RETROSPECTIVE

Arthur Kornberg (1918–2007)

One of the greatest biochemists of the 20th century and a "lover of enzymes" is remembered.

Paul Berg and I. R. Lehman

Arthur Kornberg, who had a life-long love affair with enzymes, died on 26 October surrounded by his family and mourned by his extended family of students and colleagues. It is not surprising that only 2 weeks before, he had been actively summarizing decades of work on polyphosphate for a review article.

In his autobiography, *For the Love of Enzymes: The Odyssey of a Biochemist*, Arthur described his entry into science and evolution from clinician to nutritionist to biochemist. He was born in Brooklyn, New York, on 3 March 1918, the son of parents who had emigrated from Eastern Europe and ran a small hardware store. He majored in chemistry and biology at City College of New York. After receiving an M.D. from the University of Rochester, he entered the U.S. Public Health Service and served briefly as a ship's doctor during World War II.

But he was enormously influenced by the great biochemists of the 1930s and 1940s—F. G. Hopkins, Otto Warburg, and Otto Meyerhoff—and then by Carl and Gerti Cori and Severo Ochoa, in whose laboratories he worked. His career in medicine changed to research in biochemistry. By exploiting the power of enzyme purification to reconstitute biochemical pathways—what he called "the hammer of enzyme purification"—Arthur undertook the formidable problem of synthesizing DNA. While at Washington University from 1953 to 1959, he discovered the first DNA polymerase and established DNA synthesis as a template-driven process, for which he shared the 1959 Nobel Prize in Physiology or Medicine.

Together with talented students and postdoctoral fellows, Arthur accomplished what some described as the creation of life in a test tube—recreating a bacteriophage chromosome with purified enzymes, substrates, and cofactors. Unfazed by that success, his laboratory reconstituted the complex process of bacterial chromosome replication in vitro. That monumental achievement influenced a generation of biochemists to undertake problems seemingly as intractable as gene expression, signal transduction, and intracellular protein transport. The ability to clone, amplify, and sequence genes, and the "biological revolution" that followed, were possible largely because of the enzymes that emerged from Arthur's pioneering work.

In the early 1990s, Arthur turned from DNA replication to the study of polyphosphate (polyP), a molecule that had intrigued him since the 1950s when he and his first wife Sylvy isolated polyphosphate kinase (PPK), which synthesizes polyP. His studies of polyP and PPK, which, as he put it, "disinterred a molecular fossil," led to the discovery of polyP's role in bacterial growth and survival, quorum sensing, biofilm formation, and virulence. He was convinced that future work would reveal the clinical importance of polyP in microbial infections.

Beyond his scientific achievements, Arthur's considerable expository gifts and the ability to project his ideas are exemplified by his superb 1980 textbook, *DNA Replication*, which educated a generation of molecular biologists. Fred Sanger conceived the "dideoxy" DNA sequencing method while reading the chapter on DNA polymerase I. In *The Golden Helix: Inside Biotech Ventures*, Arthur drew on his experience as a founder of the DNAX Research Institute of Molecular and Cellular Biology to provide a unique perspective on biotechnology. His last book, *Germ Stories*, a collection of poems for children, reveals the wonders and hazards of the microbial world.

Arthur's contributions to science did not go unrecognized. In addition to the Nobel Prize, he received the National Medal of Science, the Cosmos Club Award, and the Gairdner Foundation Award, among others. He served as president of the American Society of Biological Chemists, was elected to membership in the U.S. National Academy of Sciences, the American Academy of Arts and Sciences, and the American Philosophical Society, and was a Foreign Member of the British Royal Society. He was also awarded honorary doctorates from 12 universities.

Arthur revealed his gift as a leader by organizing the Enzyme and Metabolism Section of the National Institute of Arthritis and Metabolic Diseases. He assembled an outstanding Department of Microbiology at the Washington University School of Medicine in St. Louis, Missouri, as well as the Department of Biochemistry at Stanford. We accompanied him to Stanford along with Melvin Cohn, David Hogness, Dale Kaiser, and Robert Baldwin. Five of the six faculty members who accompanied him from St. Louis in 1959 have remained at Stanford, a tribute to Arthur's leadership.

In an unusual and much admired arrangement initiated by Arthur at Washington University and maintained at Stanford, the department's graduate students and postdoctoral fellows were provided available space in common laboratories. This encouraged research groups to interact and share reagents and methods, practices that greatly facilitated development of recombinant DNA technology at Stanford.

Both of us knew Arthur for more than 50 years, from the time we joined his laboratory at Washington University as postdoctoral fellows. But our relationships with him went beyond that of student and mentor. We were embraced as members of his family and shared many special occasions and achievements that they celebrated. Arthur's style of doing science, his passion for experimentation rather than theory, and excitement about discovery inspired us. We remember the late-night calls inquiring how our experiments had fared. He was a serious and superb teacher and a generous and compassionate leader. The success of the faculties he assembled attests to his gift of forsaking the limelight and encouraging his colleagues to flourish on their own. Above all, Arthur was devoted to his students and colleagues and fiercely loyal to his family and friends. Perhaps Arthur's greatest legacy, and certainly the one of which he was most proud, was his extraordinary family of three sons and eight grandchildren. We will miss him greatly.

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