James F. Crow
1916–2012

BIOGRAPHICAL *Memoirs*

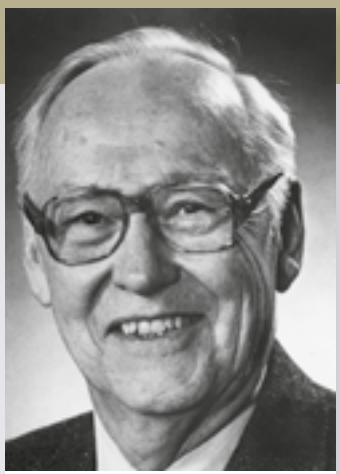
A Biographical Memoir by
Daniel L. Hartl
and Rayla Greenberg Temin

NATIONAL ACADEMY OF SCIENCES

JAMES FRANKLIN **CROW**

January 18, 1916–January 4, 2012

Elected to the NAS, 1961



By Daniel L. Hartl and Rayla Greenberg Temin

James F. Crow enjoyed relating how he and the first issue of the journal Genetics were scheduled to arrive on the same day—January 18, 1916—and how he was delivered on time, whereas the journal was delivered several weeks late (Crow 2000a). The coincidence was altogether fitting, as Crow became one of the leading geneticists of the twentieth century.

Renowned as scholar, teacher, mentor, author, and historian, he had a career in science that spanned seventy years, primarily at the University of Wisconsin–Madison. Professor Crow's research was in theoretical and experimental population genetics, focusing on Drosophila as his model organism and extending his theory and results to human genetics. He had further influence on the field of genetics as a writer and speaker, a synthesizer and disseminator of knowledge, and he performed service to his colleagues and to society as a whole in many different capacities.

James Crow was born in Phoenixville, Pennsylvania. At the time, his father taught biology at Ursinus College in nearby Collegeville. In 1918 the family moved to Wichita, Kansas, where his father, who was able to obtain a position teaching biology at Friends University, could care for his own aging parents. Crow's mother and father had both studied at Friends; his father later attended the University of Kansas and earned a masters degree with Clarence E. McClung, the famous grasshopper geneticist who discovered the X chromosome. The family's return to Wichita took place while the 1918 flu pandemic was in full force, and the two-year-old baby Crow became infected and barely survived (Harper 2005).

The family was poor, but not destitute, and as devout Quakers, Crow's parents practiced a life of modesty and simplicity. Intellectual pursuits were encouraged, and the young

Crow had reading and music lessons as a child. His parents thought he had deep sensitivity to music because whenever they played a recording of Edward MacDowell's "To a Wild Rose" on their wind-up Victrola—a selection that Crow later called "pretty corny music"—the boy would go off into a corner and sob (Crow 2005). Actually, the song reminded him of the leaping flames that had frightened him when a neighboring house had burned down (Crow 2005). But his reaction inspired his parents to start him on piano lessons at age six, and at eight he switched to violin.

As a first grader, James was enrolled in a rural two-room school, but a few years later he moved to the urban Wichita system (Crow 2000a). He went on to the newly built Wichita North High School on the banks of the Little Arkansas River, where his favorite subjects were music, mathematics, chemistry, and physics. At first he planned to be a professional musician and he studied violin and viola diligently, but soon Crow realized that while he loved music and was good at it, his talent was not that of a professional. Nevertheless, music became a lifetime avocation (Crow 2005).

He polished his social skills working nights as a soda jerk in a drugstore that was a hangout for high school and college students. In his senior year of high school he took a job at the Wichita Public Library, working five hours every afternoon and all day Saturday as a reference librarian, looking up whatever people asked to know. In this activity, he said (Crow 2005), "I think I learned a comparable amount to what I was learning in school."

For college, Crow attended Friends University, and with characteristic energy he was a full-time student while continuing to work as a reference librarian. He also played viola in dance orchestras, in a string quartet broadcast weekly on the radio, and in what eventually became the Wichita Symphony Orchestra. Having decided against a career in music, he successively considered physics, chemistry, and biology. His interest in biology was piqued by a genetics course in his junior year (Crow 2006a), and he graduated with high honors in 1937 with majors in biology and chemistry.

The Texas years 1937–1941

For graduate school in biology or genetics, Crow had several options, but he chose the first school that accepted his application, the University of Texas at Austin (Crow 2005). Turned down by Harvard and Caltech, he did receive an offer from the University of Wisconsin–Madison in biochemistry. He later reflected:

> *The Texas offer came first, and I was so insecure [it was 1937, the depths of the Great Depression] that I accepted it almost immediately. I expect that if I'd been offered...a good...fellowship at Wisconsin, I'd have accepted that...and been a biochemist.*

Crow began graduate studies at the University of Texas in the fall of 1937. He had initially hoped to work with Hermann J. Muller, Drosophila geneticist nonpareil, who ten years earlier had discovered that x-rays cause mutations, for which he was awarded the Nobel Prize in 1946. However, Muller, who had communist sympathies at the time and was involved in leftist political activities, had gone on leave, first to Germany in 1932 and then to Russia, and he never did return to Austin (Crow and Abrahamson 1997).

Crow decided to work with John T. Patterson and Wilson S. Stone. Patterson, already well known for his work on polyembryony in the armadillo, which usually gives birth to four genetically identical offspring, had become increasingly interested in genetics. "Dr. Pat," as he was known, was a gruff and portly man with a dark complexion, who introduced himself to his new graduate student by saying, "You are blonder and skinnier than I thought you would be," whereupon he talked about his collection of Indian arrowheads (Wagner and Crow 2001). Crow later described Patterson as "my crusty and earthy major professor" (Crow 1988a).

The Patterson and Stone laboratory at the University of Texas was to evolutionary genetics of the fruit fly *Drosophila* what the Thomas Hunt Morgan laboratory at Columbia University was to the formal genetics of *Drosophila*. Thanks to these two groups, *Drosophila* was developed as a classic model organism for the study of evolution and genetics.

The Texas lab provided a lively intellectual environment, and Crow had a happy experience as a student and as a teaching assistant in the cytology and embryology laboratories. In his first year he helped Stone solve a problem in mathematics, whereupon Stone encouraged him to read the papers of Sewall Wright and Ronald A. Fisher, the famous founders (along with J. B. S. Haldane) of modern population genetics. Crow found this work fascinating and decided to specialize in population genetics himself. Assigned to study species in the *Drosophila* mulleri group, he discovered a mutation that caused lethality between, but not within, species. This mutation formed the basis of his thesis for his PhD degree, which he received in 1941.

J. F. Crow, his wife Ann, and their family in 1957. Son Franklin is behind the couch, Laura (with pearls) is to Ann's left, and Catherine (with braids) is between Jim and Ann. The dog's name is Socks.

While a graduate student, Crow played viola in the University Orchestra, where he met Ann Crockett, who played clarinet. They married in 1941 after his graduation (Crow 2005) and were together for sixty years; Ann Crockett Crow passed away in 2001. They had three children: Franklin, Laura, and Catherine.

A memorable incident from Crow's days in the University Orchestra melded his musical and scientific activities. One day he left his viola in the lab, so that he could pick it up later on his way to a concert. One of his lab mates took the opportunity to stealthily place thousands of anesthetized fruit flies inside the viola, timing it so that as Crow began to play at the performance, the flies gradually awakened and fluttered up out of the F-holes. He often recounted this as "one of the diabolically cleverest jokes that anyone ever perpetrated" (Crow 2005).

Dartmouth 1941–1947

Crow had hoped to do postdoctoral studies with Sewall Wright at the University of Chicago, but by then it was clear that the United States would become involved in World War II, and plans changed. Crow accepted a one-year teaching position at Dartmouth College substituting for James V. Neel, who had taken leave to try a year in medical school. Neel never came back and went on to establish a brilliant career in human genetics. Crow stayed on at Dartmouth.

"When I was in graduate school," he recalled, "I really expected to be a teacher. I wasn't sure that I was cut out for research" (Crow 2000a). His Dartmouth years gave him ample opportunity to teach. He was hired to teach genetics and general zoology, but, following his own desire, he added embryology and comparative anatomy to his teaching load.

Of this dizzying schedule, he later reflected: "At least one student and possibly half a dozen had six or seven courses all taught by me—so I was totally responsible for whatever these students knew... Much of the time, need I say, I was barely ahead of the class, but I never regretted the broadening experience."

Once the war was on, he took a course in navigation, in case he might be drafted, and he found the subject quite easy. He passed the exam with a score high enough to qualify him as an instructor, and so he taught navigation, too. But he was the only one around who had ever studied parasitology, and his arm was twisted to teach that course also, which he did by staying only a day or two ahead of his students. Part of his study of tropical diseases and parasitology was in a month-long course in Guatemala and Costa Rica, which he very much enjoyed (Crow 2005). The medical school decided soon after that they needed a course in statistics, and Crow was the logical instructor. All this transpired while he was teaching mathematics to undergraduates. As a member of the biology department, he could teach whatever mathematics he wanted, and so he included analytical geometry and three semesters of calculus. Of this dizzying schedule, he later reflected:

> *At least one student and possibly half a dozen had six or seven courses all taught by me—so I was totally responsible for whatever these students knew...Much of the time, need I say, I was barely ahead of the class, but I never regretted the broadening experience (Crow 2006a).*

Until the war, Crow had been a pacifist, and as a graduate student he was active in peace groups that later proved to be fronts for the Communist Party. This caused him anxiety during the McCarthy years (1950–1956), but nothing ever came of it. At Dartmouth he informed his draft board that he was willing to serve in the armed forces if called, but evidently his teaching led to his continued deferment (Crow 2006a).[1]

Amidst the heavy teaching, the turmoil of war, and a new baby (Franklin was born in 1943), Crow managed to carry out and publish original research. Always interested in mathematics, he found a mathematical series that made the significance level of a chi-square test essentially a linear function of the chi-square value. He set out to produce a set of graphs of significance level against chi-square for various degrees of freedom, which he did by expanding the series, which proved to converge very slowly:

> *And it took me all afternoon with [an] old-fashioned kind of chunk, chunk, chunk calculator...[and] I finally finished this graph and published*

> *it in the Journal of the American Statistical Association (Crow 1945)....[It is] far and away the most popular thing I've ever done in the sense of the number of copies and reprints requested (Crow 2005).*

During this period, he also pondered the phenomenon of heterosis, in which hybrids of inbred lines usually show improved performance over the parental inbreds. He suggested two hypotheses: (1) "nicking," which means that inbred lines are inferior because each is homozygous for many recessive deleterious mutant alleles of small effect, and (2) "overdominance," which means that hybrids are superior because, on a gene-by-gene basis, heterozygous genotypes are better than homozygous genotypes (Crow 1948). The distinction set off decades of research, and while more than a handful of individual genes showing overdominance have been discovered, the overwhelming evidence favors nicking.

Among the most sociable people that either of us has ever met, Crow kept up his professional contacts even while under pressure of work at Dartmouth. For example, H. J. Muller was at Amherst College in Massachusetts, and Crow drove to meet him on several occasions. After the war, when Muller moved to Indiana University in Bloomington, Crow took a semester of leave and spent some of the time in Bloomington, interacting on a daily basis with Muller, for whom he had enormous respect.

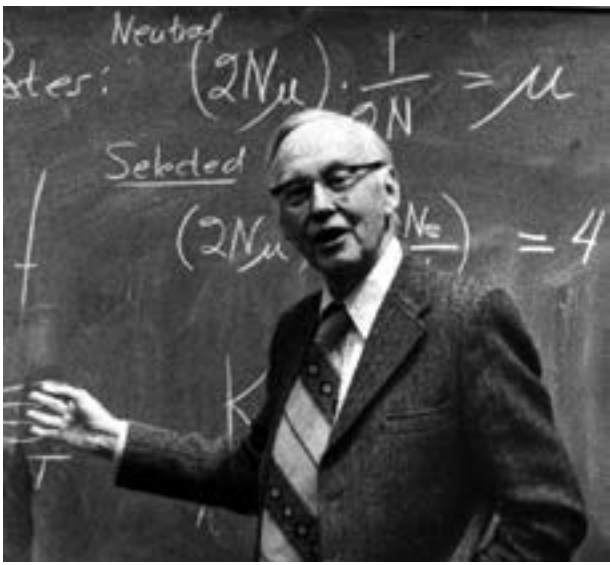
Wisconsin 1948–2012

It was the University of Wisconsin–Madison that opened Crow's door to the broad sunlit uplands of his career. It all started in the summer of 1947 when he attended a Cold Spring Harbor Symposium and met Joshua Lederberg. Lederberg had given a talk on recombination in bacteria, and Crow asked a question about crossover interference. Lederberg was impressed that anyone in the audience knew enough about crossover interference to ask an intelligent question, and the two men had a lengthy conversation afterward. Lederberg was just about to start a position at the University of Wisconsin, and the next year Crow received a job offer from "out of the blue," though presumably at Lederberg's behest (Crow 2000a). Lederberg became one of Crow's closest personal friends and a valued scientific colleague. They talked almost every day.

It was a great disappointment when Lederberg left Wisconsin for Stanford in 1958, shortly after being awarded the Nobel Prize. Lederberg had hoped to entice Crow to join him at Stanford, but Crow decided to stay in Wisconsin. This seems to be the only time that Crow seriously considered leaving the University of Wisconsin (Crow 2000a).

Teacher and mentor

From the beginning, Crow regarded his teaching career as at least as important as his research. He was a popular and successful teacher and won several teaching awards. Almost every year from 1948 until his retirement in 1986, he taught a large enrollment undergraduate genetics course, General Genetics 560. The course was legendary. He obviously loved to teach, and came so well prepared that his lectures seemed extemporaneous. Relying mainly on blackboards and chalk, he could explain a complex concept so lucidly that a student could seemingly understand it clearly during the lecture, but then realize after class that the concept was not so simple after all.



J. F. Crow lecturing on population genetics, 1979.

His lectures were enlivened with humorous anecdotes and historical asides. And, to spare students the chore of taking notes while listening, he published his lecture notes as a book, *Genetics Notes*, referred to by everyone as "Crow's Notes." Eventually it went into eight editions (Crow 1983) and was translated into several languages. Crow's Notes included interesting and challenging problems, which were educational in their own right. The early editions had a spiral wire binding and were printed only on the left side pages, leaving the right side pages blank for students to take additional notes. By the sixth edition (1966), there had been so many advances in genetics that Crow's Notes had to be printed on both sides of the page. Crow often joked that genetics was such a fast-moving field that he could ask the same exam questions every year and merely change the answers.

In addition to General Genetics, Crow taught courses in population genetics, human genetics, segments of other courses, and various graduate seminars. The content of his population genetics course formed the framework of his influential book with Motoo Kimura, *An Introduction to Population Genetics Theory* (Crow and Kimura 1970).

Crow also spent time in Hollywood consulting on a short 1960 Warner Brothers film, *The Thread of Life*, which dealt with genetics and heredity in humans, showing various traits and the methods used to study their inheritance.[2]

While undergraduate teaching was a pleasure for him and he did it most willingly, Crow excelled at mentoring graduate students. He later commented, "Part of my legacy is students...I've been conspicuously successful with graduate students" (Hartl 2011). And so he was. Many of his former graduate and postdoctoral students went on to make distinguished careers of their own.[3] He often singled out two of these students for special mention: Newton Morton, a pioneer in human genetics and genetic epidemiology; and Motoo Kimura, a major figure in theoretical population genetics. Both were students in the mid-1950s, when Lederberg was on the faculty. Crow spoke of these years with such fondness that it is hard to escape the suspicion that these were some of the happiest years in the life of a generally happy man (Crow 2000a, 2005, 2006a; Harper 2005).

J. F. Crow on a bicycle with parasol in Mishima, Japan, 1957.

His mentoring of Kimura led to a long-lasting collaboration, with Crow traveling to Japan and Kimura to Wisconsin on many occasions. (Ann Crow often accompanied him; she was fluent in Japanese and admired Japanese culture.) It also led to Crow mentoring a series of Japanese students, with each successive student recommending the next in line. In 1985 Crow was made an honorary member of the Japan Academy, and at his induction the Emperor cited his contributions to training Japanese geneticists.

Colleague

Crow was a geneticist who played on the international stage. In his early years, his self-assertiveness got him acquainted with many famous geneticists, including Muller and Lederberg, with whom he quickly made friends. While at Dartmouth, Crow attended a summer statistics course in Raleigh, North Carolina, at which the famous statistician and population geneticist R. A. Fisher lectured. One evening Fisher spoke about his new

three-locus model for the genetic determination of rhesus blood groups, after which Crow asked a question, and then approached Fisher as the audience began to disperse. Fisher asked whether he'd like a glass of beer, and they adjourned to a nearby bar. Alas, the pub had no beer, nor any wine. What it did have was a bottle of champagne, which they were not allowed to drink owing to a North Carolina blue law. So they took the champagne to Crow's dorm room and forged a friendship that lasted the rest of Fisher's life (Crow 1990).

Crow likewise cultivated a friendship with Sewall Wright. He often drove from Madison to Chicago to visit Wright, who was teaching at the University of Chicago. In 1954, when Wright turned sixty-five, he was forced to retire from Chicago, and Crow arranged an appointment for him at the University of Wisconsin. Wright was a professor at Wisconsin until his retirement at age seventy, and then he remained active in his professional life for another twenty-five years. Crow called Wright "the best bargain Wisconsin ever had" (Crow 1988b). To Wright, he was a good friend and showed his characteristic generosity. Crow got the department to buy Wright one of the first electronic calculators; Wright was at first rather suspicious of the contraption, until he discovered that it could calculate exact factorials up to sixty-nine!

In Wright's later years, when he suffered from macular degeneration, Crow bought him a special magnifying machine so that he could continue to read. Crow was a joyful and beloved friend of his colleagues at the University of Wisconsin. One example: In December 1960, Crow and Seymour Abrahamson, who had been a student of Muller, set off to New York to help celebrate Muller's seventieth birthday. During the dinner, which was at Columbia University, Muller collapsed and was rushed to a hospital, where he fortunately recovered. But during the commotion, Crow was heard to remark, sotto voce, that when he celebrated his own seventieth birthday, he hoped he would be young enough to enjoy it. Upon returning to Madison, Seymour, his colleague Larry Sandler, and others in the lab began to plan a surprise mock "seventieth birthday party" for Crow on January 18, 1961, when he would actually turn forty-five. It was carefully and elaborately planned—kept secret even from Ann, his wife—and it came off perfectly with songs and skits and numerous (fabricated) messages from geneticists living and dead (including Gregor Mendel). Crow kept all of his "seventieth birthday" Western Union telegrams, delivered by messenger, among his mementoes (Abrahamson 2012).

One such telegram read:

Roses are red,
Violets are blue.
I say balanced,
You say mu.

—Th. Dobzhansky.

This reflected the ongoing debate about genetic variation in populations, whether attributable mainly to hidden, mostly recessive mutations, or more largely to balancing selection for genes at loci where the heterozygote is superior in fitness to either homozygote.

In 1986 there was a real seventieth birthday celebration, an International Genetics Symposium, the "Crowfest," presented by Crow's large and illustrious cohort of students, postdocs, and colleagues, and he was indeed still healthy enough in mind and body to fully enjoy it.

Research

Most of Crow's research was in experimental and theoretical population genetics, making use of mathematical and statistical methods. After Dartmouth, much of his work was collaborative.

Crow's experimental research focused on the model organism *Drosophila melanogaster*. His early work included studies of the evolution of DDT resistance as an example of natural selection in action (Crow 1954). A recurring theme in Crow's experimental work was hidden genetic variation—variation with no great or visible manifestation. How much of this hidden variation, for example, in natural populations at equilibrium between mutation and selection, is due to genes which, when made homozygous, have large or drastic effect (such as lethals), and how much to genes with individually very small effect ("detrimentals")? Crow was especially interested in the total impact of the latter, those minor-viability mutations, which in the long run, acting cumulatively, may even have as much overall effect as the lethals (Crow 1979). An associated issue was whether the "recessive" mutations that affect viability are fully recessive, or whether they have mildly deleterious effects even in heterozygous carriers. His research showed that such "partial dominance" is, in fact, usually the rule (Hiraizumi and Crow 1960, Crow and Temin 1964, Mukai et al. 1972, Temin 1978).

Crow's group likewise investigated new mutations, spontaneous or induced by radiation or chemicals, and estimated their rates and effects both when homozygous and heterozygous, including effects on fertility and other facets of total fitness (Mukai et al. 1972, Simmons and Crow 1977). Crow also considered how principles of *Drosophila* fitness might extend to humans. He made major contributions, both by mathematical modeling and experimental measurement, to the concept of "genetic load," which estimates the amount by which average population fitness is reduced by mutation, selection, or other evolutionary processes.

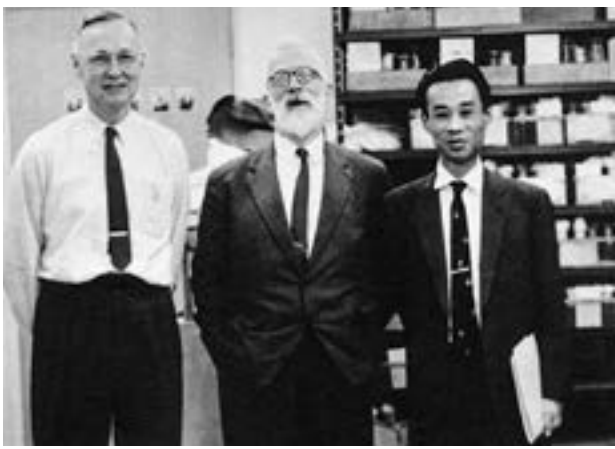
J. F. Crow and Rayla Greenberg Temin, 2006. (Courtesy of Hilde Adler, Madison, Wisconsin.)

Crow was fascinated by genes that violate Mendel's rules by giving themselves an advantage in genetic transmission from one generation to the next. A remarkable case in *Drosophila*, known as segregation distortion, was first discovered in his laboratory in the course of the fitness studies (Hiraizumi et al. 1960). Segregation distortion works by interrupting the development of sperm carrying the normal gene. A diagram of the spiraling approach to equilibrium of three genotypes involved in segregation distortion in nature graces the cover of Crow's book, *Basic Concepts on Population, Quantitative, and Evolutionary Genetics* (Crow 1986). Another important exception to Mendelism was elucidated in Crow's lab: the P factor, a transposable element responsible for hybrid dysgenesis, a set of genetic instabilities observed in hybrids from particular crosses between males of one *Drosophila* population and females from another (Crow 1988c, Engels 1988).

Crow had an abiding interest in human genetics, especially in aspects related to population genetics. He made estimates of the genetic load of deleterious mutations in the human genome, often using insightful indirect methods that made use of inbreeding data (Morton, Crow, and Muller 1956). One contribution he especially enjoyed was related to isonymy, the analysis of surname frequencies in a population and among mates to

estimate the extent of inbreeding and make inferences about population structure (Crow and Mange 1965). In studies of mutation rates of human genes, he found much greater rates in males than in females, and during his retirement he wrote frequently on the paternal age effect (Crow 1993, 1997, 2000b, 2006b).

One thread running through all of Crow's research is that of population genetics theory. Undoubtedly his great interest in theory reflected his lifelong love of mathematics. He extended the concept of effective population number to distinguish inbreeding (inbreeding effective size) from random drift effects (variance effective size). He studied the consequences of small population size, inbreeding, and non-random mating, and he developed the infinite-alleles model of mutation, in which each new mutation yields a new type of allele not already present in the population. He studied the conditions in which a subdivided population can lead to the evolution of altruism. He worked on the theory regarding the evolutionary benefits of sexual reproduction maintained by two different sexes. Fascinated by the theoretical foundations of Fisher's "fundamental theorem of natural selection," which deals with the rate of increase in average fitness under natural selection, Crow also studied the conditions under which the theorem holds and the limits to its applicability.



J. F. Crow with Ronald Aylmer Fisher (center) and Motoo Kimura, Madison, Wisconsin, 1961.

Crow's interest in theory was also sustained by his long-term collaboration with Kimura, who began as a graduate student working out the mathematics of fixation of neutral alleles. This early work eventually culminated in Kimura's neutral theory of molecular evolution, with its many applications in modern studies of genomic DNA sequences, such as estimating rates and times of species divergence and serving as the null hypothesis in tests for natural selection. Through the years, the two remained close friends and collaborators, and Kimura rarely published anything he thought important without first seeking Crow's opinion.

Consistently of the highest quality, Crow's research was characterized by the breadth and diversity of topics on which it touched. In a self-appraisal of his research, he explained, "I don't regard any particular discoveries as being outstanding...I would say that the most important thing really is not any one experiment but a more or less persistent study of the variability in natural populations and how it is maintained with partial dominance, and the other things that grew out of this. I also think that I've made some substantial contribution to theoretical population genetics, but mostly these have been in collaboration...My life has been characterized more by diversity than by systematic concentration on one or two subjects. It's been richer for that reason and enjoyable, but I'm not sure what that means from the standpoint of contributions" (Crow 2000a). Of contributions there were many: His full publication list includes almost four hundred citations and can be accessed at http://www.genetics.wisc.edu/documents/CrowCV2010_1.pdf.

To honor Crow's significant contributions to evolutionary theory, the J. F. Crow Institute for the Study of Evolution was established at the University of Wisconsin, comprising an affiliation of more than seventy faculty members throughout the campus.[4] When it was named in his honor in 2010, Crow noted with characteristic humor: "I am honored. Usually these things are named after a person who has died. But I am not going to take the hint."

Service

Much of Crow's time was spent in university, national, and community service. He was highly personable, able to get along with nearly anyone, which made him a superb leader, committee member, and chair. At the University of Wisconsin he chaired the Department of Medical Genetics from 1958 until 1963, was acting dean of the Medical School from 1963 until 1965, and served as chairman of the departments of Genetics and Medical Genetics from 1965 until 1972 and from 1975 until 1977. Throughout his long career, he was an active member of the Genetics Society of America (serving as vice president in 1959 and president in 1960) and the American Society for Human Genetics (serving as president in 1962).

Crow was elected to the National Academy of Sciences in 1961. He was active in the Academy and on numerous committees of the National Research Council, often as chair. With his research in population genetics, including that on the impact of new mutations, Crow was able to bring his expertise and knowledge to bear on public policy. The committees included those set up to measure the effects of radiation on human health

following the atomic bombing of Hiroshima and Nagasaki in World War II, and those on related public health issues[5], namely the following:

Committee on Biological Effects of Atomic Radiation (BEAR, Genetics section 1955–1963, chair from 1960)

Committee on Biological Effects of Ionizing Radiation (BEIR, Genetics Section 1969–1972), chair

Committee on Nuclear and Alternative Energy Systems (1977–1982), Risk/Impact Panel chair

Committee on Chemical Environmental Mutagens (1979–1983), chair

Scientific Advisory Committee of the Radiation Effects Research Foundation (RERF) in Hiroshima (1975–1983)

Committee for Scholarly Communication with the People's Republic of China, Science and Engineering Committee chair (1983–1985)

Committee on DNA Technology in Forensic Science (1994–1995), chair

The committees dealing with radiation took up questions of mutational damage, of how to get estimates of genetic risk from exposure to low doses of radiation, and of the impact of radioactive fallout from atomic weapons testing. The work extended to general health risks from radiation, in particular carcinogenicity, and thus the effects of radiation exposure on current and future generations. Concerns arising from the work helped to ban above ground testing of nuclear weapons. Further, the work pointed attention to chemical and environmental mutagens, and the essential need to focus on those. Crow's committee on forensic DNA tests and his skills in explaining the underlying genetic theory to those in the justice systems helped lead to widespread use of such tests in the courts (Abrahamson 2012).

Consider just one example of Crow as conciliator: Warren Weaver, whose work as director of the Division of Natural Sciences at the Rockefeller Foundation was instrumental in supporting the early years of research in molecular biology, chaired the first meetings of the BEAR committee. He was soon caught between two factions, one led by Muller and the other by Wright. The Muller faction argued that considerations of genetic load were relevant to evaluating the biological effects of radiation, whereas the Wright faction felt that the theory of genetic load was too simplistic for practical application.

The two leaders, each a giant of genetics in his own right, squared off and each stuck stubbornly to his position. A potential fiasco was in the making until Crow, masterful manager of strong personalities and friend of both protagonists, got them to a reasonable compromise. The final report introduced the concept of "doubling dose" of radiation—the dose expected to double the spontaneous mutation rate—which is still used today in the evaluation of human genetic risk (Crow 1995, Abrahamson 2012).

Crow was also active with the National Institutes of Health. He served on the Advisory Committee to the Director from 1971 until 1973; on the Genetics Study Section from 1959 until 1963 and as chair of the section from 1965 until 1968; on the Genetics Training Grant Committee from 1980 until 1983; and on the Mammalian Genetics Study Section from 1984 until 1988, serving as chair from 1986 until 1988. Of his work on review panels, he remarked:

> *I had one nice privilege for comparative purposes. I was Chairman of the Genetics Study Section when it was quite young [1965–1968] and then again just a few years ago [1986–1988], and there's a big contrast…In the early days when there was enough money to go around and almost every good project got funded, it was fun being on the study section; but now, when you know that a lot of good work is not going to be supported, it is very discouraging, at least for me (Crow 2000a).*

J. F. Crow and viola, 1995. (Courtesy of Wolfgang Hoffman, College of Agricultural and Life Sciences, University of Wisconsin–Madison.)

Crow was, as noted, a lifetime musician, and gave generously of his time to share his musicianship with his local community. He played viola in the Madison Symphony Orchestra for about forty-five years and continued playing in chamber groups throughout the city for the rest of his life. He was president of the Madison Civic Music Association (1973–1974) and president of the Madison Symphony Orchestra (1984–1986).

Later years

Although officially retired in 1986 at age seventy, Crow remained very active in his profession. He no longer taught his own courses, but gave guest lectures and seminars, traveled, and served on committees. When home in Madison he was in his office nearly every day. Fittingly, he was the recipient of numerous honors, many awarded prior to his retirement, including, at the University of Wisconsin, Bascom Professorship Award for Distinguished Service and Teaching (1965), College of Agricultural and Life Sciences Teaching Award (1972), Senior Distinguished Research Professorship (1984), Distinguished Teaching Award (1985), and Distinguished Service Award from the UW College of Agricultural and Life Sciences (1995).

More widely, too, the recognition and awards continued to roll in: election as honorary member of the Japan Academy (1985); Thomas Hunt Morgan Medal of the Genetics Society of America (1987); honorary degree from the University of Chicago (1991); election to the Royal Society of London (2000); and University of California San Diego Merck Life Sciences Achievement Award (2009).

Much of Crow's time in retirement was spent writing short general and historical essays on genetics and geneticists. In 1987, Jan Drake, editor of the journal *Genetics*, asked him to take on the editorship of a new monthly column to be called Perspectives. Crow explained that he had been asked because Drake knew "I was a person who knew how to meet a deadline" (Crow 2000a). Crow accepted the assignment, and with Wisconsin colleague William Dove, he oversaw a valuable and popular new feature of this venerable publication. Most of the Perspectives were written by others, either by invitation or direct submission, but Crow wrote more than fifty of these essays himself, often on short-deadline after a promised piece never materialized. This was his métier. He was perfect for the job, preadapted to it by his friendly and direct style of writing, his seemingly inexhaustible store of anecdotes, his encyclopedic knowledge of genetics, and personal ties and connections with geneticists extending back to his youth.

James F. Crow passed away peacefully in Madison on January 4, 2012, two weeks before his ninety-sixth birthday. We are quite sure that if he could, he would share a fitting anecdote or witty remark to help us bear his passing. We remember him as a man of uncommon energy, superior intellect, joyful disposition, friendly manner, quick wit, and high culture. He had an unusual ability to make others feel at ease, to understand and respect their opinions, to foresee and avert potential conflict, and to help people with divergent views find consensus. No longer will we be able to get an answer to almost any

question about the history of genetics by saying, “Let’s ask Jim,” although we will have his writings and his extraordinary legacy to treasure.

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NOTES

1. Much of his teaching between 1943 and 1946 was in connection with the V-12 Navy College Training Program, designed to increase the number of commissioned officers in the Navy and Marine Corps during World War II. Dartmouth was one of 131 colleges and universities in the United States that participated in this program.
2. This film is available online at http://archive.org/details/thread_of_life.
3. Table 1 in Hartl (2011) includes what is believed to be a complete list of fifty-two scientists who studied with him, including undergraduates, graduate students, postdoctoral students, and visiting senior scientists who carried out research in his lab.
4. For more information on the J. F. Crow Institute for the Study of Evolution, see http://www.evolution.wisc.edu.
5. Crow also served on the United Nations Scientific Committee on the Effects of Atomic Radiation, Genetics section, in 1957; the Department of Energy Health and Environmental Research Advisory Committee, from 1985 to 1988; and the Board of Scientific Overseers for the Jackson Laboratory, in Bar Harbor, Maine, from 1961 until 1988.

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