

John Tyler Bonner

The establishment and growth of developmental-evolutionary biology owes a great debt to the work of John Tyler Bonner. Bonner's studies of cellular slime molds have shed light on some of the big questions of biology including the origins of multicellularity and the nature of morphogenesis. The second child of Lilly Marguerite Stehli and Paul Bonner, John Tyler was born 12 May 1920 in New York City and spent his early years in Locust Valley, Long Island (late 1920s), France (1930), and London (1932). His love for science was ignited as a young boy in England where he was inspired by visits to St. James's Park and the Natural History Museum.

The Bonner family returned to America in 1934 so that the four Bonner boys could attend Phillips Exeter Academy in New Hampshire like their father. In 1937 Bonner began studying biology at Harvard University. During his freshman year he took a botany course taught by William H. Weston who became his mentor and later on, his graduate supervisor. Bonner was fascinated by embryology but troubled by the complexity of animal embryology. He therefore decided to study development in lower plants, algae, and fungi which also enabled him to continue working with Weston. Kenneth Raper had also studied with Weston; it was Raper's PhD thesis on slime molds that inspired Bonner to investigate their unusual life cycle for his undergraduate thesis. Bonner received his BS degree from Harvard in 1941 and stayed on to continue working with slime molds and with Weston for graduate school.

Bonner's graduate education was interrupted by WWII. In 1942, shortly after his marriage to Ruth Anna Graham, he joined the Air Force. Wearing the rank of first lieutenant, Bonner conducted research on high-altitude physiology. He was discharged in 1946 and immediately returned to Harvard to finish his graduate studies.

Bonner's PhD work investigated the mechanisms that control the aggregation process in the life cycle of slime molds, a process triggered by starvation of the amoebae. Slime molds have a particularly unusual life cycle characterized by periods of unicellularity and multicellularity. During the unicellular stage the amoebae feed on bacteria and repeatedly divide to expand their population. When they have consumed all of the bacteria in a region, the independent amoebae cease all feeding, growth, and division and enter a period of aggregation during which they stream together to form a single aggregate, or slug. It is this period of aggregation that interested Bonner, for the aggregation period allowed him to investigate the mechanisms of morphogenetic movements without the complicating factor of growth.

Bonner hypothesized that some sort of chemotaxis was responsible for aggregation. This idea did not coincide with the recent findings of developmental biologist Paul Weiss, who had shown that contact guidance, rather than chemotaxis was responsible for cell migration. Bonner therefore did not limit his search to chemical attraction but also investigated other possibilities such as electrical forces. Fortunately a clever experiment revealed that indeed chemical attraction was the mechanism behind the aggregation; social amoebae were attracted to an unknown chemical that was given off by the center of the aggregate.

Bonner's discovery of chemotaxis involved a technique he had developed that allowed the amoebae to aggregate on the bottom of a glass dish under a layer of water. To test whether water current effected the orientation of the aggregating amoebae he placed a bent stirring rod over the aggregating amoebae and turned on the motor. He observed that the current generated by the stirring rod produced an asymmetrical aggregation pattern. The amoebae upstream of the current wandered aimlessly, rather than forming characteristic streaming patterns. In contrast, the amoebae downstream of the current were oriented normally and formed regular streaming patterns. This ob-

ervation led Bonner to conclude that the amoebae must be attracted to some sort of chemical that was disrupted by the introduction of the stirring rod. He suspected that diffusion of this chemical was responsible for the characteristic patterns that occurred during the aggregation period.

Bonner christened this unknown substance "Acrasiales" after the witch in Edmund Spenser's *Faerie Queene*. This demonstration of chemotaxis served as the foundation for a great deal of work in Bonner's laboratory as well as the laboratories of many others. For this work Bonner was awarded his PhD in 1947.

As part of his education Bonner spent summers at the Marine Biological Laboratory (MBL) in Woods Hole, Massachusetts. There he met such renowned embryologists as Thomas Hunt Morgan, Oscar Schotté, Ross Granville Harrison, Edmund Beecher Wilson, and Edward Grant Conklin, who let Bonner share his office. Bonner was an instructor in the Embryology Course at the MBL in 1956 and 1957.

In 1947 Bonner accepted a position as an assistant professor at Princeton University where he spent the duration of his career and where today he is a Professor Emeritus. The first student to obtain his doctorate with Bonner was David Stadler, who went on to a successful career at the University of Washington. Although his lab began with students working on other lower organisms, it quickly became a slime mold lab. This concentration helped lead to a number of exciting discoveries including thermotaxis, which was not confirmed until the 1970s, the mobility of individual cells within the migrating slug, and the role of repelling gases in the slime mold life cycle. Bonner was the Chairman or Acting Chairman of the department of biology during the periods 1965-1977; 1983-1984; and 1987-1988. His long and rich career as a researcher and administrator continues to help bring many changes to biology, especially with the growth of molecular biology and genetics.

During his career Bonner took a number of sabbaticals to Edinburgh, Scotland to focus on writing. In addition to producing over 160 articles in peer reviewed journals, Bonner is also an accomplished author of widely-accessible books. He described the publication of his first book, *Morphogenesis: An Essay On Development* in 1952, as one of his greatest accomplishments. He was pleased and relieved when his ideas were well received, for his agenda in *Morphogenesis* was ambitious: to provide an overview of the most important aspects of development, across a wide range of species, and to search for shared developmental mechanisms. A gifted writer with a talent for synthesizing material and making the big picture clear, Bonner further developed ideas about evolution and development in a number of books, including: *Cells and Societies* (1955); *The Evolution of Development* (1958); *The Cellular Slime Molds* (1959); *The Ideas of Biology* (1962); *Size and Cycle* (1965); *The Scale of Nature* (1969); *On Development: The Biology of Form* (1974); *The Evolution of Culture in Animals* (1980); *The Evolution of Complexity* (1988); *Researches on Cellular Slime Moulds* (1991); *Life Cycles: Reflections of an Evolutionary Biologist* (1992); *Sixty Years of Biology: Essays on Evolution and Development* (1996); *First Signals: The Evolution of Multicellular Development* (2000); *Lives of a Biologist: Adventures in a Century of Extraordinary Science* (2002); *Why Size Matters: from bacteria to blue whales* (2006) . He also edited and abridged a version of D'Arcy Thompson's *Growth and Form* (1961).

For his accomplishments Bonner has received many awards, including Fellow, American Academy of Arts and Sciences (1969); Member, American Philosophical Society (1972); Member, National Academy of Sciences (1973); Fellow, American Association of the Advancement of Science (1981); DSc Middlebury College (1970); LLD Concordia University (2003). Bonner is also an Honorary Fellow, Indian Academy of Sciences (1992) since he spent time as a Raman Professor at the Indian Academy of Sciences (1990) and as a visiting professor at the Jawaharal Nehru Centre for Advanced Scientific Research (1993). Bonner was awarded an honorary D Litt from the University College of Cape Breton (2004) where he has spent many summers writing and fishing at his home in Margaree Harbour, Cape Breton, Nova Scotia.

Bonner's highly readable and unusually clear written contributions have made many complicated ideas of biology accessible to a wide audience. His long and rich career as a researcher and administrator continues to help bring many changes to biology, especially with the growth of molecular biology and genetics. He has dedicated his career to studying the life cycle of slime molds and as a result has informed many key questions in evolution and development and helped to create an

extensive international community of slime mold researchers. When Bonner first starting working with cellular slime molds there were only two people in the field; today there are hundreds who study these creatures. In fact Dictyostelium is recognized as a model organism by the National Institutes of Health and therefore has a significant amount of resources committed to its development as a research organism for the biomedical sciences.

Sources

1. Bonner, John Tyler. An Extract from "Memoirs for Family and Friends." *Genetics* 150 (1998): 519-21.
2. Bonner, John Tyler. *Lives of a Biologist*. Cambridge: Harvard University Press, 2002.