

Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life

by Eva Jablonka and
Marion J. Lamb

Reviewed by Bernhard Haubold,
Fachhochschule Weihenstephan,
Germany

In *The Origin of Species*, published in 1859, Charles Darwin described evolution as a process subject to diverse influences. Natural selection, of course, leads to adaptation in a manner similar to the changes elicited by breeders of pets or livestock. However, organisms might also display neutral characteristics, which have no effect on their fitness. In addition, and rather surprisingly for the modern biologist, Darwin went along with the conventional wisdom of his day and believed acquired characteristics to be heritable. Since then, genetics and computers have been the decisive additions to evolutionary thought. Their combination has led to a distinctive reinterpretation and refinement of Darwin's great idea. In 1976, the UK evolutionary biologist Richard Dawkins succinctly stated the resulting new paradigm in the preface to his influential book, *The Selfish Gene*: "we are survival machines – robot vehicles blindly programmed to preserve the selfish molecules known as genes." From this point of view, the sequence of the human genome published in 2001 holds the promise of

revealing the entire software that comes with the human hardware.

Darwin's open-mindedness about the possible forces of evolution is the starting point for *Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life* by the evolutionary biologists Eva Jablonka and Marion J. Lamb. Their book is aimed at anyone interested in evidence that undermines a strictly gene-based perspective, as the authors hope to convince their readership that "DNA is not the be all and end all of heredity". Ever since that winter day in 1953 when Francis Crick told astonished lunch guests at the Eagle pub in Cambridge that he and Jim Watson had just solved the secret of life by unravelling the double helical structure of DNA, this molecule has, to all intents and purposes, been the 'be all and end all of heredity'. For biologists brought up in the growing excitement of molecular biology that culminated in the Human Genome Project, the supremacy of DNA is part of a shared culture that has become so entrenched that it is hard even to recognise. But Jablonka and Lamb make a convincing and level-headed case for a more pluralistic view of evolution and heredity. The authors avoid the antagonistic tone of *The Selfish Gene* school of debating and patiently explain the nuts and bolts, as well as the implications, of the four dimen-

sions of evolution that they consider important. In each of these dimensions, they present up-to-date ideas but at the same time remind the reader of classical observations that would have undermined the 'DNA as software' metaphor had their significance been fully acknowledged.

The first dimension they discuss is the genetic. A central tenet of contemporary evolutionary thinking is that mutations, the raw material of evolution, are random. In other words, it is believed that there is no code for changing the code. Jablonka and Lamb introduce the reader to the debate about non-random, adaptive mutations among microbiologists during the late 1980s and 1990s. More persuasive, however, is their insistence on the significance of the well-known fact that cells can alter their own DNA through various mechanisms, including somatic mutation and selective amplification.

The second dimension is the epigenetic, which encompasses all those characteristics of cells and organisms that are heritable without being written into a genome's DNA sequence. Although liver and brain cells contain the same DNA, they have very different heritable morphologies and functions. Behaviour constitutes the third dimension. The behaviour of the young is guided in non-genetic ways by that of their parents. Finally, symbolic inheritance systems, foremost

among them language, make up the fourth dimension.

Having described their four-dimensional model of evolution, Jablonka and Lamb continue by showing how these dimensions interact. As before, it is classical work that is most illuminating. For example, the authors cite Waddington's experiments from the 1940s with heat-shocked *Drosophila* which demonstrated the phenomenon of 'genetic assimilation'. Here, selecting for an inducible phenotype leads to it becoming constitutive and stably heritable after only a few generations.

Today, genetic assimilation as well as many other genetic phenomena are understood in molecular detail and the reader is given some of this information where appropriate. The moderately technical nature of these passages is mitigated by careful avoidance of unnecessary jargon. In addition, each chapter concludes with a delightful dialogue in which the themes introduced in the main section are playfully varied. This makes the book not only thought-provoking, but also fun to read. We may be blind robots, but some of these robots are perceptive enough to see the limited fruitfulness of this point of view. I thoroughly recommend Jablonka and Lamb's book to anyone interested in an exciting alternative.

Details

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The Ancestor's Tale: A Pilgrimage to the Dawn of Life

by Richard Dawkins

Reviewed by Bernhard Haubold,
Fachhochschule Weihenstephan,
Germany

There is a natural way to tell a tale: begin at the beginning and end at the end. Standard biographies, for example, start with the forebears, in many cases the grandparents, and end with the protagonist's death. So the end is clear, but the beginning is potentially fraught with the difficulty of deciding which ancestors to describe. After all, one person has two parents, four grandparents, and 2^{n+2} n-great-grandparents. An elegant technique to avoid the thicket of ancestors is contained in the Bible, in which Luke, the biographer of Jesus, tells the genealogy of his subject by starting with Jesus and ending with Adam. As a man of his time, Luke only mentions the fathers, thereby converting an exponentially growing, unmanageably large bi-parental genealogy into a lean uni-parental genealogy.

In contrast to human individuals, two animal or plant species are usually derived from a single ancestral species. Biological species therefore naturally form uni-parental genealogies. In his latest book, *The Ancestor's Tale: A Pilgrimage to the Dawn of Life*, Oxford biologist Richard Dawkins takes advantage of this fact by giving a popular but richly detailed account of evolution starting at the end and time-travelling backwards to the beginning of life.

Today, the inversion of the arrow of time has a strong tradition among evolutionary biologists. If we start with, say, three copies of the human alpha-haemoglobin gene and look back in time, we will reach a point at which two of the three genes were derived from a common ancestral gene. At that point, two alpha-haemoglobin lineages fuse. Such a fusion is also known as a coalescence event, and hence the corresponding theory is called coalescent theory. Moving further back in time, we reach a point where the last two remaining lineages fuse in another coalescence event. This is known as the most recent common ancestor of the genes. It is of fundamental importance for evolution, since any mutation that happened further in the past affected all genes equally and hence is invisible in the present copy of the genes.

Consequently, there is no use in pursuing the history of a sample of genes beyond their most recent common ancestor. Similarly, there is no sense in telling the history of life beyond the last common ancestor of all creatures alive today. So, as with biographies, the end of the story is clear, while the beginning is less clear, because evolution has as many ends as there are extant species. But of course, we are mainly interested in ourselves and this is where Dawkins starts his magnificent account.

Moving backward in time, we are joined along our lineage by 39 other branches of the tree of life. These include, among others, apes, mon-