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Perspectives

Anecdotal, Historical and Critical Commentaries on Genetics

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"IN THE AIR"—THEODOSIUS DOBZHANSKY'S *GENETICS AND THE ORIGIN OF SPECIES*

THEODOSIUS DOBZHANSKY's *Genetics and the Origin of Species* was first published 50 years ago. Many, myself included, would argue that it is the most important and influential book on evolution of the twentieth century. Certainly, taken together with later editions as well as with *Genetics of the Evolutionary Process* (1970) (which was meant to be a fourth edition), the book has been the cornerstone of genetic studies of evolutionary change for much of the last 50 years. It is perhaps difficult for us today to understand why a book integrating Mendelian genetics and Darwinian evolution was so important—or, indeed, even necessary—some 37 years after the rediscovery of MENDEL and 25 years after MORGAN and his associates confirmed and so elegantly extended Mendelian principles. Perhaps equally difficult to appreciate is how this book continues to influence not only genetical studies of evolution but also such fields as systematics and paleontology.

To understand the book's initial impact, it is necessary to realize that in the 1930s it was far from established that Mendelian genetics could account for evolutionary changes observed in nature [see MAYR (1980) for thought-provoking documentation]. In particular, two factors delayed the synthesis (as it was to be called) between the Darwinian tradition and Mendelism. The first was misunderstanding, lack of communication and, at times, mistrust between geneticists and evolutionists (the latter group consisting primarily of systematists, natural historians and paleontologists). As BATESON stated in a famous lecture in 1922:

> I am convinced that biology would greatly gain by some cooperation among workers in several branches. I had expected that genetics would provide at once common ground for the systematist and laboratory worker. This hope has been disappointed. Each still keeps apart. Systematic literature grows precisely as if the genetical discoveries had never been made and the geneticists more and more withdraw each into his special "claim"—a most lamentable result. Both are to blame.

A main issue of contention was the genetic basis for the origin of species, the phrase from both DOBZHANSKY's and DARWIN's major contributions. It was clear enough that Mendelian rules of inheritance could predict patterns of inheritance of many traits within populations, but could Mendelian factors account for the origin of new species, genera, and all higher taxa? One problem before 1937 was that some geneticists who often wrote about evolution (DEVRIES, BATESON and GOLDSCHMIDT) believed that new species (and all higher taxa) arose by some form of special "mutation" (macromutations, hopeful monsters, systemic mutations, etc.) which immediately established a recognizably discontinuous form of a new species. Yet the evolutionist studying nature saw a quite different pattern: there were subtle geographic differences blending into subspecific recognition followed by the gradual accumulation of sufficient distinctness to warrant the designation of a new species. This continuous, gradual formation of species was a far cry from the genetic explanation offered by DEVRIES, BATESON and GOLDSCHMIDT. No wonder evolutionists doubted that the new Mendelian genetics was their key to the mechanism of evolution. This led evolutionists to consider other forms of inheritance, in particular what MAYR (1980) has termed "soft inheritance" theories including various forms of Lamarckism, Geoffroyism, and other environmentally induced adaptive changes. That this was still an issue is illustrated by the serious consideration given to the infamous case of KAMMERER (1924).

A second cause of the schism between geneticists and evolutionists is illustrated by T. H. MORGAN, the most influential geneticist of his time. Contrary to some population notions, MORGAN had a keen interest in evolution and, in fact, wrote three books on the subject (1903, 1925, 1932). Why did MORGAN fail to bridge the gap and set in motion the synthesis? His books reveal at least three reasons. First, he did not believe in species. He felt that species designations were arbitrary, the result of "a scholastic distinction that arose when species were regarded as specially created" (MORGAN 1932, p. 105). Second, MORGAN had an unorthodox view of natural selection [see WEINSTEIN (1980) for detailed discussion] and felt that it was not the primary force of change. He emphasized the role of mutation as the driving force of evolution—indeed, the creative force. After discussing his view of the importance of mutation, he states:

> This consideration shows that even without natural selection evolution might have taken place. What the theory does account for is the absence of many kinds of living things that could not survive . . . Natural selection may then be invoked to explain the absence of a vast array of forms that appeared, but this is saying no more than that most of them have not had a survival value. The argument shows that natural selection does not play the role of a creative principle in evolution (MORGAN 1932, p. 131).

Finally, MORGAN was one of the original staunch reductionists in approaching all biological problems. He believed that the key to understanding evolution was a more thorough knowledge of the physicochemical basis of heredity. Two examples will suffice. In discussing the origin of sterility of the mule, he points out that great strides have been made in discovering that the sterility is due to failure of proper synapsis of chromosomes. Then he states, "Until we learn more concerning the conditions that bring about the union of chromosomes, it may be unsafe to offer any explanation of the process" (MORGAN 1925, p. 50). In his 1932 book he devotes a whole chapter to "The Theory of Sexual Selection and Hormones." He makes a plea that the key to understanding sexual dimorphism is to learn more about ways in which hormones differentially affect development in the sexes. Nowhere in his writings on evolution is there a serious concern for populational phenomena. Evolutionists would be concerned with trying to understand what population histories might have caused the horse and donkey to possess different chromosomes. What interaction with the environment might have caused selection, drift, or whatever, to fix these differences? Such issues did not concern MORGAN. In this context it is interesting to see how MORGAN treated the emerging field of population genetics as exemplified by WRIGHT, FISHER and HALDANE. By 1932 he must certainly have been aware of their writings, yet none of their theoretical papers is referenced or discussed. (Curiously, none of MORGAN's books on evolution and genetics is cited by DOBZHANSKY despite the fact that MORGAN was the chairman of DOBZHANSKY's department!)

MORGAN was not alone among geneticists in not appreciating populational phenomena. MAYR (1980, p. 29) states: "GOLDSCHMIDT thought of the origin of new types in terms of proximate causation. In 1952 I asked GOLDSCHMIDT how the population in which a new hopeful monster occurred would react to it. He answered, after considerable pause, 'I have never thought of it that way.'"

Why, then, did DOBZHANSKY succeed in 1937 when his predecessors had failed to bridge the gap? The usual (*e.g.*, GOULD 1982) and probably largely valid explanation is that he was trained in and understood genetics, systematics and natural history. This was due to his initial education in natural history and systematics in Russia followed by training in MORGAN's laboratory. Thus, he could appreciate as could few others the different approaches, concerns, and vocabularies of the two groups of biologists. (A. H. STURTEVANT was perhaps another who had the required breadth and background; however, he was not one to indulge in the necessarily speculative arguments which were needed. In England, J. HUXLEY had gone very far toward realizing the beginning of a synthesis, although his definitive treatise, *Evolution, The Modern Synthesis*, did not appear until 1943. However, in his Preface, HUXLEY states that "DOBZHANSKY's valuable and distinctive book did not appear until much of the present volume was in proof.") The highlights of DOBZHANSKY's 1937 book are, briefly:

- The various theories of "soft inheritance" were untenable, whereas the geneticists' insistence on the importance of spontaneous mutations as the source of variation was valid.
- While mutation was the source of variation, natural selection was the prime agent of adaptation. Thus, DOBZHANSKY reinstated the Darwinian tradition (as practiced by natural historians) as the central tenet in understanding the "creative" aspect of evolution.
- The integration of genetics with systematics and natural history could best be achieved by adopting a populational approach. The theoretical basis for this approach was being developed by WRIGHT, FISHER and HALDANE. WRIGHT's models in particular appealed to DOBZHANSKY because they emphasized population structure (size, fluctuations, geographic isolation, etc.) which students of natural populations saw as vital in understanding evolution.
- Species, as a stage in the evolutionary process, are real and are one of the crucial steps in all evolutionary change. The biological species concept was introduced and defended. The importance of isolating mechanisms was emphasized: with the establishment of genetic isolation (speciation), lineages are free to independently explore new adaptive peaks, *sensu* WRIGHT.
- For the first time it was emphasized that, in addition to being an adaptive process, evolutionary change leads to diversity (thus DOBZHANSKY's emphasis on the speciation process as a multiplication of life forms).
- The genetic basis for species differences and, by extension, the speciation process, is not qualitatively

different from intraspecific genetic variation.

Thus, in a sense, there was something for everyone. Concepts like soft inheritance and macromutations or hopeful monsters were discounted. The familiar Mendelian genes and chromosomes geneticists studied in the laboratory were more than trivial curiosities; they could account for larger biological phenomena. For the natural historian, the gradual changes observed in nature were shown to be perfectly compatible with Mendelian genetics, natural selection regained its central role as the agent of adaptive change, and populational concepts were brought to the forefront. For the systematist, the reality of species as natural units was defended and their importance as a crucial stage of evolutionary change was emphasized. Thus, systematics took on greater importance than the merely "pigeon-holing" role detractors had assigned to the field. To be sure, each group had to relinquish some cherished beliefs, but many were willing to, given the logic, internal consistency and supportive data that weave through the book.

It is often said that timing is important in presenting new ideas and 1937 seemed to be the right time for this first attempt to present the synthesis. "It was, so to speak, in the air" (DOBZHANSKY 1962). This is not to imply that the 1937 book was the final word, far from it. DOBZHANSKY himself stated in 1962: "As I look it (the First Edition) over now, I see quite a lot of things which are simply naive, and a lot of other things which are plain wrong." What it did supply was a common ground, a starting point for the next several decades of attempting to fully integrate genetics with evolution. Several seminal books were directly inspired by DOBZHANSKY's book: E. MAYR's *Systematics and the Origin of Species* (1942), G. G. SIMPSON's *Tempo and Mode in Evolution* (1944) and G. L. STEBBINS' *Variation and Evolution in Plants* (1950). These books and their successors greatly broadened the synthesis to include paleontology, systematics and botanical studies. Thus, the authors and work stimulated by *Genetics and the Origin of Species* have been at least as important as the book itself.

A second major impact of this book, especially in its later editions, was to establish the field of experimental population and evolutionary genetics. Largely through his own experimental work, DOBZHANSKY was able to show that many problems of evolution were amenable to experimental study. His earlier exposure to the Russian school of CHETVERIKOV, TIMOFEEF-RESSOVSKY, SEREBROVSKY, etc., who had begun programs in experimental evolutionary genetics, no doubt predisposed him to pursue such studies. (The rise of LYSENKO snuffed out this pioneering Russian research program; had it not, the history of evolutionary genetics would have been very different.) Probably the best illustration in the 1937 edition is the study of the genetic basis of the sterility of F_1 males from crosses of *Drosophila pseudoobscura* and *D. persimilis* (then called Races A and B). Using mutant markers, he was able to demonstrate that the factors causing sterility resided on the chromosomes and that many factors spread over the genome were involved. This was clearly at odds with many theories of species differences. Perhaps more importantly, he showed that the degree of sterility varied with the geographic origin of the strains used in the crosses. A similar study by HOLLINGSHEAD (1930) demonstrated that geographic variation in the production of viable hybrids in the plant *Crepis* was due to a single Mendelian factor. These were crucial demonstrations that intraspecific variation existed for the very traits which define interspecific distinctions. This was the key in demonstrating the microevolution (intraspecific) and macroevolution (interspecific or higher taxonomic level) were qualitatively the same in the sense that they relied on the same genetic basis: Mendelian genes and chromosomal rearrangements.

A final observation worth considering, especially in light of contemporary ideas, is the role of random genetic drift in evolution. An insistence on the primacy of natural selection in adaptive evolution does not exclude a role for drift. Indeed, DOBZHANSKY was very much enamored of WRIGHT's views on the importance of random changes, especially for characters under weak or no selection. DOBZHANSKY began his study of the third-chromosome inversion polymorphism of *D. pseudoobscura* precisely because he wanted to test WRIGHT's theories. He thought the inversion polymorphism to be the ideal candidate for a neutral trait; no gene mutations were thought to be involved, only a rearrangement of existing genetic information. As the evidence became overwhelming that this polymorphism is under remarkably strong selection, DOBZHANSKY began to de-emphasize a role for drift in later editions. After all, if precisely the character one chooses to study as the ideal neutral trait turns out to be under strong selection, it is quite understandable that one would begin to doubt the importance of genetic drift. GOULD (1982) has called this the "hardening of the synthesis," by which he means the panselectionist attitudes so prevalent in the 1950s and 1960s.

With the introduction of molecular techniques to the study of natural genetic variation in the 1960s and 1970s, the attitude toward the importance of drift changed radically. With so much genetic variation at the nucleotide level, it seems virtually impossible that all such variation is subject to selection at all times. The theories of neutral molecular evolution, especially as developed by KIMURA and his associates, have been most influential. While DOBZHANSKY initially resisted, he eventually recognized the importance of these new developments. He told me in 1974, "I began as a drifter and then became a selectionist. Now, in my old age, I find myself becoming a drifter again."

Most evolutionary geneticists today have a healthy respect for the interaction of the various forces which can drive evolutionary change. The days of panselectionism, or pan anything, are over. The first edition of DOBZHANSKY's *Genetics and the Origin of Species* has, in this context, a curiously modern ring to it. It is still worth reading. It was crucial in helping to set into motion one of the great advances in biology as well as an agenda for research which continues today.

I thank H. CARSON, J. CROW, D. FUTUYMA, E. MAYR and W. PROVINE for comments on an earlier draft of this essay. Needless to state, not all of their advice was heeded.

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LITERATURE CITED

BATESON, W., 1922 Evolutionary faith and modern doubts. Science **55:** 55–61.

DOBZHANSKY, TH., 1937 *Genetics and the Origin of Species.* Columbia University Press, New York. Second edition, 1941; third edition, 1951; first edition republished, 1982.

DOBZHANSKY, TH., 1962 The reminiscences of Theodosius Dobzhansky. Transcript of interview conducted by B. LAND for the Oral History Research Office of Columbia University, New York.

DOBZHANSKY, TH., 1970 *Genetics of the Evolutionary Process.* Columbia University Press, New York.

GOULD, S. J., 1982 Introduction. pp. xvii–xli. In: *Genetics and the Origin of Species* by TH. DOBZHANSKY. Columbia University Press, New York.

HOLLINGSHEAD, L., 1930 A lethal factor in Crepis effective only in interspecific hybrids. Genetics **15:** 114–140.

HUXLEY, J., 1943 *Evolution, The Modern Synthesis.* Harper & Brothers, New York.

KAMMERER, P., 1924 *The Inheritance of Acquired Characteristics.* Boni & Liveright, New York.

MAYR, E., 1942 *Systematics and the Origin of Species.* Columbia University Press, New York.

MAYR, E., 1980 Prologue: Some thoughts on the history of the evolutionary synthesis. pp. 1–48. In: *The Evolutionary Synthesis*, Edited by E. MAYR and W. PROVINE. Harvard University Press, Cambridge, Mass.

MORGAN, T. H., 1903 *Evolution and Adaptation.* Macmillan, New York.

MORGAN, T. H., 1925 *Evolution and Genetics.* Princeton University Press, Princeton, N. J.

MORGAN, T. H., 1932 *The Scientific Basis of Evolution.* W. W. Norton, New York.

SIMPSON, G. G., 1944 *Tempo and Mode in Evolution.* Columbia University Press, New York.

STEBBINS, G. L., 1950 *Variation and Evolution in Plants.* Columbia University Press, New York.

WEINSTEIN, A., 1980 Morgan and the theory of natural selection. pp. 432–445. In: *The Evolutionary Synthesis*, Edited by E. MAYR and W. PROVINE. Harvard University Press, Cambridge, Mass.