James F. Crow and the Art of Teaching and Mentoring

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ABSTRACT To honor James F. Crow on the occasion of his 95th birthday, GENETICS has commissioned a series of Perspectives and Reviews. For GENETICS to publish the honorifics is fitting, as from their birth Crow and GENETICS have been paired. Crow was scheduled to be born in January 1916, the same month that the first issue of GENETICS was scheduled to appear, and in the many years that Crow has made major contributions to the conceptual foundations of modern genetics, GENETICS has chronicled his and other major advances in the field. The commissioned Perspectives and Reviews summarize and celebrate Professor Crow's contributions as a research scientist, administrator, colleague, community supporter, international leader, teacher, and mentor. In science, Professor Crow was the international leader of his generation in the application of genetics to populations of organisms and in uncovering the role of genetics in health and disease. In education, he was a superb undergraduate teacher whose inspiration changed the career paths of many students. His teaching skills are legendary, his lectures urbane and witty, rigorous and clear. He was also an extraordinary mentor to numerous graduate students and postdoctoral fellows, many of whom went on to establish successful careers of their own. In public service, Professor Crow served in key administrative positions at the University of Wisconsin, participated as a member of numerous national and international committees, and served as president of both the Genetics Society of America and the American Society for Human Genetics. This Perspective examines Professor Crow as teacher and mentor through the eyes and experiences of one student who was enrolled in his genetics course as an undergraduate and who later studied with him as a graduate student.

THIS essay is one of a planned series of Perspectives and Reviews honoring James F. Crow on the occasion of his 95th birthday. Professor Crow was born in Phoenixville near Valley Forge, Pennsylvania, in January 1916, the same month in which the first issue of a new journal called GENETICS was scheduled to arrive. He relates with evident satisfaction that he himself arrived on time whereas the journal was a month or two late (Crow 2000). His father had worked his way through college as a newspaper carrier and house painter and eventually earned an M.S. degree from the University of Kansas studying with C. E. McClung, discoverer of the X chromosome (Crow 2005). The elder Crow taught biology at Ursinus College in Collegeville, Pennsylvania, for a few years, but in 1918 accepted a position at Friends University in Wichita, Kansas, which allowed him to relocate his family

so that he could take care of his parents (Crow 2005). The young James Crow attended public school, studied piano and violin, became interested in physics, chemistry, and biology, and eventually matriculated at Friends University and earned a B.A. degree in Biology and Chemistry (1937). He joined the graduate program at the University of Texas, hoping that H. J. Muller might return from his sojourn in the Soviet Union, but this never happened and Crow worked instead with J. T. Patterson and W. S. Stone on premating reproductive isolation in the *Drosophila mulleri* species group (Wagner and Crow 2001; Crow 2006). Crow received his Ph.D. in 1941 and in that same year married Ann Crockett.

In his 95 years, James F. Crow has become one of the most admired, beloved, and accomplished geneticists in the world. He is renowned as a research scientist, administrator, colleague, community supporter, international leader, teacher, and mentor. His achievements in these diverse occupations will be recounted in forthcoming issues of GENETICS by other authors. In this piece, I have been asked to profile him as a teacher and mentor, to give an account of his undergraduate course, and to relate as best

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doi: 10.1534/genetics.111.135160

This article is dedicated to the memory of Yuichiro Hiraizumi, Terumi Mukai, Takeo Maruyama, Motoo Kimura, and Carter Denniston.

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I can what it was like to be a graduate student in his laboratory. "When I was in graduate school," Crow says, "I really expected to be a teacher" (Crow 2000)—and as teacher and mentor he shaped himself into a Jedi Master. This account is necessarily personal although I hope not idiosyncratic. My perspective is privileged because I was enrolled in Crow's course as an undergraduate in 1963 and studied under his supervision as a graduate student in 1965–1968. These are the years in which, as Professor of Genetics and Zoology, Crow published two editions of *Genetics Notes* and 32 research papers as well as serving variously as Chairman of the Department of Medical Genetics (1958–1963), Acting Dean of the Medical School (1963–1965), Chairman of Genetics and Medical Genetics (1965–1972), Chairman of the Genetics Study Section of the National Institutes of Health (1965–1968), member of the Board of Overseers of The Jackson Laboratory (1961–1988), and Chairman of the National Academy of Sciences Committee on Effects of Atomic Radiation (1960–1963).

My account begins in the fall of 1963 when I had the good fortune to be able to attend the University of Wisconsin at Madison on a Sputnik-inspired scholarship designed to encourage young people to study science and engineering. As a junior transferring from a 2-year program at the Marathon County campus in Wausau, Wisconsin, I enrolled in the course General Genetics 560 taught by Professor James F. Crow. I met him personally only after the midterm exam when an anonymous grader had marked my fill-in answer "plieotropy" as wrong without explanation. I made my way to the New Genetics Building (now called the Old Genetics Building) on Henry Mall, where I introduced myself to Professor Crow and inquired why the answer was marked wrong. He cheerfully explained that that answer was wrong because the spelling was incorrect. I argued that, given the context, any reasonable person would have known what I meant. But he countered genially with the remark that grading must be based on what students write, not what they mean. I grumbled but admired his rigor and consistency. I was also taken by his extraordinary amiability and charm. I remember thanking him when I left, rather like thanking a friendly and courteous policeman for a speeding ticket.

James F. Crow was already a celebrated teacher who had taught genetics almost every year since 1948 when he joined the University of Wisconsin from Dartmouth College where, during World War II, he had taught parasitology, hematology, mathematics, and statistics as part of the V-12 Navy College Training Program for commissioned officers. Tall and slim, sharp featured with graying hair, impeccably dressed usually in a gray, single-breasted suit, white shirt, and dark narrow necktie, there was little to identify him as an academic except for the Hush Puppy loafers and his tendency to clip a ballpoint pen to the placket of his shirt between buttons concealed by his tie. Lectures began promptly when Professor Crow came into the lecture hall and ended precisely on time. He obviously loved to lecture,

enjoyed playing with ideas in his mind, liked interacting with students, and came so well prepared that he seemed to speak impromptu. To make life easier for students, he published his lecture notes as a book, *Genetics Notes*, usually called "Crow's Notes," which eventually went through eight editions (Crow 1983). The earliest versions had a spiral wire binding and were printed only on even-numbered pages so students could use the blank odd-numbered pages to take notes. His lectures were punctuated with historical asides, humorous anecdotes, and clear, intuitive explanations of highly complex processes. Following one lecture a confused student questioning him was suddenly enlightened by an apt analogy and exclaimed "Oh, Professor Crow, you make everything so clear. I believe you're the most simple-minded person I ever met." On occasion, a few hours or days later when you were studying your lecture notes or for an exam, you became aware that some of the concepts that he explained so simply were not quite as simple after all, and you experienced a sinking, uh-oh feeling when you realized that the understanding of some elusive concept you thought you had firmly in your grasp had somehow slipped away.

To illustrate his lectures, Professor Crow used chalk and blackboard, with only occasional pictures or diagrams projected overhead. When asked the perennial question of what would be on the exam, he joked that genetics as a field was moving forward so fast that he could ask many of the same questions year after year and merely change the answers. For many students Genetics 560 was the best of their undergraduate courses, but for me it proved the adage that an excellent teacher can change your life. Seeing Professor Crow so cheerful and happy as a geneticist inspired me to want to become a geneticist, too—and I have never been disappointed in that decision.

But what kind of geneticist? Molecular genetics or population genetics? The tedium of a senior-year research project in A. S. Fox's lab carrying out starch gel electrophoresis with F. M. Johnson, not to mention my tendency to spatter boiling starch solution over myself, militated strongly for population genetics. Hoping for personal reasons to stay at the University of Wisconsin for graduate studies, I was delighted when admitted to the Genetics Training Program and honored with one of the National Aeronautics and Space Administration fellowships created as another response to Sputnik. Soon after joining the program I asked Professor Crow whether I could join his lab as a graduate student. He thought for a moment and then said, "Yes, Dan, provided you understand that population genetics is a recondite field that will never be of great interest except to a small group of specialists." I remember this because afterward I hurried to look up "recondite" in the dictionary. His admonition made population genetics seem like some variety of monasticism, which, being an admirer of Gregor Mendel, was all right by me. Little did either of us foresee that genetics would be transformed in our lifetimes by genomic sequencing on a population scale and the development of computer technologies capable of analyzing

terabytes of data and that population genetics would become a key approach for understanding human evolutionary history as well as for identifying genetic risk factors for common diseases.

Professor Crow's laboratory consisted of one large room with low benches providing space for six or eight stations for counting flies, plus several smaller rooms that served as offices. When he was not in meetings elsewhere on campus or out of town, he could be found in his office across the hall. He was always accessible, although conversations were usually short. He could often understand your question and formulate an answer while you were still in the middle of asking it. I have never known anyone whose mind was so quick. If you wanted a more leisurely interaction, you could sometimes find him in the lab at night where he would return after dinner to transfer his fly cultures. He kept a few dozen stocks and clearly took pleasure in maintaining them himself.

Professor Crow ran his laboratory on the principles of bringing smart people together to pursue their passions and encouraging interaction, mutual respect and support, constructive criticism, and the free sharing of ideas and resources. There were no formal group meetings or reports, as there was so much daily interaction that group meetings would have been superfluous. He would advise, suggest, and encourage, but never direct or cajole. The standard of mutual respect was set by Professor Crow himself and extended not only to members of the lab but also to everyone in the field. I never heard him utter an unkind word about anyone. He also treated everyone in the lab as a colleague. One day he came to me and said, "Dan, there's a matter on which I'd like your advice." He must have seen how flattered I was at being asked because he quickly added, "That doesn't mean I'll take it. It only means I want to hear it."

In the 1960s Crow's laboratory was a crossroads of evolutionary genetics with many visitors for weeks, months, or years. Motoo Kimura visited one summer. Slightly built, soft-spoken, and formal, he would enter the lab each morning at 8 AM dressed in a three-piece suit, sharpen a dozen #2 yellow wooden pencils with a mechanical sharpener affixed to the wall, and disappear into his office until precisely noon when he would emerge to meet Professor Crow for lunch, return at around 1 PM, sharpen the pencils, and disappear again until precisely 5 PM. His work habits denoted discipline, not unfriendliness. He was always glad to answer questions or chat if you caught him between the pencil sharpener and his office. Sewall Wright was as disciplined as Kimura and even more shy and difficult to corner, but if you peeked through the small window placed high in his office door you could see him almost every day checking his work on a Marchant electromechanical calculator the size of a car battery equipped with a 9×10 array of numeric keys.

Among Crow's experimental research interests at the time was the degree of partial dominance of new mutations and those segregating in natural populations. Terumi Mukai

had joined the lab and was studying the heterozygous effects of new mutations, while Rayla Greenberg Temin was studying mutations in natural populations. Rayla was an important personage in the lab, providing continuity on a day-to-day basis when Professor Crow was out of town and stability from year to year. She was also interested in the *SD* system of non-Mendelian segregation, which so captivated me that I chose to study it for my thesis research. Elaine Mange was finishing her research on the temperature sensitivity of *SD* chromosomes, and Yuichiro Hiraizumi, one of Crow's former students who had discovered *SD*, had returned to the lab for research in 1967. Yuichiro was the most meticulous fly researcher I ever worked with. He planned his experiments in exquisite detail, maintained his cultures with loving care, and had an elaborate system for labeling cultures and recording data. I had conceived what I thought was a pretty clever idea for an experiment, but everyone I mentioned it to assured me that it would never work. Hiraizumi encouraged me to do it anyway, with his help, asserting that while you could always think of many reasons why an experiment might not work, many of them actually do. This one worked beautifully beyond expectation, and, thanks to Hiraizumi, my thesis research was launched. Together we were able to show that the distorted segregation in *SD* males was due to the production of dysfunctional sperm (Hartl *et al.* 1967).

Professor Crow sustained a keen interest in population genetics theory. His reminiscences hint of nostalgia for the mid-1950s when Newton Morton and Motoo Kimura were both graduate students and when Joshua Lederberg had not yet moved to Stanford and he and Crow would talk nearly every day (Crow 2000, 2005, 2006). But he had fun with theory in the 1960s, too, when Carter Denniston was working on two-locus measures of identity by descent, and Takeo Maruyama was augmenting his theoretical studies with some of the field's first computer simulations. Crow's main theoretical interests in the 1960s seemed to be genetic load, the amount by which average population fitness is reduced by mutation, selection, and other evolutionary processes (Crow 1970), and also isonymy, the sharing of names, which is an idea he admits to having the most fun with "just because it was cute" (Crow 2000). The germ of the theory of isonymy was a lecture that Muller gave at Dartmouth in the 1940s in which he remarked that "the last name is linked to the Y chromosome" (Crow 2000). A similar idea had also occurred to Haldane (Haldane 1938). Crow began to work out the relation between the probability of isonymy and the genetic coefficient of relationship and found some simple rules that were valid for most human matings (Crow 1980). Arthur Mange later put this idea to good use in his study of inbreeding among the Hutterites, an isolated religious group (Crow and Mange 1982).

Course work was also an important part of graduate education. I was surprised that, in addition to recommending courses in probability and statistics, Professor Crow urged me to study physical chemistry to come to understand how a relatively

small number of fundamental equations could be used in various combinations to solve an astonishing variety of problems. This background was important, he stressed, because it was the structure of population genetics. In the genetics program itself, there was a huge menu of course offerings, and I enrolled in courses by Millard Susman (microbial genetics), Allen Fox (advanced genetics), Seymour Abrahamson (experimental *Drosophila* genetics), Charles Cotterman (combinatorial problems in genetics), Stanley Peloquin (cytogenetics), and James F. Crow (population genetics).

Crow's teaching skills were again in evidence in his course in population genetics. At the time he and Kimura had mostly finished the first draft of what was to become *An Introduction to Population Genetics Theory* (Crow and Kimura 1970). As each chapter was written, a stencil was prepared for a mimeograph machine that produced copies in a slow-drying purple ink smelling of naphthenic distillate. I still have my handouts, lecture notes, problem sets, exams, and other materials from the course, which I later sent off for sewing and binding into a volume as thick as a dictionary. My students today look at the old mimeographed sheets as if they were printed in ancient runes.

Professor Crow and his wife Ann were generous in opening their home to visitors and guests, including graduate students and postdocs. In the 1960s, the Department of Genetics at the University of Wisconsin was arguably the best in the world, and it drew countless distinguished visitors including giants such as H. J. Muller, A. H. Sturtevant, J. B. S. Haldane, and R. A. Fisher, as well as equally accomplished younger geneticists. As a student or postdoc in genetics, you had the thrill of swimming in these waters. (If "gene pool" of geneticists is not a collective noun, it should be.) I visited Professor Crow's home on several occasions, but one I recall in particular provided an opportunity to meet Dan L. Lindsley, one of the doyens of *Drosophila* genetics. I had just returned from taking advantage of a generous invitation from Hiraizumi to visit his lab at the University of Hawaii before he moved to the University of Texas at Austin. I had taken an inordinate number of pictures, all of which I thought were wonderful, that I showed to everyone in the lab unable to make an escape, oblivious to their boredom. Professor Crow must have been warned because when he telephoned to invite me to his home, he said "By the way, I hear that you have some lovely pictures of Hawaii, and I would like to see some. Please bring your two best."

My graduate studies drew nearer their end one evening when I encountered Professor Crow in the lab. We had a short discussion about one thing or another, and after a while I eventually screwed up enough courage to declare "I think I've done enough experiments now and should start to write my thesis." He thought for a long minute and said "Yes, well, I suppose that's right." During my time with Professor Crow I received a lot of advice from him, mostly in the form of offhand comments. It was sound advice, and I have tried to abide by it. He told me that you can learn something important from almost every article, even those that turn out

Table 1 Former students and postdocs of James F. Crow

Seymour Abrahamson	Kenichi Aoki
Bruce S. Baker	Jack Bennett
James J. Bull	Yong Jai Chung
Loring Craymer	Carter Denniston
William R. Engels	Joseph Felsenstein
Lawrence Friedman	Ove Frydenberg
A. (Sasha) Gimelfarb	Rayla Greenberg Temin
Thomas Gregg	Daniel L. Hartl
Yuichiro Hiraizumi	Branch Howe
Wen-Hsiung Li	Elaine Johansen Mange
Warwick E. Kerr	Motoo Kimura
Alexey S. Kondrashov	Russell Lande
Charles H. Langley	Cathy Laurie
William R. Lee	Terrence W. Lyttle
Russell Malmberg	Arthur P. Mange
Etan Markowitz	Takeo Maruyama
Muneo Matsuda	Joyce Mitchell
Michael Moody	Newton E. Morton
Terumi Mukai	Thomas Nagylaki
Taisei Nomura	Ohmi Ohnishi
Paulo A. Otto	Janardan Pandey
Patrick Phillips	Michael R. Rose
Larry Sandler	Edward L. Schwartz
Frank Seto	Michael J. Simmons
Samuel Skinner	Robert Tamarin
W. Y. Tan	Chung-I Wu

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to be wrong. On peer review Crow said that a reviewer should judge the work by whether the experiments were properly designed and competently performed and by whether the conclusions were supported by the data, and not by whether the authors had carried out the experiments that the reviewer would have performed had the reviewer done the work. He remarked that teachers should limit the number of anecdotes they include in their lectures because students will remember the anecdotes and forget the principles. (How true: I vividly remember an anecdote with which Bill Stone began a guest lecture in Genetics 560, one that modern sensibilities prohibit my repeating, but I cannot for the life of me remember what the rest of the lecture was about.) Crow also prophesied that I would one day be asked to do more than I could possibly accomplish, and this has turned out to be all too true.

In October of 2000 I had the privilege and the pleasure of interviewing Professor Crow for a project of the Genetics Society of America called *Conversations in Genetics*, described on the jacket of the DVD as "a collection of videotaped conversations with geneticists who have made major contributions to the conceptual foundations of modern genetics" (Crow 2000). Toward the end of our conversation I asked him about his legacy, and he said "If I have a legacy, part of it is the collaborative work that I've done with other people. But I want to say that part of my legacy is students. I've had an unusually good group of graduate students and postdocs [Table 1], many of which have gone on to make names for themselves in genetics, and I like to think of that as my real

legacy.” I am proud to say that I have had many very successful graduate students and postdocs of my own and am pleased to admit they are the second-generation beneficiaries of a style of teaching and mentoring learned from a master.

Acknowledgments

My indebtedness to Professor James F. Crow knows no bounds. I am also grateful to Bill Stone, Millard Susman, and Rayla Greenberg Temin for their helpful comments and advice on the manuscript. I thank the taxpayers of the State of Wisconsin for undergraduate scholarships and those of the United States of America for a National Aeronautics and Space Administration graduate fellowship. I am also grateful to the National Institutes of Health for many years of research support, most recently through grants GM084236, GM065169, and GM079536.

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