

PERSONALITIES IN SCIENCE

THEODOSIUS DOBZHANSKY AND THE SYNTHETIC THEORY OF EVOLUTION - 30 YEARS AFTER THE DEATH OF THE “20TH CENTURY’S DARWIN”

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When Tshetverikov (1926) published his classic paper showing that natural populations of an organismic species such as *Drosophila melanogaster* contain an enormous amount of genetical variation, this was a new argument for anti-Darwinists against the theory of natural selection. To be specific, the newly discovered populational genetic loads of prevalently recessive mutations were much too large to be in accordance with the intensive selectional events that occur in nature, supposedly leading to survival of the best-adapted and permanent elimination of deleterious variants. Quite the opposite, the existing loads of mutations reduce the survival of their carriers, especially when they are in homozygous states.

Another postulate of Darwinian theory of natural selection was that individuals of a particular species are the units of this selection, and their survival (more or less in an alternative way) can be considered as a basis for estimation of the chance of leaving their genes in following generations. Darwin’s theory of evolution was based in part on an assumption of blending inheritance, and Mendel’s theory of heredity filled the gap, leading directly to population genetics and evolutionary synthesis. Darwinism, however, was rejected by three of the founders of Mendelism, Bateson, de Vries, and Johannson, who failed to appreciate the nature of species as a group of biological populations, denied the importance of natural selection, and considered mutation pressure as the major force in evolution.

Accumulation of data in the fields of genetics, taxonomy, paleontology, physiology, and developmental sciences contributed to a body of new information about evolutionary events. A new synthesis was necessary, and it occurred almost 80 years after Darwin’s “The Origin of



Species” with the appearance of Th. Dobzhansky’s (1937) book “Genetics and the Origin of Species” (title suggested by Thomas Morgan!).

Accepting as a basic theory of organic evolution Darwin’s theory of natural selection, Dobzhansky (1937) emphasized that:

- (1) **populations** are the basic units of evolution;
- (2) **fitness** of specific genotypes determines the chance of increasing or decreasing their frequency in future generations;
- (3) differential **reproduction rates**, rather than survival rates, are of more importance for determination of the genetic constitution of a population;
- (4) **balancing selections** are the basic forces maintaining the genetic variability of a population.

In the light of only these four postulates, it was now possible to explain the paradoxical effects of natural selection and other evolutionary factors, which result in a systematic **increase** of biological variation during processes of evolution, as well as in maintenance of genetic loads in natural populations. With his populational thinking Dobzhansky proved that Darwin’s evolutionary theory and Mendelian genetics are mutually supportive, and demonstrated that various other discoveries in paleontology, zoological systematics, and in botany are compatible with this approach.

Dobzhansky (1937) further emphasized the importance of the Hardy-Weinberg principle (Hardy, 1908) as to the maintenance of genetic equilibria in populations and the existence of counterbalances between a permanent tendency toward biological equilibrium and effects of surrounding evolutionary forces (i.e., selection, mutations, migration, and genetic drift). He succeeded in

synthesizing many contemporary discoveries in the fields of paleontology, taxonomy, genetics, cytology, ecology, and behavior, but concentrated his attention on processes of speciation, i.e., on the mechanisms of diversification of organismic populations into different races, subspecies, siblings, and “good” species.

At the same time, Dobzhansky succeeded in bringing together the broad experimental and synthetical work of Russian geneticists from 1920s and 1930s (such as Vavilov, 1926; Tshetverikov, 1926; Philiptshenko, 1927; Timofeev-Ressovsky, 1927; Dubinin, 1931) with the theoretical foundations of population genetics given by Fisher (1930), Wright (1931), and Haldane (1932) during the same period. He himself collected a huge amount of data, in the field as well as in the laboratory, demonstrating the basic mechanisms of speciation, using *Drosophila* as a model organism (see, for example, Dobzhansky, 1970). It was his contention, proved later with the Llanos strain of *D. paulistorum*, that minor differences in behavior can be the first steps in the processes of speciation and reproductive isolation of two groups of individuals (Dobzhansky and Pavlovsky, 1966). His classical studies of ecology, behavior, inversion polymorphism, and fitness properties of the American species *Drosophila pseudoobscura* lasted more than 40 years and yielded an incomparable amount of information about the synchronous contribution of genetic and environmental factors in numerous evolutionary adaptations of a species (see, for example, Dobzhansky *et al.*, 1966). Cold-temperature resistance is just one of adaptive response characterized by numerous carriers of chromosomal inversion types (Marinković and Crumpacker, 1967), although Dobzhansky himself initially stated that chromosomal inversion types may not have specific adaptive meaning.

Although neither a biochemist nor a mathematician, Dobzhansky in many of his papers contributed clearly to a synthesis of these two fields with experimental approaches to prove the genetic mechanisms governing variation of a specific trait. He always collaborated with excellent mathematicians (S. Wright in the 1930s, H. Levene in the 1940-60s), some of whom were his Ph.D. students of his (e.g., B. Wallace, R. Lewontin, F. J. Ayala, W. W. Anderson). His students were broadly educated, later becoming the founders of new fields in evolutionary genetics, especially biochemical population genetics (e.g., R. Lewontin, F. J. Ayala, R. Richmond, J. R. Powell). Most of them later founded well-known population-ge-

netics laboratories (e.g., J. A. Beardmore in Great Britain, C. Krimbas in Greece, D. Sperlich in Germany, D. Brnčić in Chile, A. Cordeiro in Brazil, Oshima, Ohba and Kitagawa in Japan, S. Lakovaara in Finland, etc.). There is probably no scientist or professor of biology in the world who produced such a pleiade of famous and successful followers as Dobzhansky did. Most of his students, however, received their Ph.D.s in the last fifteen years of Doby's professional activity, i.e., from the mid-1950s to the early 1970s. John Moor (from the USA) and C. C. Tan (from China) were among the rare students who earned their Ph.D.s earlier. It should not be forgotten that Dobzhansky was elected to the National Academy of Sciences of the USA already in 1943 and by the late 1950s had published more than 300 papers and many books.

In early 1940s, a number of distinguished books followed Dobzhansky's “Genetics and the Origin of Species”. These were: Huxley's “Evolution, the Modern Synthesis” (1942), Mayr's “Systematics and the Origin of Species” (1942), Simpson's “Tempo and Mode of Evolution” (1944), Rensch's “Evolution Above the Species Level” (1947), and Stebbins “Variation and Evolution of Plants” (1950). They all contributed to a much better understanding of the mechanisms of evolutionary processes which were first explained synthetically by Dobzhansky (1937).

Known for hundreds of excellent papers on *Drosophila* genetics, Dobzhansky also contributed ingenious suggestions about the scope and origins of human variation. In his famous book ‘Mankind Evolving’, Dobzhansky (1962) extended the synthesis of Mendelism and Darwinism to the understanding of human nature and origins. This book also was a synthesis of genetics, evolutionary theory, anthropology, and sociobiology, emphasizing the two dimensions of human evolution, i.e. biological and cultural. On page 18 he writes “*Human evolution cannot be understood as a purely biological process, nor can it be adequately described as a history of culture. It is the interaction of biology and culture*”. Dobzhansky considered human diversity as a natural phenomenon and emphasized that populations or groups of populations differ from each other in the frequencies of some genes. Human races are polymorphic for the same genetic variants that can be used to distinguish one race from another, and there is more genetic variation within any human race than between them. He wisely compared genetic diversity and human equality, pointing out that equality in law and opportunity is the

best strategy to maximize the benefits of human biological diversity (Dobzhansky, 1973). He fought for years in the USA against the creationists and for a broad and progressive understanding of scientific discoveries. His anti-racial views contributed greatly to a proper understanding of human differences by claiming explicitly that human populations, rather than races, are the units of human variation and evolution.

A broad scope of interests, profound wisdom, great knowledge and memory, and exceptional energy were just some of the characteristics of Theodosius Dobzhansky as a scientist, thinker, and writer. He always knew what he wanted and had a rigorous discipline for a systematic work and talent for excellent organization of his working plans and obligations. "A month gone by without a paper sent to press, is a wasted month", he liked to say.

The greatness of Dobzhansky lay not merely in his numerous activities and significant discoveries, nor in his wisdom to visualize the most important phenomena in evolutionary processes. More than this it lays in his humanity and optimistic criticism, which spread to colleagues and scientists around him. Dobzhansky's God was Nature, and probably nobody in the world understood the proper meaning and complexity of this entity as well as he did. After his death in December of 1975, his ashes were scattered over the grounds of the Mather Experiment Station in the Sierra Nevada Mountains. He thereby became a permanent part of the Nature which he so much tried to understand during his lifetime.

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