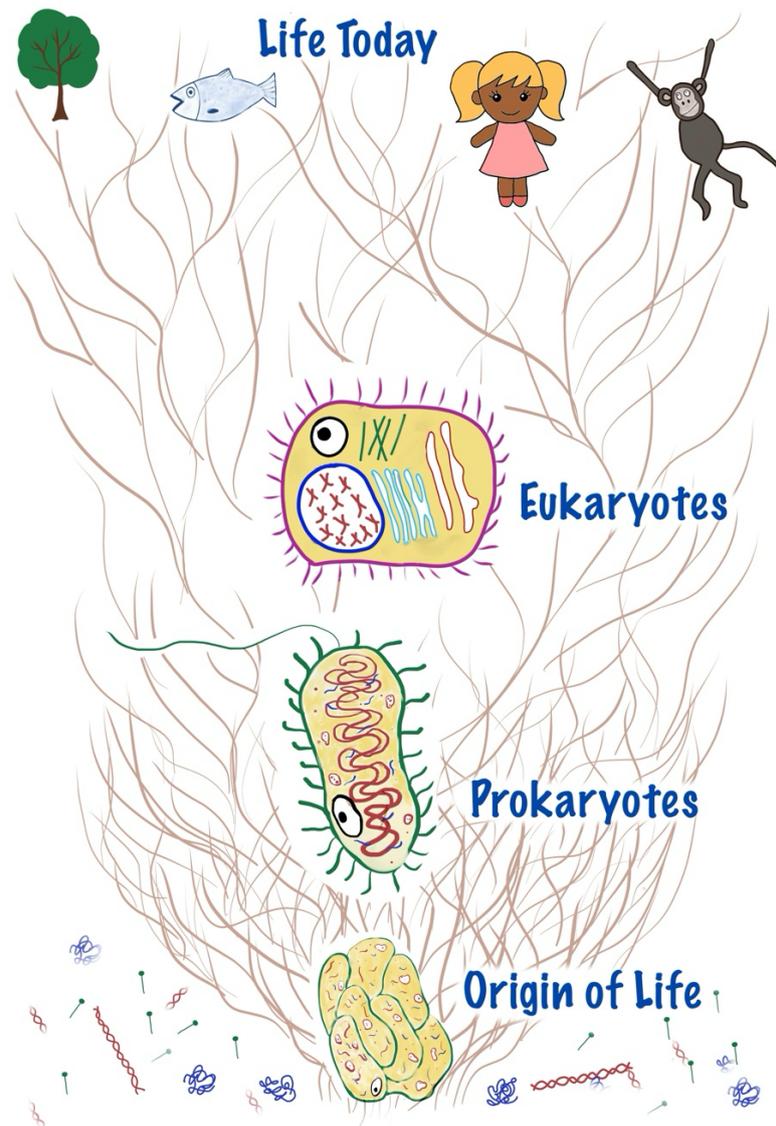


## The Microbial Origin of Life

*Mom: where do we come from?*



Cartoon image of the origin of life and evolution of life forms, courtesy of Joane C. Xavier

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## The Microbial Origin of Life

### Storyline

All life on Earth is part of a great, old story: for around 4 billion years of our planet's existence, we have been evolving together. Us, all animals we know, all plants, and all microorganisms: we are all leaves in the Great Tree of Life. When we draw our own family trees, we can look at a very minuscule portion of that great tree. How minuscule? The distance from us to our great-great grandparents (100 years) compared to the distance from us to the root of our tree (4 billion years), is as small as the thickness of a sheet of paper compared to the height of Mount Everest.

Since its origins, life has been spreading vertically – that is, through inheritance of key genetic information from parents to offspring at birth. Other information that shapes our behaviour and activities can be obtained after birth: elephants teach their youngsters routes to water, human societies depend on sharing culture and education. But even genes can be transmitted after birth! We call this process Lateral (or horizontal) Gene Transfer–LGT. Amongst microorganisms like bacteria, LGT is extremely prevalent, but LGT also happens between other life forms (including viruses and animals – look up information on the origins of the placenta!). Because of LGT (and how complex life is), the Great Evolutionary Tree looks more like a mycelium—a giant fungal network—and its history is very hard to decipher. The root of our Great Tree, or of our Great Mycelium, is one of the deepest mysteries for science today. Where does life come from in the first place??

Some things we do know, starting with: microorganisms were the first life forms; they are our great-great-great-great ancestors. The ancient evolution of microorganisms, near the root of the Great Tree, is much more mycelium-like because microorganisms do a lot of LGT. All microorganisms, just like us and all other life on this planet, use a group of very special molecules: DNA, RNA, protein, lipid, some carbohydrates, and some very special small molecules: cofactors (or vitamins), metals, and water. The story of the origin of life is the story of how these strange small molecules got together and started to share information, laterally, and vertically. So, who are the great-great ancestors of microorganisms?

### The Microbiology and Societal Context

*The microbiology:* the first microbes on Earth (origin and evolution of microbes); universal features of microbes; cooperation and emergence vs. competition and selection; the importance of the environment for microbes and their origin. *Sustainability issues:* bioproduction; bioremediation; climate change; food, water and energy.

### The Microbial Origin of Life: The Microbiology

**1. *Microbes were the first life forms on Earth.*** The details of how and where life arose on Earth are still a great mystery for science. It is important to transmit this message clearly to the wide public and students, not only to promote clarity and trust in science, but also to inspire a new generation to help in solving the problem. So, to re-emphasize, in 2024, as I write, we are still far from knowing exactly how life started. But there is a lot that we do know, and that is the starting point for our journey here.

We know that prokaryotes—the simplest microbes known, unicellular life forms with DNA free in the cytoplasm—were the first form of life populating our planet, at least 3.8 billion

## A learner-centric microbiology education framework

years ago. That is 3,800,000,000 years ago, an amount of time hard to picture, around 60 (!) times the time passed since the last dinosaurs walked on our planet. How do we know that microbes were the first life forms? There are three main sources of evidence to keep in mind:

a. geology, the study of rocks and soil. Two types of evidence are relevant here: *morphological* (microscopic fossil shapes preserved in ancient rocks, inferred to have been very ancient microbes), but most importantly, and generally accepted, *geochemical* evidence. In geochemistry, isotopic ratio determination is a very important method. It is based on the fact that atoms of the same element may contain different numbers of neutrons (see TF *How we use isotopes to study microbes and their activities*). Atoms with different numbers of neutrons have different weights and are called *isotopes*. Carbon, for example naturally exists in 3 isotopic forms:  $^{12}\text{C}$  (or C-12), the main one,  $^{13}\text{C}$  (or C-13) and  $^{14}\text{C}$  (or C-14). Determining the amount of different isotopes - isotopic ratios - in materials is relatively easy and precise. There are different processes that change isotopic ratios, but biological metabolism is a major one, because enzymes often prefer one isotope over another. For example, fossil fuel carbon deposits are the result of biomass accumulation, so are of biological origin and have more  $\text{C}^{12}$  than materials with carbon not of biological origin. Finding carbon isotope ratios typical of biological material in ancient rocks indicates a microbial presence and perhaps a role in their formation (though we need to keep in mind that some formations are unstable and, in some instances, microbes enter them after formation).

b. biology, with evolution telling us that we are all related in the great tree of life. At the bottom of the root of the great tree lie the first life forms, from which we and all other species evolved during the history of life on our planet. Scientists trace this connection using techniques like comparing genomes (the set of all genes in an organism) and using the information obtained to predict earlier forms of life that no longer exist. The results of these comparisons show us that we all have shared features inherited from common ancestors. Here, microbial ecology also plays a role, showing that ancient microbial communities were thriving on the planet as long as 3.48 billion years ago (see TF on Stromatolites).

c. (bio)chemistry, with the simple observation that we all share small chemicals that make up all cells on Earth. These include DNA, protein, lipids (or fats) that make up membranes, and even vitamins! Scientists use techniques like molecular analysis and experiments that identify these molecules and try to replicate early Earth conditions to investigate how they might have formed and been shared by the earliest life forms.

Of interest to learners of all ages may be three main stages of early evolution about which we are relatively certain (see cover image for a general illustration):

a. The origin of life itself. Very little is known about this process, neither the how, the where or the what. Often, we refer to entities at this stage as **protocells**. It is unknown if these were able to live separately or had to be together as in a **biofilm** (see below). The origin of life happened before *LUCA*, the Last Universal Common Ancestor, with multiple, much simpler molecular processes occurring in parallel.

b. *LUCA* is the life form with those features that are common to all life on Earth and its emergence is placed at around 3.8 billion years ago (see criteria b and c above). *LUCA* is the ancestor of prokaryotes (see image above). We know it existed because of evolution (there needs to be a root for the Great Tree), but also because of our shared biochemical characteristics (we all have DNA, protein, the same vitamins, etc.). For more information, see TF on *LUCA*.

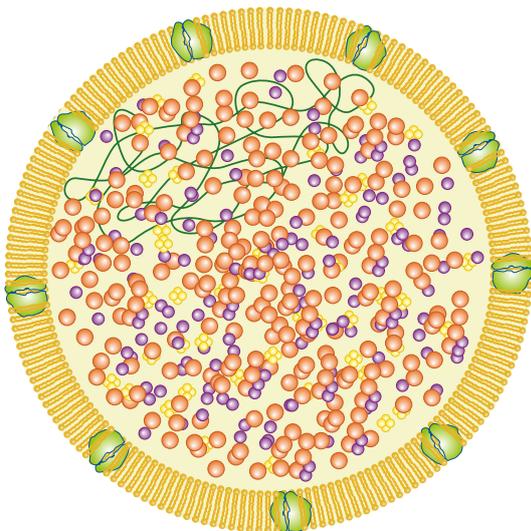
c. *LECA*, the last common ancestor of Eukaryotes, was made of cells like ours and those of plants. The details around the origin of Eukaryotes are still debated, but we know that this event involved a symbiosis (cooperation) between ancient bacteria and archaeal cells.

*2. Life, from microbes to us, uses the same very tiny components since its origins*

Prokaryotic cells arose at the beginning of the great tree of life, but they are still exquisitely complicated. How did they originate? How do we go about explaining the origins of life, also known as **abiogenesis**? There are two main ways to think about this question. In the first, we take the pieces of the cell apart – deconstruct/disassemble them – in an approach known as top-down or reductionism. When we do this, we can see that all cells (from prokaryotes to humans) have DNA and RNA (made of nucleobases), protein (made of amino acids), lipids (or fats) and other small molecules, including vitamins (for instance vitamins B1, B2 and B3 are essential not just for us – but for all life as we know it, including bacterial!).

In a top-down approach, we identify those individual components and study them separately, going deep into what each of them is capable of. In very superficial and simple terms, a short explanation follows. Proteins are responsible for copying DNA and RNA, joining together nucleotides; for making long lipids that build up the membrane, and for all the other important chemical transformations in the cell (these chemical transformations are called metabolism). Proteins that perform or accelerate these chemical transformations are called enzymes—enzymes are the workhorses of metabolism and thus of life. Vitamins and metals aid enzymes in these essential chemical transformations. DNA is the cell's memory, storing in its genes information to make more proteins. RNA is an intermediate between DNA and protein (there are different types of RNA with different functions – look up mRNA, tRNA and rRNA), and lipids make up the membrane and store energy. Very few portions of DNA are universally conserved, and especially amongst bacteria there is an exquisite variety of genes and proteins.

To go deeper into understanding how protocellular systems arose, we must think of how these molecules relate, and when we do that, we change our strategy to the second available approach: bottom-up (also known as synthetic). When using a synthetic approach, scientists put together/assemble some of those molecules in varying conditions and see what happens – this can be a vesicle (a fat bubble) that can grow and split into other vesicles; or an RNA molecule that is able, when provided with its building blocks, to build more of itself.



*A simple protocell. The lipids make-up the membrane (dark yellow bars). One type of protein appears nine times in the membrane (green). In the cytoplasm, multiple smaller proteins are shown in orange and purple, with smaller simpler molecules in yellow (circles and background). The DNA is represented as a green line spread on top of the cell. This is a hypothetical depiction for illustration and inspiration purposes – no fully-functioning protocell has been built in the lab from scratch; however we know that the ancestors of all life had protein, DNA, membranes and a cytoplasm with small molecules. Image courtesy of Joane C. Xavier*

The biggest difficulty in understanding the origins of life is this molecular complexity that makes up all cells, even the simplest ones (prokaryotes). For, to explain the origin of prokaryotes, we cannot just explain the origin of proteins, or just the origin of lipids, but of them together with the other essential molecules mentioned above. This is often misunderstood by

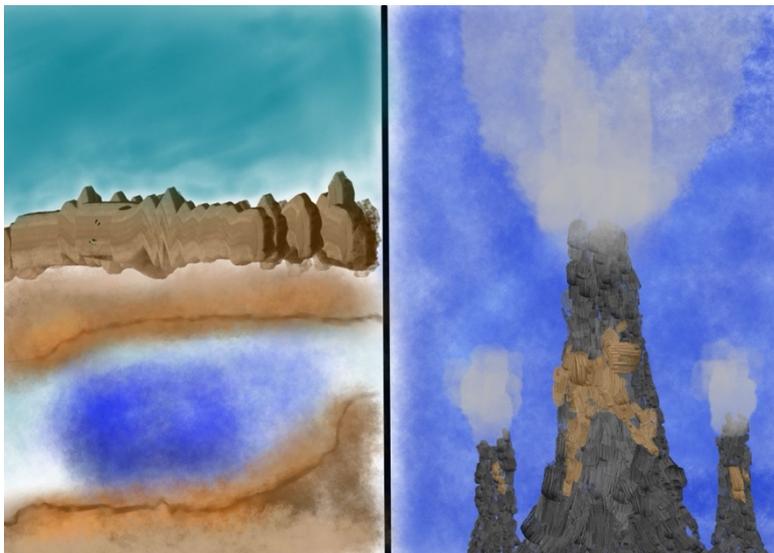
the public. Take, for instance, the famous Miller-Urey experiment of 1953. Probably the most famous experiment in life's origins, it showed that under certain conditions (electric discharges that simulate lightening on the early Earth) some amino acids (the building blocks of proteins) can form from simpler molecules. But making building blocks of proteins is very, very far from making a cell.

Today we know that some amino acids form in space, in the clouds left by star explosions, and most amino acids can form under a variety of conditions in the laboratory. So, chemistry is versatile to a large degree and gives us multiple answers together with multiple new questions. If amino acids could form naturally in only one, singular, unique set of conditions, that would point us to *the* set of conditions for the origin of cells. But amino acids can form in *many* different places and conditions, so if we look just at amino acids, we are again a bit lost in the space of possibilities. In summary, bottom-up we can synthesise many of the building blocks of life, and put them together in interesting, non-living, highly-controlled dynamic systems in the laboratory—this is a very important approach, and knowledge that we must use when moving forward. But our journey to understand the origin of cells cannot stop here – far from it. How do we go about choosing amongst many possible paths? The best way is to leave the vast space of chemistry aside for a moment and look at biology and geology. What is life, and how does it relate to the environment?

### ***3. Life is highly dependent on the environment since its origin.***

One of the major questions about the origin of microbes is quite simply: *where* did it happen? We still cannot exclude the hypothesis that it came from elsewhere; it is possible that the late heavy bombardment (LHB, 4.1 to 3.8 billion years ago – a time interval when many asteroids and comets collided with Earth) brought with it spores of prokaryotic ancestors from another planet. Life thrived here on Earth right after the LHB, so it is clear that Earth was a very welcoming place to life, even if life started elsewhere. So, as scientists, we can look at Earth as a model planet for the thriving of very early life, and build theories for the origin of life on Earth or in an Earth-like planet. We will focus on theories as such now.

There are multiple theories for the locale of the origin of microbes, but two receive the widest attention and supporting evidence. The first is hydrothermal springs (pools, or ponds) on the surface of the Earth, and the second hydrothermal chimneys at the bottom of the ocean



*Artistic depiction, courtesy of Joana C. Xavier, of the two types of ancient environments with more attention in origins of life research. On the left: a hydrothermal spring (also known as hydrothermal pond, pool or field); modern examples include the pools in Yellowstone National Park (USA). On the right, a deep-sea hydrothermal chimney (or vent) – alkaline hydrothermal vents exist in the area known as Lost City in the mid-Atlantic Ridge.*

## A learner-centric microbiology education framework

Hydrothermal springs have been known to humanity since we walked on Earth – they are quite visible and impactful at the surface. Famously, but not seen elsewhere in his writings, Charles Darwin spoke of what he thought about the origins of life in a letter to his friend Joseph Hooker in 1871, “*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*”. In part because of this, and the easy access to springs for research, these have been traditionally the favourite environment to conceive of life’s origins. More recently, in spring-like conditions, much organic chemistry (the synthesis of building blocks of life – see above) has been successful, giving more support to these environments. But, as mentioned above, making the building blocks of life is very far from making a cell. In these environments, conditions can change dramatically very rapidly and, without a protective atmosphere from the ancient sun, there would have been high exposure to aggressive levels of radiation.

Hydrothermal chimneys (or vents) are a more recent theory with a rapid growth in attention. These types of geological formation in the deep ocean were only discovered for the first time in 1976, and those first studied were the kind known as *black smoker* – too hot for life. Other types of milder vents were postulated in the 80s and found only in 2000. These are alkaline vents (or white smokers) and they come with a series of bonus points for origins: they provide a kind of geological womb that concentrates important minerals, energy and abiotically fixed carbon; they look very much like a bioreactor, with an input from the bottom and a release in the top. They are dynamic environments with gradients of temperature, pH and pressure, yet also protected from the harsh, rapidly changing conditions of high radiation at the surface. Today’s hydrothermal vents are one of the most biodiverse ecosystems on Earth, very rich in microbial communities that feed whole chains of higher forms of life all the way up to animals like worms and crabs!

Finally, it is important to point out that biologists are very familiar with a process called “terrestrialisation” which is the adaptation of life to the surface. This process took millions of years, in cyanobacteria, because cells that ventured at the surface needed to gain protective skills against high ultraviolet radiation from the sun and other challenges they did not face in water. All these features point to vents as a most likely place for the origin of cells, yet the debate is far from over. It is possible (even if quite unlikely) that life originated at the surface, lost those protective capacities when it went to the deep oceans, and gained them again. It is also possible (and more likely) that a lot of interesting chemistry happened at the surface, transforming Earth on a planetary level in terms of organic content, but that the origin of cells itself happened in the deep, protected from chaos at the surface.

Before leaving this section, it is important to highlight how dependent life is on the environment. Modern life has learned to build most of itself: provided with a simple form of carbon, metals and water, many bacteria and plants thrive. However, no organism can live isolated from the environment – we all must eat and excrete to live. When we look at the simplest life forms, with fewer genes, they are more dependent on the environment. It is most plausible that the earliest life forms were even more dependent on the environment, for to be more independent, they needed to learn new functions, and save them encoded in new genes.

In particular for origins of life research, it has become more and more evident that metals played a significant role. Metals confer upon organisms the ability to perform chemical transformations in unique ways – all life needs metals like iron, magnesium, etc. From the beginning, we needed the environment for food (carbon, hydrogen, nitrogen to make more of our building blocks) but also for aid in transforming that food into other important things. Life is never independent, and life forms themselves create the environment for other life, in a never-ending chain of evolution, from the first organic growth of protocells to us.

### 4. *Life is about cooperation, and more so at the origins*

Charles Darwin's theory of evolution has been seminal to our understanding of life, from microbes to us. Evolution occurs by natural selection, namely organisms that are better equipped to live and reproduce, in a world with limited resources, will live longer and reproduce more. It is as simple as this, yet quite hard to comprehend when one looks deeply. If the fittest survives, why do we have such a wide biodiversity on Earth, and not just one fittest organism? The story is not so simple. Perhaps the key aspect missing from this line of thought (which Darwin himself pointed to multiple times in his book) is that most often *groups* of organisms are selected. Look at the delicate balance between insects and flowers – one cannot live without the other – so the unit of selection includes both. Look at the delicate balance between us and the plants that give us food – one cannot live without the other. It is now clear to scientists that selection operates at many levels – and groups that cooperate better are in fact those more likely to thrive, rather than individuals that grow too fast and extinguish the resources around them – they are bound to die eventually.

What is striking is that now, unlike the time of Darwin, we can look at the microbial world, and here cooperation occurs in unprecedented levels. Humans cannot live without their gut microbiome; microbial communities in soil are highly interdependent, often with one species producing and sharing a certain amino acid and others producing and sharing something else. Bacteria are happiest living in biofilms, such as those in dental plaque, or in biofilms that form in the shower. It is quite likely that, at the origins of life, large organic structures like biofilms formed before individual protocells (see first image, root of the tree). The capacity of cells to go by themselves, survive and reproduce may very well have been acquired later. Beyond that, as discussed above, the origin of life implies the coming together of the molecules that make up cells. These molecules form intricate networks of interaction, and studies show that networks of small molecules simpler than those in cells are possible in the laboratory! We can see this as a kind of cooperation that exists today in every cell, and that started at the origin of life.

### Relevance for Sustainable Development Goals and Grand Challenges

The origin of life was literally the first time cells and their parts were produced. Today, we produce cells and their parts for many applications, for example, we produce vitamins to be used as supplements, we grow cells to produce drugs, etc. Understanding the natural origin of microbes and their parts will certainly impact biotechnological and biomedical applications. While some of those processes may have been slow, we expect several to have been very fast due to the relatively short time in which microbes appear on the fossil record after the formation of the Earth. There is a lot of fundamental knowledge between geochemistry and biochemistry that we are yet to discover, which is vital to understand the origins of life. This knowledge will certainly impact how we produce many of our commodities, medicines, and beyond.

### Pupil Participation

1. *Draw your own tree/mycelium of life.* Position humans and other animals or plants you know at the end of one branch, and prokaryotes originating at the bottom, eukaryotes originating in the middle. Remember: eukaryotes have a membrane around their DNA forming a nucleus; prokaryotes lack this membrane and have their DNA distributed in the cytoplasm. Make more connections in your tree/mycelium near the bottom, when DNA is widely transferred friend-to-friend. In the top, where we are, DNA is more transferred parent-to-child.

## A learner-centric microbiology education framework

2. ***Dramatize with your class a prokaryotic cell!*** Some students are lipids that should make a circle around the others – these should remain holding hands and not let go—otherwise the cell breaks! Other students are proteins: some should be fixed between lipid-students, others should be inside the circle and are free to move around! Then also inside the cell, a chain of students should make the DNA. These should remain holding hands too, but the whole rope can move as well!

3. ***Draw or build a primitive microbial cell in 3D.*** You can make it in a circle (sphere in 3D) or rod-shape (see illustrations in this article or those linked below for inspiration). Use at least three different colours: one for the membrane, one for proteins and one for DNA. The membrane is the boundary around the cell; place little blobs that are the proteins with different colours both in the middle of the membrane and inside the cell. You should also draw in a different colour a long, coiling rope to represent DNA inside the cell. Have fun!

4. ***Where did life start?*** Draw your own hydrothermal pond or your own hydrothermal chimney – get inspiration from the image above or look up images online.

5. ***Discuss the features we share with all life forms, including microbes.*** DNA carries information old and new; proteins do all the jobs, the membrane keeps everything inside and senses the environment, and vitamins make essential transformations much easier!

### The Evidence Base, Further Reading and Teaching Aids

#### Scientific articles

- [Lane N, Xavier JC \(2024\). To unravel the origin of life, treat findings as pieces of a bigger puzzle. \*Nature\* 626, 948-951.](#) A contemporary article speaking about the current state of origins of life research accessible to a wide audience.
- [Preiner M, \[...\], Xavier JC \(2020\). The future of origin of life research: bridging decades-old divisions. \*Life\*, 10:20.](#) An article written in a very accessible manner for anyone with a minimum level of education in science. It provides the current state of the art in origins of life research and what the early-career community sees for the future of the field. The authors are eager to continue to promote easy access and understanding in origins of life research – please feel free to reach out to both corresponding authors for clarification on any of the topics covered.
- [Xavier JC, Patil KR, Rocha I \(2014\). Systems biology perspectives on minimal and simpler cells. \*Microbiology and Molecular Biology Reviews\*, 78:487–509.](#) This is an article covering in depth what life *actually* is and the hard task of reducing life's complexity. What is the minimum number of genes for a genome? What is the minimum number of molecules that can make up an organism's food? What is essential vs. non-essential for life? These questions are explored in depth – for further clarification please reach out to the first author.
- [Xavier JC\\* \(2020\). The early origin of cooperation. \*Nature Ecology and Evolution\*, 4:18-19.](#) This article covers, for a wide audience, the question of the early origin of cooperation, with examples across the molecular world and prokaryotes.

#### Multimedia

- Animation covering the theory of origins in a hydrothermal spring: <https://www.youtube.com/watch?v=qKXt7zdLVR4>
- Animation covering the theory of origins in a hydrothermal vent: <https://www.youtube.com/watch?v=oplG0xYm2XY>
- Animation covering a theory for the origin of eukaryotes: <https://www.youtube.com/watch?v=x6tmovJghyY>
- Illustration on the origin of life by David Goodsell: <https://pdb101.rcsb.org/sci-art/goodsell-gallery/abiogenesis>

- Illustration of LUCA by David Goodsell: <https://pdb101.rcsb.org/sci-art/goodsell-gallery/last-universal-common-ancestor>

## Glossary

**Abiogenesis.** The natural process by which life arises from non-living matter, such as simple organic compounds.

**Alkaline Vents (White Smokers).** Openings on the seafloor that emit warm, mineral-rich water. These vents are thought to provide a supportive environment for the chemical processes that may have led to the first living cells.

**Amino Acids.** Small molecules that are the building blocks of proteins, essential for life. They perform many roles in cells, including forming enzymes that accelerate chemical reactions.

**Biofilm.** A structured community of microorganisms that stick to surfaces and to each other, often embedded in a protective matrix they produce. Early life forms may have existed as biofilms.

**Bioproduction.** The process of producing biological materials (like vitamins or proteins) using living organisms.

**Bioreactor.** A controlled container where biological processes can occur, often used in industrial microbiology or biotechnology.

**Black Smokers.** Deep-sea vents that release extremely hot, mineral-rich water, generally unsuitable for life due to high temperatures.

**Carbon Isotope Fractionation.** A process where living organisms preferentially use lighter forms of carbon (like carbon-12). This leaves a chemical signature in ancient rocks that helps scientists identify early life.

**Cofactors (Vitamins and Metals).** Small molecules or ions that assist enzymes in carrying out chemical reactions. Examples include magnesium, iron, and vitamins like B1 and B2.

**Cyanobacteria.** A group of bacteria that can perform photosynthesis, producing oxygen as a byproduct. They were among the first organisms to thrive on Earth's surface.

**Cytoplasm.** The gel-like substance that makes up the inside of a cell.

**DNA (deoxyribonucleic acid).** The molecule that stores genetic information in all living organisms. It is like a blueprint for building and maintaining an organism.

**Enzyme.** A protein that speeds up chemical reactions, generally inside cells but also outside cells, without being used up in the process.

**Eukaryotes.** Organisms whose cells have a nucleus, where the DNA is enclosed by a lipid membrane. Examples include plants, animals, fungi, and humans.

**Hydrothermal Springs.** Hot, mineral-rich pools on Earth's surface. These have been considered potential sites where life might have originated due to their ability to host complex chemical reactions.

**Lateral (Horizontal) Gene Transfer (LGT).** The transfer of genetic material between organisms that are not parent and offspring. This is common among microorganisms and contributes to genetic diversity.

**Last Universal Common Ancestor (LUCA).** The most recent shared ancestor of all current life on Earth. It lived around 3.8 billion years ago and had features common to all living organisms today, including DNA and protein.

**Last Eukaryotic Common Ancestor (LECA).** The last common ancestor of all eukaryotes.

**Late Heavy Bombardment (LHB).** A period in Earth's history marked by frequent asteroid and comet impacts, potentially influencing the origin of life.

**Lipids.** Also known as fats, organic compounds that make up cell membranes and store energy.

## A learner-centric microbiology education framework

**Microbiome.** The community of microorganisms (like bacteria, fungi, and viruses) living in a particular environment, including the human body.

**Miller-Urey Experiment.** A famous experiment simulating early Earth conditions to show that organic molecules like amino acids could form naturally.

**Mycelium.** A network of thread-like structures (hyphae) found in fungi. Used metaphorically here to describe the interconnected complexity of life's evolution.

**Nucleobases.** The basic building blocks of DNA and RNA nucleic acids, such as adenine (A), thymine (T), cytosine (C), guanine (G), and uracil (U). Nucleic acids store and transmit genetic information.

**Prokaryotes.** Simple, single-celled organisms without a nucleus. Their DNA is free in the cell's cytoplasm. Examples include bacteria and archaea.

**Protocells.** Primitive cell-like structures thought to have existed before the first true cells. They likely lacked the complexity of modern cells but could grow, divide, and carry out basic functions.

**Reductionism (Top-down Approach).** A method of understanding complex systems by deconstructing/disassembling them and studying their simpler, individual components.

**RNA (Ribonucleic Acid).** A molecule similar to DNA that plays several roles in the cell, including acting as a messenger between DNA and proteins.

**Stromatolites.** Layered structures created by the activity of microorganisms, especially cyanobacteria. These provide some of the oldest evidence of life on Earth.

**Symbiosis.** A close relationship between two different organisms where both benefit. For example, early eukaryotic cells likely formed through symbiosis between bacteria and archaea.

**Synthetic (Bottom-up Approach).** A method of studying origins by constructing/assembling life-like systems from basic molecules in the laboratory.

**Terrestrialization.** The adaptation of life from water to land environments.

**Vesicle.** A small, bubble-like structure made of lipids. In early life studies, vesicles are used as models for primitive cell membranes.

**Vitamins (e.g., B1, B2, B3).** Essential organic molecules that play key roles in cellular metabolism.