THE EARLIEST ANAEROBIC AND AEROBIC LIFE

M. Rizzotti
Department of Biology, University of Padova, Italy

Keywords: First Cells, Aerobic Microorganisms, Aerobic respiration, Anaerobic respiration, Autotrophy, Heterotrophy, Metabolism, Molecular evolution, Organelles, Phylogeny, Respiration

Contents

Summary

The first cells are thought to have been heterotrophic, i.e. to have fed on organic molecules present in the body of liquid water in which the cells originated. Reduction in the availability of dissolved organic molecules would have constituted a selection pressure favoring the emergence of autotrophy—the capacity to synthesize such molecules from carbon dioxide and other simple inorganic molecules. The first autotrophy would have occurred without oxygen.

After the appearance of oxygen-producing photosynthesis, oxygen so produced in water accumulated in the atmosphere and paved the way for to the arrival of aerobic organisms. The first large ecosystem of our planet was made up of photosynthetic bacteria and other life forms that exploited them in some way. It is likely that among these life forms were the first nucleated cells able to engulf organic particles as food by endocytosis.

Unicellular nucleated organisms gradually became more and more complex. One lineage engulfed and incorporated an aerobic bacterium that later became the mitochondrion. Some descendants of this lineage acquired in addition the plastids or chloroplasts. The origin of the cilium is more controversial as there is an exogenous as well as an endogenous hypothesis; the former states that the cilium derived from an attached spirochete, the latter that it derived from a cellular peduncle.

1. The First Cells

In the body of water where the first cell of a biosphere originates, be it on Earth or on another planet, there is no molecular oxygen (or dioxygen), or at most there is an extremely low concentration of it due to the splitting of the water molecule by ultraviolet light. This means that the earliest evolution must have taken place in anaerobic conditions, i.e. in the absence of dioxygen (simply called oxygen, O_2).

Moreover, according to most scientists (section 2), the first cell originated from a slightly simpler organic aggregate, so it can be considered heterotrophic. This means that, instead of producing its own organic molecules from carbon dioxide (or carbon monoxide), it takes organic molecules from the hydrosphere, i.e. the body of liquid water in which it lives. We may suppose that in the first cell, as well as in the organic aggregate that gave rise to it, some of the organic molecules are taken up without any metabolic modification. This does not usually happen in advanced cells, but can be considered as one of the likely primitive characteristics of the first one.

Although we are starting with the first cell, we may discuss whether the biosphere had a single or a multiple origin, i.e. whether cells originated just once or more than once. A brief consideration of complexity can help us think about this problem. Cells are undoubtedly very complex objects. We may even regard their complexity is extreme, as they are perhaps the most complex molecular objects possible. Certainly, unless we consider organized aggregates of cells, such as brains, cells are the most complex objects known in the universe.

It is usually reasonable assume that very complex objects appear just once, due to the almost zero probability of repetition of the long series of events that are needed for their appearance. For this reason, most scientists assume that a biosphere starts from a single cell or at most a single local population. In fact, we may think of a population of very similar pre-cellular aggregates that exchange some molecules with each other and perhaps also with the first cellular aggregates, so that it is not possible to strictly distinguish their individual evolution.

The descent of the first population of cells may spread in the hydrosphere and undergo differentiation due to both chance and selection. Different bodies of liquid water, sometimes isolated, sometimes in communication, or even different parts of the same hydrosphere, can have different properties and favor different primitive genes, and thus select different primitive cells. This means that the first population can undergo diversification.

If the diversity loses continuity and two populations become separated, bifurcation into separate lineages ensues as in the processes of speciation of modern organisms. We may also suppose that this splitting into separate lineages does not prevent occasional cellular fusions and mixing of genes between lineages, but the main process remains the duplication of the cells and their isolation, otherwise they lose their cellular state and disappear as elements of the biosphere. This means that if a cell fuses with another one and then separates again, it can give up to the other cell a gene that is needed to grow and duplicate, and thus it loses its cellular state and decays without the possibility of undergoing further duplication. The number of genes in primitive cells was probably quite limited, so it is unlikely that they could lose even a few of them without lethal consequences.

According to this view, as soon as the first population of cells appears, their evolution starts in a way very similar to that of advanced biospheres. New lineages (or species) arise and others become extinct. A phylogeny, i.e. a tree of life made of subsequent bifurcations, begins with the first cellular population and does not stop until the extinction of the entire biosphere. But there are no rules in the extinctions. For example, one of the two lineages produced by the first bifurcation of the first cell can go extinct soon after its origin, or two billion years later.

If we look at a biosphere a long time after its origin, we detect a number of species. They all derive from a single species that can be dubbed the last common ancestor (LCA) of that biosphere at that moment. If we go back to the moment of existence of that LCA, many more species are simultaneously present but their entire progeny becomes extinct in the future. If we look at the same planet after another long period, we detect a different set of species that derive from their own LCA. However, this LCA is not the same as in the previous observation, but a later species; it too lives together with many more species, none of which have any surviving descendants by the time of our inspection. For a while, after the origin of a biosphere, the LCA is identical to the first species, i.e. the first population of cells. But as soon as all the species derived from one of the two lineages of the first bifurcation become extinct, the LCA is no longer the first species.

This is the monogenetic line of thought. However, some scientists support polygenetic views. If the transition between the pre-cellular aggregate and the first cell is in fact a rather simple one, and if the pre-cellular aggregates were abundant, cells could have originated more than once.

The multiple originations could either have been simultaneous (unlikely) or sequential. Conceivably, a new cell could have originated at some moment after each catastrophic impact large enough to erase any preexisting biosphere. In that case, the first cell of the Earth's present biosphere would be the one that originated after the last such event, the only essential difference between it and earlier first cells being that no impact large enough to destroy its descendants occurred after its coming into being. In this view of the relatively easy origin of life, a multiple origin after every complete extinction is more likely to be accepted. A descent that rapidly spreads in the whole hydrosphere can inhibit the rise of new cells from pre-cellular aggregates because in the competition for the organic molecules of the environment it is already advanced.

Nevertheless, some scientists argue that the modern terrestrial biosphere arose from a multiple cellular origin. Moreover, only modern cells would give rise to the distinct lineages of a basically divergent evolution. Before modern cells, there was some kind of pre-cellular situation in which fusions and fissions and exchanges were the rule. The origin of modern cells almost froze, for unknown reasons, the main lineages (more than two) that thus came down to us. These scientists identify the LCA with this situation that began following the first population of cells.

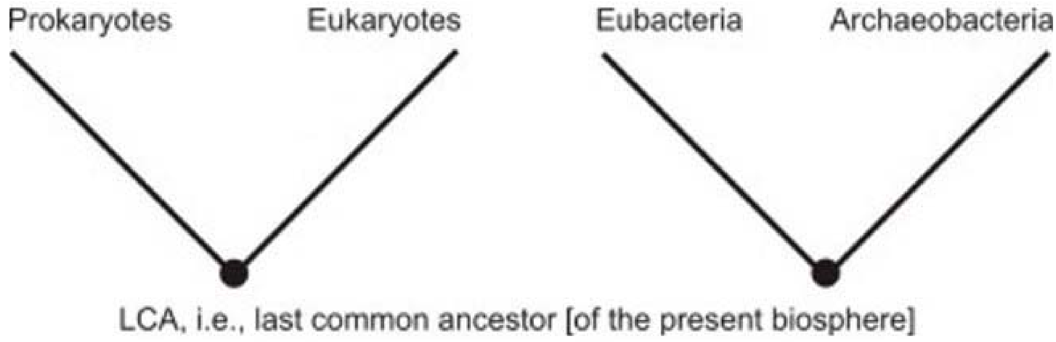

Figure 1. Two current views of bifurcation of the LCA (last common ancestor of the present terrestrial biosphere).

In the present terrestrial biosphere, the products of bifurcation of the LCA are the lineages of prokaryotes and eukaryotes or, alternatively, eubacteria and archaeobacteria (figure. 1). In the first view, the LCA was either a modern bacterium (i.e. a prokaryote) or a cell that could not yet be defined as a prokaryote or a primitive eukaryote. In the second view, the LCA could only be a modern bacterium as all its descendants are modern bacteria; the eukaryotes (i.e. the nucleated cells) are a branch of archaeobacteria or derive from a fusion between a eubacterium and an archaeobacterium.

In the first view, prokaryotes and eukaryotes are usually called superkingdoms, whereas in the second view, eubacteria, archaeobacteria, and eukaryotes are called domains and renamed, respectively, bacteria, archaea, and eukarya. Whichever of the two alternative views is the right one, all biologists support the idea that in the present biosphere there are no cellular organizations different from the prokaryotic and eukaryotic ones. In the second view, which is currently the most accepted one, the LCA is not the first cell because the rooting of the tree precisely assumes that there were more primitive cells before the LCA that evolved according to the same mechanisms as modern cells.

The discussion is by no means over. We must take into account that the first cell arose perhaps 3.9 billion years ago, according to some paleontological evidence, and that the LCA lived perhaps some 3 billion years ago, according to some pieces of evidence from genomic (or molecular) phylogeny. Whatever the method, resolving a remote event (for example, a series of phylogenetic bifurcations) is typically more difficult than resolving a recent one. Ancient phylogeny is mainly studied by means of genomic comparison, and the history of this approach tells us that the resolution of much more recent evolutionary events took decades.

For example, the attempt to resolve the bifurcations of three apes—gorillas, chimpanzees, and humans—began at the very beginning of sequence comparisons and required at least three decades, in spite of the fact that the events involved go back to only 10 to 5 million years ago. Only in the mid-1990s did scientists reach consensus that gorillas branched off before the split between chimpanzees and humans, who share a more recent common ancestor. The point is that it will be surprising if we can resolve in a few years phylogenetic bifurcations that are so much older.

-
-
-

Bibliography

Doolittle W. F. (2000). Uprooting the tree of life. *Scientific American*, February issue, 72–77. [A clear and accessible discussion of the current view on the phylogeny of the present biosphere.]

Margulis L. and Schwartz K. V. (1998). *Five Kingdoms*. 3rd edn., 520 pp., New York: Freeman. [This book sketches a brief profile of every lineage of the present biosphere in the frame of their general phylogenetic (genealogical) relationships.]

Rizzotti M. (2000). *Early Evolution: From the Appearance of the First Cell to the First Modern Organisms*. 175 pp., Basel: Birkhäuser Verlag. [This covers the rise of the first cell, the evolution of the earliest modern cells, and the origin of the major cellular organelles of the present biosphere.]

Biographical Sketch

Martino Rizzotti teaches Biological Evolution at the University of Padova, Italy. His experimental research is mainly concerned in comparing hemoglobin systems of fish groups. His theoretical research ranges from the axiomatization of genetics to the definition of life; on the latter subject he edited *Defining Life: The Central Problem in Theoretical Biology* (Univ. of Padova, 1996; www.bio.unipd.it/information/rizzotti.html). His studies on life in the universe concern the precellular organic aggregates, the origin of the main cellular organelles, and the prerequisites for the evolution of intelligence. He has advanced new hypotheses on the origin of the flagellum of bacterial cells and the origin of the cilium of nucleated cells. On these subjects, he has published *Early evolution: From the appearance of the first cell to the first modern organisms* (Birkhäuser, 2000; www.birkhauser.ch).