

Weaving a Tapestry from Threads Spun by Geneticists: The Series *Perspectives on Genetics*, 1987–2008

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ABSTRACT The *Perspectives* column was initiated in 1987 when Jan Drake, Editor-in-Chief of *GENETICS*, invited Jim Crow and William Dove to serve as coeditors of “Anecdotal, Historical, and Critical Commentaries.” As the series evolved over 21 years, under the guidance of Crow and Dove, the input of stories told by geneticists from many countries created a panorama of 20th-century genetics. Three recurrent themes are visible: how geneticists have created the science (as solitary investigators, in pairs, or in cooperative groups); how geneticists work hard, but find ways to have fun; and how public and private institutions have sustained the science of genetics, particularly in the United States. This article ends by considering how the *Perspectives* series and other communication formats can carry forward the core science of genetics from the 20th into the 21st century.

INSPIRED by Jan Drake, then Editor-in-Chief of *GENETICS*, James Crow and I (Figure 1A), both of the University of Wisconsin–Madison, founded the *Perspectives* column in 1987. Dedicated to presenting vignettes of the history of genetics, the series created a veritable tapestry of stories of the science, as told by geneticists themselves. The loom on which these stories were woven stretched back through the 20th century. The two editors’ work was greatly facilitated by the fact that, between them, they had known many of the major figures of 20th-century genetics. For example, Crow, who was born in 1916, the year in which *GENETICS* was founded, personally knew many of the geneticists active in population and evolutionary genetics in that century. Crow’s research interests were broad, bridging mutational issues from *Drosophila* (Mukai *et al.* 1972) to humans (Crow and Abrahamson 1997), and important population genetic issues in evolution (Hiraizumi *et al.* 1960). Further, Crow taught general genetics at Wisconsin from 1948 until his nominal retirement in 1986. Drake recognized the vast treasure of stories that Crow had developed, once saying “Someone should attach a recording device around Jim’s neck to capture his stories!” A generation younger, I, in contrast, had extensive research experience in molecular biology and development, as heavily influenced by

genetics, carrying out research on controlled replication in organisms ranging from bacteriophage to protists to mammals (Furth *et al.* 1979; Moser *et al.* 1990; Burland *et al.* 1993; Dove *et al.* 1998; Irving *et al.* 2014). My extensive contacts in genetics reflect that range of interests. Fortunately, from 1986 to 2006, I led Wisconsin’s Genetics Colloquium on current issues in research, bringing many of the leading geneticists in the world to the university’s campus at Madison to lecture and then engage in critical roundtable discussions with the doctoral students on the evolving craft of genetics.

Many a *Perspectives* article by an established geneticist was triggered by an early report published in *GENETICS* when the salient issue was perceived only in outline. Each year, Crow and I would scan the table of contents of *GENETICS* for articles published 5, 10, 15, 25, or 50 years previously. We supplemented this process by noting the anniversaries of classics in genetics earmarked in A. H. Sturtevant’s history (Sturtevant 1965) and trying to recruit appropriate articles for *Perspectives* to commemorate those anniversaries. This rolling process generated an ever-flowing stream of invitations to geneticists who were present at the birth of a topic and had come to preside over its maturation. Some of these writers were tapped when speaking at Wisconsin’s Genetics Colloquium. Other authors came into the fold from Crow’s and my networks of colleagues, centered in Wisconsin but extending worldwide to Japan, China, England, Scotland, Belgium, Denmark, France, Germany, and the



Figure 1 (A) Bill Dove, Jan Drake, and Jim Crow at the 1992 GSA Meeting in St. Paul, Minnesota. (B) Lucy Shapiro and Dale Kaiser at the fete for Francois Jacob in Crete, 1991. (C) Charley Steinberg and Kirsten Fischer-Lindahl, Basel Institute of Immunology, 1984. (D) Norman Horowitz, Ed Lewis, and Ray Owen in the Caltech Athenaeum, 1998. (E) David Perkins, kneeling to study a poster at the 1992 GSA Meeting in St. Paul, Minnesota. (F) Welcome Bender and Eric Lander deep in conversation, perhaps about chromosome walks in metazoans, at the 1992 GSA Meeting in St. Paul, Minnesota.

Soviet Union. With both patience and gentle prodding, articles came forward “when time permitted.” Frequently an author found, not surprisingly, that the *Perspectives* article attracted a broader response than the primary research report that triggered it. In the Crow–Dove collaboration, it helped that we were within easy reach of one another, working in neighboring buildings on the campus. Shepherding so many articles involving authors around the globe led to occasional lapses. Our good working relationship allowed us to move forward with a simple *mea culpa* (Dove and Susman 2012).

Overall, the 1987–2008 *Perspectives* series is neither a history nor a textbook of genetics. Instead, it constitutes an ensemble of stories varying in technical detail. The stories are personal, however; many sense the starting point and creative pulse of the geneticist by which the science of genetics is generated and regenerated. Here, I choose to comment on three recurrent themes: how geneticists have functioned as solitary investigators, in pairs, or in cooperative groups; how geneticists work hard but find ways

to have fun; and how public and private institutions have sustained the science of genetics, particularly in the United States. Most of the cited articles in what follows were contributions to *Perspectives*. Each selected comment represents a small sample of the original article, and the cited articles are an arbitrary subset of the 1987–2008 Crow–Dove *Perspectives* series. The interested reader can gain access to the collection of Crow–Dove *Perspectives* essays in reverse chronological order on the *GENETICS* website: <http://www.genetics.org/collection/crow-dove-perspectives>.

How Geneticists Have Functioned

As solitary investigators

Much of the popular perception of scientific progress is tied up with the Great Man theory of history, namely extraordinary individuals who were major but largely solitary pathfinders. Examples that come to mind include Galileo, Newton, Darwin, Pasteur, Einstein, and, in genetics, Mendel and McClintock. There are, however, other

exemplary individuals of this class who are far less well known. Tom Nagylaki, for example, elucidated the formative body of theoretical research carried out in apparent isolation by the French scholar Gustave Malecot:

Seldom does a doctoral dissertation substantially advance its field. Nevertheless, just such a rare dissertation, *Theorie mathématique de l'herédité mendélienne généralisée*, was submitted fifty years ago, to the Faculty of Sciences of the University of Paris, by Gustave Malecot . . . Despite the breadth, depth, originality, power, and elegance of the contributions of this great French theoretical population geneticist, much of his work is known even now only to a small minority of researchers in his area (Nagylaki 1989).

In a similar vein, but in an example in which the history of genetics collided with a larger force in political history, Jim Crow contrasted the story of the Russian plant geneticist Vavilov with that of his Japanese contemporary Kihara. Each created comprehensive collections of wild varieties of their plant species of interest. Vavilov, however, became entangled with the political force of Lysenkoism unleashed by Stalin.

On January 26, 1943, Nikolai Ivanovitch Vavilov, near starvation, died in a Soviet prison hospital. He was 55, at what should have been the peak of his career . . . Genetics was fated to be caught up in the two most devastating European dictatorships of the century. Hitler's notorious racist policies deprived Germany and the world of some of our greatest minds and clouded human genetics for decades. Stalin, by supporting Lysenko's bizarre Lamarckism, set Soviet genetics a generation behind. [Hermann Muller] had spent four years in Russia, from 1933 to 1937, at Vavilov's invitation. He had gone there with high hopes for an expanded, well supported genetic research program and had come back thoroughly discouraged. Geneticists had been disappearing—18 of Vavilov's staff members were arrested between 1934 and 1940—and the program was devastated . . .

[Vavilov's] downfall came from the ambitious Trofim Lysenko, who . . . had attracted [Stalin's] attention with the technique of vernalization, by which cold treatment of seeds altered development in a way said to hasten maturity and increase yields. Vavilov actually promoted Lysenko by praising these results. By this time Vavilov was being criticized for failing to produce the hoped-for increases in agricultural productivity. His method of collecting wild relatives of cultivars from around the world would yield only slow (but certain) improvement. Lysenko, with his naive Lamarckian views, promised quick results. The debates were vigorous and even Muller got into the act . . . [asking] what hope there could be for a proletarian revolution when the poor had suffered generations of bad environments, which on a Lamarckian interpretation would have ruined their genetic potential. The answer is not recorded (Crow 1993).

Another example of the solitary pioneer was Leo Szilard, who, after critical contributions to atomic physics, gained prominence in biology, playing a role in steering Jacob and Monod to consider a “double-negative” model for the

induction of β -galactosidase, instead of simple positive induction. Werner Maas described Szilard's career as that of a “lone wolf.”

[Szilard and his junior colleague Aaron Novick] began their entry into biology by taking the Phage Course at Cold Spring Harbor in 1947, which at that time was taught by Max Delbruck . . . Szilard spent a great deal of his time visiting other scientists in the quest for obtaining information about questions that interested him. He was very purposeful during these visits. As an example, during a party in Bernard Davis's apartment . . . Szilard suddenly appeared . . . [He] took over a bedroom and invited each guest, in turn, in for a private chat, quizzing them on their latest work and findings, suggesting new experiments and novel interpretations, and reporting how these might relate to the work of others (Maas 2004).

The genetics of *Escherichia coli*, initiated by Josh and Esther Lederberg, provided a platform from which Julius Adler carved out his own solitary niche. Julius described an epiphany that occurred while he was studying the general biology of micro-organisms with C. B. van Niel at the Hopkins Marine Station:

But my greatest accomplishment was to make a decision on my research subject as an independent scientist. I wanted to study behavior, but which behavior of which organism? The Marine Station has a grand library with journals dating back to nearly the beginning. There I found the ‘ancient’ (1880s) publications of Wilhelm Pfeffer on the chemotactic behavior of bacteria. I decided that was it! (Adler 2011)

Sandy Parkinson has described the beginnings of Julius's adventure:

Motile microorganisms exhibit surprisingly sophisticated sensory behaviors . . . These behaviors came to light in the pioneering work of Engelmann, Pfeffer, and others in the 1880s . . . but were largely overlooked until Julius Adler . . . initiated work on the chemotaxis system of *Escherichia coli* . . . Adler chose *E. coli* primarily for the genetic methods that could be brought to bear on the problem, reasoning that the flow of sensory information through stimulus transduction components should be amenable to genetic dissection much like a conventional biochemical pathway . . . The mutants isolated during those early days of *E. coli* chemotaxis were widely disseminated to workers in the chemotaxis field and have served to define most of the known components of the sensory transduction machinery: receptors, transducers, signaling elements and flagellar switching components . . . [We] owe special thanks to Julius Adler for having the foresight to pick an organism with good genetics (Parkinson 1987).

Adler's (2011) memoir “My Life With Nature” gives a broad view of the ways in which this niche has grown from its solitary beginnings.

The *Perspectives* series provides several personal stories in which a solitary investigator created a new niche by reinvention of one's self. Lee Hartwell made the transition from the molecular analysis of macromolecular synthesis in bacteria to his pioneering study of the cell cycle, thanks to yeast genetics (Hartwell 1991). His overview of his studies of genes controlling the cell cycle further illustrated reinvention. To

understand the uniform terminal phenotype that defined each of his extensive collection of “cell cycle (cdc) mutants” in *Saccharomyces cerevisiae*, and the deduction of the dependent pathway of the action of the genes involved, Hartwell and Ted Weiner proposed that:

It is likely that the dependent relations between many events of the cell cycle are due to . . . controls . . . We have termed these control points in the cell cycle ‘checkpoints’ (Hartwell 1991).

Thus, two decades after the isolation of the first cell cycle mutants, investigators began to turn attention to checkpoints.

Gerry Fink illustrated a different mode of reinvention: taking the lessons learned from yeast genetics to develop the genetic analysis of plant biology in *Arabidopsis* (Fink 1988). In his “Notes of a Bigamous Biologist” he explained how he made the transition from a fast-growing to a slower species:

Although the duration of the *Arabidopsis* life cycle seems at first interminable to the microbial geneticist, it becomes less of a psychological shock as one learns to initiate experiments in parallel rather than in series. Once this new rhythm has been acquired, the results arrive in the rapid succession to which microbial geneticists are accustomed (Fink 1988).

In contrast to the isolation of Vavilov by political forces, Jim Crow’s final *Perspectives* article on Edmund Just (1883–1941), “Just and Unjust,” illuminated the institutional and community prejudice of the 1930s that isolated this extraordinarily able biologist. Crow wrote:

Just . . . was one of the greatest biologists of the early 20th century, but being AfroAmerican, he never had a position that permitted full development of his research talent . . . Just was a superb technician and extremely careful worker. He set rigorous standards for experimentation and was openly critical of experiments that did not meet his standards. Furthermore, he trusted his observations and did not hesitate to point out disagreements with others. The most notable of these was a difference with [his Woods Hole colleague] Jacques Loeb . . . Loeb had argued that the development of the egg was initiated by two steps, a cytolysis, induced in the laboratory by butyric acid, followed by a quenching produced by hypertonic sea water. Just showed that, with careful attention to concentrations, sea water alone was sufficient.

Unfortunately for Just, Loeb’s earlier friendship changed to enmity. One of the few opportunities that Just had [to move from his teaching position at Howard University] for a position in a research environment occurred in 1923. Just was being considered for a position at the Rockefeller Institute for Medical Research. Naturally Loeb’s advice was sought and his reply left no uncertainty.

[Frank] Lillie [of the University of Chicago and Woods Hole] must have known Just better than any other American scientist . . . In his . . . restrained way, he said ‘An element of tragedy ran through all Just’s scientific career due to the limitations imposed by being a Negro in America . . . The numerous grants for research did not compensate for failure to receive an appointment in one of the large universities or research institutes . . . In Europe he was received with universal kindness, and made to feel at home in every way . . . That a man of his ability, scientific devotion, and of such

strong personal loyalties as he gave and received, should have been warped in the land of his birth must remain a matter for regret.’ (Crow 2008)

Jim Crow once testified that “A person with my name should know something about the status of African-Americans in the United States.” His article on Just combined this lifelong commitment with his appreciation of the exceptional solitary scientist.

In pairs

Indeed, the mode of the solitary investigator, plowing a unique, distinctive furrow in isolation, is far from the rule in the history of genetics. Far more striking and common is the fact that progress is often made by pairs of investigators. The creative partnerships of Watson and Crick, Meselson and Stahl, Brenner and Crick, Jacob and Monod, and Crow and Kimura are well-known examples. Several articles in the *Perspectives* series display important but more nuanced examples of what we might well call the “Power of Two.”

The Mom and Pop Editorial Shop: Indeed, the operation of *GENETICS* during much of the Crow–Dove era involved the complementary efforts of Jan and Pamela Drake. In his *sayonara* as Editor-in Chief, Jan painted a picture of the intimacy involved in what came to be called the ‘Mom and Pop Editorial Shop’:

. . . authors all over the world could be harassed directly from our office at any hour of the day. Some authors retaliated by phoning us during European or Australian working hours. The distant ring of the editorial office phone in the middle of our night was uncannily like a baby’s cry in its ability to rouse us abruptly and fully. Once awakened, we would often stay in the editorial office, secure in the knowledge that no author could see us working in our pajamas (Drake 1998).

Fostering *Neurospora*: Examples that were particularly prominent early in the century involved husband–wife combinations in which one member of the creative pair, commonly the wife, held an academic position of lower stature. Joshua and Esther Lederberg, mentioned earlier, were one example. Another was that of David and Dorothy (Dot) Perkins, who together established a focal point for the development of *Neurospora* genetics. Rowland Davis described their partnership:

[Dot’s] involvement with David’s genetic studies deepened with time, yet her publications reflect the independence with which she worked. She sought increasingly to tie up loose ends . . . It is a tribute to both David and Dot that David did not co-author publications that were truly her work, nor did either one hesitate to co-author articles on which they clearly collaborated (Davis 2007).

Cell biology meets molecular genetics: Carolyn Silflow and Pete Lefebvre represent an academically coequal husband–wife pair. Their research pairing in the 1980s reflected the emergent necessity in that era to combine expertise in the

genetic analysis of cellular phenotypes with sophisticated molecular analysis of the genotype. The rich biology of the protist *Chlamydomonas* invited study of motility at a molecular level. Silflow and Lefebvre combined mutant analysis based on motility phenotypes with genetic mapping based on restriction site polymorphisms in natural isolates (Ranum *et al.* 1988; Lefebvre and Silflow 1999):

[the scarcity of RFLPs for many cloned probes ... was solved] when an undergraduate student in our laboratories, Christian Gross, discovered a field isolate of *Chlamydomonas* (strain S1-D2) that is completely interfertile with the laboratory strains, but that shows an exceptionally high frequency of RFLPs ... (Lefebvre and Silflow 1999).

Lefebvre and Silflow have amplified their Power of Two by their effort with others to create a self-sustaining *Chlamydomonas* community for the study of the cytoskeleton, basal body, cellular motility, and photosynthesis. They summarized this group process in their *Perspective*:

Starting 20 years ago with a small roomful of enthusiasts at the *Chlamydomonas/Euglena* session, held annually for part of 1 day at the American Society for Cell Biology meetings, the *Chlamydomonas* meetings have grown to attract more than 200 participants every 2 years (Lefebvre and Silflow 1999).

Microbes pair to simulate metazoan development: Sometimes, the Power of Two pertains as much to the subject matter as to the investigators. One theme in metazoan development is lineage determination involving asymmetric cell division, while a contrasting theme is the creation of cellular differences through cell–cell interaction. The interaction between Lucille (Lucy) Shapiro and Dale Kaiser illustrates a choice of a complementary pair of microbial species to illuminate the two sides of this contrast (Figure 1B). Working in parallel at Stanford, Lucy and Dale have investigated these basic issues in developmental biology through the high-resolution lens of the molecular genetics of microbes. Lucy investigates the mechanisms and consequences of asymmetric cell division in *Caulobacter*, summarizing an early stage in these studies in her *Perspectives* article with Bert Ely:

A critical part of our strategy to dissect *Caulobacter*'s temporal and spatial control of development was the establishment of a system for genetic analysis. Accordingly, one of the first objectives ... was the isolation of a generalized transducing phage which would facilitate exchange of genetic material between *Caulobacter* strains (Ely and Shapiro 1989).

Dale investigates multicellular co-operation in *Myxobacter*, connecting these studies back a century to Roland Thaxter (Kaiser 1993). His interests expand the notion of the Power of Two by seeking commonality at a higher biological level between prokaryotic myxobacteria and eukaryotic cellular slime molds:

Slime molds and myxobacteria are found in the same habitats, and are often isolated from the same soil samples by enrichment culture. Both feed on bacteria in the soil ... The observed evolutionary convergence of these two disparate groups is presumably a consequence of natural selection in a common habitat ... Perhaps there are also rules about

the way development and morphogenesis are regulated for reliability in relatively harsh or changing environments. Use of cellular oscillators revealed by traveling waves and the expression of genes in batteries, triggered by different extracellular signals, are cases in point. Comparisons of eukaryotes and prokaryotes may give insights that would come from neither examined alone (Kaiser 1993).

Meiosis in pairs: The magic created by an interaction between two independent investigators extended around the world in a landmark investigation of meiosis in *Drosophila* by Larry Sandler and Dan Lindsley. They normally operated at the distance between Seattle (Sandler) and San Diego (Lindsley), but got together for a joint sabbatical in Rome during which they isolated a series of *Drosophila* mutants affected in the process of meiosis. Scott Hawley has described how their initiative was:

one of the earliest examples of a systematic search for, and study of, mutations affecting a complex regulatory process in higher eukaryotes. The decision to search for meiotic mutations in natural populations was based on the assumption that recessive mutations would be found as heterozygotes in natural populations at a frequency equal to the square root of their mutation rate, a frequency high enough to be detected in screens (Hawley 1993).

Mentoring new leaders for molecular immunology: The final example of the Power of Two illustrates a rare mode of interaction that normally flies below the radar of histories of science. Charley Steinberg published only rarely but served as mentor to many of the talented junior members of Niels Jerne's Basel Institute of Immunology who became leaders in molecular immunology (Figure 1C). Under Charley's guidance, these mentees solved several of the major problems in the somatic genetics of the adaptive immune system. As summarized by Gillian Wu and Kirsten Lindahl, one of his mentees, Louis Du Pasquier, said:

A mentor listens to the babblings of a scientist trying to figure out the data. Charley would hand us a chalk and say: 'Start from the beginning, I am a simpleton, I don't know anything about this area, explain it to me.' And by explaining it to him, you would begin to understand it yourself. A silent Charley made you think ... Charley helped me when I was confronted with strange results—explaining to me why the bacteriophage I used was likely not the one whose name was written on the label ... (Wu and Lindahl 2001)

Gillian and Kirsten also quoted Charley near the end of his life:

If I had it to do all over again, I would not change. I prevented a lot of atrocities in my day. I have nothing to apologize for (Wu and Lindahl 2001).

In co-operative groups

Neither solitary workers nor significant pairs, however, are the whole story of progress in genetics. A major contribution to

the substratum on which 20th-century genetics developed was the creation of open co-operative groups of investigators. The logistical barriers to genetic analysis in maize were addressed early by this strong spirit of co-operation. Lee Kass, Christophe Bonneuil, and Ed Coe described the birth of the first such group:

At the 1932 International Congress of Genetics held in Ithaca, New York, Rollins Adams Emerson . . . gave an opening address titled, 'The Present Status of Maize Genetics.' In his introduction he declared, 'I cannot refrain from noting here a very real advantage experienced by students of maize genetics . . . I am aware of no other group of investigators who have so freely shared with each other not only their materials but even their unpublished data. The present status of maize genetics, whatever of noteworthy significance it presents, is largely to be credited to this somewhat unique, unselfishly cooperative spirit of the considerable group of students of maize genetics.' (Kass *et al.* 2005)

The paradigm established by the maize group has been replicated by a number of organism-specific groups, each holding regular conferences as discussed above for *Chlamydomonas*. The success of these organism-specific groups has garnered significant conference support from the Genetics Society of America (GSA) and research support from the National Institutes of Health (NIH) and the National Science Foundation (NSF). Perhaps the epitome of group action has been that involving the nematode *Caenorhabditis elegans*. As Jonathan Hodgkin summarized in his article "Early Worms":

A final advantage . . . has been the establishment of a group of enthusiastic and dedicated workers. All of the early genetic work was due to [Sydney] Brenner, but the appeal of the system was such that more and more disciples began to accumulate. As with the mutant strains, so with the scientists: almost every worker in the field has an intellectual pedigree that traces back to a single source. Moreover, most of the early workers had a common background in either bacterial or phage genetics - especially T4. . . The 'phage' influence colored a lot of the early work, for example, the emphasis on powerful selections and rare events, the usefulness of conditional mutants . . . and the need for long-term storage (Hodgkin 1989).

The spirit of sharing strains goes beyond the organism-specific co-operative groups. In his article, Frank Stahl described the 30-year history of Robin Holliday's molecular model of genetic recombination. The model was challenged with experiments made possible by strains of a range of organisms exchanged among geneticists. Stahl concluded:

The junction is there, [except . . .]; mismatch correction contributes to conversion, [except . . .]. That's an impressive record, really. Robin's model was the lightning rod for 30 years of research, and its central assumptions, though modified, have survived every strike. Congratulations, Robin!" (Stahl 1994)

This story illustrates ways in which geneticists interact across organisms on issues that lie at the core of the science. I shall return to this point at the end of this essay.

How Geneticists Work Hard Yet Have Fun

Jim Crow's creative life gives a vibrant example of the synergy between working hard and engaging fully in a hobby. From an early age, Crow's consuming hobby was music. He described to me why he had settled upon playing the viola: "Because string quartets are always looking for a violist." Hartl and Greenberg Temin described Crow's lifelong involvement with music, telling a tale from his graduate days that illustrates this fun-loving spirit:

A memorable incident from Crow's [graduate student] days in the University [of Texas-Austin] 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.' (Hartl and Greenberg Temin 2014)

The powerful influence of a life-long passionate interest in an activity outside the laboratory is also illustrated in the life of Guido Pontecorvo, which spanned the destruction of Jewish life by Fascism in Italy, World War II, and the migration of scientists to the United Kingdom and the United States. His genetics research started in Edinburgh in 1940 with Hermann Muller (who had escaped from Stalin's USSR to Edinburgh), and then matured as a leader in fungal and mammalian cell genetics in Glasgow and London. His pervasive influence in 20th-century genetics shows up in *Perspectives* articles on bacterial genetics (Cavalli-Sforza 1992) and mammalian developmental genetics (Waelsch 1989). His colleague Bernard Cohen has captured Ponte's lifelong bond to the plant life of the Swiss Alps:

Almost invariably, Ponte's overseas academic visits were to places near alpine zones. This reflected his interest in alpine plants, which grew from early enthusiasm for the Italian Alps . . . With Leni, his Swiss wife, he built a small chalet in the Valais region of Switzerland and, from this base, made long-term studies of the ecology of alpine and compiled a major [unpublished] photographic archive. The chalet guest book . . . is an impressive record of the friends who enjoyed their hospitality. Although Leni predeceased Guido, this did not stop him from spending much of every summer and part of each winter in the chalet, often fending for himself, gardening on a 45 degree slope despite hip prostheses and entertaining in the evenings a succession of guests and 'gerisitters.' (Cohen 2000)

Jim Crow established an abiding connection with Japanese genetics, about which he wrote several *Perspectives* article. His article on Hitoshi Kihara not only described Kihara's vast

importance in collecting wild species [but] also described Kihara's life outside science:

Kihara had a life-long interest in athletics. As a student he was active in many sports. His book of photographs . . . shows him involved in baseball, archery, racing, and javelin throwing. He was a skilled skier and traveled with the Kyoto University Alpine club to the snowy heights of Japanese mountains.

. . . Kihara led the Japanese ski team at the Winter Olympics in 1960 and 1964. [On a visit to Mishima] I went to a large public gathering at which Miss Mishima was to be chosen. And who turned out to be the judge to select the most personable and comely young woman? Kihara, of course (Crow 1994).

One last colorful example of ways that geneticists find ways to have fun was described by Scott Hawley in his aforementioned article on the mutational dissection of meiosis in *Drosophila* by Larry Sandler and Dan Lindsley:

The [meiotic] mutations were recovered from wild populations collected in and around Rome at such locales as a winery in Salaria and the city's wholesale fruit market. Larry . . . claimed for years that the collections were made entirely by Dan . . . while Larry conversed with the vintners or the fruit merchants. Larry also claimed that while the fruit sellers were initially suspicious of Dan and his butterfly net, they were reassured by Larry's claims, in the vernacular, that this was the only therapy that Dan's physicians at the asylum found effective. Dan did not speak Italian and was thus fortunately unaware of these conversations (Hawley 1993).

How Public and Private Institutions Have Sustained the Science of Genetics in the United States

The science of genetics has developed along several distinct institutional tracks in the 20th century. The *Perspectives* series has given life to the role of some of these universities and independent research institutes in the United States, while illustrating the key roles of particular individuals in shaping them.

Universities are the established seats for the creation of new knowledge. Indeed, numerous private and public universities hosted the contributors to this "genetics century." Some of these large universities provided homes for the clusters of investigators with complementary interests and talents. Frequently, a university supported genetics from a commitment to agriculture—the improvement of plants and animals. John Weir's article appreciated the formative influence of the Bussey Institution at Harvard University on American genetics in the earliest decades of the 20th century (Weir's 1994).

The Bussey Institution

From a movement led by the physicist Wallace Sabine, a Graduate School of Applied Science was organized [at Harvard] in 1906 to replace the undergraduate Lawrence Scientific School. As part of the reorganization in 1908, Bussey became a graduate school for advanced instruction and research in scientific problems that relate and contribute

to practical agriculture and horticulture—this just at the time when the claims of genetics could no longer be ignored. [William] Castle moved his animals to Forest Hills, soon to be joined by the noted plant geneticist Edward Murray East from the Connecticut Agricultural Experiment Station.

Castle's early work at Harvard was concerned with vertebrate embryology, but with the rediscovery of Mendel's laws in 1900, his interest soon shifted to mammalian genetics . . . Most of his papers dealt with the genetics of mice, rats, rabbits and guinea pigs, but he also wrote on the genetics of horses, sheep and humans, and on race crossing and hybrid vigor. His textbook on Genetics and Eugenics went through four editions. Late in life he became interested in the genetics of the Palomino horse. His last two papers, both on horses, were published in 1961 when he was 94 years old. His first paper, on the plants he had collected while teaching in Ottawa, had been published in 1893, 68 years earlier.

At the Sixth International Congress of Genetics held in Ithaca, New York, in 1932, there were 399 participants from the United States, including Castle, East and 32 of their students . . . The early days of the GSA featured leaders who had trained at the Bussey: . . . 1932 L. C. Dunn Columbia; 1933 R. A. Emerson Cornell; 1934 Sewall Wright Chicago; 1935 D. F. Jones Connecticut Agricultural Experiment Station; 1936 P. W. Whiting Pennsylvania; 1937 E. M. East Harvard; 1938 L. J. Stadler Missouri (Weir 1994).

The Bussey Institution closed in 1938 when the Harvard Board of Overseers rejected the nomination of Raymond Pearl for its director, on the basis of dispute over scientific rigor (Goldman 2002). From that point, the university leadership in the development of genetics in the United States moved westward, often driven by agricultural issues. Thus, the public universities from Cornell through the Midwest to California are each reflected in articles in the Crow–Dove *Perspectives* series that deal with, for example, issues in the genetics of corn, tomatoes, and potatoes.

Caltech

Caltech, recruiting Morgan and Sturtevant in 1926, became a mecca for *Drosophila* genetics. Caltech then reinvented itself under George Beadle in 1946 (Horowitz *et al.* 2004) by recruiting a range of geneticists including Max Delbruck, who created a bacteriophage "church." My article, "Paradox Found" (Dove 1987), described the philosophical culture generated by Delbruck, the intellectual impact of the physicist Richard Feynman, and the doctoral research of the afore-mentioned Charley Steinberg. Caltech's geneticists contributed many articles to the Crow–Dove series. First, Norman Horowitz (1998), Ed Lewis (1995), and Ray Owen (Owen 1989; Owen 2000) (Figure 1D), then Bob Edgar (2004), and even Alfred Sturtevant (2001) posthumously contributed.

Beyond the universities, many of the centers that supported the flowering of genetics in the 20th century were independent research institutions. Marine biological stations gave opportunities for biologists from universities to mingle. Flanking the United States are the Woods Hole Marine Biological Laboratory on Cape Cod, Massachusetts, and the Hopkins Marine Station in Pacific Grove, California. Random

collisions outside the departmental structures of universities seeded several of the new initiatives in the growth of 20th-century genetics.

Marine biological stations: Woods Hole and Pacific Grove

Alfred Sturtevant described the importance of Woods Hole for the emergence of genetics in the United States:

[Morgan] came back [to Woods Hole] in 1890 and spent a very high proportion of the summers here for the rest of his life. 1897 was the year in which the 'Young Turks' took over the laboratory and its management, and Morgan was one of the new trustees elected at the time of that change . . . it really was a revolution in terms of the management of scientific organizations. The director . . . C. O. Whitman [promoted the idea] that a scientific organization should be owned and managed by the people who were working in it. He resisted any plans to fit this laboratory under the wing of any other organization, any university, or any foundation. This was a new idea, and it was a very difficult one to implement. One of the reasons he was able to do it was that he had this extraordinary group of people working here and, as it happened, they came from different universities. Whitman was at Chicago, Wilson was at Columbia, Morgan at that time was at Bryn Mawr, and Conklin was at Pennsylvania. They were all first-rate people and they got along very well together, and the fact that they came from different universities was a great strength in the organization (Sturtevant 2001).

Dianna Kenney and Gary Borisy (2009) described the connection to the emergence of *Drosophila* genetics provided to Morgan by the Woods Hole center. Garland Allen (1978, see footnote 108 on p. 147) has quoted Morgan:

I was, of course, familiar with the important paper of Castle, Carpenter, Clarke, Mast and Barrows and used it in my lecture on experimental zoology (Castle *et al.* 1906).

The Hopkins Marine Station, an outpost of Stanford University in Pacific Grove, California, has played a formative role in introducing molecular biologists to the biological richness of microorganisms. Jay Dunlap (2008) emphasized the role of this institution in bringing together investigators interested in circadian biology. A major force at this Station was the Dutch microbiologist C. B. van Niel. As H. A. Barker and Robert E. Hungate summarized:

[van Niel] did not believe in directing the research of his younger associates . . . As a consequence, the range of phenomena investigated in his laboratory was exceedingly wide and included . . . biology of caulobacteria, cultivation of free-living spirochetes, induction of fruiting bodies in myxobacteria, . . . and the thermodynamics of living systems (Barker and Hungate 1990).

One can trace at least indirectly to C. B. van Niel three initiatives discussed above: Julius Adler's choice of *E. coli* to study chemotactic behavior, Lucy Shapiro's choice of caulobacteria to study asymmetric cell division, and Dale Kaiser's choice of myxobacteria to study cellular interactions. He created a unique environment for microbiology in Pacific Grove.

Beyond these two marine biological stations, two other independent research centers, the Jackson Laboratory (JAX) and the Cold Spring Harbor Laboratory (CSHL), each established a center of excellence in genetics. These centers continue to maintain strong outreach initiatives that bond them with investigators around the world.

The Jackson Laboratory

Elizabeth Russell described the way that the worldwide role of JAX enabled it to survive a disastrous fire in 1947 and develop into the mecca for mouse genetics that it has become:

Would there ever again be a Jackson Laboratory? C. C. Little never doubted. He called us together in Ellsworth, on the mainland not far from the Island, assured mouse box-changers that they still had jobs, and assigned responsibilities to staff and research assistants. When he viewed the ashes around the wreck of the old Lab, he said, 'Now we can see the sea.' . . . We also needed to build up animal resources to supply critical needs of researchers in other institutions. Where would the necessary mice come from? . . . Almost immediately after the fire, a very welcome pile of letters began to pour in. Investigators who had recently received pedigreed mice from the Jackson Laboratory, and geneticists who maintained inbred mouse colonies stemming from our stocks, wrote to offer 'starts' of almost all the strains we had lost, plus some valuable new types . . . The 1947 fire came at a propitious time for the scientific community. Just as large numbers of researchers were coming to depend on animals from outside suppliers, disruption by the fire focused attention on the importance of selecting the right animals for a particular project. The Laboratory's losses in the fire, and rescue by gifts from other mouse geneticists, gave the staff a heightened sense of genetic responsibility. In addition to contributing through their own research, they now wanted to apply genetic know-how to guarantee ready availability and continuity of pertinent, genetically uniform, well-characterized mice for the growing biomedical research community. The Laboratory had added a new phase to its scientific mission (Russell 1987).

The Cold Spring Harbor Laboratory

As described in the article by Phil Hartman, the focus of CSHL on genetics developed in the research of Milislav Demerec, first with *Drosophila* and then with *Salmonella*:

Exactly fifty years ago my father-in-law, Milislav Demerec, coauthored a *GENETICS* paper on X-ray-induced chromosomal breaks in *Drosophila*. . . Then, exactly 25 years ago, he authored a paper on bacterial genetics. . . Why this migration from eukaryote to prokaryote, the opposite of present-day trends? What happened during those intervening 25 years? This is mainly the story of a man deeply involved in a search for the structure of the gene and who, at the same time, quietly developed two institutions at Cold Spring Harbor that emerged under his leadership as a hub of what is now known as molecular genetics.

In the latter part of 1941 Demerec became Acting Director [of the Laboratory] and in 1943 [also] Director of the Department of Genetics of the Carnegie. This move consolidated activities of the two institutions at Cold Spring Harbor, much to the benefit of each . . . The consolidation added to

Demerec's duties because he quietly supervised everything from budgets to mowing the grass to maintaining aging laboratory buildings to arranging purchase of laboratory land along Bungtown Road . . . he had to do much of it himself. There were also formal annual reports to be written and compiled, both for the Carnegie . . . and for the Biological Laboratory . . . Demerec's Carnegie research section includes the names of 62 people in the 19 years he was Carnegie Director; few people are listed more than 2 years in a row. This is an indication of the flow and vitality of the laboratory and the man. [Al Hershey] has said, 'When it came to decisions of importance to research, to the laboratory, or to science at large, he seemed to call on an infallible instinct.' Perhaps that's because he had an infallible instinct about honest people, upon which all the rest depends (Hartman 1988).

The political independence of CSHL was signaled by the failed recruitment of Hermann Muller, who had disavowed his support of Stalinist Russia to return to the United States. Diane Paul described this scenario:

In 1939, Demerec told Frank Blair Hanson, of the Rockefeller Foundation, that 'it would be impossible to place Muller in a State institution in this country and that most privately endowed institutions would also reject him. His long residence in Russia and his widely known book on Communism would militate against his acceptance here.' . . . Demerec suggested placing Muller at Cold Spring Harbor. This was attractive for another reason: Muller could be his own boss and thus avoid conflict with others, as was assumed would occur in a university department. But . . . the deal fell through, in large part as a result of the Carnegie trustees' 'fear of Muller's past political background.' (Paul 1988)

CSHs focus on genetics combined with its public spirit of outreach to become instrumental after World War II in the growth of two worldwide "schools" that generated major advances in genetics: the Phage Group and the Yeast Group. The Phage Group formed around the leadership of Delbruck, who with his disciples taught a hands-on course each summer from 1946 to 1970. As described graphically by Millard Susman:

Students participating in the Phage Course carried home a great deal more than a handful of useful techniques. They felt that they had been initiated into the community of biologists. The course featured seminars by leaders in the field, and the students could sit and drink beer with them on the porch at Blackford Hall or chat with them on the beach (Susman 1995).

I shared with the Belgian geneticist Rene Thomas the stimulating experience of teaching the 1970 Phage Course. Then, in 1999 my laboratory joined with those of the British cancer biologist Chris Potten and the American mammalian biologist Jeff Gordon to initiate a hands-on course in the genetics and biology of the laboratory mouse at The Jackson Laboratory. Years later, I find satisfaction in seeing the emergence of leaders who came to know one another as neophytes in a hands-on course.

After 1970, under the directorship of Jim Watson, the Phage Course at CSHL gave way to the Yeast Genetics Course.

The 30th anniversary of this influential course was celebrated by a reunion, described in an article by Peter Sherwood:

'It's hard to imagine where we'd be today without yeast,' says Watson, who kicked off the reunion on a Friday evening with opening remarks.

Owing to the prodigious talents and dynamic, fun-loving personalities of [Fred] Sherman and [Gerry] Fink, the Cold Spring Harbor Yeast Genetics Course rapidly became a classic. 'I found Fred's deadpan sense of humor always hilarious and still do. I found Gerry's electric intellect and his love of yeast genetics to be energizing and still do,' remarked Ira Herskowitz during the reunion (Sherwood 2001).

The abiding impact of JAX and CSHL on the science of genetics cannot be underestimated.

The research substratum

The substratum on which genetics developed in the 20th century included private and government organizations and modes of interaction among active geneticists. The *Perspective* series cast light on interesting ways that key individuals, communities, and organizations facilitated this emergent science of genetics.

In the United States, research support from the NIH and the NSF rests on the principle of peer review in study sections. This principle depends greatly on the operation of each study section. In a grateful tribute to one of the many outstanding study section secretaries, Jim Crow and Ray Owen described the special qualities that Kay Wilson brought to the early NIH Genetics Study Section:

What did she do that was so great? In the first place, she did her homework. She made a point of getting acquainted with people applying for grants. Often, if something was not clear she would call the applicant and straighten it out before the meeting, or she would call an appropriate person for additional expert advice. The day before the meeting she met with the Study Section Chairman and sometimes others, and they went over each application. Thus, there were very few surprises for her or for the chairman during the meeting.

At the meeting itself, she said little. She regarded it as the chairman's job to run the show. But she sat at his side and, by whispered comments or penciled notes, called attention to points that needed to be brought out. She made sure that things that were supposed to be confidential stayed that way (Crow and Ray Owen 2000).

The intersection between the peer review principle and the spirit of co-operation within groups of geneticists comes into high contrast in the review of proposed publications. As Crow has described, reviewers vary greatly, as do their reviews:

Much of the success of any journal, then and now, depends on the quality of its reviewers. *GENETICS* had good ones, often leaders in the field. [The mutual dislike between Sturtevant and Dobzhansky was well-known.] But on one occasion Sturtevant did make his feelings known, although with characteristic subtlety. *GENETICS* had received two manuscripts. One was by a young cytogeneticist and the other by Dobzhansky. Sturtevant reviewed both. His reply was essentially as follows: The first paper is careful work by

a serious, deserving young scientist, but it does not quite measure up to *GENETICS* standards. I say, reject with regret. The Dobzhansky paper must surely be published. But it is too long for its content and generally overstated. I say, accept with regret (Crow 2006).

The tensions involved in the review of an individual research report are amplified when public policy is at stake. In the aftermath of the atomic bombing in World War II, the United States Government convened a panel of geneticists to evaluate the genetic risks of radiation. Crow described the pitched battles that took place on this panel (majorly between Muller's and Wright's views of the nature of detrimental mutant alleles) and the way in which the chairman, the mathematician Warren Weaver, solved conflicts among strongly held positions:

In what at first appeared to be a strange decision, [the head of the National Research Council Detlev] Bronk appointed as chairman of the genetics committee, not a geneticist but a mathematician, Warren Weaver. The decision turned out to be providential. He had an enormous influence on the direction of biological research. One of his early decisions was to shift Rockefeller funds away from the physical sciences and toward biology, particularly those areas that made the greatest use of physics, chemistry, and mathematics. Weaver was not only instrumental in helping to found the science we now call 'molecular biology,' but is credited with coining the term as well (Crow 1995).

Summary: Sustaining the Core Science of Genetics as it Evolves

During the first part of the 20th century, the science of genetics addressed basic issues in transmission and physiological genetics, shared among organisms. By the end of the century, however, the growing power of molecular genetic analysis in the established "model organisms" focused much of the support of the GSA, NIH, and NSF on the set of organisms with sophisticated molecular genetic analysis, each representing an individual phylum. Gerry Fink referred to this set of organisms as the "Security Council":

With this volume, *GENETICS* announces that *Arabidopsis* has joined the Security Council of Model Genetic Organisms . . . the standard to which all other organisms are compared . . . The idea is that an intense concentration on the genetics of one of the representatives [of a phylum] provides a window on the biology of all the other species in that phylum (Fink 1998).

Geneticists increasingly came to see themselves as fly, worm, mouse, or other organism-centered geneticists. Focusing effort on a particular species has led to explorations wonderfully deep into the biological space occupied by that species.

This *diaspora* has been reflected in the disappearance of the general GSA meeting. Figure 1E illustrates how the 1992 general GSA meeting organized by Silflow and Lefebvre in St. Paul, Minnesota, served the needs of David Perkins to

connect with progress in the genetics of *Neurospora* (not a member of the Security Council). Figure 1F illustrates how Eric Lander, developing the genetic map of the mouse, had deep commonality with Welcome Bender, who had carried out a "chromosome walk" in *Drosophila*. In continuing to support the *Perspectives* series, Jan Drake, Jim Crow, and I aimed to provide a platform on which geneticists at large could converse, in the absence of the annual general GSA meeting (Figure 1A).

Ironically, the transition to a focal organization of genetical research coincided with the period when developmental geneticists were discovering myriad hidden links in the developmental programs used by distinct animal genera. Thus, the science itself is undergoing a degree of synthesis as its practitioners are diverging into different methodological streams. In the 21st century, geneticists are creating methods that transcend individual species, the classic model systems: efficient random mutagenesis by ethylnitrosourea, targeted genomic editing by CRISPR/Cas, and an increasing number of ways to group gene activities into functional clusters. Growth of the science of genetics and its partnership with genomics has led to an explosion in understanding the structure and evolution of populations of living and extinct creatures. Mutational analysis, now commonly reaching molecular resolution, satisfies the demand of experimental biologists to perturb a system to help understand its logic. Will this extensive radiation into many branches of evolutionary and experimental biology make the science of genetics fade as a separate discipline?

An understanding of a biological process of interest requires an organism that displays that process and acquires at least the rudiments of genetic analysis; for instance, mutational perturbation by genomic editing. The science of genetics, evolving along these lines, can serve the community of investigators interested in evolution, or those focused on a particular biological process, whether newly described or previously known as displayed by a member of the Security Council. Geneticists can promote development of genetic analysis in new organisms of biological interest; they can bring to light new genetic phenomena; and they can promote the integration of the information garnered by the reductionist paradigm of 20th-century genetics. For example, each of these transcendent issues at the core of genetics was foreshadowed by particular articles in the Crow–Dove *Perspectives* series: the emergence of *C. elegans* genetics (Hodgkin 1989), the phenomenon of paramutation (Chandler and Alleman 2008), understanding the basis for convergence of function between two phyla (Kaiser 1993), and the respective determinative and homeostatic roles of positive and negative feedback loops elucidated by "the grandfather of systems genetics" Rene Thomas (Brenner *et al.* 1990).

The GSA plays an essential role in supporting the core science of genetics going forward. Its journals, *GENETICS* and *G3*, provide a direct route to primary research data for investigators worldwide, across species. The *Perspectives* column creates a tapestry of personal stories that embody the distinct

culture of the geneticist. I look forward to observing the patterns along which this fabric grows.

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Adam Wilkins has gone beyond the call of editorial duty to give critical advice. His contribution even preceded the Crow–Dove effort when he created the “Roots” column as the former Editor of *BioEssays*. The *GENETICS* editorial office has been a flexibly helpful partner throughout. In Wisconsin, Ilse Riegel and Alexandra Shedlovsky have critiqued matters of style, while Linda Clipson has enhanced the quality of images and graphics. Readers of the articles in this series will appreciate the care invested by each author. Finally, on the occasion of his centennial, I raise a toast to Jim Crow. He will live forever in the hearts of those privileged to work with him, and in the minds of those who will enjoy reading the articles of the *Perspectives* series.

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