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THEODOSIUS DOBZHANSKY

1900—1975

A Biographical Memoir by

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Biographical Memoir

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Th. Dobzhansky

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January 25, 1900–December 18, 1975

BY FRANCISCO J. AYALA

THEODOSIUS DOBZHANSKY was born on January 25, 1900 in Nemirov, a small town 200 kilometers southeast of Kiev in the Ukraine. He was the only child of Sophia Voinarsky and Grigory Dobrzhansky (precise transliteration of the Russian family name includes the letter "r"), a teacher of high school mathematics. In 1910 the family moved to the outskirts of Kiev, where Dobzhansky lived through the tumultuous years of World War I and the Bolshevik revolution. These were years when the family was at times beset by various privations, including hunger.

In his unpublished autobiographical *Reminiscences* for the Oral History Project of Columbia University, Dobzhansky states that his decision to become a biologist was made around 1912. Through his early high school (*Gymnasium*) years, Dobzhansky became an avid butterfly collector. A schoolteacher gave him access to a microscope that Dobzhansky used, particularly during the long winter months. In the winter of 1915–1916, he met Victor Luchnik, a twenty-five-year-old college dropout, who was a dedicated entomologist specializing in Coccinellidae beetles. Luchnik convinced Dobzhansky that butterfly collecting would not lead anywhere, that he should become a specialist. Dobzhansky chose to work with ladybird beetles, which would be the subject of his first scientific publication in 1918.

Dobzhansky graduated in biology from the University of Kiev in 1921. Before his graduation, he was hired as an instructor in zoology at the Polytechnic Institute in Kiev. He taught there until 1924, when he became an assistant to Yuri Filipchenko, head of the new Department of Genetics at the University of Leningrad. Filipchenko was familiar with Morgan's work in the United States and had started a *Drosophila* laboratory, where Dobzhansky was encouraged to investigate the pleiotropic effects of genes.

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 was working at the time 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 Dobzhansky's had only one child, Sophie, who is married to Michael D. Coe, professor of anthropology at Yale University.

In a routine medical check-up 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. The disease took a conspicuous turn for the worse in the summer of 1975. In mid-November Dobzhansky started to receive chemotherapy, but continued living at home and working at the laboratory. 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, in my car as I was rushing him to the hospital. The previous day Dobzhansky had been, as usual, working in the laboratory.

THE MODERN SYNTHESIS OF EVOLUTIONARY THEORY

Theodosius Dobzhansky was one of the most influential biologists of the twentieth century; he also was one of the most prolific. His first publication appeared in 1918 when Dobzhansky was eighteen years old. The complete list of his publications comprises nearly 600 titles, including a dozen books. The gamut of subject matter is enormous, and includes results of experimental research in various biological disciplines, works of synthesis and theory, and essays on humanism and philosophy, to name but three. The incredibly numerous and diversified published works of Dobzhansky are nevertheless unified—biological evolution is the theme that threads them together. The place of biological evolution in human thought was, according to Dobzhansky, best expressed in a passage that he often quoted from Pierre Teilhard de Chardin: "[Evolution] is a general postulate to which all theories, all hypotheses, all systems must hence forward bow and which they must satisfy in order to be thinkable and true. Evolution is a light which illuminates all facts, a trajectory which all lines of thought must follow—this is what evolution is."

Dobzhansky's most significant contribution to science doubtless was his role in formulating the modern synthesis of evolutionary theory. His *Genetics and the Origin of Species*, first published in 1937, may be considered the most important book of evolutionary theory in the twentieth century. The title of the book suggests its theme: the role of genetics in explaining the origin of species; a synthesis of genetic knowledge and Darwin's theory of evolution by natural selection. Considerably revised editions of this book were published in 1941 and 1951. *Genetics of the Evolutionary Process*, published in 1970, was considered by Dobzhansky as the fourth edition of the earlier book, except that it had changed too much to appear under the same title.

By the early 1930s the work of R. A. Fisher, S. Wright, and J. B. S. Haldane had provided a theoretical framework accounting for the process of evolution, particularly natural selection, in genetic terms. This work had a limited impact on the biology of the time for various reasons: it was formulated for the most part in mathematical language; it was almost exclusively theoretical with little empirical corroboration; and it was limited in scope. In *Genetics and the Origin of Species*, Dobzhansky completed the integration of Darwinism and Mendelism in two ways. First, he gathered the empirical evidence that corroborated the mathematico-theoretical framework. Second, he extended the integration of genetics with Darwinism much beyond the range of issues treated by the mathematicians, and into critical evolutionary issues—such as the process of speciation—not easily subject to mathematical treatment. Moreover, Dobzhansky's book was written in prose understandable to all biologists.

The line of thought of *Genetics and the Origin of Species* is surprisingly modern—in part, no doubt, because that book established the pattern that successive evolutionary treatises would largely follow. The book starts with a consideration of organic diversity and discontinuity. Successively, it deals with mutation as the origin of hereditary variation, the role of chromosomal rearrangements, variation in natural populations, natural selection, the origin of species by polyploidy, the origin of species through gradual development of reproductive isolation, physiological and genetic differences between species, and the concept of species as natural units.

Genetics and the Origin of Species was received with great excitement by the biological community of the time. The book would inspire other biologists to bring into the modern synthesis of evolutionary theory the contributions of such fields as systematics (E. Mayr, 1942), paleontology (G. G. Simpson, 1944), and botany (G. L. Stebbins, 1950). Equally or more important, *Genetics and the Origin of Species* provided a conceptual framework that would stimulate experimental research for many years.

HUMAN EVOLUTION, HUMAN INDIVIDUALITY, AND THE CONCEPT OF RACE

Dobzhansky extended the synthesis of Mendelism and Darwinism to the understanding of human nature in *Mankind Evolving* (1962), a book that some think to be as important as *Genetics and the Origin of Species.*

Mankind Evolving remains an unsurpassed synthesis of genetics, evolutionary theory, anthropology, and sociology. Dobzhansky expounded that human nature has two dimensions: the biological, which mankind shares with the rest of life, and the cultural, which is exclusive to man. These two dimensions result from two interconnected processes, biological evolution and cultural evolution:

> The thesis to be set forth in the present book is that man has both a nature and a "history." Human evolution has two components, the biological or organic, and the cultural or superorganic. These components are neither mutually exclusive nor independent, but interrelated and interdependent. 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. There exists a feedback between biological and cultural processes [*Mankind Evolving*, p. 18].

Two principal topics of *Mankind Evolving* are the interrelated concepts of human diversity and race. Dobzhansky's first major publication on these topics was *Heredity, Race, and Society* (1946), a book coauthored with L. C. Dunn, which was translated into many languages and sold more than one million copies. The two topics are the main subject of *Genetic Diversity and Human Equality* (1973), the last of Dobzhansky's books published before his death. (Dobzhansky left his manuscript completed for another book, *Evolution*, coauthored with F. J. Ayala, G. L. Stebbins, and J. W. Valentine, which appeared in 1977.)

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 foundation of human individuality and leads to demystification of the much abused concept of race. Dobzhansky emphasized that populations or groups of populations differ from each other in the frequencies of some genes. These differences may be recognized by distinguishing populations of a given species as races. The number of races and the boundaries between them are largely arbitrary, because rarely if ever are populations of the same species separated by sharp discontinuities in their genetic makeup. Most important is the fact that races are polymorphic for the same genetic variants that may be used to distinguish one race from another. There is more genetic variation within any human race than there are genetic differences between races. It follows, as Dobzhansky saw it, that individuals should be evaluated by what they are, not by the race to which they belong.

Dobzhansky considered human diversity a fact belonging to the realm of observable natural phenomena: "People are innately, genetically, and therefore irremediably diverse and unlike" (*Genetic Diversity and Human Equality*, p. 4). Biological distinctiveness is not, however, a basis for inequality. Equality—as in equality in law and equality of opportunity—"pertains to the rights and the sacredness of life of every human being" (*loc. cit.*). Dobzhansky pointed out that equality in law and equality of opportunity are the best strategy to maximize the benefits of human biological diversity. "Denial of equality of opportunity stultifies the genetic diversity with which mankind became equipped in the course of its evolutionary development. Inequality conceals and stifles some people's abilities and dissembles the lack of abilities in others. Conversely equality permits an optimal utilization of the wealth of the gene pool of the human species" (*Mankind Evolving*, p. 285). Dobzhansky had little patience with racial prejudice or social injustice, and castigated those who pretended to base them on what he called "bogus 'science' of race prejudice."

Dobzhansky's lasting interest in the relevance of biology, and particularly evolutionary theory, to human affairs is evident in scores of articles that he wrote on the subject and in the titles of some of his books: *Heredity, Race, and Society* (1946), *Evolution, Genetics, and Man* (1955), *The Biological Basis of Human Freedom* (1956), *Radiation, Genes, and Man*

(1959, with B. Wallace), *Mankind Evolving* (1962), *Heredity and the Nature of Man* (1964), *The Biology of Ultimate Concern* (1967), and *Genetic Diversity and Human Equality* (1973).

EXPERIMENTAL POPULATION GENETICS

Dobzhansky was not only a great theorist of evolution, he also was an eminent and extremely productive experimentalist. During half a century of intensive research and publication, he made fundamental empirical contributions to virtually every major problem of population genetics.

Dobzhansky's first contribution to population genetics appeared in 1924—an investigation of 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 results of the same fundamental evolutionary processes. Some cardinal themes of Dobzhansky's evolutionary theory are already present in this work: the pervasiveness of genetic variation, geographic variation as an extension of local polymorphism, and as the first but reversible step toward species differentiation. Dobzhansky continued the study of natural populations of ladybird beetles until the time he left Russia in 1928, and on occasion returned thereafter to them (for example, the 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* races A and 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 a 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. Dobzhansky introduced in 1935, and formally proposed in 1937 (*American Naturalist,* 71:404–20), the term "isolating mechanisms" to designate the phenomena that impede gene exchange between species. He identified, classified, and throughout his life 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 standard terminology of evolutionary biology.

The experimental contributions of Dobzhansky to population genetics are so numerous, and so diversified, as to defy the possibility of a brief summary. I shall mention a few principal areas of research and list the years in which he published some of the major papers in each subject.

His classical studies on the geographical and temporal variation of chromosomal arrangements in *Drosophila pseudoobscura* and its relatives started with a publication in 1936; in 1938 he published a paper on altitudinal variation; in 1943 a paper on seasonal variation, followed in 1946 by a laboratory study (in collaboration with Sewall Wright) showing adaptive differences (with respect to temperature) between chromosomal arrangements. Numerous other publications on this subject appeared through the 1930s and 1940s, and would continue throughout Dobzhansky's life. Starting in the 1950s the study of geographical variation in chromosomal arrangements was extended to the *D. willistoni* group of tropical species, which exhibit even greater degrees of local polymorphism and geographical variation than *D. pseudoobscura*.

Dobzhansky, in collaboration with A. H. Sturtevant, realized that the evolutionary phylogeny of chromosomal arrangements can be reconstructed by deciphering the patterns of overlapping chromosomal inversions found in natural populations of *Drosophila*; the first phylogeny was published in 1936. This technique became a major tool in the reconstruction of evolutionary history and was applied to many species by Dobzhansky and others. A notable example of the success of this method is the reconstruction of the phylogeny of Hawaiian species by H. L. Carson and his colleagues.

Originally Dobzhansky thought that the various chromosomal arrangements of *D. pseudoobscura* were adaptively equivalent (see the 1941 edition of *Genetics and the Origin of Species*), and hence that their geographical and temporal variation was the result of genetic drift. Eventually he became convinced that the chromosomal polymorphisms are adaptive, but remained interested in the roles that migration, mutation, and drift play in the maintenance of variation in natural populations. Estimates of rates of mutation and accumulation of lethals were first published in 1941 (again in collaboration with Sewall Wright); estimates of the critical parameter *Nm* (the product of effective population size times migration rate) in natural populations appeared in 1942, 1952, and 1954. He developed techniques for the experimental study of migration in nature and published pioneering works in the 1940s; he would return later to this research and did spend most of the last few summers of his life at the beloved cabin in Mather, near Yosemite in Sierra Nevada, measuring the rates of dispersion in *Drosophila*.

Dobzhansky realized early the need to investigate the ecological basis of natural variation. He investigated the nutritional preferences first of *D. pseudoobscura* and later of other species (papers in the 1950s). Several papers (late 1950s) were devoted to ascertaining—particularly in *D. willistoni*—the relationships between the ecological diversity of the environment and the degree of genetic polymorphism. He also investigated the physiological basis of adaptation, starting with studies of fecundity and rates of oxygen consumption published in 1935.

Genetic variation is a necessary condition for evolution. Dobzhansky probably dedicated more research effort to the study of genetic variation in natural populations than to any other single problem. He studied morphological variations, but saw that physiological variation—i.e., variation affecting fitness—would be most important in evolution. Taking advantage of genetic methods to produce flies homozygous for full chromosomes, he first investigated the frequency of lethal mutations in nature. In 1942 he published a classical paper showing that variation in fitness is a pervasive phenomenon: virtually every chromosome found in nature carries genes that are deleterious in homozygous condition; most individuals in nature are well adapted because they are heterozygous for the deleterious variants. "It is the adaptive level of individuals heterozygous for various chromosomes which is most important" (*Genetics*, 27[1942]:487). Dobzhansky pursued the study of this "concealed variation" affecting fitness for two and a half decades. When the techniques of gel electrophoresis were first applied to population genetics in the mid-1960s, he became quite enthusiastic. He appreciated that these studies made it possible to obtain quantitative measures of genetic variation. He also saw that there is a trade-off between electrophoretic studies and the former methods of studying concealed variation: the adaptive role of electrophoretic variation is not immediately apparent.

In the 1940s Dobzhansky started work with the *D. willistoni* group of species that would result in contributions to evolutionary genetics comparable in significance to those derived from the study of *D. pseudoobscura* and its relatives. The most unique results with this group concern the process of speciation and concommitant development of reproductive isolation. The *willistoni* group contains several sibling species. One of these, *D. paulistorum*, is a cluster of semispecies, or species *in statu nascendi*, where varying degrees of hybrid sterility, and particularly sexual isolation, can be observed. He discovered and took advantage of this favorable state of affairs for the experimental study of a fundamental evolutionary problem—speciation. He also used *D. paulistorum* as the organism for the laboratory study of sexual isolation by selection. This work brought about some unsought publicity in such journals as *The New York Times* and *Time* magazine.

From around 1960 until the time of his death, Dobzhansky worked on the geotactic and phototactic behavior of *Drosophila.* His interest in this work encompassed the determination of the genetic basis of some simple behavioral traits, but his main interest was to model the interaction among selection, gene flow, and population size for a behavioral trait with low heritability. There were some unexpected but instructive results, such as the observation of what *prima facie* appeared as a case of negative heritability.

CONTRIBUTIONS TO GENERAL GENETICS AND OTHER EXPERIMENTAL WORK

Dobzhansky made significant contributions to other areas of population biology, particularly ecology and systematics, in addition to his work in population genetics. As pointed out above, much of Dobzhansky's population genetics research had an ecological component: geographical and temporal variation in population characteristics, food resource preferences of *Drosophila* species, rates of dispersion, ecological diversity of environments, and so on. Among his other ecological investigations, two at least deserve mention. One is the study of species' diversity in tropical forests, which led him to a hypothesis to account for the high level of species diversification in the tropics (1950). Then, in the early sixties, he published several papers on the estimation of the innate capacity for increase in numbers in diverse *Drosophila* populations.

Dobzhansky also made significant contributions to "classical" genetics, particularly during the 1920s and 1930s. I shall mention but 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 (1929). This linear correspondence had been postulated before, but proof was first provided by Dobzhansky (and independently by Muller and Painter in the same year). Also in 1929, Dobzhansky advanced the first sophisticated *cytological* map of a chromosome—chromosome III of *D. melanogaster*. He showed that the relative distances between genes are different in the linkage and in the cytological map; 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*, and propounded that the centromere (the "spindle fiber attachment" in the terminology of the time) is 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 demonstrated that the determination of femaleness by the X chromosome is not the result of a single or a small group of genes, but to multiple factors distributed throughout the chromosome (1931). His publications on the genetic and environmental factors affecting sex determination started in 1928 and continued for more than a decade. These studies included work on *bobbed* mutants in the Y chromosome and their role in male sterility (1933), as well as numerous publications on gynandromorphs and "superfemales." His publications concerning developmental genetics started in 1930 and continued for many years.

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 (1927), a phenomenon that held his interest for many years (e.g., *Genetics*, 28[1943]:295–303). Dobzhansky's contributions to the study of position effects started in 1932 and continued for several years (a review appeared in 1936).

HUMANISM

Dobzhansky's interest in the interface between biology and human problems was expressed in numerous publications that flowed as a continuous stream from the mid-1940s onward. Dobzhansky's concern was probably kindled by several convergent influences. One factor was the racial bigotry in Europe that contributed to the triggering of World War II; another, Lysenko's suppression of genetics and geneticists in the USSR; a third, his association as a colleague and intimate friend with L. C. Dunn, whose compassion for the human predicament was much revered by Dobzhansky, and who became greatly involved in providing shelter in the United States for scientists fleeing from Nazi persecution. Doubtless there was also Dobzhansky's own personal and intellectual maturation that made him willing to tackle social and socio-political questions.

As pointed out above, Dobzhansky published with L. C. Dunn *Heredity, Race, and Society* in 1946, and continued publishing on race questions from a biological perspective until the end of his life. Publications criticizing eugenic movements appeared in 1952 and 1964; the subject of eugenics was treated in other papers and several books. In 1946 he translated into English T. D. Lysenko's *Heredity and Its Variability* as a way to expose Lysenko's quackery. Dobzhansky criticized Lysenko's "science," and particularly Lysenko's eradication of genetics and geneticists, in several articles published between 1946 and 1958.

Dobzhansky was concerned with the role of religion in human life, and he explored the evolutionary basis of religion in several articles in the 1960s and 1970s, as well as in *The Biology of Ultimate Concern* (1967). Yet he did not hesitate to criticize (1953) the antievolutionist stand of Pope Pius XII in the encyclical *Humani Generis*, or that of fundamentalist Protestants (1973).

Dobzhansky often expressed his frustration at the limited influence of biology on the thinking of philosophers. He saw that evolutionary biology raises new philosophical problems and throws light on old ones. He wrote several essays on philosophical questions, such as the concepts of determinism and chance (1963, 1966, 1974), transcendent phenomena (1965, 1967), organismic, or compositionist, approaches in the philosophy of biology (1967, 1968), and the "creative" character of biological evolution (1954, 1967, 1974).

PERSONAL TRAITS

Dobzhansky was excellent in the classroom, and a truly distinguished educator of scientists. Throughout his academic career Dobzhansky had more than thirty graduate students, and an even greater number of postdoctoral and visiting associates, many of them from foreign countries. Some distinguished geneticists and evolutionists in the United States and abroad are his former students. Dobzhansky spent long periods of time in foreign academic institutions, and was largely responsible for the establishment or development of genetics and evolutionary biology in various countries, notably Brazil, Chile, and Egypt.

Dobzhansky gave generously of his time to other scientists, particularly to young ones and to students. On the other hand, he resented time spent in committee activities, which he shunned as much as he reasonably could. Throughout his academic career, Dobzhansky avoided administrative posts; he alleged, perhaps correctly, that he had neither temperament nor ability for management. Most certainly, he preferred to dedicate his working time to research and writing rather than to administration.

Dobzhansky was a world traveler and an accomplished linguist, able to speak fluently six languages and to read several more. He was a good naturalist, and never lacked time for a hike, whether in the California Sierras, the New England forests, or the Amazonian jungles. He loved horseback riding but practiced no other sports. Dobzhansky's interests covered a broad spectrum of human activities, including the plastic arts, music, history, Russian literature, cultural anthropology, philosophy, religion, and, of course, science. His artistic preferences were unsystematic and definitely traditional. His favorite composer was Beethoven, followed by Bach and other baroques; he loved Italian operas, but had little appreciation for most twentieth century music and a definite distaste for atonalism. In painting, Dobzhansky admired the Italian Renaissance as well as the Dutch and Spanish painters of the seventeenth century; he appreciated the French Impressionists but detested cubism and all subsequent styles and schools.

Dobzhansky's most obvious personality 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 during his trips. He was conspicuously affectionate and loyal toward his friends; he expected affection and loyalty in return. Dobzhansky's exuberant personality was manifest not only in his friendships but also in his antipathies, which he was neither able nor often willing to hide.

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 conviction 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 progressed from primitive forms of life to mankind. Dobzhansky held that, in man, biological evolution has transcended itself into the realm of self-awareness and culture. He believed that somehow mankind would eventually evolve into higher levels of harmony and creativity.

Dobzhansky's prodigious scientific productivity was made possible by incredible energy and very disciplined work habits. His enormous success as the creator of new ideas and as a synthesizer was, at least in part, based on his broad knowledge, his phenomenal memory, and an incisive mind able to see the relevance that a new discovery or a new theory might have with respect to other theories or problems. His success as an experimentalist depended on a wise blending of field and laboratory research; whenever possible he combined both in the study of a problem, using laboratory studies in order to ascertain or to confirm the causal processes involved in the 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 suitable experimental apparatus or experimental method.

Dobzhansky 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.

RECOGNITION AND AWARDS

Dobzhansky was elected to the National Academy of Sciences in 1943. He was also elected to the American Academy of Arts and Sciences, the American Philosophical Society, and many foreign academies, including the Royal Society of London, The Royal Swedish Academy of Sciences, The Royal Danish Academy of Sciences, The Brazilian Academy of Sciences, the Academia Leopoldina, and the Academia Nazionale dei Lincei.

He was president of the Genetics Society of America (1941), the American Society of Naturalists (1950), the Society for the Study of Evolution (1951), the American Society of Zoologists (1963), the American Teilhard de Chardin Association (1969), and the Behavior Genetics Association (1973).

Dobzhansky received more than twenty honorary degrees from institutions that include the Universities of São Paulo in Brazil (1943), Münster in Germany (1958), Montreal in Canada (1958), Sydney in Australia (1960), Oxford in England (1964), Louvain in Belgium (1965), Padua in Italy (1968), and in the United States, Chicago (1959), Columbia (1964), Michigan (1966), Syracuse (1967), Berkeley (1968), and Northwestern (1968).

He received the Daniel Giraud Elliot Medal (1946) and the Kimber Genetics Award (1958) from the National Academy of Sciences, the Darwin Medal from the Academia Leopoldina (1959), the Anisfield-Wolf Award (1963), the Pierre Lecomte du Nouy Award (1963), the Addison Emery Verrill Medal from Yale University (1966), the Gold Medal Award for Distinguished Achievement in Science from the American Museum of Natural History (1969), and the Benjamin Franklin Medal from the Franklin Institute (1973). In 1964 he received the National Medal of Science from President Lyndon Johnson.

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