Lawrence Bogorad

Lawrence Bogorad, Marie Moors Cabot Professor of Biology Emeritus at Harvard University and former president of the American Society of Plant Biologists, died from a stroke December 28, 2003, at the age of 82, while vacationing with his family in Puerto Vallarta, Mexico.

Dr. Bogorad was an influential leader in the movement to bring the techniques of molecular biology to bear on problems in plant biology. He will be remembered for his groundbreaking contributions to the understanding of the biogenesis of chloroplasts and the photosynthetic apparatus in plants, algae, and cyanobacteria. He also will be remembered for and honored by five decades of graduate students, postdoctoral fellows, and visiting scientists who trained in his lab and whom he mentored, through example and unfailing support, into productive careers of their own.

Bogorad grew up in Chicago, earned his bachelor's degree in 1942 and, after a stint in the U.S. Army, received his Ph.D. degree in botany in 1949 from the University of Chicago. He taught as an instructor there before beginning a postdoctoral fellowship in Sam Granick's lab at the Rockefeller Institute for Medical Research in 1951. The work that he began in Granick's lab, the interactive and wide-ranging academic community that he encountered at Rockefeller, and his own personal enthusiasm and energy formed the stable base from which he launched his extremely

productive and influential career.

In Granick's lab, Bogorad began using a combination of biochemical genetics (pigment-deficient mutants of Chlorella and porphyric mutants of humans and cows) and biochemistry to characterize the pathway of porphyrin biosynthesis. When he returned to the University of Chicago as an assistant professor in 1953, he continued this work, leading to the identification of two enzymes in uroporphyrin II synthesis. As his research attracted more and more students anxious to work with him, Bogorad's boundless curiosity pushed a diversification of his group's research scope. They studied biosynthesis of bilipigments and phycobiliproteins in cyanobacteria and in Cyanidium. They undertook studies of the physiology of complementary chromatic adaptation in Fremyella and the greening process in etiolated seedlings. In the latter case, they used George Beadle's favorite organism at the time, maize, which was readily available in the greenhouse.

In 1962, when Hans Ris and Walter Plaut published histochemical evidence for the presence of DNA in chloroplasts, Bogorad immediately understood the importance of determining the role of this DNA in chloroplast biogenesis. Primed initially by a fruitful collaboration with Hewson Swift, they and their students began more detailed studies of chloroplast DNA, ribosomes, and RNA synthesis. This shift in research emphasis also fueled Bogorad's personal fascination with the evolutionary pathway that connects modern-day chloroplasts with their cyanobacterium-related endosymbiont ancestors.

By the time Bogorad moved to Harvard University in 1967, the tools of molecular biology were beginning to become sufficiently sharp to make central contributions to the study of chloroplast biogenesis and function. Pushed by a focal desire to understand the molecular mechanisms of transcription and its control in chloroplasts, Bogorad's group led the charge into plant molecular biology with key contributions in a number of areas. In 1971, they were among the first to provide strong evidence that genes encoding proteins localized in the chloroplast were distributed between the nuclear and chloroplast genomes. They constructed the first restriction map of chloroplast DNA (maize, in 1976) and determined the first complete DNA sequence of a chlo-

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roplast gene for a known protein (rbcL, in 1980). They were also the first to identify a key component of the photosynthetic apparatus via its DNA sequence before it had been recognized by biochemical means (psaA or psaB—only one of these proteins had been identified at the time). This latter finding was particularly important for studies of photosynthesis because it provided the first definitive evidence that Photosystem I was composed of a heterodimeric core, analogous to the structure of PS II and bacterial photosynthetic reaction center complexes. Bogorad's group was also in the vanguard of using molecular techniques to identify and characterize nuclear genes involved in chloroplast biogenesis and function. They made effective early use of transgenic methods for dissecting the cis-acting elements essential to the regulation of both chloroplast and nuclear genes.

At critical junctures in the development of the fields that excited him, Bogorad helped to organize influential symposia. At Strasbourg in 1976, he and Jaques-Henry Weil organized an advanced workshop and symposium on nucleic acids and protein synthesis in plants (Bogorad and Weil, 1977). At Cold Spring Harbor Laboratory in 1984, he helped to organize a symposium on the molecular biology of the photosynthetic apparatus (Steinback et al., 1985). In both cases, the discussions helped to galvanize the efforts of the assembled international community of investigators just at a time when technical advances had opened broad new horizons. In retrospect, the published proceedings are really beginning words rather than final words on their subjects. Bogorad had a unique gift for seeing ahead.

Bogorad took seriously the leadership responsibilities that his scientific successes thrust on him. He served as president of the American Society of Plant Physiologists from 1968 to 1969, the Society for Developmental Biology in 1983, and the American Association for the Advancement of Science in 1987. He was elected to the American Philosophical Society in 1985, the American Academy of Arts and Sciences in 1968, and the National Academy of Sciences (NAS) in 1971. At NAS, he served on the editorial board of the *Proceedings of the National Academy of Sciences,* constantly seeking and promoting publication of work on the leading edge of plant molecular biology. As chairman of the editorial board from 1991 to 1995, he initiated many changes in the review process designed to increase its rigor and also effected change in the cover design from plain gray to the present, more colorful format. He served on the NAS Committee on Science, Engineering, and Public Policy and on the Space Studies Board.

Bogorad was one of the first scientists to recognize the power of molecular biology to generate improvements in agriculture and pushed for accelerated investments in the necessary basic research by federal agencies. After gaining experience as a valued member of National Science Foundation review panels, he played an important role in advocating high standards of scientific review as the USDA competitive grants program was in its critical early years. He understood the importance of capitalizing on the vested interests of agribusiness to stimulate its support of research that would escalate the rate of scientific discovery. He played an important role in the founding of Advanced Genetic Systems, Inc., one of the first publicly traded agricultural biotechnology companies, and served on its science advisory board during its early growth phase. As befit his global view of science, he also served on the science advisory board of Plant Genetic Systems n.v. in Belgium. He served as an adviser to the Rockefeller Foundation and more recently on the board of directors of the Boyce Thompson Institute at Cornell. His experience and broad perspective in these advisory roles will be missed.

As a mentor for young scientists, Bogorad had a style that earned him their devotion. He was continually upbeat and supportive of their work and pushed them to develop projects of their own. There were several direct consequences. Because of his encouragement of both effort and independence, the students felt vested in their projects and were generally happy and productive, but collectively they ended up working

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on a very wide variety of topics and study organisms. The activity on so many different projects contributed immensely to the academic excitement of the lab. The sense of independence and adventure that Bogorad nurtured in his students contributed to a remarkable progression of reinvention within the lab as it kept at the forefront of a field that was undergoing continual technical change. He even treated the tragic fire that destroyed much of the lab in 1984 as an opportunity for renewal, encouraging people to think about the great experiments they were going to do in the new and improved facility. Bogorad himself actively sought out technical advances, embraced them, and then pushed their limits. He would frequently return from a scientific meeting (preferably one in some exotic locale) flush with excitement over an idea for a new strategy that would achieve dramatic progress in the lab. He occasionally stepped into the lab himself to show the way. Late one night in 1971, he could be seen excitedly preparing purified rubisco protein to raise the antibodies that he knew could be used for isolating the genes that encode its subunits. This simple but important start led to the cloning of the first plant gene some five years later.

Teaching and writing were twin passions for Bogorad. In spite of preparation through experience as an instructor at the University of Chicago, he viewed the challenge of teaching while beginning his independent research career with trepidation (Bogorad, 2001). With characteristic energy, he focused on the challenge and succeeded, earning one of the university's highest honors, the Quantrell Award for Excellence in undergraduate education, in 1959. The receipt of this award stood as one of his most cherished honors throughout his career. A continual effort to find and define the broader context of his laboratory research through both teaching and writing was a distinctive component of his scholarship.

Bogorad was a warm, gregarious, and generous person, equally at ease in conversation with influential scientists, politicians, or movie stars as with his long-time dishwasher, Olga Mili, or with the janitors who came to suppress the occasional insect infestations in the lab. In each case, he commanded respect and admiration as quickly as he gained friendship. He loved exploration of the places, peoples, and gastronomy of the world almost as much as he loved exploration of new frontiers in science. A favorite pasttime was sitting at table with a group of his colleagues and regaling them with some epic story with an always clever but often obscure punch line. These gatherings often included mixtures of the eminent and the aspiring, and Bogorad always took care to make sure that the former knew the accomplishments of the latter, which he would describe with fatherly pride. Always supportive of his students and his family, always inquisitive, Bogorad embraced science and life together as a combined adventure. In his own words, "my worst career error was to be born too early! I will miss the next exciting chapter in biology. This one has been wonderful to behold!" (Bogorad, 2001).

Bogorad is survived by his wife of 60 years, Rosalyn, who suffers from Alzheimer's disease; by his daughter, Kiki Bogorad-Gross of Newton, Massachusetts; by his son Leonard of Bethesda, Maryland; by four grandchildren; and by his partner Kathleen Mullinix. A memorial service in his honor will be held Friday, May 7, 2004, at Harvard University.

In lieu of flowers, the family requests that tax-deductible contributions be made to ASPB to endow the Lawrence Bogorad Award for Research Excellence in Plant Biology. This will be a triennial award for investigators who have continued the Bogorad tradition of tackling and solving the critical biological questions of their time.

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