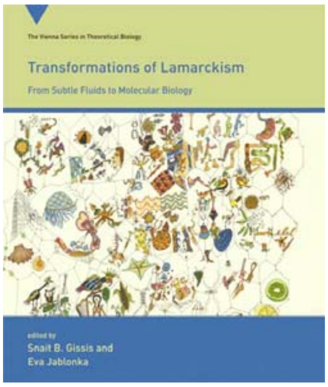

Transformations of Lamarckism. From Subtle Fluids to Molecular Biology. S. B. Gissis and E. Jablonka (eds), The MIT Press, 55 Hayward Street, Cambridge, MA02142, Cambridge, USA. 2011. xvi + 457 pp. US$ 50.00/£37.95.

This is the latest volume in the *Vienna Series in Theoretical Biology*, of which an impressive 13 have come out so far. The theme of biological evolution runs through most of them (cognition and culture are distant seconds). *Transformations of Lamarckism* is based on talks given at a workshop held in Israel in 2009 to mark the 200th anniversary of the publication of Jean-Baptiste Lamarck's *Philosophie Zoologique*, which contained 'the first comprehensive and systematic theory of biological evolution'. This is a substantial offering made up of 41 articles packaged into six chapters titled *Introductory Essays*, *History*, *The Modern Synthesis*, *Biology*, *Philosophy and Ramifications* and *Future Directions*.

Ostensibly the main aim is to raise doubts concerning the sufficiency of the standard view of evolution, namely that by and large it takes place by natural selection as Darwin and Wallace first said in 1858. As we will see, there is more to it than that. A second aim is to suggest that many of the non-selectionist ideas being advanced today were anticipated by Lamarck, a biologist of the 18 century (in fact he was the first to use 'biology' in its present-day sense). The irony is that Lamarck is, or has been, remembered mostly as the originator of an incorrect theory of evolution. Despite the effort to link contemporary discoveries with Lamarck's prescience being somewhat forced, the book makes a useful contribution to evolutionary discourse.

Transformations is unusual in three respects. One, the supposed independence of science from human affairs is shown up for the fiction it is. The editors inform us that the Israeli government prevented an invitee from participating in the workshop because of her French–Iranian nationality and that another contributed to the book but did not attend as a mark of protest against Israeli policies. Two, art is used in the aid of science. Imaginative line drawings by Anna Zeligowski are interspersed through the text and allow the reader to pause for reflection now and then (though comments by the artist would have helped). Three, many articles are devoted to historical and philosophical issues, not natural science. While the contents must have stimulated the participants, the mix of speculative thought and factual information leads to a loss of focus for the reader. On top of that the philosophical portions are rather heavy going.

Among the alternatives to natural selection as the principal explanation for evolutionary change, two are especially interesting. On the one hand, they deal with findings showing that individuals with the same DNA sequences (the same *genotype*) can possess different traits (different *phenotypes*) and pass them on to their progeny. On the other hand they hark back to what was thought to be a long-discarded evolutionary hypothesis associated with the name of Lamarck. The first part of the hypothesis is uncontroversial; it states that the attributes of organisms can be modified during a lifetime by use and disuse (training and exercise can improve muscles and memory).

The nub is the second part. Lamarck held that the attributes so modified could be passed on from parents to children. The doctrine of inheritance of acquired characters, as it is called, would imply that a person who develops strong muscles will tend to have children who are predisposed to develop muscles that are stronger than average. Termed 'soft inheritance', this element of Lamarckism strikes at the heart of conventional DNA-based heredity. As might be guessed from the latter half of the title, the intention is to make Lamarck's opinions respectable on the grounds that they prophesied contemporary findings.

Not surprisingly, plants and microorganisms get special attention. The sequestration of the germ line that is supposed to make it impossible for somatic variations to be transmitted simply does not exist in plants. And if there is only one cell, the germ line and soma are identical. Beyond that, in the history of genetics doubts persisted for a long time as to whether microorganisms had genes at all – or if they did, whether their inheritance followed the rules discovered by Mendel. Antibiotic resistance in bacteria was associated with metastable phenotypic states (Bigger, 1944), long-lasting adaptation in yeast seemed to have a non-genetic basis (Winge and Roberts, 1948) and a surgically altered pattern on the cell surface was propagated faithfully through successive cell divisions in a ciliate (Sonneborn and Beisson, 1965). What is new is that there are plausible molecular-level explanations for these uncommon modes of inheritance. Interacting systems of genes or proteins can exist in more than one steady state, reversible modifications can occur in DNA without affecting the primary sequence, and genetic material can be found outside the nucleus. But such phenomena continue to attract attention. In order to appreciate why, we need to take a look at natural selection, evolution's Standard Model.

Natural selection has been long believed to be the most important factor behind organismal evolution. It rests on three postulates that are testable and, if valid, lead to evolution. The postulates are that the members of a species differ from each other in respect of traits that impinge on their survival and reproduction; traits in parents and offspring are positively correlated; and the bearers of some traits leave behind more offspring than others. It follows that given enough time the distribution of traits between ancestral and descendant populations will be very different; evolution will have taken place. The features that characterize an individual constitute its phenotype, and the phenotypes of parents and offspring are correlated because of shared genes. 'Genotype' is the name for something that is assumed to be a signature of the individual, its genetic constitution. To summarize, natural selection leads to evolution whenever (a) individuals vary with regard to survival or reproduction because of their phenotypes and (b) the phenotype is influenced by its genotype. Natural selection has nothing to say about the origin of variation.

The advent of molecular biology strengthened natural selection's claim to primacy among explanations for organismal evolution. DNA, RNA and proteins provided the underpinning that natural selection had lacked till then. The nature of a living organism depends fundamentally on the proteins in its cells and bodies. DNA sequences or genes act as templates for the synthesis of complementary RNAs that in turn carry encoded information for making proteins. DNA sequences also regulate where, when and how much of a given protein is synthesized; small molecules, RNA or other proteins act as intermediaries. In common with all chemical reactions, the duplication of DNA is prone to rare errors or mutations. A mutation has the potential to cause variation, to change the organism's phenotype. As far as we can tell mutations are undirected ('random'). Because of this either large mutations or small mutations of large effect are liable to be harmful to the organism; small mutations of small effect may be neutral or harmful. But occasionally, a small mutation with a small effect may turn out to be advantageous for survival or reproduction. If so, over generations it will spread through the population. The sequential accumulation of beneficial mutations can gradually change the species. This line of reasoning agrees with what we have learnt about genes, proteins and organisms. Importantly, it also accounts for the observation that the structures and internal workings of plants and animals give the impression that they are precisely suited or adapted to fulfill particular functions – as if they had been designed with that end in view.

Natural selection is the only explanation there is for adaptation. Taken together with its intrinsic plausibility, that would appear to clinch the issue. However, other routes to evolutionary change are known. Many plant species arose more or less at one stroke: the genetic material of two different species fused and gave rise to a new species. Also evolution can come about from purely statistical effects without the intervention of natural selection: when plant seeds are transported by ocean currents, chance decides which ones strike land and become 'successful ancestors'. A broad consensus developed by the 1950s regarding the ways in which evolution could occur. Natural selection was its chief but not sole component (Darwin too had mentioned alternatives to natural selection). The set of accepted explanations for evolution came to be called the neo-Darwinian or Modern Synthesis. It seemed to provide a satisfactory picture of the evolutionary process.

Given that the synthesis was forged over 50 years ago, one might wonder whether the contributors to *Transformations* are pushing at an open door. As it happens, this book is more about an urgent problem that confronts us than about revisiting the Modern Synthesis (though two articles challenge its sufficiency). That problem is to blend unexpected experimental findings from cell and molecular biology into a coherent evolutionary picture. The real significance of the book is that it draws attention to instances of phenotypic variation and inheritance in which the role of DNA as a carrier of information is unimportant or secondary or unclear. The examples are many: a form of developmental plasticity in which the offspring can respond adaptively after the mother is exposed to a stimulus (plants and crustaceans; Sultan); plasticity of genetic regulatory systems, whereby existing metabolic pathways can be modified in the course of the organism's response to environmental stress and the modified state can be inherited (yeast; Braun and David); non-genetic stochastic variability involved in protection against a virus (bacterium; Pearl *et al.*); heritable traits that depend on the transmission of RNA, not DNA (mouse; Rassoulzadegan), and the role of the prenatal maternal environment in shaping the risk of offspring to disease (human; Gluckman *et al.*).

Markel and Trut describe an extraordinary response of a developmental system to environmental stress: after many generations of enforced domestication wild silver foxes begin to resemble dogs in their appearance and behaviour. Gilbert makes the point that the very notion of the individual, and therefore of its phenotype, can be murky. The 'individual' is frequently a conglomerate of many organisms (witness the hundreds of symbiotic bacterial species in the human gut) and the phenotype is based on inputs from many distinct genotypes. This blurs the link between an organism and 'its' genotype and requires that we regard the phenotype as being associated with a shifting consortium of reproductive units – quite unlike the view that underpins the Modern Synthesis. Newman and Bhat show that single cells came equipped with properties that could have allowed multicellular life to originate via self-organization – that is, in the absence of prior genetic alterations that specifically favoured multicellular forms (presumably the relevant single cell properties had evolved by natural selection). To the extent that their contention is valid, the claim that natural selection is responsible for phenotypic change is weakened. Jablonka gives an excellent summary of the case for including developmental plasticity and non DNA-based inheritance as factors in evolution.

The articles serve to reiterate lessons that are often disregarded. First, phenotypes are at the heart of evolution. Phenotypic variation may or may not be accompanied by genetic variation. When genotype and phenotype are strongly correlated, selection between phenotypes implies selection between genotypes. Irrespective of how an advantageous phenotype originates, genetic change can stabilize it, free it from the exigencies of chance or particular environmental conditions (Baldwin effect, Baldwin and Morgan). Second, potential phenotypic variation is strongly buffered or canalized in nature; a great many genotypes map to the same phenotype. Buffering can be because of natural selection in the past or because the pathways have a small number of stable outcomes. Stressful environments destabilize development and lower the degree of canalization. The diverse phenotypes that result are exposed to natural selection and the result can mimic the evolution of an environmentally acquired character (genetic assimilation, Waddington).

The third lesson is that phenotypic variation can propagate from one generation to the next in many ways. The familiar route presupposes variations in the primary DNA sequence; another is via the propagation of states of gene expression. A commonplace example of the latter is the stable transmission of cell and tissue differences during multicellular development. Different phenotypes, all of them associated with the same genotype, are faithfully conveyed from cell to cell within a developing embryo. It turns out that under certain circumstances they can be channelled through the germ line as well, i.e. across generations. Reversible modifications in DNA and regulatory or informational RNA molecules have been implicated in such 'epigenetic' inheritance. Unlike conventional 'genetic' inheritance, here the propagated state is relatively unstable. Epigenetic alterations revert within a time that is much smaller than the typical interval between spontaneous mutations. (Depending on the organism, base-substitution mutations occur at a frequency of $\sim 10^{-11}$ to 10^{-9} per nucleotide site per cell division.) The importance of epigenetic inheritance for evolution remains open. How common it is, generally, and the ratio of the two timescales, in particular, are going to be critical.

For an evolutionary biologist the most intriguing part of the book is a radical conjecture alluded to earlier, long advocated by Newman. According to it the role of physics in biology goes well beyond the familiar one of constraining the range of possible outcomes. The conjecture amounts to saying that living matter is more 'matter' than 'living'. It states that aspects of biological form and structure may have physical explanations as opposed to explanations based on the cumulative accumulation of mutations of small effect that occurred by chance. Spatio-temporal patterns within and among cells, the major evolutionary transition from single-celled to multicellular life and subsequent events in the evolution of multicellular organisms may have originated – at least in part – by self-organization. The physical and biochemical properties of single cells, along with their behaviours, could have predisposed them spontaneously to build multicellular morphologies of particular kinds. An illustration would be the segregation of cells into coherent sub-groups during development, which can be compared to the phase separation of two fluids with different surface tensions.

A spatial pattern that arose by self-organization could be stabilized by subsequent genetic change via the Baldwin effect. The scope for adaptation by natural selection would not be eliminated. But adaptation would amount to the fine-tuning of an outcome whose broad direction was set by physical principles. Self-organization may have been meaningful in another situation, not examined here: self-organized networks of reciprocal interactions may have seeded the evolution of social behaviour. Considering that cultural evolution proceeds largely along Lamarckian lines, it would have been interesting to see an exploration of the consequences.

Darwin lacked an understanding of the nature of heredity. He had neither read Mendel's paper nor drawn the correct conclusions from his own experiments on crossing plant varieties. He was unable entirely to discard the possibility that traits acquired during a lifetime could be inherited, or that use and disuse could lead to the heritable modification of organs. But an inner voice seems to have persuaded him that Lamarck's views on evolution could not be correct. Advances in genetics, cell and developmental biology have opened our minds to the many and varied routes that evolution can take. To say that much of this was foreseen by Lamarck is anachronistic. The motivation seems to be to restore to him the honour that is his due. True, he has been unfairly derided for being wrong; indeed the attacks began immediately after his death with an insulting eulogy by the palaeontologist Cuvier. Still, a scientist's contributions should not be judged by asking whether subsequent developments show that they pointed in the 'correct' direction. The right question to ask is how original and interesting the contributions were at the time they were made and to what extent they stimulated others. Lamarck does not require posthumous rehabilitation on either count.

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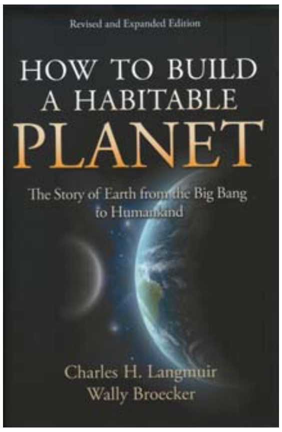

How to Build a Habitable Planet: The Story of Earth from the Big Bang to Humankind. Charles H. Langmuir and Wally Broecker. Princeton University Press, 41 William Street, Princeton, New Jersey 08540. 2012. 718 pp. Price: US$ 39.95. ISBN-978-0-691-140063.

In 1985, Wally Broecker gifted us with a brilliant account of the origin and evolution of the Earth in his book *How to Build a Habitable Planet*. This 291 page book was more like a gripping novel, but was packed with state-of-the-art scientific information and has served not only the earth sciences community, but many other inquisitive minds. Almost three decades later, a thoroughly updated second edition of this book has been presented by Langmuir and Broecker. This book covers diverse topics over 21 chapters from the Big Bang and Star formation, synthesis of elements and molecules, to planet formation and differentiation, plate tectonics and mantle convection to the ocean and atmosphere, surface processes on the Earth to origin and evolution of life, impacts of humans on the Earth to the search for extra-terrestrial life. These diverse topics are held together by a 'systems approach', i.e. how different parts of the planet influence one another and their relationship to the Solar System and the universe.

The first chapter provides a thoughtful introduction to reductionism – its power and limitations in explaining natural phenomena, chaos, self-similarity, feedback mechanisms and other characteristics of natural systems. This is followed in the subsequent four chapters by a journey through time, from the Big Bang and Galaxy formation, synthesis of elements in stars, formation of molecules, to the formation of planets. Chapter 6 switches gears and discusses about radioactive dating and is more technical than the preceding chapters. Age of the Earth and bulk meteorites are discussed along with concepts of half-life and the isochron technique. The concept of extinct radionuclides and their significance in understanding events in the first few million years of our Solar System is also briefly described. Interesting trivia is provided regarding early age estimates of the Earth – from the seventeenth century estimate of Bishop James Ussher, who calculated that the world was created in 4004 BC, to that of the nineteenth century physicist Lord Kelvin, who argued that the Earth was no more than 40 million years old. This is followed by a discussion of differentiation of the Earth into core, mantle and crust, other planetary bodies in our Solar System such as planetary satellites, asteroids, comets and impact events.

After the first eight chapters, the stage is set to zoom into our Earth and discuss why our particular planet became habit-