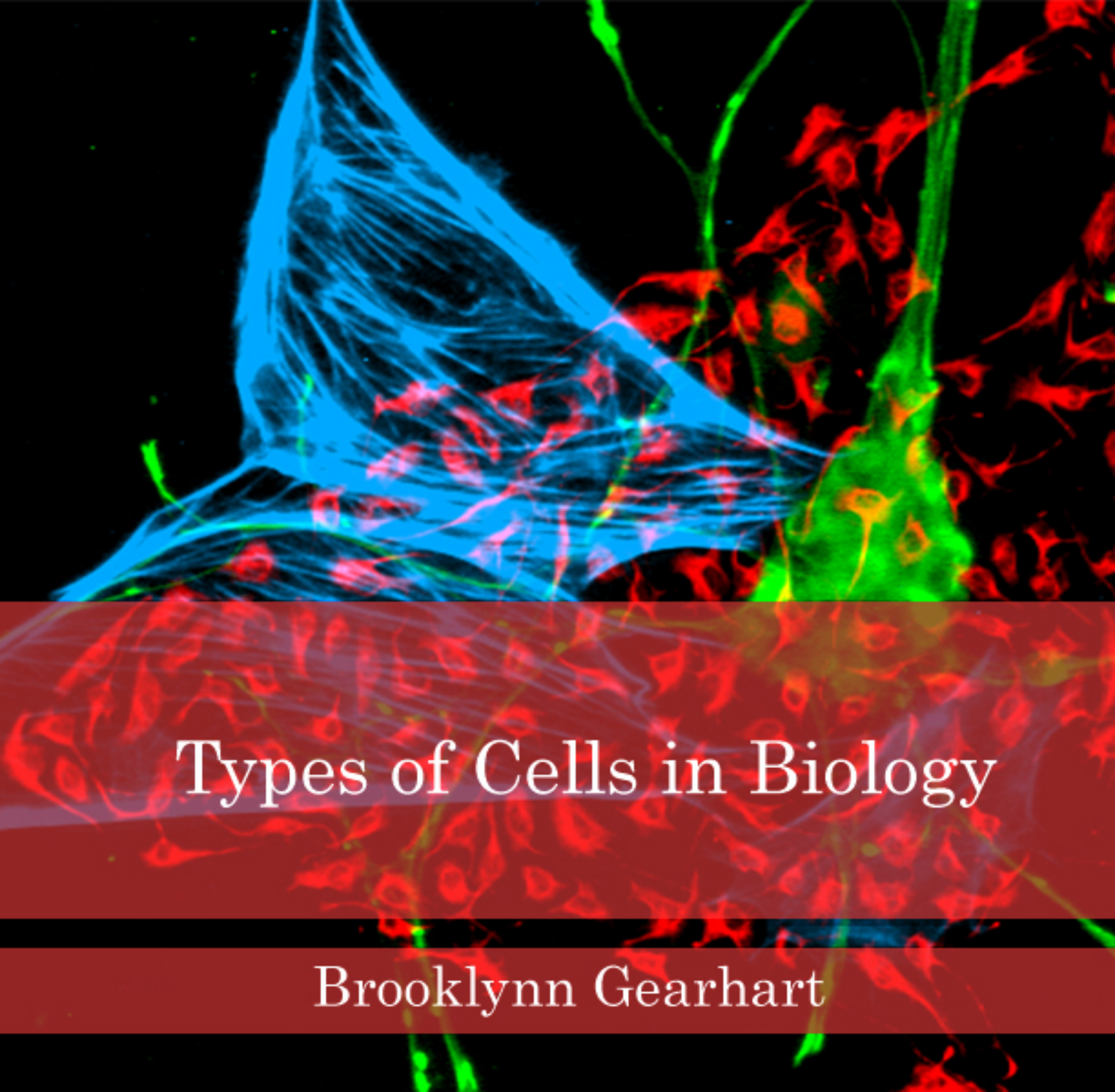

# Types of Cells in Biology

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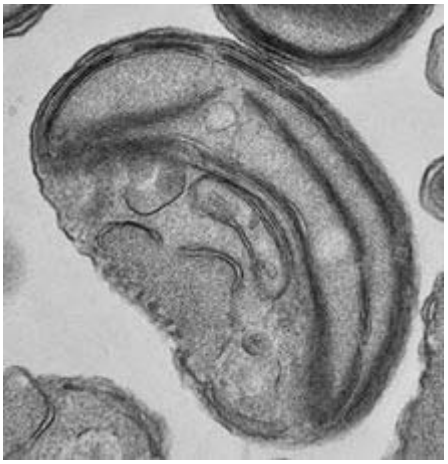
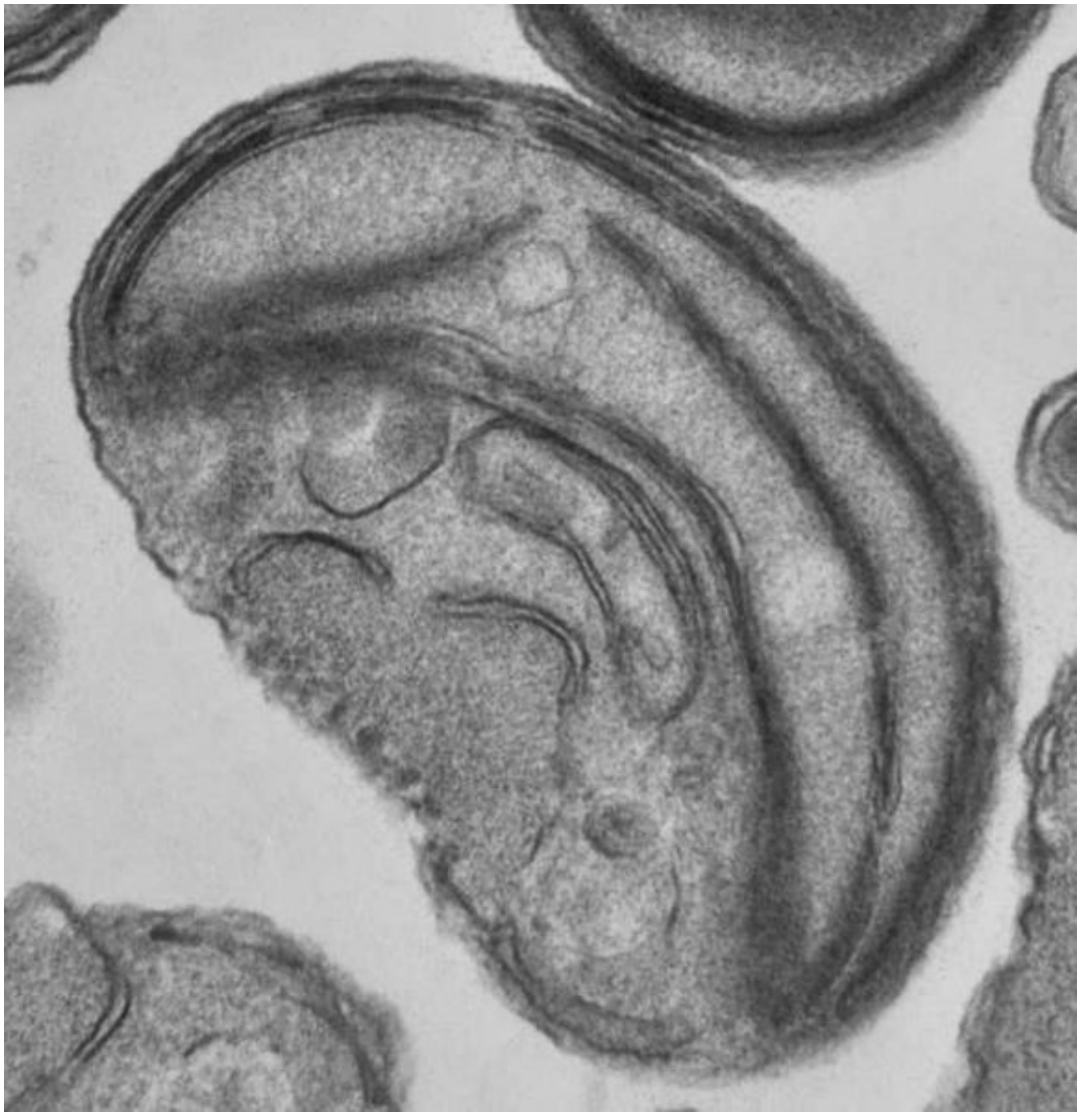
# Eukaryote

| Eukaryotes<br>**Temporal range: Proterozoic – Recent** |
|---|
|  |
| *Ostreococcus* is the smallest known free living eukaryote, with an average size of 0.8 µm. |
| **Scientific classification** |
| Domain: **Eukaryota**<br>Whittaker & Margulis,1978 |
| **Kingdoms** |
| Animalia – Animals |
| Fungi |
| Amoebozoa |
| Plantae – Plants |
| Chromalveolata |
| Rhizaria |
| Excavata |
| **Alternative phylogeny** |

- ***Unikonta***
  - **Opisthokonta**

        - Metazoa
        - Mesomycetozoa
        - Choanozoa
        - Eumycota
    - Amoebozoa
- ***Bikonta***
    - Apusozoa
    - Rhizaria
    - Excavata
    - Archaeplastida
    - Chromalveolata



Eukaryotes

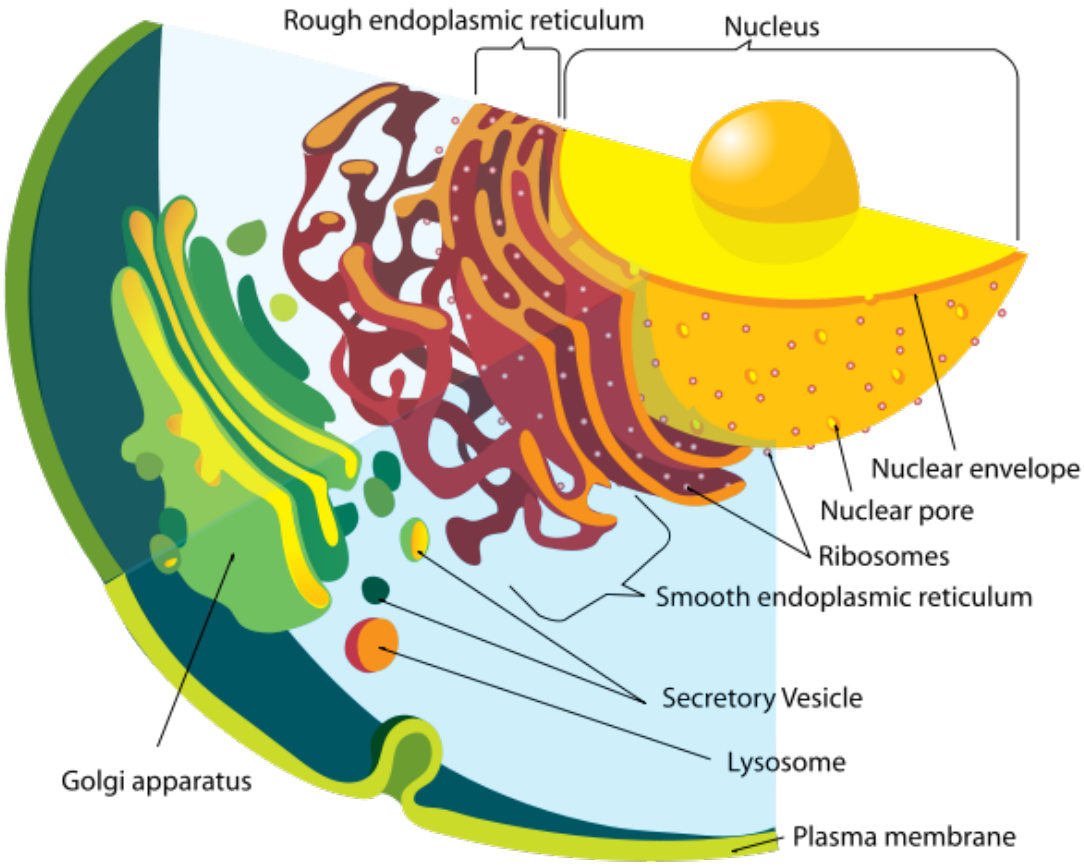
A **eukaryote** is an organism whose cells contain complex structures enclosed within membranes. The defining membrane-bound structure that sets eukaryotic cells apart from prokaryotic cells is the nucleus, or nuclear envelope, within which the genetic material is carried. The presence of a nucleus gives eukaryotes their name, which comes from the Greek ευ (*eu*, "good") and κάρυον (*karyon*, "nut" or "kernel"). Most eukaryotic cells also contain other membrane-bound organelles such as mitochondria, chloroplasts and the Golgi apparatus. All species of large complex organisms are eukaryotes, including animals, plants and fungi, although most species of eukaryotic protists are microorganisms.

Cell division in eukaryotes is different from that in organisms without a nucleus (prokaryotes). It involves separating the duplicated chromosomes, through movements directed by microtubules. There are two types of division processes. In mitosis, one cell divides to produce two genetically identical cells. In meiosis, which is required in sexual reproduction, one diploid cell (having two instances of each chromosome, one from each parent) undergoes recombination of each pair of parental chromosomes, and then two stages of cell division, resulting in four haploid cells (gametes). Each gamete has just one complement of chromosomes, each a unique mix of the corresponding pair of parental chromosomes.

Eukaryotes appear to be monophyletic, and so make up one of the three domains of life. The two other domains, Bacteria and Archaea, are prokaryotes and have none of the above features. Eukaryotes represent a tiny minority of all living things; even in a human body there are 10 times more microbes than human cells.

# Cell features

Eukaryotic cells are typically much larger than prokaryotes. They have a variety of internal membranes and structures, called organelles, and a cytoskeleton composed of microtubules, microfilaments, and intermediate filaments, which play an important role in defining the cell's organization and shape. Eukaryotic DNA is divided into several linear bundles called chromosomes, which are separated by a microtubular spindle during nuclear division.



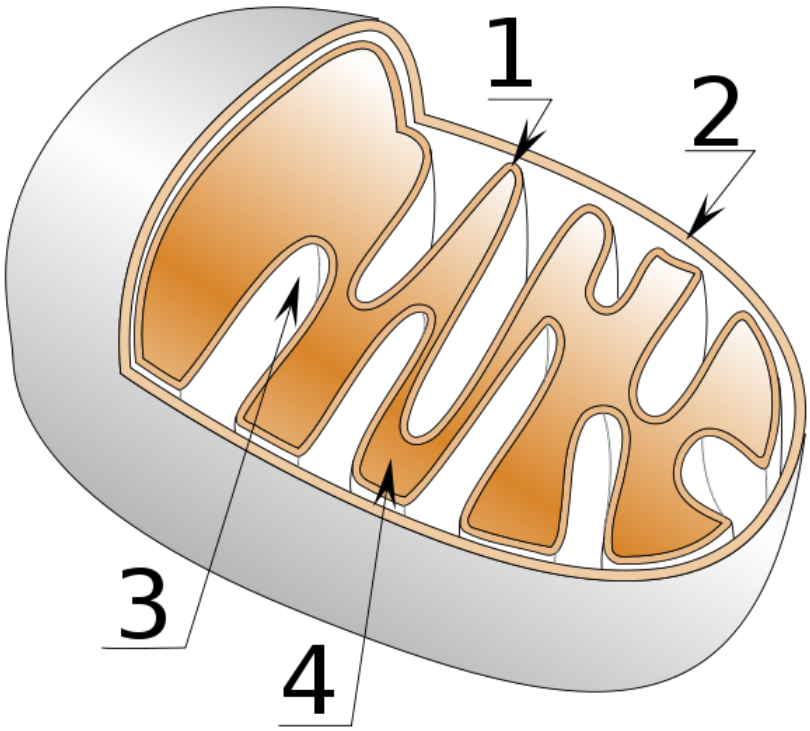

Detail of the endomembrane system and its components

## Internal membrane

Eukaryotic cells include a variety of membrane-bound structures, collectively referred to as the endomembrane system. Simple compartments, called vesicles or vacuoles, can form by budding off other membranes. Many cells ingest food and other materials through a process of endocytosis, where the outer membrane invaginates and then pinches off to form a vesicle. It is probable that most other membrane-bound organelles are ultimately derived from such vesicles.

The nucleus is surrounded by a double membrane (commonly referred to as a nuclear envelope), with pores that allow material to move in and out. Various tube- and sheet-like extensions of the nuclear membrane form what is called the endoplasmic reticulum or ER, which is involved in protein transport and maturation. It includes the rough ER where ribosomes are attached, and the proteins they synthesize enter the interior space or lumen. Subsequently, they generally enter vesicles, which bud off from the smooth ER. In most eukaryotes, these protein-carrying vesicles are released and further modified in stacks of flattened vesicles, called Golgi bodies or dictyosomes.

Vesicles may be specialized for various purposes. For instance, lysosomes contain enzymes that break down the contents of food vacuoles, and peroxisomes are used to break down peroxide, which is toxic otherwise. Many protozoa have contractile vacuoles, which collect and expel excess water, and extrusomes, which expel material used to deflect predators or capture prey. In multicellular organisms, hormones are often produced in vesicles. In higher plants, most of a cell's volume is taken up by a central vacuole, which primarily maintains its osmotic pressure.




Mitochondria structure:
1) Inner membrane
2) Outer membrane
3) Crista
4) Matrix

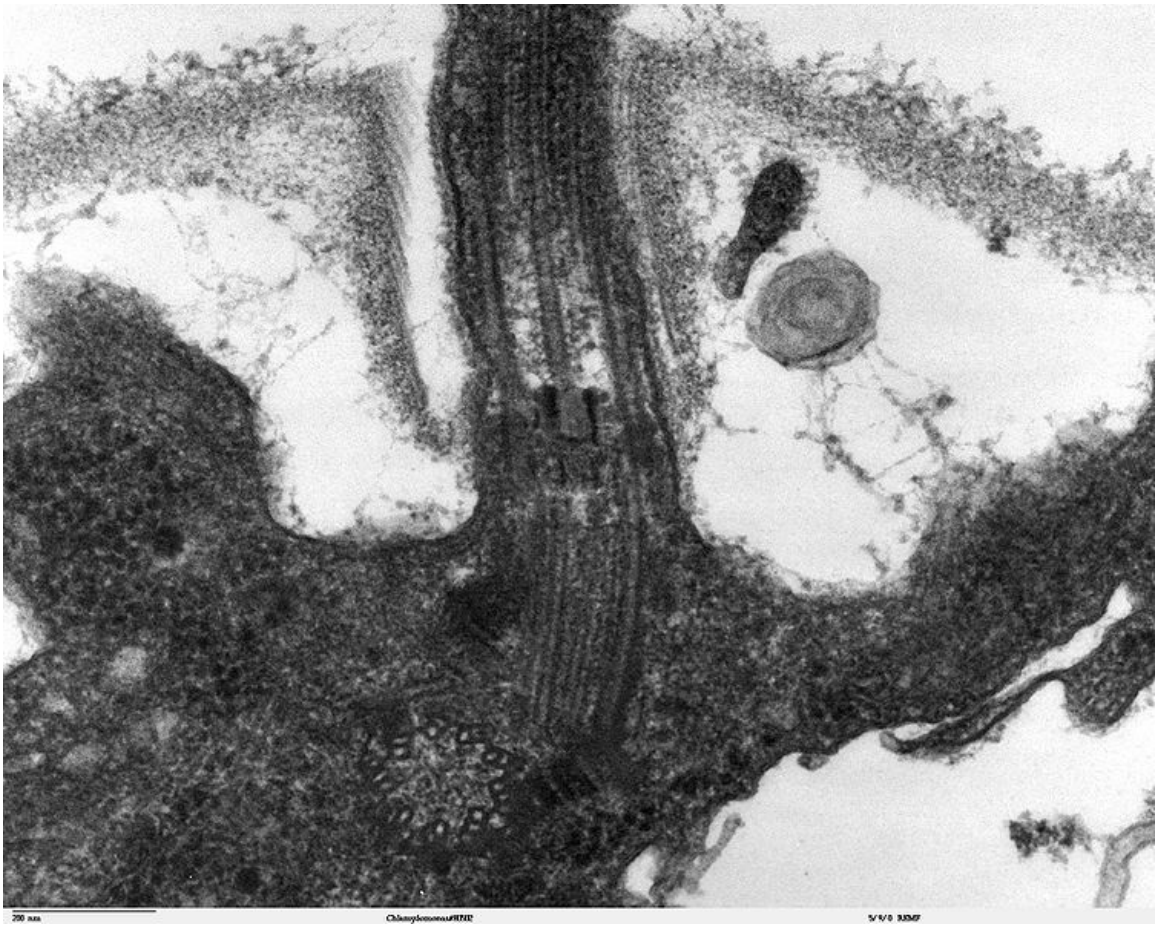
## Mitochondria and plastids

Mitochondria are organelles found in nearly all eukaryotes. They are surrounded by double membranes (known as the phospholipid bi-layer), the inner of which is folded into invaginations called cristae, where aerobic respiration takes place. Mitochondria contain their own DNA. They are now generally held to have developed from endosymbiotic prokaryotes, probably proteobacteria. The few protozoa that lack mitochondria have been found to contain mitochondrion-derived organelles, such as hydrogenosomes and mitosomes.

Plants and various groups of algae also have plastids. Again, these have their own DNA and developed from endosymbiotes, in this case cyanobacteria. They usually take the form of chloroplasts, which like cyanobacteria contain chlorophyll and produce organic compounds (such as glucose) through photosynthesis. Others are involved in storing food. Although plastids likely had a single origin, not all plastid-containing groups are closely related. Instead, some eukaryotes have obtained them from others through secondary endosymbiosis or ingestion.

Endosymbiotic origins have also been proposed for the nucleus, for which see below, and for eukaryotic flagella, supposed to have developed from spirochaetes. This is not generally accepted, both from a lack of cytological evidence and difficulty in reconciling this with cellular reproduction.

## Cytoskeletal structures



Longitudinal section through the flagellum of *Chlamydomonas reinhardtii*

Many eukaryotes have long slender motile cytoplasmic projections, called flagella, or similar structures called cilia. Flagella and cilia are sometimes referred to as undulipodia, and are variously involved in movement, feeding, and sensation. They are composed mainly of tubulin. These are entirely distinct from prokaryotic flagella. They are

supported by a bundle of microtubules arising from a basal body, also called a kinetosome or centriole, characteristically arranged as nine doublets surrounding two singlets. Flagella also may have hairs, or mastigonemes, and scales connecting membranes and internal rods. Their interior is continuous with the cell's cytoplasm.

Microfilamental structures composed by actin and actin binding proteins, e.g., α-actinin, fimbrin, filamin are present in submembraneous cortical layers and bundles, as well. Motor proteins of microtubules, e.g., dynein or kinesin and actin, e.g., myosins provide dynamic character of the network.

Centrioles are often present even in cells and groups that do not have flagella. They generally occur in groups of one or two, called kinetids, that give rise to various microtubular roots. These form a primary component of the cytoskeletal structure, and are often assembled over the course of several cell divisions, with one flagellum retained from the parent and the other derived from it. Centrioles may also be associated in the formation of a spindle during nuclear division.

Significance of cytoskeletal structures is underlined in determination of shape of the cells, as well as their being essential components of migratory responses like chemotaxis and chemokinesis. Some protists have various other microtubule-supported organelles. These include the radiolaria and heliozoa, which produce axopodia used in flotation or to capture prey, and the haptophytes, which have a peculiar flagellum-like organelle called the haptonema. An animal cell is a form of Eukaryotic cell that makes up many tissues in animals.

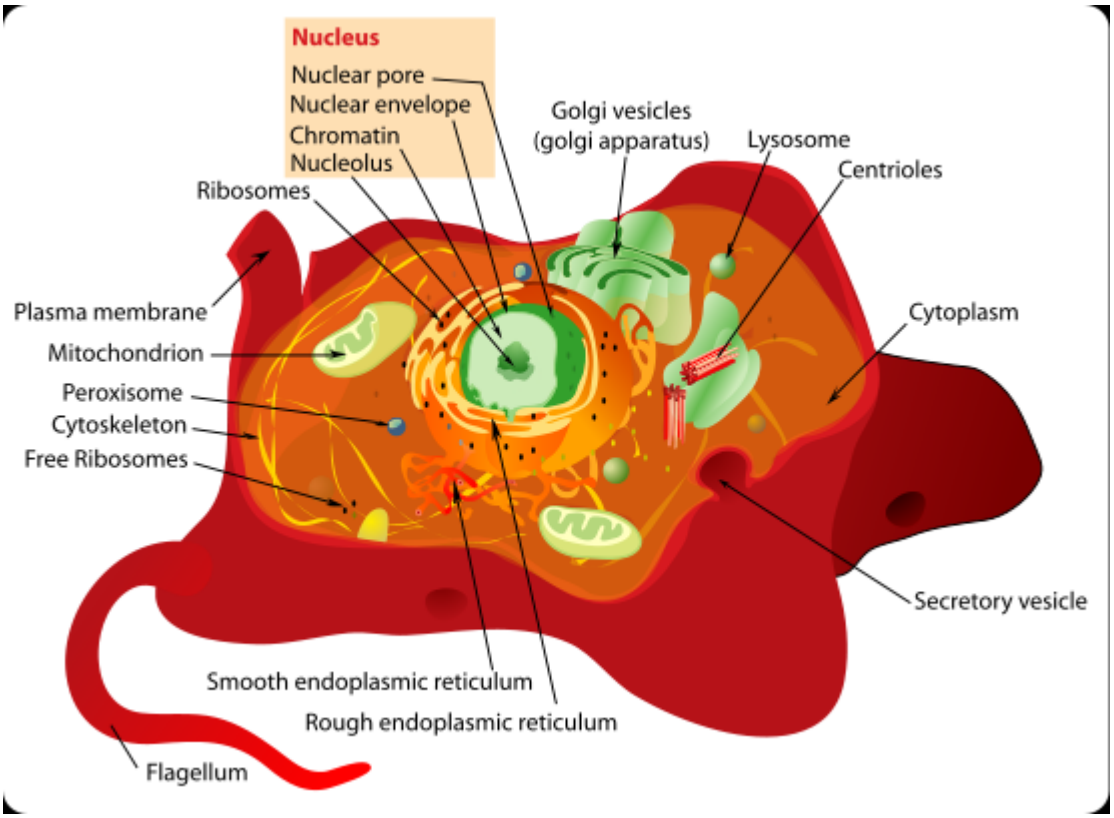
### Plant cell wall

Plant cells have a cell wall, a fairly rigid layer outside the cell membrane, providing the cell with structural support, protection, and a filtering mechanism. The cell wall also prevents over-expansion when water enters the cell. The major carbohydrates making up the primary cell wall of land plants are cellulose, hemicellulose, and pectin. The cellulose microfibrils are linked via hemicellulosic tethers to form the cellulose-hemicellulose network, which is embedded in the pectin matrix. The most common hemicellulose in the primary cell wall is xyloglucan.

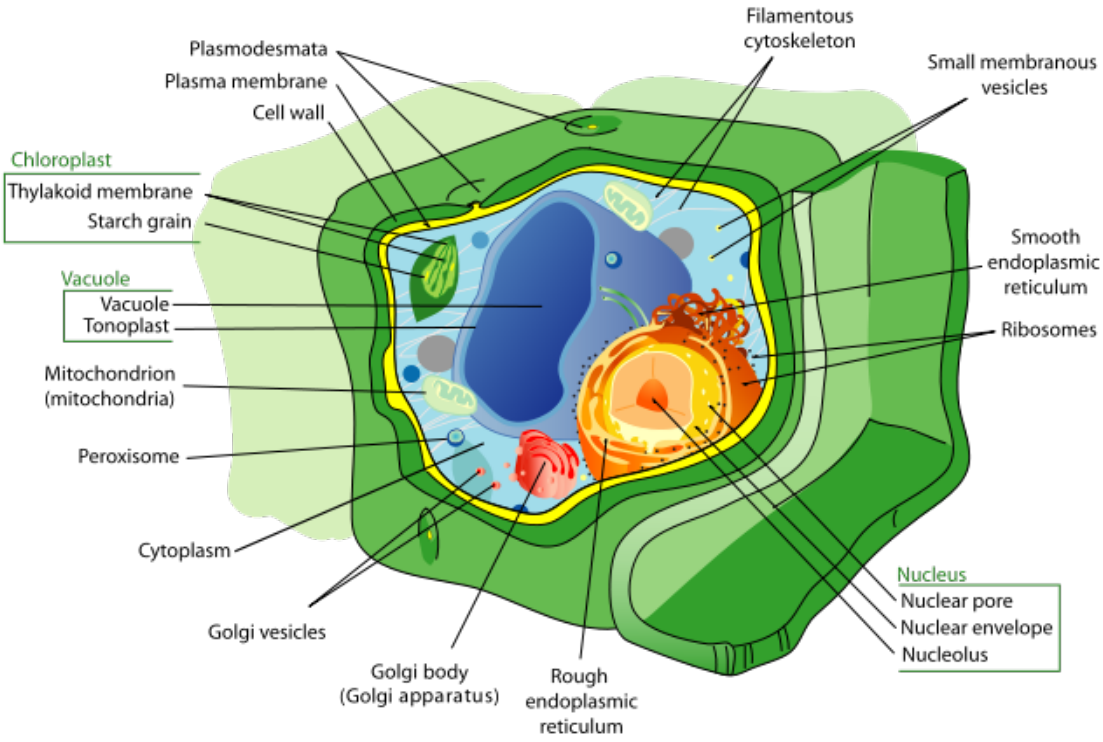
## Differences between eukaryotic cells

There are many different types of eukaryotic cells, though animals and plants are the most familiar eukaryotes, and thus provide an excellent starting point for understanding eukaryotic structure. Fungi and many protists have some substantial differences, however.

## Animal cell




Structure of a typical animal cell




Structure of a typical plant cell

An **animal cell** is a form of eukaryotic cell that makes up many tissues in animals. The animal cell is distinct from other eukaryotes, most notably plant cells, as they lack cell walls and chloroplasts, and they have smaller vacuoles. Due to the lack of a rigid cell wall, animal cells can adopt a variety of shapes, and a phagocytic cell can even engulf other structures.

There are many different cell types. For instance, there are approximately 210 distinct cell types in the adult human body.

## Plant cell

Plant cells are quite different from the cells of the other eukaryotic organisms. Their distinctive features are:

- A large central vacuole (enclosed by a membrane, the tonoplast), which maintains the cell's turgor and controls movement of molecules between the cytosol and sap
- A primary cell wall containing cellulose, hemicellulose and pectin, deposited by the protoplast on the outside of the cell membrane; this contrasts with the cell walls of fungi, which contain chitin, and the cell envelopes of prokaryotes, in which peptidoglycans are the main structural molecules

- The plasmodesmata, linking pores in the cell wall that allow each plant cell to communicate with other adjacent cells; this is different from the functionally analogous system of gap junctions between animal cells.
- Plastids, especially chloroplasts that contain chlorophyll, the pigment that gives plants their green color and allows them to perform photosynthesis
- Higher plants, including conifers and flowering plants (Angiospermae) lack the flagellae and centrioles that are present in animal cells.

### Fungal cell

**Fungal cells** are most similar to animal cells, with the following exceptions:

- A cell wall that contains chitin
- Less definition between cells; the hyphae of higher fungi have porous partitions called septa, which allow the passage of cytoplasm, organelles, and, sometimes, nuclei. Primitive fungi have few or no septa, so each organism is essentially a giant multinucleate supercell; these fungi are described as coenocytic.
- Only the most primitive fungi, chytrids, have flagella.

### Other eukaryotic cells

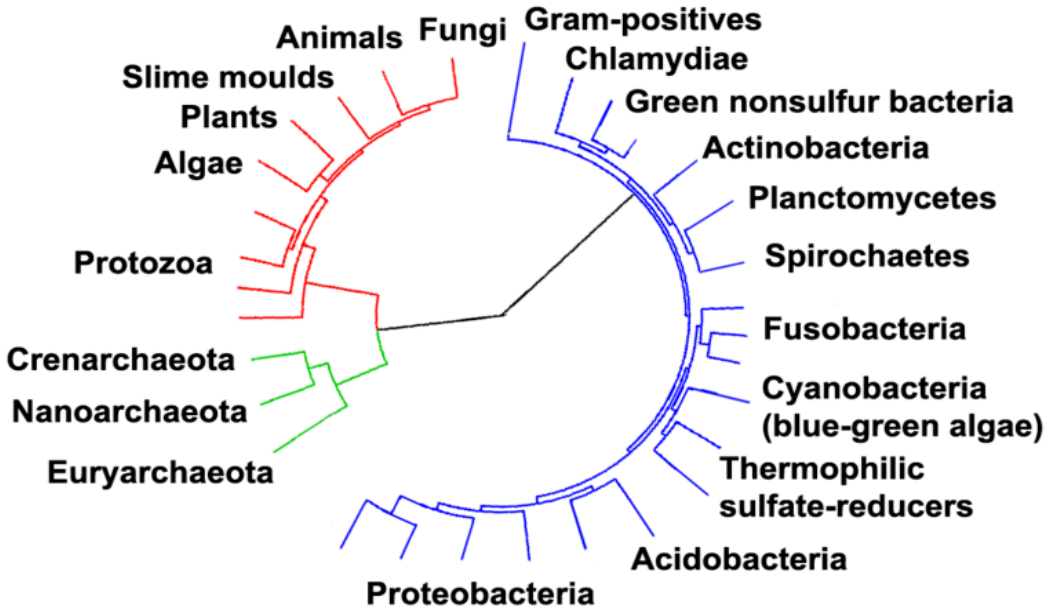
Eukaryotes are a very diverse group, and their cell structures are equally diverse. Many have cell walls; many do not. Many have chloroplasts, derived from primary, secondary, or even tertiary endosymbiosis; and many do not. Some groups have unique structures, such as the cyanelles of the glaucophytes, the haptonema of the haptophytes, or the ejectisomes of the cryptomonads. Other structures, such as pseudopods, are found in various eukaryote groups in different forms, such as the lobose amoebozoans or the reticulose foraminiferans.

## Reproduction

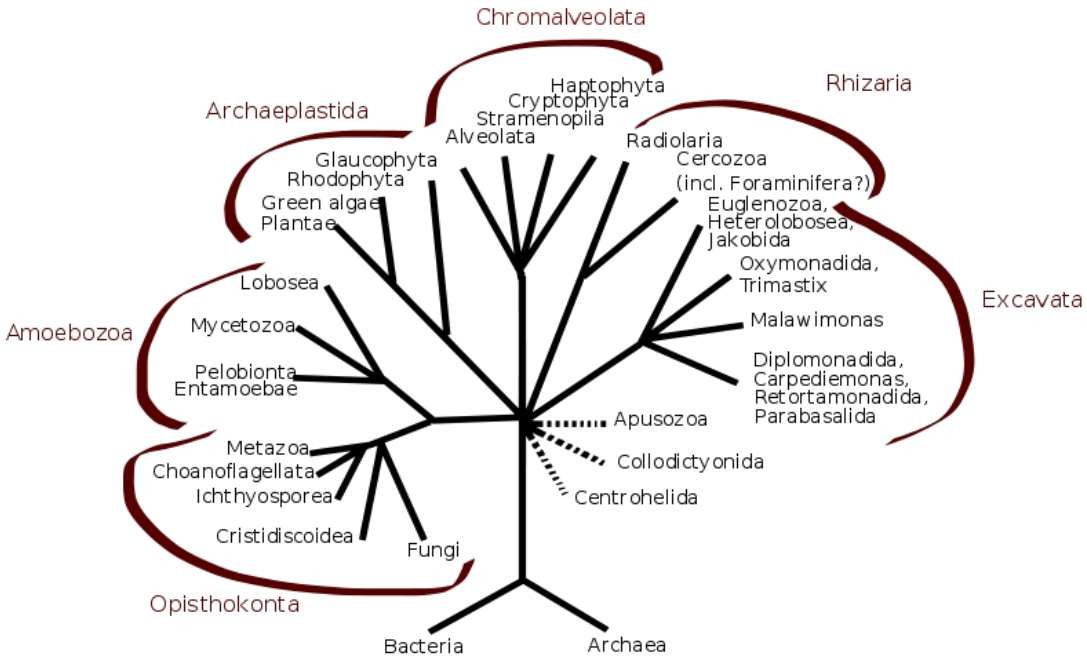
Nuclear division is often coordinated with cell division. This generally takes place by mitosis, a process that allows each daughter nucleus to receive one copy of each chromosome. In most eukaryotes, there is also a process of sexual reproduction, typically involving an alternation between haploid generations, wherein only one copy of each chromosome is present, and diploid generations, wherein two are present, occurring through nuclear fusion (syngamy) and meiosis. There is considerable variation in this pattern, however.

Eukaryotes have a smaller surface area to volume ratio than prokaryotes, and thus have lower metabolic rates and longer generation times. In some multicellular organisms, cells specialized for metabolism will have enlarged surface areas, such as intestinal vili.

# Origin and evolution




Phylogenetic tree showing the relationship between the eukaryotes and other forms of life. Eukaryotes are colored red, archaea green and bacteria blue.




One hypothesis of eukaryotic relationships

The origin of the eukaryotic cell was a milestone in the evolution of life, since they include all complex cells and almost all multi-cellular organisms. The timing of this series of events is hard to determine; Knoll (2006) suggests they developed approximately 1.6–2.1 billion years ago. Some acritarchs are known from at least 1650 million years ago, and the possible alga *Grypania* has been found as far back as 2100 million years ago.

Fossils that are clearly related to modern groups start appearing around 1.2 billion years ago, in the form of a red alga, though recent work suggests the existence of fossilized filamentous algae in the Vindhya basin dating back to 1.6 to 1.7 billion years ago.

Biomarkers suggest that at least stem eukaryotes arose even earlier. The presence of steranes in Australian shales indicates that eukaryotes were present 2.7 billion years ago.

## Phylogeny

rRNA trees constructed during the 1980s and 1990s left most eukaryotes in an unresolved "crown" group (not technically a true crown), which was usually divided by the form of the mitochondrial cristae. The few groups that lack mitochondria branched separately, and so the absence was believed to be primitive; but this is now considered an artifact of long-branch attraction, and they are known to have lost them secondarily.

**Six supergroup/kingdom model**

A classification produced in 2005 for the International Society of Protistologists, which reflected the consensus of the time, divided the eukaryotes into six supposedly monophyletic 'supergroups'. Although the published classification deliberately did not use formal taxonomic ranks, other sources have treated each of the six as a separate Kingdom.

| | |
|---|---|
| Excavata | Various flagellate protozoa |
| Amoebozoa | Most lobose amoeboids and slime moulds |
| Opisthokonta | Animals, fungi, choanoflagellates, etc. |
| Rhizaria | Foraminifera, Radiolaria, and various other amoeboid protozoa |
| Chromalveolata | Stramenopiles (or Heterokonta), Haptophyta, Cryptophyta (or cryptomonads), and Alveolata |
| Archaeplastida (or Primoplantae) | Land plants, green algae, red algae, and glaucophytes |

However, in the same year (2005), doubts were expressed as to whether some of these supergroups were monophyletic, particularly the Chromalveolata, and a review in 2006 noted the lack of evidence for several of the supposed six supergroups.

As of 2010, there is widespread agreement that the Rhizaria belong with the Stramenopiles and the Alveolata, in a clade dubbed the SAR supergroup, so that Rhizara is not one of the main eukaryote groups; also that the Amoeboza and Opisthokonta are each monophyletic and form a clade, often called the unikonts. Beyond this, there does not appear to be a consensus.

## Relationship to Archaea

Eukaryotes are more closely related to Archaea than Bacteria, at least in terms of nuclear DNA and genetic machinery, and one controversial idea is to place them with Archaea in the clade Neomura. However, in other respects, such as membrane composition, eukaryotes are similar to Bacteria. Three main explanations for this have been proposed:

- Eukaryotes resulted from the complete fusion of two or more cells, wherein the cytoplasm formed from a eubacterium, and the nucleus from an archaeon, from a virus, or from a pre-cell.
- Eukaryotes developed from Archaea, and acquired their eubacterial characteristics from the proto-mitochondrion.
- Eukaryotes and Archaea developed separately from a modified eubacterium.

There is also the Kronocyte theory for the origin of the Eukaryotic cell. This postulates that a primitive Eukaryotic cell emerged from the pre-DNA world but retained the earlier RNA based chemistry from which all modern life emerged. This primitive cell is called the Kronocyte. According to this hypothesis an RNA based Kronocyte coexisted with the DNA based Archaea (and probably eubacteria) and became the modern eukaryotic cell after a number of major endosymbioses—the first was the incorporation of an Archaea that introduced DNA metabolism and the nucleus, then the incorporation of an alphaproteobacter that became the mitochondria (and photosynthetic bacteria found in today's plants as chloroplasts). The Kronocyte hypothesis explains the large number of genes that are today only found in Eukaryotes but not in Archaea or Bacteria.

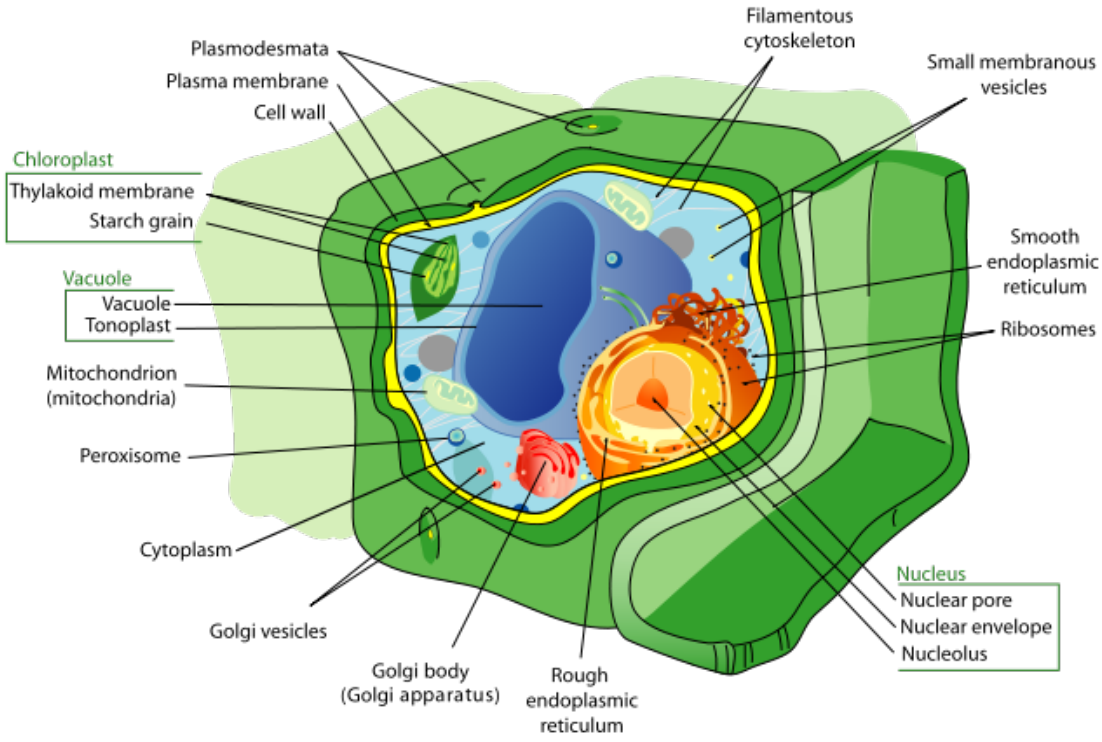
## Endomembrane system and mitochondria

The origins of the endomembrane system and mitochondria are also unclear. The **phagotrophic hypothesis** proposes that eukaryotic-type membranes lacking a cell wall originated first, with the development of endocytosis, whereas mitochondria were acquired by ingestion as endosymbionts. The **syntrophic hypothesis** proposes that the proto-eukaryote relied on the proto-mitochondrion for food, and so ultimately grew to surround it. Here the membranes originated after the engulfment of the mitochondrion, in part thanks to mitochondrial genes (the hydrogen hypothesis is one particular version).

In a study using genomes to construct supertrees, Pisani *et al.* (2007) suggest that, along with evidence that there was never a mitochondrion-less eukaryote, eukaryotes evolved from a syntrophy between an archaea closely related to Thermoplasmatales and an α-proteobacterium, likely a symbiosis driven by sulfur or hydrogen. The mitochondrion and its genome is a remnant of the α-proteobacterial endosymbiont.

## Chapter- 2

# Plant Cell




Plant cell structure

**Plant cells** are eukaryotic cells that differ in several key respects from the cells of other eukaryotic organisms. Their distinctive features include:

- A large central vacuole, a water-filled volume enclosed by a membrane known as the *tonoplast* maintains the cell's turgor, controls movement of molecules between the cytosol and sap, stores useful material and digests waste proteins and organelles.

- A cell wall composed of cellulose and hemicellulose, pectin and in many cases lignin, are secreted by the protoplast on the outside of the cell membrane. This contrasts with the cell walls of fungi (which are made of chitin), and of bacteria, which are made of peptidoglycan.

- Specialised cell-cell communication pathways known as plasmodesmata, pores in the primary cell wall through which the plasmalemma and endoplasmic reticulum of adjacent cells are continuous.

- Plastids, the notables one being the chloroplasts, which contain chlorophyll and the biochemical systems for light harvesting and photosynthesis, but also amyloplasts specialized for starch storage, elaioplasts specialized for fat storage, and chromoplasts specialized for synthesis and storage of pigments. As in mitochondria, which have a genome encoding 37 genes, plastids have their own genomes of about 100-120 unique genes and, it is presumed, arose as prokaryotic endosymbionts living in the cells of an early eukaryotic ancestor of the land plants and algae.

- Unlike animal cells, plant cells are stationary.

- Cell division by construction of a phragmoplast as a template for building a cell plate late in cytokinesis is characteristic of land plants and a few groups of algae, the notable one being the Charophytes and the Order Trentepohliales

- The sperm of bryophytes have flagellae similar to those in animals, but higher plants, (including Gymnosperms and flowering plants) lack the flagellae and centrioles that are present in animal cells.

# Cell types

- Parenchyma cells are living cells that have diverse functions ranging from storage and support to photosynthesis and phloem loading (transfer cells). Apart from the xylem and phloem in its vascular bundles, leaves are composed mainly of parenchyma cells. Some parenchyma cells, as in the epidermis, are specialized for light penetration and focusing or regulation of gas exchange, but others are among the least specialized cells in plant tissue, and may remain totipotent, capable of dividing to produce new populations of undifferentiated cells, throughout their lives. Parenchyma cells have thin, permeable primary walls enabling the transport of small molecules between them, and their cytoplasm is responsible for a wide range of biochemical functions such as nectar secretion, or the manufacture of secondary products that discourage herbivory. Parenchyma cells that contain many chloroplasts and are concerned primarily with photosynthesis are called chlorenchyma cells. Others, such as the majority of the parenchyma cells in potato tubers and the seed cotyledons of legumes, have a storage function.

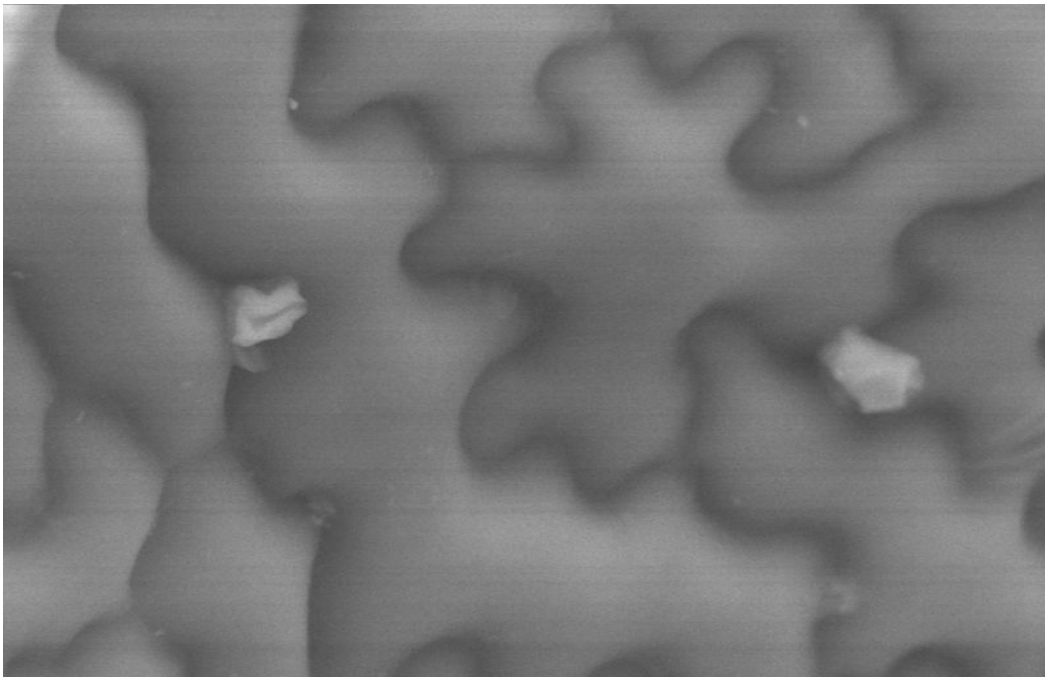
- Collenchyma cells - collenchyma cells are alive at maturity and have only a primary wall. These cells mature from meristem derivatives that initially resemble parenchyma, but differences quickly become apparent. Plastids do not develop, and the secretory apparatus (ER and Golgi) proliferates to secrete additional primary wall. The wall is most commonly thickest at the corners, where three or more cells come in contact, and thinnest where only two cells come in contact, though other arrangements of the wall thickening are possible.

Pectin and hemicellulose are the dominant constituents of collenchyma cell walls of dicotyledon angiosperms, which may contain as little as 20% of cellulose in *Petasites*. Collenchyma cells are typically quite elongated, and may divide transversely to give a septate appearance. The role of this cell type is to support the plant in axes still growing in length, and to confer flexibility and tensile strength on tissues. The primary wall lacks lignin that would make it tough and rigid, so this cell type provides what could be called plastic support - support that can hold a young stem or petiole into the air, but in cells that can be stretched as the cells around them elongate. Stretchable support (without elastic snap-back) is a good way to describe what collenchyma does. Parts of the strings in celery are collenchyma.

- Sclerenchyma cells - Sclerenchyma cells (from the Greek **skleros**, *hard*) are hard and tough cells with a function in mechanical support. They are of two broad types – sclereids or stone cells and fibres. The cells develop an extensive secondary cell wall that is laid down on the inside of the primary cell wall. The secondary wall is impregnated with lignin, making it hard and impermeable to water. Thus, these cells cannot survive for long' as they cannot exchange sufficient material to maintain active metabolism. Sclerenchyma cells are typically dead at functional maturity, and the cytoplasm is missing, leaving an empty central cavity.

Functions for sclereid cells (hard cells that give leaves or fruits a gritty texture) include discouraging herbivory, by damaging digestive passages in small insect larval stages, and physical protection (a solid tissue of hard sclereid cells form the pit wall in a peach and many other fruits). Functions of fibres include provision of load-bearing support and tensile strength to the leaves and stems of herbaceous plants. Sclerenchyma fibres are not involved in conduction, either of water and nutrients (as in the xylem) or of carbon compounds (as in the phloem), but it is likely that they may have evolved as modifications of xylem and phloem initials in early land plants.

# Tissue types



cells of *Arabidopsis thaliana* epidermis

The major classes of cells differentiate from undifferentiated meristematic cells (analogous to the stem cells of animals) to form the tissue structures of roots, stems, leaves, flowers, and reproductive structures.

Xylem cells are elongated cells with lignified secondary thickening of the cell walls. Xylem cells are specialised for conduction of water, and first appeared in plants during their transition to land in the Silurian period more than 425 million years ago. The possession of xylem defines the vascular plants or Tracheophytes. Xylem tracheids are pointed, elongated xylem cells, the simplest of which have continuous primary cell walls and lignified secondary wall thickenings in the form of rings, hoops, or reticulate networks. More complex tracheids with valve-like perforations called bordered pits characterise the gymnosperms. The ferns and other pteridophytes and the gymnosperms have only xylem tracheids, while the angiosperms also have xylem vessels. Vessel members are hollow xylem cells aligned end-to-end, without end walls that are assembled into long continuous tubes. The bryophytes lack true xylem cells, but their sporophytes have a water-conducting tissue known as the hydrome that is composed of elongated cells of simpler construction.

Phloem is a specialised tissue for food conduction in higher plants. The conduction of food is a complex process that is carried in the plant with the help of special cell called phloem cells. These cells conduct inter- and intra-cellular fluid (food - proteins and other essential elements required by the plant for its metabolism) through the process of osmosis. This phenomenon is called ascent of sap in plants. Phloem consists of two cell

types, the sieve tubes and the intimately-associated companion cells. The sieve tube elements lack nuclei and ribosomes, and their metabolism and functions are regulated by the adjacent nucleate companion cells. Sieve tubes are joined end-to-end with perforate end-plates between known as *sieve plates*, which allow transport of photosynthate between the sieve elements. The companion cells, connected to the sieve tubes via plasmodesmata, are responsible for loading the phloem with sugars. The bryophytes lack phloem, but moss sporophytes have a simpler tissue with analogous function known as the leptome.

Plant epidermal cells are specialised parenchyma cells covering the external surfaces of leaves, stems and roots. The epidermal cells of aerial organs arise from the superficial layer of cells known as the *tunica* (L1 and L2 layers) that covers the plant shoot apex, whereas the cortex and vascular tissues arise from innermost layer of the shoot apex known as the *corpus* (L3 layer). The epidermis of roots originates from the layer of cells immediately beneath the root cap.

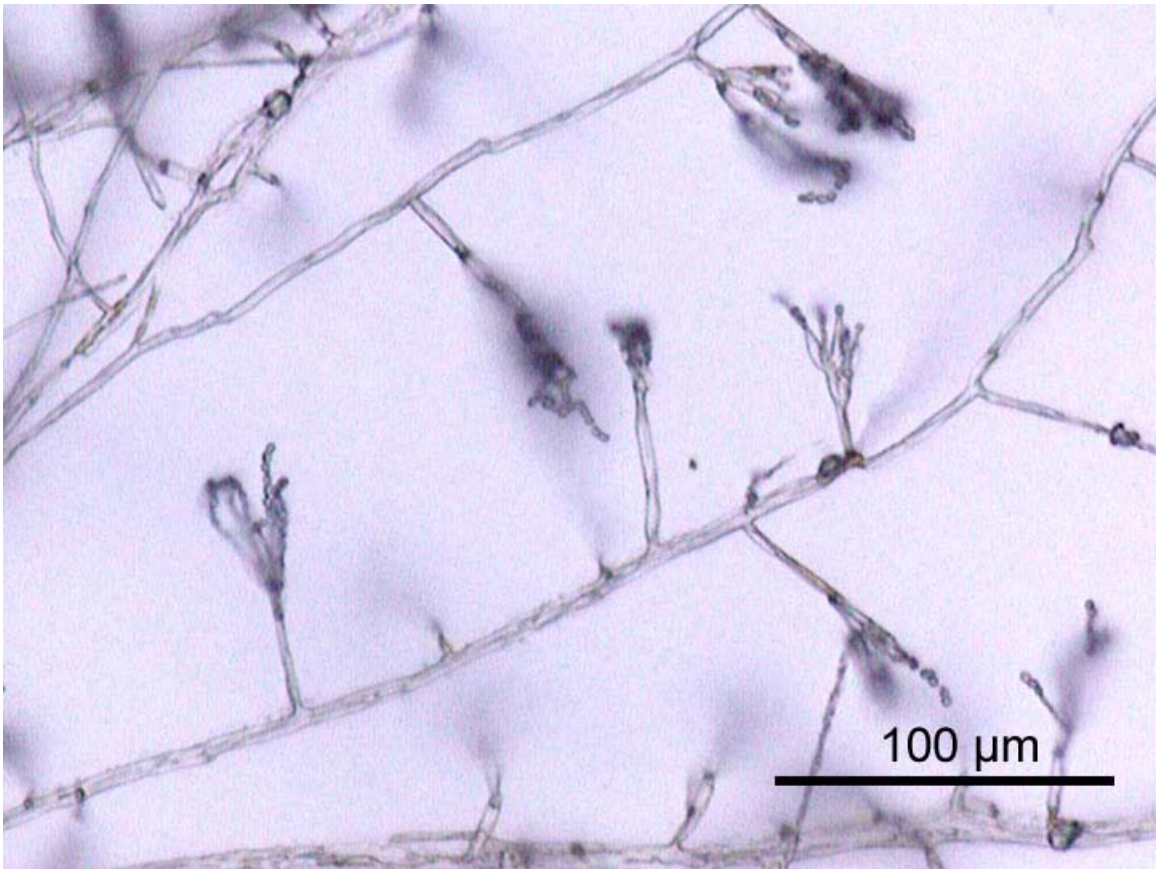
The epidermis of all aerial organs, but not roots, is covered with a cuticle made of waxes and the polyester cutin. Several cell types may be present in the epidermis. Notable among these are the stomatal guard cells, glandular and clothing hairs or trichomes, and the root hairs of primary roots. In the shoot epidermis of most plants, only the guard cells have chloroplasts. The epidermal cells of the primary shoot are thought to be the only plant cells with the biochemical capacity to synthesize cutin.

# Organelles

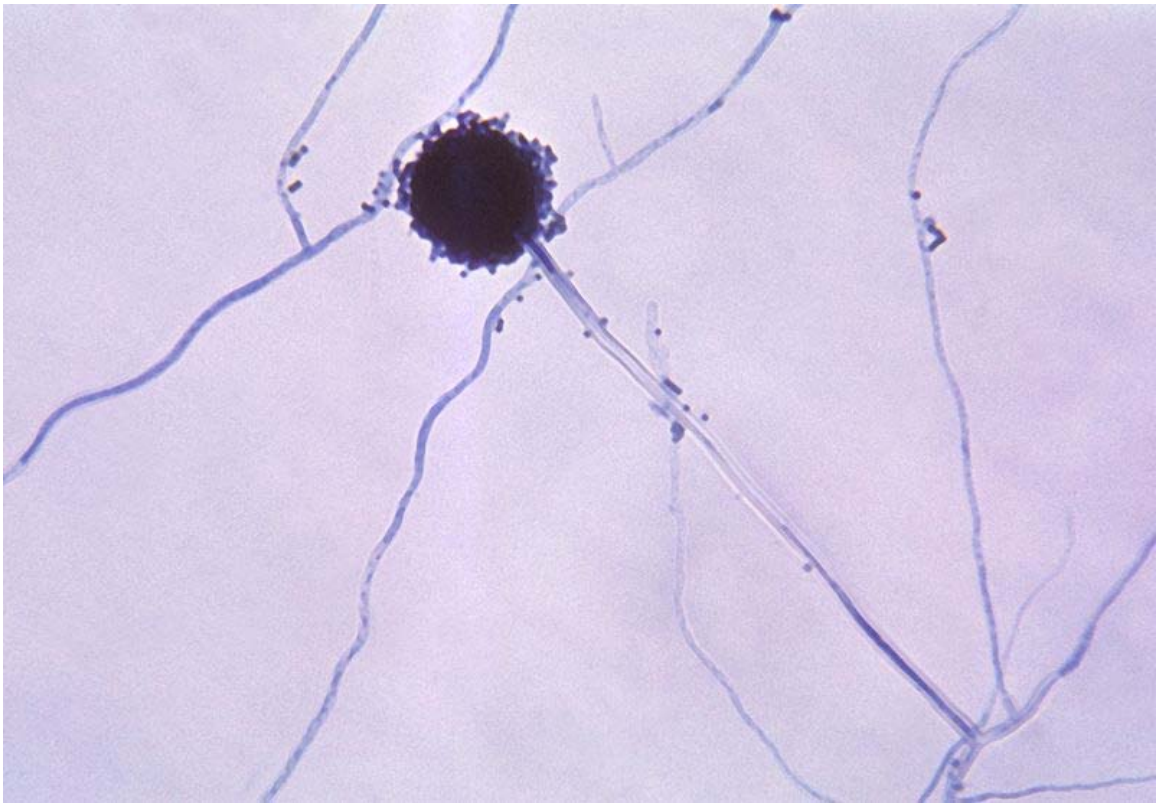
- Cell membrane
- Cell wall
- Nuclear membrane
- Plasmodesma
- Vacuole
- Plastids
- Chloroplast
- Leucoplast
- Chromoplast
- Golgi Bodies
- Ribosome
- Endoplasmic reticulum
- Mitochondrion
- Lysosome
- Cytoplasm
- Nucleus
- DNA
- Chromatin
- RNA
- Cytoskeleton
- Nucleolus

**Chapter- 3**

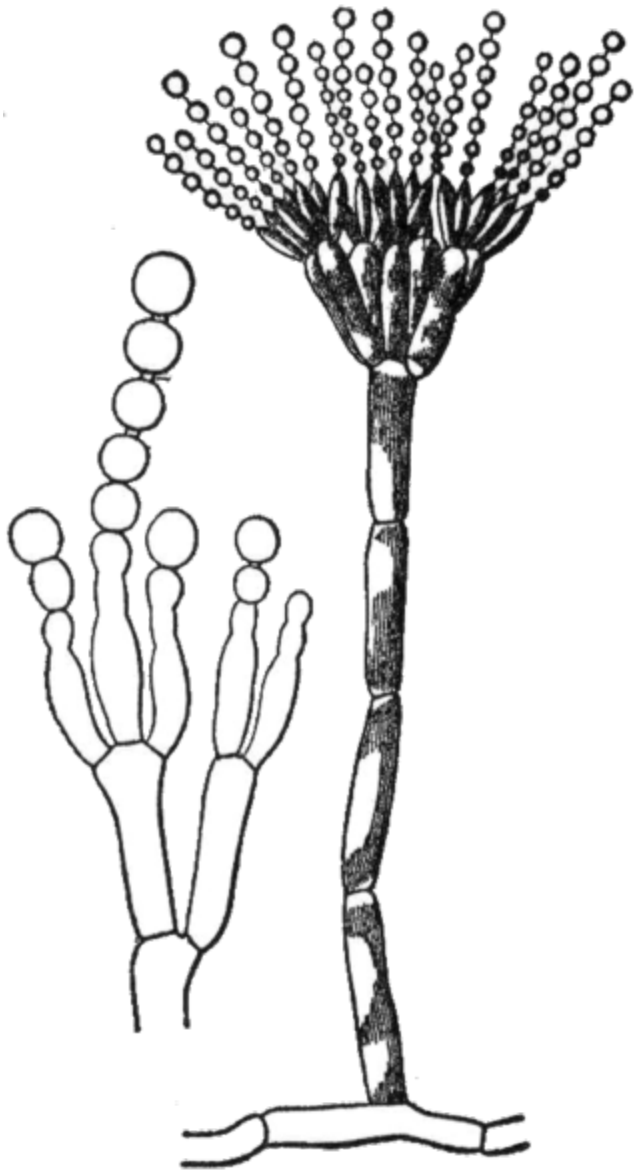
# Hypha




Hyphae of Penicillium



Aspergillus niger



Conidia on conidiophores

A **hypha** (plural **hyphae**) is a long, branching filamentous structure of a fungus, and also of unrelated Actinobacteria. In most fungi, hyphae are the main mode of vegetative growth, and are collectively called a mycelium; yeasts are unicellular fungi that do not grow as hyphae.

# Structure

A hypha consists of one or more cells surrounded by a tubular cell wall. In most fungi, hyphae are divided into cells by internal cross-walls called "septa" (singular septum). Septa are usually perforated by pores large enough for ribosomes, mitochondria and

sometimes nuclei to flow between cells. The major structural polymer in fungal cell walls is typically chitin, in contrast to plants that have cellulosic cell walls. Some fungi have aseptate hyphae, meaning their hyphae are not partitioned by septa.

# Growth

Hyphae grow at their tips. During tip growth, cell walls are extended by the external assembly and polymerization of cell wall components, and the internal production of new cell membrane. The spitzenkörper is an intracellular organelle associated with tip growth. It is composed of an aggregation of membrane-bound vesicles containing cell wall components. The spitzenkörper is part of the endomembrane system of fungi, holding and releasing vesicles it receives from the Golgi apparatus. These vesicles travel to the cell membrane via the cytoskeleton and release their contents outside the cell by the process of exocytosis, where it can then be transported to where it is needed. Vesicle membranes contribute to growth of the cell membrane while their contents form new cell wall. The spitzenkörper moves along the apex of the hyphal strand and generates apical growth and branching; the apical growth rate of the hyphal strand parallels and is regulated by the movement of the spitzenkörper.

As a hypha extends, septa may be formed behind the growing tip to partition each hypha into individual cells. Hyphae can branch through the bifurcation of a growing tip, or by the emergence of a new tip from an established hypha.

# Modifications

Hyphae may be modified in many different ways to serve specific functions. Some parasitic fungi form haustoria that function in absorption within the host cells. The arbuscules of mutualistic mycorrhizal fungi serve a similar function in nutrient exchange, so are important in assisting nutrient and water absorption by plants. Hyphae are found enveloping the gonidia in lichens, making up a large part of their structure. In nematode-trapping fungi, hyphae may be modified into trapping structures such as constricting rings and adhesive nets. Mycelial cords can be formed to transfer nutrients over larger distances.

# Types

## Classification based on cell division

- Septate (with septa)
    - *Aspergillus* and many other species have septate hyphae.

- Aseptate or coenocytic (without septa)
    - Non-septate hyphae are associated with Mucor, some zygomycetes, and other fungi.

- "Pseudohyphae" are distinguished from true hyphae by their method of growth, relative frailty and lack of cytoplasmic connection between the cells.
    - Yeast can form pseudohyphae. They are the result of a sort of incomplete budding where the cells remain attached after division.

## Classification based on cell wall and overall form

Characteristics of hyphae can be important in fungal classification. In basidiomycete taxonomy, hyphae that comprise the fruiting body can be identified as generative, skeletal, or binding hyphae.

- **Generative** hyphae are relatively undifferentiated and can develop reproductive structures. They are typically thin-walled, occasionally developing slightly thickened walls, usually have frequent septa, and may or may not have clamp connections. They may be embedded in mucilage or gelatinized materials.
- **Skeletal** hyphae are of two basic types. The classical form is thick-walled and very long in comparison to the frequently septate generative hyphae, which are unbranched or rarely branched, with little cell content. They have few septa and lack clamp connections. Fusiform skeletal hyphae are the second form of skeletal hyphae. Unlike typical skeletal hyphae these are swollen centrally and often exceedingly broad, hence giving the hypha a fusiform shape.
- **Binding** hyphae are thick-walled and frequent branched. Often they resemble deer antlers or defoliated trees because of the many tapering branches.

Based on the generative, skeletal and binding hyphal types, in 1932 E. J. H. Corner applied the terms monomitic, dimitic, and trimitic to hyphal systems, in order to improve the classification of polypores.

- Every fungus must contain generative hyphae. A fungus which only contains this type, as do fleshy mushrooms such as agarics, is referred to as **monomitic**.

- Skeletal and binding hyphae give leathery and woody fungi such as polypores their tough consistency. If a fungus contains all three types (example: *Trametes*), it is called **trimitic**.

- If a fungus contains generative hyphae and just one of the other two types, it is called **dimitic**. In fact dimitic fungi almost always contain generative and skeletal hyphae; there is one exceptional genus, *Laetiporus* that includes only generative and binding hyphae.

Fungi that form fusiform skeletal hyphae bound by generative hyphae are said to have **sarcodimitic** hyphal systems. A few fungi form fusiform skeletal hyphae, generative hyphae, and binding hyphae, and these are said to have **sarcotrimitic** hyphal systems. These terms were introduced as a later refinement by E. J. H. Corner in 1966.

## Classification based on refractive appearance

Hyphae are described as "gloeoplerous" ("gloeohyphae") if their high refractive index gives them an oily or granular appearance under the microscope. These cells may be yellowish or clear (hyaline). They can sometimes selectively be coloured by sulphovanillin or other reagents. The specialized cells termed cystidia can also be gloeoplerous.

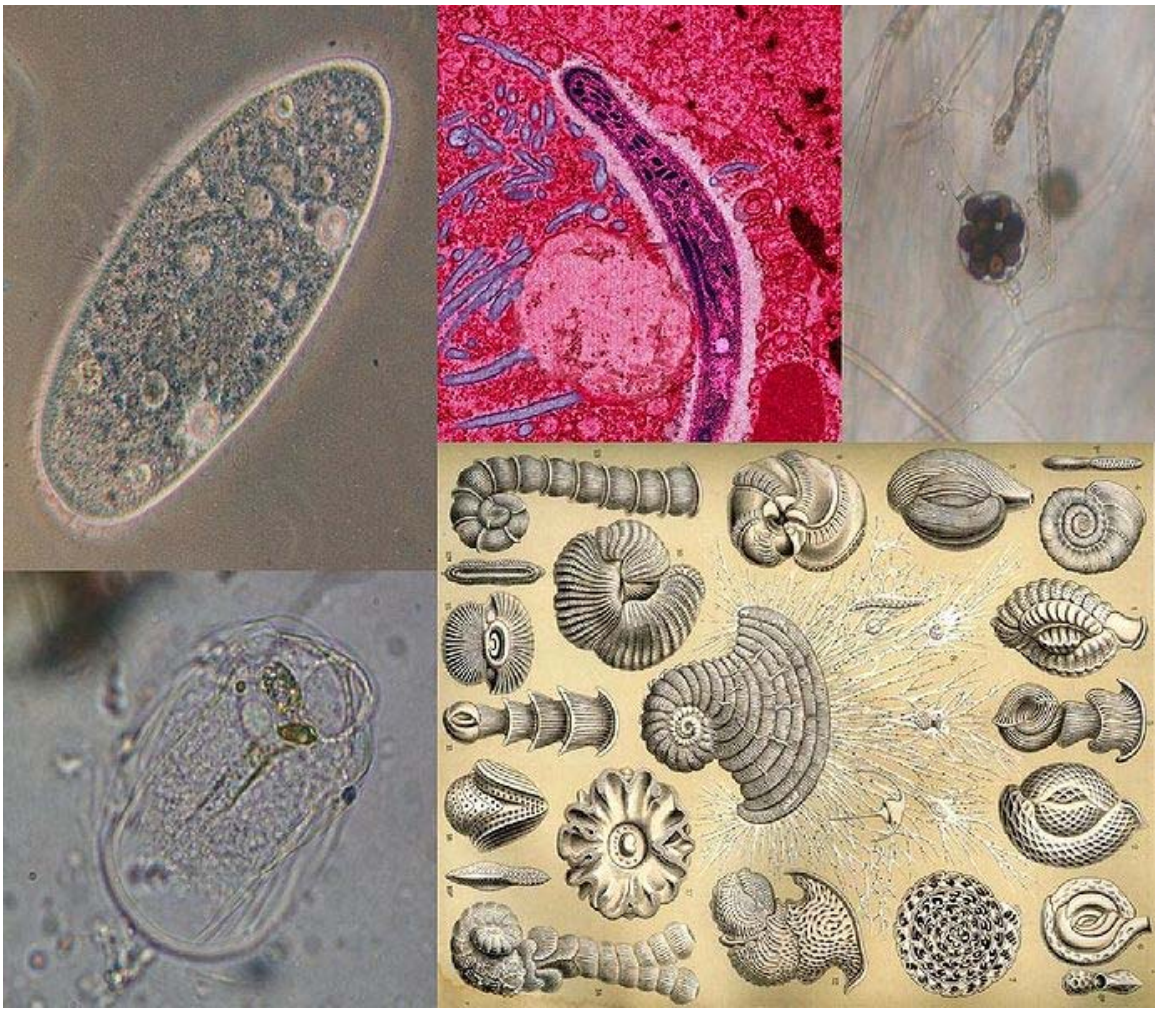
## Chapter- 4

# Protist

| Protist<br>Temporal range: Neoproterozoic - Recent |
|---|
|  |
| **Scientific classification** |
| Domain: **Eukarya** |
| Kingdom: **Protista*** <br> Haeckel, 1866 |
| **Typical phyla** |

- **Chromalveolata**
  - Heterokontophyta
  - Haptophyta
  - Cryptophyta (cryptomonads)
  - **Alveolata**
    - Dinoflagellata
    - Apicomplexa
    - Ciliophora (ciliates)
- **Excavata**
  - Euglenozoa
  - Percolozoa
  - Metamonada
- **Rhizaria**
  - Radiolaria

    - Foraminifera
    - Cercozoa
- **Archaeplastida (in part)**
    - Rhodophyta (red algae)
    - Glaucophyta (basal archaeplastids)
- **Unikonta (in part)**
    - Amoebozoa
    - Choanozoa



**Protists** are a diverse group of eukaryotic microorganisms. Historically, protists were treated as the kingdom **Protista**, which includes mostly unicellular organisms that do not fit into the other kingdoms, but this group is contested in modern taxonomy. Instead, it is "better regarded as a loose grouping of 30 or 40 disparate phyla with diverse combinations of trophic modes, mechanisms of motility, cell coverings and life cycles."

The protists do not have much in common besides a relatively simple organization—either they are unicellular, or they are multicellular without specialized tissues. This simple cellular organization distinguishes the protists from other eukaryotes, such as fungi, animals and plants.

The term *protista* was first used by Ernst Haeckel in 1866. Protists were traditionally subdivided into several groups based on similarities to the "higher" kingdoms: the one-celled animal-like protozoa, the plant-like protophyta (mostly one-celled algae), and the fungus-like slime molds and water molds. Because these groups often overlap, they have been replaced by phylogenetic-based classifications. However, they are still useful as informal names for describing the morphology and ecology of protists.

Protists live in almost any environment that contains liquid water. Many protists, such as the algae, are photosynthetic and are vital primary producers in ecosystems, particularly in the ocean as part of the plankton. Other protists, such as the Kinetoplastids and Apicomplexa, are responsible for a range of serious human diseases, such as malaria and sleeping sickness.

# Classification

## Historical classifications

The first division of the protists from other organisms came in the 1830s, when the German biologist Georg A. Goldfuss introduced the word *protozoa* to refer to organisms such as ciliates and corals. This group was expanded in 1845 to include all "unicellular animals", such as Foraminifera and amoebae. The formal taxonomic category *Protoctista* was first proposed in the early 1860s by John Hogg, who argued that the protists should include what he saw as primitive unicellular forms of both plants and animals. He defined the Protoctista as a "fourth kingdom of nature", in addition to the then-traditional kingdoms of plants, animals and minerals. The kingdom of minerals was later removed from taxonomy by Ernst Haeckel, leaving plants, animals, and the protists as a “kingdom of primitive forms”.

Herbert Copeland resurrected Hogg's label almost a century later, arguing that "Protoctista" literally meant "first established beings", Copeland complained that Haeckel's term *protista* included anucleated microbes such as bacteria. Copeland's use of the term *protoctista* did not. In contrast, Copeland's term included nucleated eukaryotes such as diatoms, green algae and fungi. This classification was the basis for Whittaker's later definition of Fungi, Animalia, Plantae and Protista as the four kingdoms of life. The kingdom Protista was later modified to separate prokaryotes into the separate kingdom of Monera, leaving the protists as a group of eukaryotic microorganisms. These five kingdoms remained the accepted classification until the development of molecular phylogenetics in the late 20th century, when it became apparent that neither protists nor monera were single groups of related organisms (they were not monophyletic groups).

### Modern classifications

Currently, the term *protist* is used to refer to unicellular eukaryotes that either exist as independent cells, or if they occur in colonies, do not show differentiation into tissues. The term *protozoa* is used to refer to heterotrophic species of protists that do not form filaments. These terms are not used in current taxonomy, and are retained only as convenient ways to refer to these organisms.

The taxonomy of protists is still changing. Newer classifications attempt to present monophyletic groups based on ultrastructure, biochemistry, and genetics. Because the protists as a whole are paraphyletic, such systems often split up or abandon the kingdom, instead treating the protist groups as separate lines of eukaryotes. The recent scheme by Adl *et al.* (2005) is an example that does not bother with formal ranks (phylum, class, etc.) and instead lists organisms in hierarchical lists. This is intended to make the classification more stable in the long term and easier to update. Some of the main groups of protists, which may be treated as phyla, are listed in the taxobox at right. Many are thought to be monophyletic, though there is still uncertainty. For instance, the excavates are probably not monophyletic and the chromalveolates are probably only monophyletic if the haptophytes and cryptomonads are excluded.

## Metabolism

Nutrition in some different types of protists is variable. In flagellates, for example, filter feeding may sometimes occur where the flagella find the prey. Other protists can engulf bacteria and digest them internally, by extending their cell membrane around the food material to form a food vacuole. This is then taken into the cell via endocytosis (usually phagocytosis; sometimes pinocytosis).

Nutritional types in protist metabolism

| Nutritional type | Source of energy | Source of carbon | Examples |
|---|---|---|---|
| Phototrophs | Sunlight | Organic compounds or carbon fixation | Algae, Dinoflagellates or Euglena |
| Organotrophs | Organic compounds | Organic compounds | Apicomplexa, Trypanosomes or Amoebae |

## Reproduction

Some protists reproduce sexually (conjugation), while others reproduce asexually (binary fission).

Some species, for example *Plasmodium falciparum*, have extremely complex life cycles that involve multiple forms of the organism, some of which reproduce sexually and others asexually. However, it is unclear how frequently sexual reproduction causes genetic exchange between different strains of *Plasmodium* in nature and most populations of parasitic protists may be clonal lines that rarely exchange genes with other members of their species.

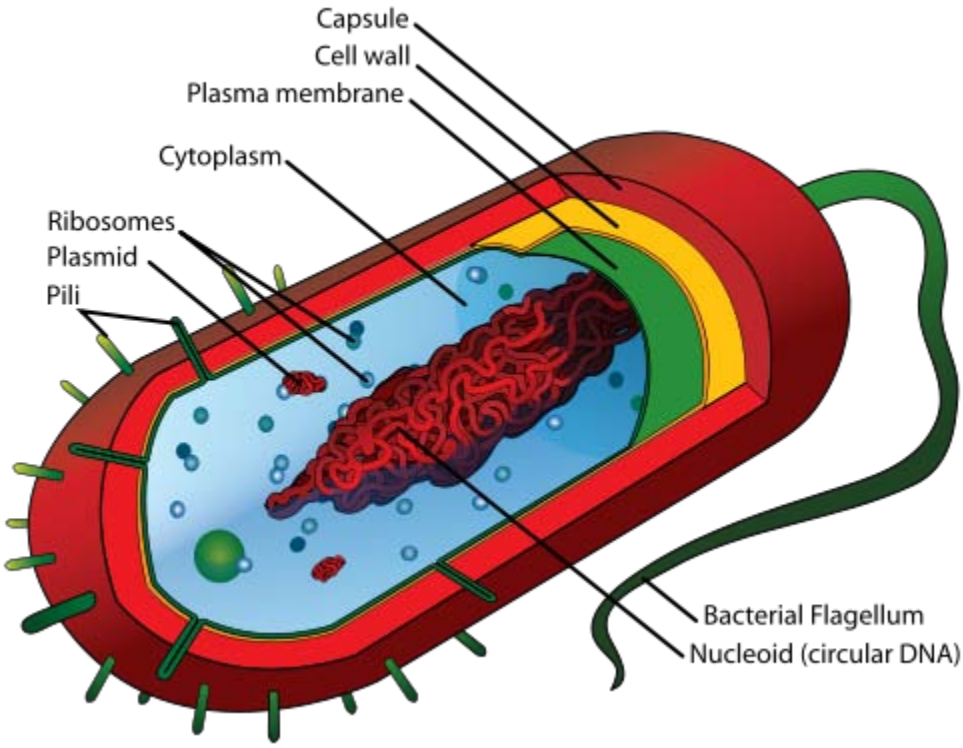
## Role as pathogens

Some protists are significant pathogens of both animals and plants; for example *Plasmodium falciparum*, which causes malaria in humans, and *Phytophthora infestans*, which causes potato blight. A more thorough understanding of protist biology may allow these diseases to be treated more efficiently.

Researchers from the Agricultural Research Service are taking advantage of protists as pathogens in an effort to control red imported fire ant (*Solenopsis invicta*) populations in Argentina. With the help of spore-producing protists such as *Kneallhazia solenopsae* the red fire ant populations can be reduced by 53-100%. Researchers have also found a way to infect phorid flies with the protist without harming the flies. This is important because the flies act as a vector to infect the red fire ant population with the pathogenic protist.

## Chapter- 5

# Prokaryote




Cell structure of a bacterium, one of the two domains of prokaryotic life.

The **prokaryotes** are a group of organisms that lack a cell nucleus (= karyon), or any other membrane-bound organelles. They differ from the eukaryotes, which have a cell nucleus. Most are unicellular, but a few prokaryotes such as myxobacteria have multicellular stages in their life cycles. The word *prokaryote* comes from the Greek *πρό- (pro-)* "before" + *καρυόν (karyon)* "nut or kernel".

The prokaryotes are divided into two domains: the bacteria and the archaea. Archaea were recognized as a domain of life in 1990. These organisms were originally thought to

live only in inhospitable conditions such as extremes of temperature, pH, and radiation but have since been found in all types of habitats.

## Relationship to eukaryotes

A distinction between prokaryotes and eukaryotes (meaning true kernel, also spelled "eucaryotes") is that eukaryotes do have "true" nuclei containing their DNA, whereas the genetic material in prokaryotes is not membrane-bound. Eukaryotic organisms may be unicellular, as in amoebae, or multicellular, as in plants and animals. The difference between the structure of prokaryotes and eukaryotes is so great that it is sometimes considered to be the most important distinction among groups of organisms. However, a criticism of this classification is that the word "prokaryote" is based on what these organisms are not (they are not eukaryotic), rather than what they are (either archaea or bacteria). In 1977, Carl Woese proposed dividing prokaryotes into the Bacteria and Archaea (originally Eubacteria and Archaebacteria) because of the major differences in the structure and genetics between the two groups of organisms. This arrangement of Eukaryota (also called "Eukarya"), Bacteria, and Archaea is called the three-domain system replacing the traditional two-empire system.

The cell structure of prokaryotes differs greatly from that of eukaryotes. The defining characteristic is the absence of a nucleus. Also the size of Ribosomes in prokaryotes are smaller than in eukaryotes, which is now where respiration takes place.The genomes of prokaryotes are held within an irregular DNA/protein complex in the cytosol called the nucleoid, which lacks a nuclear envelope. Prokaryotes generally lack membrane-bound cell compartments: such as mitochondria and chloroplasts. Instead processes such as oxidative phosphorylation and photosynthesis take place across the prokaryotic plasma membrane. However, prokaryotes do possess some internal structures, such as cytoskeletons, and the bacterial order Planctomycetes have a membrane around their nucleoid and contain other membrane-bound cellular structures. Both eukaryotes and prokaryotes contain large RNA/protein structures called ribosomes, which produce protein. Prokaryotes are usually much smaller than eukaryotic cells.

Prokaryotes also differ from eukaryotes in that they contain only a single loop of stable chromosomal DNA stored in an area named the nucleoid, while eukaryote DNA is found on tightly bound and organized chromosomes. Although some eukaryotes have satellite DNA structures called plasmids, these are generally regarded as a prokaryote feature, and many important genes in prokaryotes are stored on plasmids.

Prokaryotes have a larger surface-area-to-volume ratio giving them a higher metabolic rate, a higher growth rate and consequently a shorter generation time compared to Eukaryotes.

## Sociality

While prokaryotes are still commonly imagined to be strictly unicellular, most are capable of forming stable aggregate communities. When such communities are encased in a stabilizing polymer matrix ("slime"), they may be called "biofilms". Cells in biofilms often show distinct patterns of gene expression (phenotypic differentiation) in time and space. Also, like multicellular eukaryotes, these changes in expression appear to often result from cell-to-cell signaling, a phenomenon known as quorum sensing.

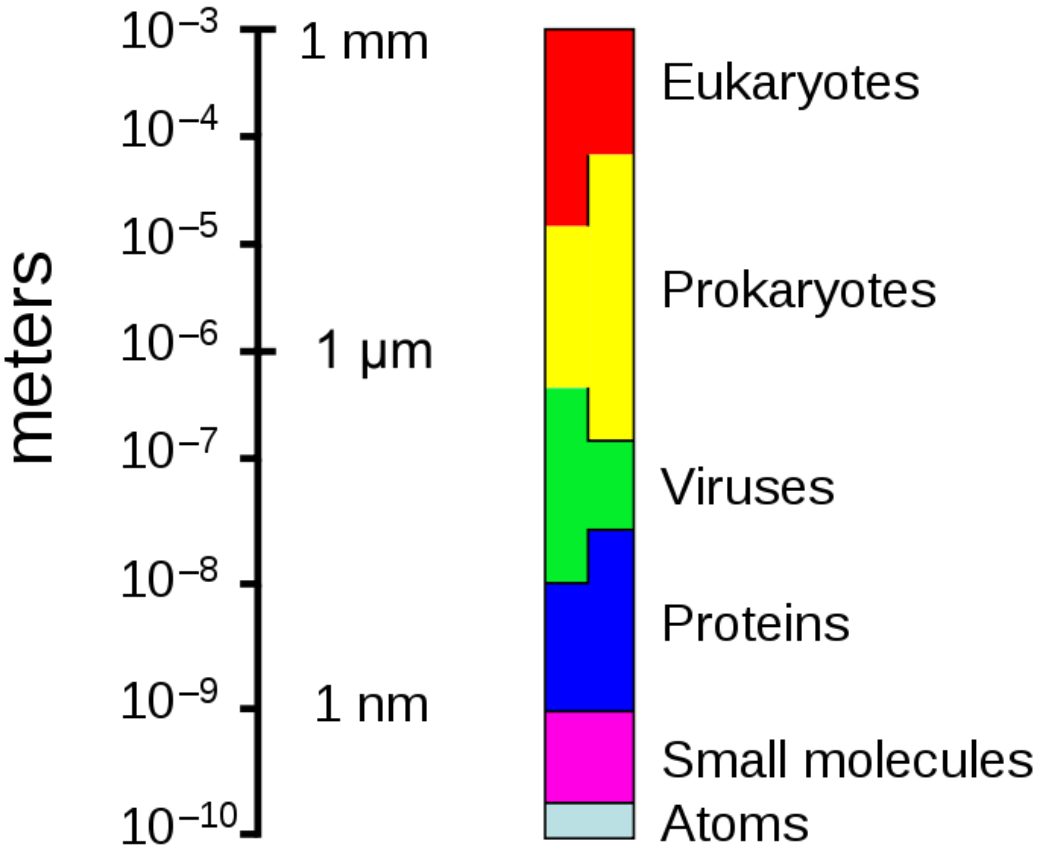
Biofilms may be highly heterogeneous and structurally complex and may attach to solid surfaces, or exist at liquid-air interfaces, or potentially even liquid-liquid interfaces. Bacterial biofilms are often made up of microcolonies (approximately dome-shaped masses of bacteria and matrix) separated by "voids" through which the medium (e.g. water) may flow relatively uninhibited. The microcolonies may join together above the substratum to form a continuous layer, closing the network of channels separating microcolonies. This structural complexity—combined with observations that oxygen limitation (a ubiquitous challenge for anything growing in size beyond the scale of diffusion) is at least partially eased by movement of medium throughout the biofilm—has led some to speculate that this may constitute a circulatory system and many researchers have started calling prokaryotic communities multicellular (for example ). Differential cell expression, collective behavior, signaling, programmed cell death, and (in some cases) discrete biological dispersal events all seem to point in this direction. However, these colonies are seldom if ever founded by a single founder (in the way that animals and plants are founded by single cells), which presents a number of theoretical issues. Most explanations of co-operation and the evolution of multicellularity have focused on high relatedness between members of a group (or colony, or whole organism). If a copy of a gene is present in all members of a group, behaviors that promote cooperation between members may permit those members to have (on average) greater fitness than a similar group of selfish individuals.

Should these instances of prokaryotic sociality prove to be the rule rather than the exception it would have serious implications for the way we view prokaryotes in general and the way we deal with them in medicine. Bacterial biofilms may be 100x more resistant to antibiotics than free-living unicells and may be nearly impossible to remove from surfaces once they have colonized them. Other aspects of bacterial cooperation—such as bacterial conjugation and quorum-sensing mediated pathogenicity—present additional challenges to researchers and medical professionals seeking to treat the associated diseases.

## Reproduction

Bacteria and archaea reproduce through asexual reproduction, usually by binary fission or budding. Genetic exchange and recombination still occur, but this is a form of horizontal gene transfer and is not a replicative process, simply involving DNA being transferred between two cells, as in bacterial conjugation.

## Structure




The sizes of prokaryotes relative to other organisms and biomolecules

Recent research indicates that all prokaryotes actually do have cytoskeletons, albeit more primitive than those of eukaryotes. Besides homologues of actin and tubulin (MreB and FtsZ) the helically arranged building block of the flagellum, flagellin, is one of the most significant cytoskeletal proteins of bacteria as it provides structural backgrounds of chemotaxis, the basic cell physiological response of bacteria. At least some prokaryotes also contain intracellular structures which can be seen as primitive organelles. Membranous organelles (a.k.a. intracellular membranes) are known in some groups of prokaryotes, such as vacuoles or membrane systems devoted to special metabolic properties, e.g. photosynthesis or chemolithotrophy. Additionally, some species also contain protein-enclosed microcompartments, which have distinct physiological roles (e.g. carboxysomes or gas vacuoles).

Most prokaryotes are between 1 µm and 10 µm, but they can vary in size from 0.2 µm to 750 µm (Thiomargarita namibiensis).

### Prokaryotic cell Structure

Flagellum
Cell membrane
Cell wall (except genus Mycoplasma)
Cytoplasm
Ribosome
Nucleoid
Glycocalyx
Inclusions

## Morphology of prokaryotic cells

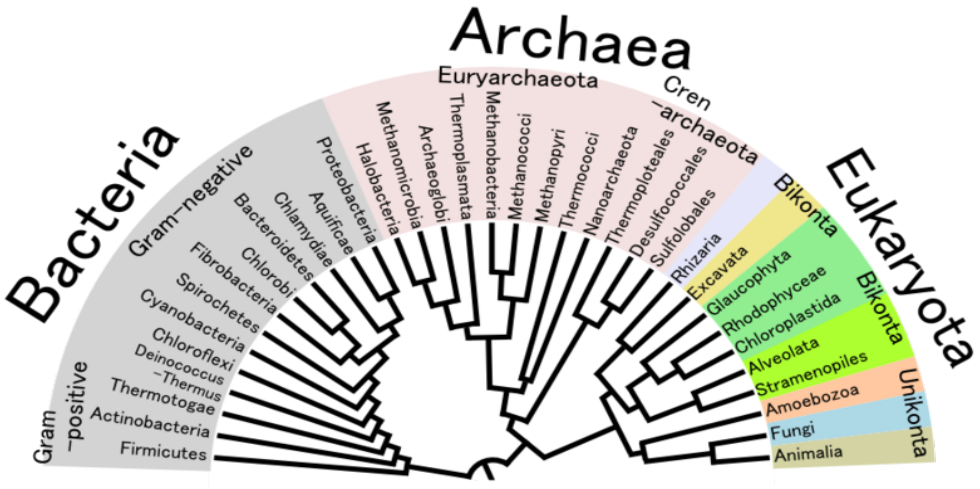
Prokaryotic cells have various shapes; the four basic shapes are:

- Cocci - spherical
- Bacilli - rod shaped
- Spirochaete - spiral shaped
- Vibrio - comma shaped

## Environment

Prokaryotes live in nearly all environments on earth where there is liquid water. Some archaea and bacteria thrive in harsh conditions, such as high temperatures (thermophiles) or high salinity (halophiles). Organisms such as these are referred to as extremophiles. Many archaea grow as plankton in the oceans. Symbiotic prokaryotes live in or on the bodies of other organisms, including humans.

## Evolution of prokaryotes



Phylogenetic tree showing the diversity of prokaryotes, compared to eukaryotes.

The current model of the evolution of the first living organisms is that these were some form of prokaryotes, which may have evolved out of protobionts. The eukaryotes are generally thought to have evolved later in the history of life. However, some authors have questioned this conclusion, arguing that the current set of prokaryotic species may have evolved from more complex eukaryotic ancestors through a process of simplification. Others have argued that the three domains of life arose simultaneously, from a set of varied cells that formed a single a gene pool. This controversy was summarized in 2005:

There is no consensus among biologists concerning the position of the eukaryotes in the overall scheme of cell evolution. Current opinions on the origin and position of eukaryotes span a broad spectrum including the views that eukaryotes arose first in evolution and that prokaryotes descend from them, that eukaryotes arose contemporaneously with eubacteria and archeabacteria and hence represent a primary line of descent of equal age and rank as the prokaryotes, that eukaryotes arose through a symbiotic event entailing an endosymbiotic origin of the nucleus, that eukaryotes arose without endosymbiosis, and that eukaryotes arose through a symbiotic event entailing a simultaneous endosymbiotic origin of the flagellum and the nucleus, in addition to many other models, which have been reviewed and summarized elsewhere.

The oldest known fossilized prokaryotes were laid down approximately 3.5 billion years ago, only about 1 billion years after the formation of the Earth's crust. Even today, prokaryotes are perhaps the most successful and abundant life forms. Eukaryotes only appear in the fossil record later, and may have formed from endosymbiosis of multiple prokaryote ancestors. The oldest known fossil eukaryotes are about 1.7 billion years old. However, some genetic evidence suggests eukaryotes appeared as early as 3 billion years ago.

While Earth is the only place in the universe where life is known to exist, some have suggested that there is evidence on Mars of fossil or living prokaryotes; but this possibility remains the subject of considerable debate and skepticism.

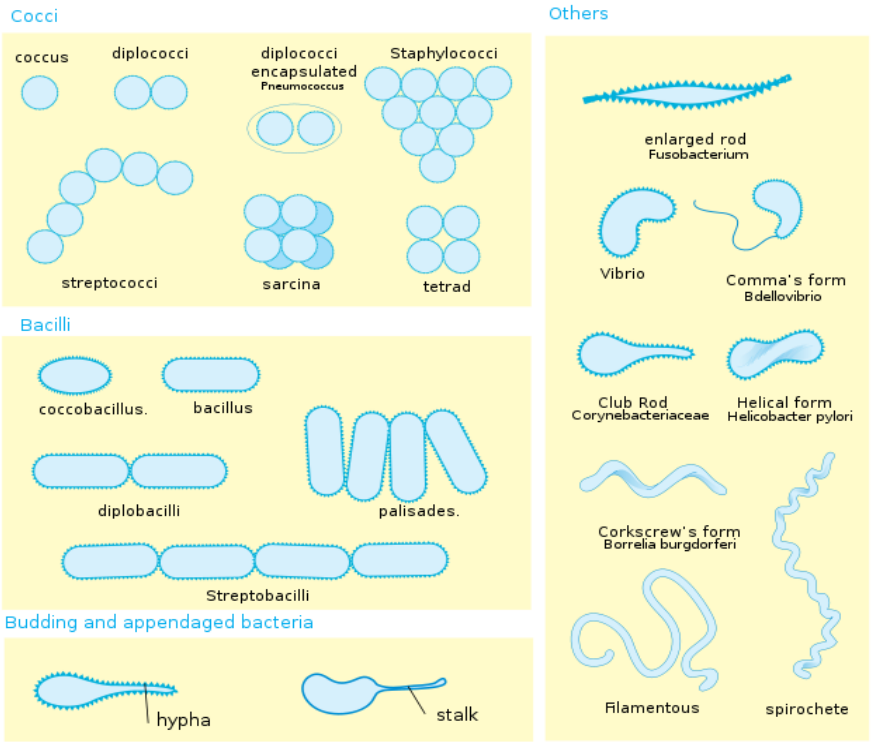
Prokaryotes have diversified greatly throughout their long existence. The metabolism of prokaryotes is far more varied than that of eukaryotes, leading to many highly distinct prokaryotic types. For example, in addition to using photosynthesis or organic compounds for energy, as eukaryotes do, prokaryotes may obtain energy from inorganic compounds such as hydrogen sulfide. This enables prokaryotes to thrive in harsh environments as cold as the snow surface of Antarctica, and as hot as undersea hydrothermal vents and land-based hot springs.

Chapter- 6

# Bacterial Cell Structure

Bacteria, despite their simplicity, contain a well developed cell structure which is responsible for many of their unique biological properties. Many structural features are unique to bacteria and are not found among archaea or eukaryotes. Because of the simplicity of bacteria relative to larger organisms and the ease with which they can be manipulated experimentally, the cell structure of bacteria has been well studied, revealing many biochemical principles that have been subsequently applied to other organisms.

## Cell morphology




Bacteria come in a wide variety of shapes

Perhaps the most elemental structural property of bacteria is cell morphology (shape). Typical examples include:

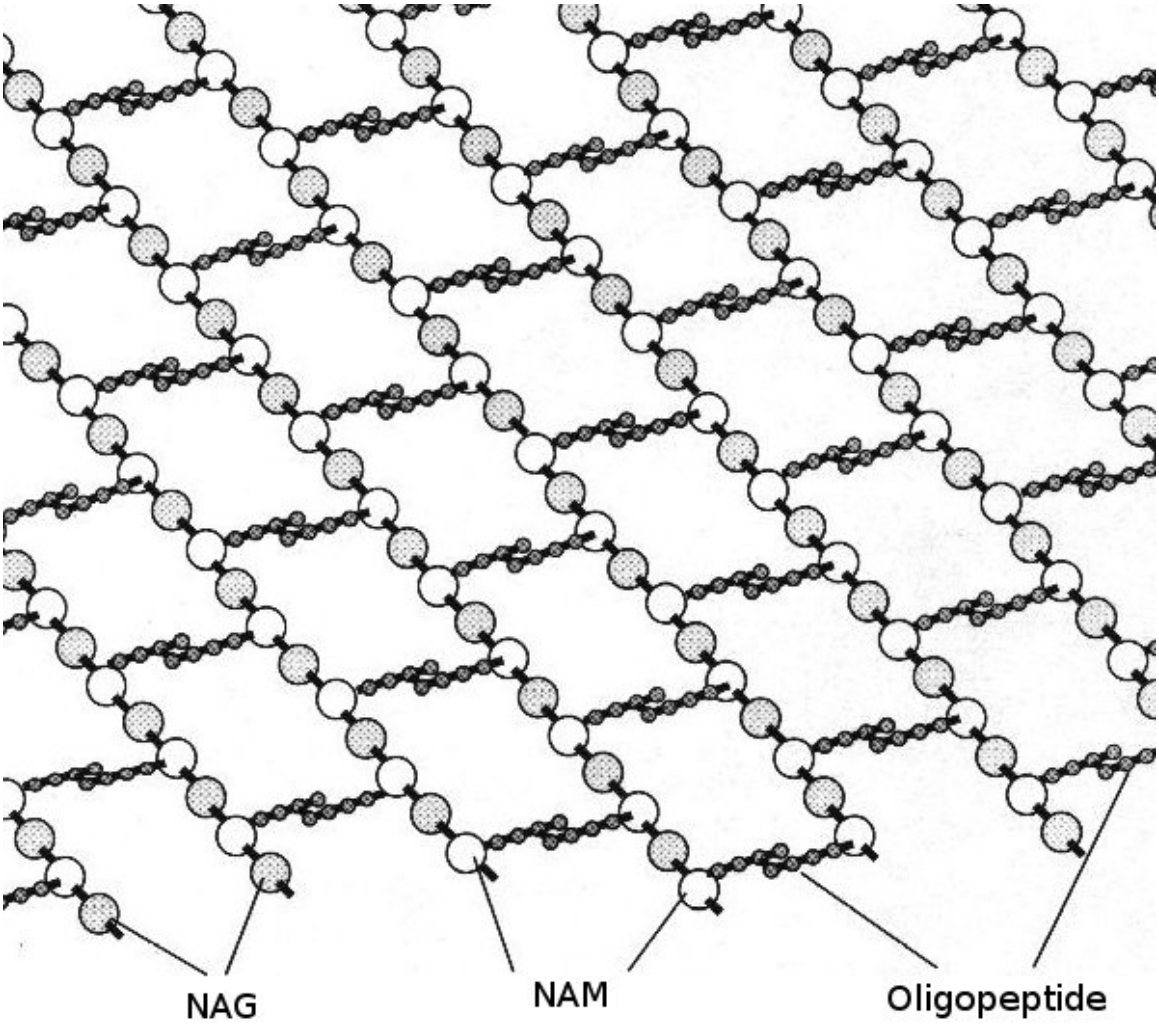
- coccus (spherical)
- bacillus (rod-like)
- spirillum (spiral)
- filamentous

Cell shape is generally characteristic of a given bacterial species, but can vary depending on growth conditions. Some bacteria have complex life cycles involving the production of stalks and appendages (e.g. *Caulobacter*) and some produce elaborate structures bearing reproductive spores (e.g. *Myxococcus*, *Streptomyces*). Bacteria generally form distinctive cell morphologies when examined by light microscopy and distinct colony morphologies when grown on Petri plates. These are often the first characteristics observed by a microbiologist to determine the identity of an unknown bacterial culture.

# The importance of cell size

Perhaps the most obvious structural characteristic of bacteria is (with some exceptions) their small size. For example, *Escherichia coli* cells, an "average" sized bacterium, are about 2 micrometres (μm) long and 0.5 μm in diameter, with a cell volume of 0.6 - 0.7 $\mu m^3$. This corresponds to a wet mass of ca. 1 pg, assuming that the cell consists mostly of water. The dry mass of a single cell can be estimated as 20 % of the wet mass, amounting to 0.2 pg. About half of the dry mass of a bacterial cell consists of carbon, and also about half of it can be attributed to proteins. Therefore, a typical fully grown 1-liter culture of *Escherichia coli* (at an optical density of 1.0, corresponding to ca. $10^9$ cells/ml) yields ca. 1 g wet cell mass.

Small size is extremely important because it allows for a large surface area-to-volume ratio which allows for rapid uptake and intracellular distribution of nutrients and excretion of wastes. At low surface area-to-volume ratios the diffusion of nutrients and waste products across the bacterial cell membrane limits the rate at which microbial metabolism can occur, making the cell less evolutionarily fit. The reason for the existence of large cells is unknown, although it is speculated that the increased cell volume is used primarily for storage of excess nutrients.




The structure of peptidoglycan.

As in other organisms, the bacterial cell wall provides structural integrity to the cell. In prokaryotes, the primary function of the cell wall is to protect the cell from internal turgor pressure caused by the much higher concentrations of proteins and other molecules inside the cell compared to its external environment. The bacterial cell wall differs from that of all other organisms by the presence of peptidoglycan (poly-*N*-acetylglucosamine and *N*-acetylmuramic acid), which is located immediately outside of the cytoplasmic membrane. Peptidoglycan is responsible for the rigidity of the bacterial cell wall and for the determination of cell shape. It is relatively porous and is not considered to be a permeability barrier for small substrates. While all bacterial cell walls (with a few exceptions e.g. extracellular parasites such as *Mycoplasma*) contain peptidoglycan, not all cell walls have the same overall structures. Since the cell wall is required for bacterial survival, but is absent in eukaryotes, several antibiotics (penicillins and cephalosporins) stop bacterial infections by interfering with cell wall synthesis, while having no effects on human cells.

There are two main types of bacterial cell walls, Gram positive and Gram negative, which are differentiated by their Gram staining characteristics. For both Gram-positive and Gram-negative bacteria, particles of approximately 2 nm can pass through the peptidoglycan.

### The Gram positive cell wall

Peptidoglycans(mucopeptides, glycopeptides, mureins) are the structural elements of almost all bacterial cell walls. They constitute almost 95% of the cell wall in some Gram positive bacteria and as little as 5-10% of the cell wall in Gram negative bacteria. Peptidoglycans are made up of a polysaccharide backbone consisting of alternating muramic acid(MA) and glucose amine(GA) residues in equal amounts. The cell wall of some Gram positive bacteria is completely dissolved by lysozyme, as this enzyme attacks the bonds between GA and MA. In other Gram positive bacteria, e.g. Staphylococcus aureus, the walls are resistant to the action of lysozyme. They have O-acetyl groups on carbon-6 of some MA residues. The matrix substances in the walls of Gram positive bacteria may be polysaccharides or teichoic acids. The latter are very widespread, but have been found only in Gram positive bacteria. There are two main types of teichoic acid: ribitol teichoic acids and glycerol teichoic acids. The latter one is more widespread. These acids are polymers of ribitol phosphate and glycerol phosphate, respectively, and only one type is found in the wall of any particular strain of bacteria. Teichoic acids form receptor sites for bacteriophages, and at least some of them are located on the surface of many Gram positive bacteria.

### The Gram negative cell wall

Unlike the Gram positive cell wall, the Gram negative cell wall contains a **thin** peptidoglycan layer adjacent to the cytoplasmic membrane. This is responsible for the cell wall's inability to retain the crystal violet stain upon decolourisation with ethanol during Gram staining. In addition to the peptidoglycan layer, the Gram negative cell wall also contains an outer membrane composed by phospholipids and lipopolysaccharides, which face into the external environment. As the lipopolysaccharides are highly-charged, the Gram negative cell wall has an overall negative charge. The chemical structure of the outer membrane lipopolysaccharides is often unique to specific bacterial strains (i.e. sub-species) and is responsible for many of the antigenic properties of these strains.

## The bacterial cytoplasmic membrane

The bacterial cytoplasmic membrane is composed of a phospholipid bilayer and thus has all of the general functions of a cell membrane such as acting as a permeability barrier for most molecules and serving as the location for the transport of molecules into the cell. In addition to these functions, prokaryotic membranes also function in energy conservation as the location about which a proton motive force is generated. Unlike eukaryotes, bacterial membranes (with some exceptions e.g. *Mycoplasma* and methanotrophs) generally do not contain sterols. However, many microbes do contain structurally related compounds called hopanoids which likely fulfill the same function. Unlike eukaryotes,

bacteria can have a wide variety of fatty acids within their membranes. Along with typical saturated and unsaturated fatty acids, bacteria can contain fatty acids with additional methyl, hydroxy or even cyclic groups. The relative proportions of these fatty acids can be modulated by the bacterium to maintain the optimum fluidity of the membrane (e.g. following temperature change).

As a phospholipid bilayer, the lipid portion of the outer membrane is impermeable to charged molecules. However, channels called porins are present in the outer membrane that allow for passive transport of many ions, sugars and amino acids across the outer membrane. These molecules are therefore present in the periplasm, the region between the cytoplasmic and outer membranes. The periplasm contains the peptidoglycan layer and many proteins responsible for substrate binding or hydrolysis and reception of extracellular signals. The periplasm it is thought to exist as a gel-like state rather than a liquid due to the high concentration of proteins and peptidoglycan found within it. Because of its location between the cytoplasmic and outer membranes, signals received and substrates bound are available to be transported across the cytoplasmic membrane using transport and signalling proteins imbedded there.

# Other bacterial surface structures

## Fimbrae and Pili

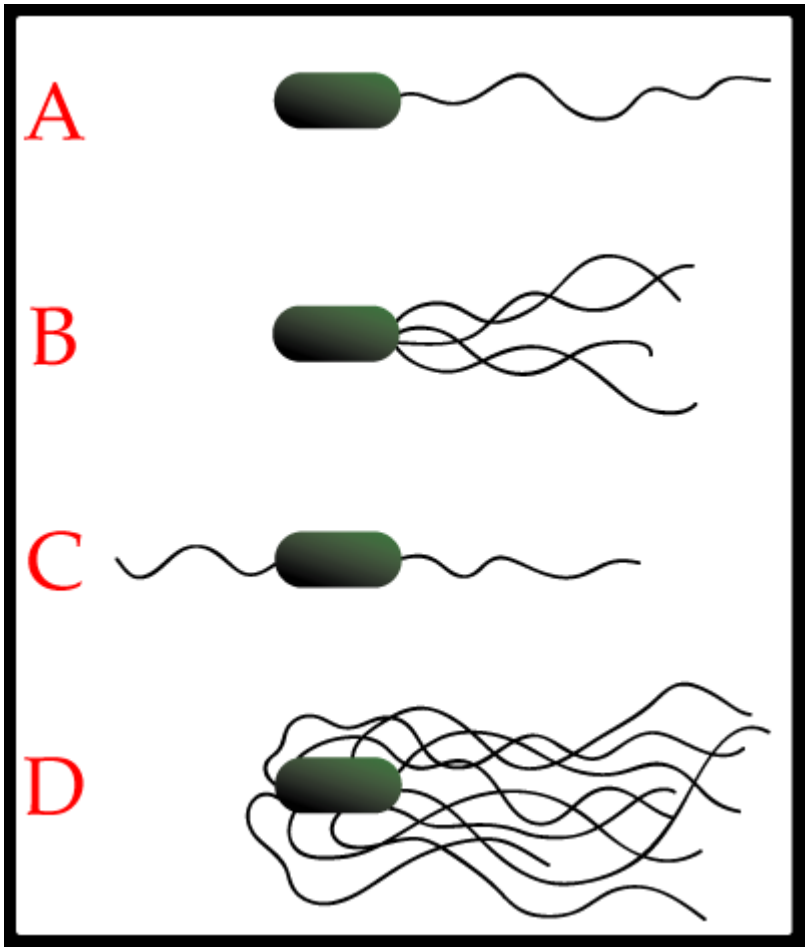
Fimbrae are protein tubes that extend out from the outer membrane in many members of the Proteobacteria. They are generally short in length and present in high numbers about the entire bacterial cell surface. Fimbrae usually function to facilitate the attachment of a bacterium to a surface (e.g. to form a biofilm) or to other cells (e.g. animal cells during pathogenesis)). A few organisms (e.g. *Myxococcus*) use fimbrae for motility to facilitate the assembly of multicellular structures such as fruiting bodies. Pili are similar in structure to fimbrae but are much longer and present on the bacterial cell in low numbers. Pili are involved in the process of bacterial conjugation. Non-sex pili also aid bacteria in gripping surfaces.

## S-layers

An S-layer (surface layer) is a cell surface protein layer found in many different bacteria and in some archaea, where it serves as the cell wall. All S-layers are made up of a two-dimensional array of proteins and have a crystalline appearance, the symmetry of which differs between species. The exact function of S-layers is unknown, but it has been suggested that they act as a partial permeability barrier for large substrates. For example, an S-layer could conceivably keep extracellular proteins near the cell membrane by preventing their diffusion away from the cell. In some pathogenic species, an S-layer may help to facilitate survival within the host by conferring protection against host defence mechanisms.

## Capsules and Slime Layers

Many bacteria secrete extracellular polymers outside of their cell walls. These polymers are usually composed of polysaccharides and sometimes protein. Capsules are relatively impermeable structures that cannot be stained with dyes such as India ink. They are structures that help protect bacteria from phagocytosis and desiccation. Slime layer is involved in attachment of bacteria to other cells or inanimate surfaces to form biofilms. Slime layers can also be used as a food reserve for the cell.




A-Monotrichous; B-Lophotrichous; C-Amphitrichous; D-Peritrichous;

## Flagella

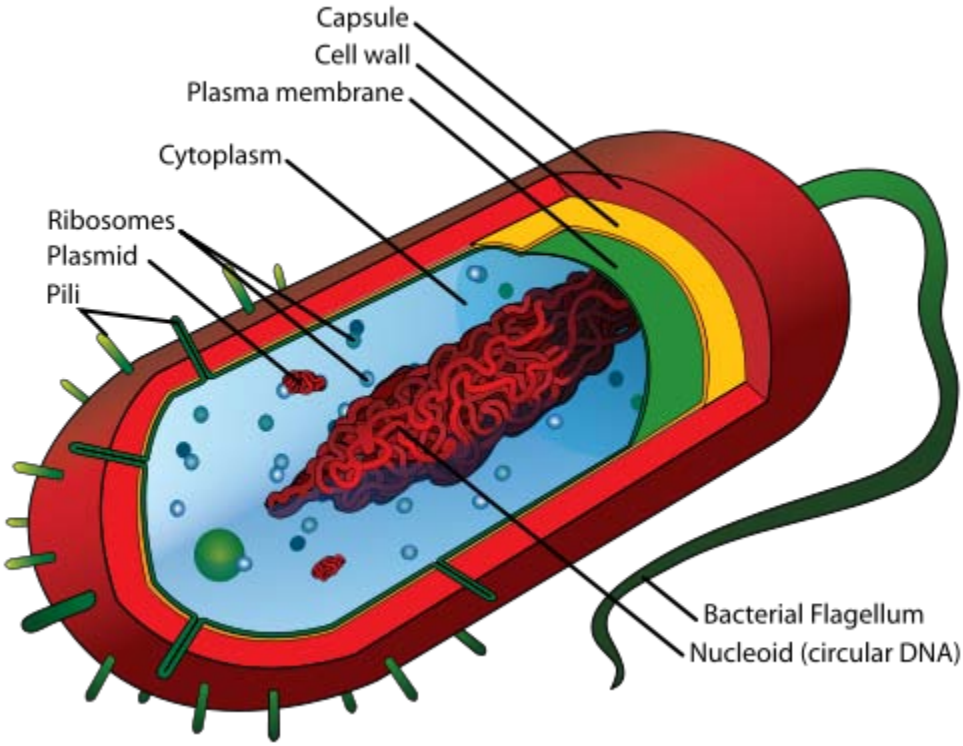
Perhaps the most recognizable extracellular bacterial cell structures are flagella. Flagella are whip-like structures protruding from the bacterial cell wall and are responsible for bacterial motility (i.e. movement). The arrangement of flagella about the bacterial cell is unique to the species observed. Common forms include:

- Peritrichous - Multiple flagella found at several locations about the cell
- Polar - Single flagellum found at one of the cell poles

- Lophotrichous - A tuft of flagella found at one cell pole

Flagella are complex structures that are composed of many different proteins. These include flagellin, which makes up the whip-like tube and a protein complex that spans the cell wall and cell membrane to form a motor that causes the flagellum to rotate. This rotation is normally driven by proton motive force and are found in the body of the cell.

# Intracellular bacterial cell structures




Cell structure of a Gram positive prokaryote

In comparison to eukaryotes, the intracellular features of the bacterial cell are extremely simple. Bacteria do not contain organelles in the same sense as eukaryotes. Instead, the chromosome and perhaps ribosomes are the only easily observable intracellular structures found in all bacteria. There do exist, however, specialized groups of bacteria that contain more complex intracellular structures, some of which are discussed below.

## The bacterial chromosome and plasmids

Unlike eukaryotes, the bacterial chromosome is not enclosed inside of a membrane-bound nucleus but instead resides inside the bacterial cytoplasm. This means that the transfer of cellular information through the processes of translation, transcription and DNA replication all occur within the same compartment and can interact with other

cytoplasmic structures, most notably ribosomes. The bacterial chromosome is not packaged using histones to form chromatin as in eukaryotes but instead exists as a highly compact supercoiled structure, the precise nature of which remains unclear. Most bacterial chromosomes are circular although some examples of linear chromosomes exist (e.g. *Borrelia burgdorferi*). Along with chromosomal DNA, most bacteria also contain small independent pieces of DNA called plasmids that often encode for traits that are advantageous but not essential to their bacterial host. Plasmids can be easily gained or lost by a bacterium and can be transferred between bacteria as a form of horizontal gene transfer.

## Ribosomes and other multiprotein complexes

In most bacteria the most numerous intracellular structure is the ribosome, the site of protein synthesis in all living organisms. All prokaryotes have 70S (where S=Svedberg units) ribosomes while eukaryotes contain larger 80S ribosomes in their cytosol. The 70S ribosome is made up of a 50S and 30S subunits. The 50S subunit contains the 23S and 5S rRNA while the 30S subunit contains the 16S rRNA. These rRNA molecules differ in size in eukaryotes and are complexed with a large number of ribosomal proteins, the number and type of which can vary slightly between organisms. While the ribosome is the most commonly observed intracellular multiprotein complex in bacteria other large complexes do occur and can sometimes be seen using microscopy.

## Intracellular membranes

While not typical of all bacteria some microbes contain intracellular membranes in addition to (or as extensions of) their cytoplasmic membranes. An early idea was that bacteria might contain membrane folds termed mesosomes, but these were later shown to be artifacts produced by the chemicals used to prepare the cells for electron microscopy. Examples of bacteria containing intracellular membranes are phototrophs, nitrifying bacteria and methane-oxidising bacteria. Intracellular membranes are also found in bacteria belonging to the poorly studied Planctomycetes group, although these membranes more closely resemble organellar membranes in eukaryotes and are currently of unknown function.

## Cytoskeleton

The prokaryotic cytoskeleton is the collective name for all structural filaments in prokaryotes. It was once thought that prokaryotic cells did not possess cytoskeletons, but recent advances in visualization technology and structure determination have shown that filaments indeed exist in these cells. In fact, homologues for all major cytoskeletal proteins in eukaryotes have been found in prokaryotes. Cytoskeletal elements play essential roles in cell division, protection, shape determination, and polarity determination in various prokaryotes.

## Nutrient storage structures

Most bacteria do not live in environments that contain large amounts of nutrients at all times. To accommodate these transient levels of nutrients bacteria contain several different methods of nutrient storage in times of plenty for use in times of want. For example, many bacteria store excess carbon in the form of polyhydroxyalkanoates or glycogen. Some microbes store soluble nutrients such as nitrate in vacuoles. Sulfur is most often stored as elemental ($S^0$) granules which can be deposited either intra- or extracellularly. Sulfur granules are especially common in bacteria that use hydrogen sulfide as an electron source. Most of the above mentioned examples can be viewed using a microscope and are surrounded by a thin nonunit membrane to separate them from the cytoplasm.

## Gas vesicles

Gas vesicles are spindle-shaped structures found in some planktonic bacteria that provides buoyancy to these cells by decreasing their overall cell density. They are made up of a protein coat that is very impermeable to solvents such as water but permeable to most gases. By adjusting the amount of gas present in their gas vesicles bacteria can increase or decrease their overall cell density and thereby move up or down within the water column to maintain their position in an environment optimal for growth.

## Carboxysomes

Carboxysomes are intracellular structures found in many autotrophic bacteria such as Cyanobacteria, Knallgasbacteria, Nitroso- and Nitrobacteria. They are proteinaceous structures resembling phage heads in their morphology and contain the enzymes of carbon dioxide fixation in these organisms (especially ribulose bisphosphate carboxylase/oxygenase, RuBisCO, and carbonic anhydrase). It is thought that the high local concentration of the enzymes along with the fast conversion of bicarbonate to carbon dioxide by carbonic anhydrase allows faster and more efficient carbon dioxide fixation than possible inside the cytoplasm. Similar structures are known to harbor the coenzyme B12-containing glycerol dehydratase, the key enzyme of glycerol fermentation to 1,3-propanediol, in some Enterobacteriaceae (e. g. Salmonella).

## Magnetosomes

Magnetosomes are intracellular organelles found in magnetotactic bacteria that allow them to sense and align themselves along a magnetic field (magnetotaxis). The ecological role of magnetotaxis is unknown but it is hypothesized to be involved in the determination of optimal oxygen concentrations. Magnetosomes are composed of the mineral magnetite or greigite and are surrounded by a lipid bilayer membrane. The morphology of magnetosomes is species-specific.

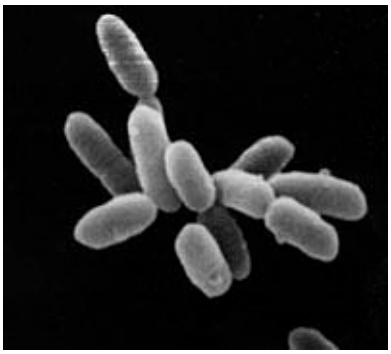
# Endospores

Perhaps the most well known bacterial adaptation to stress is the formation of endospores. Endospores are bacterial survival structures that are highly resistant to many different types of chemical and environmental stresses and therefore enable the survival of bacteria in environments that would be lethal for these cells in their normal vegetative form. It has been proposed that endospore formation has allowed for the survival of some bacteria for hundreds of millions of years (e.g. in salt crystals) although these publications have been questioned. Endospore formation is limited to several genera of Gram-positive bacteria such as *Bacillus* and *Clostridium*. It differs from reproductive spores in that only one spore is formed per cell resulting in no net gain in cell number upon endospore germination. The location of an endospore within a cell is species-specific and can be used to determine the identity of a bacterium.

## Chapter- 7

# Archaea

**Archaea**
**Temporal range: Paleoarchean – Recent**



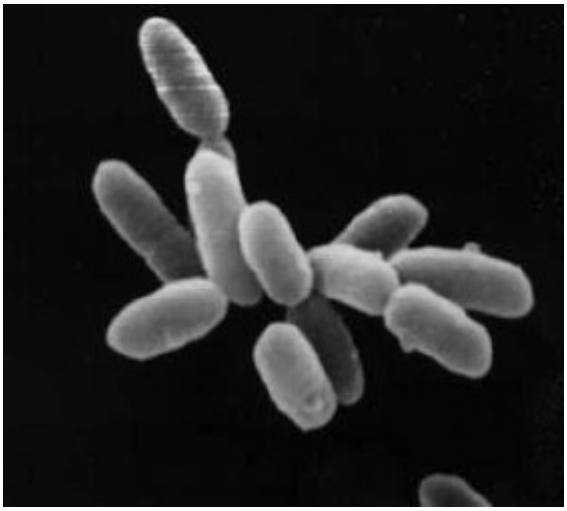
*Halobacteria* sp. strain NRC-1, each cell about 5 μm long

**Scientific classification**

**Archaea**
Domain: Woese, Kandler & Wheelis, 1990

**Kingdoms and phyla**

Crenarchaeota
Euryarchaeota
Korarchaeota
Nanoarchaeota
Thaumarchaeota



The **Archaea** are a group of single-celled microorganisms. A single individual or species from this domain is called an *archaeon* (sometimes spelled "archeon"). They have no cell nucleus nor any other membrane-bound organelles within their cells. In the past they were viewed as an unusual group of bacteria and named **archaebacteria**, but since the Archaea have an independent evolutionary history and show many differences in their biochemistry from other forms of life, they are now classified as a separate domain in the three-domain system. In this system the phylogenetically distinct branches of evolutionary descent are the Archaea, Bacteria and Eukaryota. Archaea are divided into four recognized phyla, but many more phyla may exist. Of these groups the Crenarchaeota and the Euryarchaeota are most intensively studied. Classification is still difficult, since the vast majority have never been studied in the laboratory and have only been detected by analysis of their nucleic acids in samples from the environment. Although archaea have, in the past, been classed with bacteria as *prokaryotes* (or Kingdom Monera), this classification is regarded by some as outdated.

Archaea and bacteria are quite similar in size and shape, although a few archaea have very unusual shapes, such as the flat and square-shaped cells of *Haloquadratum walsbyi*. Despite this visual similarity to bacteria, archaea possess genes and several metabolic pathways that are more closely related to those of eukaryotes: notably the enzymes involved in transcription and translation. Other aspects of archaean biochemistry are unique, such as their reliance on ether lipids in their cell membranes. The archaea exploit a much greater variety of sources of energy than eukaryotes: ranging from familiar organic compounds such as sugars, to using ammonia, metal ions or even hydrogen gas as nutrients. Salt-tolerant archaea (the Halobacteria) use sunlight as an energy source and other species of archaea fix carbon; however, unlike plants and cyanobacteria, no species of archaea is known to do both. Archaea reproduce asexually and divide by binary fission, fragmentation, or budding; in contrast to bacteria and eukaryotes, no known species form spores.

Initially, archaea were seen as extremophiles that lived in harsh environments, such as hot springs and salt lakes, but they have since been found in a broad range of habitats, including soils, oceans, and marshlands. Archaea are particularly numerous in the oceans,

and the archaea in plankton may be one of the most abundant groups of organisms on the planet. Archaea are now recognized as a major part of Earth's life and may play roles in both the carbon cycle and the nitrogen cycle. No clear examples of archaeal pathogens or parasites are known, but they are often mutualists or commensals. One example is the methanogens that inhabit the gut of humans and ruminants, where their vast numbers aid digestion. Methanogens are used in biogas production and sewage treatment, and enzymes from extremophile archaea that can endure high temperatures and organic solvents are exploited in biotechnology.

# Classification

## New domain

For much of the 20th century, prokaryotes were regarded as a single group of organisms and classified based on their biochemistry, morphology and metabolism. For example, microbiologists tried to classify microorganisms based on the structures of their cell walls, their shapes, and the substances they consume. However, a new approach was proposed in 1965, using the sequences of the genes in these organisms to work out which prokaryotes are genuinely related to each other. This approach, known as phylogenetics, is the main method used today.

Archaea were first found in extreme environments, such as volcanic hot springs.

Archaea were first classified as a separate group of prokaryotes in 1977 by Carl Woese and George E. Fox in phylogenetic trees based on the sequences of ribosomal RNA

(rRNA) genes. These two groups were originally named the Archaebacteria and Eubacteria and treated as kingdoms or subkingdoms, which Woese and Fox termed *Urkingdoms*. Woese argued that this group of prokaryotes is a fundamentally different sort of life. To emphasize this difference, these two domains were later renamed Archaea and Bacteria. The word *archaea* comes from the Ancient Greek ἀρχαῖα, meaning "ancient things".

At first, only the methanogens were placed in this new domain, and the archaea were seen as extremophiles that exist only in habitats such as hot springs and salt lakes. By the end of the 20th century, microbiologists realized that archaea is a large and diverse group of organisms that are widely distributed in nature and are common in much less extreme habitats, such as soils and oceans. This new appreciation of the importance and ubiquity of archaea came from using the polymerase chain reaction to detect prokaryotes in samples of water or soil from their nucleic acids alone. This allows the detection and identification of organisms that cannot be cultured in the laboratory, which generally remains difficult.

## Current classification

The classification of archaea, and of prokaryotes in general, is a rapidly moving and contentious field. Current classification systems aim to organize archaea into groups of organisms that share structural features and common ancestors. These classifications rely heavily on the use of the sequence of ribosomal RNA genes to reveal relationships between organisms (molecular phylogenetics). Most of the culturable and well-investigated species of archaea are members of two main phyla, the Euryarchaeota and Crenarchaeota. Other groups have been tentatively created. For example, the peculiar species *Nanoarchaeum equitans*, which was discovered in 2003, has been given its own phylum, the Nanoarchaeota. A new phylum Korarchaeota has also been proposed. It contains a small group of unusual thermophilic species that shares features of both of the main phyla, but is most closely related to the Crenarchaeota. Other recently detected species of archaea are only distantly related to any of these groups, such as the Archaeal Richmond Mine Acidophilic Nanoorganisms (ARMAN), which were discovered in 2006 and are some of the smallest organisms known.

The ARMAN are a new group of archaea recently discovered in acid mine drainage.

**Species**

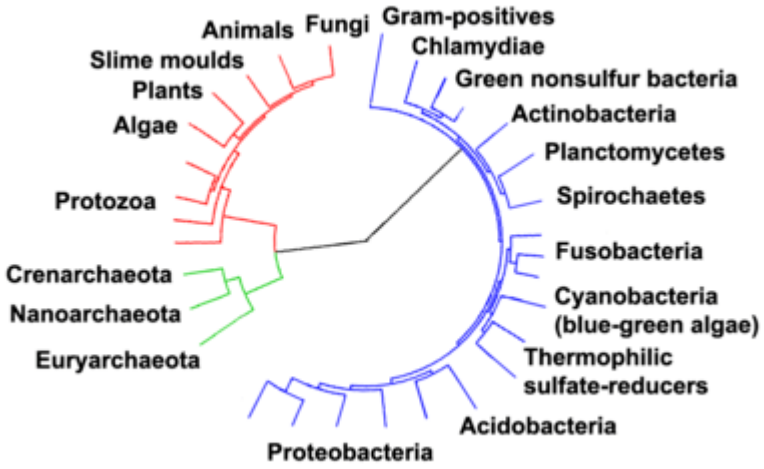
The classification of archaea into species is also controversial. Biology defines a species as a group of related organisms. The familiar exclusive breeding criterion (organisms that can breed with each other but not with others), is of no help because archaea reproduce asexually.

Archaea show high levels of horizontal gene transfer between lineages. Some researchers suggest that individuals can be grouped into species-like populations given highly similar genomes and infrequent gene transfer to/from cells with less-related genomes, as in the genus *Ferroplasma*. On the other hand, studies in *Halorubrum* found significant genetic transfer to/from less-related populations, limiting the criterion's applicability. A second concern is to what extent such species designations have practical meaning.

Current knowledge on genetic diversity is fragmentary and the total number of archaean species cannot be estimated with any accuracy. Estimates of the number of phyla range from 18 to 23, of which only 8 have representatives that have been cultured and studied directly. Many of these hypothesized groups are known from a single rRNA sequence, indicating that the diversity among these organisms remains obscure. The Bacteria also contain many uncultured microbes with similar implications for characterization.

# Origin and evolution

Although probable prokaryotic cell fossils date to almost 3.5 billion years ago, most prokaryotes do not have distinctive morphologies and fossil shapes cannot be used to identify them as Archaea. Instead, chemical fossils of unique lipids are more informative because such compounds do not occur in other organisms. Some publications suggest that archaean or eukaryotic lipid remains are present in shales dating from 2.7 billion years ago; such data have since been questioned. Such lipids have also been detected in Precambrian formations. The oldest such traces come from the Isua district of west Greenland, which include Earth's oldest sediments, formed 3.8 billion years ago. The archaeal lineage may be the most ancient that exists on earth.




Phylogenetic tree showing the relationship between the archaea and other forms of life. Eukaryotes are colored red, archaea green and bacteria blue. Adapted from Ciccarelli *et al.*

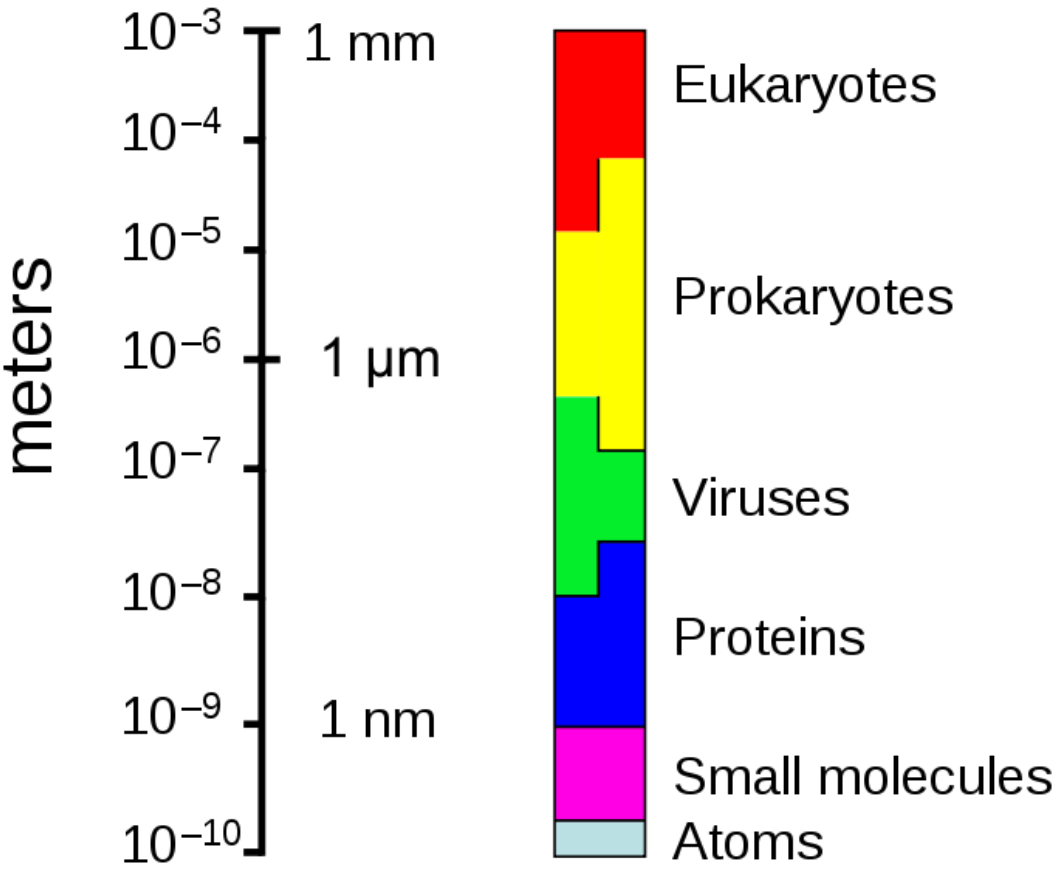
Woese argued that the bacteria, archaea, and eukaryotes represent separate lines of descent that diverged early on from an ancestral colony of organisms. A few biologists, however, argue that the Archaea and Eukaryota arose from a group of bacteria. In any case it is thought that viruses and archaea began relationships approximately two billion years ago, and that co-evolution may have been occurring between members of these groups. It is possible that the last common ancestor of the bacteria and archaea was a thermophile, which raises the possibility that lower temperatures are "extreme environments" in archaeal terms, and organisms that live in cooler environments appeared only later. Since the Archaea and Bacteria are no more related to each other than they are to eukaryotes, the term *prokaryote*'s only surviving meaning is "not a eukaryote", limiting its value.

### Archaea and eukaryotes

The relationship between archaea and eukaryotes remains problematic. Aside from the similarities in cell structure and function that are discussed below, many genetic trees group the two.

Complicating factors include claims that the relationship between eukaryotes and the archaeal phylum Euryarchaeota is closer than the relationship between the Euryarchaeota and the phylum Crenarchaeota and the presence of archaean-like genes in certain bacteria, such as *Thermotoga maritima*, from horizontal gene transfer. The leading hypothesis is that the ancestor of the eukaryotes diverged early from the Archaea, and that eukaryotes arose through fusion of an archaean and eubacterium, which became the nucleus and cytoplasm; this accounts for various genetic similarities but runs into difficulties explaining cell structure.

## Morphology




The sizes of prokaryotic cells relative to other cells and biomolecules (logarithmic scale)

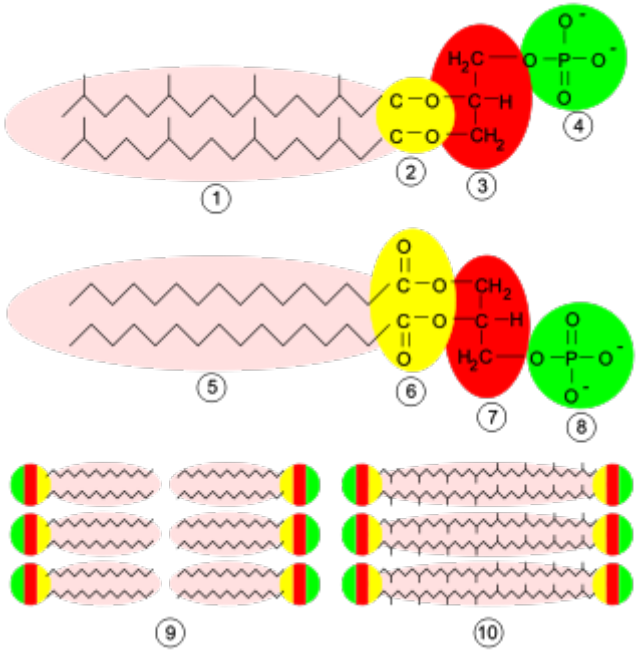
Individual archaea range from 0.1 micrometers (μm) to over 15 μm in diameter, and occur in various shapes, commonly as spheres, rods, spirals or plates. Other morphologies in the Crenarchaeota include irregularly shaped lobed cells in *Sulfolobus*, needle-like filaments that are less than half a micrometer in diameter in *Thermofilum*, and almost perfectly rectangular rods in *Thermoproteus* and *Pyrobaculum*. *Haloquadratum walsbyi* are flat, square archaea that live in hypersaline pools. These unusual shapes are probably maintained both by their cell walls and a prokaryotic cytoskeleton. Proteins related to the cytoskeleton components of other organisms exist in archaea, and filaments form within their cells, but in contrast to other organisms, these cellular structures are poorly understood. In *Thermoplasma* and *Ferroplasma* the lack of a cell wall means that the cells have irregular shapes, and can resemble amoebae.

Some species form aggregates or filaments of cells up to 200 μm long. These organisms can be prominent in biofilms. Notably, aggregates of *Thermococcus coalescens* cells fuse together in culture, forming single giant cells. Archaea in the genus *Pyrodictium* produce an elaborate multicell colony involving arrays of long, thin hollow tubes called *cannulae* that stick out from the cells' surfaces and connect them into a dense bush-like agglomeration. The function of these cannulae is not settled, but they may allow communication or nutrient exchange with neighbors. Multi-species colonies exist, such as the "string-of-pearls" community that was discovered in 2001 in a German swamp. Round whitish colonies of a novel Euryarchaeota species are spaced along thin filaments that can range up to 15 centimetres (5.9 in) long; these filaments are made of a particular bacteria species.

# Structure, composition development, operation

Archaea and bacteria have generally similar cell structure, but cell composition and organization set the archaea apart. Like bacteria, archaea lack interior membranes and organelles. Like bacteria, archaea cell membranes are usually bounded by a cell wall and they swim using one or more flagella. Structurally, archaea are most similar to gram-positive bacteria. Most have a single plasma membrane and cell wall, and lack a periplasmic space; the exception to this general rule is *Ignicoccus*, which possess a particularly large periplasm that contains membrane-bound vesicles and is enclosed by an outer membrane.

## Membranes




Membrane structures. **Top**, an archaeal phospholipid: **1**, isoprene chains; **2**, ether linkages; **3**, L-glycerol moiety; **4**, phosphate group. **Middle**, a bacterial or eukaryotic phospholipid: **5**, fatty acid chains; **6**, ester linkages; **7**, D-glycerol moiety; **8**, phosphate group. **Bottom**: **9**, lipid bilayer of bacteria and eukaryotes; **10**, lipid monolayer of some archaea.

Archaeal membranes are made of molecules that differ strongly from those in other life forms, showing that archaea are related only distantly to bacteria and eukaryotes. In all organisms cell membranes are made of molecules known as phospholipids. These molecules possess both a polar part that dissolves in water (the phosphate "head"), and a "greasy" non-polar part that does not (the lipid tail). These dissimilar parts are connected by a glycerol moiety. In water, phospholipids cluster, with the heads facing the water and the tails facing away from it. The major structure in cell membranes is a double layer of these phospholipids, which is called a lipid bilayer.

These phospholipids are unusual in four ways:

- Bacteria and eukaryotes have membranes composed mainly of glycerol-ester lipids, whereas archaea have membranes composed of glycerol-ether lipids. The difference is the type of bond that joins the lipids to the glycerol moiety; the two types are shown in yellow in the figure at the right. In ester lipids this is an ester bond, whereas in ether lipids this is an ether bond. Ether bonds are chemically more resistant than ester bonds. This stability might help archaea to survive extreme temperatures and very acidic or alkaline environments. Bacteria and eukaryotes do contain some ether lipids, but in contrast to archaea these lipids are not a major part of their membranes.

- The stereochemistry of the glycerol moiety is the reverse of that found in other organisms. The glycerol moiety can occur in two forms that are mirror images of one another, called the right-handed and left-handed forms; in chemistry these are called *enantiomers*. Just as a right hand does not fit easily into a left-handed glove, a right-handed glycerol molecule generally cannot be used or made by enzymes adapted for the left-handed form. This suggests that archaea use entirely different enzymes for synthesizing phospholipids than do bacteria and eukaryotes. Such enzymes developed very early in life's history, suggesting an early split from the other two domains.

- Archaeal lipid tails are chemically different from other organisms. Archaeal lipids are based upon the isoprenoid sidechain and are long chains with multiple side-branches and sometimes even cyclopropane or cyclohexane rings. This is in contrast to the fatty acids found in other organisms' membranes, which have straight chains with no branches or rings. Although isoprenoids play an important role in the biochemistry of many organisms, only the archaea use them to make phospholipids. These branched chains may help prevent archaean membranes from leaking at high temperatures.

- In some archaea the lipid bilayer is replaced by a monolayer. In effect, the archaea fuse the tails of two independent phospholipid molecules into a single molecule with two polar heads; this fusion may make their membranes more rigid and better able to resist harsh environments. For example, the lipids in *Ferroplasma* are of this type, which is thought to aid this organism's survival in its highly acidic habitat.

## Wall and flagella

Most archaea (but not *Thermoplasma* and *Ferroplasma*) possess a cell wall. In most archaea the wall is assembled from surface-layer proteins, which form an S-layer. An S-layer is a rigid array of protein molecules that cover the outside of the cell (like chain mail). This layer provides both chemical and physical protection, and can prevent macromolecules from contacting the cell membrane. Unlike bacteria, archaea lack peptidoglycan in their cell walls. Methanobacteriales do have cell walls containing pseudopeptidoglycan, which resembles eubacterial peptidoglycan in morphology, function, and physical structure, but pseudopeptidoglycan is distinct in chemical structure; it lacks D-amino acids and N-acetylmuramic acid.

Archaea flagella operate like bacterial flagella—their long stalks are driven by rotatory motors at the base. These motors are powered by the proton gradient across the membrane. However, archaeal flagella are notably different in composition and development. The two types of flagella evolved from different ancestors. The bacterial flagellum shares a common ancestor with the type III secretion system, while archaeal flagella appear to have evolved from bacterial type IV pili. In contrast to the bacterial flagellum, which is hollow and is assembled by subunits moving up the central pore to the tip of the flagella, archaeal flagella are synthesized by adding subunits at the base.

# Metabolism

Archaea exhibit a great variety of chemical reactions in their metabolism and use many sources of energy. These reactions are classified into nutritional groups, depending on energy and carbon sources. Some archaea obtain energy from inorganic compounds such as sulfur or ammonia (they are lithotrophs). These include nitrifiers, methanogens and anaerobic methane oxidisers. In these reactions one compound passes electrons to another (in a redox reaction), releasing energy to fuel the cell's activities. One compound acts as an electron donor and one as an electron acceptor. The energy released generates adenosine triphosphate (ATP) through chemiosmosis, in the same basic process that happens in the mitochondrion of eukaryotic cells.

Other groups of archaea use sunlight as a source of energy (they are phototrophs). However, oxygen–generating photosynthesis does not occur in any of these organisms. Many basic metabolic pathways are shared between all forms of life; for example, archaea use a modified form of glycolysis (the Entner–Doudoroff pathway) and either a complete or partial citric acid cycle. These similarities to other organisms probably reflect both early origins in the history of life and their high level of efficiency.

Nutritional types in archaeal metabolism

| Nutritional type | Source of energy | Source of carbon | Examples |
|---|---|---|---|
| Phototrophs | Sunlight | Organic compounds | *Halobacteria* |
| Lithotrophs | Inorganic compounds | Organic compounds or carbon fixation | *Ferroglobus*, *Methanobacteria* or *Pyrolobus* |
| Organotrophs | Organic compounds | Organic compounds or carbon fixation | *Pyrococcus*, *Sulfolobus* or *Methanosarcinales* |

Some Euryarchaeota are methanogens living in anaerobic environments such as swamps. This form of metabolism evolved early, and it is even possible that the first free-living organism was a methanogen. A common reaction involves the use of carbon dioxide as an electron acceptor to oxidize hydrogen. Methanogenesis involves a range of coenzymes that are unique to these archaea, such as coenzyme M and methanofuran. Other organic compounds such as alcohols, acetic acid or formic acid are used as alternative electron acceptors by methanogens. These reactions are common in gut-dwelling archaea. Acetic acid is also broken down into methane and carbon dioxide directly, by *acetotrophic* archaea. These acetotrophs are archaea in the order Methanosarcinales, and are a major part of the communities of microorganisms that produce biogas.

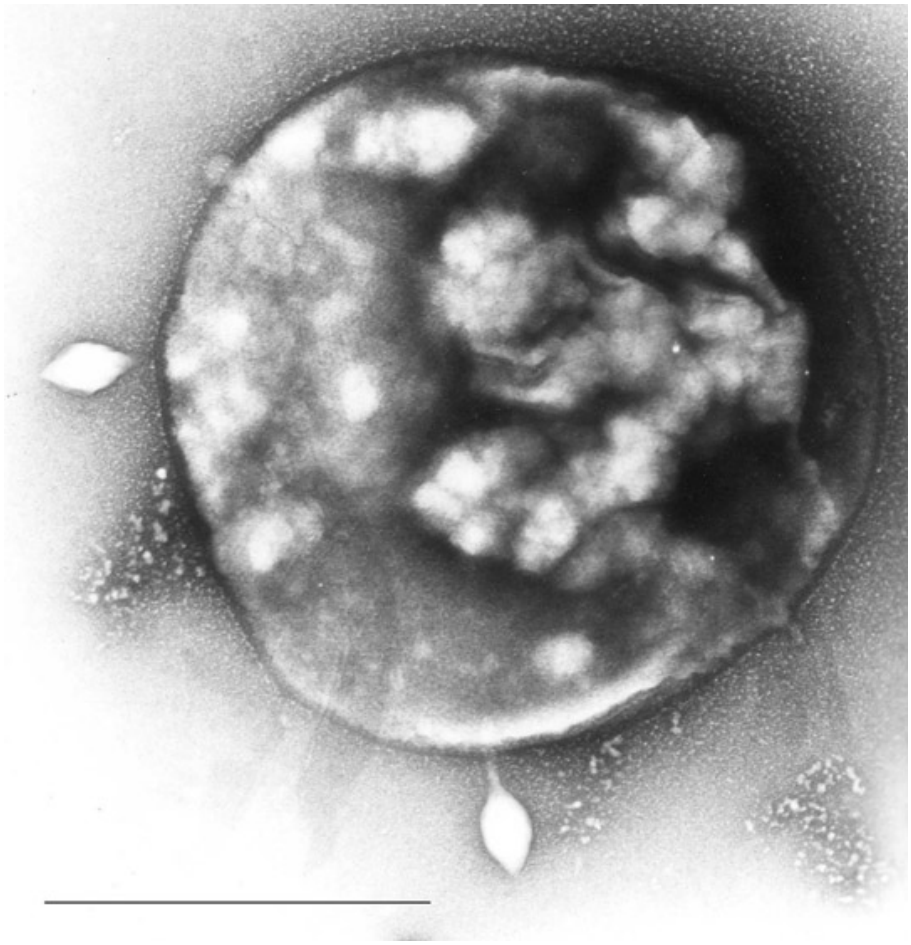
Bacteriorhodopsin from *Halobacterium salinarum*. The retinol cofactor and residues involved in proton transfer are shown as ball-and-stick models.

Other archaea use $CO_2$ in the atmosphere as a source of carbon, in a process called carbon fixation (they are autotrophs). This process involves either a highly modified form of the Calvin cycle or a recently discovered metabolic pathway called the 3-hydroxypropionate/4-hydroxybutyrate cycle. The Crenarchaeota also use the reverse Krebs cycle while the Euryarchaeota also use the reductive acetyl-CoA pathway. Carbon–fixation is powered by inorganic energy sources. No known archaea carry out photosynthesis. Archaeal energy sources are extremely diverse, and range from the oxidation of ammonia by the Nitrosopumilales to the oxidation of hydrogen sulfide or elemental sulfur by species of *Sulfolobus*, using either oxygen or metal ions as electron acceptors.

Phototrophic archaea use light to produce chemical energy in the form of ATP. In the Halobacteria, light-activated ion pumps like bacteriorhodopsin and halorhodopsin generate ion gradients by pumping ions out of the cell across the plasma membrane. The energy stored in these electrochemical gradients is then converted into ATP by ATP synthase. This process is a form of photophosphorylation. The ability of these light-driven pumps to move ions across membranes depends on light-driven changes in the structure of a retinol cofactor buried in the center of the protein.

# Genetics

Archaea usually have a single circular chromosome, the size of which may be as great as 5,751,492 base pairs in *Methanosarcina acetivorans*, the largest known archaean genome. One-tenth of this size is the tiny 490,885 base-pair genome of *Nanoarchaeum equitans*, the smallest archaean genome known; it is estimated to contain only 537 protein-encoding genes. Smaller independent pieces of DNA, called *plasmids*, are also found in archaea. Plasmids may be transferred between cells by physical contact, in a process that may be similar to bacterial conjugation.



*Sulfolobus* infected with the DNA virus STSV1. Bar is 1 micrometer.

Archaea can be infected by double-stranded DNA viruses that are unrelated to any other form of virus and have a variety of unusual shapes, including bottles, hooked rods, or teardrops. These viruses have been studied in most detail in thermophilics, particularly the orders Sulfolobales and Thermoproteales. A single-stranded DNA virus that infects halophilic archaea was identified in 2009. Defenses against these viruses may involve RNA interference from repetitive DNA sequences that are related to the genes of the viruses.

Archaea are genetically distinct from bacteria and eukaryotes, with up to 15% of the proteins encoded by any one archaeal genome being unique to the domain, although most of these unique genes have no known function. Of the remainder of the unique proteins that have an identified function, most are involved in methanogenesis. The proteins that archaea, bacteria and eukaryotes share form a common core of cell function, relating mostly to transcription, translation, and nucleotide metabolism. Other characteristic archaean features are the organization of genes of related function—such as enzymes that catalyze steps in the same metabolic pathway into novel operons, and large differences in tRNA genes and their aminoacyl tRNA synthetases.

Transcription and translation in archaea resemble these processes in eukaryotes more than in bacteria, with the archaean RNA polymerase and ribosomes being very close to their equivalents in eukaryotes. Although archaea only have one type of RNA polymerase, its structure and function in transcription seems to be close to that of the eukaryotic RNA polymerase II, with similar protein assemblies (the general transcription factors) directing the binding of the RNA polymerase to a gene's promoter. However, other archaean transcription factors are closer to those found in bacteria. Post-transcriptional modification is simpler than in eukaryotes, since most archaean genes lack introns, although there are many introns in their transfer RNA and ribosomal RNA genes, and introns may occur in a few protein-encoding genes.

# Reproduction

Archaea reproduce asexually by binary or multiple fission, fragmentation, or budding; meiosis does not occur, so if a species of archaea exists in more than one form, all have the same genetic material. Cell division is controlled in a cell cycle; after the cell's chromosome is replicated and the two daughter chromosomes separate, the cell divides. Details have only been investigated in the genus *Sulfolobus*, but here that cycle has characteristics that are similar to both bacterial and eukaryotic systems. The chromosomes replicate from multiple starting-points (origins of replication) using DNA polymerases that resemble the equivalent eukaryotic enzymes. However, the proteins that direct cell division, such as the protein FtsZ, which forms a contracting ring around the cell, and the components of the septum that is constructed across the center of the cell, are similar to their bacterial equivalents.

Both bacteria and eukaryotes, but not archaea, make spores. Some species of Haloarchaea undergo phenotypic switching and grow as several different cell types, including thick-walled structures that are resistant to osmotic shock and allow the archaea to survive in

water at low salt concentrations, but these are not reproductive structures and may instead help them reach new habitats.

# Ecology

## Habitats

Archaea exist in a broad range of habitats, and as a major part of global ecosystems, may contribute up to 20% of earth's biomass. The first-discovered archaeans were extremophiles. Indeed, some archaea survive high temperatures, often above 100 °C (212 °F), as found in geysers, black smokers, and oil wells. Other common habitats include very cold habitats and highly saline, acidic, or alkaline water. However, archaea include mesophiles that grow in mild conditions, in marshland, sewage, the oceans, and soils.

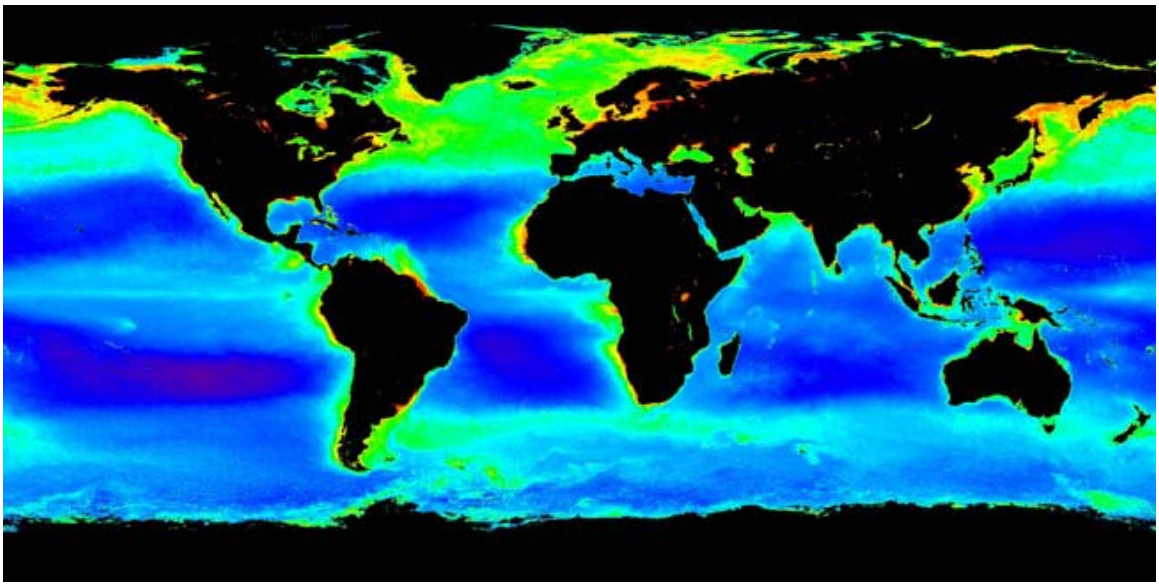


Image of plankton (light green) in the oceans; archaea form a major part of oceanic life.

Extremophile archaea are members of four main physiological groups. These are the halophiles, thermophiles, alkaliphiles, and acidophiles. These groups are not comprehensive or phylum-specific, nor are they mutually exclusive, since some archaea belong to several groups. Nonetheless, they are a useful starting point for classification.

Halophiles, including the genus *Halobacterium*, live in extremely saline environments such as salt lakes and outnumber their bacterial counterparts at salinities greater than 20–25%. Thermophiles grow best at temperatures above 45 °C (113 °F), in places such as hot springs; *hyperthermophilic* archaea grow optimally at temperatures greater than 80 °C (176 °F). The archaeal *Methanopyrus kandleri* Strain 116 grows at 122 °C (252 °F), the highest recorded temperature of any organism.

Other archaea exist in very acidic or alkaline conditions. For example, one of the most extreme archaean acidophiles is *Picrophilus torridus*, which grows at pH 0, which is equivalent to thriving in 1.2 molar sulfuric acid.

This resistance to extreme environments has made archaea the focus of speculation about the possible properties of extraterrestrial life. Some extremophile habitats are not dissimilar to those on Mars, leading to the suggestion that viable microbes could be transferred between planets in meteorites.

Recently, several studies have shown that archaea exist not only in mesophilic and thermophilic environments but are also present, sometimes in high numbers, at low temperatures as well. For example, archaea are common in cold oceanic environments such as polar seas. Even more significant are the large numbers of archaea found throughout the world's oceans in non-extreme habitats among the plankton community (as part of the picoplankton). Although these archaea can be present in extremely high numbers (up to 40% of the microbial biomass), almost none of these species have been isolated and studied in pure culture. Consequently, our understanding of the role of archaea in ocean ecology is rudimentary, so their full influence on global biogeochemical cycles remains largely unexplored. Some marine Crenarchaeota are capable of nitrification, suggesting these organisms may affect the oceanic nitrogen cycle, although these oceanic Crenarchaeota may also use other sources of energy. Vast numbers of archaea are also found in the sediments that cover the sea floor, with these organisms making up the majority of living cells at depths over 1 meter below the ocean bottom.

## Role in chemical cycling

Archaea recycle elements such as carbon, nitrogen and sulfur through their various habitats. Although these activities are vital for normal ecosystem function, archaea can also contribute to human-made changes, and even cause pollution.

Archaea carry out many steps in the nitrogen cycle. This includes both reactions that remove nitrogen from ecosystems, such as nitrate-based respiration and denitrification, as well as processes that introduce nitrogen, such as nitrate assimilation and nitrogen fixation. Archaean involvement in ammonia oxidation reactions was recently discovered. These reactions are particularly important in the oceans. The archaea also appear to be crucial for ammonia oxidation in soils. They produce nitrite, which other microbes then oxidize to nitrate. Plants and other organisms consume the latter.

In the sulfur cycle, archaea that grow by oxidizing sulfur compounds release this element from rocks, making it available to other organisms. However, the archaea that do this, such as *Sulfolobus*, produce sulfuric acid as a waste product, and the growth of these organisms in abandoned mines can contribute to acid mine drainage and other environmental damage.

In the carbon cycle, methanogen archaea remove hydrogen and are important in the decay of organic matter by the populations of microorganisms that act as decomposers in

anaerobic ecosystems, such as sediments, marshes and sewage treatment works. However, methane is one of the most abundant greenhouse gases in Earth's atmosphere, constituting 18% of the global total. It is 25 times more potent as a greenhouse gas than carbon dioxide. Methanogens are the primary source of atmospheric methane, and are responsible for most of the world's yearly methane emissions. As a consequence, these archaea contribute to global greenhouse gas emissions and global warming.

## Interactions with other organisms

Methanogenic archaea form a symbiosis with termites.

The well-characterized interactions between archaea and other organisms are either mutual or commensal. As of 2007, no clear examples of archaeal pathogens or parasites were known. However, a relationship has been proposed between some species of

methanogens and infections in the mouth, and *Nanoarchaeum equitans* may be a parasite of another species of archaea, since it only survives and reproduces within the cells of the Crenarchaeon *Ignicoccus hospitalis*, and appears to offer no benefit to its host.

**Mutualism**

One well-understood example of mutualism is the interaction between protozoa and methanogenic archaea in the digestive tracts of animals that digest cellulose, such as ruminants and termites. In these anaerobic environments, protozoa break down plant cellulose to obtain energy. This process releases hydrogen as a waste product, but high levels of hydrogen reduce energy production. When methanogens convert hydrogen to methane, protozoa benefit from more energy.

In anaerobic protozoa such as *Plagiopyla frontata*, archaea reside inside the protozoa and consume hydrogen produced in their hydrogenosomes. Archaea also associate with larger organisms. For example, the marine archaean *Cenarchaeum symbiosum* lives within (is an endosymbiont of) the sponge *Axinella mexicana*.

**Commensalism**

Archaea can also be commensals, benefiting from an association without helping or harming the other organism. For example, the methanogen *Methanobrevibacter smithii* is by far the most common archaean in the human flora, making up about one in ten of all the prokaryotes in the human gut. In termites and in humans, these methanogens may in fact be mutualists, interacting with other microbes in the gut to aid digestion. Archaean communities also associate with a range of other organisms, such as on the surface of corals, and in the region of soil that surrounds plant roots (the rhizosphere).

# Significance in technology and industry

Extremophile archaea, particularly those resistant either to heat or to extremes of acidity and alkalinity, are a source of enzymes that function under these harsh conditions. These enzymes have found many uses. For example, thermostable DNA polymerases, such as the Pfu DNA polymerase from *Pyrococcus furiosus*, revolutionized molecular biology by allowing the polymerase chain reaction to be used in research as a simple and rapid technique for cloning DNA. In industry, amylases, galactosidases and pullulanases in other species of *Pyrococcus* that function at over 100 °C (212 °F) allow food processing at high temperatures, such as the production of low lactose milk and whey. Enzymes from these thermophilic archaea also tend to be very stable in organic solvents, allowing their use in environmentally friendly processes in green chemistry that synthesize organic compounds. This stability makes them easier to use in structural biology. Consequently the counterparts of bacterial or eukaryotic enzymes from extremophile archaea are often used in structural studies.

In contrast to the range of applications of archaean enzymes, the use of the organisms themselves in biotechnology is less developed. Methanogenic archaea are a vital part of

sewage treatment, since they are part of the community of microorganisms that carry out anaerobic digestion and produce biogas. In mineral processing, acidophilic archaea display promise for the extraction of metals from ores, including gold, cobalt and copper.

Archaea host a new class of potentially useful antibiotics. A few of these archaeocins have been characterized, but hundreds more are believed to exist, especially within *Haloarchaea* and *Sulfolobus*. These compounds differ in structure from bacterial antibiotics, so they may have novel modes of action. In addition, they may allow the creation of new selectable markers for use in archaeal molecular biology.

Chapter- 8

# Gamete and Zygote

# Gamete

A **gamete** (from Ancient Greek γαμέτης *gametes* "husband" / γαμετή *gamete* "wife") is a cell that fuses with another cell during fertilization (conception) in organisms that reproduce sexually. In species that produce two morphologically distinct types of gametes, and in which each individual produces only one type, a female is any individual that produces the larger type of gamete—called an ovum (or egg)—and a male produces the smaller tadpole-like type—called a sperm. This is an example of anisogamy or heterogamy, the condition wherein females and males produce gametes of different sizes (this is the case in humans; the human ovum is approximately 20 times larger than the human sperm cell). In contrast, isogamy is the state of gametes from both sexes being the same size and shape, and given arbitrary designators for mating type. The name gamete was introduced by the Austrian biologist Gregor Mendel. Gametes carry half the genetic information of an individual, 1n of each type.

## Asexual reproduction

Asexual reproduction is a process of reproduction without the use of gametes and fertilization. Asexual reproduction only uses the genetic material from the single parent. An organism may be capable of reproducing both asexually or sexually using gametes.

## Sperm-egg distinction

Eggs are relatively few, large, and do not move, whereas sperm are many, small, and mobile. The size difference is mostly (but not entirely) accounted for by the very large cytoplasm of the egg. Eggs awaiting zygote formation may be anchored either to something in the environment or by an organ that contains them; sperm may rely solely on their own motility or may be relayed into place by an organ such as pollen to reach the

place of zygote formation. Typically many more sperm than eggs are created and wasted, in the sense of never fusing with a partner gamete.

The sperm-egg distinction is the basis for distinguishing between males and females. Since some algae and fungi have sexual reproduction by combining two identical gametes, there is no male/female distinction in these species. This raises the question as to why most large/familiar species reproduce by sperm and egg. One theory for why the male/female distinction is so common is that it facilitated encounters between gametes, in ancestral marine species.

## Dissimilarity

In contrast to a gamete, the diploid somatic cells of an individual contain one copy of the chromosome set from the sperm and one copy of the chromosome set from the egg; that is, the cells of the offspring have genes expressing characteristics of both the *father* and the *mother*. A gamete's chromosomes are not exact duplicates of either of the sets of chromosomes carried in the somatic cells of the individual that produced the gametes. They can be *hybrids* produced through crossover (a form of genetic recombination) of chromosomes, which takes place in meiosis. This hybridization has a random element, and the chromosomes tend to be a little different in every gamete that an individual produces. Additionally, base pairs in chromosomes often undergo random mutations resulting in modified DNA (and subsequently, new proteins and phenotypes). This mutation, recombination, and the fact that the two chromosome sets ultimately come from either a grandmother or a grandfather on each parental side account for the genetic dissimilarity of siblings.

## Plants

Plants which reproduce sexually also have gametes, however, they are produced in the anther and ovary. They produce pollen and ovules by meiosis, in a similar way to animals.

## Sex determination

In humans, an ovum can carry only an X chromosome (of the X and Y chromosomes), whereas a sperm may carry either an X or a Y; thus the male sperm determines the sex of any resulting zygote, if the zygote has two X chromosomes it will develop into a female, if it has an X and a Y chromosome, it will develop into a male. For birds, the female ovum determines the sex of the offspring, through the ZW sex-determination system.

# Zygote

A **zygote** (from Greek ζυγωτός *zygōtos* "joined" or "yoked", from ζυγοῦν *zygoun* "to join" or "to yoke"), or **zygocyte**, is the initial cell formed when a new organism is produced by means of sexual reproduction. A zygote is synthesized from the union of two gametes, and constitutes the first stage in a unique organism's development. Zygotes are usually produced by a fertilization event between two haploid cells—an ovum from a female and a sperm cell from a male—which combine to form the single diploid cell. Such zygotes contain DNA derived from both the mother and the father, and this provides all the genetic information necessary to form a new individual. The term *zygote* is also used more loosely to refer to the group of cells formed by the first few cell divisions, although this is properly referred to as a morula.

In mammalian reproduction, after fertilization has taken place the zygote travels down the fallopian tube, while dividing to form more cells without the zygote actually increasing in size. This cell division is mitotic, and is known as *cleavage*. All mammals go through the zygote stage of life. Zygotes eventually develop into an embryo, and then a fetus. A human zygote exists for about four days, and becomes a blastocyst on the fifth day.

## Twins

Twins and other multiple births can be monozygotic (identical) or dizygotic (fraternal). Dizygotic twins arise from one or several—strictly, two—fertilization events. Polyspermic zygotes in mice have been manipulated so as to remove one of the two male pronuclei and made to survive birth.

Conjoined twins, sometimes called "Siamese twins", occur once in every two hundred identical twin pregnancies and are always identical. Actual numbers for conjoined births vary from 1 in 20,000 to 1 in 100,000 pregnancies; 40–60% are stillborn, with many others dying within the first few days after birth. About 70% of conjoined twins are female, the reason for which is unknown.

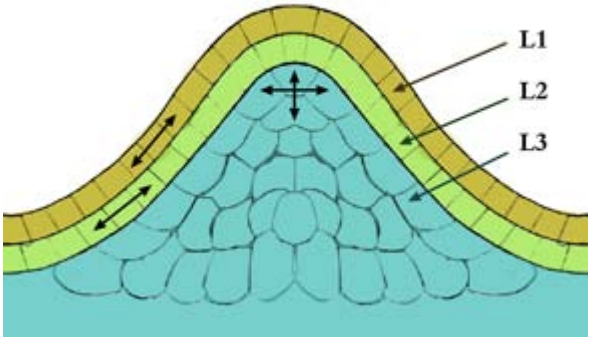
The first successful separation of conjoined twins was performed in Basle, Switzerland in 1689 on twin girls born joined by a ligament at the sternum (xiphopagus). The first to be successfully separated in modern times are generally believed to be Catherine and Caroline Mouton of Louisiana, born joined at the lower back (pygopagus) and separated in 1953 at eight days of age. Both survived the operation. Separation has been attempted on almost all conjoined twins born since the 1950s, with varying results.

## In other species

A **biparental zygote** is a Chlamydomonas (a kind of algae) zygote that contains chloroplast DNA (cpDNA) from both parents.

## Chapter- 9

# Meristem




**Tunica-Corpus model** of the apical meristem (growing tip). The epidermal (L1) and subepidermal (L2) layers form the outer layers called the tunica. The inner L3 layer is called the corpus. Cells in the L1 and L2 layers divide in a sideways fashion which keeps these layers distinct, while the L3 layer divides in a more random fashion.

A **meristem** is the tissue in most plants consisting of undifferentiated cells (**meristematic cells**), found in zones of the plant where growth can take place.

The term *meristem* was first used in 1858 by Karl Wilhelm von Nägeli (1817–1891) in his book *Beiträge zur Wissenschaftlichen Botanik*. It is derived from the Greek word *merizein* (μερίζειν), meaning to divide, in recognition of its inherent function.

Differentiated plant cells generally cannot divide or produce cells of a different type. Therefore, cell division in the meristem is required to provide new cells for expansion and differentiation of tissues and initiation of new organs, providing the basic structure of the plant body.

Meristematic cells are analogous in function to stem cells in animals, are incompletely or not at all differentiated, and are capable of continued cellular division (youthful). Furthermore, the cells are small and protoplasm fills the cell completely. The vacuoles are extremely small. The cytoplasm does not contain differentiated plastids (chloroplasts or chromoplasts), although they are present in rudimentary form (proplastids).

Meristematic cells are packed closely together without intercellular cavities. The cell wall is a very thin *primary cell wall*.

Maintenance of the cells requires a balance between two antagonistic processes: organ initiation and stem cell population renewal.

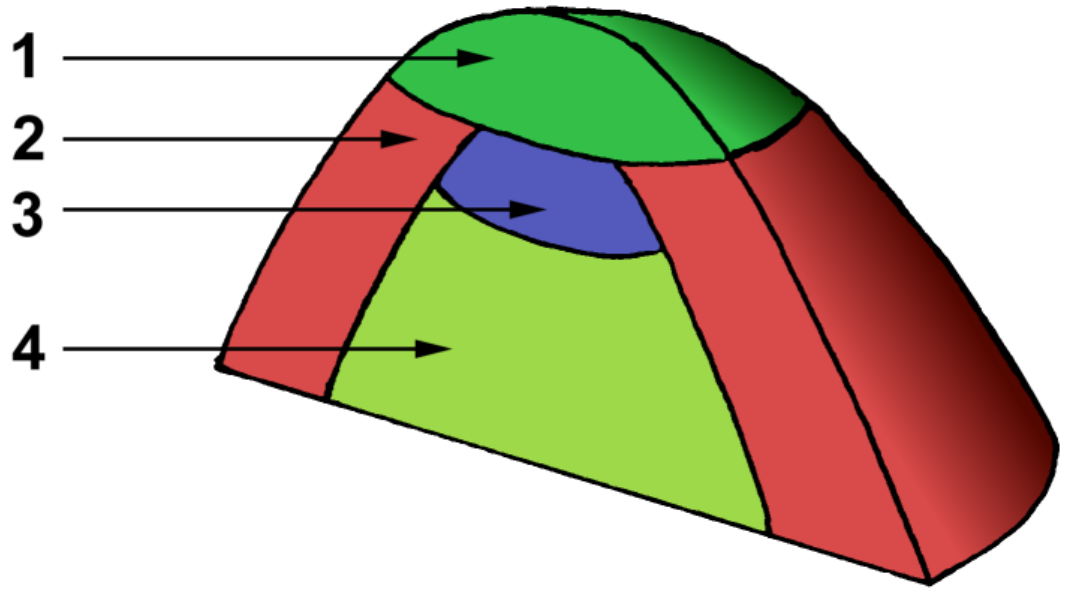
# Meristematic zones

Apical meristems are the completely undifferentiated (indeterminate) meristems in a plant. These differentiate into three kinds of primary meristems. The primary meristems in turn produce the two secondary meristem types. These secondary meristems are also known as lateral meristems because they are involved in lateral growth.

At the meristem summit there is a small group of slowly dividing cells which is commonly called the central zone. Cells of this zone have a stem cell function and are essential for meristem maintenance. The proliferation and growth rates at the meristem summit usually differ considerably from those at the periphery.

Meristems also are induced in the roots of legumes such as soybean, *Lotus japonicus*, pea, and *Medicago truncatula* after infection with soil bacteria commonly called Rhizobium. Cells of the inner or outer cortex in the so-called "window of nodulation" just behind the developing root tip are induced to divide. The critical signal substance is the lipo-oligosaccharide Nod-factor, decorated with side groups to allow specificity of interaction. The Nod factor receptor proteins NFR1 and NFR5 were cloned from several legumes including *Lotus japonicus*, *Medicago truncatula* and soybean (Glycine max). Regulation of nodule meristems utilizes long distance regulation commonly called "Autoregulation of Nodulation" (AON). This process involves a leaf-vascular tissue located LRR receptor kinases (LjHAR1, GmNARK and MtSUNN), CLE peptide signalling , and KAPP interaction, similar to that seen in the CLV1,2,3 system. LjKLAVIER also exhibits a nodule regulation phenotype though it is not yet known how this relates to the other AON receptor kinases

# Apical meristems




Organisation of an apical meristem (growing tip)
1 - Central zone
2 - Peripheral zone
3 - Medullary (i.e. central) meristem
4 - Medullary tissue

The **apical meristem**, or growing tip, is a completely undifferentiated meristematic tissue found in the buds and growing tips of roots in plants. Its main function is to begin growth of new cells in young seedlings at the tips of roots and shoots (forming buds, among other things). Specifically, an active apical meristem lays down a growing root or shoot behind itself, pushing itself forward. Apical meristems are very small, compared to the cylinder-shaped lateral meristems.

Apical meristems are composed of several layers. The number of layers varies according to plant type. In general the outermost layer is called the **tunica** while the innermost layers are the **corpus**. In monocots, the tunica determine the physical characteristics of the leaf edge and margin. In dicots, layer two of the corpus determine the characteristics of the edge of the leaf. The corpus and tunica play a critical part of the plant physical appearance as all plant cells are formed from the meristems. Apical meristems are found in two locations: the root and the stem. Some Arctic plants have an apical meristem in the lower/middle parts of the plant. It is thought that this kind of meristem evolved because it is advantageous in Arctic conditions.

## Shoot apical meristems

The source of all above-ground organs. Cells at the shoot apical meristem summit serve as stem cells to the surrounding peripheral region, where they proliferate rapidly and are incorporated into differentiating leaf or flower primordia.

The shoot apical meristem is the site of most of the embryogenesis in flowering plants. Primordia of leaves, sepals, petals, stamens and ovaries are initiated here at the rate of one every time interval, called a plastochron. It is where the first indications that flower development has been evoked are manifested. One of these indications might be the loss of apical dominance and the release of otherwise dormant cells to develop as axillary shoot meristems, in some species in axils of primordia as close as two or three away from the apical dome. The shoot apical meristem consists of 4 distinct cell groups: -.

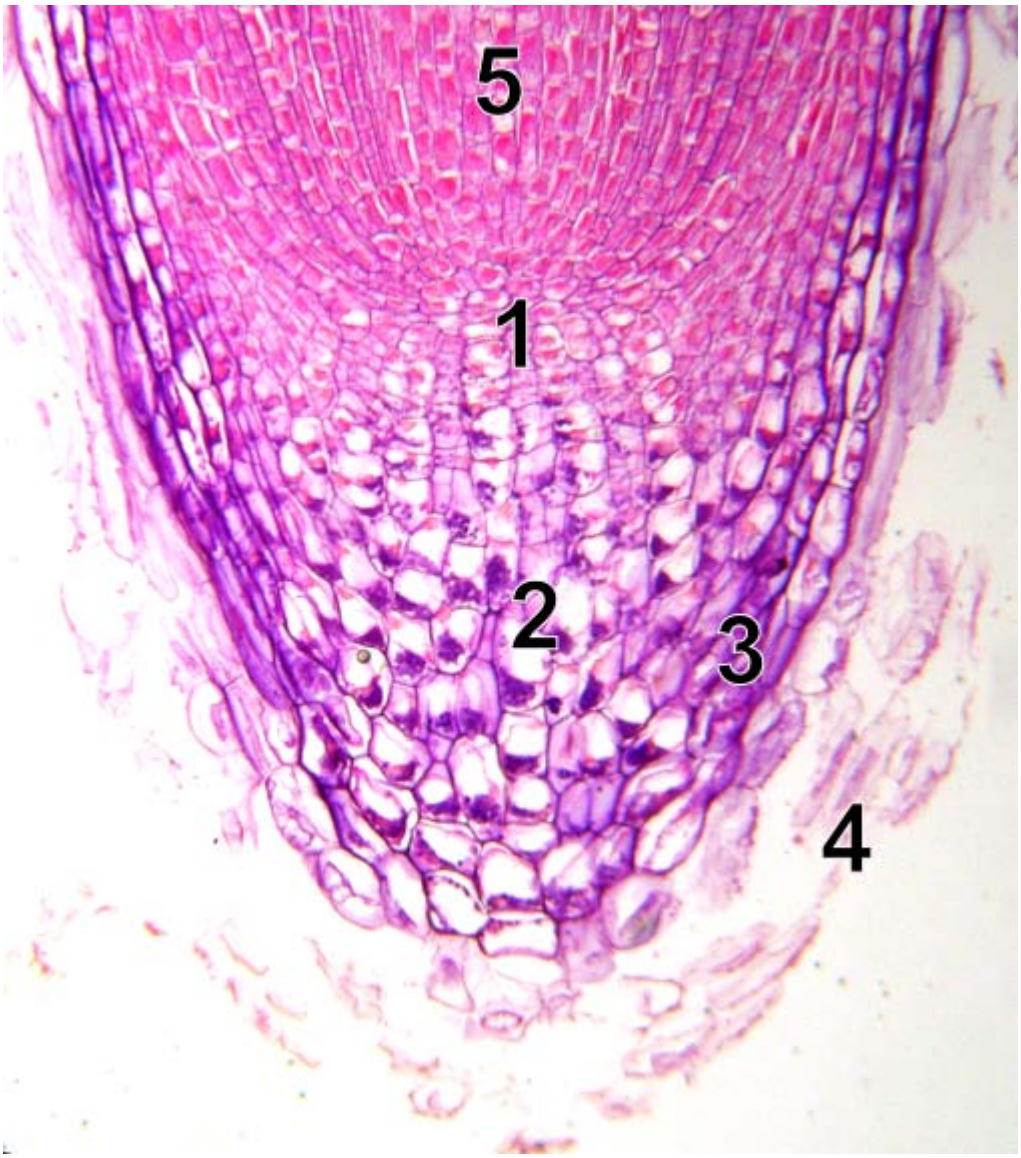
- Stem cells
- The immediate daughter cells of the stem cells
- A subjacent organising centre
- Founder cells for organ initiation in surrounding regions

The four distinct zones mentioned above are maintained by a complex signalling pathway. In *Arabidopsis thaliana* , 3 interacting *CLAVATA* genes are required to regulate the size of the stem cell reservoir in the shoot apical meristem by controlling the rate of cell division. CLV1 and CLV2 are predicted to form a receptor complex (of the LRR receptor like kinase family) to which CLV3 is a ligand. CLV3 shares some homology with the ESR proteins of maize, with a short 14 amino acid region being conserved between the proteins. Proteins that contain these conserved regions have been grouped into the CLE family of proteins.

CLV1 has been shown to interact with several cytoplasmic proteins that are most likely involved in downstream signalling, for example the CLV complex has been found to be associated with Rho/Rac small GTPase related proteins. These proteins may act as an intermediate between the CLV complex and a mitogen-activated protein kinase (MAPK) which is often involved in signalling cascades. KAPP is a kinase-associated protein phosphatase that has been shown to interact with CLV1. KAPP is thought to act as a negative regulator of CLV1 by dephosphorylating it.

Another important gene in plant meristem maintenance is *WUSCHEL* (shortened to *WUS*), which is a target of CLV signalling. *WUS* is expressed in the cells below the stem cells of the meristem and its presence prevents the differentiation of the stem cells. CLV1 acts to promote cellular differentiation by repressing *WUS* activity outside of the central zone containing the stem cells. *STM* also acts to prevent the differentiation of stem cells by repressing the expression of Myb genes that are involved in cellular differentiation.

## Root apical meristems




10x microscope image of root tip with meristem
1 - quiescent center
2 - calyptrogen (live rootcap cells)
3 - rootcap
4 - sloughed off dead rootcap cells
5 - procambium

Unlike the shoot apical meristem, the root apical meristem produces cells in two dimensions. It is covered by the root cap, which protects the apical meristem from the rocks, dirt and pathogens. Cells are continuously sloughed off the outer surface of the root cap. The center of the root apical meristem is occupied by a quiescent center which has low mitotic activity. Evidence suggests the quiescent center does function as the zone of initials. Infrequent division of initial cells in the quiescent center is the source of cells

for the root apical meristem. These initial cells and tissue patterns become established in the embryo in the case of the primary root and in the new lateral meristems in the case of secondary roots.

## Intercalary meristem

In angiosperms, intercalary meristems occur only in monocot (particularly grass) stems at the base of nodes and leaf blades. Horsetails also exhibit intercalary growth. Intercalary meristems are capable of cell division and allow for rapid growth and regrowth of many monocots. Intercalary meristems at the nodes of bamboo allow for rapid stem elongation, while those at the base of most grass leaf blades allow damaged leaves to rapidly regrow. This leaf regrowth in grasses evolved in response to damage by grazing herbivores, but is more familiar to us in response to lawnmowers.

## Floral meristem

When plants begin the developmental process known as flowering, the shoot apical meristem is transformed into an inflorescence meristem which goes on to produce the floral meristem which produces the familiar sepals, petals, stamens, and carpels of the flower.

In contrast to vegetative apical meristems and some exflorescence meristems, floral meristems are responsible for determinate growth, the limited growth of the flower to a particular size and form. The transition from shoot meristem to floral meristem requires floral meristem identity genes, that both specify the floral organs and cause the termination of the production of stem cells. *AGAMOUS* (*AG*) is a floral homeotic gene required for floral meristem termination and necessary for proper development of the stamens and carpels. *AG* is necessary to prevent the conversion of floral meristems to inflorescence shoot meristems, but is not involved in the transition from shoot to floral meristem. AG is turned on by the floral meristem identity gene *LEAFY* (*LFY*) and *WUS* and is restricted to the centre of the floral meristem or the inner two whorls. This way floral identity and region specificity is achieved. WUS activates AG by binding to a consensus sequence in the AG's second intron and LFY binds to adjacent recognition sites. Once AG is activated it represses expression of WUS leading to the termination of the meristem.

Through the years scientists have manipulated floral meristems for economics reasons. An example is the mutant tobacco plant "Maryland Mammoth" In 1936 the department of agriculture of Switzerland performed several scientific tests with this plant. "Maryland Mammoth" is peculiar in this sense that it grows much faster than other tobacco plants.

## Apical dominance

Apical dominance is phenomenon where one meristem prevents or inhibits the growth of other meristems. As a result the plant will have one clearly defined main trunk. For example, in trees the tip of the main trunk bears the dominant meristem. Therefore the tip

of the trunk grows rapidly and is not shadowed by branches. If the dominant meristem is cut off, one or more branch tips will assume dominance. The branch will start growing faster and the new growth will be vertical. Over the years the branch may begin to look more and more like an extension of the main trunk. Often several branches will exhibit this behaviour after the removal of apical meristem, leading to a bushy growth.

The mechanism of apical dominance is based on the plant hormone auxin. It is produced in the apical meristem and transported towards the roots in the cambium. If apical dominance is complete, it prevents any branches from forming as long as apical meristem is active. If the dominance is incomplete, side branches will develop.

Recent investigations into apical dominance and the control of branching have revealed a new plant hormone family termed strigolactones. These compounds were previously known to be involved in seed germination and communication with mycorrhizal fungi and are now shown to be involved in inhibition of branching.

# Primary meristems

Apical meristems may differentiate into three kinds of primary meristem:

- **Protoderm** - lies around the outside of the stem and develops into the epidermis.
- **Procambium** - lies just inside of the protoderm and develops into primary xylem and primary phloem. It also produces the vascular cambium, a secondary meristem.
- **Ground meristem** develops into the pith. It produces the cork cambium, another secondary meristem.

These meristems are responsible for primary growth, or an increase in length or height which were discovered by scientist Joseph D. Carr of North Carolina in 1943.

# Secondary meristems

There are two types of secondary meristems, these are also called the *lateral meristems* because they surround the established stem of a plant and cause it to grow laterally (i.e. larger in diameter).

- Vascular cambium - produces secondary xylem and secondary phloem, this is a process which may continue throughout the life of the plant. This is what gives rise to wood in plants. Such plants are called arborescent. This does not occur in plants which do not go through secondary growth (known as herbaceous plants).
- Cork cambium - gives rise to the periderm which replaces the epidermis

# Indeterminate growth of meristems

Though each plant grows according to a certain set of rules, each new root and shoot meristem can go on growing for as long as it is alive. In many plants meristematic growth is potentially **indeterminate**, making the overall shape of the plant not determinate in advance. This is the **primary growth**. Primary growth leads to lengthening of the plant body and organ formation. All plant organs arise ultimately from cell divisions in the apical meristems, followed by cell expansion and differentiation. Primary growth gives rise to the apical part of many plants.

The growth of nitrogen fixing nodules on legume plants such as soybean and pea is either determinate or indeterminate. Thus soybean (or bean and Lotus japonicus) produce determinate nodules (spherical), with a branched vascular system surrounding the central infected zone. Often Rhizobium infected cells have only small vacuoles. In contrast, nodules on pea, clovers, and Medicago truncatula are indeterminate; to maintain (at least for some time) an active meristem that yields new cells for Rhizobium infection. Thus zones of maturity exist in the nodule. Infected cells usually possess a large vacuole. The plant vascular system is branched and peripheral.

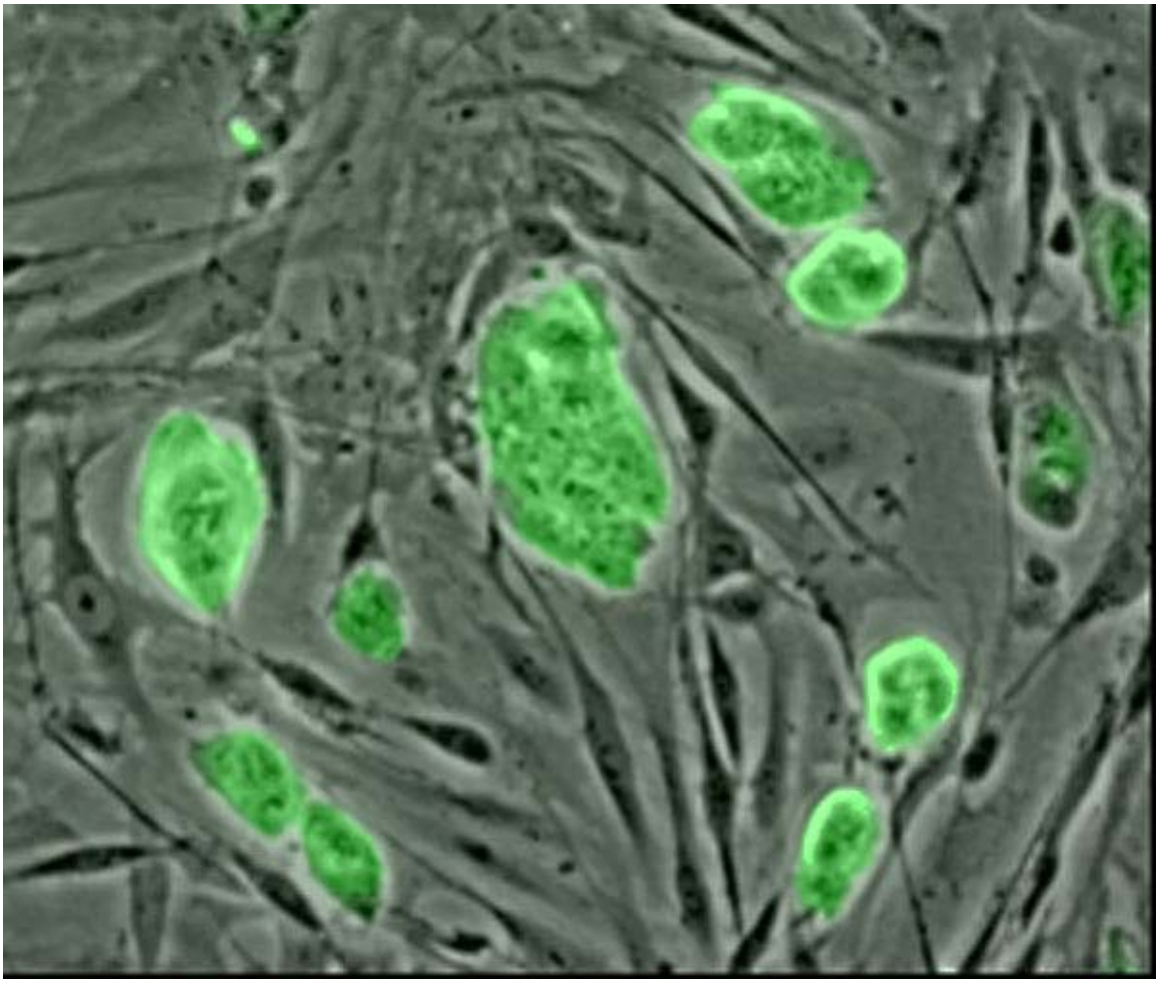
# Cloning

Under appropriate conditions, each shoot meristem can develop into a complete new plant or clone. Such new plants can be grown from shoot cuttings that contain an apical meristem. Root apical meristems are not readily cloned, however. This cloning is called **asexual reproduction** or **vegetative reproduction** and is widely practiced in horticulture to mass-produce plants of a desirable genotype. This process is also known as mericloning.

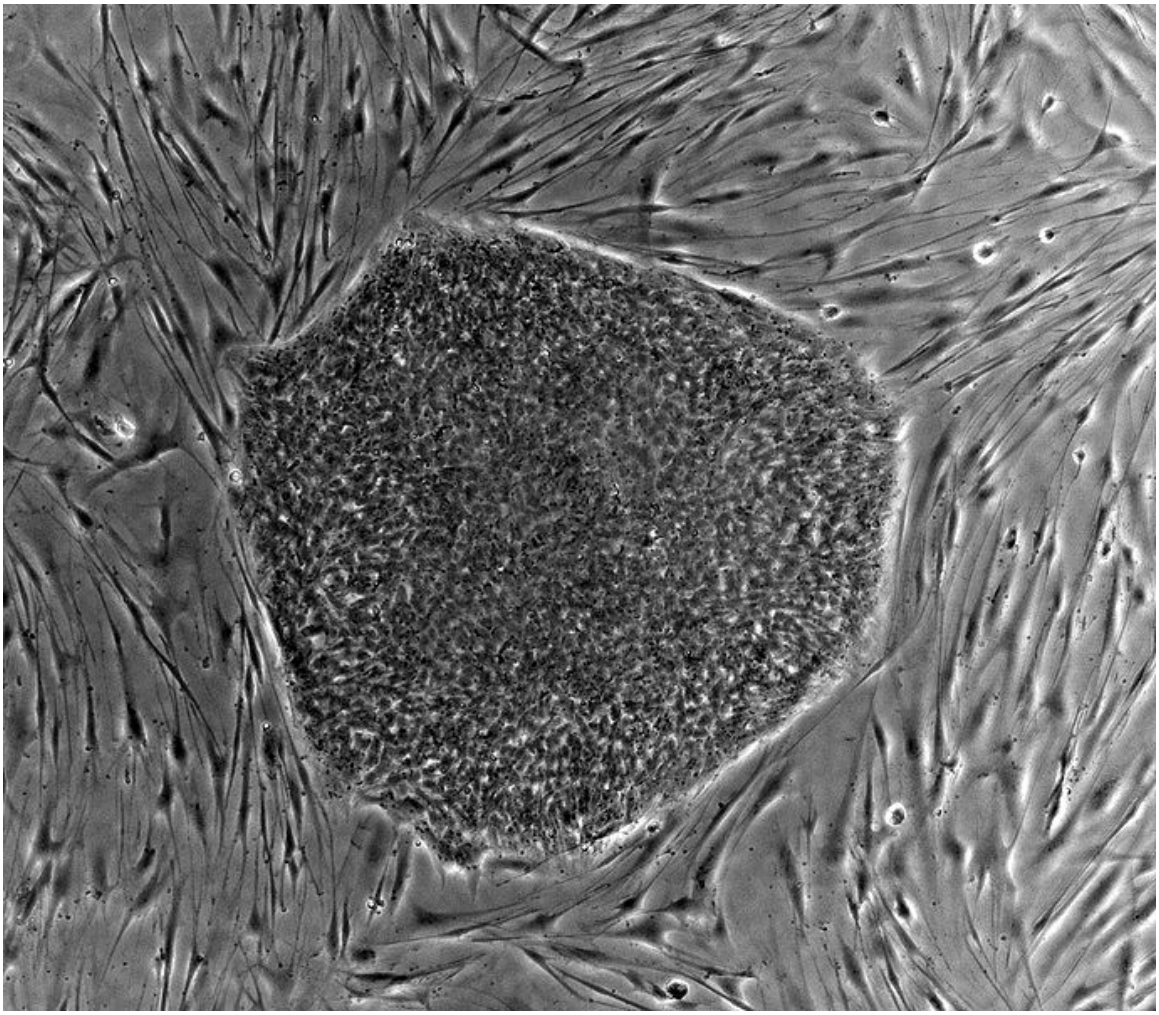
Propagating through cuttings is another form of vegetative propogation that initiates root or shoot production from secondary meristematic cambial cells. This explains why basal 'wounding' of shoot-borne cuttings often aids root formation.

**Chapter- 10**

# Stem Cell



Mouse embryonic stem cells with fluorescent marker



Human embryonic stem cell colony on mouse embryonic fibroblast feeder layer

**Stem cells** are cells found in all multi cellular organisms. They are characterized by the ability to renew themselves through mitotic cell division and differentiate into a diverse range of specialized cell types. Research in the stem cell field grew out of findings by Ernest A. McCulloch and James E. Till at the University of Toronto in the 1960s.

The two broad types of mammalian stem cells are: embryonic stem cells that are isolated from the inner cell mass of blastocysts, and adult stem cells that are found in adult tissues. In a developing embryo, stem cells can differentiate into all of the specialized embryonic tissues. In adult organisms, stem cells and progenitor cells act as a repair system for the body, replenishing specialized cells, but also maintain the normal turnover of regenerative organs, such as blood, skin, or intestinal tissues.

Stem cells can now be grown and transformed into specialized cells with characteristics consistent with cells of various tissues such as muscles or nerves through cell culture. Highly plastic adult stem cells from a variety of sources, including umbilical cord blood and bone marrow, are routinely used in medical therapies. Embryonic cell lines and

autologous embryonic stem cells generated through therapeutic cloning have also been proposed as promising candidates for future therapies.

# Properties

The classical definition of a stem cell requires that it possess two properties:

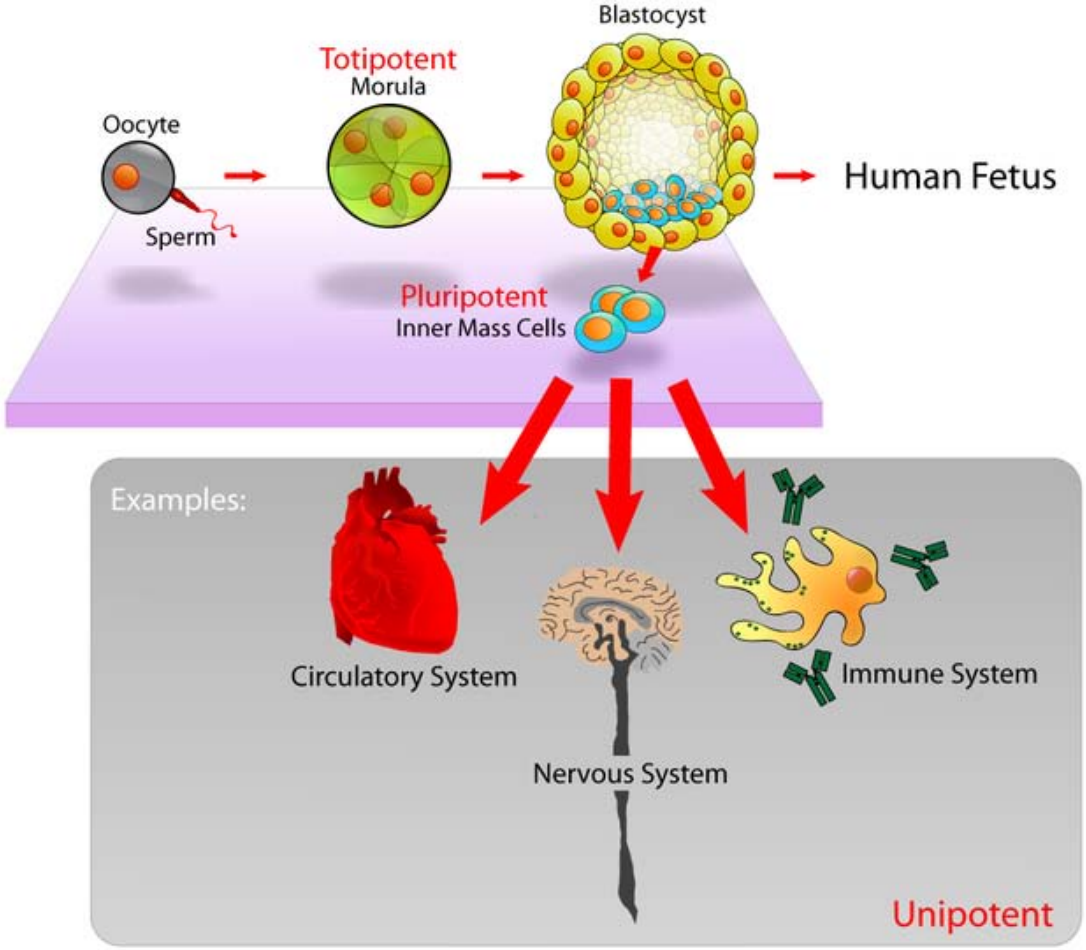
- *Self-renewal* - the ability to go through numerous cycles of cell division while maintaining the undifferentiated state.
- *Potency* - the capacity to differentiate into specialized cell types. In the strictest sense, this requires stem cells to be either totipotent or pluripotent - to be able to give rise to any mature cell type, although multipotent or unipotent progenitor cells are sometimes referred to as stem cells.

## Self-renewal

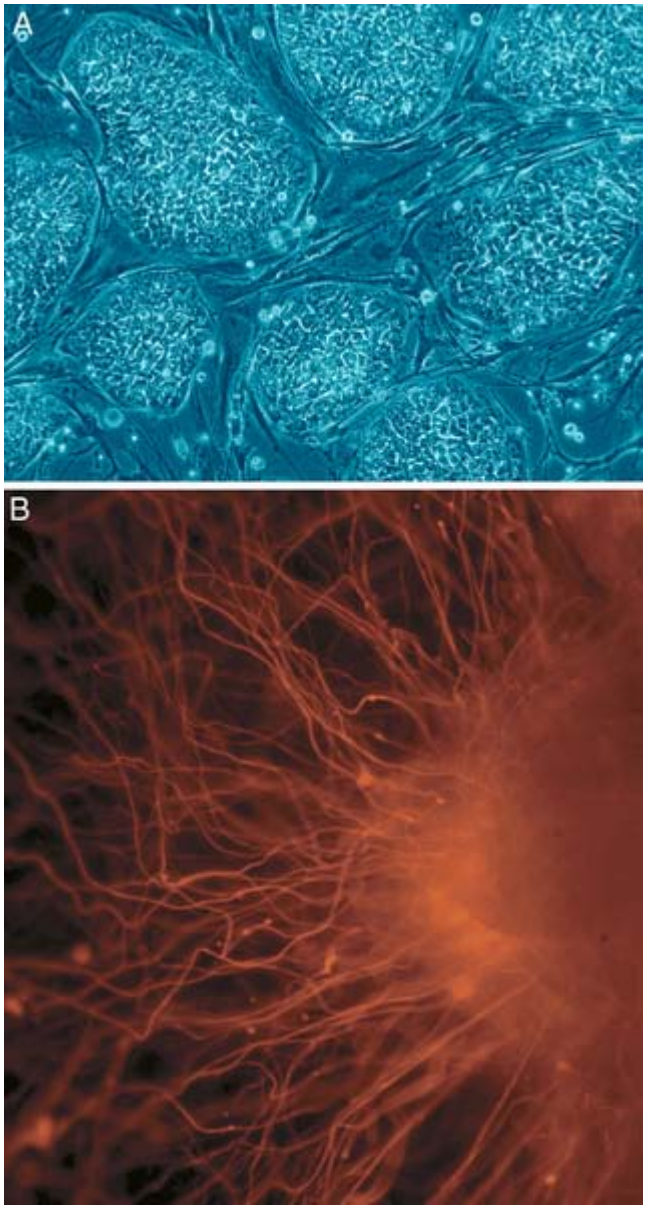
Two mechanisms exist to ensure that the stem cell population is maintained:

1. Obligatory asymmetric replication - a stem cell divides into one father cell that is identical to the original stem cell, and another daughter cell that is differentiated
2. Stochastic differentiation - when one stem cell develops into two differentiated daughter cells, another stem cell undergoes mitosis and produces two stem cells identical to the original.

## Potency definitions




Pluripotent, embryonic stem cells originate as inner mass cells within a blastocyst. The stem cells can become any tissue in the body, excluding a placenta. Only the morula's cells are totipotent, able to become all tissues and a placenta.




Human embryonic stem cells
A: Cell colonies that are not yet differentiated.
B: Nerve cell

*Potency* specifies the differentiation potential (the potential to differentiate into different cell types) of the stem cell.

- Totipotent (a.k.a omnipotent) stem cells can differentiate into embryonic and extraembryonic cell types. Such cells can construct a complete, viable, organism. These cells are produced from the fusion of an egg and sperm cell. Cells produced by the first few divisions of the fertilized egg are also totipotent.
- Pluripotent stem cells are the descendants of totipotent cells and can differentiate into nearly all cells, i.e. cells derived from any of the three germ layers.

- Multipotent stem cells can differentiate into a number of cells, but only those of a closely related family of cells.
- Oligopotent stem cells can differentiate into only a few cells, such as lymphoid or myeloid stem cells.
- Unipotent cells can produce only one cell type, their own, but have the property of self-renewal which distinguishes them from non-stem cells (e.g. muscle stem cells).

### Identification

The practical definition of a stem cell is the functional definition - a cell that has the potential to regenerate tissue over a lifetime. For example, the gold standard test for a bone marrow or hematopoietic stem cell (HSC) is the ability to transplant one cell and save an individual without HSCs. In this case, a stem cell must be able to produce new blood cells and immune cells over a long term, demonstrating potency. It should also be possible to isolate stem cells from the transplanted individual, which can themselves be transplanted into another individual without HSCs, demonstrating that the stem cell was able to self-renew.

Properties of stem cells can be illustrated *in vitro*, using methods such as clonogenic assays, where single cells are characterized by their ability to differentiate and self-renew. As well, stem cells can be isolated based on a distinctive set of cell surface markers. However, *in vitro* culture conditions can alter the behavior of cells, making it unclear whether the cells will behave in a similar manner *in vivo*. Considerable debate exists whether some proposed adult cell populations are truly stem cells.

## Embryonic

Embryonic stem cell lines (ES cell lines) are cultures of cells derived from the epiblast tissue of the inner cell mass (ICM) of a blastocyst or earlier morula stage embryos. A blastocyst is an early stage embryo—approximately four to five days old in humans and consisting of 50–150 cells. ES cells are pluripotent and give rise during development to all derivatives of the three primary germ layers: ectoderm, endoderm and mesoderm. In other words, they can develop into each of the more than 200 cell types of the adult body when given sufficient and necessary stimulation for a specific cell type. They do not contribute to the extra-embryonic membranes or the placenta.

Nearly all research to date has taken place using mouse embryonic stem cells (mES) or human embryonic stem cells (hES). Both have the essential stem cell characteristics, yet they require very different environments in order to maintain an undifferentiated state. Mouse ES cells are grown on a layer of gelatin and require the presence of Leukemia Inhibitory Factor (LIF). Human ES cells are grown on a feeder layer of mouse embryonic fibroblasts (MEFs) and require the presence of basic Fibroblast Growth Factor (bFGF or FGF-2). Without optimal culture conditions or genetic manipulation, embryonic stem cells will rapidly differentiate.

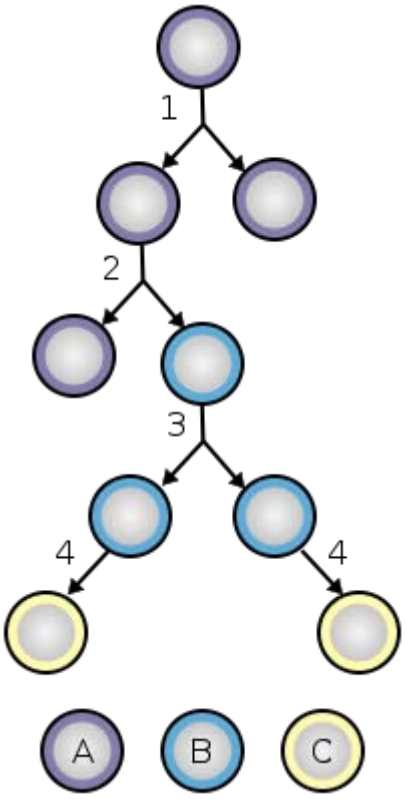
A human embryonic stem cell is also defined by the presence of several transcription factors and cell surface proteins. The transcription factors Oct-4, Nanog, and Sox2 form the core regulatory network that ensures the suppression of genes that lead to differentiation and the maintenance of pluripotency. The cell surface antigens most commonly used to identify hES cells are the glycolipids SSEA3 and SSEA4 and the keratan sulfate antigens Tra-1-60 and Tra-1-81. The molecular definition of a stem cell includes many more proteins and continues to be a topic of research.

After nearly ten years of research, there are no approved treatments using embryonic stem cells. The first human trial was approved by the US Food & Drug Administration in January 2009. However, as of August 2010, the first human trial had not yet been initiated. The first human medical trial for embryonic stem cells started in Atlanta on October 13, 2010 for spinal injury victims. ES cells, being pluripotent cells, require specific signals for correct differentiation - if injected directly into another body, ES cells will differentiate into many different types of cells, causing a teratoma. Differentiating ES cells into usable cells while avoiding transplant rejection are just a few of the hurdles that embryonic stem cell researchers still face. Many nations currently have moratoria on either ES cell research or the production of new ES cell lines. Because of their combined abilities of unlimited expansion and pluripotency, embryonic stem cells remain a theoretically potential source for regenerative medicine and tissue replacement after injury or disease.

# Fetal

Fetal stem cells are primitive cell types found in the organs of fetuses.

# Adult




Stem cell division and differentiation. A - stem cell; B - progenitor cell; C - differentiated cell; 1 - symmetric stem cell division; 2 - asymmetric stem cell division; 3 - progenitor division; 4 - terminal differentiation

Also known as somatic (from Greek Σωματικός, "of the body") stem cells and germline (giving rise to gametes) stem cells, they can be found in children, as well as adults.

Pluripotent adult stem cells are rare and generally small in number but can be found in a number of tissues including umbilical cord blood. A great deal of adult stem cell research has focused on clarifying their capacity to divide or self-renew indefinitely and their differentiation potential. In mice, pluripotent stem cells are directly generated from adult fibroblast cultures. Unfortunately, many mice don't live long with stem cell organs.

Most adult stem cells are lineage-restricted (multipotent) and are generally referred to by their tissue origin (mesenchymal stem cell, adipose-derived stem cell, endothelial stem cell, dental pulp stem cell, etc.).

Adult stem cell treatments have been successfully used for many years to treat leukemia and related bone/blood cancers through bone marrow transplants. Adult stem cells are also used in veterinary medicine to treat tendon and ligament injuries in horses.

The use of adult stem cells in research and therapy is not as controversial as embryonic stem cells, because the production of adult stem cells does not require the destruction of an embryo. Additionally, because in some instances adult stem cells can be obtained from the intended recipient, (an autograft) the risk of rejection is essentially non-existent in these situations. Consequently, more US government funding is being provided for adult stem cell research.

An extremely rich source for adult mesenchymal stem cells is the developing tooth bud of the mandibular third molar. While considered multipotent they may prove to be pluripotent. The stem cells eventually form enamel (ectodrm), dentin,periodontal ligament, blood vessels, dental pulp, nervous tissues, including a minimum of 29 different unique end organs. Because of extreme ease in collection at 8–10 years of age before calcification and minimal to no morbidity will probably constitute a major source for personal banking, research and multiple therapies. These stem cells have been shown capable of producing hepatocytes.

# Amniotic

Multipotent stem cells are also found in amniotic fluid. These stem cells are very active, expand extensively without feeders and are not tumorigenic. Amniotic stem cells are multipotent and can differentiate in cells of adipogenic, osteogenic, myogenic, endothelial, hepatic and also neuronal lines. All over the world, universities and research institutes are studying amniotic fluid to discover all the qualities of amniotic stem cells, and scientists such as Anthony Atala and Giuseppe Simoni have discovered important results.

From an ethical point of view, stem cells from amniotic fluid can solve a lot of problems, because it's possible to catch amniotic stem cells without destroying embryos. For example, the Vatican newspaper "Osservatore Romano" called amniotic stem cell "the future of medicine".

It's possible to collect amniotic stem cells for donors or for autologuous use: the first US amniotic stem cells bank opened in 2009 in Medford, MA, by Biocell Center Corporation and collaborates with various hospitals and universities all over the world.

# Induced pluripotent

These are not adult stem cells, but rather reprogrammed cells (e.g. epithelial cells) given pluripotent capabilities. Using genetic reprogramming with protein transcription factors, pluripotent stem cells equivalent to embryonic stem cells have been derived from human adult skin tissue. Shinya Yamanaka and his colleagues at Kyoto University used the transcription factors Oct3/4, Sox2, c-Myc, and Klf4 in their experiments on cells from human faces. Junying Yu, James Thomson, and their colleagues at the University of Wisconsin–Madison used a different set of factors, Oct4, Sox2, Nanog and Lin28, and carried out their experiments using cells from human foreskin.

As a result of the success of these experiments, Ian Wilmut, who helped create the first cloned animal Dolly the Sheep, has announced that he will abandon nuclear transfer as an avenue of research.

Frozen blood samples can be used as a source of induced pluripotent stem cells, opening a new avenue for obtaining the valued cells.

# Lineage

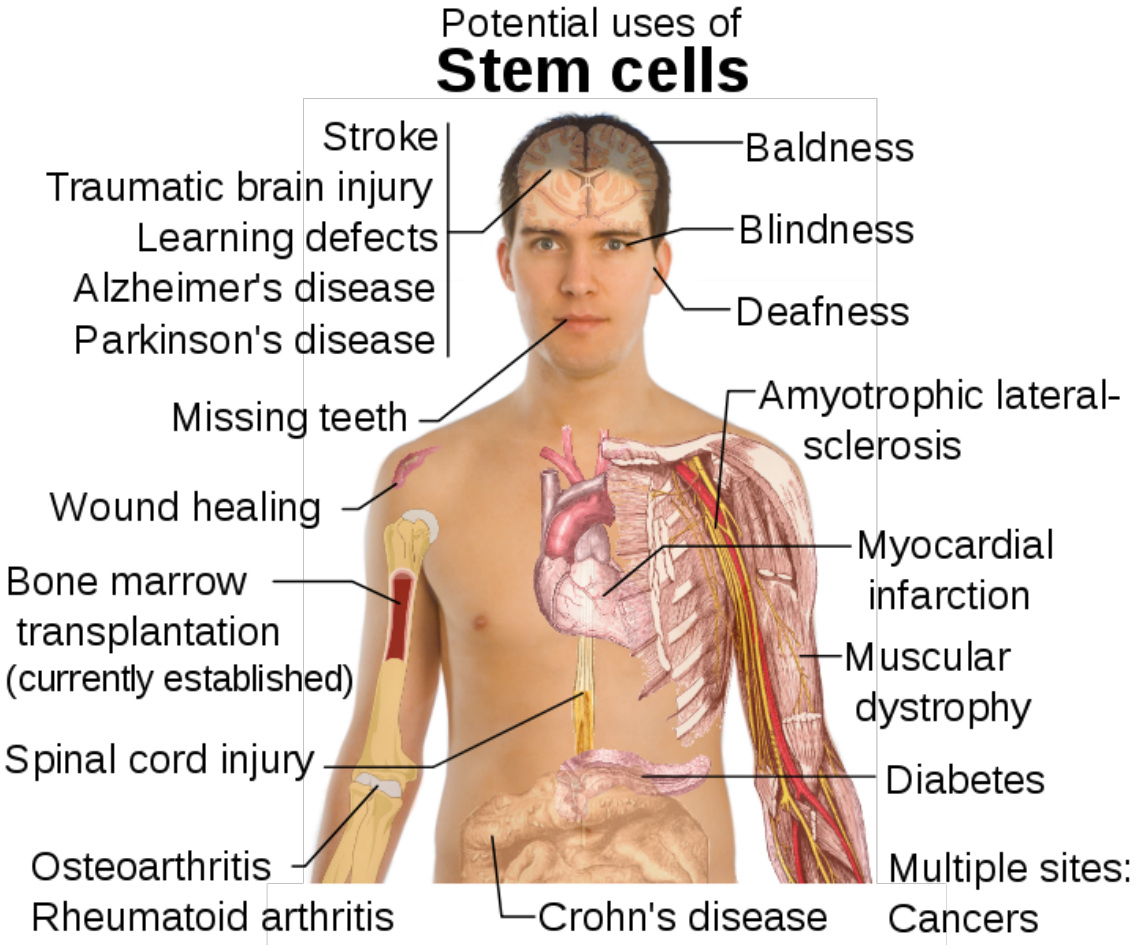
To ensure self-renewal, stem cells undergo two types of cell division. Symmetric division gives rise to two identical daughter cells both endowed with stem cell properties. Asymmetric division, on the other hand, produces only one stem cell and a progenitor cell with limited self-renewal potential. Progenitors can go through several rounds of cell division before terminally differentiating into a mature cell. It is possible that the molecular distinction between symmetric and asymmetric divisions lies in differential segregation of cell membrane proteins (such as receptors) between the daughter cells.

An alternative theory is that stem cells remain undifferentiated due to environmental cues in their particular niche. Stem cells differentiate when they leave that niche or no longer receive those signals. Studies in *Drosophila* germarium have identified the signals dpp and adherens junctions that prevent germarium stem cells from differentiating.

The signals that lead to reprogramming of cells to an embryonic-like state are also being investigated. These signal pathways include several transcription factors including the oncogene c-Myc. Initial studies indicate that transformation of mice cells with a combination of these anti-differentiation signals can reverse differentiation and may allow adult cells to become pluripotent. However, the need to transform these cells with an oncogene may prevent the use of this approach in therapy.

Challenging the terminal nature of cellular differentiation and the integrity of lineage commitment, it was recently determined that the somatic expression of combined transcription factors can directly induce other defined somatic cell fates; researchers identified three neural-lineage-specific transcription factors that could directly convert mouse fibroblasts (skin cells) into fully functional neurons. This "induced neurons" (iN) cell research inspires the researchers to induce other cell types implies that *all* cells are totipotent: with the proper tools, all cells may form all kinds of tissue.

## Treatments




Diseases and conditions where stem cell treatment is promising or emerging. Bone marrow transplantation is, as of 2009, the only established use of stem cells.

Medical researchers believe that stem cell therapy has the potential to dramatically change the treatment of human disease. A number of adult stem cell therapies already exist, particularly bone marrow transplants that are used to treat leukemia. In the future, medical researchers anticipate being able to use technologies derived from stem cell research to treat a wider variety of diseases including cancer, Parkinson's disease, spinal cord injuries, Amyotrophic lateral sclerosis, multiple sclerosis, and muscle damage, amongst a number of other impairments and conditions. However, there still exists a great deal of social and scientific uncertainty surrounding stem cell research, which could possibly be overcome through public debate and future research, and further education of the public.

One concern of treatment is the possible risk that transplanted stem cells could form tumors and have the possibility of becoming cancerous if cell division continues uncontrollably.

Stem cells, however, are already studied extensively. While some scientists are hesitant to associate the therapeutic potential of stem cells as the first goal of the research, they find the investigation of stem cells as a goal worthy in itself.

Contrarily, supporters of embryonic stem cell research argue that such research should be pursued because the resultant treatments could have significant medical potential. It is also noted that excess embryos created for in vitro fertilization could be donated with consent and used for the research.

The recent development of iPS cells has been called a bypass of the legal controversy. Laws limiting the destruction of human embryos have been credited for being the reason for development of iPS cells, but they are less efficient and reliable than natural stem cells. Various methods are being developed to bypass this problem by removing mutation.

## Research patents

The patents covering a lot of work on human embryonic stem cells are owned by the Wisconsin Alumni Research Foundation (WARF). WARF does not charge academics to study human stem cells but does charge commercial users. WARF sold Geron Corp. exclusive rights to work on human stem cells but later sued Geron Corp. to recover some of the previously sold rights. The two sides agreed that Geron Corp. would keep the rights to only three cell types. In 2001, WARF came under public pressure to widen access to human stem-cell technology.

These patents are now in doubt as a request for reviewing the US Patent and Trademark Office has been filed by non-profit patent-watchdogs The Foundation for Taxpayer & Consumer Rights, and the Public Patent Foundation as well as molecular biologist Jeanne Loring of the Burnham Institute. According to them, two of the patents granted to WARF are invalid because they cover a technique published in 1993 for which a patent had already been granted to an Australian researcher. Another part of the challenge states that these techniques, developed by James A. Thomson, are rendered obvious by a 1990 paper and two textbooks.

The outcome of this legal challenge is particularly relevant to the Geron Corp. as it can only license patents that are upheld.

Chapter- 11

# Germ Cell and Somatic Cell

## Germ cell

In biology, **germ cells** are the cells that give rise to the gametes of organisms that reproduce sexually. In many animals, the germ cells originate near the gut and migrate to the developing gonads. There, they undergo cell division of two types, mitosis and meiosis, followed by cellular differentiation into mature gametes, either eggs or sperm. Unlike animals, plants do not have a germ line set aside in early development. Instead, germ cells can come from somatic cells in the adult floral meristem.

## Introduction

Multicellular eukaryotes are made of two fundamental cell types. Germ cells produce gametes and are the only cells that can undergo meiosis as well as mitosis. These cells are sometimes said to be immortal because they are the link between generations. Somatic cells are all the other cells that form the building blocks of the body and they only divide by mitosis. The lineage of germ cells is called germ line. Germ cell specification begins during cleavage in many animals or in the epiblast during gastrulation in birds and mammals. After transport, involving passive movements and active migration, germ cells arrive at the developing gonads. In humans, sexual differentiation starts approximately 6 weeks after conception. The end-products of the germ cell cycle are the egg or sperm.

Under special conditions *in vitro* germ cells can acquire properties similar to those of embryonic stem cells (ES). The underlying mechanism of that change is still unknown. These changed cells are then called embryonic germ cells (EG). Both EG and ES are pluripotent. Recent studies have demonstrated that it is possible to give rise to primordial germ cells from ES.

# Specification

There are two mechanisms to establish the germ cell lineage in the embryo. The first way is called preformistic and involves that the cells destined to become germ cells inherit the specific germ cell determinants present in the germ plasm (specific area of the cytoplasm) of the egg (ovum). The unfertilized egg of most animals is asymmetrical: different regions of cytoplasm contain different amounts mRNA and proteins. By this germ cells obtained by the first divisions of the fertilized egg are characterized by specific molecules of a particular region of the egg cytoplasm. The second way is found in birds and mammals, where germ cells are not specified by such determinants but by signals controlled by zygotic genes. In mammals, a few cells of the early embryo are induced by signals of neighboring cells to become primordial germ cells. Mammalian eggs are somewhat symmetrical and after the first divisions of the fertilized egg, the produced cells are all totipotent. This means that they can differentiate in any cell type in the body and thus germ cells.

# Migration

Primordial germ cells, germ cells that still have to reach the gonads, also known as PGCs, precursor germ cells or gonocytes, divide repeatedly on their migratory route through the gut and into the developing gonads.

## Invertebrates

In the model organism *Drosophila*, pole cells passively move from the posterior end of the embryo to the posterior midgut because of the infolding of the blastoderm. Then they actively move through the gut into the mesoderm. Endodermal cells differentiate and together with Wunen proteins they induce the migration through the gut. Wunen proteins are chemorepellants that lead the germ cells away from the endoderm and into the mesoderm. After splitting into two populations, the germ cells continue migrating laterally and in parallel until they reach the gonads. Columbus proteins, chemoattractants, stimulate the migration in the gonadal mesoderm.

## Vertebrates

In the *Xenopus* egg, the germ cell determinants are found in the most vegetal blastomeres. These presumptive PGCs are brought to the endoderm of the blastocoel by gastrulation. They are determined as germ cells when gastrulation is completed. Migration from the hindgut along the gut and across the dorsal mesentery then takes place. The germ cells split into two populations and move to the paired gonadal ridges. Migration starts with 3-4 cells that undergo three rounds of cell division so that about 30 PGCs arrive at the gonads. On the migratory path of the PGCs, the orientation of underlying cells and their secreted molecules such as fibronectin play an important role.

Mammals have a migratory path comparable to that in *Xenopus*. Migration begins with 50 gonocytes and about 5,000 PGCs arrive at the gonads. Proliferation occurs also during migration and lasts for 3-4 weeks in humans.

PGCs come from the epiblast and migrate subsequently into the mesoderm, the endoderm and the posterior of the yolk sac. Migration then takes place from the hindgut along the gut and across the dorsal mesentery to reach the gonads (4.5 weeks in human beings). Fibronectin maps here also a polarized network together with other molecules. The somatic cells on the path of germ cells provide them attractive, repulsive, and survival signals. But germ cells also send signals to each other.

In reptiles and birds, germ cells use another path. PGCs come from the epiblast and move to the hypoblast to form the germinal crescent (anterior extraembryonic structure). The gonocytes then squeeze into blood vessels and use the circulatory system for transport. They squeeze out of the vessels when they are at height of the gonadal ridges. Cell adhesion on the endothelium of the blood vessels and molecules such as chemoattractants are probably involved in helping PGCs migrate.

# Sex determining region of Y (*Sry*) gene

The sex of a mammalian individual is determined by the *Sry* gene on the Y chromosome. It induces the somatic cells of the gonadal ridge to develop into a testis. *Sry* is expressed in a small group of somatic cells of the developing gonad and influence these cells to become Sertoli cells (supporting cells in testis). Sertoli cells are responsible for sexual development along a male pathway in many ways. One of these ways involves stimulation of the arriving primordial cells to differentiate into sperm. In the absence of the *Sry* gene, primordial germ cells differentiate into eggs. Removing genital ridges before they started to develop into testes or ovaries results in the development of a female, independent of the carried sex chromosome.

# Gametogenesis

Gametogenesis, the development of diploid germ cells into either haploid eggs or sperm, (respectively oogenesis and spermatogenesis) is different for each species but the general stages are similar. Oogenesis and spermatogenesis have many features in common, they both involve:

- Meiosis
- Extensive morphological differentiation
- Incapacity of surviving for very long if fertilization does not occur

Despite their homologies they also have major differences:

- Spermatogenesis has equivalent meiotic divisions resulting in four equivalent spermatids while oogenic meiosis is asymmetrical: only one egg is formed together with three polar bodies.
- Different timing of maturation: oogenic meiosis is interrupted at one or more stages (for a long time) while spermatogenic meiosis is rapid and uninterrupted.

## Oogenesis

After migration primordial germ cells will become oogonia in the forming gonad (ovary). The oogonia proliferate extensively by mitotic divisions, up to 5-7 million cells in humans. But then many of these oogonia die and about 50,000 remain. These cells differentiate into primary oocytes. In week 11-12 *post coitus* the first meiotic division begins (before birth for most mammals) and remains arrested in prophase I from a few days to many years depending on the species. It is in this period or in some cases at the beginning of sexual maturity that the primary oocytes secrete proteins to form a coat called zona pellucida and they also produce cortical granules containing enzymes and proteins needed for fertilization. Meiosis stands by because of the follicular granulosa cells that send inhibitory signals through gap junctions and the zona pellucida. Sexual maturation is the beginning of periodic ovulation. Ovulation is the regular release of one oocyte from the ovary into the reproductive tract and is preceded by follicular growth. A few follicle cells are stimulated to grow but only one oocyte is ovulated. A primordial follicle consists of an epithelial layer of follicular granulosa cells enclosing an oocyte. The pituitary gland secrete follicle-stimulating hormones (FSHs) that stimulate follicular growth and oocyte maturation. The thecal cells around each follicle secrete estrogen. This hormone stimulates the production of FSH receptors on the follicular granulosa cells and has at the same time a negative feedback on FSH secretion. This results in a competition between the follicles and only the follicle with the most FSH receptors survives and is ovulated. Meiotic division I goes on in the ovulated oocyte stimulated by luteinizing hormones (LHs) produced by the pituitary gland. FSH and LH block the gap junctions between follicle cells and the oocyte therefore inhibiting communication between them. Most follicular granulosa cells stay around the oocyte and so form the cumulus layer. Large non-mammalian oocytes accumulate egg yolk, glycogen, lipids, ribosomes, and the mRNA needed for protein synthesis during early embryonic growth. These intensive RNA biosynthese are mirrored in the structure of the chromosomes, which decondense and form lateral loops giving them a lampbrush appearance. Oocyte maturation is the following phase of oocyte development. It occurs at sexual maturity when hormones stimulate the oocyte to complete meiotic division I. The meiotic division I produces 2 cells differing in size: a small polar body and a large secondary oocyte. The secondary oocyte undergoes meiotic division II and that results in the formation of a second small polar body and a large mature egg, both being haploid cells. The polar bodies degenerate. Oocyte maturation stands by at metaphase II in most vertebrates. During ovulation, the arrested secondary oocyte leaves the ovary and matures rapidly into an egg ready for fertilization. Fertilization will cause the egg to complete meiosis II. In human females there is proliferation of the oogonia in the fetus, meiosis starts then before birth and stands by at meiotic division I up to 50 years, ovulation begins at puberty.

**Egg growth**

A 10 - 20 μm large somatic cell generally needs 24 hours to double its mass for mitosis. By this way it would take a very long time for that cell to reach the size of a mammalian egg with a diameter of 100 μm (some insects have eggs of about 1,000 μm or greater). Eggs have therefore special mechanisms to grow to their large size. One of these mechanisms is to have extra copies of genes: meiotic division I is paused so that the oocyte grows while it contains two diploid chromosome sets. Some species produce many extra copies of genes, such as amphibians, which may have up to 1 or 2 million copies. A complementary mechanism is partly dependent on syntheses of other cells. In amphibians, birds, and insects, yolk is made by the liver (or its equivalent) and secreted into the blood. Neighboring accessory cells in the ovary can also provide nutritive help of two types. In some invertebrates some oogonia become nurse cells. These cells are connected by cytoplasmic bridges with oocytes. The nurse cells of insects provide oocytes macromolecules such as proteins and mRNA. Follicular granulosa cells are the second type of accessory cells in the ovary in both invertebrates and vertebrates. They form a layer around the oocyte and nourish them with small molecules, no macromolecules, but eventually their smaller precursor molecules, by gap junctions.

### Spermatogenesis

Mammalian spermatogenesis is representative for most animals. In human males, spermatogenesis begins at puberty in seminiferous tubules in the testes and go on continuously. Spermatogonia are immature germ cells. They proliferate continuously by mitotic divisions around the outer edge of the seminiferous tubules, next to the basal lamina. Some of these cells stop proliferation and differentiate into primary spermatocytes. After they proceed through the first meiotic division, two secondary spermatocytes are produced. The two secondary spermatocytes undergo the second meiotic division to form four haploid spermatids. These spermatids differentiate morphologically into sperm by nuclear condensation, ejection of the cytoplasm and formation of the acrosome and flagellum.

The developing male germ cells do not complete cytokinesis during spermatogenesis. Consequently cytoplasmic bridges assure connection between the clones of differentiating daughter cells to form a syncytium. In this way the haploid cells are supplied with all the products of a complete diploid genome. Sperm that carry a Y chromosome, for example, is supplied with essential molecules that are encoded by genes on the X chromosome.

## Diseases

Germ cell tumor is a rare cancer that can affect people at all ages. 2.4 children out of 1 million suffer the disease, and it counts for 4% of all cancers in children and adolescents younger than 20 years old.

Germ cell tumors are generally located in the gonads but can also appear in the abdomen, pelvis, mediastinum, or brain. Germ cells migrating to the gonads may not reach that intended destination and a tumor can grow wherever they end up, but the exact cause is still unknown. These tumors can be benign or malignant.

## Induced differentiation from stem cells

Culture of human embryonic stem cells in mitotically inactivated porcine ovarian fibroblasts (POF) causes differentiation into germ cells, as evidenced by gene expression analysis.

# Somatic cell

**Somatic cells** (diploid) are any cells forming the body of an organism, as opposed to germline cells. In mammals, germline cells (also known as "gametes") are the spermatozoa and ova which fuse during fertilization to produce a cell called a zygote, from which the entire mammalian embryo develops. Every other cell type in the mammalian body—apart from the sperm and ova, the cells from which they are made (gametocytes) and undifferentiated stem cells—is a somatic cell: internal organs, skin, bones, blood, and connective tissue are all made up of somatic cells.

The word "somatic" is derived from the Greek word *sōma*, meaning "body".

## Genetics and chromosome content

A simple definition of a somatic cell is that it is a non-sex cell In humans, somatic cells contain 46 individual chromosomes, organized into 23 pairs of chromosomes. Each pair comprises one chromosome inherited from the father and one inherited from the mother. Human somatic cells contain twice as many chromosomes as gametes ("sex cells"). Gametes contain only 23 chromosomes. When two gametes (i.e. a spermatozoon and an ovum) meet during conception, they "fuse" together, creating a zygote. The sex of the child is dependent on the sex chromosome that the spermatozoon contains (X or Y). Due to the "fusion" of the two gametes, a zygote contains 46 chromosomes (i.e. 23 pairs).

In other species, the situation is more complex. Humans, and other species whose somatic cells contain chromosomes arranged in pairs, are known as "diploid" organisms (their gametes, which contain only single unpaired chromosomes, are known as "haploid"). However, a large number of species arrange the chromosomes in their somatic cells in fours ("tetraploid") or even sixes ("hexaploid") which means that they can have diploid or even triploid germline cells. An example of this is the modern cultivated species of wheat, *Triticum Aestivum L.*, a hexaploid species whose somatic cells contain six copies of every chromatid.

# Somatic cells and cloning technology

In recent years, the technique of cloning whole organisms has been developed in mammals, allowing almost identical genetic clones of an animal to be produced. Any retention of existing mitochondrial DNA prevents the new cell from being identical. One method of doing this is called "somatic cell nuclear transfer" and involves removing the nucleus from a somatic cell, usually a skin cell. This nucleus, which contains all of the genetic information needed to produce the organism it was removed from is then injected into an ovum of the same species which has had its own genetic material removed. The ovum now no longer needs to be fertilized as it contains the correct amount of genetic material (a diploid number of chromosomes) and, in theory, it can be implanted into the uterus of a same-species animal and allowed to develop. The resulting animal will be a genetically identical clone to the animal from which the nucleus was taken. In practice, this technique has so far been problematic, although there have been a few high profile successes, such as Dolly the Sheep and, more recently, Snuppy, the first cloned dog.

Chapter- 12

# List of Distinct Cell Types in the Adult Human Body

There are several hundred distinct **human cell types** , . There are between 50 and 75 trillion cells in the human body.

Cell types can be classified by their tissue of origin. However, it is possible for some cells to have their behavior induced by surrounding tissue.

## Cells that are derived primarily from endoderm

### Gland cells

**Exocrine secretory epithelial cells**

- Salivary gland mucous cell (polysaccharide-rich secretion)
- Salivary gland serous cell (glycoprotein enzyme-rich secretion)
- Von Ebner's gland cell in tongue (washes taste buds)
- Mammary gland cell (milk secretion)
- Lacrimal gland cell (tear secretion)
- Ceruminous gland cell in ear (ear wax secretion)
- Eccrine sweat gland dark cell (glycoprotein secretion)
- Eccrine sweat gland clear cell (small molecule secretion)
- Apocrine sweat gland cell (odoriferous secretion, sex-hormone sensitive)
- Gland of Moll cell in eyelid (specialized sweat gland)
- Sebaceous gland cell (lipid-rich sebum secretion)
- Bowman's gland cell in nose (washes olfactory epithelium)
- Brunner's gland cell in duodenum (enzymes and alkaline mucus)
- Seminal vesicle cell (secretes seminal fluid components, including fructose for swimming sperm)
- Prostate gland cell (secretes seminal fluid components)
- Bulbourethral gland cell (mucus secretion)Alaina and emma cell

- Bartholin's gland cell (vaginal lubricant section)
- Gland of Littre cell (mucus secretion)
- Uterus endometrium cell (carbohydrate secretion)
- Isolated goblet cell of respiratory and digestive tracts (mucus secretion)
- Stomach lining mucous cell (mucus secretion)
- Gastric gland zymogenic cell (pepsinogen secretion)
- Gastric gland oxyntic cell (hydrochloric acid secretion)
- Pancreatic acinar cell (bicarbonate and digestive enzyme secretion)
- Paneth cell of small intestine (lysozyme secretion)
- Type II pneumocyte of lung (surfactant secretion)
- Clara cell of lung

## Hormone secreting cells

- Anterior pituitary cells
    - Somatotropes
    - Lactotropes
    - Thyrotropes
    - Gonadotropes
    - Corticotropes
- Intermediate pituitary cell, secreting melanocyte-stimulating hormone
- Magnocellular neurosecretory cells
    - secreting oxytocin
    - secreting vasopressin
- Gut and respiratory tract cells
    - secreting serotonin
    - secreting endorphin
    - secreting somatostatin
    - secreting gastrin
    - secreting secretin
    - secreting cholecystokinin
    - secreting insulin
    - secreting glucagon
    - secreting bombesin
- Thyroid gland cells
    - thyroid epithelial cell
    - parafollicular cell
- Parathyroid gland cells
    - Parathyroid chief cell
    - Oxyphil cell
- Adrenal gland cells
    - chromaffin cells
    - secreting steroid hormones (mineralcorticoids and gluco corticoids)
- Leydig cell of testes secreting testosterone
- Theca interna cell of ovarian follicle secreting estrogen
- Corpus luteum cell of ruptured ovarian follicle secreting progesterone

    - Granulosa lutein cells
    - Theca lutein cells
- Juxtaglomerular cell (renin secretion)
- Pia-arachnoid squamous cell
- Pigmented ciliary epithelium cell of eye
- Nonpigmented ciliary epithelium cell of eye
- Corneal endothelial cell
- Peg cell (of Fallopian tube)

### Ciliated cells with propulsive function

- Respiratory tract ciliated cell
- Oviduct ciliated cell (in female)
- Uterine endometrial ciliated cell (in female)
- Rete testis ciliated cell (in male)
- Ductulus efferens ciliated cell (in male)
- Ciliated ependymal cell of central nervous system (lining brain cavities)

## Derived primarily from ectoderm

### Integumentary system

#### Keratinizing epithelial cells

- Epidermal keratinocyte (differentiating epidermal cell)
- Epidermal basal cell (stem cell)
- Keratinocyte of fingernails and toenails
- Nail bed basal cell (stem cell)
- Medullary hair shaft cell
- Cortical hair shaft cell
- Cuticular hair shaft cell
- Cuticular hair root sheath cell
- Hair root sheath cell of Huxley's layer
- Hair root sheath cell of Henle's layer
- External hair root sheath cell
- Hair matrix cell (stem cell)

#### Wet stratified barrier epithelial cells

- Surface epithelial cell of stratified squamous epithelium of cornea, tongue, oral cavity, esophagus, anal canal, distal urethra and vagina
- basal cell (stem cell) of epithelia of cornea, tongue, oral cavity, esophagus, anal canal, distal urethra and vagina
- Urinary epithelium cell (lining urinary bladder and urinary ducts)

## Nervous system

### Sensory transducer cells

- Auditory inner hair cell of organ of Corti
- Auditory outer hair cell of organ of Corti
- Basal cell of olfactory epithelium (stem cell for olfactory neurons)
- Cold-sensitive primary sensory neurons
- Heat-sensitive primary sensory neurons
- Merkel cell of epidermis (touch sensor)
- Olfactory receptor neuron
- Pain-sensitive primary sensory neurons (various types)
- Photoreceptor cells of retina in eye:
    - Photoreceptor rod cells
    - Photoreceptor blue-sensitive cone cell of eye
    - Photoreceptor green-sensitive cone cell of eye
    - Photoreceptor red-sensitive cone cell of eye
- Proprioceptive primary sensory neurons (various types)
- Touch-sensitive primary sensory neurons (various types)
- Type I carotid body cell (blood pH sensor)
- Type II carotid body cell (blood pH sensor)
- Type I hair cell of vestibular apparatus of ear (acceleration and gravity)
- Type II hair cell of vestibular apparatus of ear (acceleration and gravity)
- Type I taste bud cell

### Autonomic neuron cells

- Cholinergic neural cell (various types)
- Adrenergic neural cell (various types)
- Peptidergic neural cell (various types)

### Sense organ and peripheral neuron supporting cells

- Inner pillar cell of organ of Corti
- Outer pillar cell of organ of Corti
- Inner phalangeal cell of organ of Corti
- Outer phalangeal cell of organ of Corti
- Border cell of organ of Corti
- Hensen cell of organ of Corti
- Vestibular apparatus supporting cell
- Taste bud supporting cell
- Olfactory epithelium supporting cell
- Schwann cell
- Satellite cell (encapsulating peripheral nerve cell bodies)
- Enteric glial cell

**Central nervous system neurons and glial cells**

- Astrocyte (various types)
- Neuron cells (large variety of types, still poorly classified)
- Oligodendrocyte
- Spindle neuron

**Lens cells**

- Anterior lens epithelial cell
- Crystallin-containing lens fiber cell

# Derived primarily from mesoderm

## Metabolism and storage cells

- Hepatocyte (liver cell)
- Adipocytes:
  - White fat cell
  - Brown fat cell
- Liver lipocyte

## Barrier function cells (Lung, Gut, Exocrine Glands and Urogenital Tract)

**Kidney**

- Kidney glomerulus parietal cell
- Kidney glomerulus podocyte
- Kidney proximal tubule brush border cell
- Loop of Henle thin segment cell
- Kidney distal tubule cell
- Kidney collecting duct cell
- Type I pneumocyte (lining air space of lung cell)
- Pancreatic duct cell (centroacinar cell)
- Nonstriated duct cell (of sweat gland, salivary gland, mammary gland, etc.)
  - principal cell
  - Intercalated cell
- Duct cell (of seminal vesicle, prostate gland, etc.)
- Intestinal brush border cell (with microvilli)
- Exocrine gland striated duct cell
- Gall bladder epithelial cell
- Ductulus efferens nonciliated cell
- Epididymal principal cell
- Epididymal basal cell

## Extracellular matrix secretion cells

- Ameloblast epithelial cell (tooth enamel secretion)
- Planum semilunatum epithelial cell of vestibular apparatus of ear (proteoglycan secretion)
- Organ of Corti interdental epithelial cell (secreting tectorial membrane covering hair cells)
- Loose connective tissue fibroblasts
- Corneal fibroblasts (corneal keratocytes)
- Tendon fibroblasts
- Bone marrow reticular tissue fibroblasts
- Other nonepithelial fibroblasts
- Pericyte
- Nucleus pulposus cell of intervertebral disc
- Cementoblast/cementocyte (tooth root bonelike cementum secretion)
- Odontoblast/odontocyte (tooth dentin secretion)
- Hyaline cartilage chondrocyte
- Fibrocartilage chondrocyte
- Elastic cartilage chondrocyte
- Osteoblast/osteocyte
- Osteoprogenitor cell (stem cell of osteoblasts)
- Hyalocyte of vitreous body of eye
- Stellate cell of perilymphatic space of ear
- Hepatic stellate cell (Ito cell)
- Pancreatic stelle cell

## Contractile cells

- Skeletal muscle cells
    - Red skeletal muscle cell (slow)
    - White skeletal muscle cell (fast)
    - Intermediate skeletal muscle cell
    - nuclear bag cell of muscle spindle
    - nuclear chain cell of muscle spindle
- Satellite cell (stem cell)
- Heart muscle cells
    - Ordinary heart muscle cell
    - Nodal heart muscle cell
    - Purkinje fiber cell
- Smooth muscle cell (various types)
- Myoepithelial cell of iris
- Myoepithelial cell of exocrine glands

## Blood and immune system cells

- Erythrocyte (red blood cell)

- Megakaryocyte (platelet precursor)
- Monocyte
- Connective tissue macrophage (various types)
- Epidermal Langerhans cell
- Osteoclast (in bone)
- Dendritic cell (in lymphoid tissues)
- Microglial cell (in central nervous system)
- Neutrophil granulocyte
- Eosinophil granulocyte
- Basophil granulocyte
- Mast cell
- Helper T cell
- Suppressor T cell
- Cytotoxic T cell
- Natural Killer T cell
- B cell
- Natural killer cell
- Reticulocyte
- Stem cells and committed progenitors for the blood and immune system (various types)

### Pigment cells

- Melanocyte
- Retinal pigmented epithelial cell

### Germ cells

- Oogonium/Oocyte
- Spermatid
- Spermatocyte
- Spermatogonium cell (stem cell for spermatocyte)
- Spermatozoon

### Nurse cells

- Ovarian follicle cell
- Sertoli cell (in testis)
- Thymus epithelial cell

### Interstitial cells

- Interstitial kidney cells