

RETROSPECTIVE

Paul D. Boyer (1918–2018)

Pioneer of molecular machines and inspirational leader

By David S. Eisenberg

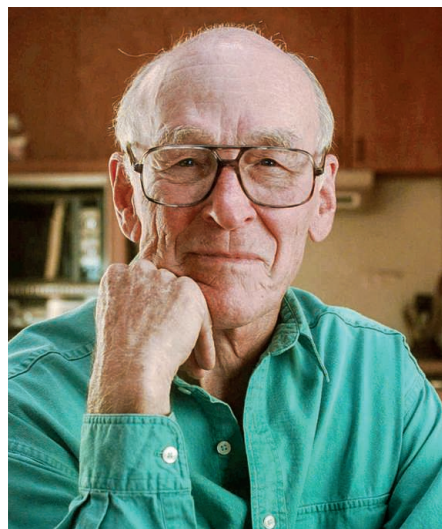
On 2 June, 2 months before his 100th birthday, Paul Boyer died peacefully, surrounded by family, including Lyda, his wife of nearly 79 years. Paul was deeply admired by his students, colleagues, and friends for his many talents. He was skilled in mechanics, science, diplomacy, administration, and athletics. Beyond his scientific success, culminating in a share of the 1997 Nobel Prize in Chemistry, Paul contributed to the community by serving as a role model, demonstrating the wisest path forward in tough situations.

Paul died at his home in Los Angeles, which he built, serving as his own general contractor. Recalling Paul's mechanical skills, his daughter Gail said that they had never had a repairman in the house. Earlier, while at the University of Minnesota, Paul and Lyda had designed their first home, for which Paul was the plumber, electrician, and cabinet maker. Paul was teaching his class at the university when the inspector arrived at their homesite to evaluate the plumbing. He lingered intently over each fitting and junction and then confronted Lyda with the question, "Who did this work?" Her heart fell as she told him it had been her husband. "He must have been trained in the old country," said the inspector, "they don't do fine work like this anymore."

In fact, Paul was raised in Provo, Utah, the fourth of seven children, a descendant of what he called "hardy Mormon pioneer stock." Although he rejected the religious tenets of his church, he attributed his scientific career to parental and community devotion to education. He attended Brigham Young University, a few blocks from his home, graduating with a degree in chemistry in 1939. That autumn, he left for graduate school at the University of Wisconsin–Madison armed with \$150 in cash, a \$400-per-year scholarship, and his new bride, Lyda. He soon developed a second love—for biochemistry. After earning his Ph.D. in the subject in 1943, he did war research on blood proteins at Stanford University, joined the faculty at the University of Minnesota, where he introduced chemical and isotopic methods for the study of enzyme mechanisms, and then settled for good at the University of California, Los

Angeles (UCLA), in 1963. Starting at age 70, Paul and Lyda enjoyed an active retirement of tennis, golf, bridge, and travel throughout the American West, interrupted only by the award of Paul's Nobel Prize at age 79.

Paul's most profound discovery was that adenosine triphosphate (ATP), the energy currency of life, is synthesized in living cells by a rotary molecular engine, ATP synthase. The inference of this unprecedented mechanism from measurements of chemical rates could have been made only by a scientist with Paul's deep mechanical understanding. He applied mass spectrometry to monitor oxygen-18 exchange kinetics to understand the enzymatic mechanism of ATP synthase. His experiments suggested that the energy of oxi-



dation is coupled to the release of ATP from the enzyme, rather than to ATP synthesis (his so-called "binding change mechanism"), and that the enzymatic reaction of ATP synthase must involve more than one catalytic site. From these insights, he correctly proposed a rotary molecular engine, later gloriously illuminated by the crystal structure of ATP synthase by British chemist John E. Walker. For this work, he and Walker shared half of the Nobel Prize in Chemistry in 1997.

Paul had the curiosity and confidence to grapple with big questions and big projects. Though he studied some 20 enzymes during the course of his career, he kept returning to ATP synthase. As he said in a biographical memoir, "Although the larger questions [about oxidative phosphorylation] were not

likely to be answered, at least I wanted to try." He knew that "effort is difficult without optimism, and accomplishment is rare without effort."

Soon after moving from Minnesota to UCLA, Paul applied his optimism and effort to founding the Molecular Biology Institute (MBI). He immediately set out to recruit faculty (around 20 over time, including me) and students (some 400 have completed molecular biology Ph.D.s as of 2018). With phenomenal persistence, he put together a mosaic of funding sources for construction of the laboratory now known as Boyer Hall. However, not every project of Paul's came to fruition. In 1980, he envisioned a set of bicycle freeways emanating from UCLA that would change the character of Los Angeles. Clearly, that idea was before its time, but Paul could once again say "at least I wanted to try."

Active in the national leadership of the biochemical community, Paul served as president of the society now called the American Society for Biochemistry and Molecular Biology, as well as chair of the Division of Biological Chemistry of the American Chemical Society. With Lyda's assistance, he produced 18 volumes of the review series *The Enzymes*.

Paul's many achievements were made possible by his optimism, effort, ambition, and know-how, but there was something more: character. In my every encounter with Paul, from the first in 1967 to my last shortly before his death 50 years later, I sensed his drive to get at the truth, his generous judgments of others and their work, and his modesty. Together, these traits made him the most effective leader that many of us have ever personally known. Under his 18-year directorship of the MBI, faculty meetings were amicable and short. Paul had discussed the issues beforehand with each of us and had forged a consensus prior to the meeting. A generous author, Paul carefully noted the advances made by each of his graduate students and postdoctoral fellows in his several scientific autobiographies. In appreciation of these contributions, Paul donated to UCLA part of his Nobel Prize stipend for awards to his current UCLA postdoctoral fellows. Paul also invariably took care to credit the results from the labs of other scientists. Even when he disagreed, the tone was one of respect, sometimes noting where in hindsight his own interpretation had been wrong.

In the present era, when science and reason are under attack, facts are considered optional, lying by leaders is not unexpected, and bullying and falsely hogging credit are tolerated, Paul Boyer's life stands as a model of the proper path for all of us who have had the privilege of knowing him. ■

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