NATIONAL ACADEMY OF SCIENCES

LAWRENCE BOGORAD
1921—2003

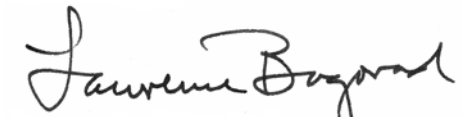
A Biographical Memoir by
SABEEHA S. MERCHANT

Any opinions expressed in this memoir are those of the author and do not necessarily reflect the views of the National Academy of Sciences.

Biographical Memoir

COPYRIGHT 2009
NATIONAL ACADEMY OF SCIENCES
WASHINGTON, D.C.

Biology Department, Harvard University, Photograph by Bachrach



LAWRENCE BOGORAD

August 29, 1921–Decemer 28, 2003

BY SABEEHA S. MERCHANT

Lawrence Bogorad is renowned for his breadth of achievement in chloroplast biology. As a post-doctoral fellow in 1951 with Sam Granick at the Rockefeller Institute, he applied cross-species biochemical genetics to deduce steps in the complex tetrapyrrole biosynthetic pathway. This resulted subsequently in the discovery of two key enzymes, PBG deaminase and uroporphyrinogen III cosynthetase (Bogorad, 1958a, b), in his own laboratory at the University of Chicago. The work on tetrapyrrole biosynthesis led to studies of greening in maize, synthesis of biliproteins in cyanobacteria and algae, and complementary chromatic adaptation, topics that he investigated with passion until he closed down his laboratory shortly before his death at the age of 82.

After the discovery of DNA in chloroplasts in 1962, Bogorad collaborated with Hewson Swift[1] at the University of Chicago on detailed studies of the plastid genetic system, showing the presence of smaller ribosomes in the organelle relative to the cytosol, and eventually establishing in his group at Harvard University that chloroplast ribosomes were encoded by genes in both the plastid and nuclear genomes (Mets and Bogorad, 1971). This suggested to him that endosymbiosis involved either the transfer of genes from the symbiont to the host or that host genes could take over the

function of symbiont genes (Bogorad, 1975). Bogorad's group applied techniques of DNA cloning and sequencing to the chloroplast genome, resulting in the first restriction map of a plastid genome in 1976 and eventually the cloning of the gene, *rbcL*, for the large subunit of Rubisco (Bedbrook and Bogorad, 1976; Bedbrook et al., 1979).

The sequence of *rbcL* represented the first sequence of a gene for a plant protein (McIntosh et al., 1980). The work was considered a remarkable achievement at that time (Krogmann and Key, 1981). In the following two decades, the Bogorad group continued to identify and sequence components of the photosynthetic apparatus and illuminate the mechanisms of gene regulation in the context of chloroplast function. His group was among the first to use anti-sense "knock-down" technology in plants to downregulate an abundant protein in photosynthesis, pioneering a popular approach for manipulating metabolic pathways (Rodermel et al., 1988). He appreciated the power of molecular genetics and pushed the use of cyanobacteria as a model system for understanding chloroplast function.

The number of fundamental discoveries in Lawrence Bogorad's group is attributed to his facility for unconventional thinking, his passion for new technology and his fearless application of it, and his consistent ability to attract talented scientists to his laboratory.

HIS LIFE AND FAMILY

Lawrence Bogorad was born in Tashkent, Uzbekistan, then a part of the Soviet Union, on August 29, 1921 into a Jewish family with roots in the Ukraine and Moldavia. His mother, Florence, was a nurse and his father Boris was a physician. The Bogorads emigrated to the USA thanks to sponsorship by family in Chicago. They were almost turned back at the time of entry because the two-year-old Lawrence had an eye

infection. Fortunately, he was hospitalized at Ellis Island, and eventually became a US citizen as a youth. Despite his medical training, Lawrence Bogorad's father worked in a fish market in Chicago; the family therefore was not affluent. The parents spoke Russian at home, but Lawrence Bogorad wanted to assimilate (like the immigrants of today) and spoke English as much as possible. As an adult he regretted that he did not speak Russian; he tried to learn it but without much success. Yearnings for the days of his youth are evident from his postretirement trips to Brighton Beach, where he could enjoy poppy seed cake and hear the language of his childhood spoken.

Bogorad was an excellent student; he was president and valedictorian of his high school class, which opened the door to a first-class university education. Although he had been admitted to the University of Chicago, Bogorad was planning to attend City College instead, because his family could not afford to send him to a private university. A benefactor heard of this unfortunate situation and arranged a scholarship for him. He remembered this kindness and reciprocated with a bequest for a fellowship for undergraduates at the University of Chicago. As a youngster, Bogorad enjoyed visits to the Field Museum in Chicago, which perhaps stimulated his interest in science. He graduated in 1942 with a degree in botany.

Bogorad hitchhiked to northern Minnesota to meet Rosalyn Sagen, who would become his wife, on a blind date. Roz told us the story of Bogorad working an ice and milk delivery route as a young man. He had a fondness for cream (which lasted throughout his life) and he would regularly consume the best part of the goods that he was supposed to deliver. Bogorad's enjoyment of ice cream was well-known by his research group at Harvard. It suggested a means to get time with him in the middle of the day. If we in the laboratory

took up a collection and brought in several quarts of various flavors from Herrell's in Harvard Square, it would guarantee that Prof. Bogorad would join us in the break room.

Bogorad was close to his sister Lois, who was 10 years his junior. He made the long drive from Chicago to Los Angeles every three years for several summers so that he and his family could spend time with his parents, Lois, and her daughter Judi. Lois was very intelligent but she did not have the same opportunities as he did and became a bookkeeper. Perhaps because of this he was especially supportive of women in his laboratory, providing them opportunities that had not been available to his sister. Mary Clutter, former assistant director for the National Science Foundation, recalled that Bogorad, who was already a distinguished scientist and a member of the National Academy of Sciences (elected in 1971), came up to her at a meeting in St. Louis in the 1970s to discuss her research.[2] She remembers that type of attention to a female scientist as being uncommon in that period. A former coworker remembers that after she left the group of a Harvard colleague who was not comfortable with a pregnant woman in his laboratory, she joined Bogorad's group as a postdoctoral fellow. In fact, the Bogorad laboratory housed many talented women. He was very supportive of his coworkers' life-styles and provided a family friendly work environment before it was fashionable to do so. His wife, Roz, was especially helpful to laboratory members with young children and helped them locate schools and childcare, and Bogorad ensured that postdoctoral fellows with children were adequately compensated.

Bogorad wanted to join the Navy after graduating in 1942 because he had a curiosity about the world and love of travel even at that age; but his uncorrected vision was poor and he therefore joined the Army as a supply officer and was restricted to Natchez, Mississippi. Bogorad subsequently

headed up a school for returning soldiers to help them get a fresh start. Len Bogorad, his son, recalls a "basement full of Army-looking textbooks."

After his military service, Bogorad started graduate school, and this opened the door to many travel opportunities during his academic life. His son Leonard was born during these graduate student years. Len Bogorad is now an urban planner and estate consultant in Bethesda, Maryland. Bogorad's doctoral research was on chlorophyll synthesis in dark-grown pine seedlings, and he earned a Ph.D. at University of Chicago in 1949 in plant physiology. Bogorad maintained an interest in this area throughout his scientific career. He joined Sam Granick at the Rockefeller in 1951 as a Merck National Research Council postdoctoral fellow, and his second child, Kiki, now an interior designer, was born during those years. They lived on York Avenue. He looked back on those postdoc days fondly. He loved to show his family the places he had been and the things he liked to do in New York. His research at the Rockefeller showed unusual insight and intuition about metabolic relationships. Bogorad realized that compounds in the urine of patients resembled pigments used by photosynthetic organisms. Therefore, he fed the urine of porphyric patients (which contained various tetrapyrrole intermediates and degradation products) to mutant algae and showed cross-species biochemical complementation as the tetrapyrrole compounds in the urine could be used as substrates for the synthesis of pigments by the algae. This work resulted eventually in the discovery of two key enzymes in the biosynthesis of tetrapyrroles, porphobilinogen deaminase and uroporphyrinogen III cosynthetase.

SCIENCE AND CAREER

Bogorad returned to the University of Chicago as an assistant professor in 1953 eager to be an independent

researcher (Bogorad, 2001). He continued his work on tetrapyrrole pigments and added *Cyanidium* (eukaryotic alga) and *Fremyella* (cyanobacterium) as experimental systems. Cognizant of the work of George Beadle, Bogorad deduced steps in the photosynthetic pigment biosynthesis pathways through biochemical analyses of mutants he isolated. He was fascinated by complementary chromatic adaptation in which the organism synthesizes pigments in response to the quality of incident light—green pigments to absorb red light and red pigments to absorb green light.

Studies of pigment biosynthesis led naturally to studies of plastid development during the etioplast-to-chloroplast transition, during which the synthesis of pigments and the photosynthetic apparatus are initiated by exposure to light. For this purpose, maize served as an excellent model organism because the seed reserve allowed plant material to be synthesized in the dark in the absence of photosynthesis in amounts sufficient for subsequent biochemical and microscopic analyses. The transition from an iron-deficient chlorotic state to an iron-replete green chloroplast was another system of interest to him. Although he did not continue this work, he remained very interested in the problem and was delighted when the maize *yellow stripe 1* locus was identified in 2001 as a phytosiderophore transporter (Curie et al., 2001). We had been communicating at that time because I had started working on iron deficiency around 2000 and Bogorad had sent me a set of his reprints dating back to the late 1950s and he told me about his own work on *ys1*. He was pleased that my work on trace metals led me circuitously to the discovery of enzymes in the tetrapyrrole pathway (Moseley et al., 2000; Tottey et al., 2003). When I was in his group, I had not worked on the projects close to his heart despite

his many attempts to lead me there, but the path of science eventually brought me to those projects.

After the plastid was shown to contain DNA, Bogorad collaborated with his colleague at the University of Chicago, Hewson Swift, to discover the presence of ribosomes in the etioplast that were smaller than the ones in the cytosol, and they noted a change in their abundance during the etioplast-to-chloroplast transition (Jacobson et al., 1963). Eventually, after he moved to Harvard, Bogorad showed that the genetic information for plastid ribosomes was shared between the nucleus and the plastid (Mets and Bogorad, 1971). Bogorad was recruited to Harvard in 1967. The timing was right for the move; the teaching obligations and research support allowed his program greater potential and the research facilities were "more comfortable" (Bogorad, 2001). He waited a year to move to accommodate the children's lives. His son, Len, had just graduated from high school at the time of the move and his daughter, Kiki, had turned 14 and would be attending high school after the move.

Lawrence Bogorad was chairman of the Department of Biological Sciences at Harvard University from 1974 to 1976, director of the Maria Moors Cabot Foundation in 1976, and became the Maria Moors Cabot Professor of Biology in 1980 until his formal retirement in 1991 (his laboratory remained active for another decade) just shortly before the opportunities in photosynthesis and plant biology exploded with the publication of the sequence of the genome of *Synechocystis* 6803 (representing the first bacterial genome) and eventually the sequence of *Arabidopsis* in 2000. As he saw the possibilities for the future, his regret was that he was born too early (Bogorad, 2001). Indeed, had he been born only a few months later, he would have been young enough to have avoided mandatory retirement. He was prescient about

the possibility of manipulating cyanobacteria to understand plastid-based photosynthesis and organized a Cold Spring Harbor meeting in 1984 to bring the relationship between prokaryotic and eukaryotic phototrophs to the attention of the photosynthesis community.

At Harvard, Lawrence Bogorad changed the focus of his research to concentrate on the molecular biology of the chloroplast. He had the idea to look for light-regulated genes on the entire chloroplast chromosome to identify photogenes: this was in the days before genomics and microarrays and it is an example of his vision in science. Other examples include his early use of epitope exposure studies for determining the topology of thylakoid membrane proteins, and antisense technology to knock down Rubisco and, in so doing modify metabolic flux (Rodermel et al., 1988; Quick et al., 1991). Bogorad had exceptional ability to learn new things because he was curious and he was not too proud to show enthusiasm for new ideas of others. He thought about horizontal gene transfer in the mid-1970s as he pondered the origins of the chloroplast. He would have been so excited to read Penny Chisholm's work on the role of cyanophages in gene transfer (Sullivan et al., 2006).

Bogorad was entranced by technology. If he heard about a new method, he wanted to apply it to the ongoing projects, and if a new gadget reached the market, he had to have it —whether it was a simple dot blot apparatus, the prototype gene gun, or a continuous-flow centrifuge. Maureen Hanson recalled that because of his enthusiasm for purchasing the latest gadget, he often ended up with a quirky beta version such as the continuous-flow centrifuge that deposited leaf extract all over the floor. Bogorad was very careful about spending his supply budget and I have often wondered whether it was because he wanted to splurge the savings on some fancy new equipment. Unfortunately, the latest "toy"

often was used only once and then set aside forever after. Yet he was not a spendthrift, and some enzymes or reagents were produced in the laboratory for some time after they were commercially available, until the Ph.D. students and postdoctoral scholars could convince him that the quality and time saving of the commercial product was commensurate with the expense. Some of us have fond memories of Iggy and Enno working at the Bally cooler making *E. coli* RNA polymerase, but some of us have not-so-fond memories of redistilling phenol.

Bogorad loved gadgets at home too. He bought a video recorder when I was in his laboratory and took movies of the group at parties at his house and then played them back for us. He would be behind the video camera as he interviewed his grandchildren. Bogorad just loved the camera. He took pictures of all of us and had large prints of the group members on a wall outside his office. He would take lots of pictures on his trips and have slide shows for family and friends on his return. Bogorad had an eye for composition and artistic talent for taking travel photographs; he would capture a local in an interesting costume or an architectural detail of a temple or historical monument. Pictures of him taken by others on these trips invariably show him with a camera around his neck. It is too bad he did not live to see the iPhone. He would have been the first in line to buy one —all his favorite things in one small toy: the telephone that he could answer immediately, a camera, music, and a map to go places.

I remember visiting him shortly after he shut down his laboratory. Bogorad showed me the old equipment that he could not bear to discard. He was so happy when one of us had a use for it. He was sorry that the Bionebulizer I coveted had been claimed by someone else, but he was eager to give

me his entire collection of Pipetman pipettors because I told him that the company had a deal where I could get a new one for half the price with a trade-in of an old one. Since he loved a deal, he excitedly went through all the cabinets to find as many as he could.

Lawrence Bogorad received many honors. He was elected to the National Academy of Sciences in 1971, the American Philosophical Society in 1985, and the American Academy of Arts and Sciences in 1968. In 1982, the American Society of Plant Physiologists honored his lifetime achievements with the Stephen Hales Award. He was also recognized as a foreign member of the Royal Danish Academy of Sciences and Letters, and in 2004, he received posthumously the Distinguished Service Award from the University of Chicago's Alumni Association. After his death, the American Society of Plant Biologists created a biennial award in his name to honor a scientist "whose work both illuminates the present and suggests paths to enlighten the future."

SERVICE

Lawrence Bogorad was a master of public service—to a fault. He spent his prime daytime hours on work for committees of various academies, professional organizations and granting agencies, editorial boards; and scientific advisory boards of public and private institutions and companies. It was only during the late evening hours and weekends that he had time for science. In addition to service on numerous committees of the National Research Council and the National Academy of Sciences, Bogorad served as chair of the Botany Section of the National Academy of Sciences, from 1974-1977, a member of the Council from 1989 to 1992, and he served as the Editor of the *Proceedings* from 1991-1995. From 1990 to 1992, Bogorad served on the Committee on Science Engineering and Public Policy for the joint Academies. Frank

Press, who was then President of the National Academy of Sciences, indicated that very few members made the type of commitment to its activities as did Bogorad, who served on 13 committees of the Academy[3]. In his work for the Academy, Bogorad was particularly interested in relations with Russia, Eastern Europe, India and China, where the problems of agriculture, energy, and sustainable development—all of great interest to him—were so pressing. I wonder whether his dedication to service was a form of payback to his country for the opportunities that it had offered him.

As a member of the Policy Advisory Group for the U.S. Department of Agriculture, Bogorad championed the use of outside scientific peer review to ensure the success of the Competitive Grants Program in its formative years, and he was persuasive on the Advisory Committee for the Biological, Behavioral, and Social Sciences Directorate at National Science Foundation for establishing the Plant Postdoctoral Program. His service to professional organizations included the American Society of Plant Physiologists of which he was President from 1968 to 1969, the Society for Developmental Biology from 1982-1984 and the American Academy of Arts and Sciences from 1986 to 1987. He also served on the Council and Executive Committee of the American Society for Cell Biology between 1971 and 1974.

As one of the first plant physiologists to use the techniques of molecular cloning, Bogorad was a recognized authority in molecular plant biology. With Jacques Weil, he organized the first international meeting on plant molecular biology, in 1976 in Strasbourg, and he founded the highly successful Gordon Research Conference in Plant Molecular Biology in 1980. He served as an adviser to the Rockefeller Foundation for many years, and subsequently he was on the board of directors of the Boyce Thompson Institute for Plant Research.

Bogorad was cognizant that the science of plant molecular biology would rapidly lead to biotechnological applications. Together with John Bedbrook, a Bogorad lab alumnus, he played an important role in the founding of Advanced Genetic Sciences (AGS), one of the first startup plant biotechnology companies, located in California, USA. He then served a distinguished role on the Scientific Advisory Board that was shared by AGS and another startup plant biotechnology company in the late 1970s and 1980s, Plant Genetic Systems (PGS) in Gent, Belgium. In that role he helped both companies gain scientific credibility, set their technical courses, and remain linked to cutting edge developments in the academic arena.

In 1995, as Chairman of the Editorial Board of *Proceedings of the National Academy of Sciences*, Bogorad instituted a number of small changes that set into motion a series of substantial changes aimed at moving the journal from an archive of papers from members of the Academy to a more popular and high-impact journal of general scientific interest (Bogorad, 1995). The traditional grey cover daring from around 1915 was replaced in 1995 with illustrations representing various decorative elements of the rotunda at the National Academy of Sciences building in Washington, D.C. Between the covers, Bogorad and his editorial board instituted front matter such as commentaries to highlight articles of especially broad interest and invited reviews to bring exciting topics to the timely attention of readers of the *Proceedings*. The publication of a collection of papers around National Academy of Sciences colloquia was also instituted at that time.

THE PERSON AND MENTOR

Bogorad was a workaholic. I remember him being in his office early in the morning, going home for dinner, and returning after dinner to work till midnight or later. We always knew when he was around because he loved to answer the telephone. Despite his workload, he would answer both office and laboratory phone (with a sense of urgency) and page us over the intercom. The best time to talk to him was around 10 at night. He had probably accomplished enough for the day by then, and if you were still in the laboratory, he would come by and chat and he could be very relaxed. These conversations were a mixture of story-telling (although I never understood the punch line) and a discussion of his latest ideas, and he had many of those. Some of the postdocs interpreted the ideas as potential projects he wanted them to work on, and perhaps he did, but he offered a dozen ideas in every conversation, so one could not actually implement most of them. But in retrospect he had some really good ones. At the time, I thought them crazy—for instance, the idea of combining domains from different proteins to generate new functionalities—but today they seem prescient. He worked all the time, even in hospital while waiting for bypass surgery.

The Bogorads' first grandchild was born in 1983. He enjoyed spending time with the grandchildren, telling stories around the dinner table, usually about his travels accompanied by pictures and slides. His daughter, who lives in the nearby town of Newton, said that the only break he took from his workaholic life was to spend quality time with the grandchildren.

Bogorad had a well-developed sense of ethics and morals. For instance, he did not share with his coworkers information from manuscripts or proposals that he received to review.

In 1996, just after he retired as editor of the *Proceedings*, he said, "If one could gain a material advantage from knowing what is in a manuscript, one has a potential conflict of interest and should not review the paper" in the context of the Cistron vs. Immunex case (Marshall, 1996). And this was not merely lip service to the mantra of confidential peer review. Lawrence Bogorad genuinely believed this and acted on this principle throughout his scientific life. In the three-and-a-half years in his group I never saw a manuscript or proposal from another group, and many of his former students and postdoctoral fellows have the same recollection.

Bogorad was unusually honest and forward thinking about personal issues as well. He was nonjudgmental of others and accepted alternative life-styles without comment. Bogorad was distraught and took responsibility for the loving care of his wife, Roz, when she was diagnosed with Alzheimer's disease and institutionalized in 1998, but he was open also about his love for Kathleen Mullinix who was his companion in the years before he passed away.

Travel was one of Bogorad's passions, especially international travel. He was genuinely interested in the people of other cultures and he welcomed individuals from all over the world to his laboratory. As an academic, Bogorad had many opportunities to travel and he took advantage of as many as possible. Besides short conference trips, he spent six months in Australia in 1960 as a Fulbright Scholar at the CSIRO (Commonwealth Scientific and Industrial Research Organisation) in Canberra and the following year spent six months in Sweden at the Karolinska Institute as a National Science Foundation senior postdoctoral fellow. Bogorad's passion extended to wanting everyone to travel, his family and his coworkers, and he took them to exotic destinations. Indeed, after retirement, in his late 70s and early 80s, he planned long-haul trips for his extended family to places he

had loved on his professional trips. He was excited about exposing his grandchildren to countries that were culturally significant, including Thailand, Vietnam and Cambodia.

I remember a trip to Taiwan with him in the late 1980s. I had just started my own group and was too busy to go on what I considered a National Science Fundation-funded "junket" (in reality a U.S.-Taiwan workshop) but Bogorad persuaded me that it was a wonderful opportunity, and indeed it was. Once there he told me that attending the scientific sessions for a few days was quite enough, and I could skip the last day and join him and Roz for a visit to the museum in Taipei. I learned much later that the National Palace Museum was one of his favorite places. Bogorad had arranged for a car so that we could break off from the group. Once we were at the museum he advised me on which rooms I should focus, given the limited time we had. He also told me that the prints in the museum gift shop were a good buy (US$2), and when I commented on the inconvenience of carrying large prints in my luggage, Bogorad promptly showed me how to roll them and protect them in cardboard. There was no excuse for not seeing things and not taking advantage of a good deal. He often brought back little gifts for the group, and occasionally these were chosen specifically for the recipient: for instance, a former student recalled that he brought her a vinyl record from Russia because she was a musician. Bogorad travelled all over the world, but China was the place he loved most. He was one of the first U.S. scientists to visit China and he led the first Botanical Exchange to the People's Republic of China, in 1978, a six-week-long expedition made successful by his charm and diplomacy. He sustained a long-term relationship with science in China by warmly reciprocating the hospitality and by hosting several Chinese students and postdoctoral workers in his laboratory

subsequently. How he would have loved to see the status of science in China today.

Some years ago, Jen Sheen (one of Bogorad's Ph.D. students) and I found ourselves to be roommates at a conference. We discussed the "good old days" late into the night and especially our common experience with Bogorad as a mentor. The training environment was old-school. He protected us from responsibilities that were his own (such as the review of manuscripts and proposals), leaving us free to concentrate on our experiments. To stimulate creativity and support our independence, Bogorad did not teach us how to write papers and proposals, discuss experimental approaches, work with us on our presentation skills, or discuss laboratory, budget and personnel management. I suppose we learned all that by osmosis in an environment where we were free to explore and seek out exciting activities. But on the one occasion during my three and a half years in his laboratory, when advice was called for, he offered it to me unsolicited. I had been interviewing for faculty positions and had declined two offers (including one from the University of California, Los Angeles) and was on the point of turning down a third one. I had not discussed the job search with him, a not uncommon situation in his group. Bogorad initiated the conversation. On hearing that I had not yet accepted a position, he told me that job offers were not really offers until I turned them into offers that I was likely to accept. "Tell them what you want," he said. When I told him that I had done that, he said, "Well, tell them again and again until they give you what you want; then, you have an offer. Go back to UCLA and tell them what you want. That is where you should be." Bogorad recognized that negotiation was an under-developed skill (in me) in the context of an important decision in my life, and he took the time to have a discussion with me. Of course it was a typical late evening

discussion. He subsequently wrote about choice of employment and choice of project being the two most important decisions for a scientist (Bogorad, 2001). Despite the absence of formal mentoring, the Bogorad laboratory was a great place for making discoveries. The resources were unlimited (or at least it seemed that way to me): we were surrounded by first class groups developing state-of-the-art methods in molecular biology, and he would not hold back anyone who had an idea or wanted to try something new.

Bogorad was an intensely private person. A rather inconvenient consequence of this is that he did not inform the laboratory when he was travelling. His secretary knew, but the group did not. This was a bit problematic when he left for sabbatical in Australia without informing his students. It was also inconvenient on the day that his laboratory burned down. The authorities needed to contact him, but no one knew where he was, not even his wife, although she did tell us that it was AAAS business, which helped us to locate him at a meeting in New York.

The fire devastated Bogorad, but he did not let us or even his immediate family see how he felt. When he was reached by telephone, he only asked "Is everyone OK?" and on hearing yes, his response was, "That is what matters". Of course, his life's work was at risk, but his immediate and only thought was about us. Bogorad had designed the laboratory to be aesthetically pleasing with beautiful wood benches and cabinets; so the loss had a personal component as well. He kept the stress of the fire aftermath from his wife and children. It happened during a hot summer in Boston, and I had never seen him work harder. He was in the laboratory every day, helping with the clean up, ensuring that his coworkers had a place to work (arrangements were made to occupy the space of Walter Gilbert on the third floor), raising funds so that his laboratory could be set up again, arranging

for everyone's notebooks to be photocopied, working with architects to redesign the laboratory, and probably a myriad other tasks to which we were oblivious.

Because Bogorad was a private person, some of his younger colleagues in the scientific community did not know him well, and could hold misguided opinions about him. I remember that he asked me to write a proposal to the U.S. Department of Agriculture Competitive Grants Program to fund my work on copper-responsive gene expression. He indicated that it would be a good experience for me, and that I could take the grant with me to my own academic position. My proposal was funded, and any number of individuals told me that Bogorad would never let me move the grant (since at the time I was not qualified to be a principal investigator and had to be listed on the proposal as a coinvestigator with Bogorad as the principal investigor). But despite popular wisdom, when I moved to UCLA, Bogorad cooperated fully to transfer resources to my laboratory. In fact, I learned later that he had mentioned the grant in his recommendation letter. Bogorad was not the type of person to go back on his word or to be deceptive. I learned after his death that contrary to the generally held opinion, Bogorad was modest about his achievements and, in fact, invariably offered credit to a younger coworker if the opportunity presented itself. I wish I had thanked him for the opportunities he gave me as a scientist. I was young and cocky when I was in his laboratory and accepted the resources of his group as my right. Today, I recognize the privilege that it was.

A characteristic that Bogorad shared with many great scientists was his enthusiasm for young people and their ideas. At conferences and on seminar trips he always spoke to students and discussed their projects attentively and without distraction. This was in distinct contrast to other professors I had met, who at a conference, made no effort to engage the

students at the table in a discussion and spoke only with their colleagues. As a classroom teacher, Bogorad was dedicated and committed. He was not an entertaining teacher, but he inspired students with his passion about the subject matter. At the University of Chicago he taught three courses a year and although he did find them a "wearing obligation" (Bogorad, 2001) (because they took time away from research), he looked forward to the opportunity to impart knowledge to a younger generation. In 1959 he was awarded the University of Chicago's highest honor, the Quantrell Award for Excellence in undergraduate education.

Bogorad was always a gentleman. One could sense when he was displeased, but I never heard him raise his voice. Every individual in his path, from the dishwashers and janitors to the postdoctoral scholars and visiting scientists in his group, was treated with warmth and respect. The student and postdoctoral trainees were viewed as adult colleagues. There was never a disparaging comment about someone's work at a group meeting presentation and all ideas were fairly considered and evaluated. Because he never pushed anyone or made demands of anyone in his group, there was a tendency for some people to get lost.

Despite Bogorad's kindness, the group was not a relaxed place to work, at least not in the day time hours, perhaps because of his formality with his coworkers or perhaps because of the pressure we put on ourselves. The atmosphere did become more comfortable at night though. At the time I was in the group in the mid-1980s, there was a sense that it was easier for the women in the group than the men. Certainly, the women who were there at the time—Alice Cheung, Jen Sheen, Jean Lukens and I—worked long hours, and we had the opportunity to talk to him when he returned to his office after dinner. Perhaps this contributed to our more open, although always distinctly formal, relationship

with him. None of us would refer to him by his first name and even after 20 years as an independent scientist, I cannot imagine calling him "Laurie." We always called him "Dr. Bogorad" in his presence, but in private amongst ourselves, he was "LB." We knew who his friends were because they called him "Laurie," whereas people who did not know him and presumed familiarity called him "Larry."

Because my relationship with Dr. Bogorad was so formal during my postdoctoral years at the Biolabs, I initiated very few communications with the group or with him after I left. Our correspondence was restricted to the exchange of greeting cards during the Christmas holidays each year and occasional communications about science when necessary. Nevertheless, I did attend some of the postretirement reunions that were organized by other alumni, including Richard Sayre, Maureen Hanson, André Steinmetz, Alice Cheung, and Steven Rodermel. I did not realize that Bogorad cared deeply about his former coworkers until years later when we developed a warmer friendship and discussed our personal lives. I remember now that the first telephone call I received after the Northridge earthquake in 1994 was from Bogorad and when I told him that I could not reach my parents, he immediately assured me that he would call them and anyone else I needed to reach. He continued to call me frequently for the next few days. When I gave the Shull Award lecture at the American Society of Plant Biologists meeting in San Diego in 2000, he came to the conference just to hear the lecture although he had stopped attending meetings by that time. In retrospect, I realize that he was proud of the accomplishments of his former coworkers although he never communicated that to them directly.

Lawrence Bogorad suffered a stroke at the age of 82 on December 28, 2003, while he was doing what he loved best:

he was in Puerto Vallarta with his family for the holidays. He died a few hours later. He was survived by his wife of 60 years, Rosalyn, who suffered from Alzheimer's disease and died in 2006; his daughter Kiki Bogorad-Gross, his son, Leonard; four grandchildren; and his partner, Kathleen Mullinix. He had lived a full life, but there were still places to visit, books to read, plays to see.

Lawrence Bogorad was a luminary in plant biology. He was dedicated to science and to public service. In his early work he made key contributions to deducing the pathways of synthesis of tetrapyrroles, the pigments of life. After he saw ribosomes in the etioplast, he was enchanted with the endosymbiotic origin of plastids and applied the then-new tools of molecular cloning to define the plastid genome and provide a molecular description of changes in gene expression during chloroplast development. His laboratory was responsible for the cloning of the first plant gene, *rbcL*, which raised the possibility of engineering plants for agricultural benefit; and he pioneered the concept of light-regulated gene expression through the identification of photogenes. Bogorad was excited about applying the latest technologies to problems in photosynthesis and chloroplast biology. He was not entrenched in dogma or bound by prevailing paradigms: he encouraged his co-workers to explore the possibilities and to think independently. His contribution to the field through tireless service has left us a legacy of scholarship and an infrastructure for fundamental discovery in plant biology.

I am grateful to Kiki Gross-Bogorad and Len Bogorad for information on their father's childhood and early career and Kathleen Mullinix for her perspective on Lawrence Bogorad's enthusiasm for life and science. I thank Alice Cheung, Enno Krebbers, Maureen Hanson, Laurens Mets, Steven Rodermel and Jen Sheen for reading the manuscript and offering comments and personal anecdotes, and Charles Arntzen, Winslow Briggs, Woody Hastings, and

Diter von Wettstein for sharing their recollections. Other sources were the obituary by L. Mets (*ASPB News*, vol. 31. No 1:18-19, 2003), the eulogies by his children and others at http://mcb.harvard.edu/Bogorard/Guestbook.html, and the following notes.

NOTES

1. Swift, H. (1985) *Science* 229:353-354
2. Mary Clutter statement at Memorial Service on May 7, 2004.
3. Frank Press statement read by Woody Hastings at Memorial Service on May 7, 2004.
4. Mets, L. Obituary of Lawrence Bogorad, *ASPB News*, 31:18-19.
5. http://mcb.harvard.edu/Bogorad/Guestbook.html

REFERENCES

Bedbrook, J.R., and L. Bogorad. 1976. Endonuclease recognition sites mapped on *Zea mays* chloroplast DNA. *Proc Natl Acad Sci U S A.* 73, 4309-4313.

Bedbrook, J.R., D. M. Coen, A. R. Beaton, L. Bogorad, and A. Rich. 1979. Location of the single gene for the large subunit of ribulosebisphosphate carboxylase on the maize chloroplast chromosome. *J Biol Chem.* 254, 905-910.

Bogorad, L. 1958a. The enzymatic synthesis of porphyrins from porphobilinogen. I. Uroporphyrin I. *J Biol Chem.* 233, 501-509.

Bogorad, L. 1958b. The enzymatic synthesis of porphyrins from porphobilinogen. II. Uroporphyrin III. *J Biol Chem.* 233, 510-515.

Bogorad, L. 1975. Evolution of organelles and eukaryotic genomes. *Science.* 188, 891-898.

Bogorad, L. 1995. About the Proceedings. *Proc Natl Acad Sci U S A.* 92, i-ii.

Bogorad, L. 2001. Samples from fifty years of career decisions. *Plant Physiol.* 126, 1345-1346.

Curie, C., Z. Panaviene, C. Loulergue, S. L. Dellaporta, J. F. Briat, and E. L. Walker. 2001. Maize *yellow stripe1* encodes a membrane protein directly involved in Fe(III) uptake. *Nature* 409, 346-349.

Jacobson, A.B., H. Swift, and L. Bogorad. 1963. Cytochemical studies concerning the occurrence and distribution of RNA in plastids of *Zea mays*. *J Cell Biol.* 17, 557-570.

Krogmann, D.W., and J. Key. 1981. The Agriculture Grants Program. *Science*. 213, 178-182.

Marshall, E. 1996. Trial set to focus on peer review. *Science*. 273, 1162-1164.

McIntosh, L., C. Poulsen, and L. Bogorad. 1980. Chloroplast gene sequence for the large subunit of ribulose bisphosphate carboxylase of maize. *Nature* 298, 556-560.

Mets, L.J., and L. Bogorad. 1971. Mendelian and uniparental alterations in erythromycin binding by plastid ribosomes. *Science*. 174, 707-709.

Moseley, J., J. Quinn, M. Eriksson, and S. Merchant. 2000. The *Crd1* gene encodes a putative di-iron enzyme required for photosystem I accumulation in copper deficiency and hypoxia in *Chlamydomonas reinhardtii*. *Embo J.* 19, 2139-2151.

Quick, W.P., U. Schurr, K. Fichtner, E.-D. Schulze, S. R. Rodermel, L. Bogorad, and M. Stitt. 1991. The impact of decreased Rubisco on photosynthesis, growth, allocation and storage in tobacco plants which have been transformed with antisense *rbcS*. *Plant J.* 1, 51-58.

Rodermel, S.R., M. S. Abbott, and L. Bogorad. 1988. Nuclear-organelle interactions: nuclear antisense gene inhibits ribulose bisphosphate carboxylase enzyme levels in transformed tobacco plants. *Cell*. 55, 673-681.

Sullivan, M.B., D. Lindell, J. A Lee, L. R. Thompson, J. P. Bielawski, and S. W. Chisholm. 2006. Prevalence and evolution of core photosystem II genes in marine cyanobacterial viruses and their hosts. *PLoS Biol.* 4, e234.

Tottey, S., M. A. Block, M. Allen, T. Westergren, C. Albrieux, H. V. Scheller, S. Merchant, and P. E. Jensen. 2003. Arabidopsis CHL27, located in both envelope and thylakoid membranes, is required for the synthesis of protochlorophyllide. *Proc Natl Acad Sci U S A* 100, 16119-16124.

SELECTED BIBLIOGRAPHY

1952

With S Granick. Precursors of protoporphyrin in *Chlorella*. *Nature*. 170, 321.

1953

With S Granick. The Enzymatic Synthesis of Porphyrins from Porphobilinogen. *Proc Natl Acad Sci U S A*. 39, 1176-1188.

1958

The enzymatic synthesis of porphyrins from porphobilinogen. II. Uroporphyrin III. *J Biol Chem*. 233, 510-515.

1963

With A. B. Jacobson and H. Swift. Cytochemical studies concerning the occurrence and distribution of RNA in plastids of *Zea mays*. *J Cell Biol*. 17, 557-570.

1964

With S. Klein and G. Bryan. Early stages in development of plastid fine structure in red + far-red light. *J Cell Biol*. 22, 433-438.

1965

With N. Kislev and H. Swift. Nucleic Acids of Chloroplasts and Mitochondria in Swiss Chard. *J Cell Biol*. 25, 327-344.

1967

With M. Gassman. Studies on the Regeneration of Protochlorophyllide after Brief Illumination of Etiolated Bean Leaves. *Plant Physiol*. 42, 781-784.

1971

With L. J. Mets. Mendelian and uniparental alterations in erythromycin binding by plastid ribosomes. *Science*. 174, 707-709.

1973

Wit A. Bennett. Complementary chromatic adaptation in a filamentous blue-green alga. *J Cell Biol*. 58, 419-435.

1974

With L. J. Mets. Two-dimensional polyacrylamide gel electrophoresis: an improved method for ribosomal proteins. *Anal Biochem.* 57: 200-210.

1975

Evolution of organelles and eukaryotic genomes. *Science* 188:891-898.

Phycobiliproteins and complementary chromatic adaptation. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 26: 369-401.

1977

With J. R. Bedbrook and R. Kolodner. L. *Zea mays* chloroplast ribosomal RNA genes are part of a 22,000 base pair inverted repeat. *Cell* 11:739-749.

With D. M. Coen, J. R. Bedbrook, and A. Rich. Maize chloroplast DNA fragment encoding the large subunit of ribulosebisphosphate carboxylase. *Proc Natl Acad Sci U S A.* 74:5487-5491.

1978

Bedbrook, J.R., Link, G., Coen, D.M., and Bogorad, L. Maize plastid gene expressed during photoregulated development. Proc Natl Acad Sci U S A. 75, 3060-3064.

With G. Link and D. M. Coen. Differential expression of the gene for the large subunit of ribulose bisphosphate carboxylase in maize leaf cell types. *Cell* 15:725-731.

1980

With L. McIntosh and C. Poulsen. Chloroplast gene sequence for the large subunit of ribulose bisphosphate carboxylase of maize. *Nature* 298:556-560.

1981

With K. E. Steinback, L. McIntosh, and C. J. Arntzen. Identification of the triazine receptor protein as a chloroplast gene product. *Proc Natl Acad Sci U S A.* 78: 7463-7467.

1982

With K. E. Krebbers, I. M Larrinua, and L. McIntosh. The maize chloroplast genes for the beta and epsilon subunits of the photosynthetic coupling factor CF1 are fused. Nucleic Acids Res. 10, 4985-5002.

1985

Fish, L.E., Kuck, U., and Bogorad, L. Two partially homologous adjacent light-inducible maize chloroplast genes encoding polypeptides of the P700 chlorophyll *a*-protein complex of photosystem I. J Biol Chem. 260, 1413-1421.

Rodermel, S.R., and Bogorad, L. Maize plastid photogenes: mapping and photoregulation of transcript levels during light-induced development. J Cell Biol. 100, 463-476.

1986

Merchant, S., and Bogorad, L. Regulation by copper of the expression of plastocyanin and cytochrome c_{552} in *Chlamydomonas reinhardtii*. *Mol Cell Biol* 6, 462-469.

Sayre, R.T., Andersson, B., and Bogorad, L. The topology of a membrane protein: The orientation of the 32 kd Qb-binding chloroplast thylakoid membrane protein. *Cell* 47, 601-608

1987

Sheen, J.Y., and Bogorad, L. Differential expression of C4 pathway genes in mesophyll and bundle sheath cells of greening maize leaves. *J Biol Chem.* 262, 11726-11730.

1988

Rodermel, S.R., Abbott, M.S., and Bogorad, L. Nuclear-organelle interactions: nuclear antisense gene inhibits ribulose bisphosphate carboxylase enzyme levels in transformed tobacco plants. *Cell.* 55, 673-681.