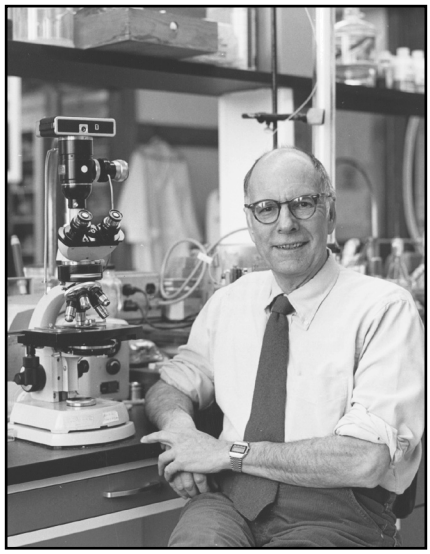
JOHN T. BONNER



12 MAY 1920 · 7 FEBRUARY 2019

PROCEEDINGS OF THE AMERICAN PHILOSOPHICAL SOCIETY VOL. 163, NO. 4, DECEMBER 2019

John T. Bonner, distinguished biologist and dedicated teacher, died on February 7, 2019, just short of his 99th birthday. He is recognized as a pioneer in developmental biology when it was dominated by embryology and before the rise of molecular genetics, and is applauded for his numerous contributions to a wide range of topics in biology, from the life cycle of lowly slime molds to problems of scaling and the evolution of complexity. He was a man of small organisms and big ideas.

His contributions to developmental biology were fundamental and were made through imaginative, lifelong studies of slime molds. In John's words, they chose him for a lifetime's work. Slime molds are social amoebae that live much of their life as independent cells feeding on bacteria in the soil, but when food runs short, they aggregate on the surface where they merge into a multicellular slug with a stalk that supports a fruiting body full of spores. Later the body bursts and the spores disperse. All this fascinated John when he first learned about them as an undergraduate at Harvard University. In graduate research, also at Harvard, he took up the challenge of trying to understand how this complex behavior was coordinated. His studies were interrupted by war and completed in 1947. He then moved to Princeton University, where he stayed until he retired in 1990 as the George M. Moffett Professor of Biology. For the next 29 years, John treated retirement as a sabbatical, volunteering his teaching for most of those years and writing several books and essays in lucid prose and plain English.

John is probably best known for his early discovery of a diffusible signaling molecule, later identified as acrasin (cyclic AMP), that causes the independent slime mold cells to aggregate (Kessin 2019). The discovery opened up research possibilities and questions across a surprisingly broad spectrum of biology, including differentiation and pattern formation, self-recognition, the evolution of multicellularity, the sociobiology of unicellular organisms, and the evolution of cooperation. He pursued them in the lab, and the discoveries he made led him to generalize beyond the lab, to seek principles applicable to organisms far removed from slime molds. Thus, he relished exploring issues of scaling, complexity, and social organization that flowed directly from understanding his microscopic subjects. The conceptual framework for all of this was evolution by natural selection. For many years, his numerous books on these large issues made an important contribution to the education of the public. A sample of book titles illustrates the breadth of his canvas: *Morphogenesis: An Essay on Development* (1952), *The Cellular Slime Molds* (1959), *The Ideas of Biology* (1962), *Evolution and Development* (1982; a very influential Dahlem conference), *The Evolution of Complexity by Means of Natural Selection*

(1988), *Life Cycles: Reflections of an Evolutionary Biologist* (1993), and *Why Size Matters: From Bacteria to Blue Whales* (2006). Several of them were translated into multiple languages.

John was an outstanding lecturer in introductory biology. I once asked an alumnus how he became an ecologist, and he replied that he came to Princeton to study chemical engineering, but the course on Introductory Biology changed all that:

> It was taught by John Bonner. He was inspirational. For one thing, he wore a white lab coat. He was obviously a scientist! And for another, he was extraordinarily enthusiastic about strange animals: worms and slime molds! I had to know why he had this enthusiasm, and the more I learned the more I was drawn into biology.

Thousands of students could tell a similar story. This little anecdote touches on two parts of the professional persona of John Bonner: a laboratory scientist of great distinction and an outstanding and memorable teacher. A third and very important part of his professional life was spent in summer months at Margaree Harbour in Nova Scotia, where he wrote essays and books on the large themes of biology. And when he was not doing that, he went fishing.

My most memorable interactions with John took place either in his office or mine, where we regularly had lunch together and exchanged news, views, and occasional gossip laced with much humor. Always courteous, polite, and respectful, John was interested in good conversation for what he could gain as well as contribute. John was an ideas man, and wanted material for exploring evolution in both research and teaching. These he molded into stories that he told to students in Intro Bio. He was a superb storyteller, an entertainer, witty, employing hyperbole to great effect, and his sense of timing was as good as a professional actor's. My wife Rosemary and I encouraged him to tell us stories about important figures in science from his early days, like D'Arcy Wentworth Thompson, J. M. Mitchison, and J. B. S. Haldane. He relished the opportunity, and his supply of stories was never-ending. One I remember most vividly I have recounted many times, because I wanted to believe it was literally true:

> In about 1950, the phone rings.
> "Is that you, Bonner? President of the National Science Foundation, here. How are you?"
> "Fine," John replies.
> "We have funded your research. How is it going?"
> "Really very well, we have found . . ."
> But before he could go any further, he was cut short with the words, "You are probably running short of money."

> "No," says John. "I still have some left."
> "Well, if the research is going well you will need some more in the future and we are going to fund you for another three years!"

If you have ever wondered exactly when the "Golden Era" was . . .

On matters of science we debated ideas. John worked them out by himself, and even if they had been developed by others, he refused to copy them but instead constructed his own way of expressing whatever he had on his mind. Independence he admired in others. Independence he had himself. John unapologetically acknowledged his own stubbornness. His self-awareness can be traced back to his Swiss mother. "My mother wrote in her diary when I was a small child, 'John is pig-headed and argumentative, but strangely thoughtful and sweet. Very bright'" (email to Mary Jane West Eberhard; Brigandt et al. 2019, 369). Stubbornness served him very well when, as chairman for 14 years, he had to deal with particularly powerful, opinionated, and irate faculty. He may have had a light touch as a chairman, but his hand was firm and unyielding. This attribute, combined with courtesy and collegiality, independence and originality, formed the core features of his social and scholarly personality. To Stuart Newman,

> He was the most low-key originator of radical ideas I have known. John was a campaigner, even a propagandist, for major departures from the prevailing ideas in developmental and evolutionary biology. But you would never know it from his humorous, self-effacing manner, and his kind disposition toward those who had not yet seen the light. (Brigandt et al. 2019, 369)

In a volume celebrating his retirement John wrote, ". . . as the years progressed, I have become increasingly obsessed with the idea that natural selection is the most useful, the most important, the most all-enveloping concept in all of biology" (Bonner 1992, 3). Many biologists would say the same. Yet toward the end of his life he became convinced it could not account for the enormous morphological variation among microorganisms. John spent five years working on an alternative, his final treatise, a small and stimulating book entitled *Randomness in Evolution* (2013). This was more a viewpoint than a theory. He makes the case that natural selection affects small and large organisms differently, less stringently when applied to morphological features of eukaryotic microorganisms. Variants are more likely to accumulate unchecked in small organisms because, in the absence of long and complex development, they are less subject to purifying or stabilizing selection. The argument applies to differences between species, while being largely silent on variation within species. With this,

his final fling as it were, he threw down a challenge to developmental biologists, and many have received it enthusiastically (Brigandt et al. 2019). What a way to end an exceptionally long, happy, and productive career! Well, not quite the end, for a recent issue of the *Journal of Experimental Zoology* devoted to celebrating his life contained his swansong, a paean to evolution. Fitting, because he published his first paper in the journal 72 years earlier!

John was elected to the APS in 1972 as a Resident Member in Class 2. He often attended APS Meetings and twice presented a paper at an APS Meeting ("Size and Living Form," April 1973; "The Biological Basis of Culture," April 1978). He was a Councilor (1983–1986), served on the Class 2 Committee (1975–1982), on the Committee on Nomination of Officers (1985), and on the Research Committee (1980–1989). In 2011, he donated his papers and some other material to the APS. He was a fellow of the American Academy of Arts and Sciences and a member of the National Academy of Sciences, among other distinctions. He took particular pride in the honorary degree he received from Princeton, the institution he served so well throughout his long career.

Elected 1972

Peter R. Grant
Class of 1877 Professor of Zoology Emeritus
Princeton University

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