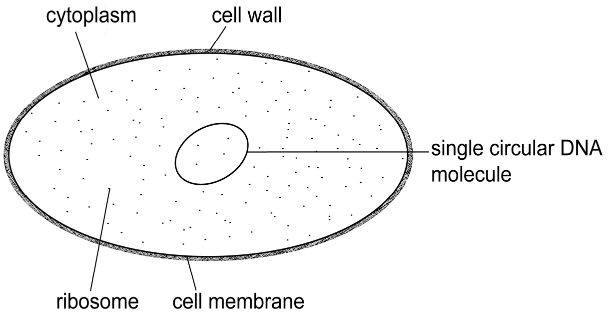
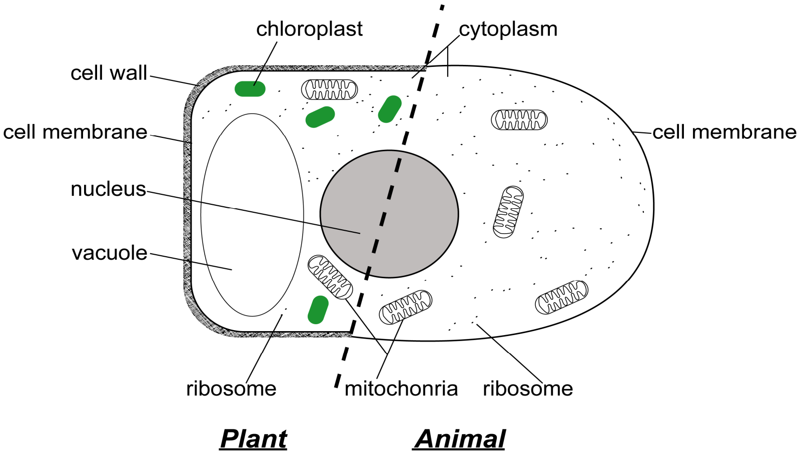
Abiogenesis & Early Life

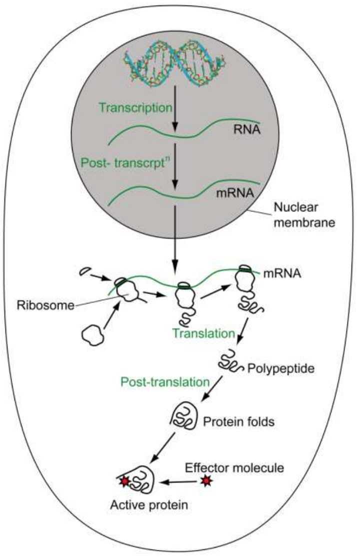
Living organisms have self-sustaining biological processes, and replicate imperfectly. They fall into two basic cell structures. Prokaryotes (Archaea and Bacteria) are generally <10µm; they lack a nucleus or internal membrane-bound structures (organelles), and contain a single loop of DNA within the cytoplasm:



There is great variation in the processes by which prokaryotes obtain energy. They are generally unicellular, and reproduce by simple (asexual) fission. Genetic exchange and recombination occur through horizontal gene transfer. Eukaryotes (e.g. Fungi, Plants, Animals, Amoebozoa) tend to be larger (10-100µm) and differ from prokaryotes in that they possess organelles – membrane bound structures within the cytoplasm. The nucleus houses the DNA, mitochondria are key to providing cellular energy, and in some organisms chloroplasts are responsible for photosynthesis:



The DNA is found in linear molecules which form chromosomes, and organisms are often multicellular with differentiated cells. Cell reproduction occurs by mitosis, with meiosis for sexual reproduction.

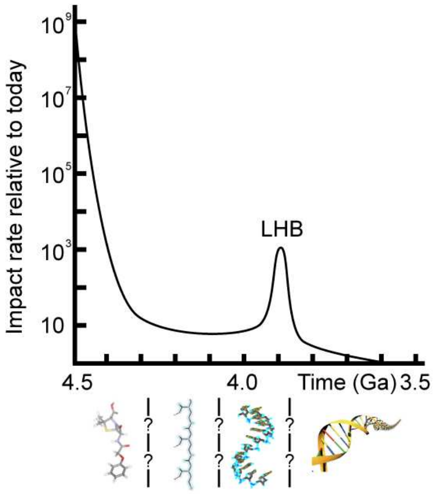


Both forms create proteins from their DNA through protein synthesis; the process is shown to the left for a eukaryote cell, but is similar for prokaryotes. Thus even the ‘simplest’ examples of life are complex, and investigating the origin of these systems is problematic because evidence is limited, and the fundamental steps in cellular evolution occurred so long ago. Nevertheless, in the last century numerous major advances have been made.

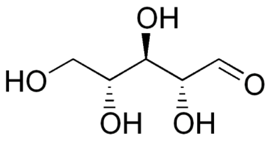
Timescale

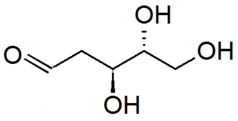
Early earth had an accretionary phase starting at 4.54 billion years ago (4.54 Ga, =4540 million years), during which high temperatures would have made the presence of liquid water and an extensive organic carbon reservoir unlikely. Water would have been present as steam, and the high temperatures would have incinerated organic compounds. This phase would be followed by cooling, in a period where water and simple organic compounds could accumulate. Oxygen isotopes of ~4.4 Ga detrital zircons indicate the presence of liquid water about 100–200 million years after accretion, and suggest that from 4.4 to 4.0 Ga extensive liquid water oceans existed for long periods. These would have been cool enough to allow the survival of organic compounds. Moon cratering suggests this period was relatively impact free, and it was in this quiescent interval that the key steps in the origin of life probably occurred.

At 3.9 Ga the late heavy bombardment – a spike in impact rates – occurred (right). This is currently thought to have been between 20 and 200 million years in duration, with the most recent estimates falling around the lower limit. Life need not post-date the LHB; recent computer models demonstrate no plausible situation in which the habitable zone was fully sterilised on Earth during this period. Thus organic molecules could have survived since the termination of primary accretion of the planets and postulated impact origin of the Moon. The earliest evidence for life on Earth comes from isotopically light carbonaceous inclusions within apatite, reported from 3,800 Myr banded iron formation deposits (Isua formation, western Greenland). The earliest tentative fossil evidence – which requires the existence of cell-like membrane structures – is dated at 3.4 Ga; anything older than this is generally obliterated by metamorphism.



There are three major divisions in the origin of life, whose duration and dates are poorly constrained. The prebiotic / pre-RNA world is the earliest, and it was during this time that early biotic chemistry developed. Following this was the RNA world, during which early biotic chemistry developed into self-replicating RNA molecules (Ribonucleic acid, much like DNA but usually single-stranded, and with ribose [left, five oxygen atoms] as opposed to deoxyribose [right, four oxygen atoms] nucleotides).





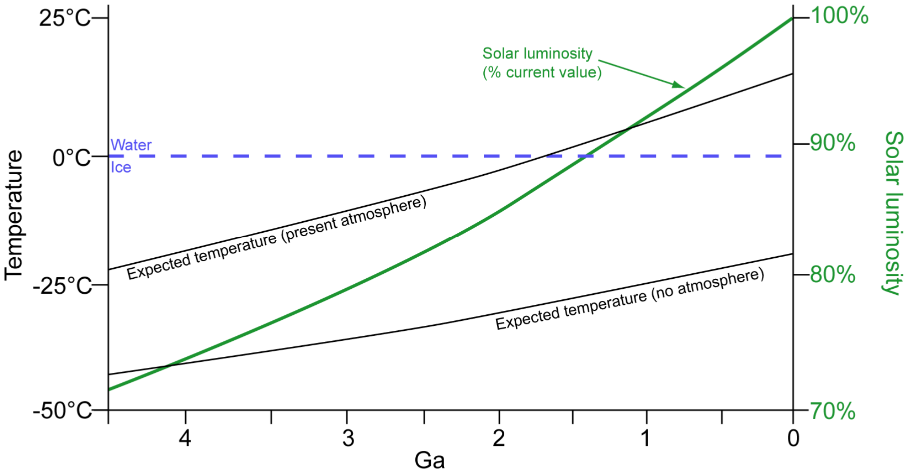
By the end of this period the first molecular entities capable of multiplication, heredity and variation emerged, which marks the origin of life and evolution. The third division is the DNA/protein world, marked by the switchover from RNA for storing genetic information, to modern biochemistry – the use of DNA coupled with protein synthesis (page 1, bottom left). Early in this period the last common ancestor to all life on Earth would have lived.

Source of material

Life as we know it requires liquid water and organic polymers for survival. Water is an effective solvent, with a large liquid temperature range, so is vital to many functions of life. Water on the early Earth was derived from degassing of hydrated mantle minerals, and in-fall of asteroids and comets. All cells rely upon organic chemistry for their central biological functions and structure. These were probably derived from a combination of direct Earth-based syntheses (see Experimental Approach) and input from space; interplanetary dust particles (IDPs), comets, asteroids and meteorites contain a wide assortment of organic compounds, including amino acids, nucleobases, methane and hydrogen cyanide (HCN). These sources led to the accumulation of simple abiotic organic monomers (small molecules which can be bonded together to create polymers) in early oceans and other bodies of water. For most hypotheses of abiogenesis (the formation of life from inanimate matter) this provides the raw material for the subsequent reactions.

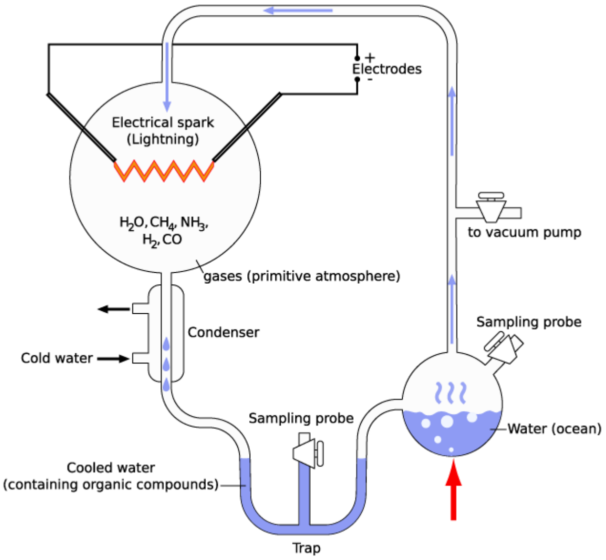
Early climate

During the early history of the Earth the sun was ~30% less luminous than today (the faint young Sun paradox, diagram on page three). This gives two options for the early Earth; without an enhanced greenhouse effect global surface temperatures would have been -40ºC, and thus the early oceans could have been totally ice covered. They would not have completely frozen, however, due to heat from the Earth’s interior. This would cause a deep ocean beneath the ice layer, much like Lake Vostok at the base of the Antarctic ice sheet. Heat flow during this period was around three times the present day value, which would have resulted in an ice thickness of ~300±100 m. Melting could have been aided by the LHB.



Alternatively, as there were few continents, there would be little weathering, thus less CO_2 removal and storage, causing higher atmospheric CO_2 levels and increased greenhouse effect. It is generally accepted that the early environment was a weakly reducing mixture of CO_2, N_2, and CO, with smaller amounts of more reducing gases, such as H_2, SO_2 and H_2S.

<u>Experimental Approach</u>

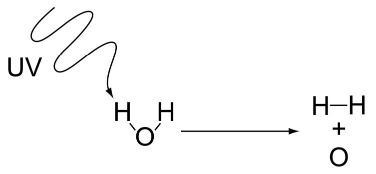


The prebiotic world can be investigated in the lab with plausible geochemical conditions. In 1953 Stanley Miller and Harold Urey, of the University Of Chicago, demonstrated the ease with which important biomolecules could be synthesised. Using the equipment shown above, the pair sealed a 'primitive atmosphere' of H_2, CH_4 and NH_3 in a loop of sterile glass tubes and flasks. One flask was half-full of liquid water to represent early oceans, while the other contained a pair of electrodes. The water was heated and the electrodes were continually sparked to simulate lightning through the atmosphere and water vapour. A condenser cooled the atmosphere, allowing water to return to the 'ocean' and create a continuous cycle. After a week, up to 15% of the carbon had been incorporated into organic compounds: 2% in amino acids (the 'building blocks' of proteins). Also present were sugars, lipids, hydroxy acids, HCN, aldehydes, and ketones such as glycine, adenine and guanine, the latter two of which are nucleotide bases. This synthesis took place in an aqueous solution – proof that on early Earth amino acids could have been produced in bodies of water, provided the necessary reagents were present. HCN – also found in meteorites – proved a critical reagent, central to synthesis of aldehydes and ketones.

It is often-overlooked that the main product was oily goo, which would have created a global oil slick. This would have acted as both a protective layer shielding compounds in the ocean from UV light, and an anhydrous solvent to promote polymerisation. It would have also increased the lifetimes of reducing reagents. We now know that the atmosphere used in these initial experiments was too reducing, but studies since have shown that a large assortment of organic molecules can be synthesised using a variety of gaseous mixtures and energy sources, and most of the molecules that play an essential role in modern biochemistry have been synthesised under plausible geochemical conditions. For oceanic theories of abiogenesis these reagents must be concentrated, which could have occurred through either the eutectic freezing of dilute aqueous solutions, or the evaporation of tidal regions. Eutectic freezing of dilute reagent solutions has also been found to promote the synthesis of key biomolecules, and salty brines could have played a role in the polymerisation of amino acids and other important biopolymers.

Energy Sources

The localised release of reduced gases by volcanic eruptions would lead to an eruption column, a feature which typically produces intense lightning. This could represent one source of prebiotic reagents, which could wash out of the atmosphere and become involved in the synthesis of organic molecules. Another likely energy source (one implicated in the origin of interstellar organics) is UV light from the sun. Wavelengths of <200nm can dissociate H_2O (below) and CH_3 to radicals, and initiate synthesis of larger molecules.



Abiogenesis: Prebiotic Soup

This cold and oceanic hypothesis for abiogenesis requires the accumulation of organic compounds in primordial oceans, from home-grown chemical synthesis reactions on Earth, and in-fall of organic rich material from space. Further reactions would lead to increasing complexity of the molecules present. Some of these reactions could take place at the interfaces of mineral deposits with primitive ocean water, and others through concentration, as mentioned above. Eventually polymerisation could have occurred, to form oligomers (=compound of limited number of monomers). These would become more varied, and some could acquire functions by chance, such as the ability to catalyse other reactions. As increasingly complex macro-molecules form, some could become capable of catalysing self-replication. Initially these would have represented only a tiny fraction of the large array of macromolecules; but because they could catalyse their own replication, they would become increasingly abundant. This would mark the transition from purely abiotic chemistry to primitive biochemistry, starting an evolutionary cascade culminating in the RNA, and then eventually, DNA world.

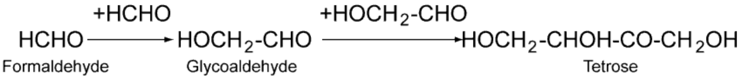
Abiogenesis: Metabolist

In contrast to the prebiotic soup model, the metabolist hypothesis suggests a hot and volcanic origin. It posits a primitive type of ‘metabolic life’ characterised by a continuous chain of sulphide-mineral catalysed self-sustaining chemical reactions. This was based on organic monomeric compounds, created directly from simple constituents such as CO_2, and CO in the vicinity of mineral-rich hydrothermal systems. The vital difference here is that the first ‘life’ did not have need for informational molecules. A system of self-sustaining reactions would have evolved in complexity, and eventually this would require genetic molecules to be incorporated in order for this ‘metabolic life’ to develop into modern biochemistry. While details of this ‘genetic takeover’ are lacking, recently it has been suggested that an elaborate cascade of metabolic reactions entrained within sulphide minerals around hydrothermal vents developed all the way to RNA molecules and even primitive cells.

It is worthy of note that self-sustaining reaction chains could have played an important role in enriching the prebiotic soup in molecules either more difficult to synthesise by other abiotic reactions, or unstable, and thus requiring continual synthesis in order to be available for subsequent reactions. In this respect, the prebiotic soup and metabolist theories are synergistic and complementary.

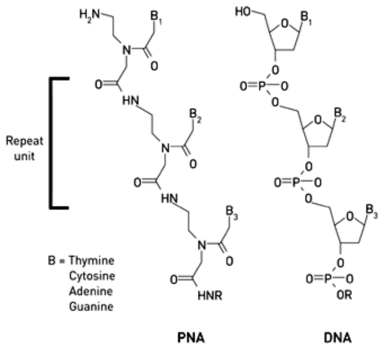
Precursors to RNA

It is quite possible that there were precursor ‘worlds’ which evolved into the RNA world. Following one of the above schemes, polymerised molecules would have been created, and these would increase in length and complexity. Eventually they would begin to fold into configurations that could bind and interact with other molecules. Life requires replication, and thus the survival of the ‘living’ molecules long enough to ensure replication. RNA is complex, unlikely to be a product of just the models above: a simpler self-replicator is far more likely. Prebiotic soup theories require the first molecular self-replicating living entities to have the capacity to store information (and were thus probably nucleic acid based), but the nucleobases and the backbone of the molecules were not necessarily the same as those in modern RNA and DNA. There are two widely discussed possibilities. Peptide nucleic acid (PNA) would require a backbone of linked amino-acid derivatives (diagram at top of page 5). This would be a good choice because the backbone is achiral (lacking handedness), eliminating the need for selecting chirality before the origin of life. All components are produced easily under simulated prebiotic conditions, but the PNA molecule is not as stable as the ideal precursor to RNA would be.



$$\underset{\text{Formaldehyde}}{HCHO} \xrightarrow{+HCHO} \underset{\text{Glycoaldehyde}}{HOCH_2\text{-}CHO} \xrightarrow{+HOCH_2\text{-}CHO} \underset{\text{Tetrose}}{HOCH_2\text{-}CHOH\text{-}CO\text{-}CH_2OH}$$

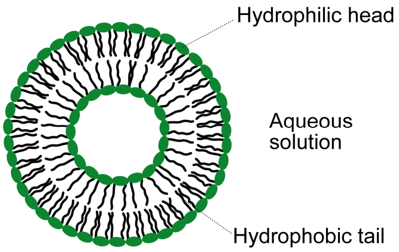
The other possibility is threose nucleic acid (TNA), where the backbone is made up of L-threose. This has good base-pairing attributes, and it is easy to explain its origin, as the tetrose precursor readily forms through the above reaction. This would require early selection of chirality.



Both, however, lack any demonstrated process of formation under prebiotic conditions, and neither have been shown to have catalytic properties. It is also possible that, for example, PNA preceded TNA.

RNA world

RNA is an all-in-one molecule – it stores information and catalyses reactions. Experiments show that RNA molecules can act as catalysts (ribozymes), and have the capacity to carry out a wide range of important biochemical reactions. It is likely that by the time RNA-based life appeared on Earth, the supply of simple abiotic organic compounds had greatly diminished, and thus the raw materials needed to sustain primitive life were exhausted. Hence, the first simple metabolic-like pathways must have arisen at this point, to supply the components needed to sustain primitive life. RNA could have been encapsulated in fatty acid vesicles:



Due to the properties of fatty acids (hydrophilic head and hydrophobic tail), these can spontaneously form, grow, and divide, all of which have been demonstrated experimentally. They can further retain a portion of their contents - an attribute necessary to support RNA replication. This is the currently accepted origin of cell membranes.

It is thought that during this period protein synthesis and the encapsulation of reaction machinery needed for replication may have taken place; four of the basic reactions involved in protein biosynthesis are catalysed by ribozymes.

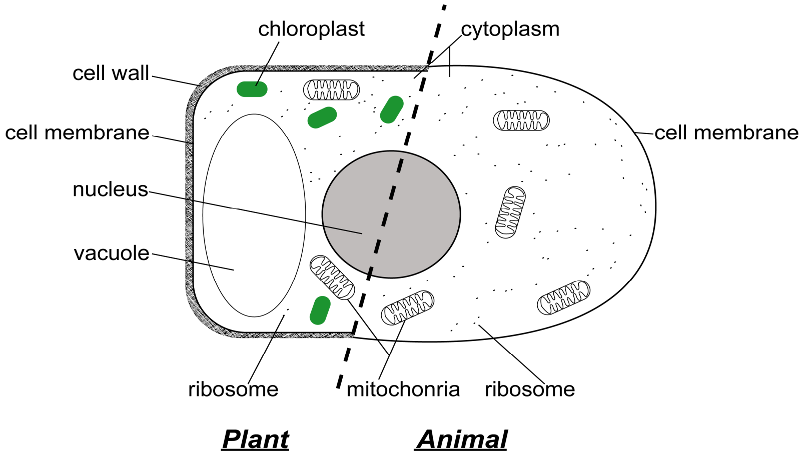
Prokaryotes (DNA/Protein world)

RNA is still relatively unstable compared to DNA. Ribozymes could have arisen to catalyse the polymerisation of DNA during this period, and RNA-stored information could have been transferred to DNA. The resulting increased stability would allow longer oligomers to develop, enhancing the storage capacity of genetic material. The discovery of deoxyribozymes (DNA molecules with catalytic action; associated only with gene replication) suggests that some DNA inherited catalytic abilities from ancestors in RNA world, strengthening the hypothesis that RNA preceded DNA as a genetic molecule. RNA was then demoted to a messenger and transcriber of DNA.

It is early in this period that life’s last universal common ancestor (LUCA) was alive. Recent opinion has been divided on whether this was a specialist, living in high temperature environments – an idea which came about because the tree of life seems to be rooted in hyperthermophillic organisms. While this could be the case, there is little conclusive proof, and several problems with the idea exist. First, there is little scientific consensus on whether the tree of life is truly rooted in hyperthermophillic bacteria. It is likely that lateral gene transfer of thermoadaptive traits has compromised the genetic record of modern organisms, making assumptions about where DNA originated questionable. Further, it is thought that hyperthermophillic organisms possess a single specific 'high temperature' enzyme; the rest are heat-adapted versions of those found in other organisms. Even if LUCA was such an organism, it does not mean that the origin of life lies in such an environment; hyperthermophilly could be an evolutionary relic from early Archaen high temperature regimes associated with bolide impacts during the late heavy bombardment, and LUCA could be a survivor from this event. The origin of DNA-based life could predate this.

Milestones: Origin of Eukaryotes

Eukaryotes differ from prokaryotes in a number of ways, described on page 1. The most notable of these is that they possess membrane-bound organelles, which have their own DNA:



It is thought that such structures are endosymbiotic in origin: they come from the long-term symbiosis of prokaryotes. The earliest such structure – and also that with the most uncertain origin – is the nucleus, which could be the result of a symbiotic relationship between archaea similar to modern methanogenic archaea or sulfidogens, and a bacterium. The former could have eventually formed the early nucleus. Other theories include an autogenous origin (i.e. the nucleus evolved without the need for endosymbiosis) based on extant bacteria that possess more complex internal structures, including nuclear material within a membrane. This hypothesis is supported by the chemical similarity between the nuclear membrane and other internal eukaryotic membranes. Another possible but controversial model suggests that the nucleus results from the infection of a prokaryote by a virus. Whatever the origin of the nucleus, at this stage eukaryotes are likely to have developed swimming motility and mitosis.

The story for mitochondria and plastids (e.g. chloroplasts) is much less ambiguous. Mitochondria post-date the formation of the nucleus, based on eukaryotic Archaeoprotists which (primitively) have a nucleus, but no mitochondria. Mitochondria probably represent endosymbiotic proteobacteria which could respire aerobically within an anaerobic fermentor with a flexible surface (i.e. no cell wall). The symbionts would have utilised some of the end products of fermentation (e.g. lactate) while the host passed proteins back to the mitochondria. With time the symbionts would rely on each other totally, and mitochondria would lose their cell wall, and transfer some of their genetic material to the host.

Plastids are the last major endosymbiosis, have evolved numerous times in the history of life. Plastids, such as chloroplasts, are more independent of their host than mitochondria, and often resemble cyanobacteria. A symbiosis could rely upon carbon compounds supplied by the cyanobacteria, and mineral nutrients supplied by the host. Such symbiosis is seen in modern eukaryotes, which can contain smaller eukaryotes such as algae to supplement or replace their food supply.

The oldest unequivocal eukaryotes date from 1.5 Ga, while possible algae fossils have been found in 2.1 Ga rocks. Geochemical evidence based on the composition of bitumen, which contains membrane lipids found only in Eukaryotes, suggests the presence of Eukaryotes at 1.7 Ga.

Milestones: Sexual Reproduction

This is most common in Eukaryotes, and requires diploidy (two sets of chromosomes) in at least one phase of life. Sexual reproduction has a two-fold cost: in asexual species any individual can bear young, while only half can in a sexual species, and sexual reproduction requires the males to find the females. Yet it is a common mode of reproduction, especially in animals and plants, and thus must improve the fitness of any progeny. Most notably, sex outcompetes asexuality when some factor kills a large proportion of populations, is sensitive to genetic variation, and changes rapidly between generations.

There are several explanations for what this factor could be. The Red Queen Hypothesis relies upon parasites and pathogens to explain the increased fitness of progeny. Parasites and pathogens co-evolve with their hosts, and as such change rapidly, even between generations. This can cause previously neutral or deleterious traits to become favourable, and sexual reproduction increases variation and speeds the dispersion of novel traits – this helps counteract the effect of pathogens. This is one of the most widely accepted explanations for the dominance of sexual reproduction. Another, also well supported, hypothesis relies on the fact that replication is often imperfect. Sex can result in the combination of beneficial mutations within an individual, increasing the fitness, and it can similarly lead to the removal of deleterious genes by reducing fitness when these are combined in an individual. Deleterious mutations are often recessive, and thus sexual reproduction can minimise their expression when individuals inherit only one such mutation.

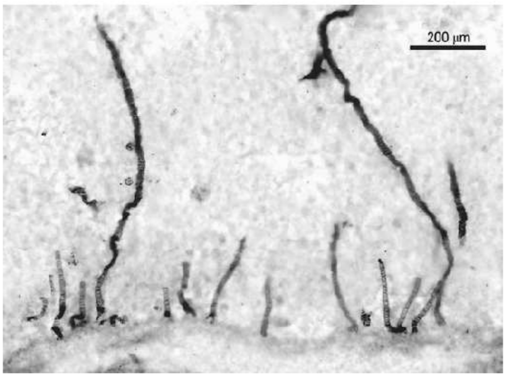
It is often suggested that sexual reproduction dates back to the origin of Eukaryotes, while an evolutionary radiation at 1.2 Ga could also be a result of the advent of sexual reproduction.

Milestones: Multicellularity

There are more than twenty independent instances of multicellularity in the living world - for example, plants, fungi, and animals evolved multicellularity separately. It is clearly beneficial, allowing asymmetric cell division, and thus intraorganismal divisions of labour, and increased specialisation. The morphological disparity possible with multicellularity allows for greater complexity in mode of life, ontogeny, and evolution. All but the simplest multicellular creatures have a single-celled stage in their life cycle, such as the egg – this genetic bottleneck helps weed out deleterious mutations and allows the aforementioned differentiation of cell lines and associated varied morphology.

There are three principle theories as to how multicellularity may have evolved. The first relies upon symbiosis; this would mean cooperation between different species of single celled organisms, each taking a different role in the multicellular organism. It would require the incorporation of the different species' genetic material into a single genome, for which there is no known mechanism, and in other examples of endosymbiosis (for example mitochondria) the organelles have retained some DNA, and replicate separately. The second theory, based upon the fact that some single-celled organisms have more than one nucleus, suggests that a unicellular forerunner could develop internal membranes around separate nuclei, leading to the evolution of a multicellular organism. Many consider this unlikely because no mechanism is known by which this could occur, and in cases where organisms have multiple nuclei they typically perform different roles. The third hypothesis relies upon the symbiosis of organisms of the same species (not different species, as in the symbiotic theory) to create colonies with different individuals having specialised roles. This has been seen to occur numerous times in the living world, to the extent that the boundary between colonial organisms and a multicellular entity is a diffuse one. As such this is the most widely accepted theory for the origin of multicellularity.

The first convincing evidence of multicellularity in the fossil record dates from ~1.7 Ga, with the first reliable cellular differentiation placed at ~1.2 Ga (the red algae, *Bangiomorpha pubescens,* below):



Other Milestones

Other milestones in the history of life include the evolution of biomineralisation (hard parts), predation, terrestrialisation, and sociality. The most recent milestone could be considered consciousness, depending upon the anthropogenicity of one's world view.

Recommended reading. Relevant chapters in:
Evolution: The First Four Billion Years, Michael Ruse & Joseph Travis, ISBN: 067403175X
Evolution: A Biological and Palaeontological Approach, Peter Skelton, ISBN: 0201544237

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