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WILLIAM DAVID McELROY
1917–1999

A Biographical Memoir by

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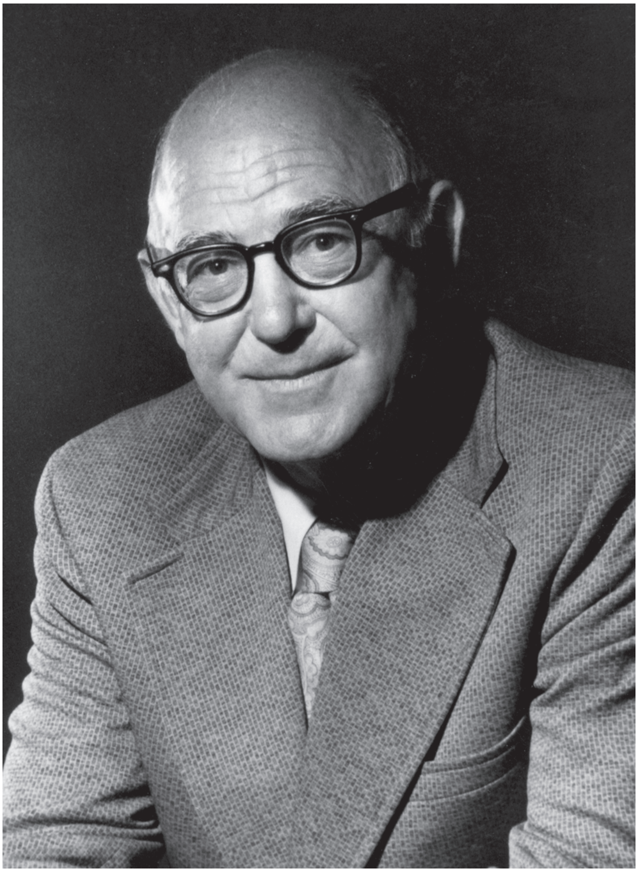

Photo by Anthony di Gesu, La Jolla, California

WILLIAM DAVID McELROY

January 22, 1917–February 17, 1999

BY J. WOODLAND HASTINGS

WILLIAM DAVID MCELROY, a biologist who made groundbreaking discoveries in bioluminescence and was an administrator of great talent, died of respiratory failure at Scripps Memorial Hospital in San Diego, California, at the age of 82. He was an innovative and internationally prominent scientist and administrator, with a continuing agenda for experimental projects and research support for all areas of science, both basic and applied.

At the time of his death McElroy was a professor emeritus at the University of California, San Diego, having served as its chancellor from 1972 to 1980. He was on the faculty at the Johns Hopkins University, where from 1946 until 1969 he was the founding director of the McCollum-Pratt Institute, and from 1956 to 1969 the chairman of the biology department. He was a member of many professional scientific societies and served as president of several, including three of the largest: the American Society of Biological Chemists, the American Institute of Biological Sciences, and the 116,000-member American Association for the Advancement of Science. He served on the President's Science Advisory Committee under both Kennedy and Johnson (1962-1966), was elected to the National Academy of Sciences in 1963, was director of the National Science Foundation under Nixon

(1969-1972), and was a member of the President's Committee on the National Medal of Science Award (1972). He was the recipient of honorary degrees from some twelve institutions, including Johns Hopkins University, the University of California, San Diego, and the University of Bologna, Italy, and was an honorary member of Phi Beta Kappa. He was a member of the American Philosophical Society and the American Academy of Arts and Sciences, and he received from the latter the Rumford Prize, given in recognition of important discoveries concerning "heat or light." He was also a recipient of the Barnett Cohen award in bacteriology from the American Society for Microbiology.

McElroy was born on January 22, 1917, in Rogers, Texas, the son of William D. and Ora Shipley McElroy. He completed high school in McAllen, Texas, and graduated from Pasadena Junior College in 1937. In 1939 he obtained a B.A. from Stanford University, where he played right end on the football team in 1938 and 1939; he continued studies at Reed College in Portland, Oregon, where he received his M.A. in biology in 1941. There he met a fellow student, Nella Amelia Winch; they were married on December 23, 1940.

McElroy continued as a graduate student in biology at Princeton University with E. Newton Harvey as his mentor, receiving a Ph.D. in 1943, and continuing there with Harvey and others on a research project for the U.S. Office of Scientific Research and Development (1946) during World War II. From 1945 to 1946 he held a National Research Council Fellowship at Stanford, working with George Beadle, where he also developed close scientific relationships with Edward Tatum and Cornelius van Niel.

Mac, as he was called in the early days, began his career in 1946 as an instructor of biology at Johns Hopkins University, where the noted embryologist Benjamin H. Willier was chairman. With fireflies abundant on campus, he carried out an experiment that was to become the signature of his career (1947), in which he showed that light emission in extracts of the firefly lantern required adenosine triphosphate (ATP), a recently identified "high-energy" molecule in metabolism (Lipmann, 1941). He had earlier explored this possibility with Robert Ballentine using a different luminous species in a publication from Princeton (McElroy and Ballentine, 1942).

As it turned out, ATP alone could not be the energy source for light emission, as suggested by the title of his 1947 publication, since the energy released by ATP hydrolysis (~ 7 kcal) is far less than the energy of a photon in the yellow (~ 50 kcal). He later showed the role of ATP in the light-emitting reaction to be analogous to the activation of amino acids in protein synthesis, reacting with luciferin to form the luciferyl-adenylate intermediate (1968), which then reacts with oxygen to form a high-energy peroxy intermediate, the breakdown of which provides enough energy to emit light. This work highlighted the relatedness of different biochemical systems and the importance of understanding basic biochemistry. One should not recount this experiment without recalling that ATP was not found in the freezer or in a catalog in those days; indeed, few biochemical reagents could be purchased. McElroy obtained the ATP by purifying it himself from rabbit muscle.[1]

Research on the firefly system continued briskly in McElroy's laboratory at Hopkins over the decades of the 1950s and 1960s. Arda Green spearheaded the purification and crystallization of luciferase (1956), while other students pursued the discovery that coenzyme A could stimulate light emission (1958), which had its explanation later from the discovery that firefly luciferase and CoA ligase are homologous (Schroder, 1989). With White and McCapra in the

Hopkins chemistry department, the structure of firefly luciferin was determined (1961). Howard Seliger joined the lab in the late 1950s and determined the quantum yield of the reaction to be close to 1.0 (1960); he also measured the spectral composition of the light in relation to the structure of the luciferase (1964).

McElroy and his group also researched other luminescent organisms, including bacteria (1953, 1955), fungi (1959), and dinoflagellates (1961, 1971). The first and last are now biochemically well described. He later coauthored an influential book with Seliger (Seliger and McElroy, 1965), in which the evolutionary origins of bioluminescence were interestingly associated with the appearance of oxygen in geological time, promulgating the provocative hypothesis that luciferase originated as an oxygen scavenger. An article in *Scientific American* (1962) reached scientists in many areas, as well as laypersons.

Upon Willier's retirement McElroy assumed the chairmanship of the biology department at Hopkins and built a very strong department, in both research and teaching. Andre Jagendorf testifies to his effectiveness as chair, saying that Mac shielded faculty from administration, meaning, however, that faculty might not be consulted in many important decisions. Those who did not agree with this approach went elsewhere. In teaching, he himself was dedicated and effective. His lectures in biochemistry were dynamic and provocative, as recounted by Gilbert Levin, a NASA engineer who, while developing biology experiments for the first Mars mission, returned to Hopkins for a Ph.D. in biology. "He was certainly a far cry from the typical JHU prof! The first thing he did was to doff his suit coat and loosen his tie. [He used] . . . simple English, including plenty of vernacular. . . [and] taught us a lot of stuff in each session." Levin credits McElroy's lectures with providing him with the understanding of optical isomers that led to NASA's "labeled release" experiments in the search for life on the 1976 *Viking* mission to Mars (Levin and Straat, 1979). "The chirality issue started by Bill's lecture has kept the space biology community riled for 28 years."

McElroy's strong beliefs in quality education for all led to his involvement in the Baltimore city schools and junior college; he served as a member of the Board of School Commissioners for the city from 1958 to 1968 and chairman of the Board of Trustees for Baltimore Junior College in 1968 and 1969. He was also greatly concerned with the problem of overpopulation of humans and was active in promoting measures to address the problem (1969).

In the 1960s McElroy was divorced from Nell. He met and married Marlene Anderegg DeLuca, a fellow scientist at Johns Hopkins, in 1967. In 1969 he was appointed director of the National Science Foundation by President Nixon, and he moved to Washington, D.C. His tenure saw increases in funding from $400 million to $650 million, and the introduction of important new programs, especially in the area of applied science, with no compromises on basic research (1975).

Eloise Clark and Sig Suskind, who were at the National Science Foundation at the time, recall that "shortly after his arrival at NSF the Office of Management and Budget proposed a major reduction in the science education budget of NSF. There was speculation that this was simply the first step in further reductions on the path toward elimination of the agency. Recognizing that the decision to cut the education budget was irreversible, McElroy is said to have persuaded OMB to leave the money in the budget by orienting the targeted funds to applied research."

He was recently remembered by the later NSF Director Rita Colwell as "a visionary who expanded NSF's mission beyond the 'core' disciplines . . . [who] recognized that NSF could not fulfill its mission without incorporating fully the engineering and social sciences, and extending greatly its public outreach activities. [He] fought to keep the basic research 'edge' on a larger effort to link research investments with societal needs."

As director McElroy made bold moves. As an example, it was said that in a meeting to discuss research funding at Caltech, an undergraduate asked why students could not apply for grants. McElroy asked that they describe their proposed research and its cost on a single sheet of paper, then on the spot signed the authorization for a grant in support of the work.

In 1972 Mac, now more often called Bill, was appointed chancellor at the fledgling 12-year-old campus of the University of California, San Diego, in La Jolla. He oversaw the tripling of the budget, the expansion of arts, humanities, and social sciences, which he strongly supported, and significantly, he involved community leaders in the governance of the university by establishing a Board of Overseers. But his strong administrative style, which had been so successful earlier, met opposition from other administrators and faculty; therefore, in 1980 he returned to full-time research and teaching as a professor of biology. A distinguished lectureship in biology was endowed in his honor, and a garden and terrace adjacent to the Mandeville Auditorium named for him.

During those years as chancellor, McElroy maintained an active participation in research and scholarship. He organized a Southern California bioluminescence group, bringing together colleagues from as far north as Santa Barbara for discussions of research. Ken Nealson, then a faculty member at Scripps Institution of Oceanography remembers "some great meetings at the chancellor's house, where a lot of nice interactions were started due to him" and that he was "a strongly positive influence who appreciated the subtleties of the science across a wide range of disciplines, and encouraged everyone, but especially the young scientists."

During the next decade with his wife, Marlene, he directed work leading to the cloning of the firefly luciferase gene and its expression in several organisms, including tobacco plants, with many important implications for applications (de Wet et al., 1985, 1987; Ow et al., 1986). Queried on National Public Radio about "lighting up tobacco" with luciferase, Marlene joked that her next project would be to clone the gene in yeast and produce "lite" beer. Keith Wood and other students participated in those studies, which included the discovery in a single beetle of different genes coding for luciferase isoforms eliciting different colors of bioluminescence (1989). Thus the enzyme, not just the luciferin (the product of which is the emitter), has an important role in determining the color of the light emitted. Marlene's untimely death in 1987 was a shock, and his activities were greatly reduced in the 1990s. In 1997 he met and married Olga Robles, with whom he spent the last years of his life.

The many practical applications of firefly luciferase were already evident and underway by the early 1950s. Bernard Strehler, one of McElroy's first graduate students at Hopkins, promoted and exploited the use of luciferase for the determination of ATP (1957). At the Oak Ridge National Laboratory, with William Arnold, Strehler used luciferase to try to demonstrate photosynthetic phosphorylation in *Chlorella*. In that, they were frustrated by the occurrence of luminescence in controls lacking luciferase, which thereby led to their important discovery of delayed light emission in plants (Strehler and Arnold, 1951; Arnold, 1986). But its use in the detection of ATP became widespread, especially for the detection and quantification of living organisms (Chapelle and Levin, 1968; Holm-Hansen and Booth, 1976). NASA pioneered this work as a possible way to detect life on Mars; it was instrumented but never flown. It is now widely used to test for the presence of organisms contaminating foods, for example, soft drinks and beef carcasses after slaughter (Hastings and Johnson, 2003). Even more widespread is the use of luciferase as a reporter of gene expression in biology and medical research and diagnostics. In 2004 a search of literature on the Web gave hundreds of hits yearly for firefly luciferase, the great majority being concerned with clinical and research applications.

In La Jolla, Bill and Marlene established one of the early biotech firms, the Analytical Luminescence Laboratory, which provided many of the agents and reagents for various uses. Later, the ProMega Corporation (Madison, Wisc.) obtained rights and became a major supplier of luciferase-related reagents, with former student Keith Wood as director of research in that area.

I joined Mac's lab in the early summer of 1951 after completing my Ph.D. at Princeton, also with E. Newton Harvey. Mac put me in charge of firefly collection, the now-legendary operation in which children were paid a penny for each firefly collected. He instructed me in the fundamentals of negotiation and bluffing, which he sometimes made use of later at the higher levels of government and university administration, and always at the poker table. "It's good to over-pay, but when the claim is ridiculous, make it double or nothing on a number that you can win. If they claim 700 fireflies and it's clear that there are less than 300, offer to pay them for 400. If they do not agree, say that you will count them and pay for 800 if there are more than 400, and to pay nothing if there are fewer." After a few losses the word got around and the kids claimed more reasonable numbers.

The firefly collection operation had an enormous, positive impact on the perception of and interest in science nationwide. There were innumerable articles in newspapers and magazines describing the collection and explaining the importance of such research in basic science, even though significant applications were not so evident at the time (*Johns Hopkins Magazine,* 1952). Unfortunately, there were concurrent political efforts to ridicule basic science, for example, the "golden fleece" awards, promulgated by a member of the U.S. Congress, directed at deriding studies based on perhaps less appealing organisms, such as snakes. Years later, as director of the National Science Foundation, Mac strongly opposed such political intervention and was a strong and effective spokesman in supporting basic research in all areas.

Photometers were not commercially available in 1951, so based on Ted MacNicol's design, I built a photomultiplier photometer, which later became the first such instrument to be marketed. Baltimore's humid climate favored fireflies but not photomultipliers, so Mac agreed that I could buy a window air conditioner for my lab. These had just become generally available; indeed, this was the only air-conditioned room at the time in the biology department, probably in all of Johns Hopkins. So it came about that on certain very hot summer evenings my lab was reserved for a poker game hosted by Mac, with the dean of faculty, the provost, and a few other key players as guests. Thus the title of my salutatory address on the occasion of his honorary degree from Bologna was "Firefly Flashes and Royal Flushes: Life in a Full House" (Hastings, 1989). His was indeed a full life.

Later Mac transferred the poker game custom to Thursday nights in Woods Hole, where in 1956 he was appointed director of the renowned summer course in physiology at the Marine Biological Laboratory. His impact at the MBL was profound; he transformed the course, and it became the flagship offering, attracting many postdoctoral fellows and physicians for advanced training in research. He was elected a trustee of the MBL and participated actively in laboratory governance. The Thursday poker game still continues there, and derivative games are located in many places around the country. Veterans attest to Mac's uncanny ability to regularly finish the evening with sizable winnings, and he typically wore a cap with a green celluloid visor with Magic Marker writing, "Make checks payable to W. D. McElroy." Andrew Szent-Gyorgyi, a regular participant, also recalls that a bottle of champagne was transferred each week to the home of the host, so as to be prepared for a celebration if Mac should ever lose, which he eventually did, but only once according to legend. John Riina, Mac's editor at Prentice-Hall, says that "over 15 years, I recall only one game in which he was not a winner" and attributes to McElroy the observation that "the declared winnings always exceeded the sum of the reported losses." Riina characterized McElroy as "unique in many ways, he was interdisciplinary, thinking, acting and bringing together science, academia, government and society."

In 1948 John Lee Pratt, a trustee of the Johns Hopkins University and self-styled "plain dirt farmer" from Fredericksburg, Virginia (also, incidentally, a former vice-president of General Motors), donated $500,000 to establish a fund for the study of "micronutrients" in animal and plant nutrition. As recalled by Lawrence Grossman, who later occupied McCollum's chair, Pratt had served on a presidential committee during World War II with nutritionist Elmer McCollum, professor of biochemistry at the Johns Hopkins school of public health, discoverer of vitamin A, and codiscoverer of vitamin D. Pratt mentioned that his cattle were suffering from "disease X," and McCollum suggested that this might be alleviated by adding small quantities of copper and molybdenum to the diet. This proved to be successful, probably triggering the idea for a gift; Hopkins President Bowman then appointed a committee, with both McElroy and McCollum as members, to recommend its implementation. Many on the committee were at a loss as to how a gift with such specific directives could be used (with McCollum retired there were no longer any Hopkins faculty working in the area of nutrition). Mac convinced the committee to establish a research institute associated with the biology department, and he volunteered to be its first director. Never mind that he had no special credentials or expertise in the area; good basic research, he argued, would inevitably lead to advances in an understanding of animal and plant nutrition. The success of the institute is well known; Mr. Pratt added another million to the fund in 1952, and upon his death in 1975, bequeathed $55 million to colleges and universities, including $5.5 million to Hopkins.

Who were McElroy's first appointments to the institute? Not nutritionists, but four of the best young biochemists in the country, now deceased: Sidney Colowick and Nate Kaplan, who later initiated the series "Methods in Enzymology" (Colowick and Kaplan, 1955), which is still going strong today, 50 years later, with over 380 volumes; Al Nason, a plant biochemist with whom McElroy later collaborated on effects of micronutrients on enzyme activity (1953); and Robert Ballentine, with whom he had authored the first paper on the possible involvement of ATP in luminescence. Over his career he engaged in collaborations with many other scientists, well exemplified by his work with Nelson Leonard from the University of Illinois (Leonard, 1997), who recalls his "very pleasant and fruitful collaborations with Bill and Marlene."

McElroy was keen on the importance of communication; he wanted everybody to attend scientific meetings and to exchange results and ideas. In those years $100 was equal to about $1,000 today, and I recall him passing out $100 bills to all graduate students who were planning to go to the Federation Meeting in Chicago in 1953. No accounting needed, but they could not submit a voucher and get more.

He was also keen on the importance of timely publication of the latest findings. He was one of the first to organize stand-alone topic-oriented symposia, doing so initially with funds from the McCollum-Pratt Institute on subjects closely related to vitamins and nutrition, in keeping with the institute's mission. Indeed, the first was on "disease X." Together with Bentley Glass, who wrote extended summaries that typically also clarified the obscure paper, they edited (in my air-conditioned lab) questions and answers recorded from the talks within weeks and had the volume published within months. Altogether there were nine such symposia, embracing such seemingly far-afield topics as heredity, development, and enzyme action, yet all were arguably, indeed evidently, of great fundamental importance for the progress of the mission of the institute. The last symposium, "Light and Life," included such topics as molecular structure and excited states, photosynthesis, vision, and, of course, bioluminescence (McElroy and Glass, 1961).

Believing that "the latest news" would greatly stimulate students and researchers, Mac was also very active in the promotion of publishing. He was very active on editorial boards of many professional journals and was a founding editor of *Biochemical and Biophysical Research Communications.* In 1958 he became the editor with Carl Swanson of Prentice-Hall's "Foundations of Modern Biology" series, possibly the first paperback monographs that served as textbooks. John Riina, the Prentice-Hall editor with whom he worked, testifies to McElroy's leadership in identifying the best authors and convincing them to write. McElroy himself authored *Cellular Physiology and Biochemistry,* and with Carl Swanson provided the editorial direction for an outstanding list of books in the biological sciences.

McElroy was a true pro at obtaining funding for research. The National Science Foundation was started while I was in his laboratory, and I recall sitting with him for the 30 minutes or so that it took him to write his first proposal—for $10,000, I think. And it was successful!! In later years, as chairman of the biology department at Hopkins, he obtained some of the first grants from the NSF, National Institutes of Health, Office of Naval Research, and other agencies in support of term-time faculty salaries, relieving them of some teaching and allowing him to build a strong research department.

He was so imaginative and effective, one might infer, that the NSF decided that it would be wise to hire him as director, a post that he assumed in 1969. As the *New York Times* reported in its obituary (1999), he was the second choice, after an offer to Franklin Long of Cornell was withdrawn when it was learned that Long had opposed Nixon's proposed antiballistic missile system. McElroy was said to have been similarly opposed but was quiet about it, viewing government service as a way to promote science and to get increased funding for research. In this, and in his numerous other enterprises, and in his service to science and society, he was a leader and an achiever of the first rank.

William D. McElroy was survived by his wife, Olga Robles McElroy; his four children by his wife, Nell: Mary Elizabeth McElroy of Boston, Mass.; Ann Reed McElroy of Hickory, N.C.; Thomas Shipley McElroy of Glen Arm, Md.; William David McElroy, Jr., of Woods Hole, Mass.; and his son by his second wife, Marlene: Eric Gene McElroy of San Marcos, Calif. He also left a sister Lola Rector of Pismo Beach, Calif.; a nephew Mark Heinz; three grandchildren: Heather McElroy Holman, William D. McElroy III, and Michael James McElroy; and three great-grandchildren: Timothy Alexander Holman, Jr., Emily Madison Holman, and Nicholas Holman.

NOTE

1. As it happened, a business of isolating and selling ATP, stimulated by the firefly work, led to the founding of the Sigma Chemical Co. in St. Louis, subsequently and still now a premier biochemical supplier. This started as a side activity of Dan Broida's shoe polish company, and Broida became a good friend of many biochemists. In later years Sigma itself developed a network of children (some well over the age of 21) to collect fireflies, which it marketed to biochemists.

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