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Review article

GENETIC BASES OF THE EVOLUTION OF ORGANISMS

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Biological progress consists of the continuous increase of divergence with simultaneous maintenance and the increase of conformance (harmoniousness) of living systems. A mutual balance between divergence of forms and the degree of perfection of their structure and function indicates a level of the evolutionary development of a particular group of organisms, i.e. a level and prospects of their evolutionary progress. An enormous potential of combined genetic polymorphousness is reduced to adaptive landscapes of a limited number of developmental programmes that make actual units of inheritance and variability within each species.

Key words: evolution, genetic bases

INTRODUCTION

The beginning of life (3.7 billion years ago) started in the form of multiple reproducibility of a number of biochemical processes based on:

- (1) the genetic information on a single stranded nucleotide sequence (RNA)
- (2) the protein structure of the simplest "living" system
- (3) deterioration and recovery of systems of the identical structure
- (4) catalysts that speed processes of synthesis (minerals, active ions).

The evolution of living systems has been developing by (1) maintenance of homogeneity of newly developed systems (through ever more perfect reproduci-

bility-heritability of the structure and function), (2) a gradual input of changes in genetic and physical structures, which simultaneously with natural selection, leads to the development of more stable and perfect, but at the same time, more diverse systems.

The improvement of conformity with a permanent increase of diversity of living systems characterizes the evolution at the genetic and phenotypic levels and occurs associated and synchronous at all levels of the organization of living creatures.

For about 1.5 billions years, a genome was increasing from the initial "genes" with not more than several hundreds nucleotides in a single stranded sequence to about three millions nucleotides by the evolution of primordially developed bacteria. Another two billions years were necessary for the development of the lowest plants in which the genome was only 10-fold higher than in bacteria, but a prokaryotic system of the gene regulation was replaced with the eukaryotic one. After another half a billion years primitive animals, with the number of nucleotides in DNA greater by about 100 times, were developed. The nucleic material in higher plants and vertebrates (developed 4-5,000 millions years ago) is even 1000 fold higher than in bacteria, their general structure is possibly more than 1000 fold more complex, but still it can be stated that a degree of harmoniousness of such a structure, especially of metabolic processes, is far more perfect than in systems at an evolutionary lower system.

All these changes are usually attributed to natural selection i.e. Darwinian selection, but we should not neglect a forewarning of our great biologist Prof. Borivoje Milivojević (1938, 1956) that a gradual and directional autosynthesis of certain living systems, with an accumulative superstructure in a conformational and functional sense, has a special significance in the origination of numerous and specific forms of living organisms. Nowadays we are aware that natural selection does not have all possible combinations of parental gametes (approximately 70 trillions combinations of parental chromosomes can be theoretically accomplished in one pair of parents) "at its disposal", but only a very limited number of genetic combinations that have been developed by the evolution and complied within a species.

With all these complex processes the question on the basic evolution unit, i.e. essential target or aim of natural selection inevitably arises. A concept that these units are single individuals of each species had been dominating for a long time till the 1930's when the idea of Theodosius Dobzhansky ("Darwin of the 20th century") that natural populations were the basic units of evolutionary changeability was accepted. Not denying this allegation, cytogeneticists put forward the idea that chromosomes, as essential segregational units of cell division, are a very realistic target of natural selection because they are carriers of the entire packages of differently conformed genes. Population geneticists define gene alleles as main objects of manipulation by natural selection and also determine a genetic structure of populations of certain species according to the frequency of specific alleles, but at the same time they do not avoid to consider gene arrangements (e.g. chromoso-

mal inversions, etc.) as a major target of selection. Molecular biologists find out possible targets of selection even in the essential structures of proteins (amino acids) or at the DNA and RNA levels (nucleotides, their repeated sequences, introns, exons, etc.).

Beside the "structural" approach, a "functional" one has been increasingly applied with the acceptance that a "basic selection unit" could be at the same time an individual, cell chromosome, gene alleles, direct gene product, as well as, a fundamental structure of protein and nucleic acids, and with the fact that all these responses to selections were synthesized (caught up) at the population level of organisms of a certain species.

The "functional approach" warns of the fact that metabolic processes, as basic ones, are processes that have been changing over the evolution and that survival and the evolutionary development of more and more complex living systems depended on their harmoniousness, i.e. conformance of changeability. It can be naturally assumed that primordial metabolic systems (e.g. phosphor-sucrose, Krebs or any other metabolic cycle) were significantly less complex than these later developed by the evolution, i.e. that genes controlling the order of processes were mainly monomorphic. Newly derived alleles in a cyclic system have been strictly tested in order to determine whether they disturbed harmony (i.e. reproducibility and conformance of the process) that already existed and whether they provided any improvement within the existing metabolic system. The analysis of such a complex system in 400 individuals of fruit fly of the species *Drosophila melanogaster* shows that out of 30 analyzed genes determining the phosphorus-sucrose metabolic cycle only 10 are polymorphic, while the rest have only one allelic form, by which the system stability is provided. Furthermore, the most frequent allele among polymorphic loci is usually in the homozygous state, suggesting that it was primordially formed during the evolution of this system, while other, less frequent alleles were formed in the course of the evolution. Such an order (from monomorphic to ever more polymorphic metabolic systems) of the evolutionary development can be a model for other biochemical (metabolic) cycles, which could be one of the principal aims (targets) of selection, rather than individual genes or their alleles could be.

The conventional genetical approach (at any of the following levels: molecular, cytogenetic, individual or population) focuses on the changes of particular structures such as a gene, chromosome, etc., while nowadays it is accepted that more complex coadaptive systems are of actual significance for monitoring the evolution of living organisms. Namely, certain parts of developmental programmes are in fact inherited by the transmission of hereditary factors from parents to progenies; this approach is far more complex than the one indicating that "dominant" or "recessive" alleles are transferred from parents to progenies, which can be applied only to a relatively low number of qualitative traits. Even the later is interpreted quite differently due to the most recent discoveries at the biochemical and molecular levels. For instance, the genomic map of human chromosomes reveals that genes controlling formation of dark, i.e. red hair pigments are located on the

long arm of chromosomes 15 and 19 (just "below" the centromere), i.e. on the peripheral part of the long arm of chromosome 4, respectively. This means that inter-allelic interactions of the same locus are here of less significance than interactions of different loci, i.e. the broadest-sense epistasis is significantly more often present than we have ever imagined.

The essential assumption of the conventional genetics also includes the idea that prospects of survival of natural populations are based on the magnitude of their genetic polymorphousness and that the greater genetic divergence of the system is, the greater changes for its further evolution and survival are ("Fisher's Fundamental Theorem"). There was a question on bounds of this genetic diversity and since it has been comprehended that they were very high, scientists have been orientating themselves to giving answers related to the mode in which such a potentially enormous divergence of genotypes and phenotypes was reduced to 'adaptive landscape', i.e. to adapted forms that survive in nature. One of the modes is a presence of a great number of monomorphous loci that provide a basic "skeleton" of necessary structures and functions in organisms of a certain species. Hence, if we shift between any of pairs of human chromosomes (which is provided by contemporary biochemical analyses) we shall find out that different alleles are present in only 7-8% of gene loci, while same alleles in all others will be recorded on opposite loci. At that, these 3-4000 polymorphous loci can produce more allelogenic combinations (more than 10^{600}) than a total number of particles in the Einsteinian Universe (about 10^{76}). Therefore, whereas biologists of the last century occupied themselves with discovering diversity of forms of life and the way that diversity occurred, nowadays, their studies are aimed at determining the modes in which such enormous diversity is controlled in nature and is reduced to adaptive landscapes.

When the mentioned phosphorus-sucrose metabolic cycle was analyzed, it was determined that nine polymorphous loci involved into control of this system could theoretically obtain over 78,000 combinations of existing alleles, while it was estimated that no more than 200-220 genotypes of these loci existed in the population of fruit fly that was analyzed in the present study. In other words, adaptive polymorphousness for this complex system is reduced to less than 0.5% of one that would be achieved by a free combination of allelogenes. Such a reduction is presumably performed in the stages prior to the completion of gametogenesis, hence the existence of not more than 800-1000 types of gametes were determined (for this system) prior to selection for the best zygotes, while selection during the development depends not only on genetic disposition of zygotes, but also on environmental conditions.

Based on everything stated it can be comprehended that enormous divergence of parental allelogenic combinations is reduced to a relatively limited number of compiled developmental programmes that are implemented and that these developmental programmes, i.e. specific metabolic cycles they consist of, are actual units of selection, and also of inheritance and variability of organisms. Thereby, it can be explained how the complete set of traits, e.g. a face appearance

of humans, or of any other part of a body of one of parents is almost in full expressed in a similar way in several generations of their offspring's, or ('horizontally') in close or distant relatives. The number of such conformities of developmental programmes within each species is far lower than the number of free combinations of existing allelogenes, hence scientists still have to understand the way in which such complied developmental programmes are formed and to what extent they are conservative ("inheritance"), and to what extent they are flexible, changeable and combinable.

The existing knowledge on the evolution of living systems indicates that both, genetic and somatic structures with their permanent conformance became more complex over previous almost four billions years. A human organism, with approximately 13-16,000 billions cells that could be classified into about 250 different types of which each contains somewhat less than 100,000 genes, is one of bioevolutionary products. A eukaryotic epigenic type of development provides the expression of genes in a quite particular way according to a certain order and frames that are strictly outlined for each species separately. Conformity of certain developmental and metabolic processes in this enormously complex system seems to be a fundamental criterion of survival of that living system (individual, population, species) in nature.

The approaches to these branches of studies on living processes should be altered in future in order to move from the description of complex phenomena (from a molecular over a physiological to a population level) to comprehension of how they are conjoint in living systems in nature. At present, it is necessary to shift from a descriptive representation of the 'evolution of divergence of living organisms' to causality of the course of the 'evolution of conformity' of coadaptive systems that exit in nature, which will be a scientific task much more difficult than the one prevailing in the previous century. If biology answers this important question it will earn to be proclaimed, as predicted, a "science of the 21st century".

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