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CURT STERN

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A Biographical Memoir by
JAMES V. NEEL

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Biographical Memoir

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Curt Stern

CURT STERN

August 30, 1902– October 23, 1981

BY JAMES V. NEEL

THERE HAVE BEEN three remarkable periods in the history of modern genetics. The first of these, in the early years of this century, encompasses the rediscovery and confirmation of Mendel's findings and the enunciation of the chromosomal theory of inheritance. The second period is characterized by a concatenation of discoveries regarding the more precise mechanisms of chromosomal behavior, largely based on the use of *Drosophila* and emanating from the "fly room" at Columbia University. The third is the period in which we now find ourselves, initiated in the 1940s by the seminal observations of Avery and collaborators and the later phage work demonstrating that the essential genetic material was DNA and the demonstration, using *Neurospora*, that genes have essential and specific roles in the synthesis of proteins. This was followed by the elucidation of the structure of DNA, leading to a cascade of discoveries concerning DNA fine structure and how it can be manipulated. Each of these flowerings dominated the conceptual biological thinking of the time.

NOTE: This memoir is an expanded version of a manuscript published in the *Annual Review of Genetics*. I am deeply indebted to the many people who have contributed their remembrances and perspective to the writing of this memoir.

THE EARLY YEARS

Curt Stern, the subject of this memoir, must be regarded as one of the principal participants (and last survivors) of the fly room period.¹ Born in Hamburg, Germany, on August 30, 1902, the first son of Barsed and Anna Stern, he early displayed a strong interest in natural history, ranging from microscopic studies of pondwater to the zoological collections that enliven parental responsibilities. In these interests he received unusual support from two extraordinary high school teachers, who encouraged him to undertake the study of zoology. His father, who was in the dental supply business, and his mother, a schoolteacher, were also highly supportive as their son's biological interests unfolded. Following the family's move to a suburb of Berlin, he entered the University of Berlin in 1920. He must almost immediately have found his way to the Kaiser Wilhelm Institute, where he conducted his doctoral studies. He received a Ph.D. from the University of Berlin in 1923, at that time the youngest person ever to receive the degree from the university. There is no record of an undergraduate degree. Attendance at the university required one to two hours of commuting each way. To achieve his degree so early under these circumstances was an early, clear signal of the remarkable combination of high intellectual ability, photographic memory, and stamina that was to characterize his career.

Stern's Ph.D. thesis was a descriptive cytological study of mitosis in a protozoan of the order *Heliozoa*, under the direction of one of the truly eminent protozoologists of that era, Max Hartmann. One perceives here the momentum of a high school fascination with microscopic pond life. By the time he finished his thesis, he knew he would not remain a

¹ The only remaining survivor of the "fly room" known to the author is Helen Redfield (Mrs. Jack) Schultz.

protozoologist. Reading widely, he became intrigued by genetics. A paper by Richard Goldschmidt, then director of the Institute, on the basis for crossing-over caught his attention. Stern felt Goldschmidt's interpretation was incorrect and wrote a critique, which, after great hesitation, he submitted to Goldschmidt. (He was at that time probably the most junior fellow at the Kaiser Wilhelm Institute.) Some six months later, Goldschmidt returned the paper without comment, but shortly thereafter called Stern into his office. Those of us privileged to see Goldschmidt in action after his immigration to the United States will recall the personification—at least superficially—of the Geheimrat Professor. One can imagine the trepidation with which Stern approached the meeting. With few preliminaries, Goldschmidt offered Stern a fellowship, recently funded by the International Education Board of the Rockefeller Foundation, to study genetics with the Morgan group. There apparently was never any discussion of the critique.

DROSOPHILA

Stern arrived at Columbia in 1924. The fly room was near or at its zenith. Morgan in 1910 had demonstrated sex-linked inheritance in *Drosophila* and then the recombination of two sex-linked alleles, one responsible for white eye and the other for rudimentary wing. These exciting discoveries, along with the obvious potentiality of *Drosophila* as an experimental organism, had attracted to Morgan's laboratory a now historic triumvirate—Sturtevant, Bridges, and Muller. The publication by Morgan, Sturtevant, Muller, and Bridges of "The Mechanisms of Mendelian Heredity" in 1915, which brought together the early data on autosomal as well as X-chromosome inheritance and linkage, with linkage maps and the evidence for nondisjunction, had made clear how major the developments at Columbia were. One result was a rising

number of students and visiting investigators, who, together with Sturtevant, Muller, and Bridges, were all crowded into a room 16 by 23 feet in size, which contained eight working desks! (For a forthright statement of the physical “togetherness” of this setting, and especially the space allotted to Stern, see Provine 1981.)

There quickly ensued several “beginner papers,” but the first major result of this fellowship, published in 1926–1927, was the demonstration by a combination of genetic and cytological techniques that the anomalous genetic behavior of the “bobbed bristles” trait could be explained by the Y-linked inheritance of the responsible allele (plus a homologous locus on the X). Until then, the Y-chromosome of *Drosophila*, although associated with male fertility, had been considered as otherwise genetically empty. Although Y-linked inheritance had previously been demonstrated by Schmidt in the fish, *Lebistes reticulatus*, this demonstration that abnormalities of Y-chromosome behavior (that is, the occurrence of XXY females) accounted for abnormalities in the inheritance of the bobbed trait was unusually elegant for the times, no doubt benefiting greatly from the cytological demands of Stern’s Ph.D. thesis.

His second major contribution appeared in 1931: the demonstration, using cytologically abnormal X-chromosomes, one with an X-Y translocation, one with an X-IV translocation, that the genetic phenomenon of crossing-over was accompanied by a physical exchange between the chromosomes. (Simultaneously, Creighton and McClintock quite independently demonstrated the same phenomenon in corn.) This was shortly followed by an ingenious demonstration (back to the Y-chromosome) that as he added supernumerary Y-chromosomes bearing the bobbed allele to *Drosophila*, the trait gradually disappeared, understandable now that we know the bobbed alleles are characterized by varying

degrees of underproduction of ribosomal RNA. At that time the demonstration that adding enough defective genes would produce normality was novel.

Stern's last major contribution to our understanding of the chromosomal basis of inheritance was published in 1936. He had returned to Germany in 1926, but had come back to the United States in 1932, on a second fellowship from the Rockefeller Foundation, spending the year at the California Institute of Technology in the company of a remarkable collection of geneticists: Morgan, Sturtevant, Dobzhansky, Bridges, Schultz, Emerson, Darlington, Kaufmann, and Lindgren. He had married an American citizen, Evelyn Sommerfield, in 1931. In 1933, when he was due to return to Germany, Hitler came to power, a development whose tragic implications for German Jews has been only too well documented. While Stern remained in the United States, Evelyn returned to Germany to seek some cautious advice from his colleagues. What she learned convinced them it would be wise not to return. (He became a U.S. citizen in 1939.) Stern accepted a temporary position at Western Reserve University, but quickly moved to the University of Rochester, where he was to remain until 1947, serving from 1941 to 1947 both as chairman of the Department of Zoology and chairman of the Division of Biological Sciences.

Shortly after he arrived at Rochester, he began to investigate what was then a puzzling phenomenon: the occurrence in female flies heterozygous for one or several sex-linked recessive alleles of epidermal spots manifesting the effects of one or all of these alleles or even, if the alleles were on different but homologous chromosomes, "twin spots," exhibiting the phenotypes associated with both alleles. A classical analysis revealed that the only consistent explanation required a previously unrecognized phenomenon, mitotic crossing-over. I would like to suggest that this paper was the

end of the “chromosomal era” in the history of *Drosophila* as an experimental organism. It was to continue to provide insights on other problems, but the story of how its chromosomes behaved (in the classical sense) was now essentially complete.

In several autobiographical sketches, Stern has emphasized that he never attempted any grand research design, but simply “followed his nose.” The beauty of *Drosophila* was how quickly one could move from one major issue to the next, providing you knew how to manipulate the fly stocks—at which Stern was probably second only to Muller. That nose led him unerringly to basic issues. Space permits mention of only three of the outstanding contributions subsequent to 1936 that depended on experiments with *Drosophila*.

1. *Isoalleles*. The recessive allele *cubitus interruptus* (*ci*), located in the fourth chromosome, causes a gap of variable length in the fourth wing vein. Working with strains thought to be isogenic except for fourth chromosomes of different origins, as well as with strains in which a deficiency of the region encompassing the *ci* locus was present, and manipulating temperature, Stern in 1943 demonstrated that normal alleles of *ci* differed greatly in their potency, as measured by their ability to modify the expression of the *ci* trait in heterozygotes or hemizygotes for this locus. He termed these different normal alleles “isoalleles.” This demonstration of a range of genetic variation beyond that easily envisioned presaged (and may now find an explanation in) the demonstration years later of extensive inapparent biochemical variation. At that time there was still concern amounting to disbelief among some biologists and paleobiologists that the kinds of traits arising through mutation in *Drosophila* could possibly serve as the stuff of evolution. Since these alleles of small effect presumably arose from the mutational process, this direction of attention to traits of lesser effects played a signifi-

cant role in what Mayr has termed “the evolutionary synthesis” (Mayr and Provine 1980).

2. *Genetic effects of low-level radiation.* During and after World War II, Stern, in collaboration with Spencer, Caspari, and Uphoff, was drawn into studies of low-level radiation effects, studies sponsored by the Rochester branch of the U.S. Army’s Manhattan Engineering District. The question, in the context of the advent of the atomic bomb, was obvious: Was there a threshold in the genetic effects of radiation? The finding—now a cornerstone of radiation genetics—was clear: “Viewing all experiments together, it appears that radiation at low doses, administered at low intensity, induces mutation in *Drosophila* sperm. There is no threshold below which radiation fails to induce mutations” (Uphoff and Stern 1949). It was undoubtedly this background that led to a term (1950–1953) on the Advisory Committee to the Division of Biology and Medicine of the Atomic Energy Commission, a critical period in the development of the AEC’s policy of broadly based research into radiation effects.

The work on the effects of low-level radiation had used sex-linked lethals as indicator traits. Since it was felt that radiation produces disproportionate numbers of lethals (as the normal spectrum of mutation is understood), an important question was the effect of these “recessives” when heterozygous. Given the ratio of heterozygotes to homozygotes predicted by the Hardy-Weinberg formulation, for a rare allele even a small heterozygote effect for an autosomally inherited recessive lethal could outweigh the impact of the occasional homozygote. Stern—with Carson, Kinst, Novitski, and Uphoff—in 1952 established that under their conditions, the average viability of heterozygotes for sex-linked lethals was 96.5 percent normal, a figure still standard. Their data did not permit any distinction between the effects on viability of spontaneous and induced mutation.

3. *The extent of cell autonomy in gene expression and the genetic control of patterns.* In 1947, Stern left Rochester to become professor of zoology and, in 1958, professor of genetics as well, at the University of California, Berkeley; he retired from these positions in 1970. At Berkeley he returned to an old problem; the basis of the attack had been laid with the 1936 paper on somatic crossing-over and segregation. These studies had demonstrated a high degree of cell autonomy in the expression of genetic constitution in *Drosophila*. On the other hand, transplantation experiments (with Hadorn) had demonstrated that the color of the vasa efferentia was dependent on that of the testis attached to them and not on the genetic constitution of the ducts themselves, and that the shape of the testis (spiral or oval) was dependent on the genetic constitution of the sperm ducts to which it was attached (1939–1941). In the 1950s and much of the 1960s, most of Stern's research efforts, often in collaboration with his students, were directed toward the difficult problem of the genetic control of differentiation, and especially of patterns, still using *Drosophila* as an experimental organism.

The various types of regularly arranged chaetae, so obvious when one inspects a fly, proved most useful in these interests. Studies with Hannah-Alava, employing genetic mosaics of various derivations, demonstrated a new level of complexity in embryological determination: Differentiation of the male sex-comb (a specialized row of chaetae) depended on a field effect within which the development of the sex-comb teeth was determined—down to very small patches of cells—by the sex (maleness) of the cells. These and other studies led to what Stern in 1954 termed the “prepattern hypothesis.” Prepattern was a descriptive term for any kind of spatial differentiation in development, development being regarded as a succession of prepatterns. Within the prepat-

tern there are singularities, to which developing cells respond according to their genetic competences. Much of his later work on this subject, well summarized in 1978 by his colleague and collaborator Dr. C. Tokunaga, was directed toward defining, largely through the use of genetic mosaics, the nature of prepatterns, singularities, and competences. The familiarity with *Drosophila* mosaics these inquiries demanded inspired an omnivorous interest in mosaics of all types, reflected in the Prather Lectures at Harvard in 1965, in which he summarized his activities in this field.

One of Stern's last papers on *Drosophila*, in 1969, once again illustrated his ability to take full advantage of *Drosophila* as an experimental organism. The earlier studies on somatic cell crossing-over had not provided a clear approach to the relative frequency of somatic cell versus meiotic crossing-over. Since then, in the 1950s, compound or complex loci had been recognized in *Drosophila melanogaster*, such as the "white eye" (*w*) locus, within which meiotic crossing-over could occur. As a manifestation of the remarkable degree of cell autonomy in *Drosophila*, each individual facet of its compound eye expresses its genotype as regards pigmentation independently of the other. Stern scored female flies heterozygous for two different *w* alleles between whose mutational sites the frequency of meiotic crossing-over had been determined, for red-colored spots in their white eyes. Four such spots were found in a total of 6,137 flies. No such spots were observed in the eyes of 27,557 controls. On the assumption that the red spots resulted from somatic cell recombination in a cell of the developing eye disc, and that the eyes of the flies scored collectively provided a minimum of 9×10^6 mitoses in which the results of somatic recombination could be observed, these 4 spots suggested a frequency of recombination between these mutational sites of less than 1 or 2 in

2×10^6 mitoses (1 if the exchange was nonreciprocal, 2 if reciprocal). This was 400 to 800 times less common than meiotic crossing-over in the same region.

HUMAN GENETICS

Technically, Stern's advent into the other field of genetics with which his name is so prominently associated, human genetics, dates from a paper entitled "Welche Möglichkeiten die Ergebnisse der experimentellen Vererbungslehre dafür, dass durch verschiedens Symptome charakterisierte Nervenkrankheiten auf gleicher erblicher Grundlage beruhen?", published in 1928 in *Nervenarzt*. It is a very clear statement, directed to physicians, of a principle now commonly accepted: Indistinguishable phenotypes may have very different genetic bases. His serious entry into the field, however, can be dated more precisely to 1939. That year he supervised his first graduate student seminar in the field of human genetics. As one of the half-dozen students who met weekly for a semester, I still have the list of papers he chose for review. Two impressions stand out. First, he had managed to select what little solid data existed; the contrast between the then and the now of human genetics, developments within a single generation, is simply staggering. Second, given the excesses of American eugenicists, and especially the Nazi racism from which he personally had suffered, one might have expected some bitterness and an occasional diatribe on these monstrous perversions; Stern kept the discussion all science.

This occasion must mark the beginning of the most successful textbook on human genetics ever written. In the course of three English editions (1949, 1960, 1973), *Principles of Human Genetics* sold 62,337 copies; there is no way to estimate accurately the number of copies sold of the German, Japanese, Spanish, Portuguese, Hindi, Polish, and Russian

translations! Lest I seem to be equating success with sales, it should be made clear that the content of this book was a major factor in the coming of age of human genetics. Each edition was a major rewrite; the last, which appeared in 1973 and encompassed 891 pages, occupied much of his time during the last years of his tenure at Berkeley. Although Stern himself, in an autobiographical note written in 1974, attributed the genesis of his book primarily to the needs of premedical students, the psychoanalytically oriented must wonder if its scrupulous objectivity was not a Stern response to the perversion of genetic thought to which he had been so intimately exposed.

Stern also authored a dozen papers on human genetics, albeit none with the impact of his *Drosophila* work. He was for many years interested in Y-linked inheritance in man, and devoted his presidential address to the American Society of Human Genetics in 1957 to this topic. There he pointed out that of the fourteen traits that were candidates for Y-linked inheritance, all but one (hypertrichosis of the pinnae) were known from only a single pedigree—strange indeed from what we know of recurrent mutation. This fact—along with the ambiguities in most of the pedigrees—made him most suspicious of the validity of the evidence for such linkage, the single exception being hypertrichosis of the pinnae. His interest in this trait led to field work in India, his only field work in human genetics. The resulting 1964 publication, with Centerwall and Sakar, left the issue open, simple autosomal dominance or recessiveness being possible alternative explanations.

THE MAN

Stern was a small man whose whole being was dominated by eyes that could be both probing and dancing simulta-

neously. His tact and consideration of others were legendary. Yet beneath that gentle exterior was one of the toughest, most uncompromising (on principle) men I have ever met.

He and his wife Evelyn (née Sommerfield) had three daughters, Hildegard, Holly Elizabeth, and Barbara Ellen. The successive generations of graduate students who passed through the Stern home as these children were maturing sensed an extraordinary warmth of family life, and as we passed on to family responsibilities ourselves, we also realized the extra burden we had inflicted on Mrs. Stern in connection with the many meetings held in their home, and the charm and equanimity with which she treated us.

Stern's ability to present complex issues with simplicity and lucidness made him a popular teacher and sought-after lecturer. This ability was not restricted to his scientific peers and graduate students; at Berkeley, his course on general genetics regularly drew between 120 and 150 students, and his course on human genetics for nonscience majors for years drew some 300 students. (He also found time for genetic counseling.) The series of twelve half-hour films on genetics that he narrated, sponsored by the American Institute of Biological Sciences in 1961, has been used all over the world. Two lectures that illustrate the why of this popularity are the Prather Lectures delivered in 1965 at Harvard, entitled "Genetic Mosaics and Other Essays," and "Genes and People," delivered in 1966 as a special lecture for laymen in connection with the Third International Congress of Human Genetics.

As best the record can be reconstructed (primarily by his longtime associate, Dr. C. Tokunaga), Stern supervised the doctoral theses of some thirty students, and at least another dozen individuals had postdoctoral associations of varying durations. We, his students, have had very different scientific experiences with Stern, depending on the nature of his work

as we passed through his laboratory. But one experience we have all shared has been the exposure to an uncompromising perceptiveness and adherence to standards. Nevertheless, even as he drew attention to some less than brilliant act on our part, he somehow left us reassured there was still hope we would make it someday (see also Lucchesi 1983). During my first year of graduate work with Stern, I committed a major genetic faux pas. I do not remember what it was, but it would be impossible to forget how Stern handled it. Having straightened me out, he paused a minute. I was waiting for the next blow to fall when he smiled and said, "You know, Jim, in Germany we have a proverb—great men make great mistakes." The application of this amazing quality was not restricted to his graduate students—how many nervous young scientists delivering an almost-first paper have had their day made by the right comment from Stern.

More than most scientists, Stern kept an eye on the historical and philosophical aspects of his discipline. It was he who in 1943 directed geneticists' attention to Weinberg's independent formulation of what we now term the Hardy-Weinberg Law. Likewise, in 1950 he felt obligated to point out how Boveri, far from having delayed the recognition of the chromosomal basis of genetic linkage, as suggested by Punnett in his historical account in 1950, had with amazing insight predicted genetic linkage in 1904. He was cosignatory on a little note in *Lancet* that led to the replacement of the unfortunate term "mongolian idiocy" by "Down's syndrome." Finally, impressed by inaccuracies in the available translations into English of Mendel's papers and the source material concerning their rediscovery, he collaborated with Sherwood on a *Mendel Source Book*, published in 1966. And repeatedly during his career, he returned to the thoughts expressed in "The Journey, Not the Goal," in 1944, a plea for a "a wider and deeper realization of the value of science as an expression of a de-

tached essence of human existence." While of course aware of the significance of his own contributions, his two autobiographical notes (and all his papers) are scrupulous in their recognition of his intellectual debts to others (Stern 1971, 1974).

LATER YEARS

Honors came early to Stern, and continued to accumulate until his final, incapacitating illness. He was in turn president of the Genetics Society of America (1950), the American Society of Human Genetics (1957), the American Society of Naturalists (1962), and the Thirteenth International Congress of Genetics (1973). He served as editor of *Genetics* from 1947 to 1951. Elections to learned societies included the National Academy of Sciences (1948), the American Philosophical Society (1954), and the American Academy of Arts and Sciences (1959). He was twice a fellow of the Guggenheim Foundation (1955, 1963). Awards included the Kimber Genetics Medal of the National Academy of Sciences in 1963, the Mendel Silver Medal of the Czechoslovakia Academy of Sciences in 1965, the Adair Award of the American Gynecological Society in 1967, and the Allan Award of the American Society of Human Genetics in 1974. He was Benjamin Franklin Lecturer at the University of Pennsylvania in 1951, Faculty Research Lecturer of the University of California in 1964, and Prather Lecturer at Harvard University in 1965. He received honorary degrees from McGill University (1966) and the University of Munich (1972). His bibliography encompasses five books (*Multiple Allelie*, 1930; *Faktorenkoppelung u. Faktorenaustausch*, 1933; *Principles of Human Genetics*, 1949, 1960, 1973; *The Origin of Genetics*, with Eva Sherwood, 1966; and *Genetic Mosaics and Other Essays*, 1968) and approximately 230 individual coauthored journal publications.

Earlier it was suggested that Stern's passing severs almost the last personal link with the "fly room" era. There is perhaps another symbolism in his death. During his productive years—mid 1920s to the end of the 1960s—a front-rank geneticist was expected to be conversant with *all* important contemporary genetic developments. This Stern was, and if his encyclopedic memory failed him on a point, his ability—in his cluttered office—to put his hands on just the right paper was amazing. The incredible burgeoning of genetics in the last twenty years seems to have signaled the end of the comprehensive intellects in this field. Indeed, read carefully, the last edition of his text on human genetics (1973) was showing the strains of one man writing a text doing justice to all the developments even in a single field of genetics.

The diagnosis of Parkinson's disease was made in 1970. He confronted the slow progression of this insidious and tragic disorder with insight and dignity, withdrawing from intellectual activities before the cognitive impairment characteristic of the late stages of the disease was apparent to the uninitiated. His last major presentation was, fittingly, the Presidential Address to the Thirteenth International Congress of Genetics, in 1973. In 1974, upon the receipt of the Allan Award of the American Society of Human Genetics, he declined to give the usual address, saying quietly (and well in advance) "Jim, I am not up to it; please speak for me." He died of cardiac failure complicating his Parkinsonism on October 23, 1981.

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