NATIONAL ACADEMY OF SCIENCES

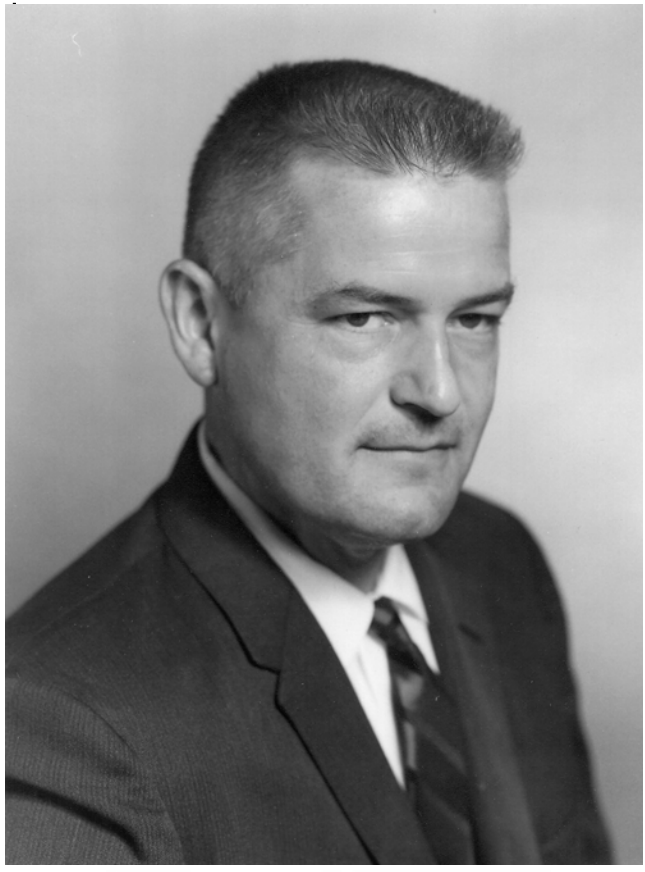
DAVID MAHLON BONNER
1916–1964

A Biographical Memoir by

MAARTEN J. CHRISPEELS

Biographical Memoirs, VOLUME 88

PUBLISHED 2006
NATIONAL ACADEMY OF SCIENCES
WASHINGTON, D.C.



David Bonner

DAVID MAHLON BONNER

May 15, 1916—May 2, 1964

BY MAARTEN J. CHRISPEELS

DAVID MAHLON BONNER'S short scientific career—he died at the age of 48—spanned the bloom period of *Neurospora* biochemical genetics and he was one of its main practitioners and contributors. He started life as a plant physiologist and became a biochemical geneticist working with *Neurospora crassa* after joining the group of George Beadle and Edward Tatum as a postdoctoral researcher at Stanford University. Initially he explored the use of *Neurospora* for biochemical investigations and identified intermediary steps in biochemical pathways. Finding that mutations that affect one enzyme are located on the same small segment of genetic material, he provided support for the "one gene, one enzyme" theory proposed by Beadle and Tatum in 1941. The nature of the genetic unit fascinated him: Was a genetic unit simple or complex? By analyzing 25 different mutants altered at the *td* (tryptophan desmolase) locus and a number of *td* revertants, he came to the conclusion that the genetic material controlling the formation of one enzyme represents a genetically indivisible unit, but admitted that (in 1955) it was still too early to decide whether this conclusion was fantasy or fact. His research group also found mutations that appeared to affect the rate at which an en-

zyme is formed, rather than its structure, and work by them and others then led to the realization that enzyme formation is regulated by repressors. After going to Yale (with Tatum) in 1942 he advanced through the ranks and became a professor of microbiology at the School of Medicine. In 1960 he was lured to San Diego to become the founding chair of the Department of Biology at the then newly established University of California, San Diego (UCSD). He had the major role in setting the direction of that department and in formulating a novel plan for integrating the teaching of the basic sciences into the curriculum of the new School of Medicine.

FAMILY MATTERS AND THE SOURCES OF HIS INSPIRATION

David Bonner was born on May 15, 1916, in Salt Lake City, Utah, the fourth child in a large family with seven children. His father, Walter D. Bonner, was head of the chemistry department at the University of Utah. His mother, Grace Gaylord, also studied chemistry at Nebraska Wesleyan University, where they were classmates, and graduated in 1906. She briefly taught chemistry at the secondary level. The family moved to Utah from Kingston, Ontario, the year before David was born. The Bonner siblings in addition to David were James (b. 1910), Lyman (b. 1912), Priscilla (b. 1914), Robert (b. 1917), Walter (b. 1919), and Francis (b. 1921). Five of the children received doctoral degrees; four of them became biochemists, two became physical chemists, and one (Robert) became an applied mathematician and computer specialist. The family lived in a semirural environment on the outskirts of Salt Lake City. These surroundings were chosen by the parents so the children could have the opportunity to experience the rewards of gardening and work in an agricultural setting. The homestead included a fully developed 2-acre orchard, and the respon-

sibility for managing, maintaining, harvesting, and marketing fell to each of the boys in succession. Spraying of orchards was still done with lead arsenate in those days. Profits from the enterprise were applied to college tuitions. According to their brother Francis, it is likely that this intense agriculture experience influenced first James and then David and also Walter to become plant biologists. One might assume that a large family in Salt Lake City would be affiliated with the Mormon Church, but this was never the case. (All the details about family life were kindly supplied by Francis T. Bonner, the youngest brother.)

In 1929, when Dave was 13 years old, his father took a sabbatical leave at the California Institute of Technology in Pasadena. James and Lyman, the two older sons attended Caltech with tuition scholarships. It was an exciting time for the family because of the close contact with renowned Caltech scholars. For example, brother James was a research assistant for Theodosius Dobzhansky during the family's year in Pasadena. After returning to Salt Lake City and graduating from high school, David majored in chemistry at the University of Utah and received his honors A.B. degree in 1936. For his doctoral work he followed in the footsteps of his brothers James and Lyman who both obtained Ph.D.s from Caltech. Just as Dave moved to Caltech for graduate work, his brother James became a biology instructor there after spending a year abroad. A year after receiving his Ph.D. at Caltech, on August 2, 1941, Dave married Miriam Thatcher. Many years later they had two sons, Matthew (b. 1956) and Nicholas (b. 1958). Nicholas was afflicted with cerebral palsy and needed crutches to get around, but Dave and Miriam treated him like any other child.

DAVID AS PLANT PHYSIOLOGIST

In the late 1930s and early 1940s the Caltech Division of Biology was a hotbed not only for *Drosophila* genetics but also for plant physiology, having attracted several famous European plant biologists, including the Dutchmen Herman E. Dolk, Fritz W. Went, and Arie J. Haagen-Smit. Working in the Netherlands, Went had discovered the first plant growth hormone, which he named auxin. The Caltech group of plant physiologists, including Kenneth V. Thimann, was trying to find the chemical identity of auxin. They isolated indole-acetic acid from human urine and showed that it had auxin activity in the *Avena* coleoptile elongation test. Factors (chemicals) that affect the growth of plants either in situ or in vitro (organ culture) were then a major field of research. David Bonner's Ph.D. thesis with Arie Haagen-Smit dealt with leaf growth factors. He found that "adenine in the presence of potassium nitrate largely replaces the effect of crude pea diffusate in promoting leaf growth in excised pea embryos and in immature excised leaves. Adenine too exerts a marked positive effect upon the vegetative growth of plants in sand culture. . . . Adenine should, therefore, be included in the list of phytohormones." Much later, adenine derivatives called cytokinins were found to be plant growth hormones in the laboratory of Folke Skoog.

Between 1937 and 1943 David Bonner published a number of articles (I found at least seven) dealing with various plant growth factors. A paper by David as sole author, published in 1937 in *The Botanical Gazette,* was entitled "Activity of the Potassium Salt of Indole-Acetic Acid in the Avena Test."[1] In 1938 he published an article with his brother James that dealt with the effect of ascorbic acid on the growth of excised pea embryos.[2] After completing his Ph.D. in 1940, David was appointed as a research assistant at Caltech,

and during this time he continued his work on plant growth factors.

David greatly enjoyed the out-of-doors and went on numerous outings, taking full advantage of the proximity of the Sierra Nevada and the Pacific Ocean. Fred Addicott, James Bonner's first graduate student, recalled a two-week camping trip with the two Bonner brothers (David and James) where David learned the fine points of trout fishing.

FROM NUTRITIONAL GROWTH FACTORS IN PLANTS TO AUXOTROPHIC MUTANTS IN *NEUROSPORA*

David is best known for his work on the chemical genetics of the bread mold *Neurospora crassa.* The switch from plants to molds occurred in 1942 when he became a research associate at Stanford University in the integrated research group of George Beadle, a geneticist who was then professor of biology, and Edward Tatum, a biochemist who had been a research associate and had just become an assistant professor. At Stanford, Beadle and Tatum were exploring the relationship between genes and metabolism. From 1937 to 1941 they concentrated on the biosynthesis of eye pigments in *Drosophila melanogaster.* Beadle visited Haagen-Smit's lab (where David was a Ph.D. student) to learn microchemical techniques to isolate and characterize chemical substances.[3] In 1941, as a result of a course on the nutrition of yeasts and fungi that Tatum had organized at Stanford, the group also started working on *Neurospora.* It had been shown that *Neurospora* could be grown on a defined medium and only required biotin. They used X-ray-irradiation-induced mutants of *Neurospora* that had specific nutritional deficiencies (auxotrophic mutants) to identify the genes associated with specific metabolic enzymes. In a landmark paper published in 1941[4] they showed that each nutritional deficiency was associated with a mutation in a

single gene. George Beadle gave a memorable seminar about this work at Caltech.[5]

When David Bonner joined the group in 1942 it was but a small step to go from nutritional growth factors in plants to growth requirements of auxotrophic mutants in *Neurospora* and from indole acetic acid (a tryptophan derivative) in plants to tryptophan synthesis in *Neurospora* (1944). David also studied mutants of *Neurospora* requiring choline, isoleucine, valine, and anthranilic acid and in 1945 the group summarized its findings in a review article that was published in the *American Naturalist*.[6] They showed that their analysis of mutants made it possible to describe biosynthetic pathways. By all accounts these were exciting times for the Stanford research group: They were breaking new ground in understanding the connection between the genetic material and metabolism or biochemistry. In 1958 George Beadle and Edward Tatum shared the Nobel Prize in physiology or medicine with Joshua Lederberg. They were cited for their discovery that "genes act by regulating chemical events," work to which David Bonner contributed substantially while at Stanford. At Stanford, David was also engaged in isolating strains of *Penicillium notatum* that overproduce penicillin; this was a major project in the Beadle and Tatum group and was their contribution to the national war effort.

GOING TO YALE UNIVERSITY.

In 1945 Edward Tatum accepted an appointment at Yale University in the newly named Department of Botany and Microbiology. Apparently, Edmund Sinnott, the chair of the Department of Botany and dean of the Graduate School at Yale at the time Tatum was hired, had the department's name changed to Botany and Microbiology to be welcoming to Tatum. David Bonner was appointed as a research associate in Tatum's group in 1946. A year later he became

an associate professor in microbiology in the Medical School and the Graduate School. At Yale he continued his research on *Neurospora* mutants, exploring nicotinamide and nicotinic acid mutants. A talk presented at the "Symposium on Genes and Cytoplasm" held in Washington, D.C., during the centennial celebration of the American Academy of Arts and Sciences and published in *Science* (1948) chronicled the advances that had been made up to that point: (1) mutations were inherited as single genes; (2) mutants could be grouped in biochemical classes leading to the understanding of pathways; (3) mutants were available for the seven chromosomes of *Neurospora* (The chromosome number was determined by Barbara McClintock who later received the Nobel Prize for her work on transposons in maize.); and (4) extracts of some mutants could be shown to lack a specific activity, such as splitting lactose into galactose and glucose, or joining serine and indole to make tryptophan. These advances supported the one gene, one enzyme postulate, but instances in which several independent genes were shown to affect a single enzyme were troubling to the investigators.

BUILDING A RESEARCH GROUP AT YALE

In 1948 Ed Tatum returned to Stanford University and left Dave in charge of what remained of his research group, providing Dave with the opportunity to build his own group. In the late 1940s it was not yet known that the genetic material was DNA. Yanofsky recalled that Dave was committed to find "*the* best system" to understand the gene-enzyme relationship. Several young people soon joined his lab, including Otto Landman, Naomi Franklin, Gabriel Lester, William Jacoby, André Jagendorf, Elga Wasserman, and Charles Yanofsky. According to his own account[7], Yanofsky had applied both to Caltech to work with Beadle and to

Yale to work with Tatum. He ended up working with neither, because he was turned down by Caltech, and although admitted to Yale, Tatum had returned to Stanford. He decided to work with Bonner, who gave him the task of identifying the intermediates in niacin biosynthesis. This work led to the identification of quinolinic acid and verification of kynurenine as biosynthetic intermediates because they accumulated in different auxotrophic mutants. Using indole labeled with ^{15}N, Elga Wasserman showed that this was converted to niacin in a niacin auxotroph. Other studies by Chester Partridge in the lab showed the conversion of ^{15}N tryptophan to niacin. Since niacin is an important vitamin, they also explored the utilization of niacin by rats. For this body of work on the biosynthesis of niacin and the interrelationship between tryptophan and niacin, David Bonner received the Eli Lilly Award in Biological Chemistry in 1952. Shortly afterward *Chemical and Engineering News* did a special feature on David and his research. These were happy times for the Bonner group.

Much of the lab at this time was devoted to the further exploration of the one gene, one enzyme hypothesis. Some in the group were working on α-galactosidase in *Neurospora* (Otto Landman and Naomi Franklin), and Gabriel Lester worked on the same enzyme in *E. coli*. They were all looking for the best system. However, what was lacking to make real progress was an assay for a specific enzyme catalyzing a specific biochemical reaction postulated to occur on the basis of genetic analyses. In the third year of his dissertation research Charley Yanofsky turned his attention to tryptophan desmolase (now called tryptophan synthase), the enzyme that catalyzes the coupling of L-serine with indole to form L-tryptophan. An assay for this enzyme had been developed in the laboratory of W. W. Umbreit, and Yanofsky showed that two tryptophan-requiring mutants that

could not use indole for growth lacked this enzyme activity. This discovery energized the entire Bonner lab to look for other mutants at this locus (*td*). Use of these mutants allowed them to show that all mutations inactivating this single enzyme appeared to be located in the same gene or genetic segment.[8] Joseph A. Roper had made the same discovery in *Aspergillus nidulans* at the same time.[9]

André Jagendorf, who joined the group as a graduate student in 1948, did the last work on plants with which Dave's name is associated. However, Dave was principally immersed in biochemical genetics of *Neurospora*, and most of Jagendorf's guidance on a project involving the effect of the synthetic auxin 2,4-D on root growth in cabbage seedlings came from Aubrey Naylor, then a young faculty member at Yale.

LIFE'S PLEASURES AND PAINS

In Connecticut David and Miriam lived out in the country, first in Woodbridge and later in Bethany, a small town of 3,000 people, where they purchased the house built by Henry and Mary ("Polly") Bunting. The house, long located on a dirt road, was a favorite gathering place of the grad students to play croquet and have barbecues. There was an apple orchard and small animals. André Jagendorf recalled that the Bonners kept two "bovines" named Porterhouse and Sirloin. Undoubtedly, David who thought of himself as a country boy, wanted to recreate the atmosphere of his own youth in Utah, when as a boy, he had been in charge of a cow on his parents little farm. It was always open-house at the Bonner home.

Miriam was not only a welcoming hostess but also the no-nonsense presence in Dave's lab. She was in charge of the *Neurospora* crosses and of the culture collection and coordinated the work of several other technicians, includ-

ing Carol Yanofsky, Charley's wife. Grad students came back to the lab most evenings to hand-wash the dishes and discuss science. A large sign over the front door proclaimed it to be the Bonner Institute of Fundamental Research. A major advantage of being a student in this lab was that the congeniality of the group was accompanied by serious but lively discussions of scientific issues. Dave took a personal interest in every student and in every project.

David had no formal training in genetics because he had studied chemistry at the University of Utah and later worked with chemists (Haagen-Smit, a chemist, was his Ph.D. advisor and Tatum was a biochemist). According to his own account, his understanding of genetics greatly profited from his interactions with Lewis J. Stadler, the renowned maize geneticist, who spent a sabbatical semester in the Bonner lab in 1950.

In 1952 David was diagnosed with Hodgkin's lymphoma and to get the needed treatment (first surgery and then periodic radiation therapy) he would have to travel to New York and elsewhere. The disease was then considered incurable, and he managed to keep the disease at bay for 13 years until the side effects of the massive radiation therapy finally took their toll in 1964 and he died. His doctors initially predicted that he could last at most five years. According to his friends, he lived life as if he were immortal, even riding his motorcycle after his radiation treatment caused him to develop a tendency to bleeding. As the years went by and David survived, they began to believe their own wishes, and his death came as a great shock. Following David's death in 1964, Miriam Bonner and her two sons moved to Stanford University, where she worked in the laboratory of Charley Yanofsky as a laboratory assistant until her retirement.

CROSS-REACTING MATERIAL

An examination of suppressor mutations of *td* mutants showed that they were allele-specific. Most suppressor mutations only restored enzyme activity when they were combined with the respective *td* mutant allele. The group at the Institut Pasteur had started to use an antiserum against α-galactosidase as a tool to understand gene activity and this prompted Sigmund Suskind, a grad student in the Bonner lab to explore the possibility of making an antiserum against tryptophan desmolase partially purified by Yanofsky. In 1953 the Bonner group moved from the Osborn botanical laboratory to Brady Hall (a Medical School building), and this permitted greater interaction with the immunochemists housed there. Peter Treffers, an immunochemist, was chair of the Microbiology Department, and the Bonner lab grad students interacted with grad students like Stanley Mills who were using immunochemical techniques. Antibodies against enzymes were then known as antienzymes. After graduating in 1954, Sig Suskind became a postdoc in the immunology laboratory of A. M Pappenheimer at New York University, where he continued to collaborate with Charley Yanofsky and the Bonner group. The immunochemical approach opened the way to find out whether mutants that lacked enzyme activity might nevertheless contain inactive protein as shown by the presence of cross-reacting material (which they called CRM). All the suppressible mutants were shown to be CRM-positive and the nonsuppressible ones were shown to be CRM-negative (1955). This work led to the conclusion that the genetic unit may be more complex than anticipated and may be composed of genetically separable subunits. Bonner presented this view in a tightly argued paper (1956) entitled "The Genetic Unit" at the 1955 Cold Spring Harbor Symposium. He wrote: "We have an increas-

ing number of facts with which to work and from these facts each of us enjoys a number of fantasies. At present, however, neither facts nor fantasies give rigorous proof of the nature of the genetic unit nor its action." (1956, pp. 163-170).

Meanwhile, the group worked on the biochemistry of tryptophan synthetase (subsequently renamed tryptophan synthase) as the enzyme became known around that time. However, Charley Yanofsky, who had moved to Case Western Reserve University School of Medicine in 1954, was now a friendly competitor rather than a valued collaborator. Yanofsky had decided to study tryptophan synthetase in *E. coli,* and *E coli* extracts were found to catalyze three reactions: the reversible hydrolysis of indole-3-glycerol phosphate to indole and triose phosphate; the condensation of indole and serine to form tryptophan; and the overall reaction, the conversion of indole-3-glycerol phosphate (InGP) and serine to form tryptophan. These findings suggested that the reaction proceeded in two steps: conversion of InGP to indole and condensation of indole and serine to form tryptophan; and *E. coli* was found to have a separate enzyme for each step. The Bonner lab applied these biochemical findings to *Neurospora* and showed that in this organism both steps were catalyzed by the same enzyme (1959). The use of sera to detect CRM led much later—after Bonner had moved to San Diego—to fine mapping of the antigenic sites of the enzyme and an understanding that mutations can affect the structure of an enzyme in different ways. David Bonner's contributions to our understanding of gene structure and function resulting from his work on the biochemical genetics of *Neurospora* were recognized in 1958 by his election to the American Academy of Arts and Sciences and in 1959 by his election to the National Academy

of Sciences. Charles Yanofsky was elected to the National Academy of Sciences in 1966.

A SQUARE PEG IN A ROUND HOLE

David Bonner's style was not exactly a good fit for an Ivy League school. He was not only outspoken in his views but he could also be loud and outrageous. His attire (khakis or jeans) and his favorite mode of transport (a motorcycle)—typical of the rough and tumble West where he grew up—were not in keeping with the decorum expected of Yale faculty. No doubt many Yalies did not care for his persona. Dave was variously described as "straight talking," "irreverent," and "speaking his own version of the English language, laced with strong verbals." Some may have been put off by this straight-talking cowboy, but David had many close friends as well, and he inspired much affection and loyalty among the people to whom he was close. In 1953 space became available in Brady Hall, a building on the school of medicine campus, and the group moved there. It is likely that this move was facilitated by Henry Bunting, a medical faculty member who was one of David's closest friends. In 1956 David was promoted to full professor in the Medical School and the Graduate School.

According to Stanley Mills, a graduate student with Peter Treffers in the Microbiology Department in the mid-1950s, Dave's status at Yale was a subject of discussion and speculation among the students. He had the biggest and most active lab in the Microbiology Department, he had all the prerogatives of a professor, but he was said not to be "on the tenure track." Dave's not being on the tenure track is one of the most pervasive myths I have encountered in writing this memoir. According to Yale records, Dave's appointment was in the Medical School and the Graduate School. After he was appointed to full professor, it was an

"appointment without term," meaning that it was a tenured appointment. However, appointments in the Medical School were different from appointments in Yale College (liberal arts and sciences); Medical School appointees were not automatically allowed to teach Yale undergraduates. Around 1958 Dave told several colleagues that he saw no future for himself at Yale and started looking for other positions. Henry Bunting's sudden and tragic death may have contributed to his gloomier outlook at that moment in his life. David's Hodgkin's disease appeared to be in remission, but he had an insurance policy at Yale that he could not afford to give up. A move depended on the new institution's willingness to pick up the policy.

At about that time the head of the Oak Ridge National Laboratory offered David the opportunity to come to Oak Ridge to pursue his research with abundant and secure research support. David invited Charley Yanofsky and Gabe Lester to move with him. They all went to Oak Ridge to scout out the possibilities. The Biology Division at Oak Ridge was located within the most secure area of the national laboratory and working there required Q-level security clearance. On the basis of an FBI investigation, David was told that questions had been raised about his "fitness" to obtain a clearance. A number of "charges" were listed, the most serious of which resulted from an "incident" in a Spanish language class that David and several other Yale faculty attended. Asked to make a controversial statement in Spanish so the class could discuss it, David stated that the United States had invaded North Korea. This is exactly what the North Koreans and Chinese were claiming as their excuse for invading South Korea. We can only speculate that someone in the class had passed this information to the FBI in a malevolent spirit. Dave fought the charges and after George Beadle testified on his behalf, the charges were eventually

dropped. After this experience he lost interest in going to Oak Ridge but also did not see his own future at Yale.

THE CALL OF THE WEST COAST

In the 1950s the administration of Governor Pat Brown decided to add three new campuses to the University of California system as part of the new Master Plan for Education for the state. One of these was to be located in the San Diego area. In 1960 Dave accepted an appointment as professor of biology in the School of Science and Engineering at the newly created University of California, San Diego (then still—and only briefly—called the University of California in La Jolla). David, who had always abhorred administrative duties, was now charged with the challenging tasks of setting up not only a new Department of Biology but also becoming the unofficial acting dean to initiate a new school of medicine at UCSD, and to play a key role in the choice of founding faculty in the planned social sciences and humanities departments on campus. His enthusiasm was unbounded. At the invitation of Roger Revelle, Dave moved his entire lab to La Jolla and invited several colleagues from Yale to come along, including S. Jonathan Singer of the Department of Chemistry. Together with other former or present Yale grad students or postdocs like Stanley Mills and Jack DeMoss they would nucleate the new department. What attracted these Yale scholars and other Ivy Leaguers to come Out West was "the youthful vigor of the new campus and the clear dedication of its leaders to the long-term development of an uncompromisingly first-rate institution," according to S. J. Singer. Dave and the others were attracted by Revelle's concept of "building from the top down," meaning that Revelle would hire department chairs, who would have a free hand to appoint faculty, who would

bring and attract grad students. This would all have to occur before the first undergraduates showed up on campus.

It was a wrenching tragedy that David had so few years left to begin all of this work. Nevertheless, he left an indelible mark upon UCSD. Even those who knew him fairly well did not expect him to exhibit such academic administrative skills and extraordinary vision of the future of academic biology and medicine, in contrast to his devil-may-care and free-wheeling approach to everyday matters at Yale.

Having experienced the benefits of an integrated biology department at Stanford and the drawbacks of the fragmentation of biology into different departments at Yale as well as their partitioning between the main campus and the Medical School, Dave saw the opportunity to create "a forward-looking community of scholars, teachers, and students in biology and medicine, unhindered by the dead hand of the past."[10] His vision was that UCSD would have only one group of science departments that would provide the education for all graduate students (Ph.D. and M.D.) as well as undergraduates. There was to be no biochemistry department, but biochemists were to be hired by both the biology and the chemistry departments. The Basic Science Building of the new Medical School housed faculty from the biology, pediatrics, chemistry, medicine, engineering, and surgery departments, all side by side. In addition, Bonner was totally opposed to staffing the Medical School with part-time faculty, whose attention would be diverted by their private practice. This was still the common practice at the University of California medical schools in San Francisco and Los Angeles. Bonner vowed that San Diego would be different and encountered much opposition from the Office of the President of the university. However, in fighting these battles he had the full support of his faculty. In writing about these early years, Robert Hamburger, who had also come from

Yale, noted: "The initial results were astounding and exciting but as with most radical innovations, with time, they tended to drift back toward the 'norm.'" In his four years at UCSD Bonner began the creation of a Department of Biology that emphasized molecular and cellular processes. The department had strong ties to other departments, chemistry for example, and strong ties to the medical faculty.

Research went on as well, although Dave's major effort was in the organization of the campus. In 1961 Prentice Hall published his small paperback *Heredity* in its Foundations of Modern Biology Series. In the lab he had never been a hands-on man, but he was always ready to discuss ideas and experiments with students and postdocs. Certain lifelong traditions continued in La Jolla: camping trips and life in the country. After moving west, David and Miriam bought a home in Sorrento Valley, an area of San Diego that in the early 1960s was rural and yet close to UCSD. Although he was busy, research on the problems close to his heart was carried out in his lab and collaboratively in the labs of two associates he had brought to UCSD: Jack DeMoss and Stanley Mills, who were now UCSD faculty members. In 1961 David spearheaded the organization of the first *Neurospora* conference, which was held in La Jolla with about 100 scientists in attendance.

Soon after the untimely death of this visionary scientist in 1964, UCSD honored him by naming its first biology building after him. "The loss of this uncommon man is a tragedy for his friends, his colleagues in science, and his university associates who knew his intellectual force, his physical vitality, his impatience with sham, his courage, his audacity," wrote his former colleagues in their obituary. "Although rough around the edges, he had a warm personality, was generous, and had a sensitive and liberal nature."

I am indebted to many former associates of David Bonner who contributed details and remembrances: Eliot Meyerowitz, Stanley Mills, Debbie Delmer, Sam Kaplan, Fred Addicott, Sigmund Suskind, Robert Hamburger, S. Jonathan Singer, Elga Wasserman, André Jagendorf, William Loomis, Donald Helinski, Arthur Galston, and Sue Bonner. I am especially grateful to Charles Yanofsky for his careful editorial and substantive corrections. Donna Harris from the provost's office at Yale University verified the employment history. Many details about David's life were supplied by his brother Francis T. Bonner, and some are at variance with the description of the Bonner family in the National Academy of Sciences biographical memoir of James Bonner.

NOTES

1.Bonner, D. M. Activity of the potassium salt of indole (3) acetic acid in the avena test. *Bot. Gaz.* 99 (1937): 408-497.
2.Bonner, D. M. and J. Bonner. On the influence of various growth factors on the growth of green plants. Amer. Journ. Bot 27 (1940): 38-42.
3.For details see J. Lederberg. Edward Lawrie Tatum. In *Biographical Memoirs National Academy of Sciences*, vol. 59, pp. 356-387. Washington, D.C.: National Academy Press, 1990.
4.G. W. Beadle and E. L. Tatum. Genetic control of biochemical reactions in *Neurospora. Proc. Natl. Acad. Sci. U. S. A.* 27(1941):499-506.
5.For details see N. H. Horowitz. George Wells Beadle. In *Biographical Memoirs National Academy of Sciences*, vol. 59, pp. 26-53. Washington, D.C.: National Academy Press, 1990.
6.*Am. Nat.* 79(1945):304-317.
7.*J. Biol. Chem.* 278(2003):10859-10878.
8.*Genetics* 35(1950):655-656.

9.*Nature* 166(1950):956.
10.J. A. DeMoss, S. E. Mills, S. J. Singer, and C. Yanofsky. David Mahlon Bonner. Online. *University of California: In memoriam, April1965*. Available from the online Archive of California; http://ark.cdlib.org/ark:/13030/hb338nb1j4. Accessed November 10, 2005

SELECTED BIBLIOGRAPHY

1938

With A. J. Haagen-Smit. The activity of pure substances in leaf growth. *Proc. Natl. Acad. Sci. U. S. A.* 25:185-188.

1943

With E. L. Tatum. Synthesis of tryptophan from indole and serine by *Neurospora*. *J. Biol. Chem.* 151:349.

1944

With E. L. Tatum. Indole and serine in the biosynthesis and breakdown of tryptophan. *Proc. Natl. Acad. Sci. U. S. A.* 30:30-37.

1946

Biochemical mutations in *Neurospora*. *Cold Spring Harb. Symp. Quant. Biol.* 11:14-24.

1948

Genes as determiners of cellular biochemistry. *Science* 108:735-739.

1949

With C. Yanofsky. Quinolinic acid accumulation in the conversion of 3-hydroxyanthranilic acid to niacin in *Neurospora*. *Proc. Natl. Acad. Sci. U. S. A.* 35:576-581.

1950

With C. Yanofsky. Accumulation of a substance possessing niacin activity by a mutant strain of *Neurospora*. *Fed. Proc.* 9:250.

With C. Yanofsky. Evidence for the participation of kynurenine as a normal intermediate in the biosynthesis of niacin in *Neurospora*. *Proc. Natl. Acad. Sci. U. S. A.* 36:167-176.

1951

With C. Yanofsky. Studies on the conversion of 3-hydroxyanthranilic acid to niacin in *Neurospora*. *J. Biol. Chem.* 190(1):211-218.

Gene-enzyme relationships in *Neurospora*. *Cold Spring Harb. Symp. Quant. Biol.* 16:143-57.

1955

With C. Yanofsky. Gene interaction in tryptophane synthase formation. *Genetics* 40:761-769.

With S. R. Suskind and C. Yanofsky. Allelic strains of *Neurospora* lacking tryptophan synthetase: A preliminary immunochemical characterization. *Proc. Natl. Acad. Sci. U. S. A.* 41:577-582.

1956

The genetic unit. *Cold Spring Harb. Symp. Quant. Biol.* 21:163-170.

1959

With J. A. DeMoss. Studies on normal and genetically altered tryptophan synthetase from *Neurospora crassa*. *Proc. Natl. Acad. Sci. U. S. A.* 45:1405-1412.

1961

With A. M. Lacy. Complementation between alleles of the Td locus in *Neurospora crassa*. *Proc. Natl. Acad. Sci. U. S. A.* 47:72-77.

1962

With H. M. Schulman. A naturally occurring DNA-RNA complex from *Neurospora crassa*. *Proc. Natl. Acad. Sci. U. S. A.* 48:53-63.

1964

With S. Kaplan, S. E. Mills, and S. Ensign. Genetic determination of the antigenic specificity of tryptophan synthetase. *J. Mol. Biol.* 12:801-813.

With S. Kaplan, S. Ensign, and S. E. Mills. Gene products of CRM—Mutants at the TD locus. *Proc. Natl. Acad. Sci. U. S. A.* 51:372-378.

With Y. Suyama and A. M. Lacy. A genetic map of the TD locus of *Neurospora crassa*. *Genetics* 49:135-144.