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BERWIND PETERSEN KAUFMANN
1897–1975

A Biographical Memoir by

EDWARD B. LEWIS

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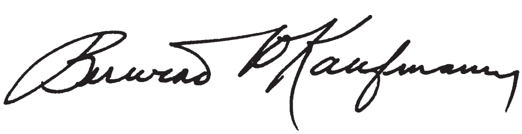

BERWIND PETERSEN KAUFMANN

April 23, 1897–September 12, 1975

BY EDWARD B. LEWIS

Berwind P. Kaufmann began his career as a botanist but turned from studies of plant chromosomes to making pioneering contributions to three principal fields: the induction of chromosomal rearrangements by ionizing radiation; identification of nucleolar organizer and heterochromatic regions of the somatic chromosomes of Drosophila; and determination of the biochemical composition of plant and animal chromosomes using purified enzymes.

Berwind Petersen Kaufmann was born on April 23, 1897, in Philadelphia, Pennsylvania. He graduated from the University of Pennsylvania with the B.Sc. degree in 1918, the M.A. in 1920, and the Ph.D. in 1925. While attending the university, he was an assistant and lecturer in the Department of Botany and at one point taught biology and drafting in Northeast High School in Philadelphia. His Ph. D. thesis dealt with the structure of the chromosomes of Tradescantia and led to his first major publication (1926). In 1926 Kaufmann went to Southwestern College, Memphis, Tennessee, where he taught biology. He left in 1929 to become a professor and the chairman of the Department of Botany at the University of Alabama.

In 1924 he married Jessie Thomson McCulloch, of Philadelphia. They had three sons: Berwind Norman, deceased; and surviving, Carl B. and Anders J., and 10 grandchildren.

On a sabbatical in 1932-1933 Kaufmann was a National Research Council fellow at the California Institute of Technology. In 1936 he left the University of Alabama to become a guest investigator in the Department of Genetics of the Carnegie Institution of Washington at Cold Spring Harbor, Long Island. He became a member of the permanent staff in 1937 and remained there for the next 25 years.

Kaufmann was elected a member of the National Academy of Sciences in 1952. He had been nominated by both the genetics and botany sections of the Academy, an unusual honor. He chose to join the Genetics Section. He served on the Biology Council of the National Research Council and was on the Council's Executive Committee. As the result of his radiation studies, described below, he was appointed a member of the National Research Council's Committee on Genetic Effects of Atomic Radiation.

Kaufman was elected president of the Genetics Society of America in 1961, after serving as secretary and treasurer. He served on the editorial boards of the *Journal of Morphology*, the *International Journal of Radiation Biology*, and *The Nucleus.* He was a member of the Marine Biology Corporation, Woods Hole, Massachusetts, and served as secretary and director of the Long Island Biological Association.

Kaufmann became director of the Department of Genetics of the Carnegie Institution of Washington in 1960, succeeding Milislav Demerec, who had been forced to retire because of a strict age limit of 65 that was then in force. Upon retirement in 1962 at age 65 Kaufmann moved to the University of Michigan, where he held joint appointments as a professor of zoology and botany and as a senior research scientist at the Institute of Science and Technology. In 1967 he was named professor emeritus. In his final years Kaufmann suffered from Parkinson's disease and a gradual decline in his mental faculties. He died on September 12, 1975, in a retirement home in Myrtle Beach, South Carolina.

I am indebted to family members and archival materials for events that influenced his life and reveal aspects of his personality. His father was a painting contractor and his mother a housekeeper. Kaufmann's interest in science was stimulated by his paternal grandfather, who was an ardent naturalist and collector of plants and animals in the Philadelphia area. Kaufmann was the first member of his family to receive a university education. While at the University of Pennsylvania he was on the fencing team and played tennis. He was a member of the Varsity Club and of the Philomathean Dramatic Society. He worked summers while in high school and college, helping on his father's construction projects. Kaufmann's wife, Jessie, had a long career in social work, having graduated from the University of Pennsylvania with an M.A. degree in that field. As a young man Kaufmann played the mandolin and violin. Later he and family members formed a mini-orchestra, his wife on piano, he on violin, and sons Berwind on flute and Carl on clarinet.

At Southwestern College in western Tennessee, where he arrived in 1926, Kaufmann taught the theory of evolution, only one year after the Scopes trials in Dayton in eastern Tennessee. This surely took some courage on Kaufmann's part, even though Southwestern College was a moderately liberal college.

His life at the University of Alabama was made miserable at one point when he was unwilling to pass some members of the football team. He had them over to his house and not only patiently tutored them but even watered down the tests somewhat, but they still could not pass. He was told by the administration that the team was Rose Bowl material and that he had to pass them. When he refused, the administration put the low-scoring students in the hands of a more malleable faculty member, with the result that the team kept on winning. Kaufmann was so disheartened that, even though tenured, he left the University of Alabama in 1936 to take up a staff position at the Carnegie Institution of Washington at Cold Spring Harbor. It could not have been a better outcome for a sorry episode.

In going to Caltech for the academic year 1932-1933, the family drove to California in an old car. While crossing the desert on the way, the radiator boiled over and cracked. There were no gas stations in sight. To illustrate Kaufmann's practical approach to getting things done, the story is told that he poured oatmeal into the hot water, which promptly sealed the leak.

During the years at Cold Spring Harbor, Kaufmann's family saw him mainly at mealtimes, since he worked all day, including weekends and holidays, in his laboratory starting at about 9:00 a.m. After coming home for dinner he would return and work till midnight, "catching up on the literature," a way of life not uncommon among Drosophila workers then as now.

He is said to have hated administrative work that he was required to do during the few years he was the director of the Department of Genetics at Cold Spring Harbor. It kept him away from his research.

He was fond of classical music and was an avid reader of the *New York Times* and the *New Yorker* magazine.

A paper (1931) published while at the University of Alabama indicates he had already begun work on Drosophila. Remarkably, this paper shows drawings of short sections of salivary gland chromosomes from two Drosophila species, *melanogaster* and *virilis*. Evidently they were drawn from sectioned material, and the full significance of these chromosomes was not understood until later when E. Heitz and

H. Bauer (1933) introduced a method of fixing and squashing the salivary gland chromosomes of the midge Bibio that revealed their true nature. It seems likely that Kaufmann's work on Drosophila chromosomes led to his taking a sabbatical in 1932-1933 at the California Institute of Technology as a National Research Council fellow. Two papers resulted and appeared as publications of the Kerckhoff Biological Laboratories of Caltech. In the first (1933) he developed an important method, still in use today, of preparing slides of squashes of neuroblast chromosomes from the larval ganglia as a source of somatic mitoses. Previously, oogonia had been used, however their chromosomes are smaller than those of the neuroblast cells, as well as more difficult to prepare. In the second paper (1934) he used his new method to demonstrate that detachments of attached-X chromosomes are the result of recombination between the X and Y sex chromosomes in their heterochromatic regions.

His next major publication (1937) dealt with the morphology of the chromosomes of *Drosophila ananassae*. Similarities and differences between this species and *D. melanogaster* are discussed, particularly in regard to their heterochromatic regions and the location of their nucleolar organizing (NO) regions.

In a series of papers Kaufmann undertook an analysis of the types and frequencies of chromosomal rearrangements induced by ionizing radiations, using the salivary gland chromosomes of Drosophila. Although genetic methods for detecting such rearrangements had been developed, they were labor intensive and required several generations of matings before the various types of rearrangements could be identified. By contrast, such rearrangements could be scored in the first generation of matings between, for example, irradiated wild-type males with unirradiated females. It sufficed to examine the salivary gland chromosomes of mature third instar larvae of such matings without waiting for the adult stage. This was an advantage over genetic methods that had to rely not only on survival of the adult stage but also on being able to breed it. Because the larvae had to be sacrificed to prepare their salivary gland chromosome, rearrangements detected in the larva could not be perpetuated. The goal, however, was not to create new rearrangements but to quantify the relationship between their frequency and the dose of X radiation. Major findings are described below.

- In a collaborative study (1938) based on analyzing over 1,700 slides, the frequency of induction of chromosomal rearrangements over a dose range of 1,000 to 5,000 r (or in the newer unit, centiGray [cG]) departed significantly from linearity. This contradicted a hypothesis that the dose-response relationship should be linear on the basis that rearrangements result from a single X-ray hit at a point where two (or more) chromosomal regions are in contact. Instead, strong support was provided for their being a dose-response that approached a 2.0 power of the dose, supporting an alternative hypothesis in which separate, more or less independent breakages are induced by X rays that later, unless restituted, take part in producing a chromosomal rearrangement. For a history of the controversy over whether the total break production varies linearly with dose or approaches a 2.0 power, see (1941,2).
- X-ray-induced breakages in the heterochromatic regions of a chromosome occur in approximately the same proportion that such regions occupy in the mitotic chromosome (e. g., in the case of the mitotic X chromosome the heterochromatic region constitutes one-third of the length of the entire chromosome), whereas in the salivary gland chromosome that region is only a small fraction of the length of

the chromosome, owing to the highly condensed state of its heterochromatin. The best estimate of the frequency of breakages in the heterochromatic region of the salivary gland X chromosome was 28 percent (1941,1) or close to the value of one-third based on the relative physical length of that region in the mitotic chromosome.

- Interchanges occur more or less at random between the various chromosomal arms.
- The yield of rearrangements from irradiation of Drosophila sperm is essentially the same whether a given X-ray dose was given all at once or when the interval between successive fractions was 16 days (1941,2). This result strongly supported the view that breakages in Drosophila sperm remain open and do not participate in forming rearrangements until the sperm fertilizes the egg.
- A study (1946) of over 1,400 breakages in the X chromosome showed that some sections had a statistically significant excess of breakages in proportion to the number of bands they contained. Kaufmann concluded that such regions contained interstitial heterochromatin.

Kaufmann was quick to take advantage of the wealth of rearrangements generated in the X-ray studies to map the location of the NOs in salivary gland chromosomes (1938,2) Although it was inferred that the NOs were associated with the X and Y sex chromosomes, he provided a proof of this by selecting rearrangements in which the NOs had been translocated to euchromatic regions of the chromosomes.

In the early 1950s Kaufmann and collaborators (1951, 1953) made use of purified enzymes to determine the composition of chromosomes. These studies were begun before it was known that genes are made of DNA and not, as dogma had it, protein. As a result complexes of DNA and histone-like proteins in chromosomes were identified before these associations were to become well defined biochemically. The role of such complexes is now one of the most active fields of molecular biology.

With M. Demerec, Kaufmann wrote the student handbook *Drosophila Guide,* which went through several editions and was used extensively in laboratory courses in genetics in high schools and colleges in the United States and abroad. At Cold Spring Harbor, Kaufmann maintained a strong interest in science education, and his laboratory attracted several young biologists from the United States and abroad.

I was fortunate to have been able to spend the summer of 1941 under his tutelage. He provided bench space, a research microscope, and the collection of slides that were the source of the data on which the radiation studies already described were based. He was very kind and generous of his time. I spent the summer, when not taking time out for the beach and playing Ping-Pong, analyzing as “unknowns” the slides that contained the various types of rearrangements. This involved determining the breakage points to the nearest section on the standard maps of the chromosomes (Bridges, 1935). Especially challenging were rearrangements that involved more than two breakage points. These were frequent following exposures to doses above 3,000 r. Kaufmann was especially proud of a slide that he showed me in which a rearrangement involved at least 32 breakages, 30 of which he was able to decipher. Kaufmann published this example (1942) and concluded that it furnished further support for the hypothesis that breakages in Drosophila sperm chromosomes remain open for either reunion or rearrangement until the sperm enters the egg. Representative rearrangements were photographed and illustrated in a publication (1939). It also contains a remarkable photograph of a nucleus that has all five major chromosome arms well spread without any overlaps or contact loops.

At the University of Michigan, Kaufmann and Marcia Iddles (1963) made an extensive study of ectopic pairing involving intercalary heterochromatin-like associations and their relation to puffing as measured in salivary gland chromosomes. One of the final papers of that period was a study carried out with Helen Gay, a former staff member of the Carnegie Department of Genetics (1969) and a long-time collaborator with Kaufmann at Cold Spring Harbor. They were able to quantitate how ends of chromosomes in the salivary glands have affinities for one another that become especially clear in the case of translocations involving the fourth chromosome and tips of the second chromosomes. Such affinity studies had long engaged other workers as well and were inspired by H. J. Muller's invention of the concept of the telomere. These studies have taken on new significance as the molecular basis for the telomere has been determined at the level of its DNA sequences. The possible role of telomeres in carcinogenesis and aging of cells is currently an active field of research.

I WAS INVITED to prepare this memoir in 2001. I was pleased to do so because of my admiration for Kaufmann as a person and as a scientist and for his many contributions to the cytogenetics of Drosophila. I am indebted to Kaufmann's sons, Carl and Anders, and Bobbie Stephens, Kaufmann's widow, for help in preparing this memoir—as well as Mila Pollock, director, Library and Archives, and Clare Bunce, archivist, of the Cold Spring Harbor Laboratory and Ellen Carpenter, archivist of the Carnegie Institution of Washington. An important source was an interview with Carl Kaufmann that is part of an oral history collection in the Cold Spring Harbor archives.

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