Chapter 2: Life's diversity and origins

In which we consider what biology is all about, namely organisms and their diversity. We discover that organisms are built of one or more, sometimes many cells. We consider the origins of organisms, their basic properties, and their relationships to one another.

Biology is the science of organisms, how they function, behave, interact, and, as populations, have and can evolve. As we will see, organisms are discrete, highly organized, bounded but open, non-equilibrium, physicochemical systems. Now that is a lot of words, so the question is what do they mean? How is a rock different from a mushroom that looks like a rock? What exactly, for example, is a bounded, non-equilibrium system? The answer is not simple, it assumes a knowledge of thermodynamics, a topic that we will address more directly in Chapter 5. For the moment, when we talk about a non-equilibrium system, we mean a system that can do various forms of work. Of course that means we have to define what we mean by work. For simplicity, we will start by defining work as something that takes the input of energy. In the context of biological systems, work involves generating and maintaining molecular gradients, driving unfavorable, that is energy-requiring, reactions, such as the synthesis of various biomolecules including nucleic acids, proteins, lipids, and carbohydrates required for growth and reproduction, and the generation of movement, and so on. Much of this involves the concept of energy, which is itself quite abstract and difficult to master. For our purposes, we will focus on what is known as free energy, which is what enables things to happen. When a system is at equilibrium its free energy is 0, which means that there are no macroscopic (visible) or net changes occurring. The system is essentially static, even though at the molecular level there are still movements due to the presence of heat. Organisms maintain their non-equilibrium state (their free energy is much greater than zero) by importing energy in various forms form the external world. They are different from other such systems in that they contain a genetic (heritable) component. For example, while non-equilibrium systems occur in nature – hurricanes and tornados are non-equilibrium systems – they differ from organisms in that they are transient. They arise *de novo* and when they dissipate they leave no offspring. In contrast, each organism alive today arose from one or more pre-existing organisms (its parent) and each organism, with some special exceptions, has the ability to produce offspring. As we see, the available evidence indicates that each and every organism, past, present, and future, has (or will have) an uninterrupted history stretching back billions of years. This is a remarkable conclusion, given the obvious fragility of life.

Biology has only a few over arching theories. One of these, the Cell Theory of Life, explains the historic continuity of organisms, while the Theory of Evolution by Natural Selection (and other processes), explains how populations of organisms have changed over time. Finally, the Physicochemical Theory of Life explains how it is that organisms can display their remarkable properties without violating the laws that govern physical and chemical systems.

What is life, exactly?

Clearly, if we are going to talk about biology, and organisms and cells and such, we have to define exactly what we mean by life. This raises a problem peculiar to biology as a science. We cannot define life generically because we know of only one type of life. We do not know whether this type of life is the only type of life possible or whether radically different forms of life exist elsewhere in the universe or even on Earth, in as yet to be recognized forms.

While you might think that we know of many different types of life, from mushrooms to whales, from humans to the bacterial communities growing on the surfaces of our teeth (that is what dental plaque is, after all), we will see that the closer we look the more these different "types of life" are in fact simply versions of a common underlying motif, they are one type of life. Based on their common chemistry, molecular composition, cellular structure, and the way that they encode hereditary information in the form of molecules of deoxyribonucleic acid (DNA), all topics we will consider in depth later on, there is little reasonable doubt that all organisms are related, that is they are descended from a common ancestor.

We cannot currently answer the question of whether the origin of life is a simple, likely, and predictable event given the conditions that existed on the Earth when life first arose, or whether it is an extremely rare and unlikely event. In the absence of empirical data, one can question whether scientists are acting scientifically or more as lobbyists for their own pet projects when they talk about doing astrobiology or speculating on when we will discover alien life forms.[20] That said, asking seemingly silly questions, provided that empirically-based answers can be generated, has often been the critical driver of scientific progress. Consider, for example, current searches for life on Earth, almost all of which are based on what we already know about life. Specifically, the methods used rely on the fact that all known organisms use DNA to encode their genetic information; they would not recognize types of life that are dramatically different. In particular, they would not detect organisms that used a different method (not DNA) to encode genetic information. But if we could generate, de novo, living systems in the laboratory we would have a better understanding of what functions are necessary for life and how to look for such "non-standard" organisms in new ways. It might even lead to the discovery of alternative forms of life right here on Earth, assuming they exist.[21] That said, until someone manages to create or identify such non-standard forms of life, it seems quite reasonable to concentrate on the characteristics of life as we know them.

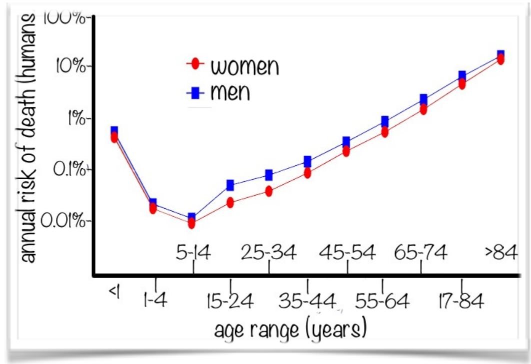
So, let us start again in trying to produce a good definition, or given the fact that we know only of one version of life, a useful description of what we mean by life. First, the core units of life are organisms, which are individual living objects. From a structural and thermodynamic perspective, each organism is a bounded, non-equilibrium system that persists over time and, from a practical point of view, can produce one or more copies of itself. Even though organisms are composed of one or more cells, it is the organism that is the basic unit of life. It is the organism that reproduces new organisms.[22]

[20] The possibility of alternative microbial life on Earth: http://www.ncbi.nlm.nih.gov/pubmed/18053938

[21] Signatures of a shadow biosphere: http://www.ncbi.nlm.nih.gov/pubmed/19292603

[22] In Chapter 4, we will consider how multicellular and social organisms come to be.

Why the requirement for and emphasis on reproduction? This is basically a pragmatic criterion. Assume that a non-reproducing form of life was possible. A system that could not reproduce runs the risk of death (or perhaps better put, dissolution) by accident. Over time, the probability of death for a single individual will approach one, that is certainty.[23] In contrast, a system that can reproduce makes multiple copies of itself and so minimizes, although by no means eliminates, the chance of accidental extinction (the death of all descendants). We see the value of this strategy when we consider the history of life. Even though there have been a number of mass extinction events over the course of life's history, organisms descended from a single common ancestor that appeared billions of years ago continue to survive and flourish.



So what does the open nature of biological systems mean? Basically, organisms are able to import, in a controlled manner, energy and matter from outside themselves, to export waste products into their environment.[24] This implies that there is a distinct boundary between the organism and the rest of the world. All organisms have such a barrier (boundary) layer, as we will see, and the basic barrier appears to be a homologous structure of organisms - that is, it was present in and inherited from the common ancestor. What is important about this barrier is that it is selective, it allows the capture or entry of energy and matter. As we will see, the importation of energy, specifically energy that can be used to drive various cellular processes, is what enables the organism to maintain its non-equilibrium nature and its dynamic structure. The boundary must be able to retain the valuable structures generated, while at the same time allow waste products to leave. This ability to import matter and export waste enables the organism to grow and to reproduce. We assume that you have at least a basic understanding of the laws of thermodynamics, but we will review the basic ideas captured in these laws later, in Chapter 5.

We see evidence of the non-equilibrium nature of organisms most obviously in the ability of organisms to move, but it is important for all aspects of the living state. In particular, organisms use energy, captured from their environment, to drive various chemical reactions and mechanical processes that by themselves are thermodynamically unfavorable. To do this, they use networks of thermodynamically favorable reactions coupled to thermodynamically unfavorable reactions. An organism that reaches thermodynamic or chemical equilibrium is dead.

There are examples of non-living, non-equilibrium systems that can "self-organize" or appear de novo. Hurricanes and tornados form spontaneously and then disperse. They use energy from their environment, which is then dispersed back into their environment (a process associated with increased entropy). They differ from organisms in that they cannot produce offspring - they are the result of specific atmospheric conditions. They are individual entities, unrelated to one another, which do not and cannot evolve. Tornados and hurricanes that formed billions or millions of years ago would (if we could

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[23] image modified from "risk of death" graph: http://www.medicine.ox.ac.uk/bandolier/booth/Risk/dyingage.html

[24] In fact, this is how they manage to organize themselves, by exporting entropy. So be careful when people (or companies) claim to have a zero-waste policy, which is an impossibility according to the laws of thermodynamics that all systems obey.

observe them) be similar to those that form today. Since we understand (more or less) the conditions that produce them, we can predict fairly reliably the conditions that will lead to their formation and how they will behave once they form. In contrast, organisms present in the past were different from those that are alive today. The further in the past we go, the more different they appear. Some ancient organisms became extinct, some gave rise to the ancestors of current organisms. In contrast, all tornados and hurricanes originate anew, they are not derived from parental storms.

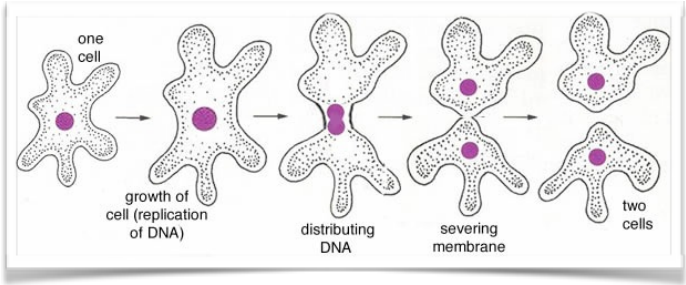
Question to answer and ponder:

- Using the graph on risk of death as a function of age in humans, provide a plausible model for the shape of the graph.
- Why are the points connected? Wouldn't it make more sense to draw a smooth line between them? which better captures the reality of the situation?
- Extrapolate when the probability of death reaches 1 and explain why it is never 0.
- What factors would influence the shape of the curve? How might the curve differ for different types of organisms?
- Make a model of what properties a biological boundary layer needs to possess. Using your current knowledge, how would you build such a boundary layer?

The cell theory and the continuity of life

Observations using microscopes revealed that all organisms examined contained structurally similar "cells." Based on such observations, a rather sweeping conclusion were drawn by naturalists toward the end of the 1800's. Known as the Cell Theory, it has two parts. The first is that every organism is composed of one or more cells (in some cases billions of cells) and non-cellular products produced by cells, such as bone, hair, scales, and slime. The cells that the Cell Theory deals with are defined as bounded, open, non-equilibrium physicochemical systems (a definition very much like that for life itself). The second is that cells arise only from pre-existing cells. The implication is that organisms (and the cells that they are composed of) arise in this way and no other way. We now know (and will consider in great detail as we proceed) that in addition to their basic non-equilibrium nature, cells also contain a unique material that encodes hereditary information in a physical and relatively stable form, namely molecules of double-stranded deoxyribonucleic acid (DNA). Based on a wide range of data, the Cell Theory implies that all organisms currently in existence (and the cells from which they are composed) are related through an unbroken series of cell division events that stretch back in time. Other studies, based on comparing the information present in DNA molecules, as well as careful comparisons of how cells are constructed, at the molecular level, suggests that there was a single common ancestor that lived between 3.5 to 3.8 billion years ago. This is a remarkable conclusion, given the (apparent) fragility of life - it implies that each cell in your body has a multibillion year old history. What the cell theory does not address is the processes that lead to the origin of the first organisms (cells).

The earliest events in the origin of life, that is, exactly how the first cells originated and what they looked like are unknown, although there is plenty of speculation to go around. Our confusion arises in large measure from the fact that the available evidence indicates that all organisms that have ever lived on Earth share a single common ancestor, and that that ancestor, likely to be a singled-cell organism, was already quite complex. We will discuss how we came to these conclusions, and their implications, later on in this chapter. One rather weird point to keep in mind is that the "birth" of a new cell involves a continuous process by which one cell becomes two. Each cell is defined, in part, by the presence of a distinct surface barrier, known as the cell or plasma membrane. The new cell is formed when that original membrane pinches off to form two distinct cells (FIG→). The important point is that there is no discontinuity, the new cell does not "spring into life" but rather emerges from the preexisting cell. This continuity of cell from cell extends back in time back billions of years. We often define the start of a new life with the completion of cell division, or in the case of humans and other sexually reproducing multicellular organisms, a fusion event, specifically the merger of an egg cell and a sperm cell. But again there is no discontinuity, both egg cell and sperm cell are derived from other cells and when they fuse, the result is also a cell. In the modern world, all cells, and the organisms they form, emerge from preexisting cells and inherit from those cells both their cellular structure, the basis for the non-equilibrium living system, and their genetic material, their DNA. When we talk about cell or organismic structures, we are in fact talking about information, stored in the structure, information that is lost if the cell/organism dies. The information stored in DNA molecules (known as an organism's genotype) is more stable, it can survive the death of the organism, at least for a while. In fact, information-containing DNA molecules can move between unrelated cells or from the environment into a cell, a process known as horizontal gene transfer (which we will consider in detail toward the end of the book).



The organization of organisms

Some organisms consist of a single cell, others are composed of many cells, often many distinct types of cells. These cells vary in a number of ways and can be extremely specialized (particularly within the context of multicellular organisms), yet they are all clearly related to one another, sharing many molecular and structural details. So why do we consider the organism rather than the cell to be the basic unit of life? The distinction may seem trivial or arbitrary, but it is not. It is a matter of reality versus abstractions. It is organisms, whether single or multicellular, that produce new organisms. As we will discuss in detail when we consider the origins of multicellular organisms, a cell within a multicellular organism normally can neither survive outside the organism nor produce a new organism - it depends upon cooperation with the other cells of the organism to reproduce. In fact, each multicellular organism is an example of a cooperative, highly integrated social system. The cells of a typical multicellular organism are part of a social system in which most cells have given up their ability to reproduce a new organism; their future depends upon the reproductive success of the organism of which they are a part. It is the organism's success in generating new organisms that underlie evolution's selective mechanisms. Within the organism, the cells that give rise to the next generation of organism are known as germ cells, those that do not (and die with the organism) are known as somatic cells.[25] All organisms in the modern world, and for apparently the last ~3.5 billion years, arise from a pre-existing organism or,

[25] If we use words that we do not define and that you do not understand, look them up!

in the case of sexually reproducing organisms, from the cooperation of two organisms, another example of social evolution which we will consider in greater detail in Chapter 4. We will also see that breakdowns in such social systems can lead to the death of the organism or disruption of the social system. Cancer is the most obvious example of an anti-social and evolutionarily short-sighted behavior of cells within a multicellular organism.

Spontaneous generation and the origin of life

The ubiquity of organisms raises obvious questions: how did life start and what led to all these different types of organisms? At one point, people believed that these two questions had a single answer, but we now recognize that they are really two quite distinct questions and their answers involve distinct mechanisms. An early commonly held view (by those who thought about such things) was that supernatural processes produced life in general and human beings in particular. The articulation of the Cell Theory and the Theory of Evolution by Natural Selection, which we will discuss in detail in the next chapter, concluded quite persuasively that life had a single successful origin and that various natural evolutionary processes generated the diversity of life.

But how did life itself originate? It used to be widely accepted that various types of organisms, such as flies, frogs, and even mice, could arise spontaneously, from non-living matter.[26] Flies, for example, were thought to appear from rotting flesh and mice from wheat. If true, on-going spontaneous generation would have profound implications for our understanding of biological systems. For example, if spontaneous generation based on natural processes was common, there must be a rather simple process at work, a process that (presumably) can produce remarkably complex outcomes (all bets are off if the process is supernatural). Also, if each organism arose independently, we might expect that the molecular level details of each would be unique, since it presumably arose independently from different stuff and under different conditions compared to other organisms of the same type. However, we know this is not the case, since all organisms are clearly related and can be traced back to a single ancestor (a conclusion to which we return, repeatedly.)

A key event in the conceptual development of modern biology was the publication of Francesco Redi's (1626 –1697) paper entitled "Experiments on the Generation of Insects" in 1668. He hypothesized that spontaneous generation did not occur. His hypothesis was that the organisms that appeared had developed from "seeds" deposited by adults. His hypothesis led to a number of clear predictions. One was that if adult flies were kept away from rotting meat, for example, maggots (the larval form of flies) would never appear no matter how long one waited. Similarly, the type of organism that appeared would depend not on the type of rotting meat, but rather on the type of adult fly that had access to the meat. To test his hypothesis Redi set up two sets of flasks - both contained meat. One set of flasks were exposed directly to the air and so to flies, the other was sealed with paper or

He who experiments increases knowledge. He who merely speculates piles error upon error.
- Arabic epigraph quoted by Francisco Redi.

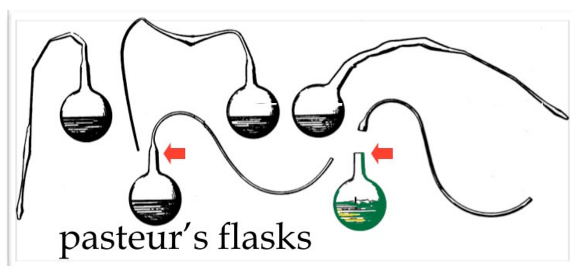
[26]Farley, J., The spontaneous generation controversy (1700-1860): The origin of parasitic worms. J. Hist. Biol., 1972. **5**: 95-125 (http://link.springer.com/article/10.1007%2FBF02113487) and The spontaneous generation controversy (1859-1880): British and German reactions to the problem of abiogenesis. J. Hist. Biol., 1972. 5: 285-319 (http://www.jstor.org/stable/4330578)

cloth. Maggots appeared only in the flasks open to the air. Redi concluded that organisms as complex as insects (and too large to pass through the cloth) could arise only from other insects, or rather eggs laid by those insects – that life was continuous.

The invention of the light microscope and its use to look at biological materials by Antony van Leeuwenhoek (1632-1723) and Robert Hooke (1635-1703) led to the discovery of a completely new and totally unexpected world of microbes or microscopic organisms. We now know these as the bacteria, archaea, protozoa, unicellular algae, and microscopic fungi, such as yeasts. Although it was relatively easy to generate compelling evidence that macroscopic (that is, big) organisms, such as flies, mice, and people could not arise spontaneously, it seemed plausible that microscopic and presumably much simpler organisms could form spontaneously.

The discovery of microbes led a number of scientists to explore their origin and reproduction. Lazzaro Spallazani (1729-1799) showed that after a broth was boiled it remained sterile (that is, without life) as long as it was isolated from contact with fresh air. He concluded that microbes, like larger organisms, could not arise spontaneously but were descended from other microbes, many of which were floating in the air. Think about possible criticisms to this experiment – perhaps you can come up with ones that we do not mention!

One criticism was that it could be that boiling the broth destroyed one or more key components that were necessary for the spontaneous formation of life. Alternatively, perhaps fresh air was the "vital" ingredient. In either case, boiling and isolation would have produced an artifact that obscured rather than revealed the true process. In 1862 (note the late date, this was after Charles Darwin had published *On the Origin of Species* in 1859), Louis Pasteur (1822-1895) carried out a particularly convincing set of experiments to address both of these concerns. He sterilized broths by boiling them in special "swan-necked" flasks. What was unique about his experimental design was the shape of the flask neck; it allowed air but not airborne microorganisms to reach the broth. Microbes in the air were trapped in the bended region of the flask'a neck. This design enabled Pasteur to address a criticism of previous experiments, namely that access to air was necessary for spontaneous generation to occur. He found that the liquid, even with access to air, remained sterile for months. However, when the neck of the flask was broken the broth was quickly overrun with microbial growth. He interpreted this observation to indicate that air, by itself, was not necessary for spontaneous generation, but rather was normally contaminated by microbes. On the other hand, the fact that the broth could support microbial growth after the neck was broken indicated that the heating of the broth had not destroyed some vital element needed for spontaneous generation or standard growth to occur. In the language of modern scientific experimentation, breaking the flask served as a positive control – it showed that the boiled media could have supported spontaneous generation if such a process were possible. Of course, not all (in fact, probably not any) experiment is perfect. For example, how would one argue against the objection that the process of spontaneous generation normally takes tens to thousands of years to occur? If true, this would invalidate Pasteur's conclusion. Clearly an experiment to address that possibility has its own practical issues. Nevertheless, the results of various experiments on spontaneous generation led to the



conclusion that neither microscopic nor macroscopic organisms could arise spontaneously, at least not in the modern world. The problem, at least in this form, became uninteresting to working scientists.

Does this mean that the origin of life is a supernatural event? Not necessarily. Consider the fact that living systems are complex chemical reaction networks. In the modern world, there are many organisms around who are actively eating complex molecules to maintain their non-equilibrium state and to grow and reproduce. If life were to arise by a spontaneous but natural process, it is possible that it could take thousands to hundreds of millions of years to occur. We can put some limits on the maximum time it could take from geological data using the time when the Earth's surface solidified from its early molten state to the first fossil evidence for life (about 100 to 500 million years). Given the tendency of organisms to eat one another, one might argue (as did Darwin) that once organisms had appeared in a particular environment they would have suppress any subsequent spontaneous generation events - they would have eaten the molecules needed for the process. But, as we will see, evolutionary processes have led to the presence of organisms essentially everywhere on Earth that life can survive - there are basically no welcoming and sterile places left within the modern world. Here we see the importance of history. According to the current scientific view, life could arise *de novo* only in the absence of life; once life had arisen, the conditions had changed. The presence of life is expected to suppress the origin of new forms of life.

It is often said that all the conditions for the first production of living organisms are now present. But if (and oh! what a big if!) we could conceive in some warm little pond, with all sorts of ammonia and phosphoric salts, light, heat, electricity, etc. present, that a proteine compound was formed, ready to undergo still more complex changes, at the present day such matter would be instantly devoured or absorbed, which would not have been the case before living creatures were formed.
- Charles Darwin (1887).

The death of vitalism

Naturalists originally thought that life itself was a type of supernatural process, too complex to obey or be understood through the laws of chemistry and physics.[27] In this vitalistic view, organisms were thought to obey different laws from those acting in the non-living world. For example, it was assumed that molecules found only in living organisms, and therefore known as organic molecules, could not be synthesized outside of an organism; they had to be made by a living organism. In 1828, Friedrich Wöhler (1800 –1882) challenged this view by synthesizing urea in the laboratory. Urea is a simple organic molecule, $O{=}C(NH_2)_2$ found naturally in the waste derived from living organisms. Urine contains lots of urea. Wöhler's *in vitro* or "in glass" (as opposed to *in vivo* or in life) synthesis of urea was simple. In an attempt to synthesize ammonium cyanate (NH_4NCO), he mixed the inorganic compounds ammonium chloride (NH_4Cl) and silver cyanate ($AgNCO$). Analysis of the product of this reaction revealed the presence of urea. What actually happened was this reaction:

$$AgNCO + NH_4Cl \rightarrow NH_4NCO + AgCl \rightarrow O{=}C(NH_2)_2 + AgCl.$$

Please do not memorize the reaction, what is of importance here is to recognize that this is just another chemical reaction, not exactly what the reaction is.

[27] In a sense this is true since many physicists at least do not seem to understand biology.

While simple, the *in vitro* synthesis of urea had a profound impact on the way scientists viewed so called organic processes. It suggested that there was nothing supernatural involved in the synthesis of urea; it obeyed the laws of chemistry. Based on this and similar observations on the *in vitro* synthesis of other, more complex organic compounds, we (that is, scientists) are now comfortable with the idea that all molecules found within cells can, in theory at least, be synthesized outside of cells, using appropriate procedures. Organic chemistry has been transformed from the study of molecules found in organisms to the study of molecules containing carbon atoms, although a huge amount of time and effort is now devoted to the industrial synthesis of a broad range of organic molecules.

Questions to answer & to ponder:

- General a scheme that you could use to determine whether something was living or not.
- Why does the continuity of cytoplasm from generation to generation matter? What (exactly) is transferred?
- Why did the discovery of bacteria reopen the debate on spontaneous generation?
- How is the idea of vitalism similar to and different from intelligent design creationism?
- Is spontaneous generation unscientific? Explain your answer.

Thinking about life's origins

There are at least three possible approaches to the study of life's origins. A religious (i.e. non-scientific) approach would likely postulate that life was created by a supernatural being. Different religious traditions differ as to the details of this event, but since the process is supernatural it cannot, by definition, be studied scientifically. Nevertheless, intelligent design creationists often claim that we can identify those aspects of life that could not possibly have been produced by natural processes, by which they mean various evolutionary and molecular mechanisms, which we will discuss in the next chapter. It is important to consider whether these claims would, if true, force us to abandon a scientific approach to the world around us in general, and the origin and evolution of life in particular. Given the previously noted interconnectedness of the sciences, one might well ask whether a supernatural biology would not also call into question the validity of all scientific disciplines. For example the dating of fossils is based on geological and astrophysical (cosmological) evidence for the age of the Earth and the Universe, which themselves are based on physical and chemical observations and principles. A non-scientific biology would be incompatible with a scientific physics and chemistry. The lesson of history, however, is different. Predictions as to what is beyond the ability of science to explain have routinely been demonstrated by scientists to be wrong, often only a few years after such predictions were made!

Another type of explanation for the appearance of life on Earth, termed panspermia, assumes that advanced aliens brought (or left) life on Earth. Perhaps we owe our origins to casually discarded litter from these alien visitors. Unfortunately, the principles of general relativity, one of the best confirmed of all scientific theories, limit the speed of travel and given the size of the Universe, travelers from beyond the solar system seem unlikely, if not totally impossible. Moreover panspermia simply postpones but does not answer the question of how life began. Our alien visitors must have come from somewhere and panspermia does not explain where they came from. Given our current models for the history of the Universe and the Earth, understanding the origin of alien life is really no simpler than understanding the origin of life on Earth. On the other hand, if there is life on other planets and moons in our solar system, and we retrieve and analyze it, it would be extremely informative, particularly if it could be shown that it originated independently rather than being splashed from the Earth through various astronomical impact events.[28]

Experimental studies on the origins of life

One strategy to understanding how life might have arisen involves experiments to generate plausible precursors of living systems in the laboratory. The experimental studies carried out by Stanley Miller (1930-2007) and Harold Urey (1893-1981) were early and influential example of this approach.[29] These two scientists made an educated, although now apparently incorrect, guess as to the composition of Earth's early atmosphere. They assumed the presence of oceans and lightning. They set up an apparatus to mimic these conditions and then passed electrical sparks through their experimental atmosphere. After days they found that a complex mix of compounds had formed. Included in this mix were many of the amino acids found in modern organisms, as well as lots of other organic molecules. Similar experiments have been repeated with combinations of compounds more likely to represent the environment of early Earth, with similar results: various biologically important organic molecules accumulate rapidly.[30] Quite complex organic molecules have been detected in interstellar dust clouds, and certain types of meteorites have been found to contain complex organic molecules. During the period of the heavy bombardment of Earth, between about 4.1 and 3.9 billion years ago, meteorite impacts could have supplied substantial amounts of organic molecules.[31] It therefore appears likely that early Earth was rich in organic molecules, the building blocks of life.

Given that the potential building blocks were present, the question becomes what set of conditions were necessary and what steps led to the formation of the first living systems? Assuming that these early systems were relatively simple compared to modern organisms (or the common ancestor of life for that matter), we hypothesize that the earliest proto-biotic systems were molecular communities of chemical reactions isolated in some way from the rest of the outside" world. This isolation or selective boundary was necessary to keep the system from dissolving away or dissipating. One possible model is that such systems were originally tightly associated with the surface of specific minerals and that these mineral surfaces served as catalysts, speeding up important reactions (we will return to the role of catalysts in biological systems later on). Over time, these pre-living systems acquired more sophisticated boundary structures (membranes) and were able to exist free of the mineral surface, perhaps taking small pieces of the mineral with them.

The generation of an isolated but open system, which we might call a protocell was a critical step in the origin of life. Such an isolated system has important properties that are likely to have

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[28] Top 5 Bets for Extraterrestrial Life in the Solar System: http://www.wired.com/wiredscience/2009/01/et-life/

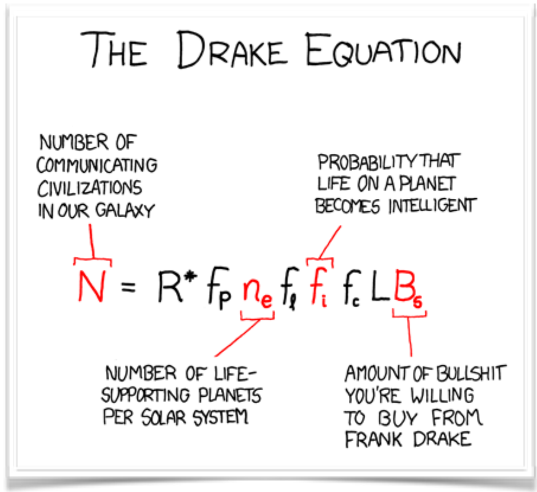
[29] The Miller-Urey experiment:http://www.ucsd.tv/miller-urey/ and http://en.wikipedia.org/wiki/Miller–Urey_experiment

[30] A reassessment of prebiotic organic synthesis in neutral planetary atmospheres: http://www.ncbi.nlm.nih.gov/pubmed/18204914

[31] A time-line of life's evolution: http://exploringorigins.org/timeline.html

facilitated the further development of life. For example, because of the membrane boundary, changes that occur within one such structure will not be shared with neighboring systems. Rather, they can accumulate and favor the survival of one system over its neighbors. Such systems can also reproduce in a crude way by fragmentation. If changes within one such system improved its stability, its ability to accumulate resources, or its ability to survive and reproduce, that system, and its progeny, would be likely to become more common. As these changes accumulate and are passed from parent to offspring, the organisms will inevitably evolve (as we will see in detail in the next chapter.)

Questions to answer & to ponder:



- If we assume that spontaneous generation occurred in the distant past, why is it not occurring today? How could you tell if it were?
- In 1961, Frank Drake, a radio astronomer, proposed an equation to estimate the number of technological civilizations that exist within the observable Universe (N).[32] The equation is $N = R^* \times f_p \times n_e \times f_l \times f_i \times f_c \times L$ where

R^*=The rate of formation of stars suitable for the development of intelligent life.
f_o = The fraction of those stars with planetary systems.
n_e = Tthe number planets, per solar system, with an environment suitable for life.
f_l = The fraction of suitable plants on which life actually appears.
fi = The fraction of life-bearing planets on which intelligent life emerges.
f_c = The fraction of civilization that develop a technology that releases detectable signs of their existence into space.
L = The length of time such civilizations release detectable signals into space.
Identify those parts of the Drake equation that can be established (at present) empirically and that cannot, and explain your reasoning.

Mapping the history of life on earth

Assuming that life arose spontaneously on early Earth, we can now look at what we know about the history of Earth and the fossil record to better understand the appearance and diversification of life. This is probably best done by starting with what we know about where the Universe and Earth came from. The current scientific model for the origin of the universe is known as the Big Bang. It arose from efforts to answer the question of whether the fuzzy nebulae identified by astronomers were located within or outside of our galaxy. This required some way to determine how far these nebula were from Earth. Edwin Hubble (1889-1953) and his co-workers were the first to realize that nebula were in fact galaxies in their own right, each very much like our own Milky Way and each composed of many billions of stars. This was a surprising result, since it made Earth, sitting on the edge of one among many, many galaxies seem less important. It is a change in cosmological perspective similar to that associated with the idea that the sun, rather than Earth, was the center of the solar system (and the Universe).

[32] The Drake equation: http://www.seti.org/drakeequation and cartoon: http://xkcd.com/384/

To measure the movement of galaxies with respect to Earth Hubble and colleagues used the Doppler shift, which is the effect on the wavelength of sound or light by an object's velocity relative to an observer. In the case of light emitted from an object moving toward the observer, the wavelength will be shortened, that is, shifted to the blue end of the spectrum. Light emitted from an object moving away from the observer will be lengthened, that is, shifted to the red end of the spectrum. Based on the observed Doppler shifts in the wavelengths of light coming from stars in galaxies and the observation that the further a galaxy appears to be from Earth, the greater that shift is toward the red, Hubble concluded that galaxies, outside of our local group, were all moving away from one another. Running time backward, he concluded that at one point in the past, all of the matter and energy in the universe must have been concentrated in a single point. A prediction of this Big Bang model is that the Universe is estimated to be ~13.8 +/- 0.2 billion (10^9) years old. This is a length of time well beyond human comprehension; it is sometimes referred to as deep time - you can get some perspective on deep time using the Here is Today website (http://hereistoday.com). Other types of data have been used to estimate the age of Earth and the other planets in the solar system as ~4.5 x 10^9 years.

After Earth first formed, a heavy bombardment of extraterrestrial materials, such as comets and asteroids, collided with it. This bombardment began to subside around 3.8 to 3.9 billion years ago and reached its current level by about 3.5 billion years ago.[33] It is not clear whether life arose multiple times and was repeatedly destroyed during the early history of Earth (4.5 to 3.6 billion years ago) or if the origin of life was a one-time event, taking hundreds of millions of years before it succeeded, which then managed to survive and expand around 3.8 to 3.5 billion years ago.

Fossils evidence for the history of life on earth

The earliest period in Earth's history is known as the Hadean, after Hades, the Greek god of the dead. The Hadean is defined as the period between the origin of Earth up to the first appearance of life. Fossils provide our only direct evidence for when life appeared on Earth. They are found in sedimentary rock, that is rock formed when fine particles of mud, sand, or dust entombed an organism before it can be eaten by other organisms. Hunters of fossils (paleontologists) do not search for fossils randomly but use geological information to identify outcroppings of sedimentary rocks of the specific age they are studying in order to direct their explorations.

Early in the history of geology, and before Darwin proposed the modern theory of evolution, geologists was recognized that fossils of specific types were associated with rocks of specific ages. This correlation was so robust that rocks could be accurately dated based on the types of fossils they contained without exception. At the same time, particularly in a world that contains young earth creationists who claim that Earth was formed less than 10,000 years ago, it is worth remembering both the interconnectedness of the sciences and that geologists do not rely solely on fossils to date rocks. This is in part because many types of rocks do not contain fossils. The non-fossil approach to dating rocks is based on the physics of isotopes and the chemistry of atomic interactions. It uses the radioactive decay of elements with isotopes with long half-lives, such as ^{235}Ur which decays into ^{207}Pb with a half-life of ~704 million years and ^{238}Ur which decays into ^{206}Pb with a half life of ~4.47 billion

[33] The violent environment of the origin of life:http://www.sciencedirect.com/science/article/pii/0016703793905436

years. Since these two Pb isotopes appear to be formed only through the decay of Ur, the ratios of Ur and Pb isotopes can be used to estimate the age of the rock.

To use isotope abundance to date rocks, it is critical that all of the atoms in a mineral measured stay there, that none wash in or away. Since Ur and Pb have different chemical properties, this can be a problem in some types of minerals. That said, with care, and using rocks that contain chemically inert minerals, like zircons, this method can be used to measure the age of rocks to an accuracy of within 1% or better. These and other types of evidence support James Hutton's (1726-1797) famous dictum that Earth is ancient, with "no vestige of a beginning, no prospect of an end."[34] We know now, however, that this statement is not accurate; while very very old, Earth coalesced around 5 billion years ago and will disappear when the sun expands and engulfs it in about 5.5 billion years from now.[35]

But, back to fossils. There are many types of fossils. Chemical fossils are molecules that, as far as we know, are naturally produced only through biological processes.[36] Their presence in ancient rock implies that living organisms were present at the time the rock formed. These first appear in rocks that are between 3.8 to 3.5 x 10^9 years old. What makes chemical fossils problematic is that there may be non-biological but currently undiscovered or unrecognized mechanisms that could have produced them, so we have to be cautious in our conclusions.

Moving from the molecular to the physical, are trace fossils. These can be subtle or obvious. Organisms can settle on mud or sand and make impressions. Burrowing and slithering animals make tunnels or disrupt surface layers. Leaves and immotile organisms can leave impressions. Walking animals can leave footprints in sand, mud, or ash. How does this occur? If the ground is covered, compressed, and converted to rock, these various types of impressions can become fossils. Later erosion can then reveal these fossils. For example, if you live near Morrison, Colorado, you can visit the rock outcrop known as Dinosaur Ridge and see trace fossil dinosaur footprints; there may be similar examples near where you live.

We can learn a lot from trace fossils, impressions can reveal the general shape of an organism or its ability to move or to move in a particular way. To move, it must have some kind of muscle or alternative mobility system and probably some kind of nervous system that can integrate information and produce coordinated movements. Movement also suggests that the organisms that made the trace had something like a head and a tail. Tunneling organisms are likely to have had a month to ingest sediment, much like today's earthworms - they were predators, eating the microbe they found in mud.

In addition to trace fossils, there are also the type of fossils that most people think about, which are known as structural fossils, namely the mineralized remains of the hard parts of organisms such as teeth, scales, shells, or bones. As organisms developed hard parts, fossilization, particularly of organisms living in environments where they could be buried within sediment before being dismembered and destroyed by predators or microbes, became more likely.

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[34] http://www.talkorigins.org/faqs/geohist.html

[35] http://www.youtube.com/watch?v=iauIP8swfBY

[36] Although as Wohler pointed out, they can be generated in the laboratory.

Unfortunately for us (as scientists), many and perhaps most types of organisms leave no trace when they die, in part because they live in places where fossilization is rare or impossible. Animals that live in wood lands, for example, rarely leave fossils. The absence of fossils for a particular type of organisms does not imply that these types of organisms do not have a long history; rather it means that the conditions where they lived and died or their body structure is not conducive to fossilization. Many types of living organisms have no fossil record at all, even though, as we will see, there is molecular evidence that they arose tens to hundreds of millions of years ago.

Life's impact on the earth

Based on fossil evidence, the current model for life on Earth is that for a period of ~2 x 10^9 (billion) years the only forms of life on Earth were microscopic. While the exact nature of these organisms remains unclear, it seems likely that they were closely related to prokaryotes, that is, bacteria and archaea. While the earliest organisms probably used chemical energy, relatively soon organisms appeared that could capture the energy in light and use it to drive various thermodynamically unfavorable reactions. A major class of such reactions involves combining CO_2 (carbon dioxide), H_2O (water), and other small molecules to form carbohydrates (sugars), and other important biological molecules such as lipids, proteins, and nucleic acids. At some point during the early history of life on Earth, organisms appeared that released molecular oxygen (O_2) as a waste product of such light-driven reactions, known generically as oxygenic photosynthesis. These oxygen-releasing organisms became so numerous that they began to change Earth’s surface chemistry - they represent the first life-driven ecological catastrophe.

The level of atmospheric O_2 represents a balance between its production, primarily by organisms carrying out oxygenic photosynthesis, and its removal through various chemical reactions. Early on as O_2 appeared, it reacted with iron to form deposits of water insoluble Fe (III) oxide - that is, rust. This rust reaction removed large amounts of O_2 from the atmosphere, keeping its levels low. The rusting of iron in the oceans is thought to be largely responsible for the massive banded iron deposits found around the world.[37] O_2 also reacts with organic matter, as in the burning of wood, so when large amounts of organic matter are buried before they can react, as occurs with the formation of coal, more O_2 accumulates in the atmosphere. Although it was probably being generated and released earlier, by ~2 billion years ago, atmospheric O_2 had appeared in detectable amounts, and by ~850 million years ago it had risen to significant levels. Atmospheric O_2 levels have changed significantly since then, based on the relative rates of its synthesis and destruction. Around 300 million years ago, atmospheric O_2 levels had reached ~35%, almost twice the current level. It has been suggested that it was these high levels of atmospheric O_2 that made possible the evolution of giant insects.[38]

Although we tend to think of O_2 as a natural and benign substance, it is in fact a highly reactive and potentially toxic compound and its appearance posed challenges and provided opportunities to

[37] Paleoecological Significance of the Banded Iron-Formation: http://econgeol.geoscienceworld.org/content/68/7/1135.abstract

[38] see Atmospheric oxygen, giant Paleozoic insects and the evolution of aerial locomotor performance: http://jeb.biologists.org/content/201/8/1043.full.pdf

many organisms. As we will see later on O_2 can be "detoxified" through reactions that lead to the formation of water and this type of reaction appears to have been co-opted for other purposes. For example, through coupled reactions O_2 can be used to capture the maximum amount of energy from food, leading to the generation of CO_2 and H_2O, both of which are very stable.

Around the time that O_2 levels were first rising, that is about 10^9 years ago, the first trace fossil burrows appear in the fossil record. These were likely to have been produced by simple worm-like, macroscopic multicellular organisms, known as metazoans, capable of moving along and through the mud on the ocean floor. About 0.6×10^9 years ago, new, more complex structural fossils begin to appear in the fossil record. Since the fossil record does not contain all types of organisms, we are left to speculate on what the earliest metazoans looked like. The first of these are the so-called Ediacaran organisms, named after the geological formation in which their fossils were first found.[39] Current hypotheses suggest they were immotile, like modern sponges but flatter and it remains unclear how they are related to later organisms. By the beginning of the Cambrian age ($\sim 545 \times 10^6$ years ago), a wide variety of organisms had appeared within the fossil record, many clearly related to modern organisms. Molecular level data suggest that their ancestors originated more than 30 million years earlier. These Cambrian organisms show a range of body types. Most significantly, many were armored. Since building armor involves expending energy to synthesize these components, the presence of armor suggests a need for armor, that is organisms gained something valuable from its presence. A plausible suggestion is that the appearance of armor was linked to the appearance of predators.

Viruses: Now, before we leave this chapter you might well ask, haven't we forgotten viruses? Well, no - viruses are often an important component of an ecosystem and an organism's susceptibility or resistance to viral infection is often an important evolutionary factor, but viruses are different from organisms in that they are non-metabolic. That means they do not carry out reactions and cannot replicate on their own, they can replicated only within a living cell. Basically they are not alive, so even though they are extremely important, we will discuss viruses only occasionally and in quite specific contexts.

Questions to answer & to ponder

- What factors would influence the probability that a particular organism, or type of organism, would be fossilized?
- What did Wöhler's synthesis of urea and the Miller/Urey experiment actually prove and what did they imply?
- Why can't we be sure about the stages that led to the origin of life?
- Can the origin of life be studied scientifically, and if so, how?
- What factors could drive the appearance of teeth, bones, shells, muscles, nervous systems, and eyes?
- What factors determine atmospheric O_2 levels?

[39] http://en.wikipedia.org/wiki/Ediacara_biota