Mid term 2

Hadean eon

After the big bang some cosmology and a little astrobiology.

Introduction

The earth is approximately 4,500 million years old but multicellular life only rose 500 million years ago. So what was going on in the intervening 4,000 million years? The first Eon in Earth's history is the Hadean and this was a very violent time in its history. Continuous bombardment and a molten planet gave way to the oceans as the earth cooled and the crust solidified. The atmosphere was unlike that of today's with the most notable exception being the absence of oxygen. Laboratory experiments have demonstrated that lightening and volcanic gases reacted and created a prebiotic soup of simple organic compounds that was supplemented by the same compounds from deep sea hydrothermal vents and even from meteorite materials. There's been no problem building most of the monomers for more complex molecules like protein and lipid; the problem is noone has been able to synthesize the required nucleotides for RNA or DNA. There is no consensus on how the first large biopolymers appear, in the soup or inside special lipid compartments of vesicles that form automatically in the soup or maybe it's a combination of both.

Geological time scale

Early palaeontologists, like Lyell and his colleagues, determined that various layers of sedimentary rocks represented very distinct times in the history of the earth. Using these layers they created the geological time scale that divides Earth's history into four eons, and within these eras and periods. Rocks that were formed during each of these periods reflect major changes in the geology and biology of the planet. While these early earth scientists weren't able to accurately date the layers more recent work using radioactive decay has, and we have fairly precise dates for these various strata. Geological time scales are hard to comprehend simply because of the magnitude of the numbers involved; hundreds of millions of years, billions of years - that's a lot of zero's!

The earth we see today, or for which there is a form of written record to consult, is short-lived. Most of the earth's history has been spent in the periods when it finally cooled to the point where organic matter makes it's first appearance (Hadean Eon from the formation of the earth 4,500 Ma - 3,800 Ma), followed by the eon when single celled prokaryote bacteria predominated (Archaean Eon from 3,800 Ma - 2,500 Ma), the single celled eukaryotes (Proterozoic Eon from 2,500 Ma- 500 Ma) and finally multicellular life (Phanerozoic Eon from 550 Ma until now). It's probably worth noting that geologists, like biologists have controversies about their taxonomy the geological time and you'll see these last three eons referred to as eras (a subdivision of eon) in a period referred to as Precambrian times. Such a division fails to recognize the immense contribution of the Archaea and the first unicellular protists to the changes in the planet - but that's a biologist's point of view.

The shortest Eon is the one we find ourselves in now, the Phanerozoic. But even during that time the appearance of the world has changed dramatically. A single large super continent has broken apart and its plates have drifted on the fluid surface of the earth's core. Landmasses, the continents, have drifted in a dance where they make close contact with each other, then drifted apart. During this dance organisms in the continental shelves and the land masses above water have been mixed, modified and isolated from each other.

Geologists recognize three major divisions, eras, in the Phanerozoic. The first starts with what has been described as the Cambrian explosion 550 Ma. This was a time where there was a tremendous diversification of animal life in the oceans and these new animals fed on the abundance of protists that populated the ancient seas. Fossils from this period show us a bewildering array of animal architectures.

This era, the Paleozoic from 550-250m Ma, sees the worlds oceans populated with animals and some of the first attempts by plants and animals to rise up from the oceans and move on land. And then it all disappears in a global catastrophic event that sees over 90% of the marine diversity disappear. During the Mesozoic (245-65 Ma) this invasion of land is perfected and plants and animals increase in numbers and variety, new species of marine animals fill the void in the oceans and global diversity recovers once again. The Mesozoic comes to an end and the disappearance of the dinosaurs marks the end of the age of reptiles as once again another global catastrophe eliminates many of the organisms that populated the earth. In a typically biased view we often refer to the next era, the Cenozoic, as the age of mammals. But there's more to this era than just the appearance and diversification of the Mammals. Birds appear and increase in numbers and more importantly, insects and plants continue their co-evolutionary war and the link between flowering plants and their insect pollinators changes the appearance of the whole planet, in the oceans a new swimming animal, chordate fish, start to appear and have a profound impact on this environment. The Cenozoic is more than just the age of mammals!

Hadean Eon

Please Note: This discussion of the Hadean Eon does not include information on the Late Heavy Bombardment - refer to your notes from class for this material.

It's impossible to understand the origins of life on planet earth without first setting the stage for its appearance, or maybe its arrival from somewhere else in the solar system or even the galaxy! Once the Big Bang ended a massive nebula of gases and dust started to contract and as it did, its centre reached a critical mass resulting in a nuclear explosion igniting our sun that still burns today. Our sun is an out of control nuclear explosion where hydrogen atoms are undergoing fusion into helium and the resulting energy is spread through our galaxy. The closer you are the greater the intensity, and its not just light! Almost 99% of the matter in our solar system is tied up in the sun with the rest swirling around the new-formed sun in a massive disk. But this wasn't a homogenous mix of material, the explosion that ignited the sun propelled the lighter gases to the edge of the galaxy and the heavier substances remained near the centre. The result is outer planets of frozen gases and the inner ones have heavy iron cores. As a result of gravitational pulls the swirling material started to stick together and the planets started to form.

One big kid on the block, Jupiter, sucked in huge amounts of material; some of it stuck and some didn't and was shot back across the solar system hitting other planets in its path. These were violent times in the solar system and huge meteorites and asteroids impacted on the new planets with enough energy to liquefy them and kept them molten and contribute their own elements to the molten mix. It was one of these impacts on planet earth that caused a huge chunk to break off and become our orbiting moon. Gradually the largest pieces were pulled into the gravitational pull of the sun and formed planets and what remained were the asteroids and meteorites that still circle within our solar system. Any impacts that did occur after this were smaller allowing the planet to cool and a crust to form on its surfaces.

Stabilization of the newly formed planet had occurred and although meteorites still ploughed into the earth they were never of a size that could cause global damage of the type seen during the building phase. Once stability occurred the various components had a chance to "settle" and the dense iron core of the earth remained molten and hot and the lighter gasses escaped. Earth was just the right size, and its gravitational field held onto the escaping gases and the first atmosphere surrounded the planet. As it cooled its surface formed a crust through which were vented the various gases from the molten central core, out gassing. Earth's first atmosphere was different from what we see today, methane gases, sulphur gases and above all no oxygen. As the earth cooled further water vapour turned to liquid and simply put, the rains began to fall and cover the earth with its first water blanket, the precursor to the present oceans. The stage was set, but at this point it was a barren and sterile world where the heating into the thousands of degrees Celsius from the molten planet insured that any life that may have occurred was killed. That would all change soon.

Prebiotic organic chemistry

To understand the origins of life on earth we're faced with a couple of realities. Life on earth is based on the versatility of the carbon atom to form the carbon-based compounds that are the basis of all living molecules. A second reality is that simple carbon molecules came first followed by the more complex.

In short, biomonomers preceded the biopolymers and all of this occurred in the water of those ancient oceans. The question then becomes what are the origins of these first monomers?

Organic chemistry is all about carbon and attaching things to it. This was the first type of chemistry to occur in the ancient oceans as carbon atoms were linked together to form the biomonomers of life. One of the first plausible explanations for how this occurred was the Miller experiment. The presumed primordial gases of methane, ammonia, and hydrogen were combined in a glass container and water (a surrogate for the ancient ocean) was boiled causing hot vapours to rise into the gas mixture. The resulting vapours were cooled and condensation occurred (ancient rain) and the condensate fell into the pool of water that was being heated into water vapour. Miller added electrical sparks, (ancient lightning) to the mix of gases and let the whole thing run for a number of days before seeing what had happened to the initially pure water. He found amino acids, a variety of carbon compounds; even some lipids had been formed. After these experiments were done it's became clear that carbon dioxide was also present in the ancient atmosphere and it's inclusion in Miller's original mix doesn't change the most significant result; that biomonomers could be produced spontaneously in the earth's early atmosphere. This experiment has been repeated under a variety of different conditions and with different starting materials and the results give us essentially every organic building block with the exception of one – the nucleotide of either RNA or DNA.

This potential source for the first organic molecules remained unchallenged until explorations to the ocean depths revealed an alternative source for the initial organic compounds. In the deepest parts of the ocean, often kilometers deep, the crust of the earth is thin and the continental plates separate from each other. Here the hydrothermal vents occur where the core of the planet releases gasses and molten rock. The temperatures are in the hundreds of degrees Celsius but the water doesn't boil because of the tremendous weight and pressure of the miles of water above the vents. Instead it heats to temperatures higher than the usual boiling point and remains liquid. The result is a brew of organic molecules and another source for the organic molecules as the precursors to the biopolymers of life.

Our understanding of the events in the ocean depths has lead to speculation that if water were present on another planet and under the same conditions as the vents, then organic molecules may have arisen elsewhere in the solar system. If so then during that building stage of the Hadean some of the large meteorites that hit the earth may have contained organic matter! Comets often have a large core of frozen water. Is it pure, or a sample of the primordial soup from another planet? The destructive heating of the planet wouldn't have destroyed these compounds and each time the earth cooled the mix in the oceans became richer and more organic. This would explain the presence of carbon which is what a dying red sun spews out as space dust.

Whether home grown as a primordial soup, from hydrothermal vents; or from outer space there is no doubt that the ancient oceans contained a rich mix of chemicals that include the organic monomers or their precursors to form a primordial soup. The question now is how did these monomers form the larger polymers?

Prebiotic biochemistry

The biopolymers fall into four broad categories, three of which are addressed in the Central Dogma of Biology: DNA, RNA and protein and each is related to the other by the dogma. The amino acid sequence in a protein is determined by the mRNA molecule which get's its information from DNA. Like a three part chicken and egg story, what came first? Was it the DNA, RNA or protein? But we need to account for more than the appearance of these polymers they must also be able to replicate themselves. Essentially if protein came first then it must be a polypeptide chain that is able to synthesize copies of itself or other proteins by stitching peptide bonds together. Same would be true if RNA if it was the first biopolymer. DNA isn't a good candidate as the first biopolymer because of the complexity and stability of the double helix that has to be unwound by a protein to even expose the neucleotide sequence. Remember were trying to figure out what came first.

Before we take a look at RNA and protein as the potential first biolpolymers let's look at another aspect of this: the simple production of linear molecules. Twenty years ago we would have said that every attempt to duplicate possible conditions that would have allowed the inanimate production of biopolymers had failed. But that's no longer the case and small peptide chains, nucleic acid polymers and the lipids have been formed under prebiotic conditions. Sure they may be simple with a single amino acid or nucleotide in the string but the strings have been made!

But one of the hallmarks of life is replication and if either protein or RNA are to be the start they will have to synthesise themselves – now that's much harder to demonstrate in the lab. When proteins were the only known enzymatic catalysts the protein first hypothesis was proposed where included in the mix of proteins formed was one that was a specialist and duplicated the other proteins. RNA strands have also been found to have autocatalytic abilities. If a folded RNA strand (that's of course what a present day ribosome is) is capable of duplicating linear RNA strands then we have replication. The assumption here is that the first replicating system was RNA based. Then a modified version of the folded RNA strand may have started stitching amino acids together using pieces of RNA that had bound to the amino acids - the first RNA translation system. Proteins are better catalysts, and RNA's role in the central dogma may have been reduced to only making the better protein based catalysts leaving it with the job of stitching the new catalyst's monomers together as it currently does by the combination of mRNA, tRNA and rRNA. The final stage was to conserve the RNA sequence that was coding for the protein in a different, more stable type of neucleotide sequence - DNA. This is the formation of life in an RNA first world.

There is a problem with both of these models that has arisen as various scientists try and get these systems to work. Protein catalysts are long chains and this is necessary to create the unique pockets and folded structure that make them to their biochemical magic. By necessity this means the RNA chain must also be long. Guess what these long chains break down rapidly in aqueous solutions meaning that they may never reach high enough concentrations for any form reaction to occur. A second troubling finding is that small peptides or nucleotide chains are usually insoluble in aqueous solution; they need all those monomeric charged groups to dissolve in polar water. Finally there is the nagging problem that no one has ever been able to build a nucleotide using prebiotic chemistry.

Compartments

One of the areas of research that is using a different approach to trying to understand how life evolved on the planet is interested how lipids interact with an aqueous environment. The reason for this is that a cell is surrounded by a phospholipid membrane that encloses an internal aqueous environment – the cytoplasm and its contents. Among the prebiotic mix are a variety of hydrophilic lipids that will do some very interesting things. If you have the right ratio of water and lipid the lipids will reorganize themselves into small spherical balls called micelles. These micelles have an internal pocket of water surrounded by a single layer of lipid. Phospholipids are to complex to have appeared in the primordial soup but there are less complex molecules with polar heads and hydrophobic tails and when these are mixed in the right ratio with water they form large bilayer membranes that surround a central core of water! Sound unusual, it gets even more interesting – you can extract lipids from carboniferous meteorites and these will no the same thing!

When they form, the vesicle trap inside of it a sample of the water that was surrounding it when it was formed. That in itself isn't interesting but if that trapped water included and enzyme and substrate the reaction will occur and for some as yet unknown reason the reaction proceeds faster in the confined space of the vesicle. If the product from the substrate hydrolyzed by the enzyme is the same lipid that is in the wall of the vesicle the product enters into the surrounding wall. More lipids in the wall and the vesicle enlarges; but only to the point where it gets big enough and then it divides in two! Unfortunately each time it divides it dilutes the enzyme and substrate that can't be replenished from outside and the vesicle dies by dilution.

Scientists have taken this further and have been able to embed proteins in the membrane of the vesicle that allow exchange with the external environment so the substrate and product can be generated for prolonged periods of time. These are what are referred to as protocells and they have been host to a variety of complex biochemical interactions including biosynthesis of DNA and RNA and RNA has even been translated into protein in artificial protocells. To be true cell though the protocell must be able to do three things: self-maintenance through metabolism and internal biochemical reactions, self reproduce and finally they will have to be able to change or evolve. To date all three of these haven't been combined – there are only experiments where one or two of the criteria have been met.

The long standing feud between the prebiotic folks and the compartmental scientists is coming to an end and both may share part of the correct answer. So much has been done in the past twenty years who knows what is coming next!

Panspermia

There is another possibility that we should mention and that is that the earth was contaminated by a living organism of some sort that already had the machinery of the Central Dogma within it. Presumably it arrived on some meteorite that landed in this rich organic soup and everything took off from there. If this were the case, it would have to be a very tough organism to with stand the conditions of travel through space and the harsh journey through the Earth’s atmosphere. The discovery of the extremophile bacteria living in the extremely harsh world of the deep undersea volcanic vents means there may be a likely candidate. The panspermia theory has gained some support from what look to be small bacteria in meteorites – although not everyone agrees.

Archean eon

A bacterial, anaerobic world and its demise.

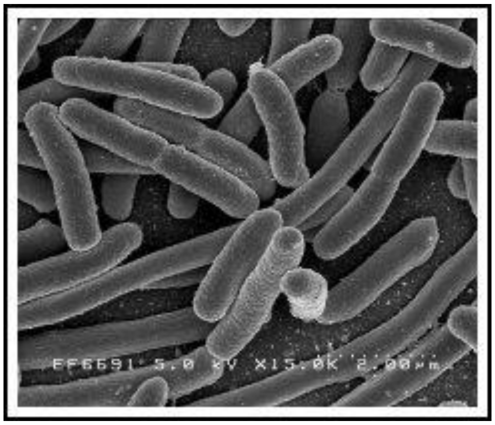
Introduction

The Archean Eon is the age of the bacteria and it starts with anaerobic forms and finishes with the aerobic forms including cyanobacteria that collectively transform the planet to the oxygen rich aerobic environment we know today. Don't let the simplicity of these little organisms fool you, they are tremendously diverse and very successful, after all they have been on the planet for 3.8 billion years, doing pretty much the same thing over that time, a notable exception being the switch from an anaerobic existence to aerobic at the end of the Archean eon. In a time when morphology was used to organize the living work it was thought that all prokaryotes were the same. But gene sequence studies of the 16S ribosomal subunit shook up the tree of life and the result was prokaryotes were divided in two: The Archea and Bacteria, or Eubacteria as they are sometimes referred to. By the time the proposal of three domains, the third is the Eukaryota, gained acceptance in the 1980's it had also become clear that the Archea and Bacteria Domains included some of the most interesting and complex organisms because of the diversity in their metabolism and horizontal gene transfer, basically gene swapping.

Eubacteria

Classification

No one knew there were single celled organisms as small as bacteria until the optics of the early microscopes improved. Once bacteria were discovered the first strategy for grouping and classifying these new organisms was to use their appearance –their morphology. It was the same method that had been successfully used for animals and plants and initially it worked with the bacteria. In the early stages of bacteriology designations of rod shaped bacilli, rounded cocoid bacteria and mobile spirochetes were enough for grouping and classification. But as more bacteria were identified it became clear there were more types than different morphologies making additional naming criteria necessary. One of these new criteria was the pathogenicity of the bacteria, another relied on the metabolic abilities that were being discovered: methanogens for methane producing forms, sulphur bacteria that were found in sulphur rich hot springs and nitrogen fixing species. As time went by, and more forms were identified by genomic structures and sequences, it became clear that this was an immensely diverse group. Simple genus and species names were not enough and numeric and other abbreviations were added to the names of different, but closely related bacteria, to describe surface proteins and genome structure. As a result, the different variants of the bacterium Escherichia coli include the enterohemoragic E. coli O157:H7, the lab strain of the bacterium E. coli BL21(DE3) and E. coli O104:H4 that caused an outbreak of gastrointestinal illness from contaminated vegetables in Germany in the summer of 2011.

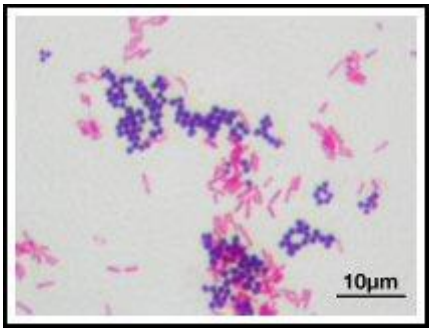


Escherichia coli is a rod shaped bacterium and a normal part of the digestive microflora. There are some types that can cause food poisoning and in some cases death. In 2000, strain O157:H7 got into the water supply of Walkerton Ontaria and resulted in the death of 7 people and about 2500 more who became ill.
U.S. National Institure of health, Wikimedia Commons

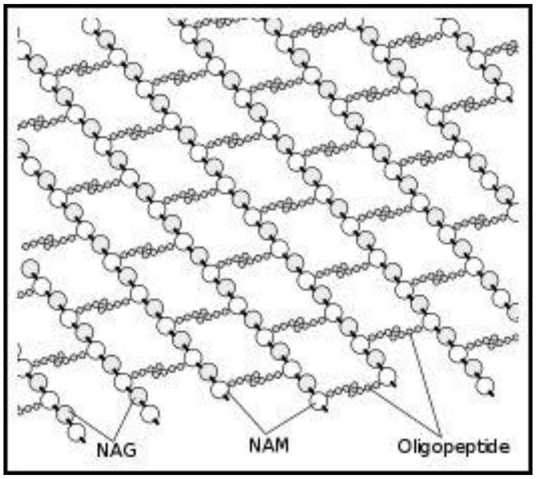
The outer limits

Bacterial Cell Walls

Many of the advances in early microscopy resulted from staining techniques that made it easier to see intracellular structures. Stains that differentiated between proteins, carbohydrate and nucleic acids revealed the organelles and nuclear materials inside cells. Of course, there are no organelles inside a bacterium and staining techniques used with eukaryote cells were not as effective in understanding the internal organization of bacterial cells. But, one staining technique differentiated between two bacterial types: the Gram-negative and Gram positive forms and their different types of cell walls.



Gram stained mix of Gram-positive cocci (*Staphylococcus aureus*, purple) and Gram-negative bacilli (*Escherichia coli*, red).
Wikimedia Commons



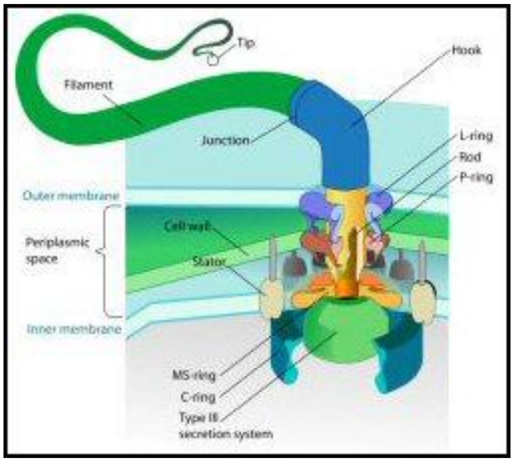
Structure of peptidoglycan in the bacterial cell wall. NAG: *N*-acetylglucosoamine and NAM:*N*-acetylmuramic acid.
Wikimedia Commons

In organisms with a cell wall, the wall consists of simple monomers strung together to form fibres that give the cell wall its strength and rigidity. In plants glucose molecules are strung together to form cellulose; N-acetyl-glucosamine monomers form the chitin of the fungal cell wall; in bacteria peptidoglycan has the same role. Like its fungal and plant counterparts, peptidoglycan is also composed of a series of repeating units. Unlike them, it does not involve linear repetition of a single monomer. Peptidoglycan is composed of two different sugars that form a dimer and these dimers are then strung together. Every second sugar, or only one sugar of the dimer, has a four amino peptide attached to it. This small peptide chain is the key for allowing two different peptidoglycan fibres to interact; an enzyme will form covalent linkages between the two terminal amino acids of the small peptide chains belonging to two different peptidoglycan molecules, which repeated multiple times, is the basis for the peptidoglycan layer’s strength and rigidity.

Peptidogylcan is common to both Gram-positive and Gram-negative bacteria but its availability for staining differs. In the Gram-positive bacteria the peptidoglycan layer is thick, and on outermost surface of the bacterium and is stained; and designated Gram-positive. In the Gram-negative bacteria the peptidoglycan layer is a thinner layer sandwiched between an inner and outer plasma membrane; yes Gram-negative bacteria have two plasma membranes, with the periplasm between. The additional outer plasma membrane prevents the staining of the peptidoglycan layer; the reason for their designation Gram-negative. But there are additional consequences of the outer membrane other than preventing the Gram-stain. Gram-negative bacteria are often pathogenic and the outer lipid layer contains the endotoxins (complex lipopolysaccharides) that make the bacteria toxic. In addition, the outer lipid layer prevents penicillin from damaging the peptidoglycan layer of Gram-negative bacteria, unlike to Gram-positive bacteria, where the thick layer of peptidoglycan is exposed and can be easily damaged.

Flagellum

Not all bacteria are motile, but those capable of movement have the same molecular motor driving the flagellum consisting of three parts: the flagellum, hook and basal structure or motor. The polymerization of thousands of copies of just one protein forms the flagellum connected to the basal structure or motor using the hook which is a coupling between the flagellum and the motor. The motor includes a series of proteins that, because of their amino acid compositions, span the plasma membrane to form rings. The number of rings depends on the whether the bacterium is Gram-positive or Gram-negative with a pair of rings associated with each membrane. Without getting bogged down in the biochemistry, the bacterial motor is driven by a proton gradient. Hydrolysis of ATP moves a proton across the inner membrane and as they accumulate a proton gradient from outside to the inside the bacterial begins to build. Proton gradients are a form of stored energy and one you may have already encountered is the electron transport chain of the mitochondria where protons accumulate between the inner and outer membrane before falling through the hollow core of the ATP synthase. The bacterial motor works the much the same way and the only way for the proton to move down the gradient is to pass through the opening in the motor proteins. As they pass through the motor protein, the energy is used to create a conformational change in the motor proteins that moves the central rotor attached to the hook that spins inside the rings embedded in the plasma membrane. Additionally, switch proteins can change whether the motor is spinning clockwise or counter clockwise and the whole complex is made of only 40 proteins of which 23 are common to all bacterial motors !



🔍 Detailed view of the bacterial flagellar motor in a Gram-negative bacterium. The L, and MS-Rings anchor the motor in the cell membrane, the P ring the cell wall, The motor consists of the secretory system pumping protons in the periplasmic space that fall back thorough the stator proteins of the motor. Mariana Ruiz Villarrael (LadyofHats) Wikimedia Commons

Odds 'n Ends

The outer surface of all bacteria is always covered by some form of mucilaginous outer capsule that forms a glycocalyx over the surface of the bacterial cell. The capsule has a number of potential functions including sticking bacterial cells together to form biofilms and as a defense against bacteriophages and phagocytosis by protists or the immune system of other organisms. The outer surface of many bacteria may also include small hair like projections called pilli that are important in conjugation, a form of reproduction that will be discussed later.

The inner space

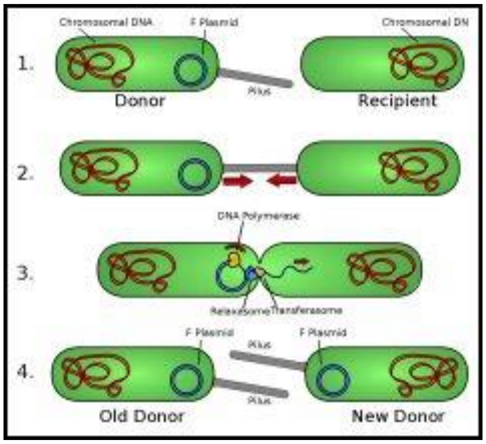
Like all prokaryotes the cytoplasm in bacteria lacks an endomembrane system or organelles. The bacterial cytoplasm is rich in 70S ribosomes consisting of 50S and 30S subunits and a genome, which is located in a specialized region of cytoplasm referred to as the nucleoid. There are no chromosomes in bacteria and instead the genome consists of a one circular piece of double stranded DNA, or in a few cases a linear piece, that loops, folds and supercoils on itself to form a compact structure suspended in the cytoplasm. How compact? The genome of E. coli is 1.5 mm long when it is unfolded, and 1µm in length when folded! The other consequence of this organization is that bacterial cells are haploid: there is no complementary second circular loop of DNA! In eukaryotes, histone proteins protect the folded DNA strand but in the bacteria, the folding pattern of the genome confers the stability. An additional piece of circular DNA, a plasmid, may also be present in the cytoplasm and they duplicate themselves independent of the bacterial cell. Plasmids are important in initiating conjugation by producing pilli and play a role in horizontal gene transfer during transformation. Plasmids have also been implicated in antibiotic resistance and toxin production. Plasmids are the work horse of many techniques in molecular biology where genes or DNA fragments are inserted into the plasmid vector that is used to make copies of the inserted DNA for subsequent analysis.

Reproductive Diversity

Binary fission

As mentioned previously, bacterial cells are always haploid and there is no second copy of the genes like in diploid, eukaryotes with paired homologous chromosomes. In terms of variability any mutations or changes in the DNA sequence of the genome that occur are going to be expressed because there is no second copy of the gene or DNA sequence as in the chromosomes of diploid organisms. The simplest form of reproduction is binary fission and when the bacterial genome is duplicated, each copy links itself to the cell wall and as the cell divides a copy of the genome ends up in each of the daughter cells. Bacteria may also contain a second piece of DNA, the plasmid and when plasmids are in the cytoplasm they replicate independent of the division cycle of the bacterial cell. When the bacterial cell divides the plasmids and other cytoplasmic inclusions, including ribosomes, are partitioned randomly between the two daughter cells. The plasmid may also be incorporated in the genome of the bacterium; if this is the case the plasmid DNA is replicated at the same time as the bacterial genome.

Conjugation



During bacterial conjugation the donor cell builds the pilus (1) that attached to and pulls in the other bacterium (2). Contrary to what is often said, the exchanged strand of DNA doesn't pass down the pilus (3). [Mike Jones, Wikimedia Commons]

Plasmids are also capable of transferring themselves between bacteria. The presence of a "fertility gene" on the plasmid produces pilli on the surface of the cell wall. They are referred to as F-positive if they have the fertility factor and F-negative if they do not. If a bacterium with pilli encounters one without, the two become connected and a single stranded copy of the plasmid DNA is transferred from the F-positive bacterium to the other F-negative bacterial cell. The complementary strand is produced and the bacterial cell now contains a plasmid that may include genes for antibiotic resistance or unique metabolic pathways. As mentioned, the plasmid can also incorporate itself into the genome of the bacterium and remain there for many generations before snipping itself out and once again becoming a separate plasmid in the cytoplasm of the bacterial cell. When this snip occurs it is not uncommon for the original piece of plasmid DNA and an adjacent part of the bacterial genome to be removed as well. This results in a new plasmid with all the original plasmid gene sequences plus some from the host bacterial cell. When this modified plasmid starts to replicate it produces pilli on the surface of its host and when conjugation occurs it passes all of the DNA contained in the plasmid to the other cell and the recipient cell receives both plasmid and bacterial DNA; a form of horizontal gene transfer.

Transduction

Bacteria often fall prey to bacteriophages, a virus that takes over the bacterial cell and kills them during the lytic phase of the viral life cycle. As is the case with all viral life cycles the virus takes over the host cells' replication, transcription and translation machinery and uses it to replicate its genome and produce the proteins of the viral case that are encoded in the viral genome. We'll learn more about these life cycles in the section on viruses. The final stage in the life cycle is to assemble the virus by encapsulating a copy of the viral genome that is floating in the bacterial cytoplasm in the viral case. Normally the DNA of the bacteria disappears during viral infections but occasionally a piece may remain intact and when the assembly step for the new viral particles is initiated, it may be encapsulated instead of the viral copy of the genome. This results in a bacteriophage containing a piece of bacterial DNA, not viral DNA. This bacteriophage is capable of injecting its genetic load into another bacterium but the consequence is the bacterium has a piece of bacterial genome that it may then incorporate it its genome. This is another form of horizontal gene transfer.

Transformation

Even more unusual is transformation; another form of horizontal gene transfer. In transformation, a bacterium can absorb a DNA strand from the external environment and splice it into their own genome! Sometimes it works and a new gene sequence is inserted and becomes active and sometimes it doesn't and the DNA is degraded and salvaged for its nucleotide building blocks. It is just another example of the gene swapping that occurs in bacteria; a key strategy in creating genetic variations in these small little organisms.

Metabolic diversity

In addition to their reproductive diversity bacteria, and this includes the Archea, are well known for their metabolic diversity. Metabolism, in its simplest sense, is the ability to harness energy and use it to build. Because we are talking about building living things, carbon is the basic building block and energy is in the form of high energy electrons. By themselves these high energy electrons don't do much but when they are combined in a redox pair where the electron is passed between two compounds there is the possibility to harness the energy. In a redox pair the recipient of the electron is reduced, with a reduced positive charge, and the donor is oxidized. The classic example of this is the mitochondrial electron transport chain where the energy of a series of redox reactions is used to pump protons in the space between the inner and outer mitochondrial membranes. So, metabolism is all about passing electrons and building with carbon.

Carbon exists in two forms, either organic or inorganic. Organic carbon is incorporated into carbon-carbon bonds and although there are various forms of pure inorganic carbon, graphite and diamonds for example, one of the most abundant and is the oxidized version of carbon - atmospheric carbon dioxide. These are the only two forms that carbon can have, but they are linked to each other and, with the exception of the small organic compounds we saw in the prebiotic soup, most complex carbon-carbon bonds are built by living organisms. If a metabolic process is capable of building organic carbon by using atmospheric carbon dioxide we refer to it as autotrophic and the complex carbon that is characteristic of living systems comes from the gaseous form of the element. The opposite of an autotroph is a heterotroph and these organisms build using carbon that already exists as part of an organic carbon-carbon bond. The link between the two is autotrophs supply the organic carbon that heterotrophs build with. So based on the source of the carbon building blocks we can divide the varied metabolism into two groups; autotrophs and heterotrophs.

We can divide metabolism based on its energy requirements. Your first thoughts about energy supplies may be ATP or others like GTP, NADH+ etc. But, each of these cellular energy sources has one thing in common. They are products of redox pairs that involved a transfer of high energy electrons. The question then becomes how do we energize this electron so that we can trap that energy later? Photons are the basic unit of electromagnetic radiation, including light, and photonic energy can be harnessed to create high energy electrons. In solar energy cells the energy of the photon knocks electrons off silicon and the flow of electrons results in electricity. Plants do the same thing and the photonic energy knocks electrons into a higher energy state and as they are transferred through redox pairs the energy is transferred into the chemical bonds of glucose. All organisms that use light's energy to build carbon-carbon bonds use the prefix photo-, and are called phototrophs. Carbon bonds can be a source for energized electrons when these high energy bonds are broken down in a gradual, controlled and step wise manner so that all the energy is not released at once. (Be careful though, we are only discussing a source of potential energy that exists in the organic carbon and the energy released when the bonds are broken - not what happens to carbon.) We refer to metabolisms that use high energy organic bonds with the prefix Chemoorgano- and chemoorganotrophs use covalent bonds in organic chemicals as their energy source. There is a third ways to generate high energy electrons. Many elements and compounds found in the inorganic world have oxidized or reduced states. A classic example is iron, which is oxidized to iron oxide, and other examples include ammonia, sulphur gases and even nitrogen which can move between their oxidized and reduced states. If a redox pair exists there is the potential to trap the high energy electron and use it. This is what our third metabolic type does. Because many of these inorganic redox pairs are a part of the earth's crust, the lithosphere, we prefix this form of metabolism with litho- and organisms with this type of metabolism are referred to as lithotrophs.

So, there are two ways to obtain carbon and three ways to get the energy to build and we have a 3x2 matrix with six possibilities and for each there is a term that describes that type of metabolism.

	Source of high energy electrons		
Carbon source	Light	Organic Carbon	Minerals

Carbon dioxide	Phototroph	Chemoorganotroph	Chemolithotroph
Organic carbon	Photoheterotroph	Chemoorganoheterotroph	Chemolithoheterotroph

What this seemingly simple table shows is that bacteria can get their energy from anything and the carbon in any form. In their two billion years of evolution they have figured out every possible way to live. But one of these combinations will change the earth. This is the use of light and the splitting of water molecules to create the carbon-carbon bonds of glucose and produce oxygen as a metabolic waste. At first the oxygen was dissolved in the water, and forced the anaerobic prokaryotes to take refuge in the deep oceans where the toxic oxygen didn't accumulate. Oxygen started to appear in the atmosphere and it oxidized the minerals of the earth - the earth began to rust. The appearance of oxidized minerals in the earth's rocks identifies the end of the Achaean eon and the start of the Proterozoic. But there's more then rusting rocks. Oxygen started to accumulate in the atmosphere where it reacted to from ozone. Ozone filtered out the ultraviolet light that caused damaging mutations in organisms that lived to close the surface of the ancient oceans. Until that happened it was hard to be a phototroph living in the narrow boundary where light penetrated the oceans waters, but not the damaging UV. Those small little bacteria produced the ozone layer we have today and all the initial oxygen that set the stage for the first unicellular eukaryotes – the Kingdom Protista. In addition to surviving on their own, these bacterial cells will ultimately become the plastids of the photosynthetic eukaryotes.

Light is one of the best sources of high energy electrons and the chemical bonds in glucose store some of the largest amounts of potential energy. The higher energy covalent carbon bonds produced using light are an excellent food for bacteria that can break the bonds. To be able to harness that much energy will require a series of electron transfer steps that will end up producing ATP. There are bacteria that still do this and at some point in the evolution of the eukaryotes a bacterium capable of oxidative phosphorylation will appear in the cytoplasm of these new cell types – more on that, and plastids, when we look at the Proterozoic.

Archea

The Archaea is a group of bacteria that thrive best under extreme conditions such as, high salt, and extreme temperatures. They're found in some of the weirdest places: hot water springs, the deep thermal ocean vents, and guts of cows and termites to name a few. They fall into a number of broad categories: methanogens (methane producers), extreme halophiles (salt loving), and extreme thermophiles (loving extreme temperatures either hot or cold). One of the more unusual features of the whole group is the unique lipid composition of the plasma membrane and these changes are no doubt the result of the extreme conditions under which these prokaryotes live.

The methanogens all live in anaerobic conditions and even a trace of oxygen is toxic to them. Bog fairies, cow flatulence, and swamp gas are all examples of methanogens at work. In their oxygen free environment they carry on life's processes of combining hydrogen and carbon dioxide to build organic molecules in a unique process resulting in methane as a by-product. It may seem like a trivial thing but these minute little prokaryotes were so abundant in the Archaean world that trapped in the pockets of water in the Earth's crust they happily carried on living and filling the spaces with their waste product of methane. In the deep oceans, water pressure has solidified the methane as methane gas hydrates. A less ancient example of their importance is their importance in landfill and garbage disposal. Landfill sites were plagued with the presence of the explosive gases methane that built up under the layers of rotting garbage. This was an anaerobic environment and the methanogens were hard at work recycling organic material! Originally a problem these landfill sites are being mined for their accumulated methane now tapped as fuel.

Halophiles love salt and as you might guess you'll find them living in some of the saltiest places on earth, the Dead Sea, the Great Salt Lake and the salt flats where ocean water is evaporated to crystalline sea salt.

Extreme thermophiles, as their name implies, adore heat or extreme cold. The hotter or colder, the better, if it's anything in between they'll stop growing. Some are aerobic and others are anaerobic but most make use of sulphur in their main energy pathways and as a consequence they're usually found in sulphur rich water. This includes geysers, hot springs and of course those deep thermal vents at the bottom of the oceans. At the opposite extreme there are others that can withstand extremely low temperatures.

Changing earth highlights

Archean period (3800 - 2500 Ma)

- 3700 Ma - Photosynthesizing bacteria
- 3500 Ma - Oldest fossils
- 3400 Ma - Small continents form
- 3100 Ma - Continents begin shifting
- 2700 Ma - First eukaryotes
- 2600 Ma - Bacteria on land
- 2500 Ma - Banded iron formations

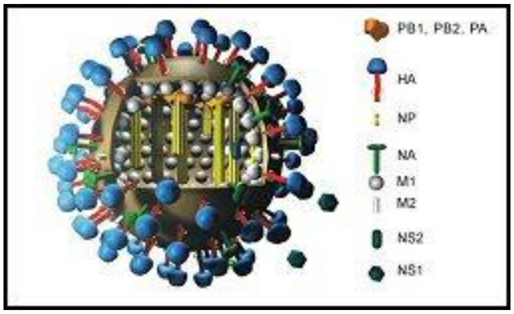
Viruses, prions and viroids

Viruses

Viruses are also capable of replication and are much smaller than bacteria and archeans. In their simplest form, a virus consists of its genome surrounded by a protective protein coat, the capsid. The viral genetic information contains the genes required to duplicate the viral genome, manufacture the capsid proteins and assemble the capsid around the copies of the genome. But, viruses lack any of the synthetic machinery to carry this out. Instead they take over the replication, transcription and translation machinery of another cell.

Like bacteria, viruses are characterized by their morphology and have one of two forms: non-enveloped or enveloped viruses. Both have the capsid casing surrounding the genome but an enveloped virus has an additional lipid bilayer membrane surrounding the capsid and the genome inside. This lipid bilayer is formed from the plasma membrane of the host and includes host membrane proteins and additional plasma membrane proteins added by the virus.

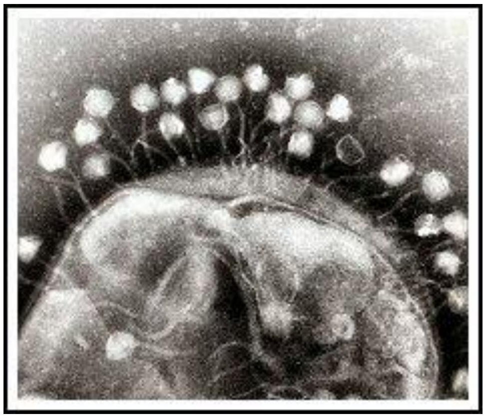
Soldiers from Fort Riley, Kansas ill with Spanish influenza at a hospital ward at Camp Funston in 1918, where the North American part of worldwide pandemic began.
US Army photograph, Wikimedia Commons



Structure of swine influenza virus showing different type of antigens present on and inside the capsid.
M Eickmann, Wikimedia Commons

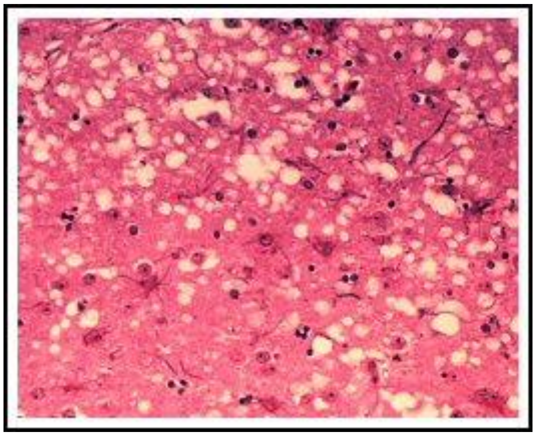
We can use the influenza virus as an example of how these additional viral proteins in the envelope are used to identify the virus. There is a set of proteins referred to as the H and N antigens embedded in the envelope of the virus. The H-antigens are important in recognizing a host cell and attaching the virus so that the genome can move into the host cell. The N-antigens are involved in the escape from the host cell when the virus has completed replication. The influenza virus is given a designation with H and N numbers and in the winter of 2010 the H1N1 variant was of great concern as a potential pandemic virus. In 1918 the Spanish flu virus killed more people returning home after the First World War than were killed in the war itself, between 50 and 100 million people around the world! The Spanish flu was also an H1N1 variant. For non-enveloped viruses, the proteins contained in the capsid itself are used to identify the different viral forms and the capsid proteins are important in recognizing the host cell and assist with the transfer of the viral genome into the host.

If we think back to the Archean eon, the oceans were filled with bacterial life and there must have been some checks and balances in place to control bacterial numbers and this was probably one of the original roles of viruses as, if you like, the predators of the bacteria. They probably have a similar role today. Viruses that invade bacteria are non-enveloped bacteriophages and they attach to the surface of the bacterium and inject their genome (DNA or RNA in retroviruses). The result, protein synthesis of host proteins is shut down and only viral nuclear material is duplicated and proteins for the new capsid produced. The virus reassembles as new virions, a term used for a single virus particle, and the bacterial cell breaks open, lysis, releasing hundreds, if not thousands of virions ready to infect another cell. This sequence is the lytic cycle. Sometimes the viral genome will incorporate itself into the bacterial DNA and remain there, dormant. Each time the bacterium duplicates the viral copy is duplicated and at later time the lytic cycle may resume. This form of viral reproduction is the lysogenic cycle. When a non-enveloped virus escapes from its host cell it kills the cell. It's a little different with the enveloped viruses. In this case during the replication cycles, the virus created the membrane proteins that are added to the mix of proteins already in the host's plasma membrane. When the virus escapes it buds from the surface of the host cell and as it buds it wraps itself in the host cell membrane.



🔍 In this electron microscope you can see the attached phage particles on the surface of the bacterial cell.
[Graham Cohen, Wikimedia Commons]

So where do viruses fit into the scheme of things? For a number of reasons viruses are not cells. They aren't surrounded by the bilipid layer that separates the inside of the cell from the outside. Although there is a plasma membrane of sorts surrounding an enveloped virus it does not have the dynamic functions of a typical cell membrane. The synthetic machinery for protein synthesis is missing, as are the mitochondria to fuel any metabolism. These last two raise the question of whether viruses should even be considered living. Our criteria for living include the following; the ability to replicate/grow, carry out metabolism, regulate, evolve and respond to internal and external stimuli. Viruses are only capable of one of these, evolving. They need their host cell to be able to do the rest. You might question whether they can evolve and it's important to realize the life cycle of a virus, lytic or lysogenic, results in duplicated nuclear material that may be different from the original - and that variation is the basis of evolution.



🔍 This micrograph shows the vacuoles in grey matter of the brain of a cow with Mad Cow Disease (Bovine spongiform encephalopathy).
[USDA, Al Jenny, Wikimedia Commons]

Prions

Prions are small proteins that can exist in two configurations: the normal, properly folded form and a misfolded form. What is interesting about prions is that if a misfolded version of the prion contacts a normal one it converts the normal one into a misfolded prion and now the two can convert other prions. This results in explosive exponential growth in the number of misfolded prions. Prion are common on the surface of cell membranes and although it is still not clear what their normal function is they are believed to be involved in cell-to cell interactions; possible adhesion or communication. In other words having prions is a normal thing. But when they are misfolded they can form fibres and add more of the altered prions at the tip, growing the fibre. The fibres often break and the number of growing points increases and as the fibres enlarge they create aggregates that appear as spongy holes in brain tissue. In animals this is "mad cow disease" and in humans Creutzfeldt–Jakob disease. What is particularly dangerous about the prion is as a small protein it is very stable and hard to destroy. When animal by-products were used as a protein feed supplement, prions passed from the food into the brain tissue. But, remember prions are not just in the brain they are in the membranes of all the cells and if ingested as meat protein they can survive the environment of the gut and infect human cells! This is why mad cow disease is such a danger – in Britain 180,000 cattle were infected and 4.4 million were slaughtered to eradicate the disease. In Canada the disease appeared in Alberta in 1993 and a second case in 2003 saw the disease spread from Canada to the US and world embargos on Canadian beef.

Viroids

Viroids are subviral particles consisting of a small piece of circular RNA that is capable of self-replication. The genome is small compared to a virus but you could consider a viroid to be a naked virus that has lost its capsid coat. When they were first discovered the ability for RNA to replicate RNA was the bases for the ribozymes and the proposal of an RNA world as the origin of the replication, transcription and translation systems of the Central Dogma of life. The RNA in viroid does not code for a protein but single stranded RNA copies are capable of binding to the mRNA of the host cell and when they do they silence the message which is not translated into a protein. These are primarily plant pathogens but it now appears the hepatitis D is an animal viroid that uses the hepatitis B envelope to move from cell to cell.

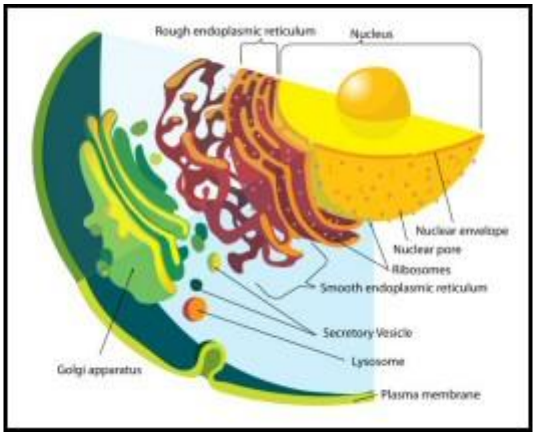
Malformed potatoes resulting from infection with the potato spindle tuber viroid.
USDA, Barry Fitzgerald

Proterozoic eon

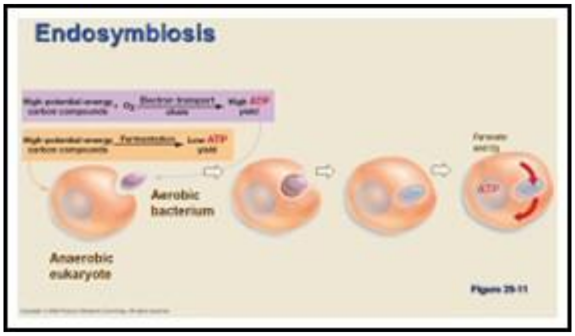
Arrival of the single celled eukaryotes - the protists.

The following topics are available: Evidence for endosymbiosis

Evidence for endosymbiosis



As was just mentioned mitochondria arose as an endosymbiotic event between a bacterium and a simple eukaryote cell with a nuclear membrane and endomembrane system. The question is, how do we know that this is what happened? There are a number of pieces of evidence that lead us to this conclusion. The first piece of evidence is that mitochondria is surrounded by a double bilipid membrane. The inner membrane is the original bacterial membrane. The outer mitochondrial membrane was produced by the cell as it surrounded the bacterium in the membrane that would have normally been a food vacuole. The second piece of evidence is that mitochondria have their own DNA which is circular, a configuration that is typical of the bacterial genome. But it's more than just a circular configuration, the genetic sequence of the mitochondrial DNA more closely resemble bacteria than the genome of the eukaryote host cell. The mitochondria also contains it own transcription and translation system using ribosomes that are bacterial in size, not the size typical of eukaryotes. Perhaps the most obvious evidence is the similarity between the size of mitochondria and bacterial and that both use binary fission as a means of replication.



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The chloroplast (plastid) also arose by endosymbiosis, only in this case an autotrophic phototroph bacterium, most likely a cyanobacterium, was internalized. Again like the mitochondria there's a double plasma membrane around the plastid that also has it's own circular DNA resembling bacterial DNA and bacterial type ribosomes. In some algae the plastid still has traces of the peptidoglycan cell wall that is typical of bacteria.

So which came first, the mitochondria or the plastid? The evidence suggests it was the mitochondria. Remember the prebiotic soup was being used as a nutrient source for initial growth and there would be a distinct advantage to have mitochondria. A photosynthetic endosymbiont was certainly an advantage once it first appeared but remember even a photosynthetic cell needs mitochondria to break down carbohydrate to produce ATP. So while glucose is produced by the plastid the usual metabolic process break it down into ATP and carbons that can be used in metabolism and that requires a mitochondria – they came first.

There is a third example of endosymbiosis in the certain algal groups. In this case a small eukaryote green algae is engulfed and surrounded by a larger eukaryote and is set up in a symbiotic relationship. Because the symbiont isn't a bacterium but anoth eukaryote this is referred to as a secondary endosymbiotic event. One of the consequences of this process, and piece of evidence for its occurrence is the membrane structure of the chloroplast. In the initial algae it would have had a double membrane but when its not host surrounds it there is another membrane resulting in third bilipid membranes surrounding plastids that have arisen from secondary endosymbiosis. There are two types of algal plastids and each uses a different set of chlorophylls. In the green algae both chlorophylls a and b are used in photosynthesis in the red algae on chlorophyll a. Secondary endosymbiosis has occurred twice with one algal group using the red algal plastids and the other the plastids from green algae. If it’s not convincing enough that it has happened at least twice there are living species that capture green algae and uses them for short periods of time when they need to obtain nutrients from photosynthesis when there are non to be consumed allowing a heterotroph to become an autotroph!

Changing earth highlights

Proterozoic eon (2500 - 543 Ma)

- 2000 Ma - Oxidation produces "red beds"
- 1900 Ma - Oxygen levels reach 3%
- 1800 Ma - Oldest eukaryote fossils
- 1200 Ma - True algae
- 1100 Ma - Rodinia supercontinent forms
- 900 Ma - Soft-bodied animals
- 800 Ma - Major glaciation period begins
- 700 Ma - Breakup of Rodinia supercontinent
- 600 Ma - Protective ozone layer in place
- 543 Ma - Vendian extinction, Hard-shelled animals