At a meeting of the FACULTY OF ARTS AND SCIENCES *on March 7, 2023, the following tribute to the life and service of the late Howard Curtis Berg was spread upon the permanent records of the Faculty.*

HOWARD CURTIS BERG

BORN: March 16, 1934
DIED: December 30, 2021

Howard C. Berg, Herchel Smith Professor of Physics and Professor of Molecular and Cellular Biology, *Emeritus*, died on December 30, 2021, at age 87. Berg, through five decades of study of bacterial motile behavior, helped establish foundations for modern quantitative biology.

Howard Berg was born in Iowa City. His father, Clarence Berg, was a biochemist at the University of Iowa. Berg entered the California Institute of Technology intending to become an electrical engineer but was attracted to basic science and switched to chemistry.

He entered Harvard Medical School but, realizing it was a mistake, returned to basic science, earning his Ph.D. in chemical physics at Harvard working on the hydrogen maser under Norman Ramsey. His storied career in biophysics began as a Junior Fellow, when he began a long collaboration with Edward Purcell. Among many honors, Berg shared the Biological Physics Prize of the American Physical Society with Purcell in 1984 for elucidating the physics of chemical sensing.

Berg began working on bacterial chemotaxis at Harvard after a conversation with Max Delbrück, a founder of molecular biology who wanted to study microorganism behavior but not with *E. coli* because he did not know how to "tame" bacteria. Berg decided that taming meant following their movements. He invented an ingenious microscope that tracked individual swimming cells in three dimensions. This microscope, which was built on the first floor of the Biological Laboratories, revolutionized the study of bacterial chemotaxis. Berg discovered that bacteria move in a random walk, biasing the walk by lengthening runs when conditions improve but not changing when conditions decline. This overturned the century-old belief that bacterial chemotaxis represented avoidance of unfavorable stimuli. Berg quipped that *E. coli* is an optimist: "If life is getting better, enjoy it more; if it is getting worse, don't worry about it!"

In 1970, Berg and his young family moved to Boulder, where Berg helped shape the newly formed Department of Molecular, Cellular, and Developmental Biology at the University of

Colorado. Stopping in Wisconsin along the way, Berg spent a sabbatical with Julius Adler. Adler had published a classic study showing that bacteria perform chemotaxis on the basis of the sensory perception of attractive molecules. This was the beginning of a lifelong friendship between the famed bacteriologist and the pioneering biophysicist.

Berg moved to Caltech in 1979 and returned to Harvard in 1986 as Professor of Biology and a member of the Rowland Institute for Science, which was funded by his friend Edwin Land, the founder of Polaroid. The two Berg labs in Cambridge continued the tradition of technological innovation in pursuit of a deeper understanding of bacterial chemotaxis by pioneering the use of optical tweezers in biology, the use of fluorescence resonance energy transfer to dissect signal transduction networks, and new methods to image the polymorphic movements of flagella and the rotation of flagellar motor components.

Berg was a quiet leader. He mentored by setting an example, not by giving instruction. He was technologically fearless. When the right tool for a measurement did not exist, he invented it. Berg's inventions opened doors to novel areas of inquiry. The patterns of bacterial behavior uncovered by the tracking microscope led to decades of work exploring its underlying mechanisms. Bacterial chemotaxis is now one of the best understood signal transduction systems in biology, a paradigm that has inspired many fields of quantitative biology, from neuroscience to systems biology.

Berg was unrelentingly focused. He studied *E. coli* at many levels, from sensory perception to signal transduction to motility, but his dedication to bacterial behavior was unwavering. Berg did not heed current trends. Every discovery in the study of his beloved *E. coli* led to new questions needing answers. He was driven solely by curiosity. Sensory responses and motility are fundamental to all life; Berg studied bacterial chemotaxis to explore their deepest principles.

Funding was sometimes challenging, partly because of his unwillingness to justify the importance of his work to others. This challenge was offset by his thrift and "do-it-yourself" attitude. Into his 80s, Berg could reliably be found in his private machine shop, building or fixing laboratory equipment.

Berg was an inspiring and effective communicator, mild and short-spoken in conversation and disciplined and concise in writing. Every word had purpose. Berg tirelessly sought the most direct way to communicate deep and hard-won insights in biology and physics. In his shop, Berg invented lecture demonstrations to teach challenging concepts in fluid mechanics, probability, statistics, and biology. Many remember his vivid demonstration of how bacteria use their flagella. Berg was the first to propose that bacteria swim by rotating rigid flagella, not bending them. In front of captivated audiences, Berg swung his helical metal wires (precisely bent to proper wavelength and pitch but scaled to human size) to demonstrate how bacteria swim and perform chemotaxis.

Berg's clarity and concision is exemplified in his slim and pithy books, *Random Walks in Biology* (1983), which emerged from years of teaching biology to physicists and physics to biologists, and *E. coli in Motion* (2004), which reviewed progress to date in his field of bacterial behavior but was not his last word on the subject. The Berg lab was active until and even after his death, funded by a grant that Berg wrote at age 87.

Berg taught biology and physics in several Harvard courses, including "Introductory Cell Biology" with Daniel Branton; "From DNA to Brain," a Core Curriculum course, with John Dowling; and "Introduction to Biophysics," the first course to be cross listed in MCB and Physics, based on *Random Walks*. Berg worked in his labs until the end. Of colleagues who passed away before retirement, he congratulated them for exiting "with [their] boots on, working until the end without going to pasture."

The work and spirit of the Berg lab continues in the many laboratories led by his former students. He is survived by Mary Guyer Berg, his wife of 57 years; his children, Henry, Alec, and Elena; and his grandchildren, Angus, Eric, India, Oliver, and Sebastian.

Respectfully submitted,

John Dowling
Paul Horowitz
Richard Losick
Aravinthan Samuel, Chair