Theodosius Dobzhansky
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THEODOSIUS DOBZHANSKY: THE MAN AND THE SCIENTIST

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Theodosius Dobzhansky was born on January 25, 1900, in Nemirov, a small town in the Ukraine 200 kilometers southeast of Kiev. He was the only child of Grigory Dobrzhansky,[1] a teacher of high school mathematics, and Sophia Voinarsky. In 1910 the family moved to the outskirts of Kiev, where Dobzhansky lived through the tumultuous years of the Bolshevik revolution and the First World War. He graduated in biology from the University of Kiev in 1921, and from 1921 to 1924 taught zoology at the Polytechnic Institute. From 1924 to 1927 he was a lecturer in genetics at the University of Leningrad.

In 1927, Dobzhansky obtained a fellowship from the International Education Board (Rockefeller Foundation) and arrived in New York on December 27 in order to work with Thomas Hunt Morgan at Columbia University. In the summer of 1928 he followed Morgan to the California Institute of Technology where Dobzhansky was appointed assistant professor of genetics in 1929, and professor of genetics in 1936. Dobzhansky returned to New York in 1940 as professor of zoology at Columbia University, where he remained until 1962, when he became professor at the Rockefeller Institute (renamed Rockefeller University in 1965) also in New York City. On July 1, 1970, Dobzhansky became emeritus at Rockefeller University; in September 1971 he moved to the Department of Genetics at the University of California, Davis, where he was adjunct professor until his death in 1975.

On August 8, 1924, Dobzhansky married Natalia (Natasha) Sivertzev, a geneticist in her own right, who at the time was working with the famous Russian biologist I. I. Schmalhausen in Kiev. Natasha was Dobzhansky's faithful companion and occasional scientific collaborator until her death by coronary thrombosis on February 22, 1969. The Dobzhanskys had only one child, Sophie, who is married to Michael D. Coe, Professor of Anthropology at Yale University.

[1]Precise transliteration of the Russian family name includes the letter "r".

In a routine medical checkup on June 1, 1968, it was discovered that Dobzhansky suffered from chronic lymphatic leukemia, the least malignant form of leukemia. He was given a prognosis of a few months to a few years of life expectancy. Over the following seven years the progress of the leukemia was unexpectedly slow and, even more surprising to his physicians, it had little if any noticeable effect on his energy and work habits. However, the disease took a conspicuous turn for the worse in the summer of 1975. In mid-November Dobzhansky started to undergo chemotherapy, but continued living at home and working. He was convinced that the end of his life was near and dreaded that he might become unable to work and to care for himself. Mercifully, this never came to pass. He died of heart failure on the morning of December 18, 1975. The previous day, Dobzhansky had been working in the laboratory as usual.

Dobzhansky had incredible energy and very disciplined work habits. The list of his publications at the time of his death consists of 568 titles, including a dozen authored books plus several others that he edited. He was a world traveler and an accomplished linguist able to speak six languages fluently and to read several more. His interests covered a broad spectrum of human activities, including the plastic arts, music, history, cultural anthropology, philosophy, religion, and of course science. He was a good naturalist, and never lacked time for a hike whether in the California Sierras, in the New England forests, or in the Amazonian jungles. He loved horseback riding, but practiced no other sports. Throughout his academic career, Dobzhansky avoided administrative posts, and participated minimally in committee activities. He alleged, perhaps correctly, that he had neither the temperament nor the ability for management. Most certainly, he preferred to dedicate his working time to research and writing rather than to administration.

Personalities can hardly be described or even characterized in a few words. Dobzhansky's most obvious traits were, perhaps, magnanimity and expansiveness. He recognized and generously praised the achievements of other scientists; he admired the intellect of his colleagues, even when admiration was alloyed with disagreement. He made many long-lasting friendships, usually started by professional interactions. Many of Dobzhansky's friends were scientists younger than himself, who either had worked in his laboratory as students, postdoctorals, or visitors, or had met him on his trips. (Throughout his academic career Dobzhansky had about 30 graduate students and an even greater number of postdoctorals.) He liked to be called "Doby" by his friends even though these might be young scientists or students. To young biologists, he freely gave his time and encouragement. He had many friends abroad, and was largely responsible for the establishment or development of genetics and evolutionary biology in various countries, notably Brazil, Chile, and Egypt. He was conspicuously affectionate and loyal towards his friends; he expected affection and loyalty in return. Dobzhansky's exuberant personality was manifest in his friendships but also in his antipathies. When he disliked a person, this was obvious.

Dobzhansky contributed to evolutionary biology perhaps more than any other scientist since Darwin. Yet his prodigious scientific productivity includes milestone contributions to several areas of genetics. I shall mention a few.

Using translocations between the second and third chromosomes of *Drosophila melanogaster*, Dobzhansky demonstrated that the linear arrangement of genes based on linkage relationships corresponds to a linear arrangement of genes in chromosomes (*Genetics* 15:347–99, 1929). This linear correspondence had been postulated but proof was first provided by Dobzhansky (and independently by Muller & Painter also in 1929). In that same paper Dobzhansky presented the first *cytological* map of a chromosome—chromosome III of *D. melanogaster*. Comparing the linkage and the cytological maps of the chromosome, he showed that the relative distances between genes are different in the two maps; genes clustered around the center of the linkage map are spread throughout a larger portion of the cytological map. He correctly inferred that the frequency of crossing-over is not evenly distributed throughout the chromosome. Later he produced cytological maps of the chromosomes II (1930) and X (1932) of *D. melanogaster*. This work led to the hypothesis that the centromere (the "spindle fiber attachment" in the terminology of the time) was a permanent feature of chromosomes. He demonstrated that translocations decrease the frequency of crossing-over and advanced a hypothesis to account for this reduction (1931).

Dobzhansky first demonstrated that the determination of femaleness by the X chromosome is not due to a single gene or to a few genes, but to multiple factors distributed throughout the chromosome (*Proc. Natl. Acad. Sci. USA* 17:513–18, 1931). His publications on the genetic and environmental factors affecting sex determination started in 1928 and extended for more than a decade. These studies included work on *bobbed* mutants in the Y chromosome, and their role in male sterility (*Genetics* 18:173–92, 1933), as well as numerous publications on gynandromorphs and "superfemales." His publications on developmental genetics started in 1930 (*Biol. Bull.* 59:128–33).

Working with *D. melanogaster* in the laboratory headed by Y. F. Filipchenko at the University of Leningrad, he made the first systematic investigation of the pleiotropic, or manifold, effects of genes (*Z. Indukt. Abstamm. Vererbungsl.* 43:330–88, 1927), a phenomenon that maintained his interest for many years (e.g. *Genetics* 28:295–303, 1943).

Dobzhansky's important contributions to the study of position effects started in 1932 and continued for several years (a review in *Biol. Rev.* 11:364–84, 1936). In the last months of his life, Dobzhansky became intrigued with the hypothesis advanced by some molecular evolutionists that position effects prompted by chromosomal rearrangements may play a critical role in evolution.

Dobzhansky has been called the founder of experimental population genetics. He doubtless was its most eminent practitioner. He may also have been the first one to name and define the field: "The third subdivision of genetics has as its province the processes taking place in groups of individuals—in populations—and therefore is called the genetics of populations" (*Genetics and the Origin of Species*, Columbia Univ., New York, 1937, p. 11).

Dobzhansky's first contributions to population genetics appeared in 1924. (He had already published four papers between 1918 and 1923 on coccinelid beetles, three dealing with taxonomic problems and one with adult diapause.) The 1924 papers investigate local and geographic variation in the color and spot pattern of two *Coccinellidae* genera, *Harmonia* and *Adalia.* These ladybird beetles exhibit local polymorphisms, which in some species vary from one to another locality. Dobzhansky explained the genetic variation within and between populations as the consequence of the same fundamental evolutionary processes. Some cardinal themes of Dobzhansky's evolutionary theory are present in this work: the pervasiveness of genetic variation, geographic variation as an extension of local polymorphism, and as the first, but reversible, step towards species differentiation. Dobzhansky continued the study of natural populations of ladybird beetles until he left Russia in 1927. He occasionally worked with coccinelids in the United States (e.g. a 94 page monograph published in 1941).

The beginning of Dobzhansky's studies on the population genetics of *Drosophila* can be traced to 1933 when he published a paper on the sterility of hybrids between *D. pseudoobscura* and *D. persimilis* (then known as *D. pseudoobscura* race B). In a series of papers, he investigated the physiological, developmental, and genetic causes of hybrid sterility. This work developed from the convergence of two independent previous lines of investigation, the genetics of translocations and the study of sex determination. It led, in 1935, to the formulation of the concept of (sexually reproducing) species still accepted today: "that stage of the evolutionary process at which the once actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding." This notion establishes that reproductive isolation is what sets species apart. It is also an evolutionary definition that sees speciation as a dynamic process of gradual change. In 1937 Dobzhansky coined the term *isolating mechanisms* (*Am. Nat.* 71:404–20) to designate the phenomena that impede gene exchange between species. He identified, classified, and investigated the various kinds of isolating mechanisms. *Isolating mechanisms* is one example of the many useful terms coined by Dobzhansky that have become part of the language of evolutionary biology.

In a brief note it is possible to name only a few of the many problems of population genetics investigated by Dobzhansky: geographical, altitudinal, and temporal variation in the frequencies of chromosomal arrangements in natural populations; the occurrence of "concealed" variation, first of lethal genes and later of genes modifying fitness components such as viability, rate of development, and fertility; the origin and evolution of sexual and the other reproductive isolating mechanisms; mutation rates, their genetic control, and the equilibrium between mutation and selection in natural populations; migration and dispersion rates; effective population size; correlation between genetic polymorphism and ecological heterogeneity; causes of species diversity; heterosis; genetic load; coadaptation of gene pools; joint effects of selection, population size, and migration on traits with low heritability; and so on. Indeed, there may be no major problem of population genetics to which Dobzhansky did not make important experimental contributions.

Some characteristics of Dobzhansky's research strategy that contributed to his enormous success deserve mention. He worked both in the field and in the laboratory; whenever possible he combined both in the study of a problem, often using laboratory studies in order to ascertain or to confirm the causal processes involved in phenomena discovered in nature. He obtained the collaboration of mathematicians in order to design theoretical models for experimental testing and to analyze statistically his empirical observations. He was no inventor or gadgeteer, but he had an uncanny ability to exploit the possibilities of any new experimental apparatus or experimental method that suited him. He selected organisms that provided the best materials to investigate the problems that interested him: the biological particularities of *D. pseudoobscura* and its relatives, and of the *D. willistoni* group, made possible many of Dobzhansky's discoveries. He always worked at the utmost level of genetic resolution possible at any given time: he took advantage of the early methods of genetic analysis, then of various cytological tools, later of the giant polytene chromosomes, and of the techniques to produce chromosomal homozygotes. When gel electrophoresis came about, he immediately recognized its enormous potential as a tool to study population genetics problems; he felt that it was too late in his life for him to learn the technique but encouraged his students and collaborators to use it and collaborated in several projects using it.

Dobzhansky was an extremely successful experimental scientist. Yet his most significant contribution to biology was his establishment of the modern synthesis of evolutionary theory. By the early 1930s the work of Fisher, Wright, Haldane, and Chetverikov had provided a theoretical framework integrating Mendelian genetics with Darwin's theory of evolution. In *Genetics and the Origin of Species* (1937) Dobzhansky completed this integration in two ways. First he gathered the empirical evidence that supported and made acceptable the mathematico-theoretical framework. Second, he extended the integration of Mendelism and Darwinism much beyond the range provided by the mathematical models and produced a comprehensive evolutionary theory that carried population genetics up to the process of speciation and beyond. The modern theory of evolution would continue to develop in the future, but it was born with Dobzhansky's 1937 book in the same way as the original theory had come about with Darwin's *Origin of Species* in 1859.

The single-most important empirical fact established and argued by Dobzhansky is the ubiquity of genetic variation. He was quick to see the momentous implications of this fact for mankind. Dobzhansky set forth that the individual is not the embodiment of some ideal type or norm, but rather a unique and unrepeatable realization in the field of quasi-infinite possible genetic combinations. The pervasiveness of genetic variation provides the biological basis of human individuality. Dobzhansky evinced that it also leads to demystification of the much abused concept of race.

Dobzhansky saw that an adequate understanding of human nature is only possible in the light of evolution. In *Mankind Evolving* (1962) he expounds the implications of the theory of evolution for mankind. This book remains an unsurpassed synthesis of genetics, evolutionary theory, anthropology, and sociology. Dobzhansky's lasting interest in the relevance of biology to human affairs is revealed in the titles of some of his books, such as *Heredity, Race, and Society* (1946, with L. C. Dunn), *The Biological Basis of Human Freedom* (1956), *Heredity and the Nature of Man* (1964), *The Biology of Ultimate Concern* (1967), *Genetic Diversity and Human Equality* (1973).

Dobzhansky was a warm and compassionate man who had little patience with obscurantism, racial prejudice, or social injustice. In the 1940s and 1950s he published several articles criticizing Lysenko's biological quackery. He attacked antievolutionists and cogently rejected claims that Christian beliefs are incompatible with evolution. He relentlessly denounced what he called "bogus 'science' of race prejudice."

Dobzhansky was a religious man, although he apparently rejected fundamental beliefs of traditional religion, such as the existence of a personal God and of life beyond physical death. His religiosity was grounded on the belief that there is meaning in the universe. He saw that meaning in the fact that evolution has produced the stupendous diversity of the living world and has in fact progressed from primitive forms of life to man. Dobzhansky beheld that in man biological evolution has transcended itself into the realm of self-awareness and culture. A metaphysical optimist, he believed that somehow mankind would eventually evolve into higher levels of harmony and creativity.

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