the **cell theory**, as articulated by Matthias Schleiden and Theodor Schwann (1839), the cell is the basic unit of structure and function in all, living organisms. When first written, the cell theory indicated that living cells could arise spontaneously through **abiogenesis**, but experiments conducted by **Louis Pasteur** and others invalidated this concept. Instead, it is now recognized that current cells arise from preexisting cells, and that they carry hereditary information (DNA) that is passed from one generation to the next through **biogenesis**.

Cells are currently divided into two general categories, **Prokaryotic** and **Eukaryotic**, on the basis of their nuclear content. The term **karyon** (karyon = nucleus) appears in both names, and is preceded by either “pro”, meaning before or “eu” meaning well or truly. Fossil and molecular evidence indicates that prokaryotic cells evolved first, and that interactions between two prokaryotic cell types (bacteria and archaea) gave rise to the larger, well-nucleated eukaryotic cells. Some of the distinguishing features of prokaryotic and eukaryotic cells are outlined below.

A typical **prokaryotic cell** (Before a nucleus):
- Does not contain a nucleus surrounded by a nuclear membrane or envelope.
- Usually contains one or more loops of covalently-closed circular DNA (ccc-DNA).
- Is not compartmentalized by membranous organelles.
- Contains 70S ribosomes.
- Is surrounded by a membrane lacking steroid lipids and involved in ATP synthesis, wall synthesis, taxis and other physiological activities.
- Is usually much smaller than a typical eukaryotic cell.
Bacteria and Archaea are groups of prokaryotic organisms; however, the Archaea have multiple features unlike those of bacteria (walls, membranes, genetics, etc.).

A typical **eukaryotic cell** (Well or truly nucleated):
Contains one or more true nuclei, each surrounded by a nuclear envelope.
Contains two or more linear chromosomes.
Is compartmentalized by many membranous organelles.
Contains 80S ribosomes.
Is surrounded by a membrane containing steroid lipids and not involved in the synthesis of ATP. Is usually much larger than a typical prokaryotic cell.

Microorganisms categorized as protozoa, algae and fungi are made up of eukaryotic cells, as are all plants and animals including humans. Some Eukaryotic cells, e.g., human red blood cells (erythrocytes), do not contain nuclei, but these cells cannot reproduce and are formed from precursor cells that do contain nuclei (hematopoietic stem cells).

Since eukaryotic cells are more familiar to many students than are prokaryotic cells, these will be covered first. Each eukaryotic cell is surrounded by a cell membrane, and most have one or more true nuclei (though there are exceptions as indicated above). The region of protoplasm between the cell membrane and the nucleus is referred to as **cytoplasm**, while the protoplasm inside the nuclear membrane or envelope is called **nucleoplasm** (all is living substance). The cytoplasm is often highly compartmentalized by internal structures called **organelles** (organelles = little organs), and makes up the bulk of the cell. The liquid matrix supporting the organelles is called the **cytosol** and contains microtubules, microfilaments, electrolytes and an assortment of organic compounds. Organelles occur in a variety of shapes and sizes, and typically carry out specific functions (like the organs found within the human body). A number of the structures found within eukaryotic cells are outlined in the lecture syllabus; keep in mind that not all of the structures listed are found within all types of eukaryotic cells.

1.  **Cell membrane** – The cell membrane surrounds and limits the cell and has the structure and functions covered in an earlier section. All cells have cell membranes that separate their cytoplasm from the external environment.

2.  **Endoplasmic reticulum** – The endoplasmic reticulum (endo = inside, plasmic = cytoplasm, reticulum = network) is a membranous organelle extending from the nuclear envelope into the cytoplasm, and occasionally connecting to the cell membrane. In composition it is like the cell membrane, but includes two membrane layers separated by a thin space. In some cells, the endoplasmic reticulum is highly folded and takes up most of the cytoplasm.
Functions associated with the smooth endoplasmic reticulum include storage, transport and the synthesis of lipids. Materials can be moved from place to place between the membrane layers, and portions of membrane can be transferred from the endoplasmic reticulum to other structures. Some regions of endoplasmic reticulum are covered with small, granular bodies called ribosomes. This is called rough endoplasmic reticulum and is involved in protein synthesis.

3. **Ribosomes** – Ribosomes are small granular bodies composed of ribosomal-RNA (rRNA) and protein (ribo = ribose, the pentose monosaccharide found in RNA, soma = body). Eukaryotic ribosomes are 80S (the S referring to Svedburg units, a measure of density), and include two subunits of 60S and 40S. **Ribosomes are the site of protein synthesis**, so are essential to cell function. The two subunits come together only when proteins are being made, and those ribosomes associated with the rough endoplasmic reticulum are attached to the membranes by the proteins they are forming. Proteins formed by ribosomes bound to the rough endoplasmic reticulum are usually exported from the cell, while those formed by ribosomes free in the cytoplasm stay inside the cell. The process of protein synthesis will be described in considerable detail later.

4. **Golgi complex** (apparatus or body) – The Golgi complex is an organelle composed of flat membranous sacs arranged in a stack and is essentially modified smooth endoplasmic reticulum. Like the endoplasmic reticulum, the Golgi is involved in transport and storage, but is also the primary site of polysaccharide synthesis. Membranous components and other materials passing from the endoplasmic reticulum (both smooth and rough) to the Golgi provide raw materials for the assembly of complex organic compounds such as lipopolysaccharides, lipoproteins and glycoproteins. The Golgi is also involved in sorting, packaging and secretion as segments of it can be pinched off to form vesicles, and these can move to the cell surface where their membranes fuse with the cell membrane. The materials contained within these vesicles can then exit the cell through exocytosis.

5. **Vacuoles and vesicles** – Vacuoles and vesicles are membranous organelles containing a variety of materials and formed in various ways. The term vacuole suggests an empty space (a vacuum) and in some cells (plants and algae) refers to a large, centrally located region filled with what appears to be clear fluid (the central vacuole). This structure helps maintain turgor pressure within cells and stores toxins that might interfere with metabolism. Vesicles are generally smaller than vacuoles, but the terminology associated with these membranous "bubbles" is inconsistent. Protozoa taking in food materials through endocytosis form food vacuoles or pinocytic vesicles depending on what was ingested. Both types of structures essentially store nutrients until they can be
digested. The membranous fragments "pinched" from the Golgi are most commonly referred to as vesicles, and these carry various materials (waste products, digestive enzymes, etc.) toward the cell surface where they can be released through exocytosis. Lysosomes are formed by the Golgi complex.

6. **Contractile vacuoles** – Contractile vacuoles are organelles found commonly in fresh-water protozoa. They vary considerably in size and complexity, but often appear as circular structures that swell and shrink in a repeating pattern. The swelling occurs when the contractile vacuole is relaxed and filling (diastole), while the shrinking occurs when it contracts, pumping water out of the cell (systole). Contractile vacuoles **pump excess water out**, so function as **osmoregulatory** structures, preventing cells from bursting due to osmosis. They are connected to the smooth endoplasmic reticulum, so also aid fluid circulation within the cell. Since liquid wastes may be eliminated along with the water, contractile vacuoles also have an **excretory function**.

7. **Lysosomes** – Lysosomes (lysis = to split, soma = body) are membranous organelles containing a variety of digestive enzymes (**hydrolases**) involved in the hydrolysis (catabolism) of organic compounds. Their primary function within microorganisms is the **digestion of food materials** taken in through endocytosis; however, they also degrade worn out organelles and help the cell recycle membrane components. The hydrolase enzymes carried within lysosomes are activated after the lysosome membrane binds with that of a food vacuole, and hydrogen ions are pumped in lowering the pH. Bacteria able to prevent this acidification can avoid digestion and may take up residence within the phagocytic cell. Lysosomes are formed and released by the Golgi complex.

8. **Peroxisomes** – Peroxisomes are membranous organelles containing enzymes involved in hydrogen peroxide metabolism. Some of these generate hydrogen peroxide by oxidizing organic compounds while others called **catalase enzymes** break down the hydrogen peroxide produced. Since hydrogen peroxide is toxic, the overall function of catalase enzymes is neutralizing toxins. Peroxisomes are not formed by the Golgi complex, but are apparently self-replicating.

9. **Mitochondria** – Mitochondria (singular mitochondrion) are self-replicating organelles each surrounded by a double layer of membrane. Each mitochondrion has an outer membrane typical of eukaryotic cells (50:50 lipid to protein ratio and steroid lipids present) and an inner membrane typical of prokaryotic cells (40:60 lipid to protein ratio, lacking steroid lipids and carrying enzymes involved in **ATP synthesis**). The surface area of the inner membrane is greatly increased by finger-like folds called **cristae**, and these are the sites of **oxidative phosphorylation** (**ATP synthesis involving the oxidation**
of coenzymes). Since quantities of ATP are produced by mitochondria, they are sometimes referred to as the "powerhouses of the cell".

In addition to their unique inner membranes, mitochondria have a number of other prokaryotic features; they carry **70S ribosomes**, have closed loops of DNA (ccc-DNA), are **damaged by antibacterial drugs** and **reproduce by means of fission**. These features provide strong evidence that mitochondria evolved from prokaryotic cells (Proteobacteria) that were taken in by larger eukaryotic-like organisms through endocytosis (**the endosymbiotic theory**). Having avoided digestion (possibly by the mechanism mentioned above), they formed a permanent symbiotic relationship, beneficial to both them and their host organisms (a **mutualistic** relationship). As **endosymbionts**, they have been significantly modified over time.

The mitochondrial genome exists as one or multiple copies of ccc-DNA within the **matrix** (area enclosed by the inner membrane), but is significantly reduced in size, i.e., much smaller than that of the original proteobacteria. This is because most of the genes encoding mitochondrial proteins have been lost or transferred to the host nucleus. Most of the enzymes involved in the **Krebs cycle** (citric acid cycle) are located in the matrix, but these plus proteins of the electron transport chain and even **ATP synthase** (the enzyme involved in ATP synthesis) are entirely or partially encoded by what are now nuclear genes, i.e., carried on the host cell’s chromosomes within the host nucleus.

**10. Chloroplasts** – Chloroplasts, like mitochondria, are self-replicating organelles each surrounded by a double layer of membrane. Within each chloroplast, the inner membrane is folded into numerous sack-like structures called **thylakoids** containing light-trapping pigments (**chlorophylls**) and enzymes involved in **ATP synthesis** through photophosphorylation, a process dependent on light energy. The chloroplast **stroma** (region enclosed by the inner membrane) contains enzymes involved in **fixing carbon dioxide**, i.e., binding CO₂ with five-carbon sugars to make six-carbon sugars. Chloroplasts are only found in certain types of cells such as Protista (algae and some protozoa) and green plants.

Like mitochondria, chloroplasts carry 70S ribosomes, have ccc-DNA and are damaged by antibacterial drugs. They apparently evolved from several different types of **cyanobacteria** ingested by eukaryotes on more than one occasion, because not all chloroplasts carry the same types of light-trapping pigments. The chloroplasts found within some protozoa are derived from green algae cells, i.e., the algae taken in by protozoa became **symbionts**. These chloroplasts have unique membrane arrangements and may even carry the remains of algae nuclei. Chloroplasts represent another fine example of mutually beneficial symbiosis.
11. **Microtubules** – Microtubules are microscopic tube-like structures (cylinders) made up of proteins called tubulins or tubulin proteins. Each tubulin unit is actually a heterodimer composed of one alpha (α) and one beta (β) tubulin (an αβ-heterodimer). The tubulin dimers polymerize (connect together in long chains) to form linear structures called **protofilaments**, each with an α-subunit at one end and a β-subunit at the other. This orientation is significant and consistent within each microtubule. The β-subunit end is called the positive end, while the α-subunit end is called the negative end. The wall of a typical microtubule is composed of thirteen protofilaments arranged as linear strands that spiral around the tubule forming imperfect helixes. In cross section these appear as thirteen globular protein dimers arranged in a circle. Microtubules can be lengthened or shortened by adding or removing tubulin dimers (and cut by Katanin proteins) so exist as dynamic structures, changing as necessary for cellular function. Addition of tubulin dimers occurs most readily at the positive end while removal occurs most readily at the negative end.

Microtubules function as support structures forming part of the **cytoskeleton**, and are also involved in intracellular motion. Proteins known as microtubule-associated proteins or MAPs interact with them in various ways. Two types of MAPs known as motor proteins are **Kinesin** and **Dynein**. Kinesin proteins (kine = movement) attach to and "walk" along protofilaments toward the positive end, and can carry cellular components such as small organelles, vesicles and other cytoskeletal elements along the microtubule. Dynein is also capable of moving along microtubules, but carries materials toward the negative end. Dynein is also involved in the movement of cilia and flagella. Both motor proteins require ATP as an energy source (have ATPase activity). Together they can allow materials to travel along microtubules in opposite directions at the same time, as though they were moving on an intracellular highway.

12. **Cilia and flagella** – Cilia (singular = cilium) and flagella (singular = flagellum) are locomotor structures found on the surfaces of some eukaryotic cells. Cilia are typically short and hair-like while flagella are longer and whip-like. Both cilia and flagella are attached to basal bodies, surrounded by the cell membrane and supported by microtubules arranged in a specific pattern; typically nine groups of two around the periphery, and two at the center, i.e., 9 x 2 + 2 (although 9 x 2 + 1 and 9 x 2 + 0 variations can occur). The center two microtubules are attached to the outer nine pairs by "spokes" made of **dynein**, and this motor protein with its ATPase activity provides the motion required to bend the cilium or flagellum. The complex formed by microtubules and MAPs within a cilium or flagellum is called an **axoneme**, and is formed in coordination with a **basal body** (a centriole-like structure recognized as one type of microtubule organizing center or MTOC).
Flagella are typically less numerous than cilia and most flagellated cells have only one or two. Cilia are usually quite numerous and often cover the entire cell surface. A single flagellum can pull a cell through its environment, or flagella in pairs can move together like the arms of a person swimming the breaststroke. Sometimes one flagellum in a pair pulls the cell forward while the other trails along at rest. Cilia move in a highly coordinated fashion, creating wave-like patterns that flow over the cell surface, or rotate around food-getting structures. Some cilia move single-celled organisms through their watery habitats while others move materials along the surfaces of stationary cells (as occurs within the human respiratory system). Many types of protozoa use cilia to sweep food materials toward and into a cellular "mouth" or cytostome.

13. **Centrioles** – Centrioles are cylindrical bodies made up of microtubules arranged in nine groups of three. They typically occur as a single pair oriented at right angles to one another within a region of the cell called the centrosome. In addition to forming the basal bodies associated with cilia and flagella, centrioles coordinate the formation of a structure known as the spindle apparatus, involved in chromosome separation during cell division (mitosis and meiosis). Some of the microtubules forming the spindle apparatus attach to chromosomes at their center (the kinetochore) and then push/pull the chromosomes apart by lengthening or shortening (a process involving the addition or removal of αβ-dimers as described above). Other microtubules move the centrosomes toward opposite sides of the cells, which also serves to pull the chromosomes apart.

14. **Actin microfilaments** – In addition to the tubulin protofilaments found in microtubules, eukaryotic cells produce microfilaments made up of actin, a protein usually thought of as being associated with muscle fibers (along with myosin). Actin monomers can be rapidly polymerized into filaments and taken apart as needed. Their microfilaments form a changeable scaffold-like complex just inside the cell membrane and are involved in a variety of cellular processes including cytokinesis (separation of the cytoplasm during cell division), endocytosis, exocytosis and the extension of the cytoplasm into finger-like locomotor structures called pseudopodia (false feet).

Certain pathogenic bacteria, e.g., *Listeria monocytogenes* can utilize the actin within host cells for locomotion. They do this by causing the polymerization of actin just outside one end of each cell. The bacteria release actin assembly-inducing proteins (ActA) and these cause rapid polymerization of actin fibers that then push each bacterium forward. The force generated by actin polymerization can propel bacteria very rapidly across a host cell, and in some cases allows them to penetrate cell membranes so they can transfer from one host cell to another.
15. **Nucleus** – The nucleus is a relatively large, centrally located organelle surrounded by a double layer of membrane called the **nuclear envelope**, and containing the **nucleoplasm**. Though separated from the cytoplasm by two layers of membrane, the nucleus maintains contact by transporting materials through **nuclear pores** (regions with greater permeability). The nuclear envelope is also connected to the endoplasmic reticulum.

Sometimes called the "brain of the cell", the nucleus is a control center involved in regulating physiological processes. Most of the DNA contained within eukaryotic cells is located here, and the associated genes determine which proteins the cell can make. The **nucleoplasm** (protoplasm enclosed by the nuclear envelope) includes a diffuse, thread-like material called **chromatin** and sometimes one or more dark-staining bodies called **nucleoli**.

Chromatin is a thread-like material made up of DNA and proteins, some of which are **homogeneous** (all of the same type) and others **heterogeneous** (of different types). Groups of homogeneous proteins called **histones** help maintain the structural stability of DNA and influence gene expression by binding with DNA in structures called nucleosomes. Each **nucleosome** contains a histone octomer wrapped with DNA, and multiple nucleosomes are bound together by other histones to form bead-like chromatin strands. Heterogeneous proteins include enzymes of various types and are involved in processes such as DNA replication and transcription. During cell division, the chromatin threads are highly folded into discrete structures called **chromosomes**. These are clearly visible with a light microscope in some types of cells.

16. **Nucleoli** (singular nucleolus) – Nucleoli are dark-staining bodies sometimes visible within the nucleoplasm of certain cells. They are composed of ribosomal-RNA (rRNA) and protein, and are sometimes referred to as the "pacemakers" of the cell because they influence protein synthesis. These bodies are the site of rRNA synthesis and the assembly of ribosomal subunits. In essence, they help make the ribosomes responsible for all protein synthesis.

17. **Spliceosomes** – Spliceosomes are small granular bodies made up of small or short-RNA (sRNA) and protein. The sRNA molecules present contain high levels of uracil (uridine nucleotides) and there are several different segments of sRNA involved. The function of spliceosomes within the nucleus is to modify RNA molecules as they are transcribed from DNA. The process is called **post-transcriptional modification** and involves cutting out some regions of RNA (introns) and splicing the remaining pieces (exons) together (this will be explained in greater detail later).
18. **Inclusions** – Inclusions are bodies of material stored within the cytoplasm of eukaryotic cells and sometimes considered to be non-living. They frequently include such materials as crystals, fat droplets, pigment granules or glycogen. Some inclusions contain materials produced by the cell, while others contain materials taken from the outside environment.

19. **Cell Walls and Skeletons** – Cell walls and skeletons are rigid layers found outside the cell membranes of certain types of eukaryotic cells including algae, fungi and certain protozoa. Cell walls are generally associated with plant-like cells such as algae, while skeletons occur on animal-like protozoa. Fungi were originally classified with plants, so their rigid coverings are also called walls.

   Cell walls are typically made of polysaccarides such as cellulose, chitin, glucan, pectin or agar, but sometimes contain glass. They give cells a characteristic shape and provide protection against changes in osmotic pressure (e.g., in hypotonic environments) and potential predators.

   Skeletons occur on some animal-like, single celled organisms (protozoa), and are typically made of glass or calcium carbonate. They also give organisms a characteristic shape and provide protection against potential predators. Most skeletons do not provide protection against the osmotic pressure exerted by hypotonic environments because they are perforated by numerous holes or are missing on some cell surfaces.

   Protozoa called **testate amoebae** can form skeleton-like structures called tests. A test may be produced by the organism (autogenic test) or made up of particles collected from the environment and then stuck together by secretions (xenogenic test). Tests can be made up of organic materials, glass, calcium carbonate or bits of sand; they are typically vase-like in shape and open at one end (allowing for the extension of pseudopodia).