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1.1.6.2. EVOLUTIONARY MECHANISMS AND PROCESSES

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Natural selection, genetic drift, molecular drive, speciation, extinction, RNA world, sexual reproduction, evolutionary plasticity, cultural evolution, meme

Contents

Glossary

Alleles: Different forms of the same gene occupying the same locus (the same place on homologous chromosomes).
Anagenesis: Processes by which the characters of organisms change during evolution.
Assortative mating: Non-random mating, involving selection of breeding partner, usually based on some aspect of its phenotype. This 'choice' may be positively assortative (the organism chooses a breeding partner that is like itself in some respect) or negatively assortative (the organism chooses a partner that is unlike itself in some respect).
Chemostat: Device for continual cultivation of a microorganism. In the chemostat, the population size is regulated by the limited availability of some resource.
Cistron: Length of DNA (or RNA in some viruses) encoding a specific and functional product, usually a protein.
Cladogenesis: Processes of sequential splitting of daughter taxa from their ancestors.
Cultural evolution: Competition and differential fixation of particular memes.
Effective size of the population: The size of an ideal population or a real population for which the influences of assortative mating, unequal proportions of males and females, fluctuation of the population size over time, fluctuation of the number of offspring between families, etc., are mathematically filtered out.
Epistatic interactions: Interactions between genes. Due to epistatic interaction the effect of an allele on the phenotype depends on the presence or non-presence of particular alleles of other genes.
Evolutionarily stable strategies (ESS): A heritable (commonly but by no means always behavioral) strategy which, if adopted by (expressed in) most members of a population, cannot be supplanted in evolution by an alternative (mutant) strategy.
Fitness: Factor describing the difference in reproductive success of one individual or genotype relative to another.
Gametogenesis: Production of gametes (germ cells). It frequently, but by no means always, involves meiosis (reduction division).
Gene: Smallest physical unit of heredity encoding a molecular product (usually a protein).
Gene pool: All of the genes contained in the genetic makeup of a population (or a species).
Genetic code: Set of rules for the assignment of each of the 64 possible combinations of triplets of nucleotides to one of 20 different amino acids.
Genotype: Genetic constitution of a cell or individual.
Homologous chromosomes: Chromosomes capable, at least potentially, of pairing during meiosis, having approximately or exactly the same order of loci. A normal (diploid) cell has pairs of such chromosomes (one copy of the same chromosome inherited from each parent).
Immunoglobulins: Molecules of antibodies.
Locus: Position on homologous chromosomes occupied by those genes which determine the state of a particular phenotypic characteristic.
Meiosis: Process whereby a cell nucleus divides in two divisions into four nuclei, each containing half the original number of chromosomes.

Meme: Cognitive or behavioral pattern that is capable of being copied by another individual of the same or even of a different species.
Mitosis: Process of division of a cell nucleus which produces two daughter nuclei, genetically identical to each other and to the original parent nucleus. It is commonly accompanied by division of parental cytoplasm around the daughter nuclei to produce two daughter cells (cell division).
Oocyte: Ovum in the stages that precede maturation.
Phenotype: Total appearance of an organism, determined by interaction during development between its genetic constitution (genotype) and the environment.
Polymorphism: Simultaneous occurrence in a species population of two or more discontinuous forms in such a ratio that the rarest of them could not be maintained solely by recurrent mutation.
Polyploidization: Amplification of a chromosomal set, usually through failure of replicated chromosomes to separate during the cell division.
Symbiogenesis: Fusion of two different organisms belonging to two distinct biological species into one integrated organism (holobiont).
Tautomeric forms of nucleotides: Two or more structures of nucleotides that differ in the placement of a hydrogen atom and its double bond, able to react in either structure.
Turbidostat: Device for continual cultivation of a microorganism. In the turbidostat, population size is regulated by the density of population-dependent elimination of organisms from the cultivation tank.

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 autoreplicative 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.

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, 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 self-organizing 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 so-called 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 one-shot 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 adaptedness 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 adaptedness of biological systems originated as an inherent product of biological evolution. The mechanism of the rise of adaptedness through natural selection was explained by Charles Darwin 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 adaptedness 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 adaptedness (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 biodiversity quickly returned to its original level and resumed its growth. Therefore, on a longer time scale biodiversity 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 artifitial	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 main mechanisms of biological evolution. *The listed properties can be understood in a common intuitive way. It means, a deterministic process is a process, a future course of which can be estimated on the basis of actual information. Adaptative traits are such traits that help an organism to survive and reproduce. As always in a 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, etc.. [1] see the Good-genes models.*

Several mechanisms are responsible for the growth of biodiversity. 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 biodiversity growth is continuous and active. An increase in the rate of biodiversity 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 biodiversity was a passive trend caused either by the wall effect (in the very beginning, biodiversity 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 nongerminal 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 Lamarckians, 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 (see sections 3.1 and 3.4). 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.

2.2. Natural Selection

The mechanism of natural selection has already been described above. Selection exists in several forms and acts on several levels. *Directional selection* preferentially eliminates individuals from one end of the distribution scale of a quantitative trait (e.g. the smallest individuals) from the population. If the trait is determined genetically, this kind of selection results in a continual shift of the population mean of the trait subjected to selective pressure. *Stabilizing selection* eliminates individuals from both ends of the distribution scale (e.g. both the largest and smallest individuals). This type of selection plays an important role in keeping the properties of a given species stable (regardless of the continuous nature of the process of generation of variation through mutagenesis). *Disruptive selection* eliminates individuals from inner parts of a distribution scale (e.g. the individuals of middle size). Under certain conditions, this kind of selection can result in the origin of a new species (see section 2.5).

Hard selection eliminates all individuals that fulfil some limit condition (e.g. all individuals with body weight less than 10 g). *Soft selection* eliminates a certain fraction of individuals from the population (e.g. the 30 % of smallest individuals).

Random selection eliminates individuals from the population randomly (regardless of their phenotypes). Such selection can result in an increase in the reproduction rate of organisms subjected to random selection.

K-selection (originally *k-selection*) occurs in so-called bottom-up-regulated populations, i.e. in populations whose size is limited (and regulated) by the available amount of some resource. On the other hand, *r-selection* occurs in top-down-regulated populations, i.e. in populations limited (and regulated) by the adverse effects of predators (herbivores) or parasites. It is very common in two-species ecosystems (predator-prey ecosystems) that the population of prey is r-selected (due to the activity of a predator), while the population of predators is K-selected (through the availability of prey). In a K-selected population the criterion of fitness is the effectiveness of transformation of resources into biomass of offspring (in bacteria growing in a chemostat, for example, the amount of energy, the number of molecules of ATP,

produced from one molecule of glucose). In r-selected populations the critical property of organisms (and the only one subject to selection) is the rate of transformation of a resource into a biomass (in bacteria in a turbidostat, for example, the growth rate).

Selection can be also classified with respect to the selecting agents. *Environmental selection* occurs due to the action of biotic and abiotic environmental factors. *Sexual selection* acts due to preferences for individuals with a certain trait (or combination of traits) by their mating partners, or due to active competition (fights or combats) among representatives of the same sex for mating partners. Sexual selection can only increase the individual fitness of an organism on account of the fitness of other members of the population. While environmental selection nearly always increases the average absolute fitness of organisms in a population (the so-called *fundamental theorem of evolutionary biology*), sexual selection can often result in the evolution of traits that have a negative influence on the average fitness of organisms. Due to sexual selection, traits with a negative influence on the viability of organisms (such as extremely long and vivid feathers in some birds) can evolve, mostly in members of only one of the sexes (usually in males). The runaway process described in the 1930s by a prominent figure of modern evolutionary biology (and modern statistics), R.A. Fisher, is probably the main factor responsible for the evolution of such sexually selected traits. When females start to prefer the males with the longest tails, they cannot stop or reverse their preferences, even if the viability of males with extremely long tails (the final products of sexual selection) is low. The attractiveness (and therefore the fitness) of viable sons of a mutant female which prefers short instead of long tails (and mates with short-tail males) would be very low because they have short tails like their father, and most females in the population prefer long-tailed males.

Alternative hypotheses (*Good genes hypotheses*) suggest that it is useful for females to mate with males with over-evolved sexual traits as the presence of these traits suggests that some other genes (genes for the utilitarian aspects of survival and reproduction) of these males are probably very good. The *Indicator hypothesis* suggests that only males in good health are able to fully express the sexual trait and the *Handicap hypothesis* suggests that among the males handicapped by prominent sexual traits only the individuals with very good genes can survive to maturity.

Some traits can evolve due to *parental selection*. For example, the glaring interior of the beak and sometimes even the colorful plumage of chicks probably evolved due to a tendency on the part of the parents to preferentially feed the chick with the most glaring beak interior or the most colorful plumage.

Artificial selection operates due to human activity, either intentional (breeding of new varieties of plants of animals) or unintentional (a systematic tendency to prefer more docile individuals or individuals with attributes resembling children).

A very important kind of selection is *frequency-dependent selection*. This occurs whenever the biological fitness of carriers of a certain trait depends on their frequency in a population. The existence of a negative correlation between the fitness of carriers and their frequency can result in the long-term preservation of a polymorphism, i.e. in the stable balanced coexistence of different alleles of a particular gene in the gene pool of a population. In many cases the fitness of carriers of a particular trait depends only indirectly on their frequency; it depends on the frequency of carriers of a second trait, while the frequency of the second trait is again dependent on the frequency of carriers of the first trait. For example, the fitness of red-beaked males can be positively influenced by the frequency of females with the gene for preferring red-beaked males. The frequency of such females must positively correlate with their fitness and this fitness can often correlate with the availability of red-beaked males in the population, i.e. with the frequency of the gene for red beaks in the gene pool of the population.

In such interconnected systems of various alleles of different genes, the relative fitness of carriers of a particular trait (and therefore also the final destiny of a new mutation) does not depend on the average fitness of carriers of a particular allele but rather on the evolutionary stability of a particular trait-associated strategy (in terms of game theory). Only the mutations (traits) associated with *evolutionarily stable strategies* (ESS) can be fixed by selection during evolution.

Competition for ESS among different alleles, rather than competition for higher fitness, is very common and probably prevails in organisms with sexual reproduction. In these organisms, the fitness of carriers of a particular allele mostly depends on the likelihood of meeting particular other alleles in the progeny (which depends on the genotypes of mating partners and therefore on the frequencies of different alleles in the population).

Selection can also be classified in terms of the nature of the units being selected. *Individual selection* was the type of selection originally described by Charles Darwin. In this type of selection individual members of a population compete for the highest biological fitness, i.e. for the highest number of offspring.

In sexually reproducing organisms, individual selection is in fact only an epiphenomenon of *interallelic selection* (most explicitly described as the theory of the selfish gene by R. Dawkins). In interallelic selection different alleles of the same gene compete for the highest number of copies transmitted to the gene pool of subsequent generations. The allele that brings the highest fitness to its carriers usually wins. Therefore, interallelic selection usually resembles classical individual selection. Some alleles, however, use quite different strategies to increase the number of copies of themselves in the gene pool of later generations. Sometimes they even do this at the expense of the biological fitness of their

carriers. Certain alleles are able to damage gametes bearing a different allele on the homologous chromosome (i.e. on the copy of the same chromosome inherited from the second parent) during or after gametogenesis. The carriers of such selfish alleles therefore produce only half the number of gametes (and consequently have lower fertility and therefore a lower biological fitness than carriers of other alleles). However, all their gametes bear the selfish allele - which results in an increase in the frequency of the selfish allele in the later generation.

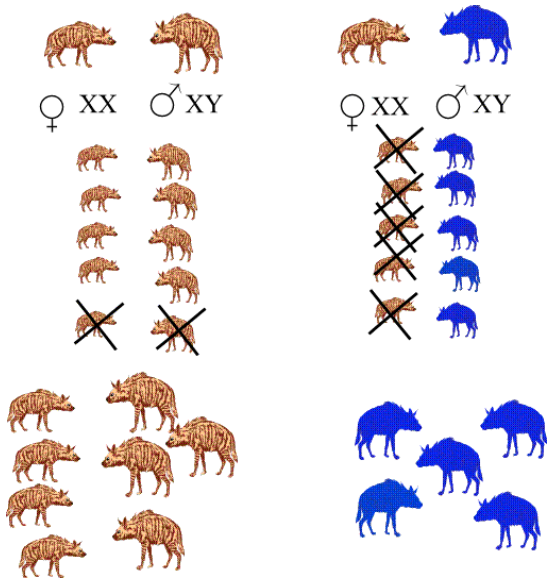

Figure 1. Model of spreading of the Bluebeard allele in a population. *This hypothetical model clearly illustrates the fundamental difference between the Darwinian model of evolution of adaptive traits based on individual selection and the current model of such evolution based on competition between alleles within the same locus. A male with a normal (inactive) allele of a Y-chromosome-localized Bluebeard gene has five daughters and five sons (only the sons have Y-chromosome and carry the copies of Bluebeard gene). In every family eight children usually survive to full age and two children die because of malnutrition. The Bluebeard (active) allele programs its carrier (male) to kill all his newborn daughters. Therefore, this allele sharply decreases the fitness of its carriers. According to Darwinian theory of individual selection the active Bluebeard allele should be quickly eliminated from the population. On the other hand, the theory of interallelic selection (theory of selfish gene) correctly predicts that the Bluebeard allele will spread through the population.*

Some alleles are able to "program" their carriers to help other carriers of the same alleles. Mostly, the carriers of such alleles help to increase the biological fitness of their relatives. This phenomenon was originally described as *kin selection*. From the point of view of an allele there is no difference between programming its carrier to produce one more young (than average members of the population) and programming its carrier to help his/her parents to produce two more sisters or brothers (or to help to his/her aunt to produce four more cousins). It is often practical to recognize two types of fitness, *exclusive fitness* (measured in terms of the number of offspring of a particular individual) and *inclusive fitness* (which also includes fitness realized by helping relatives to reproduce).

Attributes favorable from the point of view of the survival of a whole group of individuals can evolve by the process of *group selection* (interpopulation or inter-deme selection). Such an attribute might be, for example, altruistic behavior towards unrelated individuals in a group. Today, group selection is usually considered to be an unimportant mechanism for the evolution of altruistic behavior. A group containing altruistic individuals can produce more offspring than groups without altruists, yet the altruistic individuals within the group have lower fitness than selfish individuals in the group. Therefore, the frequency of altruists within the group must continuously decline. It can be argued, however, that certain types of demographic population structure (periodic breaking-up of groups and their formation anew from unrelated individuals) might improve the chance of development of altruistic behavior by group selection. Similarly, the effectiveness of group selection increases in situations where altruistic behavior requires the co-occurrence of particular alleles of several genes in the genome of one individual.

Similar and even stronger arguments to those against the importance of group selection in evolution also hold with respect to *interspecies selection*. Competition between different species can play a role in delimitation (narrowing) of niches of a particular species, or in the extinction of a species. However, the creative capacity of possible interspecies selection (evolutionary victory for the "fitter species") is highly limited. The evolution of good-for-species traits would be overpowered by the evolution of good-for-individual traits - the result of individual (or interallelic) selection. Moreover, the lifetime of a species is too long to allow sufficient species turnover, which would be a necessary precondition for cumulative evolution of adaptive traits by means of interspecies selection.

Species selection is caused by competition between species (or higher taxa) for the highest rates of speciation – i.e. for a higher rate and frequency of succession of new species – and for the lowest rates of species extinction. The taxa with a higher frequency of speciation are more successful in the long term, despite the fact that the attribute responsible for the higher rate of speciation (e.g. low mobility or narrow ecological niches of organisms) might be disadvantageous from the point of view of individual selection. It is possible that some of the most important traits of today's organisms (including sexual reproduction, which occurs in most organisms, and whose existence is very difficult to explain in terms of individual or interallelic selection) originated by means of species selection. On the other hand, all adaptive traits, which represent the most typical traits of living systems, evolved by individual selection (by interallelic selection

in sexual organisms). Only individual and interallelic selection are able to construct complex adaptive traits by gradual accumulation of favorable mutations from a pool of random (undirected) mutations.

2.3. Genetic Drift

The large majority of all mutations are fixed in the gene pool of a population (i.e. they replace other alleles of a particular gene in genomes of all members of the population) due to genetic drift. One hundred copies of each particular gene exist in the population of N=50 diploid animals. After enough time, on average after 4 N generations in an ideal population (thus, in our population, after 200 generations), only the copies of one of the 100 original alleles will remain in the gene pool. The descendants of all 99 other alleles vanish due to stochastic processes, i.e. due to genetic drift. The probability of fixation of a new mutation is the same as that of any other allele, i.e. it is equal to 1/2N. An identical number of selectively neutral mutations is fixed in small and large populations during an equal period: in small populations the probability of fixation of a mutant allele is higher, but the total number of new mutations which arise during the period depends on the size of the population and is therefore proportionally smaller in a small than in a larger population. Regardless of this fact, the effect of drift is more visible and more important in smaller populations. In small populations the effect of drift prevails over the effect of natural selection, namely over the effect of stabilizing selection. It can be shown that the destiny of mutation is determined by natural selection under the condition:

$$\mathrm{abs}(s) \geq (1/N_e) \qquad (1)$$

(s is the difference between the fitness of carriers of a mutant allele and the average fitness of the carriers of all other alleles in the population, and N_e is the effective size of the population, i.e. the size of an ideal population or a real population for which the influences of assortative mating, unequal proportions of males and females, fluctuation in the population size in time, fluctuation in the number of offspring between families, etc., are mathematically filtered out). This means that in a small population, a large fraction of mutations behave as if they were selectively neutral; that is, their destiny is determined by chance (genetic drift) rather than by natural selection. Therefore, a large number of mildly deleterious mutations (which would be eliminated by natural selection in large populations) are fixed by genetic drift in small populations.

2.4. Evolutionary Drives

Evolutionary drives are evolutionary mechanisms responsible for systematic and more or less deterministic spreading of a certain category of alleles through the gene pool of a population. These alleles are usually neutral or slightly negative from the point of view of the biological fitness of their carriers, yet they are still able to transmit more copies of themselves into later generations than their competitors.

For example, segments of so called *selfish DNA* – the segments of DNA whose presence or absence has no influence on the phenotype and therefore on the fitness of organisms – spread through the genome and through the gene pool due to *molecular drive*, i.e. due to their capacity for multiplicative self-replication. An interesting mechanism for the multiplication of selfish DNA is *gene conversion*. In gene conversion, one allele (master) acts as a template for overwriting a sequence of nucleotides of a second (slave) allele (for example, the allele on the homologous chromosome from the second parent or of a segment of DNA with a similar nucleotide sequence localized in another position in the genome).

Meiotic drive is responsible, for example, for the spreading of alleles that are able to help the chromosome in which they are located to enter the nucleus of the oocyte instead of the polar body (the dead-end product of oocyte development) during oogenesis.

Some mutations are fixed due to *mutational drive* (or mutational pressure/bias), i.e. due to their tendency to arise repetitively in the same places of a nucleotide sequence. For example, simple runs of the same nucleotide, such as AAAAA, are prone to the insertion of another A nucleotide, i.e. they have a tendency for protraction. The dinucleotides CG are highly prone to substitution by TG, and so on.

Reparation drive results in preferential reparation of certain mutations by a specific nucleotide. It can be shown that many reparation mechanisms of a modern cell are tuned to express exactly the kind of reparation drive that can neutralize a particular type of mutation drive.

2.5. Speciation

The evolutionary mechanisms described above play a role mainly in anagenesis, i.e. in the processes of the change in properties of living organisms. The second facet of evolution is cladogenesis, i.e. sequential splitting of daughter taxa from their ancestors. Organisms with similar anagenesis (which could be the result of similar selection pressures) usually have similar properties (similar phenotypes). Organisms with a common cladogenesis, i.e. phylogenetically related organisms, may be very similar (due to their common evolutionary history), but they may also be very different - if they have been subjected to very different selective pressures.

The most important mechanism of cladogenesis is speciation - the origination of new species. In evolution each species originates from some older species. The composition and structure of basic molecular and cellular systems suggest that all current species of organisms on Earth originated from a single common ancestor. The origination of a new species by the gradual transformation of all individuals of an old species is called *phyletic speciation*. True speciation (*splitting speciation*), i.e. the separation and differentiation of part of an old-species population, results in an increase in the number of species. True speciation is probably far more common than phyletic speciation and can be classified into several categories.

There is a basic categorization into *sympatric* (inhabiting the same place) and *allopatric* (inhabiting a different place) speciation. *Sympatric speciation* is the origin of a new species within the biogeographic range of the ancestral species; both species live in the same place at the time of speciation. The critical condition for sympatric speciation is the creation of a reproductive isolation barrier, a mechanism that can effectively disrupt the flow of genetic information (mating) between the new and the old species. A typical example of a genetic reproductive barrier is polyploidization (the doubling of the number of chromosomes in the cell nucleus), which can often result in the sterility of hybrids between the ancestral and the polyploid species. An example of an ethological reproduction barrier is the origination of a new allele for mating preference. The presence of such an allele can result in assortative mating, i.e. in preferential mating between individuals with a particular phenotypical trait, leading to reproductive isolation of these individuals from the ancestral species. Disruptive selection, i.e. selection against individuals with an average value of a particular quantitative phenotypical trait can also, under certain conditions, result in the splitting of a species into two new species.

Allopatric speciation is the emergence of a new species from a population that is out of contact with the main population of a species. A typical example of allopatric speciation is the genetic and phenotypical differentiation of descendants of plants or animals which colonized an island, or the differentiation of two populations of a species whose range was split by a new geographical barrier (e.g. by a glacier). The later is also called *vicariant speciation*. In allopatric speciation, genetic barriers for reproduction (the sterility or inviability of interspecies hybrids) develop gradually during the existence of the new species by the slow accumulation of incompatible mutations in the separated gene pools of both species. If the geographical barrier disappears before the end of the process of formation of the genetic barrier, the two species can again fuse as one.

A new species usually develops from a single ancestral species. In some situations a new species can originate from the fusion of two different species. In many taxa of plants, a new species can originate by hybridization of members of two different species. Sometimes, the new species are viable and fertile immediately after hybridization. Sometimes, the fertility of the hybrid is restored only after a subsequent polyploidization event (i.e. after the amplification of a chromosomal set). Such polyploidization can help to avoid problems with the separation of chromosomes during meiosis, and can therefore restore the production of fertile seeds.

The second mechanism of the origination of new species from two ancestral species is *symbiogenesis*. Symbiogenesis is a very important if relatively rare evolutionary mechanism, which undoubtedly played an enormous role in the process of biological evolution. Symbiogenesis, the fusion of two different organisms belonging to two distinct biological species into one integrated organism, is responsible for the origin of prime innovations in the history of life on Earth. Mitochondria and plastids (e.g. chloroplasts) of a modern eukaryotic cell were originally bacterial symbiotes (intracellular endosymbiotes, i.e. endocytobiotes), most of whose genes passed into the nucleus of their host cell. Notorious examples of organisms originated by symbiogenesis are lichens, products of the symbiosis of fungi (the host) and algae or blue-green algae (the extracellular endosymbiot). It is far less known, however, that many taxa of algae are in fact complex products of several serial endosymbiotic events.

2.6. Extinction

Extinction, i.e. the extinguishing of a biological species, is in some respects the opposite process to speciation. An extinction event results in a decrease in the number of species in an ecosystem and, therefore, in a decrease in the Earth's biodiversity.

Extinctions can be divided into *mass extinctions* and *background extinctions*. The duration of the existence of a species differs within as well as between taxa. For mammals the average time of existence of a species is about five million years. It is difficult to discover the causes of the extinction of one particular species. Generally, however, it can be either bad luck (the presence of the population in the wrong place at the wrong time) or an inability to adapt to changing conditions. These changes can sometimes be very rapid and very drastic and can involve a large section of the biosphere. Such dramatic changes can be caused or at least triggered by a large asteroid impact or by a sharp increase in volcanic activity. In the Earth's history, we usually identify five important periods of mass extinction, the “Big Five”. It is estimated that during the mass extinction at the end of the Permian epoch, between 80-96 % of all marine species became extinct. The intensity of current extinctions associated with human activities is often suggested to be comparable with that of a typical mass extinction.

It has been suggested that mass extinctions (including the “Big Five”) occur at more or less regular intervals of about 26

million years. For now, the evidence for this periodicity is not very convincing. If the 26 million year cycle really exists, then the length of the cycle suggests that the cause of mass extinctions is an astrophysical phenomenon (such as periodic asteroid impacts) rather than any geological or even biological phenomena.

The causes of specific background extinctions are even more diverse. A change in abiotic conditions (e.g. the climate) can be the cause of extinction of some species. However, such changes are usually only local and relatively slow, and therefore the species can react to them by changing their biogeographic range or by evolutionary change of their properties. Therefore, biotic influences (activity of a competitor, a new parasite or a new predator) are far more probable candidates for the explanation of most background extinctions (especially in species with large biogeographical ranges).

3. Major Steps in Evolution

Several fundamental events occurred in the course of evolution. These events divide the history of life on our planet into several epochs that differ in the basic nature of the processes of biological evolution. The fundamental steps in evolution are the origin of autoreplicative molecules, the beginning of the cooperation of nucleic acids and proteins, i.e. the origin of genetic code, the origin of sexuality, and the beginning of cultural evolution.

3.1. The RNA World

The origin of life and the beginning of biological evolution was closely connected with the origin of molecules or supramolecular complexes that were capable of auto-reproduction. The obvious mechanism of auto-reproduction is the replication of one-dimensional structures - linear molecules of a heteropolymer (such as DNA); theoretically, two-dimensional structures (such as biomembranes or even mineral surfaces of clays) are also possible candidates. Only those systems with the capacity for auto-reproduction are able to generate hereditary variants, which can compete for effectiveness of reproduction and therefore evolve complex adaptive structures and behavioral patterns by the mechanism of natural selection. The chemical nature of the first auto-reproducing systems is not known. Some facts, however, suggest that RNA or a molecule similar to RNA is a good candidate. Important indirect evidence for the RNA nature of the first autoreproducing molecules is the existence of ribozymes, molecules of RNA that have both the enzymatic function and also the ability to act as a template for replication. Further evidence is provided by the chemical nature of many coenzymes, i.e. nonprotein components of active centers of normal enzymes. These coenzymes are very often derivatives of ribonucleotides or their precursors. The first epoch of evolution, delimited by the origin of life at one end and the origin of genetic code at the other, is therefore often called the RNA world.

The main subject of evolution in the RNA world was the competition between different strands of RNA (or similar molecules) for the maximum rate of replication. Molecules of RNA differed in their sequences due to errors in replication. These differences in their primary structure resulted in differences in their three-dimensional structure and therefore also in their resistance to degradation and liability to replication. “Lamarckian” mechanisms of evolution (in the sense of heritability of acquired properties) may operate to an extent in the first epoch of evolution, as some of the acquired changes in the structures of organisms (in molecules of RNA) can be transmitted into later generations by the process of replication. (The second precondition for the existence of Lamarckian evolution, the existence of directional mutations (adaptive changes) induced by the environment, is however still absent).

3.2. The Asexual DNA World

Only Darwinian mechanisms of evolution can play a role in evolution in the modern DNA world. Errors in the copying of a replicator (DNA, or RNA in some viruses) result in changes in the properties of interactors (the organism’s bodies). Changes in an organism’s properties influence the efficiency of its functions, and consequently the probability of its survival until maturity, i.e. the probability of successfully passing on copies of its replicator to the next generation. However, changes in an organism’s properties (in phenotype) can not influence the replicators. The beginning of cooperation between nucleic acids (replicators) and proteins (the main building blocks of interactors) is closely linked to the origin of the proteosynthetic apparatus, namely the origin of genetic code. With some simplification we can say that in the proteosynthetic process, a sequence of four different nucleotides in a linear chain of DNA is translated into a sequence of 20 different amino acids in a linear chain of proteins. The genetic code is a set of simple rules for the assignment of each of the 64 possible combinations of triplets of nucleotides to one of 20 different amino acids. Using this Morse Code-like dictionary, the proteosynthetic apparatus translates genes into proteins, i.e. synthesizes the most important components of living organisms. The evolution of the genetic-code-based proteosynthetic apparatus is one of the two biggest evolutionary mysteries (the second being the evolution of sexual reproduction). In present-day organisms, the proteosynthetic apparatus is a very efficient device for the synthesis of tens of thousands of different proteins, using only several hundred components. However, at the beginning of evolution organisms were far simpler, probably containing between several tens and several hundreds of different molecules. Therefore, it must be asked what value complicated proteosynthetic apparatus could have had for such simple organisms. At the same time, it is also difficult to imagine the existence of a substantially simplified version of the proteosynthetic apparatus.

The second problem connected with the origin of genetic code concerns its capacity to evolve. It is very difficult to imagine a transition between a simple variant of a genetic code (e.g. a duplets code) into a more advanced one (e.g. a triplets code) without losing all the genetic information written in the DNA by the original code. At present, however, we have at least two independent lines of evidence for the genetic code's capacity to evolve. One is the existence of slightly modified genetic codes, mostly in the organelles of eukaryotic organisms. Another is the fact that similar amino acids are usually coded by similar nucleotide triplets, which suggests that the present genetic code evolved by the gradual expansion of some primitive ancestor code.

3.3. The Sexual DNA World

The third major step in the evolution of life on Earth was the origin of sexual reproduction. At the present time, most organisms are regularly or at least periodically involved in some form of sexual process. Only few lines of asexual organisms exist today and most of them represent only terminal branches within a taxon of sexual species. At the same time, asexual individuals would theoretically outcompete sexually reproducing rivals, usually within a few generations, because a population of asexual females would multiply at twice the rate of a population of sexual females. Since the 1970s, a number of different theories have been suggested to explain the existence of sexual reproduction in modern organisms.

The first group of sex-origin hypotheses supposes that sexuality is a good-for-population or good-for-species phenomenon which evolved due to either an interpopulation (group) or an interspecies selection. According to one hypothesis, sexual reproduction generates variability of individuals within populations and within species, which increases the capacity of populations or species to respond to environmental selective pressure. Another hypothesis points out that two or more different advantageous mutations can undergo fixation at the same time in a population of a sexual species (when they meet in one individual), while in an asexual population, only the best mutation can be fixed while the other (benefitial) mutations are eliminated from the population. Another hypothesis points out the fact that in an asexual population, genetic drift causes a continual accumulation of mildly deleterious mutations, a process called Müller's ratchet. In sexual populations, the deleterious mutations are repeatedly concentrated in certain individuals, selection against whom removes these mutations from the gene pool. These hypotheses are probably wrong. Under most conditions group selection is much weaker than individual selection and no force exists to intercept spreading of asexual mutants within a population of sexual organisms (regardless of the fact that the victory of asexuals decreases chances of the whole population or the whole species for long-term survival).

A second group of hypotheses suggests that sexuality increases either the exclusive or inclusive fitness of an individual. Sexual reproduction is, for example, considered to be an important mechanism for the reparation of certain classes of DNA damage. The existence of asexual species, however, contradicts the general validity of this hypothesis. Differences between offspring in sexual species lessen intra-kin competition which increases their inclusive fitness. Also, differences between offspring and parents increase the chance of sexual individuals outcompeting asexual ones under conditions of continuous attack by parasites. The evolution of parasites is usually much faster than the evolution of their host. Therefore, parasites can quickly adapt to the genotypes of the most common variants of their host. In sexual species, new (parasite-resistant) genotypes originate by genetic recombination in every generation and therefore they can (temporarily) escape their enemies.

Hypotheses of evolutionary traps suggest that the evolution of sexuality may be a one-way process. One example of such a trap is the accumulation of recessive lethal mutations in gene pools of diploid species. These mutations have only a marginal influence on the viability of sexual progeny because there is only a small probability that a child will obtain a copy of the same lethal mutation from both parents. On the other hand, asexual progeny obtain both copies of each of their genes from the same parent, which highly increases the probability of their inviability due to obtaining two copies of a lethal allele.

Another hypothesis suggests that sexuality is a product of species selection. According to this hypothesis, sexual reproduction exists because it positively influences the probability of speciation (or negatively influences that of extinction), rather than because of a positive influence on the fitness of members of sexual species.

The evolution of a sexual species differs in one very important respect from the evolution of an asexual one. While asexual organisms can easily evolve under selective pressures by classical Darwinian mechanisms, the same is not true for sexual species. The principal obstacle for evolution by natural selection is low heritability of biological fitness, and often also low heritability of polygenic traits. The fitness of an organism is determined by its phenotype. However, the influence of certain phenetic traits on fitness is highly "context-specific", i.e. the same trait can be useful in the context of certain traits, and in the context of other traits can be harmful. Similarly, the influence of a particular gene on the phenotype is often context-specific (in this case genotype-context-specific). Due to so-called epistatic interactions between genes, the effect of an allele on the phenotype depends on the presence or absence of particular alleles of other genes. In asexual organisms the genotype is transmitted between generations in an unchanged form. Therefore, a particular allele has the same influence on the phenotype (and fitness) of both parent and progeny. In sexual organisms, the genotypes of offspring arise "anew" every generation by mixing the genes from the two parents. Therefore, the same allele (mutation) occurs in every generation in the context of a different genotype, and its influence on the

phenotype and fitness might dramatically differ even in its sign. This makes an evolutionary response of a sexual species to selective pressures difficult. While asexual species are, as a rule, evolutionarily plastic for the whole duration of their existence, populations of sexual species are plastic only under conditions of low genetic polymorphism (when the allele occurs in every generation in the same or a very similar context). Such situations occur for example after a bottleneck-including speciation event or in experiments with small or inbred populations. Under normal conditions, the response of a population to selection is slow and mostly transient, i.e. after termination of the selection and breeding program the phenotypes start to return to their original values. Therefore, most anagenetic changes in the evolution of sexual species are probably concentrated only within the earliest period of the existence of a new species. After the accumulation of genetic variance the evolutionary plasticity of a species decreases or disappears. The species loses the ability to respond adaptively to changes in the biotic and abiotic environment and for the rest of its sometimes long existence only passively waits for its terminal extinction.

The freeze-up of evolutionary plasticity of sexual species is probably the reason for the punctualistic nature of evolution of most multicellular (sexual) species in the paleontological record. Current paleontological data mostly supports a punctualistic picture of the evolution of multicellular organisms, in which morphological changes of species are associated with the moments of speciation while an evolutionary stasis, i.e. an absence of anagenetic changes, is characteristic for the rest of their existence. This contradicts the gradualistic picture of evolution deduced from the neo-Darwinian model which supposed that most morphological changes should occur due to intraspecific (or interallelic) selection operating during the whole existence of the species. According to this model, most adaptive changes should occur in large populations where the effectiveness of natural selection is highest. Cladogenesis and anagenesis should be two independent processes. In contrast, the frozen plasticity model suggests that the capacity to evolve a new adaptive trait in a large stabilized population with a natural level of variance is highly limited, if it exists at all. Most adaptive changes in sexual species evolve in small, genetically isolated populations under conditions of decreased variance and increased heritability of fitness, i.e. in the earliest period of the existence of a new species.

	replicator	interactor	Lamarckian mechanism	Darwinian mechanism	horizontal transmission	gradualistic evolution
RNA world	RNA	RNA	yes	yes	no	yes
Asexual DNA world	DNA (genome)	organism	no	yes	no	yes
Sexual DNA world	gene	organism	no	yes	no	no
Cultural evolution	meme	organism	yes	yes	yes	yes

Table 2. Difference between four basic epochs of biological evolution. *The epochs (listed in the first column) differ by a nature of evolutionary replicators and interactors, by involvement and relative role of Lamarckian mechanisms in evolution of adaptive traits, by possibility of horizontal transmission of evolutionary novelties between unrelated individuals in a population, and by gradualistic or punctualistic nature of anagenesis (i.e., of process of change of properties of organisms during evolution).*

3.4. Cultural Evolution

The fourth fundamental step in evolution is the origin of cultural evolution. In cultural evolution, pieces of cultural information (memes) are transmitted within a population in a nongenetic way. A young bird learns a particular variant of a song from its father, a monkey learns from another member of its group how to separate grain from sand and pebbles by washing, and a student learns to master a computer from her teacher (or from the author of a manual). Cultural evolution, i.e. the competition and differential fixation of particular memes, is a product of biological evolution. Individuals with a higher capacity to adopt useful foreign memes beat their competitors in individual selection, and species with a higher capacity for cultural evolution (particularly one species of primates) outcompeted other species in interspecies competition. However, the evolution of particular memes very often progresses independently from the evolution of genes (including the genes for the capacity for cultural evolution). A particular meme usually spreads in the “meme pool” not because of its possible positive influence on the biological fitness of its carriers, but because of its capacity to “infect” other members of the population. The evolution of memes can sometimes proceed in the opposite direction to the main stream of biological evolution. Genes for celibacy, for taking birth-control pills or for smoking can hardly be fixed by natural selection while the corresponding memes are spreading

relatively successfully in many human populations.

The evolution of memes is much faster than the evolution of genes, i.e. than biological evolution. Two principal reasons for the high effectiveness of meme evolution exist. The first reason is that memes are not coded in DNA. Therefore, they have a capacity to spread horizontally in the population between unrelated individuals (even between members of different species). The second reason lies in the fact that memes can evolve by Lamarckian as well as by Darwinian mechanisms. The carrier of information for a particular behavioral pattern is this behavioral pattern itself. This means that, if this behavioral pattern changes, then the meme for the pattern will be transmitted to subsequent individuals in the changed (often improved) form.

It can be expected that the evolution of the human species (including the evolution of our phenotypes) will be more and more determined by the evolution of memes. Advances in medical science will probably result in the gradual accumulation of genes for genetic diseases in our gene pool, which will make our species more and more dependent on medical technologies.

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