EVOLUTIONARY MECHANISMS AND PROCESSES

J. Flegr

Department of Parasitology and Hydrobiology, Charles University, Prague, Czech Republic

Keywords: evolutionary mechanisms, natural selection, genetic drift, evolutionary drives, speciation, extinction, RNA world, cultural evolution.

Contents

- 1. Introduction
- 2. The Main Mechanisms of Biological Evolution
- 2.1 Mutations
- 3. Natural Selection
- 4. Genetic Drift
- 5. Evolutionary Drives
- 6. Speciation
- 7. Extinction
- 7.1 Major Steps in Evolution
- 8. The RNA World
- 8.1 The Asexual DNA World
- 8.2 The Sexual DNA World
- 9. Cultural Evolution
- Glossary
- Bibliography
- **Biographical Sketch**

Summary

Biological evolution is the natural and more or less stochastic process of the origination of living systems (organisms) from abiotic systems, of the cumulative change of their properties, and of their diversification and proliferation. Due to both specific mechanisms and passive trends, the organisms evolve toward higher complexity, diversity, and adaptedness of their traits. The most important mechanisms that play a role in evolution are the accumulation of mutations, natural selection, genetic drift, evolutionary drives, speciation, and extinction.

Several fundamental events occurred in the course of evolution, such as the origin of auto-replicative molecules, the origin of genetic code, the origin of sexuality, and the beginning of cultural evolution (competition of memes). These events divide the history of life on our planet into several epochs that differ in the basic nature of their major evolutionary processes. (See "*History of Earth*").

1. Introduction

Biological evolution is the natural process of the origination of living systems (organisms) from abiotic systems, of the cumulative change of their properties, and of

their diversification and proliferation. Despite the fact that some evolutionary mechanisms are more or less deterministic (selection, evolutionary drives,) others (mutations, genetic drift, and speciation) are purely stochastic. Therefore, biological evolution as a whole is a stochastic process, i.e. one in which chance plays a fundamental role. Regardless of its stochastic nature, we can recognize several distinct trends in the process of evolution. The result of these trends is the existence of certain characteristic attributes in extant organisms.

The most striking attribute of living organisms is their complexity. Whatever the criterion used for comparing the complexity of systems (the number of different elements, the number of different processes, the amount of information necessary to describe the system etc.), any organism easily beats the most complex abiotic system. Despite the fact that their complexity is a characteristic, and possibly the most prominent property of living systems, it probably does not originate as the product of an active evolutionary trend. The high complexity and level of orderliness of living systems seem to be the result of their physical nature. From the thermodynamic point of view, living organisms are dissipative systems-open systems far from thermodynamical equilibrium. All dissipative systems (including inorganic ones) are selforganizing systems, which build up and maintain their complexity, and level of order at the expense (increase of entropy) of their surroundings. The increase in the complexity of organisms throughout evolution can also be a passive trend associated with the socalled wall effect (if we have our backs to a wall, we can go nowhere but forward). A minimal complexity limit exists that is compatible with the system being alive. The complexity of the first organisms on Earth was probably not very far from this minimal complexity limit. Due to the wall effect, however, any changes to these organisms can lead only to an increase in their complexity. An evolutionary change leading to a decrease in complexity to below the minimal complexity limit would result in the loss of viability of the now oversimplified system. The evolutionary wall effect is not a oneshot phenomenon. A minimal level of complexity probably also exists for a bacterium to remain a bacterium, for a eukaryotic organism to remain a eukaryotic organism.

The second prominent property of living organisms is the adapted-ness of their traits, both structural and behavioral. Most traits of biological systems (products of biological evolution) are highly adaptive; that is, they effectively increase an organism's chance of survival and reproduction in its natural environment. In contrast to complexity, the adapted-ness of biological systems originated as an inherent product of biological evolution. Charles Darwin explained the mechanism of the rise of adapted-ness, through natural selection, in the middle of the nineteenth century. The principle of natural selection is very simple: Organisms are auto-reproducing systems. The reproduction of organisms is not precise; due to errors in the copying of genetic information (mutations) some offspring always differ from their parents. Most mutations do not influence the adapted-ness of their carriers, and therefore the chance of their carriers to survive and reproduce, i.e. their biological fitness. A large proportion of mutations decrease the adapted-ness (and fitness) of their carriers. Only a small fraction of mutations result in adaptive changes to the properties of mutants, i.e. increase their fitness. However, the carriers of these rare mutations have a higher chance of producing more offspring than an average individual in the population. The offspring inherit their genetic information (including the rare favorable mutation) from their parents. Therefore, the proportion of carriers of this mutation continuously increases from generation to generation. Such an accumulation of favorable mutations results in the gradual cumulative build-up of complex adaptive traits, (structures and behavioral patterns) which are typical for living organisms.

The third prominent property of living organisms is their diversity. The growth of biodiversity (i.e. the increase in the number of species and the number of different forms of organisms) is not a smooth trend. In the history of life on Earth, periods of mass extinction have existed. During these periods the number of species was drastically reduced. After the end of such periods, new species always seized the emptied niches and bio-diversity quickly returned to its original level and resumed its growth. Therefore, on a longer time scale bio-diversity seems to be continuously growing.

	Has foresight	Is deterministic	Builds adaptations	Builds complexity
Mutagenesis	No	No	No	No
Selection environmental	No	Yes	Yes	Yes/no
Selection sexual	No	Yes	No (yes) ¹	Yes
Selection artificial	Yes	Yes	No	Yes/no
Selection parental	No	Yes	No	Yes/no
Selection interallelic	No	Yes	Yes/no	Yes/no
Selection interspecies	No	Yes	No	No
Species selection	No	Yes	No	No
Drives	No	Yes	No	No
Genetic drift	No	No	No	No
Speciation	No	No	No	No
Extinction	No	No (yes)	No	No

Table 1. Properties of the main mechanisms of biological evolution. The listed properties can be understood in an ordinary intuitive way. Thus a deterministic process is a process, the future course of which can be estimated on the basis of actual information. Adaptive traits are traits that help an organism to survive and reproduce. As always in biology, 'yes' means more or less yes (with some exceptions), 'no' means more or less no (with some exceptions), 'no (yes)' means usually no, sometimes yes, 'yes/no' means sometimes yes, sometimes no, and so on. (¹-see the Good-genes models).

Several mechanisms are responsible for the growth of bio-diversity. The number of species on Earth grows due to the processes of speciation. Differences among species accumulate due to genetic drift, selection, and various types of evolutionary drives. To date, we are not sure whether the trend of bio-diversity growth is continuous and active. An increase in the rate of bio-diversity growth after the end of periods of mass

extinction suggests the existence of a mechanism, or mechanisms, regulating the number of species in ecosystems. We are also unable to exclude the possibility that the increase in bio-diversity was a passive trend caused either by the wall effect, (in the very beginning, bio-diversity was null) or just a manifestation of the first law of thermodynamics (the increase of entropy in a closed system).

2. The Main Mechanisms of Biological Evolution

2.1 Mutations

Most of the genetic information of present-day organisms (i.e. instructions on how to build an organism's body) is stored in DNA. A section of DNA that can be delimited according to the function of its product is now called a gene (today's conception of a gene approximately corresponds to the original conception of a cistron). The primary structure of a gene (i.e. a linear sequence of four different nucleotides in a strand of DNA) determines the primary structure of proteins, (i.e. a linear sequence of twenty different amino acids) and therefore biophysical and biological properties of these most important building, and functional molecules of present-day organisms. The genetic information is transferred from generation to generation, by copying of the DNA double helix during DNA replication. The sequence of nucleotides in the new (copied) strand of DNA directly reflects the corresponding sequence of nucleotides in the old (template) strand. However, a certain number of errors (mutations) occur during this process. The sources of these errors are either external (physical or chemical mutagens in the environment) or internal (e.g. spontaneous transitions between normal and rare tautomeric forms of nucleotides). When replication occurs in a strand of DNA containing the abnormal form of a nucleotide, the wrong nucleotide can be inserted into the new strand of DNA. Other factors can induce the deletion or insertion of a nucleotide (or group of nucleotides) or translocation of a group of nucleotides into a different position within the DNA strand. A change in the primary structure of DNA, a mutation, may result in a change of the biological properties of the product of the mutated gene. Different forms of the same gene, products of mutagenesis, are called alleles. New mutations in somatic cells (i.e. in the cells of non-germinal tissue) can influence the properties of an organism, (can change its phenotype) and can thus alter its viability (for example, a mutation can trigger a cancerous disease). They play no role in evolution, however, because they are not transmitted to subsequent generations. Mutations in germinal cells (or in tissues which later differentiate into germinal cells) are transmitted to later generations and are in fact the driving force of evolution.

The Lamarckian model of evolution presumed that new mutations are not random in respect to their direction. According to Lamarckian followers, organisms under a particular selective pressure (e.g. subjected to a new insecticide) preferentially generate mutations, which help them to avoid the negative effects of the selecting agent (for example, making them resistant to the insecticide). On the other hand, the Darwinian model of evolution presupposes that mutations are random and undirected, and are produced regardless of the direction and nature of the selective pressure. While the mechanisms of Darwinian evolution have been described in fine detail, the mechanisms of Lamarckian evolution have never been explicitly described, and their existence remains hypothetical. Some phenomena implicitly presumed by Lamarckians, namely inheritability of acquired properties, can play a role in certain stages of evolution. Others, such as the generation of directed mutations (the preferential rise of mutations that can help an organism avoid the negative effects of selective agents), may play a role in some species under certain special conditions. For example, an amplification of the genes for the enzyme that is the target of inhibition by chemotherapy has been shown to exist in some protozoa (Leishmania). A further "Lamarckian" mechanism has been described in the form of an accumulation of favorable mutations in genes for immunoglobulins during the affinity maturation of antibodies in mammals. Special and sometimes very sophisticated molecular apparatuses are necessary for such functions. They are always destined for solving a particular problem, which the members of a population encounter repeatedly during the existence of a particular biological species. There are good reasons to believe that these adaptations, as well as all other biological structures, evolved by the classical Darwinian mechanisms. Many sophisticated experiments have shown that the mutations responsible for the evolution of organisms are random (at least as concerns their direction and usefulness). Therefore, the basic principle of Darwinian evolution-selection from randomly generated variants-is correct.

- -
- _
- _
- TO ACCESS ALL THE **21 PAGES** OF THIS CHAPTER, Click here

Bibliography

Dawkins R. (1976). *The Selfish Gene*, 224 pp. Oxford: Oxford University Press. [A stimulating book in which the important mechanism of modern evolutionary biology, i.e. the theory of inter- allelic selection, which was implicitly contained in papers of W.D. Hamilton, was articulated (under the name "*Theory/Hypothesis of Selfish Gene*").]

Fisher R. A. (1958). *The Genetical Theory of Natural Selection*. New York: Dover Publications. [Classical and very influential work of neo-Darwinism. Many basic ideas of modern evolutionary biology were discussed here for the first time.]

Flegr J. (1998). On The "Origin" of Natural Selection By Means of Speciation. Rivista di Biologia– Biology Forum **91**, 291–304. [This presents a comprehensive discussion of the theory of frozen evolutionary plasticity of sexual species.]

Gould S. J., and Eldredge N. (1993). *Punctuated Equilibrium Comes of Age. Nature* **366**, 223–227. [Thoughtful review of empirical evidence for the punctuated equilibrium theory.]

Hamilton W.D. (1967). *The Genetic Evolution of Social Behavior (Part I and II). Journal of Theoretical Biology* **7**, 1–52. [This was the first presentation of basic ideas of inclusive fitness and kin selection. Later on, these ideas were developed into the theory of inter-allelic selection (selfish gene).]

Kimura M. (1983). *The Neutral Theory of Molecular Evolution*, 367 pp. Cambridge: Cambridge University Press. [This book presents a comprehensive survey of the whole theory of neutral evolution.]

Maynard Smith J., and Price G. R. (1973). *The Logic of Animal Conflict. Nature* **246**, 15–18. [Development of the conception of evolutionarily stable strategies (ESS), which represents a very important component of modern evolutionary theories.]

Mayr E. (1963). *Animal Species and Evolution*. Cambridge, MA: The Belknap Press of Harvard University Press. [A stimulating and comprehensive book about mechanisms of speciation. The elementary components of the frozen evolutionary plasticity theory were already presented here (in the chapters on genetic homeostasis, and on genetics of speciation).]

Raup D. M. and Sepkoski J. J. (1984). *Periodicity of Extinctions in the Geologic Past*. Proceedings of the National Academy of Sciences of the USA **81**, 801–805. [The authors' proposed the existence of periodicity in the mass extinction events.]

Biographical Sketch

Doc. RNDr. **Jaroslav Flegr** GR, CSc. Born 1958, Prague. Biologist, Associate Professor of Parasitology, Faculty of Sciences, Charles University, in Prague. Teaching activities: evolutionary biology, theoretical and evolutionary parasitology, molecular taxonomy, and practical methodology of sciences. Research activities: evolutionary biology, etoparasitology, (manipulation hypothesis,) and molecular systematics of parasitic protozoa. List of papers (including their electronic versions) is available at www.natur.cuni.cz/flegr. Most important papers: Flegr J., 1990: Does A Cell Perform Iso-electric Focusing? *BioSystems* 24, pps. 127–133. Flegr J., Zitková Š., Kodym P., and Frynta D.; 1996: Induction of Changes in Human Behavior by the Parasitic Protozoan Toxoplasma Gondii. Parasitology, 113, pps. 49–54. Flegr J., 1997: Two Distinct Types of Natural Selection in Turbidostat-like and Chemo stat-like Ecosystems. Theoretical Biology Journal 188, pps. 121–126. Flegr J., 1998: On the Origin of Natural Selection By Means of Speciation. Riv.Biol. /B. Forum, 91, pps. 291–304.