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LESLIE CLARENCE DUNN

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A Biographical Memoir by

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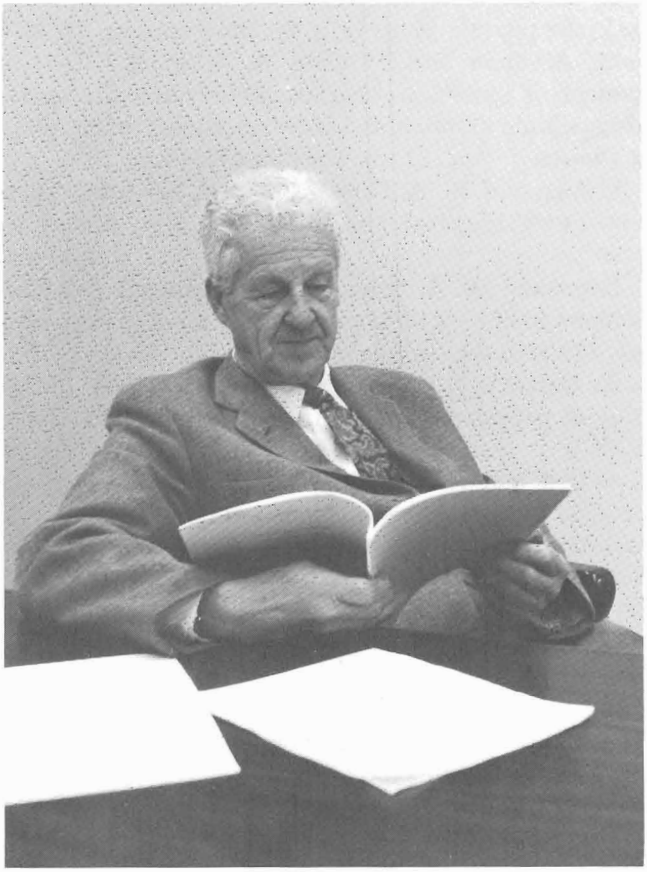
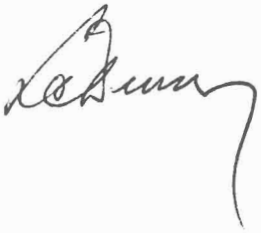
Biographical Memoir





LESLIE CLARENCE DUNN

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BY THEODOSIUS DOBZHANSKY

LESLIE CLARENCE DUNN was one of the most active and productive research geneticists in the United States. Through his many students, and even more through the textbooks and other books that he authored, Dunn was a teacher of a whole generation of American geneticists and of many foreign ones. He also generously gave much of his time and energy working for a variety of causes that his keen sense of social responsibility caused him to regard as important. Not an ivory-tower scientific specialist, he was a man of diverse human interests and accomplishments.

Born in Buffalo, New York, L. C. Dunn was a son of Clarence Leslie and Mary Eliza (Booth) Dunn, whose families were apparently moderately prosperous farmers and land dealers. Both parents were high school graduates, interested in literature —the mother especially in poetry and the father in biography and fiction. There was a library in the family home, which, according to the statement in L. C. Dunn's brief autobiography (unpublished; statement for the National Academy of Sciences, 1967), "helped to form [his] early tastes and habits." He attended a grammar school, graduating in 1907, and Lafayette High School, graduating in 1911. He was a good but not exceptional student, interested particularly in literature and later in biology. He decided to study at Dartmouth College, obtaining a scholar-

ship established by Randolph McNutt, one of the two Dartmouth alumni in Buffalo, and resisting the blandishments of the other alumnus, who offered Dunn a job with the Standard Oil Company.

At Dartmouth College (1911–1915), Dunn studied zoology under the direction of Professor J. H. Gerould, with whom he established lasting ties of mutual respect and affection. In 1914, Gerould "dropped" on Dunn's lab desk a copy of T. H. Morgan's book *Heredity and Sex*. This captured Dunn's interests entirely. A seminar organized by Gerould for a small number of students to discuss the books and papers of Morgan and R. C. Punnett on genetics made that interest permanent for life.

After the graduation from Dartmouth in 1915, Dunn was accepted as a graduate student at Harvard and given an assistantship to Professor W. E. Castle at a salary of sixty dollars per month. Dunn had experience working with laboratory mice, so he was prepared for the technical work he was to do for Castle. However, in his words, "I was surprized to be given on the first day of the fall term, soon after my arrival, charge of the discussion group of Castle's course in genetics as well as of the laboratory in which the students bred Drosophila." Castle always treated students as equals and expected them to know as much as he did. Dunn evidently lived up to his professor's assumption. As his own research problem, Dunn at first started a study of the effects of selection on recombination frequencies of sex-linked genes in Drosphila. After he was "scooped" by publication of results similar to his by one of T.H. Morgan's students, he shifted to experiments on linked genes in mice and rats.

Between 1916 and 1921, Dunn published eight papers on genetics of rodents, including his dissertation, "Linkage in Mice and Rats" (1920). When his graduate work was interrupted by the outbreak of the World War, he volunteered for officers' training, was commissioned Second Lieutenant of Infantry, soon

promoted to First Lieutenant, and sent to the American Expeditionary Force in France. He returned to resume his studies at Harvard in March 1919. In May 1918 he was married to Louise Porter, a graduate of Smith College, who survives him. Likewise surviving are two sons, Robert Leslie, born in 1921, and Stephen Porter, born in 1928.

Even before he was officially awarded his doctorate, Dunn accepted the position of poultry geneticist on the staff of the Agricultural Experiment Station at Storrs, Connecticut. Although he had never handled a chicken before accepting this position, he found poultry interesting research material and plunged into work. The years at Storrs (1920–1928) resulted in publication, alone or with co-authors, of forty-nine papers on poultry genetics. In the opinion of I. M. Lerner, the most distinguished living poultry geneticist, "The fewer than 10 years that [Dunn] spent working primarily with poultry presents a chronicle of pioneering and versatility in the use of the chicken in genetic investigation that has not been surpassed. . . ." A group of Dunn's publications deals with the relationship between egg weight and hatchability. In Lerner's words, this was "a topic whose significance to evolutionary theory did not become clear until 20 or 30 years later. Natural selection for intermediate phenotypic expression of such traits as egg size eventually became an important example of stabilizing selection. J. B. S. Haldane's student, Rendel, dealt with this phenomenon in ducks, and it was Dunn's data on chickens that figures prominently in my own 1951 analysis of what I termed genetic homeostasis."

Dunn's experiments on loss of vigor resulting from inbreeding, and the restoration of vigor following intercrossing of inbred lines of chickens, were most extensive and most carefully analyzed in his day. To quote Lerner again:

> It is, perhaps, the category dealing with skeletal variants in which Dunn was most productive of all. Not only did he investigate isolated cases of such

specific traits as chondrodystrophy, but, in collaboration with [Walter] Landauer, he also pioneered the general study of the genetics of terata. The demonstration of the lethal nature of the creeper gene was a landmark in animal genetics. The investigation of the evolution of dominance of the rumpless gene was another. The entire field dealing with the basis of production of phenocopies in vertebrates, later so brilliantly illuminated by Laundauer, was also rooted in these investigations.

Dunn's years at Storrs saw also the initiation of his career as a writer of a genetics textbook. In collaboration with his botanical colleague E. W. Sinnott, he produced *Principles of Genetics* (first edition published in 1925), which soon became one of the most widely used texts of genetics. The second edition was published in 1932, the third in 1939, and the fourth and the fifth in 1950 and 1958 in collaboration with Th. Dobzhansky (although Sinnott's name was retained as the senior author). During the last years of his life, Dunn was sketching parts of what was meant to become the sixth edition. Translations of *Principles of Genetics* appeared in several languages (and so did a pirated edition in English printed in Taiwan). Most interesting is the fate of the Russian translation in the 1930s, more copies of which were published than the English original. It was widely used for several years, until Trofim Denisovich Lysenko and the Soviet government outlawed it, whereupon it came to be passed from hand to hand like a subversive tract.

Among six other books authored by Dunn, three had a wide distribution—*Race and Biology*, published by UNESCO in 1951 (third edition, 1970); *A Short History of Genetics* (1965); and especially *Heredity, Race and Society* (1946; fourth edition, 1972). This last (in collaboration with Th. Dobzhansky) sold more than half a million copies in English and was translated into several foreign languages (including Arabic, Persian, Burmese, as well as six European ones).

A turn in Dunn's career came in 1928, when he was invited to become a full professor at the Zoology Department of Columbia University, New York City. He accepted after some hesita-

tion, being reluctant to move from a research position to one involving teaching and administrative work. Yet he quickly showed himself to be as excellent a teacher and administrator as he was a researcher. The crowded and antiquated facilities housing natural sciences in the old Schermerborn Hall were somewhat relieved by the construction of an adjacent building, with Dunn being an active member of the building committee. More graduate students wished to work with Dunn than he felt prudent to accept. A university located in the midst of a great city could not provide space for large-scale experiments on poultry. Dunn shifted back to his old research materials, mice and Drosophila, continuing however to analyze, in collaboration with Landauer, the poultry experiments made at Storrs.

Dunn's work on mouse genetics at Columbia was at first concerned mainly with pigmentation, particularly the complex phenomena of spotting patterns and gene effect interactions. By means of suitable crosses, some cryptic gene effects can be brought to light. In one of his papers, Dunn concluded that an "unspotted race contained mutant alleles which produced no spotting effects themselves but did produce spotting when combined with other spotting alleles. Such 'sub-threshold alleles' therefore act as modifiers of other factors with more extensive effects by interaction additively with them." Hardly any geneticist in 1978 will be surprised by this situation, but it was novel forty years ago!

Dunn's interest in congenital abnormalities in animals led him to study lethal and semilethal mutants in poultry, mice, and Drosophila and compare them with abnormalities described in man. Some of the genetically conditioned abnormalities are paralleled by nongenetic "phenocopies" that mimic the manifestations of the mutants. These studies, combining genetical and embryological methods and techniques, made Dunn the leader of an American school of developmental genetics. S. Gluecksom-Waelsch and D. Bennett are among the outstanding

developmental geneticists now living who were Dunn's students. The work on a group of mutants in mice that affect the tail and other axial skeletal structures opened up problems that occupied Dunn for some forty-four years, until the end of his life. At least one of the genes involved, the *T-t* locus, exhibits a high mutation rate and produces many mutant alleles (or pseudoalleles). Some of these are dominant and others recessive to the "normal" condition. Most extraordinary is that some of these mutants (but not others) so distort the segregation of the chromosomes that carry them that the mutants are transmitted to more than one-half of the male sex cells formed. No deviations from the expected 1:1 Mendelian segregations are observed in the females. *T*-locus mutants occur not only in laboratory cultures but also in wild (feral) mice populations.

This led Dunn, D. Bennett, and some of their collaborators into the field of population genetics. If a gene allele subverts the segregation mechanism in heterozygotes, so that it is transmitted to more sex cells than the alternative allele, it thereby acquires a selective advantage. If unopposed by some other factors, the selectively favored allele must eventually drive out the others from the population. But some of the *t*-alleles favored by the abnormal segregation cause lethality or sterility when homozygous. Do *t*-alleles cause mice colonies to commit genetic suicides? There is no evidence that this happens. Together with P. K. Anderson, A. B. Beasley, D. Bennett, and others, Dunn began experiments on *t*-alleles introduced in free-living and experimental laboratory populations. In 1956 and 1957 mice heterozygous for a *t*-allele were released on Gull Island, in Long Island Sound. The population living on this island before the release was apparently free of *t*-alleles. By 1961, the introduced allele had reached a high frequency in the release area, but was spreading very slowly to the rest of the island.

From his student days to the end of his life, Dunn was interested in human genetics and anthropology. By 1923 he had

already published *Some Results of Race Mixture in Hawaii.* Several general articles and some of his books are concerned with the bearings of genetics on human problems. He was elected president of the American Society of Human Genetics in 1961 and delivered a presidential address entitled "Cross Currents in the History of Human Genetics." Not satisfied with only theoretical discussions, Dunn attempted to organize an Institute for the Study of Human Variation, in which original research on the causes of evolutionary changes in human populations could be initiated and developed. The idea won the enthusiastic support of some of his colleagues, but met with antagonism from others. Not until the early 1950s was some space finally obtained in one of the old residences belonging to Columbia University and some laboratory equipment purchased for the Institute. Dunn became its director, but the opportunity to do research on human materials came simply too late in his scientific and personal life. The Institute was closed after some six years. Several investigations were carried out under the aegis of the Institute; Dunn's main work was a study entitled "The Jewish Community in Rome" (jointly with S. P. Dunn, 1957). Several students who now hold professorships in human genetics or anthropology did parts of their research at the Institute, including R. H. Osborne, W. S. Pollitzer, A. Falek, and I. L. Firschein.

In his curriculum vitae, composed in 1967, Dunn writes that:

> A long standing interest has been in improving relations between nations and cultures, using scientific collaboration as a bridge. This probably originated in disappointment with the results of political and military arrangements during and after World War I. As an army officer returning from Europe in 1919 I entered into correspondence with agencies for cultural relations with the Soviet Union, helping to provide scientific and technical literature useful in the new state which arose from the revolution in October 1917. This seemed to be the chief political event of my generation.

In 1927 Dunn toured Europe, visiting the University of Edinburgh (the laboratory of F. A. E. Crew) and Kaiser Wilhelm Institut für Biologie in Berlin (the laboratory of R. B. Goldschmidt), attending the International Congress of Genetics in Berlin, and then traveling to Russia in the company of A. S. Serebrovsky. It was the Russian part of the trip that was most memorable to Dunn. Serebrovsky was a man of wide culture, original and sometimes audacious ideas in science, and a gracious host who saw to it that Dunn received most favorable impressions from his visit. Dunn became one of the founders and an active member of the American–Soviet Friendship Council and during World War II president of the American–Soviet Science Society. He did not wave in his sympathies, even during the years of Lysenko's control of genetics, although he justifiably complained that "those who, like myself, promoted collaboration, fell into disfavor on both sides of the Iron Curtain." Indeed, the Council and the Science Society were placed on the list of subversive organizations in the United States, and Dunn was never able (or willing) to revisit the Soviet Union.

The rise of the Nazi in Germany repelled and saddened Dunn and gave a new direction to his interest in international scientific collaboration. In 1933 he became a member of the Emergency Committee for German Scholars, and during the 1930s and 1940s aided a considerable number of them to become established and to continue their work in American universities. Dunn's interest in one of the causes of human group conflict that the Nazi revolution brought into prominence, namely race prejudice, goes back to his student days. After 1933 he was repeatedly asked to speak and write about the bearings of biology on social and political problems. Three of the seven of his books are directly or indirectly inspired by his concern about racism. In 1950 he served as the rapporteur for the UNESCO Commission

on Race and was the chief author of the document *The Race Concept,* published in 1952.

The political reaction of the late forties and fifties distressed Dunn. Not only were some of the organizations to which he belonged declared subversive, but he was attacked personally in some newspapers and other publications, including a scientific journal, as a crypto-Communist or at least a Communist sympathizer. The absurdity of these accusations was evident to anybody who knew him at all well. In his memoirs he describes himself as a "Fabian socialist." Violence, cruelty, and inhumanity were repellent to Dunn, regardless of whether they came from the Right or from the Left. The attacks on his truly selfless and idealistic activities were an unexpected and therefore more bitter disappointment. He almost entirely withdrew from sociopolitical activities into himself and his science.

Following his retirement from the professorship at Columbia University in 1962, Dunn set up a "mouse lab" in a converted barn and "milk room" on the Nevis estate (belonging to Columbia University), up the Hudson River north of New York. There he worked almost full time on the analysis of the *t*-locus in the mouse. His faithful collaborator was, to the very end, his former student Dr. Dorothea Bennett, who simultaneously held a professorship at the Medical College of Cornell University. My approximately annual meetings with Dunn during his last years showed that he had reached a serene, yet intellectually active and satisfying, old age.

Dunn was the recipient of many honors. He was a member of the U.S. National Academy of Sciences (elected in 1943), American Philosophical Society, American Academy of Arts and Sciences, Norwegian Academy of Sciences, and the Italian Accademia Pataviana. He was one of the founders of the Genetics Society of America, its President in 1932, and managing editor of *Genetics* from 1935 to 1940; member of the American Society

of Naturalists, its President in 1960, and editor of *The American Naturalist,* 1951–1960; and member of the American Society of Human Genetics and its President in 1961. In 1934–1935 Dunn was visiting investigator at the Genetics Institute of the University of Oslo, Norway; in 1953–1954, visiting investigator, Istituto Superiore de Sanita, Rome; and in 1960–1961, visiting research associate, University College, London.

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KEY TO ABBREVIATIONS

Am. J. Hum. Genet. = American Journal of Human Genetics
Am. J. Phys. Anthropol. = American Journal of Physical Anthropology
Am. Nat. = The American Naturalist
Anat. Rec. = Anatomical Record
Ann. N.Y. Acad. Sci. = Annals of the New York Academy of Sciences
Biol. Rev. = Biological Reviews
Bull. Storrs Agric. Exp. Stn. = Bulletin of the Storrs Agricultural Experiment Station
Columbia Univ. Q. = Columbia University Quarterly
Eugen. Q. = Eugenics Quarterly
Genet. Res. = Genetical Research
J. Biol. Chem. = Journal of Biological Chemistry
J. Exp. Med. = Journal of Experimental Medicine
J. Exp. Zool. = Journal of Experimental Zoology
J. Genet. = Journal of Genetics
J. Hered. = Journal of Heredity
J. Mammal. = Journal of Mammalogy
J. Morphol. = Journal of Morphology
J. Reprod. Fertil. = Journal of Reproduction and Fertility
Poult. Sci. = Poultry Science
Proc. _____ Int. Congr. Genet. = Proceedings of the _____ International Congress of Genetics
Proc. Natl. Acad. Sci. USA = Proceedings of the National Academy of Sciences of the United States of America
Proc. Soc. Exp. Biol. Med. = Proceedings of the Society for Experimental Biology and Medicine
Sci. Am. = Scientific American

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