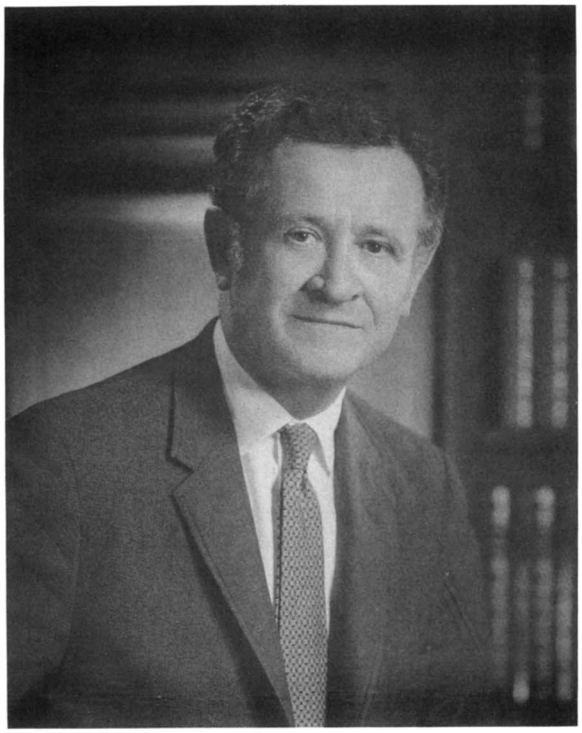

Herschel L. Roman (1914–1989)

HERSCHEL L. ROMAN was born in Poland on September 29, 1914. Before his birth, his father had left for America to establish a new home for the family, but the war intervened and ROMAN and his mother were not able to come to America until 1921. The family settled in northern Minnesota where his brother and sister were born and he attended public school. Educational opportunities were not ideal there, and ROMAN went to live with relatives in St. Louis in order to attend high school in a large city. The family followed and settled in St. Louis.

ROMAN entered the University of Missouri in 1932 and majored in chemistry with a minor in physics. He graduated with honors and had planned to enter graduate school and work in either chemistry or physics. However, in the spring of his senior year he took a position as a technical assistant to LEWIS STADLER to help develop ultraviolet filters to see which wavelength was most effective in inducing mutations. ROMAN became captivated with genetics and with STADLER and never looked back. He switched to genetics for graduate work and became LEWIS STADLER's graduate student.

Graduate school years are a good period for most people and for ROMAN the experience was unusually strong. He often spoke of this period. He not only developed a close bond with LEWIS STADLER but with the STADLER family as well, where he was treated as a sixth son. Furthermore, as ROMAN (1988) put it in his article about STADLER, this period was the beginning of the flowering of genetics at the University of Missouri. Besides STADLER, there were BARBARA MCCLINTOCK, ERNIE SEARS and GEORGE SPRAGUE, all prospective members of the National Academy (not to mention MCCLINTOCK's later Nobel Prize). It was a powerful and stimulating environment, one that would have a lasting influence on him. Besides science and the STADLER family life, the Missouri years encompassed his marriage to CARYL KAHN and the birth of their older daughter, LINDA. They had a wonderful life together of more than fifty years and were generous and charming hosts.

Considering ROMAN's strong background in chemistry and physics, and his early position with STADLER working on the physical analysis of UV-induced mutagenesis, one might have predicted that his work would have taken a chemical bent. However, this was not the case, neither in his thesis work nor in any part of his long career. He became enthralled by what he called the beauty of genetic analysis and, whether it was his early experiments in maize cytogenetics or his later studies of gene conversion in yeast, genetic analysis was always at the heart of his work.

For his thesis work, ROMAN undertook an analysis of supernumerary or B chromosomes in maize. These chromosomes vary considerably in number among different strains and have little or no phenotypic effect. To determine the source of their numerical variation, ROMAN made translocations between B chromosomes and members of the normal chromosome set. In this way he was able to track the cytogenetic behavior of the B chromosomes with markers from the regular chromosome set. In a classic study he demonstrated that a major source of variability in

B chromosome number was programmed mitotic nondisjunction in the division of the generative nucleus in the pollen cell. One product contained two of the translocation chromosomes carrying a B centromere while the other product received neither. Further analysis in a later paper showed that preferential fertilization was also involved in B chromosome phenomena. The hyperploid nucleus preferentially fused with the egg nucleus while the deficient nucleus fused with the polar nuclei to form the primary endosperm. This pattern of fertilization was several times more likely to take place than the reverse pattern in which the deficient generative nuclear product fused with the egg nucleus. These classical studies are still quoted and serve to explain the evolutionary survival of the B chromosomes. It is of interest to point out that these phenomena demonstrated by ROMAN are early precursors of programmed segregation abnormalities such as segregation distorter in Drosophila and the *t* alleles in mice.

Although ROMAN received his Ph.D. in 1942 and that same year was appointed to his first and only academic post, in the Department of Botany at the University of Washington, his first paper did not appear until 1947 (ROMAN 1947). World War II intervened and ROMAN entered military service where he served as a Captain in the U.S. Army Air Force. He returned to the University of Washington in 1946, where he prepared his thesis work for publication and extended his studies on maize cytogenetics. ROMAN found conditions for maize cultivation in Seattle to be less than ideal; he had to set up plots east of the Cascade mountains for most of his work and, in addition, had to travel to Caltech for summer studies. After several years of this pattern he decided that it was time to switch organisms. He chose yeast, a eukaryote that could be manipulated like a prokaryote. He began this endeavor with HOWARD DOUGLAS of the Department of Microbiology and DONALD HAWTHORNE, a graduate student. They became lifelong colleagues. CARL LINDEGREN was the only American yeast geneticist at this time. He accepted ROMAN's invitation to visit Seattle and to help the new group launch their program. In 1952 ROMAN spent a sabbatical with BORIS EPHRUSSI in Paris working on yeast. After his return to Seattle, he started to build the group which has made the University of Washington a leading center of yeast genetics ever since.

In 1955, while working with adenine mutants in yeast, ROMAN showed that a red to white change in the color of a colony signaled a new mutation in the adenine pathway. He used this system the following year in his classical study of multiple alleles at the adenine loci (ROMAN 1956). He developed an elegant test for the identity of two mutants in the same functional gene. This permitted him to classify some 83 different mutants at seven loci. ROMAN was excited by the simplicity of this procedure and by the contrast with the work involved in doing such an analysis in maize or other conventional genetic systems. He was so intrigued by the efficiency of these new methods that he developed a missionary zeal for telling his colleagues about them. A frequent sight at genetics meetings in the late 1950s was HERSCHEL ROMAN, seated with one or two friends in the lounge outside the lecture hall, scribbling diagrams on the back of the program and excitedly describing his latest experiment.

The basis for ROMAN's test for the identity of two allelic mutants was intragenic recombination. He immediately began studies on the mechanism of this event and, for the rest of his life, his research was always related to this question. He originally objected to the name "gene conversion" which had been given to the intragenic event by LINDEGREN. ROMAN complained that LINDEGREN had tied the name to a fallacious hypothesis that the event was actually a mutation. ROMAN proved that LINDEGREN was wrong about the mechanism, but the name "gene conversion" endured all the same and came to be accepted by all (including ROMAN).

ROMAN's work revealed the basic properties of gene conversion: that it recombined preexisting genetic sequences and that it was nonreciprocal. He also showed that mitotic gene conversion was stimulated by mutagens–a finding that presaged the later discovery of the overlapping functions of genes for recombination and genes for genetic repair.

One of ROMAN'S continuing interests was the time of recombination: at what point in mitosis or meiosis does it occur? ROMAN and FRED SHERMAN did an early experiment on this question (SHERMAN and ROMAN 1963). Later, ROMAN teamed with FRANCIS FABRE in elegant studies of this and other properties of the basic recombination event (FABRE, BOULET and ROMAN 1984).

One of ROMAN'S most important contributions was his role in bringing so many of the best minds in genetics into yeast work. This was the result of his infectious enthusiasm about the potential of the yeast system. The thing that made it irresistible was his choice of occasions for talking about his favorite experiments: over coffee after dinner in a fine restaurant or at a sidewalk cafe during a sabbatical leave in Paris or Copenhagen. To him, the game of scientific research was a supreme celebration of life, a pinnacle of human existence. Such an activity should not be limited to cluttered labs and dusty offices. It should be practiced in our most joyous celebrations: parties, picnics, visits to exotic places, fine hotels and famous restaurants.

In 1959 the University of Washington established a Department of Genetics with ROMAN as its chairman.

He immediately set about recruiting outstanding scientists to enlarge his faculty. Although faculty members were chosen mainly on the basis of research accomplishments, ROMAN devoted much of his own attention to the training program for graduate students. The success of this program is affirmed by its many graduates who are leaders in the scientific world today.

In 1965, when the Department of Genetics moved into its new quarters, ROMAN organized a modest international yeast genetics meeting. There were probably no more than 60 people at that meeting, including graduate students. Little did he know that this meeting would become a biennial event with attendance of more than 1000. When the meeting was held in Italy in 1972, GIOVANNI MAGNI dubbed ROMAN "the Pope of yeast genetics."

In 1976 ROMAN suffered a severe stroke which left his right hand immobilized and his right leg partially paralyzed. This was a devastating and humiliating shock for a proud man who had been graceful, athletic, and confident of his physical abilities. But he had the strength and determination to overcome it. With indispensable help from CARYL, he looked realistically at his changed circumstances and rebuilt his life. To his close friends, this was one of the most inspiring accomplishments of his life.

In 1980, when ROMAN stepped down from the chairmanship at age 65, a meeting was held to honor his long tenure as founder and chairman of the Department. Former graduate students and postdocs of the Genetics Department returned from all over the world for this affair. It was a touching and momentous occasion for ROMAN and gave him emphatic proof of the success of his efforts in developing the training program in genetics at the University of Washington.

ROMAN's long and distinguished career brought many honors. He was the founding editor of the *Annual Reviews of Genetics* and he served as president of the Genetics Society of America in 1968. He was elected to the American Academy of Arts and Sciences and the National Academy of Sciences. He was awarded the Morgan Medal of the GSA and a Gold Medal from the Christian Hansen Foundation in Denmark. He received honorary doctorates from the University of Paris and from his alma mater, the University of Missouri. He was particularly pleased with this last award, which came only two months before his death.

HERSCHEL ROMAN continued to be an active participant in yeast genetics to the end of his life. Unable to work at the bench after his stroke, he continued to plan and direct the experiments performed by his technician. He completed the manuscript of his last paper only a few days before his death in July of 1989.

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