



Roger Dawson Milkman
Photo courtesy of Marianne Milkman

In Memoriam Roger Dawson Milkman (1930–2011) Geneticist

Roger Dawson Milkman, professor, population geneticist, and polyglot, died from a stroke and complications of Alzheimer's disease on January 5, 2011, in Washington, DC. He was 80 years old.

Milkman's research interests were broad and interdisciplinary, embracing important issues in population genetics, evolution, embryology, and physiology. His laboratory studies of a polygenic trait in the fruit fly *Drosophila* (the crossveinless phenotype), and of the molecular genetic evolution of the bacterium *Escherichia coli*, are classic, as is his published theoretical work on the forces acting on genetic variation in natural populations.

In his novel pursuit of the genetic basis of natural variation, Dr. Milkman could be found in many grocery stores collecting fruit flies and in many zoos collecting samples of scat with *E. coli*. Well before the era of full-genome sequences, he demonstrated that natural living populations of fruit flies and bacteria have an abundant reservoir of gene variants for polygenic traits that serve as the raw material for evolution by natural selection. When sequencing DNA of *E. coli*, he discovered the first bacterial gene for a potassium ion channel, which turned out to have a sequence obviously homologous to the human ion channels that participate in the electrical excitability of our nerves. He also discovered and modeled an early example of heat shock in fly larvae that changed the later development of the vein pattern of the adult *Drosophila* wing.

As a scientist, Milkman will be most remembered for his contributions to the selectionist vs. neutralist debate, for his 1978 *GENETICS* article (volume 88, pp. 391–403) entitled "Selection differentials and selection coefficients" that unified two conceptualizations of selection, and for his development and application of a "clonal frames" theory accounting for the structure of genomic diversity in *E. coli*.

Roger Milkman was an extraordinary teacher and mentor. He had a passion for teaching, frequently using metaphor,

song, and limerick to explain and clarify complex topics in genetics in a lucid and often humorous way. His students had to re-enact the dance of chromosomes as they learned about cell division. He enjoyed working with students, teaching them the methods of research and the joys of discovery while demanding high standards. The advanced students whom he mentored or trained have gone on to highly successful careers in the life sciences, in large part because of his insistence on rigor in designing experiments and interpreting results.

J. Woodland Hastings (Harvard University) said, "My most enduring memories of talking with Roger about science is the way his face lit up, literally flashed with enthusiasm, as we engaged in a discussion. He was a very special person with whom to talk science.... He was adamant about ethics and the validity of experiments."

Donald Kennedy (former president of Stanford University) said, "He had wide-ranging interests and could see relationships between events and experimental results that most people missed. His sense of humor was wonderful. He would construct poetry from billboards or guidebooks, or political events whenever the meter of what he saw seemed appropriate. He did this regularly and unpredictably. It was one of the reasons we all wanted to be around him."

Dr. Milkman received his Ph.D. at Harvard under R. P. Levine, did postdoctoral work in Paris with Boris Ephrussi, and held professorships at the University of Michigan, Syracuse University, and the University of Iowa. He was editor or member of the editorial boards of many journals of evolution and bacteriology, a responsible officer of scientific societies, a translator of books and articles, and a frequent lecturer for the Thomas Alva Edison Foundation's conferences for high school teachers and students. Over the course of almost 50 years, he studied, taught, did population research, and sailed at the Marine Biological Laboratory in Woods Hole, Massachusetts. Bird-watching trips with him were a delight for the ecstasy with which he greeted each find. In later years, he loved strenuous hiking with his family in the Canadian Rockies.

Professor Milkman will be remembered for his vigorous engagement of people and ideas. He observed with sharp eyes, ready tongue, and keen wit. He loved his teaching, science, life, classical music, good food, fine wine, chocolate,

languages, instant repartee, and humor. He is survived by his wife of 52 years, Marianne; four children, Ruth, Louise, Janet, and Paul; and six grandchildren. Marianne Milkman can be reached at mmilkman@comcast.net.

Bertil Hille and Edward Berger