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DAVID DEXTER PERKINS
1919—2007

A Biographical Memoir by
ROWLAND H. DAVIS

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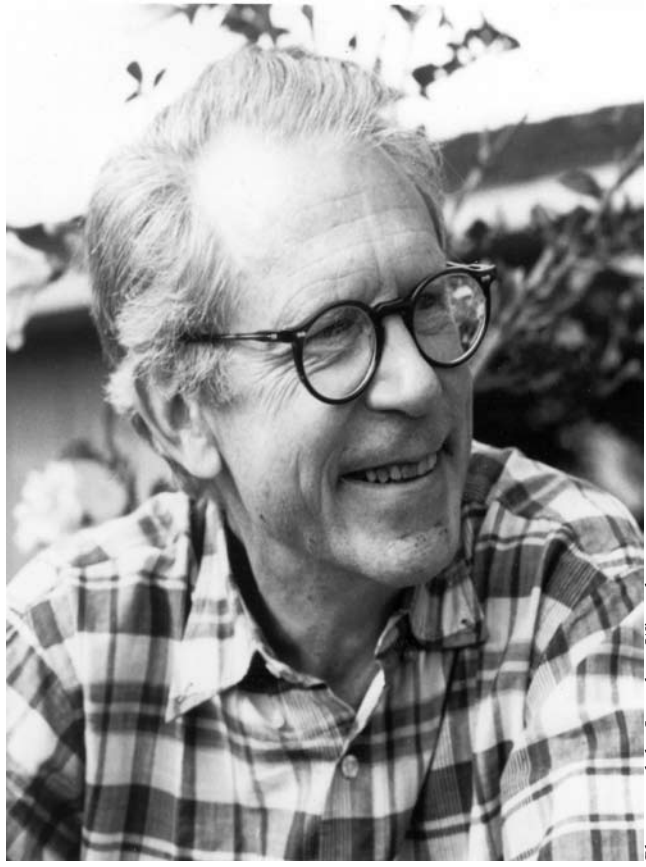
Biographical Memoir



Photograph by Jonathan Wittenberg.

David D. Perkins.

DAVID DEXTER PERKINS

May 2, 1919–January 2, 2007

BY ROWLAND H. DAVIS

DAVID PERKINS HAS A unique place in the history of fungal biology and genetics. His extensive contributions to the field began shortly after Beadle and Tatum presented clear evidence of the relation of genes and enzymes (1941, 1945). They used the filamentous fungus *Neurospora* as their experimental organism. While Beadle and Tatum popularized the use of microorganisms in the molecular revolution that followed, David Perkins assured the continuing status of *Neurospora* as a model organism used for many other types of study (Davis, 2000, 2003; Davis and Perkins, 2002). He did so largely through his extensive studies of its genetics, cytogenetics, population biology, and mating systems. In addition, his laboratory contributed, over a period of 55 years, many new techniques, compendia of all known mutant strains, updated genetic maps, and exchange of information among a global community of *Neurospora* researchers. As Charles Yanofsky said in a recent memorial tribute,[1] "Beadle and Tatum initiated research using this organism, but it was David who made certain that this interest would continue." The new field of fungal genetics and biology originated with the *Neurospora* community, and David can claim perhaps the greatest role in its origin.

PERSONAL HISTORY

David Dexter Perkins was born on May 2, 1919, to Dexter Perkins and Loretta Miller Perkins in Watertown, New York. His formative years were spent in the Great Depression, and his strong family imparted to David qualities of frugality, cooperation, hard work, and the ability to distinguish the important from the unimportant both in life and in science. He received his bachelor's degree at the University of Rochester in 1941. He joined the laboratory of Francis Ryan at Columbia University thereafter. His pacifism made him unwilling initially to join the war effort, but he decided soon that he must do so. David left Columbia to serve in military intelligence in England, studying aerial photos and briefing Air Force crews regarding bombing targets. After the war, he rejoined the Ryan laboratory and received his Ph.D. in 1949. He became a faculty member at Stanford University the same year and remained there for his entire professional life. Although he officially retired in 1989, he continued his laboratory work until his death on January 2, 2007.

David married Dorothy ("Dot") Newmeyer (b. 1922), a student of Edward Tatum, then at Stanford, in 1952. She worked for most of her professional life in David's laboratory and made many scientific contributions, both independently and jointly with David. They had one child, Susan, born in 1956. Dorothy Perkins, in poor health for many years, passed away just four days after David died.

David rode his bicycle to work at least six days a week, arrived before 6:00 a.m., took the stairs to his office even in his 80s, and rested on his back on the floor under his desk at noon daily so he would be fresh for a long afternoon's work. The stability of David's life—working this way at Stanford University for 58 years, married to Dot for 54 years, and dying four days before his wife in 2007—underlay a unique, global impact. David was remembered as much for his per-

sonal integrity, generosity, and outreach to others as he was for his considerable scientific contributions.

Hard-working and modest, David had time for others, listening to their problems, trusting them, and giving back as much as he could to help them. At the memorial website[1] many testimonials from his scientific associates speak to these traits. Alice Schroeder, one of his students, remarks,

> David also understood how to train students. He felt that your professor pointed out interesting projects, advised and critiqued experiments but let you become the expert, making decisions and mistakes that made the project your own and one you could carry with you when you left the lab. . . He hated to see an ounce of scientific ability wasted and understood the pressures that women faced if they were to be scientists and have a whole life.

Robert Lloyd, an underprivileged high-school graduate recruited as an assistant to work in the laboratory, speaks of David's and Dot's generosity:

> I was working and going to Foothill Community College at night, but David suggested I quit work and go to school full time and explained that the economics made more sense that way. I didn't see how that was possible. "We have this money that is just sitting in the bank doing nothing," he said. "You can either repay the loan when you finish your education or you can help someone else." Because of the model Dot and David set for me, I was able to do both. I became an artist and professor of photography.

These anecdotes give an inkling of the way that Dot and David personally influenced generations of students, associates, and members of his scientific community. He remained in contact with everyone who wrote or asked questions of him. He remembered everything, and gave penetrating analyses of others' problems with a sly twinkle in his eyes—never harsh, never demeaning, always helpful. The same sense of community led him, often at Dot's urging, to donate much to civic and political causes, and later to take up political activities, as her frequent illnesses restricted her own.

While I knew David most of my professional life, I got better insight into David's and Dot's lives on my sabbatical in 1985 with Charles Yanofsky, whose laboratory lay across the hall from David's. I lived for the first half of my stay in a spare room in the Perkins's plain house while he traveled in Africa to collect *Neurospora* samples from the wild. In return, I could look after Dot, who was by then in poor health, care for the house and grounds, shop for food, and cook for both of us. It gave me a chance to know Dot's love of music, literature, and I might say, cooking. Our conversations ranged widely, from the mutability of histidine mutants to Bach partitas to *The Jewel in the Crown*, then playing on their black-and-white TV. I felt that she and David would have discussed all these things and more in their normal lives, an intellectual feast for two every night. I also noted that much of their music was on 78-rpm records, under a working turntable and simple amplifier, by that time ready for the Smithsonian—just another sign of the modesty of their personal lives.

David's long letters from Africa, filled with adventure, rivaled in interest most of the science that progressed in his laboratory at the time. The letters were a regular high point in the lab's life while he was gone. He returned, with visible and poignant affection for Dot, and within a day he resumed his lab work. The atmosphere of his lab swelled with bursts of discussion and visitors eager to welcome him back and hear more of his travels. Supremely interruptible, he listened, gave advice, and smiled as he turned back to help his research associate, Barbara Turner, sort his vast collection of African *Neurospora* samples.

At this time Charley Yanofsky, long immersed in the molecular biology of bacteria, had by then returned in part to studying the molecular biology of *Neurospora*. He had

gathered a stable of students, postdoctoral fellows, and visitors like me. The two laboratories joined in a scientific and social collaboration that lasted for years, with regular lunches and coffee hours for all who could attend. David's invariant peanut-butter sandwiches at lunch and Charley's invariant cookies and cakes at 4:00 accompanied some of the most valuable modern crosstalk in the history of *Neurospora* biology. Molecular biologists learned the arcana of *Neurospora* genetics and microbiological techniques from David, and the Perkins laboratory collaborated on molecular biological research for the first time. This union of laboratories assured the renaissance of *Neurospora* research that culminated in the organism being the first filamentous fungus to have its entire genome sequenced. It remains a model for this group of organisms for that reason, and David can take no small credit for that.

SCIENTIFIC CONTRIBUTIONS

FORMAL GENETICS AND CYTOGENETICS OF NEUROSPORA

Three species of the filamentous fungus *Neurospora* were described after the discovery of the sexual phase of these organisms (Shear and Dodge, 1927). They belong to the group known as Ascomycetes. As in most fungi, their tube-like cells (hyphae) grow at their tips, branch extensively, and continuously fuse to make a reticulated mycelium. The cells contain many haploid nuclei in a common cytoplasm. Matings take place only between mycelia of opposite mating types (*mat A* and *mat a*), and the life cycle is completed by fusion, within a fruiting body, of two haploid nuclei, followed immediately by the two sexual divisions (meiosis) of the diploid nucleus. Meiosis yields the four haploid nuclei. In all three species the four products divide again to form

eight nuclei. In two species, *N. crassa* and *N. sitophila*, each of the eight nuclei is enclosed in a single spore; in the third species, *N. tetrasperma*, two nuclei of opposite mating type are included in each of four spores, rendering the spores and the mycelium derived from them self-fertile. Thus in these organisms all the products of a single meiotic process are recoverable as ascospores in a single ascus.

Dodge, after working on the sexual cytology and patterns of segregation of the mating-type genes, recognized the potential of *Neurospora* for genetic research, and encouraged others to use the organism in their genetic research. By the time Beadle and Tatum were ready to seek a simple organism for their biochemical studies, Carl Lindegren had domesticated *N. crassa* and *N. sitophila* for laboratory work, having developed standard strains, some morphological and color mutants, and a first linkage map of one chromosome of the organism (Lindegren, 1936).

The novel ability to study genetic segregation and recombination in single meiotic cells (the asci) of a simple organism was an extremely attractive opportunity for geneticists at the time. David Perkins was by then at Stanford, where Beadle and Tatum had done their first *Neurospora* work (Beadle had left Stanford for Caltech in 1946). David devoted himself to intense genetic studies of *N. crassa*, because this organism, at the heart of the tidal wave research started by Beadle and Tatum, had to be fully characterized genetically. In doing so he not only proved that *Neurospora* obeyed all the rules of genetics of higher organisms, he also greatly extended studies of chromosome interference (1954), cytogenetics (1977, 1997), the cytology of the sexual system (Raju, 1992), and made linkage maps of all mutants he could obtain from most other *Neurospora* laboratories (1982). *Neurospora* soon rivaled corn, *Drosophila*, and the mouse in the number of known genetic loci. Outside of yeast it remains genetically

the best-known microorganism among eukaryotes (organisms with true nuclei).

Most mutant strains from the Beadle-Tatum era had been derived from X-ray and ultraviolet mutagenesis. These treatments often cause chromosomal breakage. David therefore discovered many chromosomal rearrangements of *Neurospora's* seven chromosomes during his gene-mapping studies. Strains carrying aberrations yielded characteristic patterns of ascospore abortion in crosses. These patterns were easily visible under a dissection microscope, and David constructed new and valuable strains for future experimental use (Kasbekar, 2007). These chromosomally aberrant strains could be used as experimental tools with little training by the increasing numbers of biochemists entering the field of biochemical genetics. For example, David developed a widely used strain called *alcoy* for quick mapping studies (1969). The strain had visible mutations (albino, colonial, and yellow), marking three compound chromosomes (arising as reciprocal translocations). When *alcoy* is crossed to a normal strain with a new mutation, the compound chromosome on which the new mutation lay could be determined by its linkage to one of the visible markers. Only one or two follow-up crosses would be needed to reveal the location of the mutation more precisely.

The work described above, to which Dot Perkins contributed continually, underlay the rapid progress in the field of biochemical genetics of fungi in laboratories around the world. In the 1950s another fungus, *Aspergillus nidulans*, took its place beside *Neurospora* as a model organism for genetic and biochemical study, owing to the work of Guido Pontecorvo and his group (Pontecorvo et al., 1953). David, who spent a sabbatical with Pontecorvo in the early 1950s, effectively urged cooperation between the two communities, which maintained increasing contact thereafter.

Bacterial and bacteriophage genetics began with the discovery of recombination in *Escherichia coli* (Lederberg and Tatum, 1946) and developed explosively after the discovery of the structure of DNA in 1953. These milestones diverted attention from the maturing field of fungal biochemical genetics. Although work on *Neurospora* continued vigorously, the number of laboratories working with the organism remained fairly small. But by that time the community was loyal to *Neurospora,* bound in part by the standard techniques and strains propagated by David's laboratory. Even in the 1950s the Fungal Genetics Stock Center had been established. The annual *Neurospora Newsletter* began in 1961, as did the biennial *Neurospora* information conferences. David, with Raymond Barratt and others, published the first compendium of *N. crassa* mutants, genetic maps, and descriptions of the variety of different mutations (multiple alleles) of well-known genetic loci (1954). He updated this compendium twice thereafter (1982, 2001), the last appearing as a book. These resources were invaluable to the *Neurospora* community over half a century.

David's greatest personal contribution in those years was his insistence on communication, lack of competition, sharing of resources, and regular, widely distributed reports of new techniques and strains for use by others. Beyond *Aspergillus* and several genera of mushrooms, the genetics of other fungi was in a primitive state. *Neurospora* thereby became recognized as a model organism through the use of mutational analysis of attributes well beyond biochemical pathways, ranging from sexual biology, cell-to-cell recognition, mitochondrial biogenesis, circadian rhythms, population genetics, gene regulation, and development (Davis, 2000). *Neurospora* studies were sufficiently mature by 1975 that the field could attract new students in the face of the understandable attraction of the single-celled yeast *Saccharomyces cerevisiae* (often called

the eukaryotic *E. coli*) as it became domesticated for studies of biochemistry, metabolic regulation, recombination, and cell division after 1970. Without David's central role in tending *Neurospora* as a public garden of resources, the organism would almost certainly not have survived to contribute as it has in the molecular era.

POPULATION GENETICS AND EVOLUTION

We may ask whether *Neurospora* simply followed the trends now set by the technically more accessible organisms *E. coli* and *S. cerevisiae* after 1970. Most of the *Neurospora* community understandably pursued research programs that had few counterparts in bacteria or yeast. David, while maintaining his formal genetic and cytogenetic studies, began a large-scale, global collection of wild-type strains of *Neurospora spp.* in collaboration with his long-time research associate, Barbara Turner (1976). In his extensive travels and from his trusted colleagues in the United States and abroad, he gathered over 5000 samples of all conidiating species of the genus. His intent was to study the genetic diversity of the genus in terms of population genetics and evolution. The questions to be answered were whether the multiple samples from individual areas were genetically diverse, indicating largely sexual propagation, or whether they were clonal, propagated asexually after a few ascospores established a primary population. The question was biologically interesting, because conidia, the asexual spores, appeared in abundance after fires, readily recognizable as powdery orange tufts on scorched and fire-killed vegetation. In addition, almost no one had observed the sexual stage of the organisms (the perithecia that produce ascospores) in nature. Soon it became obvious that the species of the genus maintained their presence over time largely by sexual reproduction. Even in limited areas the individual colonies collected after the fires were genetically different,

as shown by their different mating types, incompatibility genes, and isozymes (1988). Moreover, the genetic diversity in small geographical areas was comparable to samples of the worldwide collection (Speith, 1975).

The second question about where sexual reproduction took place was harder to answer, but was answered eventually: the vegetative phase (mycelium) grew under the bark of trees or hidden in plant remains, where mycelia of different origin and mating type could complete the sexual phase cryptically, producing ascospores that would remain dormant for many years until activated by fire or chemical derivatives of plant decay (Pandit and Maheshwari, 1996).

The third question was the relation of one species to another. Were they variants of a single, global species, or were the species originally described truly isolated reproductively from one another? The latter was shown to be the case; so much so that fertility became a highly dependable criterion of species identity. Indeed, this led to the discovery of a new species, *N. discreta* (1986). These population studies set the stage for many genetic and evolutionary investigations, first of the productiveness of interspecies matings; then of the comparative molecular attributes of mating-type genes; then the role of incompatibility genes that limit asexual fusions of mycelia; and finally of the relatedness and probable diversification of the different species from a common ancestor. David's collections and basic work with global collections generated a host of research programs that continue vigorously to this day (e.g., Dettmann et al., 2003).

A fourth project tied in with his genetic studies, namely the discovery, with Turner, of a spore-killer trait (Sk^K is the active form) in *N. sitophila* and *N. intermedia* (1979). This chromosomal factor, carried by some strains, leads to the death, after killer × sensitive matings ($Sk^K \times Sk^S$), of the sexual spores that do not carry the Sk^K factor. This is a meiotic drive

element comparable to those in *Drosophila* and the mouse that distorts segregation ratios and blocks recombination over a large portion of the chromosome carrying it. Despite 30 years' work on this factor (Raju, 2007), its molecular nature and its mechanism of action, now being pursued by others, are still quite obscure. David was greatly disappointed that it was not, by the time of his death, more fully understood (D. J. Jacobson, personal communication).

CYTOLOGY OF THE SEXUAL PROCESS.

For many years David collected variant strains of all kinds. Many of these affected the sexual process, either in the success of matings or in the morphology of sexual structures and their products. With this collection David and long-term research associate Namboori Raju were afforded an opportunity to analyze the genetics of the steps of the mating process, from the origin of the female fruiting structure to the formation and shape of ascospores. The sexual process is now one of the best-known series of events subjected to cytological studies in any fungus (Raju, 1992). But just as important are the fruits of this knowledge in other studies. Among these was the discovery that if DNA-carrying genes indispensable for the meiotic remains unpaired with its homolog during meiosis, the mating fails. This phenomenon, meiotic silencing of unpaired DNA (MSUD) reflects the action of an RNA-silencing phenomenon, (Shiu et al., 2001). MSUD is distinct from the RNA-silencing mechanism (quelling) discovered in vegetative cells of *Neurospora* (Cogoni, 2001). Major efforts to define this process, including new mutations that disabled MSUD, were accomplished by Robert Metzenberg (NAS), who after retiring from the University of Wisconsin, spent five years as a visiting professor in David's laboratory. Bob imparted further momentum to molecular studies of the *Neurospora* sexual cycle. His analysis

of MSUD through meiotic mutations that had long perplexed the community, has defined the process as a fundamental phenomenon seen in higher organisms.[2] Another molecular study in the laboratory was the ability to detect histone gene activity, even during meiosis, through use of the green fluorescent protein (GFP) as a tag (Freitag et al., 2004).

THE GENOMIC ERA

David was not a biochemist or a molecular biologist. However, his coherent development and maintenance of data on *Neurospora* genetics and cytogenetics, and his published compendia of information on all *Neurospora* strains and mutants were indispensable factors in this organism's becoming the first filamentous fungus whose genome was sequenced (2003). Because of the extensive knowledge of chromosomal architecture, mutational landmarks, and the standardization of data, the genome was quickly annotated and compared with that of other microbes, particularly yeast and other fungi (Borkovich et al., 2004). The wealth of new genes, unshared by yeast but found in other filamentous forms, opened a major window onto the diversity of fungi, and confirmed *Neurospora crassa* as a model for the entire group. The last compendium of *Neurospora* mutants (2001) includes the molecular findings on the genes listed, and serves as a modern reference for workers on all filamentous forms.

The use of common molecular techniques by all workers on fungi transcended the diverse biology of this group of organisms, from industrial forms to plant pathogens. Because of a shared molecular language and many techniques, the *Neurospora-Aspergillus* community invited workers on all filamentous fungi to join it after 1985. The field of fungal genetics and biology was thus born and now rivals many other fields in its scientific vigor, diversity, membership, and

promise. David had long advocated attention to diversity (1991), and the massive community he left behind was one of his greatest legacies.

BUILDING A COMMUNITY

The selected bibliography below emphasizes that David's major preoccupation was the fundamental genetics of *Neurospora*. Nowadays one would ask whether this simply followed in the traditions of Morgan with the fruit fly and of the early workers with corn. This was the case, and David called attention to the parallels among all these model genetic organisms. But it was not journeyman work. In contrast with the pioneer geneticists, David accomplished as much almost single-handedly. He was the first to explore so deeply and so broadly the genetic system of a haploid, eukaryotic organism. Not only did he establish the formal genetics of *Neurospora* but the cytogenetics, the sexual biology, and almost incredibly, the population genetics of the fungus as well. This pioneer work qualified him to point the way for three later generations of workers on the organism. All the time, he promoted *Neurospora* as a research tool, "keeping the machine running," as it were, while doing original work in many areas. The later papers show that he easily contributed to molecular studies of the organism as molecular approaches overtook all of biology.

Another aspect of his bibliography is not at all obvious. David never put his name on a paper to which he had not made a hands-on experimental contribution. He had only four graduate students but many visitors and several long-term research associates: his wife, Dorothy Perkins; Raju; Turner; and later, David Jacobson. Their work was supported by his research grants, one a 42-year continuing award from the National Institutes of Health and at the end, additional support for the remaining years from the National Science

Foundation. (One reviewer of David's 2004 grant renewal application called his laboratory a "national treasure.") His full bibliography lists all work funded by his laboratory, running to over 430 titles. His intellectual contribution to many of these projects was substantial, and most major laboratory leaders nowadays would have claimed authorship on all of them.

David built his community in part by encouragement of young and foreign investigators, a process extending over many years. At meetings he would listen intently to conversations and poster sessions of those new to the group. This not only flattered these entrants to the field but also made them the targets, years later, of information and advice David would forward from obscure places in the literature or from the informal communications of workers in the field. He remained tirelessly up-to-date with the *Neurospora* literature, and could review and discuss perceptively almost any subject. Many foreign *Neurospora* researchers would automatically visit his laboratory when they were in the United States, and many began their most important work on *Neurospora* after spending longer periods with him. His loyalty to them and to others was surpassed only by his memory of the details of their work.

Because of his intellectual and historical presence in the field and at meetings, he was able to impart other characteristics to the community. These were integrity, cooperation, and noncompetitive behavior in research. He gave freely of his ideas, ideas later embodied in original research by others. Few workers were worried about being scooped, largely because David and the *Fungal Genetics Newsletter* (originally the *Neurospora Newsletter*) made clear who was working on various projects and their progress. This tradition was characteristic of much work in Mendelian genetics early in the 20th century, but David projected it upon his own field well

into the molecular era. He never copyrighted or patented a single finding or device in his own name, nor did he seek to claim any invention or technique as his own.

Finally, frugality, cleverness, and a hard work ethic drove David's years of productivity. With respect to the first two of these traits, David's contributions to the community were substantial. Given his commitment to genetic analysis on a grand scale, he devised or improved on techniques that facilitated many other research programs. He regularly published these methods in the newsletter (calling them "Stanford methods" rather than "Perkins methods"). He developed a fast method of collecting and analyzing unordered tetrads (groups of meiotic products) shot onto the lids of Petri dishes. This obviated isolation and growth of ascospore cultures for his study of spore abortion patterns. His tests of silica-gel storage of stocks allowed many people to easily maintain stock collections beyond the dreams of *Drosophila* workers. His introduction of *alcoy* and other stocks rendered mapping of new mutations rapid and routine. His compendia of mutations and their multiple alleles at all known chromosomal locations made all workers aware of what had gone before, sparing the field countless hours of work and much unnecessary duplication of findings in the literature.

PROFESSIONAL HONORS AND SERVICE

David received a National Institutes of Health Research Career Award (1964-1989) and an NIH MERIT Award (1987-1996). He assumed the job of editor in chief of *Genetics* (1963-1967) and later became president of the Genetics Society of America in 1977. He was elected to the National Academy of Sciences in 1981, was named a Guggenheim fellow from 1983 to 1985, and was awarded the Genetics Society of America Morgan Medal in 1994. The British Mycological Society made him an honorary member in 2005.

I WISH TO THANK THE following persons for help with critiques, corrections, and additions to this and an earlier account (Davis, 2007), the latter including the contributions of Dorothy Newmeyer Perkins: Namboori Raju, Charles Yanofsky, David Jacobson, Barbara Turner, Susan Perkins, and the late Robert Metzenberg. The photo of David Perkins was taken by Jonathan Wittenberg in 1978, and was provided to me by N. Raju. It is used, with thanks, by permission of Dr. Wittenberg.

NOTES

1. C. Yanovsky. In Memoriam: David Dexter Perkins 1919-2007. www.stanford.edu/group/neurospora/.
2. Sadly, Bob Metzenberg, another creative and influential geneticist of the *Neurospora* group, died in 2007 at the age of 77, as did David Stadler, whose contributions greatly illuminated the study of recombination and mutation in *Neurospora*. The *Neurospora* community is thus further and significantly diminished.

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