OVERVIEW OF CELLULAR STRUCTURE AND EVOLUTION[1]

Please read and study Campbell Chapter 6 ("Tour of the Cell") prior to class. Much of the information in this chapter is descriptive and should be review. There is not too much to say it about it in class, although we will run our own power point tour. So, learn the names of the structures, their relationships to each other and something about their functions. I will answer questions in class and may ask some of you.
Below is a list of terms and a question; let these guide your studies.

1. Terms

ultracentrifuge	prokaryote
nucleoid	cytoplasm
eukaryote	chromatin/chromosomes
nucleolus	endoplasmic reticulum (types and functions)
Golgi Apparatus (structure and functions)	lysosomes
phagocytosis	mitochondria
chloroplasts	cytoskeleton
microtubules, microfilaments	intermediate filaments (structure and function)
centrosome, centriole, centromere (see chromosomes)	cilia, flagella, basal body
extracellular matrix, collagen, proteoglycans	tight and gap junctions, desmosomes

2. What is cell fractionation?

A Bit About the Evolution of Cells

The earth dates to 4.2 b.y. It is generally believed by those who study of origin of the solar system and earth that for the first 300 million years the earth was an extremely inhospitable place and was under heavy bombardment from other condensed matter in the solar system. For much of this time, the earth's surface may have been so hot that liquid water (which was constantly arriving via comets that hit the earth) could not exist. The oldest known rocks on the earth that have persisted to present were formed about 3.8 b.y.a.; this may correspond roughly with the appearance of conditions that might allow for life.

There is much speculation about how life arose on earth. Did it arrive here from elsewhere (pushing the origin of life to another world) or did it start here? What were the events that led inorganic substances to gain the organization and characteristics that we associate with life? The answer is that we simply do not know.

However, it is very likely that cells, even very primitive ones, were not the first "living" (or proto-living) things. Instead, it is likely that organized chemical processes occurred on surfaces or perhaps within small membranes. These molecular engines somehow eventually incorporated a form of hereditary instructions that is a central characteristic of life[2]. In this process they managed to somehow connect molecules that performed functions or acted as structures with other molecules that could store instructions for making the "doer" molecules. How this happened is perhaps the central problem faced by those who study how life appeared from non-biotic precursors.

Once there is some type of heredity (including a mechanism that generates a few hereditary "mistakes"), true biotic evolution becomes possible. Thus, some simple thing we might not even recognize as alive may[3] had given rise to **true cells by 3.5 b.y.a**. This is based on microfossils of cell-like structures from west Australia. As you might expect, there is some argument about whether these are really cell fossils, but increasing numbers of fossils are found after this time (including some 3.2 (or more) b.y. old).

These earliest cells are all **prokaryote** – they show little large-scale internal structure (they are highly structured – on a molecular level) and one of the lacking structures is the nucleus. Thus, "prokaryote" – *before the nucleus*. Thus, prokaryotes have been spectacularly successful over almost the entire life of the earth. They are everywhere, covering everything. And please do not associate them all with disease – it is as accurate as thinking that all animals are deadly carnivores.

Prokaryotes do not show the size and structural diversity of eukaryotes (see below) but they are spectacularly diverse biochemically. Most enzyme and protein types were invented during the roughly 1.5 billion years the prokaryotes had the earth to themselves. This increase in diversity probably involved two interesting phenomena – duplication of genes (an even more favorite trick of eukaryotes) and gene transfer (sometimes as something we could call sex, but in other cases by a clearly different way). If a gene is duplicated, one of the copies is fee to change into something that is perhaps useful in (at first) a slightly different way and perhaps later, a very different way. The old gene continues to perform its old function (natural selection sees to that – provided the old function is still needed). You may be used to thinking about prokaryotes as organisms that only reproduce by fission. If this were true there would be no way for genes to move from one hereditary line to another. However, prokaryotes are able to pick up new genes – in some cases by transfer of small independent bits of DNA called **plasmids**, in other cases by **conjugation** where pieces of DNA are exchanged and incorporated into each cell's DNA molecule. Now, given the

[2] Probably RNA before DNA and who knows what was before RNA (If anything).

[3] I only say "may" because of the possibility that somehow cells arrived on Earth from another world.

short generation time and all this time, imagine all the new things that prokaryotes came up with. And, I must add, they continue to do this now. Prokaryotes are biochemically diverse!

One particularly important example of prokaryotic novelty was the invention of photosynthesis. In this process, energy from the sun is trapped by one or more molecules and used to split water into protons, energetic electrons (which can be used to drive chemical reactions) and a noxious waste molecule, oxygen. Around **2.7 b.y.a,** there was enough of this going on that the chemistry of the planet began to change. Free oxygen (which previously had never been present on the planet in great amounts) would react with substances such as iron and produce iron oxides (rust). Thus, a major chemical change on our planet was initiated by prokaryotes.

This in turn allowed for the evolution of forms of metabolism that used some of this oxygen in a scheme to extract stored chemical energy and use it in cellular processes. Called aerobic metabolism, it could not appear until after the "photosynthetic revolution" mentioned above. More on this in a few classes.

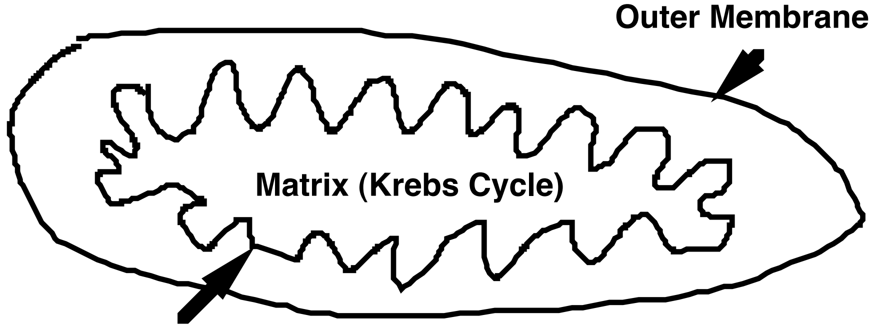
Prokaryotic cells are uniformly small. This puts some constraints on them – certainly, in terms of structural complexity. Moreover, if you are really small, there are limits on the numbers of genes you can carry. Eukaryotes represented a different way of living. Obviously we define them based on their nucleus and structural complexity but size is also a good characteristic. They are typically much larger than prokaryotes. There are advantages to this and also disadvantages. It is just a different way of doing things. Two advantages are the possibility of acquiring **endosymbionts** such as mitochondria (see below) or chloroplasts. Another is that **not only can the total number of genes increase but very complicated means of regulating the expression of these genes can also evolve**. This allows chemical processes to be turned up or down by a variety of processes or situations – we'll have more to say about this mid course. We are not sure when the first **eukaryotes** appeared – somewhere after the appearance of free O_2 in the atmosphere and certainly by 2.3 bya. Somewhere between 1.5 and 1.2 bya some eukaryotes produced what is apparently truly multicellular life. These organisms were not simply collections of identical cells. Although microscopic, the cells were somewhat specialized. Remember form and function – differences in structure are associated with differences in function. This contrasts with colonial life forms where identical cells remain associated with each other but show little if any evident specialization. Moreover, mulitcellularity usually involves a start from a single cell and some sort of increase in cell number that is accompanied by the functional **differentiation** just noted.

To complete this story, there is lots of evidence that all life continued to be microscopic up to about 570 mya with the Ediacaran life forms appeared (see our class webpage). Moreover, life experienced a major crisis between about 750 and 570 mya when much of the earth froze (due to a number of factors, especially the position of a large supercontinent that contained most (if not all dry land)). It is likely that many microscopic forms perished during this time but somehow, shortly after it ended, there was an explosion of new types leading to the appearance of most modern groups of plants, animals and fungi by 500 mya.

All About Mitochondria

Mitochondria were first described by light microscopists but they were difficult to see because of their low refractive index and the fact that they were destroyed by the common fixatives used to prepare tissue for light microscopy. Under the EM mitochondria are oval in shape and consist of two membranes: an outer limiting membrane and an inner membrane that surrounds the mitochondrial matrix. This inner membrane is thrown into folds, called cristae, which increase the membrane's surface area. The mitochondrion functions as the site for the chemical reactions that constitute the aerobic aspects of cell respiration: cellular respiration and oxidative phosphorylation. The enzymes for cellular respiration are found in the mitochondrial matrix or loosely associated with the side of the inner membrane facing the matrix. The respiratory assembly or ETS proteins are found in the inner membrane and their arrangement is not haphazard; instead, they are arranged sequentially in the order of their functional role in electron transport. The reason for cristae is to increase the number of respiratory assemblies in the inner membrane and so increase the surface area for ATP production. It is not surprising that a correlation exists between energy requirements of cells and the number of mitochondria in the cell and cristae in the mitochondria. Cells that expend much energy, e.g., muscle cells, have many mitochondria with more cristae than mitochondria found in cells that use less energy. These correlations plus the protein sequence in the inner membrane demonstrate how closely structure and function are correlated in the mitochondrion.

Mitochondrion



A model of how ATP synthesis occurs during oxidative phosphorylation, called the chemiosmotic theory or chemiosmosis, illustrates the importance of the inner membrane to mitochondrial function. The inner membrane divides the mitochondrion into two compartments: the "O" compartment or "**inner-membrane space**" between the inner and outer membrane, and the M compartment or **matrix**. The electron donors to the ETS (NADH and $FADH_2$) are located in the matrix[4]. They release electrons that are picked up by the flavoprotein, a transmembrane protein in the inner membrane (see eq. 7) . Flavoprotein passes the electrons to the rest of the respiratory assembly, and hydrogen ions (H^+) are pumped (by active transport – next class) against a concentration gradient into the inner membrane space by several ETS proteins, which act as proton pumps. Hydrogen ions accumulate in the inner membrane space because the membrane is impermeable to them and so they create a *p*H and concentration gradient across the membrane. Some of these hydrogen ions then follow this gradient and pass through and enzyme called **ATP synthase**. This transmembrane protein acts as a channel for H^+, to enter the matrix. This return movement of H^+ occurs through passive transport and drives the phosphorylation of ADP to produce ATP in the matrix

Origin of Mitochondria: Mitochondria are unique organelles in that they contain their own DNA. Thus, not all of a eukaryotic cell's DNA is confined to the nucleus! Mitochondrial DNA is of considerable interest for a number of reasons. This DNA can transcribe RNA and so enables mitochondria to produce their own proteins. It therefore is believed to reproduce within cells through a form of binary fission - a method of asexual reproduction used by many one-celled

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[4] If you've never heard of these compounds or would rather than you hadn't, don't panic. We'll visit them a little more carefully in a few classes and hopefully they'll become your friends.

organisms. This extra-nuclear DNA further suggests that mitochondria were once free-living organisms that secondarily became associated with other cells to produce a symbiotic union. This theory of evolutionary origin within eukaryotic cells is called the endosymbiotic theory, advanced by Lynn Margulis to explain the evolution of eukaryotic cell complexity. Margulis makes a case for other organelles, e.g., centrioles and chloroplasts, also becoming incorporated into eukaryotic cells through endosymbiosis. Finally, mitochondrial DNA is used extensively for forensic and phylogenetic studies because it is much less complex than nuclear DNA. Males do not contribute genetic material to mitochondria. They are passed on to offspring mainly by the female in her egg. Thus, from an evolutionary point of view they are inherited by daughters from their mother. Why? Since mitochondria are cytoplasmic components, they are largely passed on in the rich cytoplasm of the ovum or egg. Sperm, which has little cytoplasm, contributes a negligible amount relative to the egg. We will discuss the difference between egg production (oogenesis) and sperm production (spermatogenesis) and their significance to male-female reproductive behavior later in this course.