

Theodosius Dobzhansky: A Man For All Seasons

Francisco J Ayala

Francisco J Ayala obtained his Ph D with Theodosius Dobzhansky in the 1960s and is presently the Donald Bren Professor of Biological Sciences at the University of California, Irvine and a member of President Clinton's Committee of Advisors on Science and Technology. He is a member of the U S National Academy of Sciences and has been President and Chairman of the Board of the American Association for the Advancement of Science. He has worked extensively on the population ecology and evolutionary genetics of *Drosophila* species.

In 1972, Theodosius Dobzhansky addressed the convention of the National Association of Biology Teachers on the theme "Nothing in biology makes sense except in the light of evolution". The title of that address (published in *The American Biology Teacher*, Vol. 35, pp. 125-129) might serve as an epigram of Dobzhansky's worldview and life, although it is limited in scope, for Dobzhansky believed and propounded that the implications of biological evolution reach much beyond biology into philosophy, sociology, and even socio-political issues. 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".

The Modern Synthesis of Evolutionary Theory

Theodosius Dobzhansky was one of the most influential scientists of the twentieth century: he also was one of the most prolific. His first publication appeared in 1918 when Dobzhansky was 18 years old. The list of his publications at the time of his death contains 568 titles, including more than a dozen books; and he left several manuscripts in the press or at various stages of preparation. The gamut of subject matters is enormous: results of experimental research in various biological disciplines, works of synthesis and theory, essays on humanism and philosophy, and others. The incredibly numerous and diversified published works of Dobzhansky are nevertheless unified – biological evolution is the theme that threads them together. (Reference to Dobzhansky's publications can be found in the

In writing this feature, I have drawn extensively from two previous publications of mine: Nothing in biology makes sense except in the light of evolution, *The Journal of Heredity*, 68: 3-10, 1977; and Theodosius Dobzhansky 1900-1975, *Biographical Memoirs, National Academy of Sciences USA*, 55: 163-213, 1985.



detailed bibliography prepared by F J Ayala, *Biographical Memoirs, National Academy of Sciences USA*, 55:163-213, 1985.)

Theodosius Dobzhansky (1900-1975) was a key author of the Synthetic Theory of Evolution, also known as the Modern Synthesis of Evolutionary Theory, which embodies a complex array of biological knowledge centered around Darwin's theory of evolution by natural selection couched in genetic terms. The epithet 'synthetic' primarily alludes to the artful combination of Darwin's natural selection with Mendelian genetics, but also to the incorporation of relevant knowledge from biological disciplines. In the 1920s and 1930s several theorists had developed mathematical accounts of natural selection as a genetic process. Dobzhansky's *Genetics and the Origin of Species*, published in 1937 refashioned their formulations in language that biologists could understand, dressed the equations with natural history and experimental population genetics, and extended the synthesis to speciation and other cardinal problems omitted by the mathematicians.

The current synthetic theory has grown around that original synthesis. It is not just one single hypothesis (or theory) with its corroborating evidence, but a multidisciplinary body of knowledge bearing on biological evolution, an amalgam of well established theories and working hypotheses, together with the observations and experiments that support accepted hypotheses (and falsify rejected ones), which jointly seek to explain the evolutionary process and its outcomes. These hypotheses, observations and experiments often originate in disciplines such as genetics, embryology, zoology, botany, paleontology, and molecular biology. Currently, the 'synthetic' epithet is often omitted and the compilation of relevant knowledge is simply known as the theory of evolution. This is still expanding, just like one of those 'holding' business corporations that have grown around an original enterprise, but continue incorporating new profitable enterprises and discarding unprofitable ones.

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in the *Origin of Species* (1859) as follows:

“As many more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life ... Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations, useful in some way to each being in the great and complex battle of life, should sometimes occur in the course of thousands of generations? If such do occur, can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind? On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favorable variations and the rejection of injurious variations, I call natural selection”.

Darwin's argument is that natural selection emerges as a necessary conclusion from two premises: (i) the assumption that hereditary variations useful to organisms occur, and (ii) the observation that more individuals are produced than can possibly survive. The most serious difficulty facing Darwin's evolutionary theory was the lack of an adequate theory of inheritance that would account for the preservation through the generations of the variations on which natural selection was supposed to act. Theories of 'blending inheritance' then current proposed that offspring merely struck an average between the characteristics of their parents. As Darwin became aware, blending inheritance could not account for the conservation of variations, because differences among variant offspring would be halved each generation, rapidly reducing the original variation to the average of the preexisting characteristics.

The missing link in Darwin's argument was provided by Mendelian genetics. About the time the *Origin of Species* was published, the Augustinian monk Gregor Mendel was performing a

long series of experiments with peas in the garden of his monastery in Brunn, Austria–Hungary (now Brno, Czech Republic). Mendel’s paper, published in 1866, formulated the fundamental principles of a theory of heredity that accounts for biological inheritance through particulate factors (now called ‘genes’) inherited one from each parent, which do not mix or blend but segregate in the formation of the sex cells, or gametes.

Mendel’s discoveries, however, remained unknown to Darwin and, indeed, did not become generally known until 1900, when they were simultaneously rediscovered by several scientists. In the meantime, Darwinism in the latter part of the 19th century faced an alternative evolutionary theory known as neo-Lamarckism. This hypothesis shared with Lamarck’s original theory the importance of use and disuse in the development and obliteration of organs, and it added the notion that the environment acts directly on organic structures, which explained their adaptation to the ways of life and environments of each organism. Adherents of this theory rejected natural selection as an explanation for adaptation to the environment.

The rediscovery of Mendel’s theory of heredity in 1900 led to an emphasis on the role of heredity in evolution. In the Netherlands, Hugo de Vries (1900) proposed a new theory of evolution known as mutationism, which essentially did away with natural selection as a major evolutionary process. According to de Vries (joined by other geneticists such as William Bateson in England), there are two kinds of variation in organisms. One is the ‘ordinary’ variation observed among individuals of a species, which is of no lasting consequence in evolution because, according to de Vries, it could not “lead to a transgression of the species border even under conditions of the most stringent and continued selection”. The other consists of the changes brought about by mutations, spontaneous alterations of genes that yield large modifications of the organism and give rise to new species: According to de Vries, a new species originates suddenly, produced by the existing one without any visible preparation and without transition.

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Mutationism was opposed by many naturalists, and in particular by the so-called biometricians, led by the Briton Karl Pearson, who defended Darwinian natural selection as the major cause of evolution through the cumulative effects of small, continuous, individual variations (which the biometricians assumed passed from one generation to the next without being subject to Mendel's laws of inheritance).

The controversy between mutationists (also referred to at the time as Mendelians) and biometricians approached a resolution in the 1920s and '30s through the theoretical work of several geneticists (Provine 1971). These studies used mathematical arguments to show, first, that continuous variation (in such characteristics as size, number of eggs laid, and the like) could be explained by Mendel's laws; and second, that natural selection acting cumulatively on small variations could yield major evolutionary changes in form and function. Distinguished members of this group of theoretical geneticists were R A Fisher and J B S Haldane in Britain and Sewall Wright in the United States (Fisher 1930; Haldane 1932; Wright 1931). Their work contributed to the downfall of mutationism and, most importantly, provided a theoretical framework for the integration of genetics into Darwin's theory of natural selection. Yet their work had a limited impact on contemporary biologists because it was formulated in a mathematical language that most of them could not understand; because it was almost exclusively theoretical, with little empirical corroboration; and because it was limited in scope, largely omitting many issues, like speciation, that were of great importance to evolutionists.

Dobzhansky's *Genetics and the Origin of Species* advanced a reasonably comprehensive account of the evolutionary process in genetic terms, laced with experimental evidence supporting the theoretical arguments. It had an enormous impact on naturalists and experimental biologists, who rapidly embraced the new understanding of the evolutionary process as one of genetic change in populations. Interest in evolutionary studies was



greatly stimulated, and contributions to the theory soon began to follow, extending the synthesis of genetics and natural selection to a variety of biological fields.

The main writers who, together with Dobzhansky, may be considered the architects of the synthetic theory were the zoologists Ernst Mayr (1942) and Julian Huxley (1942), the paleontologist George G Simpson (1944), and the botanist G Ledyard Stebbins (1950). These researchers contributed to a burst of evolutionary studies in the traditional biological disciplines and in some emerging ones – notably population genetics and, later, evolutionary ecology. By 1950, acceptance of Darwin’s theory of evolution by natural selection was universal among biologists, and the synthetic theory had become widely adopted.

The line of thought of *Genetics and the Origin of Species* is surprisingly modern – in part, no doubt, because it established the pattern that successive evolutionary investigations and treatises largely would follow. Dobzhansky writes in the preface: “The problem of evolution may be approached in two different ways. First, the sequence of the evolutionary events as they have actually taken place in the past history of various organisms may be traced. Second, the mechanisms that bring about evolutionary changes may be studied. The present book is dedicated to a discussion of the mechanisms of species formation in terms of the known facts and theories of genetics”. 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. The book’s organization was largely preserved in the second (1941) and third (1951) editions, and in *Genetics of the Evolutionary Process* (Dobzhansky 1970), published in 1970, a book that Dobzhansky thought of as the fourth edition of the earlier one,

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but had changed too much for publication under the same title.

Human Evolution and Human Individuality

Near the end of the *Origin of Species*, Darwin wrote that “Much light will be thrown [by this theory] on the origin of man”. In the *Descent of Man* (1871) Darwin showed mankind as the outcome of biological evolution and thus kin to all life. Likewise, Dobzhansky extended the synthesis of Mendelism and Darwinism to the understanding of human nature in *Mankind Evolving* (1962), a book that many consider 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 humans. 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 co-authored with L C Dunn that was translated into many languages and sold more than one million copies.

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; Dobzhansky elucidated that it also leads to demystification of the much-abused concept of race. He 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 make-up. 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.

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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 the “bogus ‘science’ of race prejudice”.



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Dobzhansky's lasting interest in the relevance of biology, and particularly evolutionary theory, to human affairs is evident in the many 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).

A Scientist – and a Humanist and Philosopher

Dobzhansky's interest in the interface between biology and human problems was expressed in numerous publications that flow as a continuous stream since the mid-1940s. His concern was probably kindled by several convergent influences. One factor was the race bigotry that contributed in Europe to triggering 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 was greatly involved in providing shelter in the United States for scientists fleeing from Nazi persecution.

Dobzhansky was concerned with the role of religion in human life and explored the evolutionary basis of religion in several articles in the 1960s and 1970s, and in his *The Biology of Ultimate Concern* (1967).

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, transcendent phenomena, organismic, or compositionist, approaches in the philosophy of biology, and the 'creative' character of biological evolution.



A Scientist and a Teacher

Dobzhansky was an excellent teacher and distinguished educator of scientists. Throughout his academic career he had more than 30 graduate students and an even greater number of postdoctoral and visiting associates, many of them from foreign countries. Some of the most 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. But he resented time spent in committee activities, which he shunned as often as he reasonably could. Throughout his academic career, he avoided administrative posts, alleging, 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.

A Short Sketch of a Long Life

Theodosius Dobzhansky was born on January 25, 1900, in Nemirov, a small town 200 km southeast of Kiev in the Ukraine. He was the only child of Sophia Voinarsky and Grigory Dobzhansky (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. In those times the family was often 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 in about 1912. Through his early high school years, Dobzhansky became an

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avid butterfly collector. A school teacher 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 25-year-old college drop-out, who was a dedicated entomologist specializing in Coccinellidae beetles. Luchnik convinced Dobzhansky that butterfly collecting would not lead anywhere and 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 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. In 1940 he returned to New York 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. On July 1, 1970, Dobzhansky became professor 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 at the time



working with the famous Russian biologist I I Schmalhausen in Kiev. Natasha was Dobzhansky's faithful companion and occasional scientific collaborator until her death from coronary thrombosis on February 22, 1969. Dobzhansky himself died of heart failure on the morning of December 18, 1975. The previous day, he had been working in the laboratory.

Dobzhansky was a world traveller and an accomplished linguist able to fluently speak six languages and to read several more. He was a good naturalist, and never lacked time for a hike in the California Sierras, the New England forests, or the Amazon jungles. He loved horseback riding but practised no other sports. Dobzhansky's interests included the visual arts, music, history, Russian literature, cultural anthropology, philosophy, religion, and, of course, science. His artistic preferences were unsystematic and definitely traditional. His favourite 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 (of electronic and computer-composed music, he said that it is fit only for computers to listen to it). In art, Dobzhansky admired the Italian Renaissance painters as well as the Dutch and Spanish masters of the seventeenth century; he appreciated the French Impressionists but detested cubism and all subsequent styles and schools of modern art.

Dobzhansky's obvious personality traits were 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 interaction. Many of Dobzhansky's friends were scientists younger than himself, who had either worked in his laboratory as students, postdoctorals, or visitors, or had met him during his travels. 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

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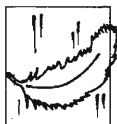


his friendships but also in his antipathies, which he was seldom able, or often willing, to hide.

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. He was a metaphysical optimist.

Address for Correspondence

Francisco J Ayala
Department of Ecology and
Evolutionary Biology
University of California
Irvine, CA 92697 - 2525, USA.
Email: fjayala@uci.edu



Francisco Jose Ayala – A Many Faceted Personality

Ayala was born in Spain, got his undergraduate degree in physics, followed by a doctorate in theology with a dissertation written in Latin. He was a Dominican priest and was pursuing graduate studies in genetics when Dobzhansky met him in Madrid in the early 1960s. Dobzhansky was impressed and persuaded Ayala to join him at Columbia University for a Ph D. After finishing his Ph D, Ayala did not want to return to Spain as he was opposed to Franco's rule. He taught for several years at the Providence College, Rhode Island (a Dominican college). By this time Dobzhansky had moved to Rockefeller University. Ayala, by now disenchanted not only with Spain, but also the Dominicans and the Catholic Church hierarchy, joined Dobzhansky as Research Associate. Finally, he moved as Associate Professor to UC Davis in 1971, with part of the deal being that the now retired Dobzhansky would come along with him. In the 1980s, Ayala moved to UC Irvine, where he is now Donald Bren Professor.

Most of what is true of Dobzhansky is also true of Ayala. Ayala, too, influenced people on several continents, especially Spain and Latin America. His graduate students include some of the best known evolutionary geneticists and ecologists (especially Drosophilists) in the 45-55 year old age group. Ayala has been a prolific writer of scientific papers, textbooks and 'general' articles. He has also been an active defender of evolution from creationist attacks with the added advantage that he too can quote the Bible chapter and verse back at them. Although English is not his native tongue, his writing is extremely clear and elegant.

Ayala's work has been an elegant blend of theoretical approaches, rigorous laboratory experimentation and field studies, a combination not often seen in one person's work. Presently, he is one of the most distinguished living evolutionary geneticists, and certainly the most illustrious of Dobzhansky's students.

Amitabh Joshi