



“The Real Point is Control”: The Reception of Barbara McClintock’s Controlling Elements

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Abstract. In the standard narrative of her life, Barbara McClintock discovered genetic transposition in the 1940s but no one believed her. She was ignored until molecular biologists of the 1970s “rediscovered” transposition and vindicated her heretical discovery. New archival documents, as well as interviews and close reading of published papers, belie this narrative. Transposition was accepted immediately by both maize and bacterial geneticists. Maize geneticists confirmed it repeatedly in the early 1950s and by the late 1950s it was considered a classic discovery. But for McClintock, movable elements were part of an elaborate system of genetic control that she hypothesized to explain development and differentiation. This theory was highly speculative and was not widely accepted, even by those who had discovered transposition independently. When Jacob and Monod presented their alternative model for gene regulation, the operon, her controller argument was discarded as incorrect. Transposition, however, was soon discovered in microorganisms and by the late 1970s was recognized as a phenomenon of biomedical importance. For McClintock, the award of the 1983 Nobel Prize to her for the discovery of movable genetic elements, long treated as a legitimation, may well have been bittersweet. This new look at McClintock’s experiments and theory has implications for the intellectual history of biology, the social history of American genetics, and McClintock’s role in the historiography of women in science.

Keywords: McClintock, Barbara, maize, corn, genetics, transposable elements, controlling elements, gene expression regulation, women scientists, development

In 1944, Barbara McClintock was already among the nation’s most respected geneticists. But that summer, she performed an experiment with maize, or Indian corn, that led to her most famous discovery. Among the progeny of the plants she grew that summer, she soon identified chromosomal elements that controlled the timing and frequency of mutation in the plant. She then found that these elements transposed, or changed position on the chromosomes. Transposition did not strengthen her reputation at the time, but it has since helped rank her among the best-known women scientists.² Biologists today recognize transposition as a fundamental type of chromosomal behavior,

widespread in nature. McClintock was awarded the 1983 Nobel Prize in Physiology or Medicine – 35 years after the discovery. The story of that three-decade interval has become one of the most powerful moral tales in the history of recent science.

McClintock discovered transposition in the course of experiments on “mutable” or spontaneously mutating genes in maize.³ In 1941, 14 years after her Ph.D., she had joined the staff of the Carnegie Institution of Washington’s Department of Genetics at Cold Spring Harbor, Long Island, New York. At Cold Spring Harbor, she continued work begun earlier on phenomena associated with the physical breakage of maize chromosomes. Chromosome breakage resulted in the loss of genes, and hence in mutations. In her 1944 experiment, McClintock had set the conditions so that the chromosomes would tear themselves apart and rejoin in new combinations, providing mutations that could be used in identifying and locating new genes. Though the technique was novel, the approach was conventional: while other geneticists generated mutations by damaging the chromosomes with X-rays, she constructed chromosomes that broke. Her intent was to produce conventional mutations, but the 1944 experiment also yielded a huge number of spontaneously mutating, “mutable” genes. When pigment genes became mutable, the result was a speckled or mottled pattern in the leaves or kernels. McClintock’s cytogenetic brilliance lay in recognizing the genetic mechanisms that underlay visible patterns of gene expression in her corn. In 1946, she identified a genetic locus responsible for breakage of one of the chromosomes. She immediately recognized that chromosome breakage at this locus was “controlled,” both in timing and frequency.⁴ Soon thereafter, she found that a second locus was also required for breakage. She named the first *Ds*, for “dissociation,” and the second *Ac*, for “activator” of dissociation. Faced with anomalies in her attempts to map these loci, by mid-April 1948 she proposed that both elements could transpose.⁵ She soon realized that breakage was only one of several effects of the movable elements. Transposition accounted for her spontaneously mutating genes: when a movable element jumped into a gene, the gene was inactivated; when it jumped out again, gene activity was restored.⁶

These results first appeared piecemeal in her annual reports to the Carnegie Institution between 1945 and 1949.⁷ In 1950 and 1951 she summarized them and exposed them to a wider audience, first with a journal article, then with a public talk before nearly 300 scientists at the annual Cold Spring Harbor Symposium, and then with a published paper in the Symposium’s proceedings.⁸ The reaction in the scientific community was portrayed vividly in Evelyn Fox Keller’s widely read biography of McClintock.⁹ Drawing heavily on interviews with McClintock herself, Keller’s narrative presents

transposition as challenging the prevailing "beads on a string" theory of the gene, by which genes were held to be static, independently acting units.¹⁰ According to this story, most geneticists, committed to the paradigm of a static genome as a requirement for the gene-mapping studies of mainstream genetics, scoffed at McClintock's findings.¹¹ Shocked at this unexpected rejection, the story continues, she amassed yet more data, only to be rejected, if anything, more firmly still. McClintock then supposedly withdrew from the genetics community, ceasing publication and lecturing, and pursued her studies with inner confidence but outer disappointment. At last, in the 1960s and 1970s, a new generation of molecular geneticists confirmed the existence of transposition in bacteria and other organisms. McClintock was exonerated, legitimated. Within months of publication of Keller's biography, McClintock was awarded an unshared Nobel Prize in Physiology or Medicine.

In Keller's arguments, McClintock's rejection was both intellectual and gender-biased. Underlying the negative reaction to McClintock's findings was a backlash against what Keller portrayed as McClintock's challenge to their masculinist style of science. Keller argued that McClintock brought intuition and empathy to genetics and thereby offered an alternative to the prevailing reductionist, impersonal style followed by most scientists. For Keller, McClintock is a guide to how a reformed science might be different from traditional, "masculine" science.¹²

Many later writers have read Keller as arguing that McClintock had a "feminine" style of science. In subsequent biographical sketches and scholarly feminist analyses, McClintock's style of science was portrayed as non-masculine, holistic, hermetic, intuitive, non-interventionist, non-reductionist, rejected by scientists.¹³ She was "a mystic by nature, who tended to think intuitively . . . utterly different from the logical thinking to which experimental scientists are accustomed."¹⁴ "Rather than separate herself emotionally from her objects of study, she became intimately involved with her corn plants."¹⁵ She worked "virtually in isolation for over thirty years," and "never gave lectures to build her career or consulted with her colleagues."¹⁶ Her science was different from "inherently masculine" normal science in its views of "nature, domination, and control."¹⁷

By the late 1980s, Keller bemoaned the fact that her book had become a "manifesto of feminine science."¹⁸ She wondered why people, feminists included, seemed able only to "count to two" to recognize only one alternative to masculine science: feminine science.¹⁹ The third alternative, non-gendered science, seemed ungraspable by her colleagues. Yet other scholars took Keller to task, arguing that she wanted it both ways: to represent the feminist critique yet not completely alienate the scientists. Which was it, they asked, was science gendered or not? Keller patiently reiterated her now-nearly-ten-year-

old argument that feminine was not the only possible alternative to masculine and by attempting to decouple “gender” and “sex.”²⁰ The story of rejection, mysticism, and redemption has remained the standard interpretation of McClintock’s life.

Among scientists, the McClintock myth was transformed. Feeling attacked by feminist outsiders, they locked arms and insisted she had never been ignored. Misunderstood, perhaps. The mysticism of the feminist and lay versions of the myth transmuted into brilliance, intuition, and a cryptic style of communication. “Her powers,” wrote one scientist, “derived from reasoning so well developed that the thesore and QEDs of her papers and conversations left others straining to catch up.”²¹ The result of this well-developed reasoning, her interpretation of transposition as a system of genetic control, was not ignored or dismissed, but rather “could not be ascertained.”²² While to the feminists, scientists had ignored McClintock’s straightforward but revolutionary discovery, the scientists themselves said they merely had been baffled by a brilliant but knotty concept, puzzlingly presented.²³

The standard McClintock narrative has been put to work in several ways. For feminist scholars, McClintock has become an icon. She has become an “inevitable example,” with Marie Curie, of a woman who achieved scientific eminence.²⁴ Her portrait graces the dustjacket of the second volume of Margaret Rossiter’s comprehensive history of the systematic discrimination faced by women scientists in twentieth century America.²⁵ For those who criticize the exploitative character of science and the clubby patriarchy of its practitioners, McClintock symbolizes both the risks women run and the prices they pay for challenging masculine norms. To them, her late awards are simultaneously a legitimization of her and a critique of her detractors. For these authors, McClintock is a tragic and noble figure. For others, she is a hero. Children’s stories exalt her as an exemplar of determination, perseverance, and individualism, and use her story to suggest that justice will come to those who wait.²⁶ The story has inspired many girls and women to enter (or remain in) science – a population as deserving of role models as it has been deprived of them.

The narrative that makes McClintock a martyr to women and a hero to children and scientists hinges on one unquestioned fact of McClintock’s science: that the main point was genetic transposition. All of the mythologies require a constant thread from what McClintock presented in the 1950s and what she was ultimately recognized for. “Barbara McClintock’s notion that genes could jump around on chromosomes was long ignored by orthodox scientists,” writes one biographer.²⁷ “Today, McClintock’s discovery is called genetic transposition,” writes another.²⁸ McClintock’s “notion that genes could jump around on chromosomes was long ignored by orthodox scien-

tists... Then in the 1960s further advances in molecular and microbial genetics proved her right.”²⁹ “To geneticists at the time,” writes a molecular biologist, McClintock’s discovery was like “claiming that the kitchen could occasionally jump into the attic in the middle of the night.”³⁰ The Introduction to a *festschrift* for McClintock’s 90th birthday discusses – amid a clear-headed discussion of the McClintock myth – McClintock’s “astounding announcement, complete with convincing evidence, that genes could move.”³¹ Her Nobel Prize was awarded “for her discovery of mobile genetic elements.”³² McClintock herself said that she was talking about transposition, and that no one could believe her.³³

Yet since McClintock’s death in 1992 a wealth of documents has become available, and these tell a different story. Foremost among these are McClintock’s voluminous research notes and much correspondence, long thought lost.³⁴ In addition, other archival collections are now open or more accessible to scholars. The most important of these are the Marcus Rhoades Collection at Indiana University’s Lilly Library and the George Beadle Collection at the California Institute of Technology Archives. Most recently, tapes and transcripts of several interviews taken with McClintock between 1978 and 1980, as well as interviews with McClintock’s friends and colleagues, have become available.³⁵ The research notes enable a detailed reconstruction of McClintock’s discovery of and continued work on controlling elements, while the interviews yield a rich, complex, and sometimes contradictory portrait of how McClintock viewed herself and how others saw her.

These documents force a revision of the standard narrative. For McClintock in the late 1940s and 1950s, transposition was a means to an end. It occurred by conventional mechanisms, was immediately accepted by other scientists, and does not seem to have shocked McClintock particularly. Transposition was only offensive to other scientists – and only interesting to McClintock – in the context of a theoretical and speculative argument in which she framed it. This argument was about gene regulation (“control”), biological development, and, eventually, evolution. The discovery of transposition in bacteria in the 1960s led to a formal rejection of McClintock’s controller argument in the scientific community; a linguistic shift from “controlling elements” to “transposable elements” – and attendant mythologizing – has buried its traces.

That McClintock was arguing for genetic control and not merely transposition has been recognized before now. Keller recognized the controller argument, even quoted McClintock talking about control, and noted that for McClintock, “the principal significance of transposition in maize lay in its regulatory function.”³⁶ This observation, a frequent undercurrent but never a

primary theme, has been utterly lost to later biographers and has been left out of the standard narrative. Scientists tend to use “transposition” as a shorthand for McClintock’s discovery; as will be shown below, when discussing McClintock at length, many acknowledge that control was her primary argument. The archival sources now available leave no doubt that the concept of control preceded the discovery of transposition, that control motivated her work on transposition, and that she continued to think about control even in work that did not involve transposition.

Showing that control was McClintock’s greatest concern does more than shift the burden of the standard narrative onto the back of new concept; it enervates the standard narrative. If the real point is control, then McClintock was not proved right when the full significance of transposition became appreciated in the 1970s. Her work was not legitimated but rather reinterpreted. The laurels heaped upon McClintock feted what was to her a secondary insight and buried what she felt was her most important contribution. Emphasizing control makes her less of an icon, more of a human.

Going Public

Outside her informal reports for the Carnegie Institution *Year Books*, McClintock’s first publication on mobile genetic elements appeared in the fall of 1950.³⁷ This paper, McClintock’s first in five years, and her first on maize in six, marked a departure from the sort of papers on which she had built her impeccable reputation as an observer and experimentalist. This one had no data.

The paper emerged from a bout of intense activity between late February and early April of that year. McClintock spent several weeks working especially intensely in the lab and then staying up late at night, writing notes to herself and letters to her close friend and colleague Marcus Rhoades, a maize geneticist at the University of Illinois. She had met Rhoades in 1928 when he came to Cornell as a Ph.D. student, and he had discovered a new mutable gene, *Dotted*, in maize in 1936.³⁸ He thus was both sympathetic and knowledgeable. In one two-week burst in March, McClintock sent him tens of pages of typescript, much of it scribbled over, lined through, and feverishly annotated between the lines and down the margins.³⁹ In these heated letters McClintock developed a theory of gene action that she felt explained one of the central problems of biology: embryological development and differentiation.

From the birth of modern genetics, embryologists had complained that genetics did not explain how one set of genes could produce the many types

of tissue that make up any complex organism – the “paradox of nuclear equivalence.”⁴⁰ Since the simplest model of the gene was as an independent, autonomous, trait-producing entity, embryologists reasoned that genes must be regulated by factors outside the nucleus, i.e., in the cytoplasm. Geneticists, meanwhile, ignored the question of gene regulation. Thomas Hunt Morgan, father of *Drosophila* genetics but an embryologist by training, was the primary architect of the split that redefined the study of heredity as the science of genetics.⁴¹ For his part, Morgan thought the problem intractable and unnecessary; there were plenty of readily soluble problems in genetics. “In a word,” Morgan wrote in 1926, “the cytoplasm may be ignored genetically.”⁴²

In her March burst McClintock reached a solution to the development problem without invoking the cytoplasm. Genes were regulated by elements within the chromosomes. The regulation was accomplished by tiny fragments of heterochromatin, a mysterious and then-fashionable form of chromosomal material that turned dark with standard stains and contained few if any genes. It tends to be located at characteristic sites on the chromosomes, such as the tips and at structures called knobs. Heterochromatin was involved in a phenomenon, known since the 1920s, called the position effect.⁴³ Geneticists sometimes induced large-scale mutations in which a large chunk of a chromosome might be broken off and then reattached upside-down or stuck on to the end of a different chromosome. In such cases, a gene formerly in the middle of a chromosome arm might be brought into proximity with a knob. Transposed – the term predates McClintock's discovery – to this new position, that gene, formerly active, could become silent. McClintock was familiar with position effects and was one of the world's experts on chromosome knobs. She became convinced she had discovered a novel type of position effect. The twist in her argument was that the heterochromatin was going to the genes, rather than the other way around.

McClintock reasoned that her movable elements were tiny fragments of heterochromatin that bounced around the chromosomes during plant growth and development. When an element landed near or in a gene, it caused a local position effect, inhibiting the gene. The inhibition was reversible: when the element transposed again, the gene was restored to normal activity. Mutable genes were explained; their on-and-off expression patterns were the result, not of chemical changes in the gene, but of a reversible modulation imposed by the transposable elements.

She then made a great speculative leap, from mutant behavior to normal activity. The plants in which she observed this behavior were sick. Their ancestors had been bombarded with X-rays and selected for their likelihood of undergoing spontaneous chromosomal rearrangements. Many died before reaching maturity; others were pale and fragile, with wrinkled leaves and

shriveled kernels. The sudden appearance of so many spontaneously mutating genes – her 1944 experiment tripled the number of mutable genes known in maize – suggested to her the disruption of the normal “stream of enzymatic reactions” that controlled development.⁴⁴ Genes were being turned on and off inappropriately. In her March burst, she concluded that *Ac* and *Ds* were dislodged fragments of a highly organized, tightly controlled system of gene regulation. It was a pathological condition that reflected a normal – and normally invisible – process.

With this theory, McClintock set out to do no less than unify all of biology. In describing all this to Marcus Rhoades, she complained that genetics had grown sterile. The “good old days of mapping genes” without a main clarifying objective are over, she told him. She hoped her theory would bring about a “phase of integration” among biochemistry, genetics, embryology, and histology. “Some of the geneticists see this very clearly,” she told him, “but a great many still cling to the good old chemical change in the gene to explain the change in phenotypic expression. The dilemma is becoming more obvious each year.”⁴⁵

McClintock was unaccustomed to such grand theorizing and did not do it lightly. She knew she could not yet prove what she believed true. But she was convinced that the field needed her theory. On March 30, 1950, she asked Rhoades to read a manuscript she was preparing. He was, she said, “the only one capable of making a judgment based on the knowledge of the material.”⁴⁶ The paper would present her theory – without the data: “I should very much like to get this information distributed about as soon as it is in the state to do so without going through a detailed discussion with all the data. If the ideas could get floating [*sic*] about, the data could follow shortly.”⁴⁷

Such a bold move indicates her professional standing and personal security. By 1950, McClintock was one of the country’s leading geneticists. At the age of 37 she had served as Vice President of the Genetics Society of America; at 43, in 1945, she served as its President. She had received prestigious fellowships, including a National Research Council award and a Guggenheim. At the young age of 41 she became the third woman to be elected to the National Academy of Sciences. She had received honorary degrees.⁴⁸ McClintock had the standing to publish a speculative paper and be listened to.

McClintock wrote the paper in late spring, sent it to Rhoades for comments, revised it, and sent it in to the *Proceedings of the National Academy of Sciences*. *PNAS* was an unusual journal. The house organ of the National Academy of Sciences, it accepted only articles written or communicated by members (today, other kinds of submissions are allowed). No peer review was required; that McClintock, or any other National Academy

member, submitted a paper was considered sufficient quality assurance. Further, the journal had high prestige and visibility, and publication was generally rapid. Sending her paper to *PNAS* thus assured McClintock a wide readership for her speculative but, she hoped, discipline-shaking theory.

Even as she wrote and revised the paper, she did not expect it to be well received. "I am not too hopeful of the reception," she told Rhoades in July, "and expect some scorn or amazement at my dive into the deep. Again, it may not be understood."⁴⁹

The published paper was indeed data-free. It contained none of the tables, kernel ratios, or photo-micrographs that were standard in cytogenetics papers, including McClintock's own. Data were relegated to a footnote, where she indicated that her Carnegie Institution reports contained "more detailed summaries of some of the observations detailed in this paper."⁵⁰ McClintock showed a remarkable rhetorical style when she acknowledged that "the accumulated observations and data" from her studies were "so extensive that no short account would give sufficient information to prepare the reader for an independent judgment of the nature of the phenomenon. It is realized that this is unfortunate."⁵¹ Surely few geneticists had the strength of reputation to make this argument: she presented no data because she had too much.

She then alluded to a series of large reports she had been sending to Rhoades since the beginning of the year: "Manuscripts giving full accounts of some of this phenomenon are in preparation. Since this task will require much time to fulfill, the author has decided to present this short account of the general nature of the study, and the conclusions and interpretations that have been drawn."⁵² She evidently intended these reports as chapters of a large monograph, but she never published them.⁵³

In the paper, she argued that her heterochromatin-based controlling mechanism explained all cases of variegation, in all organisms. The patterns on her mutable kernels and leaves were similar to those in evening primrose (*Oenothera*), which had been attributed to position effect. Also, they resembled the patterns in fruitflies (*Drosophila*) that were believed to be caused by heterochromatin position effects. McClintock could not believe the parallels were coincidental: "The similarities are too great to be dismissed as being due to causally unrelated phenomena."⁵⁴

The remainder of the paper addressed the issue of control. "There can be little question," she wrote, "that transpositions of both *Ds* and *Ac* occur and that the time of their occurrence in the development of a tissue is under precise control." She offered no suggestion of the cellular elements that might instantiate that control. McClintock recognized that she might be criticized for excessive speculation: "It may be considered that these speculations with regard to heterochromatin behavior and function have been carried

further than the evidence warrants.” She conceded that “this may be true,” but nevertheless, she continued, “it cannot be denied that one basic kind of phenomenon appears to underlie the expression of variegation in maize.”⁵⁵

McClintock then found an ally of dubious benefit: Richard Goldschmidt. A brilliant but cantankerous German emigré, Goldschmidt had infuriated geneticists for years with his gadfly attacks on classical genetics and the newly established synthesis of Mendelism and Darwinism. Goldschmidt dissented from the genetic orthodoxy by challenging the method of transmission genetics and its emphasis on mutations as definers of hereditary units. In *Physiological Genetics* (1938) and in *The Material Basis of Evolution* (1940) he argued that genes were not autonomous, independent beads, but rather their activity was set by a web of interactions determined by a given gene’s chromosomal position. The unit of heredity, to Goldschmidt, was not the gene but the entire chromosome.⁵⁶

Within months of publication of McClintock’s *PNAS* article, Goldschmidt penned an encomium to it, which he published in *The American Naturalist*.⁵⁷ Her paper gave him an opportunity to discuss her “most remarkable work on so-called mutable loci in maize.”⁵⁸ Goldschmidt was excited about McClintock’s work because it supported his own eccentric theories of the gene. After reviewing her findings and tracing the logic of her analysis as revealed in her annual reports to the Carnegie Institution, he argued that her theory explained several “facts which have been known for a long time without ever having found their proper place within the Mendelian concepts and which now fall in line with the new data under discussion.”⁵⁸ For Goldschmidt as for McClintock, a gene was not a static unit but a sensitive, dynamic structure subject to nongenetic control.⁶⁰

McClintock had been an admirer of Goldschmidt at least since the early 1930s. She had spent time in his laboratory in Dahlem while on a Guggenheim fellowship in 1933–1934, and she seems to have followed closely his speculations on the gene. Like Goldschmidt, McClintock was prepared to abandon the term “gene” altogether. In January 1951 she echoed Goldschmidt’s words in a letter to George Beadle: “It seems to me that we might well stop dealing with genes in the old sense and attempt to view the nucleus as an organized system with various types of controls of the action” of the genes.⁶¹ She began to refer to her movable elements as “controlling units” to reflect their function. McClintock was waist-deep in a major theoretical argument over the very nature of heredity and development. For a geneticist whose career had been built on observation and experiment, all this theory was discomfiting. She told Beadle, “I don’t really like working on ‘fundamental problems’ and long for the old days.”⁶²

The 1951 Symposium

The next summer she presented her theory in a paper at the 1951 Cold Spring Harbor Symposium. In the standard McClintock narrative, the talk, “dense with statistics and proofs,” was not grasped by the audience.⁶³ According to McClintock, the response to her paper was “puzzlement, even hostility.”⁶⁴ Keller wrote that the reaction from the audience was “stony silence. With one or two exceptions, no one understood. Afterward, there was mumbling – even some snickering – and [there were] outright complaints.”⁶⁵ Nearly 30 years later, McClintock herself said in an interview that in “1951 I gave a Symposium paper at the Cold Spring Harbor Symposium that nobody understood.”⁶⁶

The Cold Spring Harbor Symposium, established in 1933, had since 1941 become the most prestigious conference in genetics. Organized by Milislav Demerec, director of the laboratories at Cold Spring Harbor, and dominated by phage and bacterial geneticists such as Max Delbrück, Salvador Luria, Joshua Lederberg, and others, the Symposium became the focus of an annual pilgrimage for microbial geneticists each June.⁶⁷ Its published proceedings collected not only the papers read at the meeting in the order they were presented, but also edited accounts of discussion following the papers.⁶⁸

June, 1951 was the eve of the molecular theory of the gene. In 1952, next door to the Cold Spring Harbor auditorium, Alfred Hershey and Martha Chase performed their “blender experiment,” which convinced microbial geneticists that DNA was the hereditary material.⁶⁹ The following year, James Watson and Francis Crick published – and Watson presented at Cold Spring Harbor – their model of the DNA double helix.⁷⁰ After 1953 genes were understood as chains of nucleotides. But in 1951, a genetical old guard was battling a new group of young turks and the gene-as-black-box was under strain. In this case, however, it was the old guard who were challenging the status quo. Geneticists who worked on complex, old-fashioned organisms such as maize and fruitflies were arguing that genes were parts of great chromosomal complexes that interacted with each other and responded to the environment. On the other hand, the new school, the microbial geneticists, had found new power in the simple assumption that genes acted like beads on a string. Their interpretations of exciting new phenomena such as bacterial conjugation and viral infection depended on a simple gene model. Yet such a view could not explain many of the complex results of the maize and fly geneticists.

There were some crossovers. George Beadle had trained in maize genetics at Cornell in the 1920s, just a couple of years behind McClintock. From 1934 to 1940, at Caltech and at the Pasteur Institute, he had collaborated with Boris Ephrussi to examine the genetics of *Drosophila* eye development.

Then, at Stanford, he and biochemist Edward Tatum had taken up the genetics of biosynthetic pathways in the mold *Neurospora*. This work led to their 1941 proposal that each gene produced a single enzyme.⁷¹ The one-gene, one-enzyme hypothesis was not widely accepted in the 1940s; it was, indeed, the crux of the debate at Cold Spring Harbor in 1951.⁷²

Like Beadle, Milislav Demerec was a crossover; having trained in corn genetics, also at Cornell, he now maintained both a fruitfly and a bacterial lab. He described the crisis in the gene theory in the Foreword to the Symposium volume, writing that “the original problem of defining the unit of heredity . . . has not yet been solved.” In fact, he continued, the more geneticists learned about genes, the less they understood them:

Ten years ago they were visualized as fixed units with precise boundaries, strung along chromosomes like beads on a thread, very stable, and almost immune to external influences. Now, however, they are regarded as much more loosely defined parts of an aggregate, the chromosome, which in itself is a unit and reacts readily to certain changes in the environment.⁷³

The Symposium’s opening session, on “Theory of the Gene,” addressed this question. Papers in the session included one by a pair of young turks, Norman Horowitz and Ars Leupold, now a classic in the one-gene, one-enzyme literature, and one by a conciliatory member of the old guard, Lewis Stadler, who had brought McClintock to the University of Missouri in 1936. But the session led off with iconoclastic papers by Goldschmidt and McClintock. That Goldschmidt gave the lead paper shows not only that despite his crankiness he could still command an audience, but also that in times of intellectual upheaval dissident views are more easily tolerated. Early in his paper, he challenged Beadle, one-gene, one-enzyme, and the gene. The Beadle-Tatum hypothesis, Goldschmidt argued, reified the gene as an entity that stopped working when it was mutated. Beadle’s “extrapolation from the mutant action to the existence of the original gene” led him to a fallacy. “If the A-string on a violin is stopped an inch from the end the tone C is produced,” Goldschmidt wrote. “Something has been done to a locus in the string, it has been changed in regard to its function. But nobody would conclude that there is a C-body at that point.”⁷⁴ Similarly, a specific mutation did not prove the existence at that site of a gene “for” the mutated trait. McClintock’s “brilliant work,” he said, proved that in corn, “mutable loci are actually position effects produced by genetically controlled and repeating transpositions and translocations.”⁷⁵ This work, he argued, confirmed that “the gene” was an artifact of the way geneticists worked. The true unit of heredity was not the gene but large portions of chromosomes that interacted to produce traits.

McClintock followed Goldschmidt. Her talk was reportedly over two hours in length and in printed form it filled 35 oversized pages of small type.⁷⁶ In it, she aligned herself with Goldschmidt, both implicitly and explicitly. Twenty-three pages into her paper, she wrote, "It will be noted that use of the term gene has been avoided in the foregoing discussion."⁷⁷ This did not, she continued, imply a denial of the existence of genes. But the gene concept, she said, stemmed from studies of mutation, and so by definition excluded other kinds of chromosomal elements or metagenetic activity. "The author agrees with Goldschmidt," she wrote, "that it is not possible to arrive at any clear understanding of the nature of a gene, or the nature of a change in a gene, from mutational evidence alone."⁷⁸ McClintock invoked Goldschmidt again in her conclusion: "Evidence, derived from *Drosophila* experimentation, of the influences of various known modifiers on expression of phenotypic characters has led Goldschmidt (1949, 1951) to conclusions that are essentially similar to those given here."⁷⁹

Being a review, her paper had little data beyond her stunning micrographs of chromosomes and photographs of kernels. But what data there were demonstrated transposition, not control. She provided one table: it showed that *Ac* was in some plants unlinked to *Ds* and therefore probably physically distant, yet in those plants' descendants it was tightly linked and therefore close to *Ds*. It was solid evidence that *Ac* transposed. The mechanism of the movement was conventional, "one that can give rise to translocations, deficiencies, inversions, ring-chromosomes, etc., as well as the more frequently occurring dicentric chromatid formations" – all standard and uncontroversial phenomena.⁸⁰ The second half of the paper is mainly a theoretical argument for transposition as a means of controlling gene action in development. She later acknowledged that this was the main point of the paper: it was a "very important paper," she said, "in the way that I tried to bring out that genes had to be controlled."⁸¹

Following the meeting, McClintock's friend and colleague Ernst Caspari summarized the meeting in the pages of *Science*, the most widely read American scientific journal. Caspari noted the debate over the nature of the gene and he placed McClintock's paper squarely within it: "Among the papers dealing with this aspect of genetics," he wrote, "McClintock's representation of her work on 'Chromosome Organization and Gene Expression' aroused particular interest."⁸² Even if Caspari were inflating the impact of McClintock's paper, such a statement in a widely read journal surely influenced others' recollection or understanding of her talk. While it seems to be true that no formal discussion followed her talk, several printed comments after other papers mention McClintock's work.⁸³ Photos from the meeting show her in animated discussion during breaks between sessions. Formal

discussion is only one measure of a paper's success. McClintock's paper did arouse interest, although it seems it was expressed in small groups, rather than in the formal setting of the Symposium session.

In interviews conducted in 1996 and 1997, Symposium attendees claim it was the control theory, not transposition *per se*, that they could not understand. They understood in a general way that she was arguing these elements moved in a coordinated way to control gene action. But they could not see how the transpositions were anything but random. In 1996, bacterial geneticist Norton Zinder remembered that "*Everybody* took seriously the transposition. What she wanted was that transposition was the regulatory control of development. And nobody there, or at least the very bright geneticists in the room, could understand how stochastic processes could really be involved in something as organized as developmental regulatory stages."⁸⁴ Joshua Lederberg agrees. What made her paper difficult, he said in 1996, were her "epigenetic hypotheses about the significance of gene jumping. And she was never very clear about that. That's still part of her presentation that remains quite vague. How she brings this in as a developmental phenomenon."⁸⁵ Similarly, Waclaw Szybalski, a close friend of McClintock's who had spent hours talking with her, remembered that he could accept transposition, but that her interpretation had left him puzzled: "While I was convinced that she had good evidence that things moved, that this has any significance for development I was not convinced, because she did not present anything to me which would convince me at that time or even later."⁸⁶

Why should we believe these scientists' recollections over McClintock's own words? First, taken literally, her own recollections do not fit the available evidence. Her letters of 1950 show she had not expected her theory to be understood. After the meeting, she did not express any crushing disappointment in letters to Marcus Rhoades or George Beadle, though she confided many other black thoughts to them both before and afterward.⁸⁷ Milislav Demerec, director of the Cold Spring Harbor facility, suggested in 1953 that McClintock in fact had enjoyed the 1951 meeting. Since well before 1951, McClintock had cut back on her attendance at meetings. In 1953, Demerec wrote to George Beadle that he had "urged her many, many times to attend meetings, but she never seems to wish to do so, although when she is together with a group she enjoys it thoroughly, as was shown during the last symposium on genes here [i.e., the 1951 meeting]."⁸⁸ It seems likely, then, that the disappointment she expressed in 1981 set in some time after the summer of 1951.

Second, the scientists' statements do fit the data. Symposium attendees would have had little reason to doubt transposition. McClintock already had a long record of discovering surprising phenomena that turned out to

be true. Her technique was known to be impeccable, her analytical skills prodigious. She presented genetic evidence of a change in chromosomal location and graphic evidence of the mottling characteristic of mutable genes. Her alliance with Goldschmidt may well have contributed to skepticism about her theorizing, but could hardly have undermined the credibility of her data.⁸⁹ McClintock, who hated playing politics, may not have cared, or may even have taken a perverse pleasure in aligning herself with a dissident like Goldschmidt. Nor was transposition itself as shocking to many as it has been made out to be. It was but one of several challenges to the beads-on-a-string model. Many drosophilists and even bacterial geneticists had had some firsthand experience with maize and could easily grasp at least the thrust of her argument. The mechanism she proposed was conventional; the elements moved, she argued, by means of chromosome breakage and refusion, as she had shown conclusively in her earlier work and as others had shown in other organisms.⁹⁰ Most importantly, the essence of McClintock's argument was known to other geneticists. More than 30 symposium attendees were familiar with McClintock's transposition/controller story through personal contact with her – not counting those who may have read her Carnegie reports.⁹¹ Indeed, one highly respected member of the audience had seen transposition for himself, in his own corn plants.

Rediscovery

In the summer of 1948, Robert A. Nilan, a young Canadian biologist, began Ph.D. work in Madison, Wisconsin. His advisor was Royal Alexander Brink, a leading figure in maize genetics, chairman of the genetics department at the University of Wisconsin. Brink had a reputation for clean and trustworthy, if not dazzlingly imaginative, experiments. When Nilan joined Brink's group, Brink handed him a fistful of maize papers and told him about McClintock's new work on mutable genes. He told Nilan that his project was to be a reinvestigation of the first known mutable gene, the *P* locus. Mutations at the *P* locus produce colorful patterns in the pericarp, or outer covering of the kernels, of Thanksgiving Indian corn. Did transposition of tiny inhibitory elements explain the mutations at the *P* locus?⁹²

It did. The crucial plants were harvested in the summer of 1950, and by the time Brink and Nilan completed their analysis, in October or November, they were sure that transposition was occurring at the *P* locus.⁹³ They wrote a quick note for the *Maize Genetics Cooperation News Letter*, an informal annual publication for maize workers, which appeared the next March.⁹⁴ Nilan and Brink called their new element "*Mp*," for "modulator of pericarp." In 1952 they published their findings in *Genetics*.⁹⁵ They noted that the

patterns were very similar to those produced by McClintock's *Ac*. (It turned out that *Mp* was in fact identical to *Ac*.) Nilan finished his thesis by June 1951, at which point he headed west for a position at Washington State University. Brink headed east, for Cold Spring Harbor and the 1951 Symposium. Brink, therefore, was one audience member that June who did not doubt the existence of transposition. Lederberg, whom Brink had hired at Wisconsin, and his student Zinder, had had regular updates from Brink and were also familiar with transposition.⁹⁶

Brink admired McClintock enormously; nevertheless, through the 1950s tension mounted between them over the significance of transposition. According to Jerry Kermicle, who joined Brink's group as a student in 1957, Brink deliberately avoided use of the term "controlling elements," which McClintock began using in 1955. "That's where the nexus of the tension was" between them, he said.⁹⁷ Population geneticist James F. Crow, who lunched with Brink nearly every day during this period, recalled that "her use of the words 'controlling elements' didn't sit well, and most people here, especially [population geneticist] Sewall Wright and R.A. Brink, and by extension me, thought that she was probably wrong on that account."⁹⁸ Brink, and soon his lunch companions, used more purely descriptive terms such as "modulating element" and "transposable element" to strip away the functional connotations of "control."⁹⁹

Brink understood the essence of McClintock's argument. The implication of her work, he wrote in 1960, was that "the various loci are progressively activated during development of the individual by controllers functioning in genetically fixed ways and in a predetermined sequence."¹⁰⁰ But Brink was not convinced. One could "turn McClintock's controller argument around," he said, "without compromising the facts, and assume that what she considers primary causes are, themselves, effects."¹⁰¹ Development, in other words, influenced transposition, rather than conversely.

In 1953, transposition was discovered yet again. Peter Peterson, a corn geneticist at the University of Iowa, published a short note in the *Maize Genetics Cooperation News Letter* and also gave a paper at the meeting of the American Society of Naturalists on yet another movable element.¹⁰² He named it Enhancer (*En*), and showed that it operated at the *pale-green* (*pg*) locus. Peterson discovered the mutable *pg* in strains of maize experimentally subjected to the atomic blasts at Bikini. Both Peterson and Brink acknowledged McClintock's precedence in discovering movable genetic elements, both used the term "transposition" and compared their elements to McClintock's *Ac*.¹⁰³ But both avoided use of the term "control" and all discussion of developmental regulation as they explored their own transposition systems.¹⁰⁴

The following year, McClintock herself described yet another new transposable element, which she named "Suppressor-mutator," or (*Spm*).¹⁰⁵ This element had appeared in her cultures years before, but only now did she identify it as a unique controlling unit. Its effects were much more subtle and varied than those of the *Ac/Ds* system. It modulated gene expression in a graded manner and, depending on its state, could either activate or inactivate the gene. The complexity of *Spm* fascinated her; she spent most of the next 20 years investigating it. This very complexity made McClintock's experiments and conclusions – never easy to follow – all but impenetrable to anyone unwilling to put in months of study. To her, *Spm* was the clincher: it demonstrated that controlling elements could exert the subtlety of control that would be required to produce a complex organism. To many other geneticists, it was no more than a curiosity, a barely comprehensible special case.

What was clear was that transposable or controlling elements were widespread, at least in maize. By 1956 McClintock could cite five apparently unique controlling unit systems: *Ac/Ds*; *Spm*; Rhoades' *Dotted* gene; Brink's *Mp*; and Peterson's *En*.¹⁰⁶ Further, M. Gerald Neuffer, at the University of Missouri, had discovered two new *Dotted* loci in South American maize and another new mutable element that seemed similar to *Ac*.¹⁰⁷ In addition, she believed she had yet another controlling system in her own maize cultures and could point to the work of several other researchers whose experiments indicated (either to them or to her) the presence of controlling elements.¹⁰⁸ The number of scientists engaged in transposition or controlling unit work was growing.

McClintock published only one primary research article on genetic control in a peer-reviewed journal. It appeared in October, 1953.¹⁰⁹ This was her most empirical article on genetic control. In it, she provided ample tables giving the results of crosses, culture numbers, explanation of tests for the presence and activity of *Ac*. But her main argument derived from a highly novel approach for 1950s genetics and was unlikely to be seen as widely applicable to other work in genetics. She showed that she could create new mutable loci by setting up conditions to favor transposition of a controlling element into a specific locus. Although the 1953 paper was much less theoretical than the 1950 paper, McClintock continued to embed her work in the debate over the nature of the gene. As she was writing it, she saw the 1953 paper as the "final crucial experiment" in demonstrating genetic control.¹¹⁰ It was not received this way. At various times McClintock said she received two requests, three requests, or three requests from scientists outside her field for reprints of this paper.¹¹¹ Let us say, "not many." Citations of it have never been as numerous as for her 1951 Symposium paper. Given the import with which she freighted the 1953 paper, disappointment would be understandable at such a lackluster

reception. But if other geneticists saw it as just another transposition paper, their response too would have been rational.

Though she published no more peer-reviewed primary research articles after 1953, she hardly stopped talking about her work. Through lectures, seminars, and conference papers, McClintock brought controlling units to an increasingly wide audience. She gave a graduate course at Caltech in the spring of 1954, for which her notes state that controlling elements “serve to control specific gene actions at certain stages in development.”¹¹² She lectured at Harvard, the University of Pennsylvania, Columbia, Yale, Cornell, Minnesota, Illinois, Indiana, Wisconsin, Dallas, Brookhaven, and elsewhere in the 1950s and 1960s. Every one of these talks concerned genetic control, gene action, or developmental regulation; none focused solely on the fact and mechanism of transposition.¹¹³

In June, 1955, McClintock presented a paper at a symposium on mutation at Brookhaven National Laboratory, an hour to the east of Cold Spring Harbor. “There can be no doubt,” she concluded, “about the presence in the maize chromosome complement of elements that control the action of genes.”¹¹⁴ Her primary conclusion remained firm: “controlling elements are normal components of the chromosome complement and . . . they are responsible for controlling, differentially, the time and type of activity of individual genes.”¹¹⁵ The published proceedings record considerable discussion of her paper, much of it concerning the generality of her arguments.

A year later, she presented a more extensive review at the Cold Spring Harbor Symposium on “Genetic Mechanisms: Structure and Function.”¹¹⁶ The audience included many who had heard her 1951 paper, as well as others who knew her work well, among them George Beadle, Sterling Emerson (from Caltech, son of the great Cornell maize geneticist Rollins Emerson) and numerous Cold Spring Harbor staff members. Also present were several of a new group of young scientists actually working with McClintock’s material.

Increasingly by the late 1950s and early 1960s, other research groups were working with mobile genetic elements. Many of these were students of the maize giants of the 1930s and 1940s who had gone on to establish their own labs.¹¹⁷ McClintock was generous in responding to their questions and requests. As long as the interlocutor had done his homework, she took him seriously, often writing out many pages of analysis and explanation and tucking in numerous kernel samples.¹¹⁸

By end of the 1950s, several of McClintock’s assumptions and hypotheses about controlling elements had changed, but the core of her vision remained constant. She dropped the heterochromatin model by 1956, though for some years she continued to argue that controlling elements were made of different stuff than genes. This, however, was an inference based on their apparent

behavior, not a conclusion based on biochemistry. She acknowledged she did not know what the elements were made of, although she believed they were integral to the chromosome. Some argued that her elements were free-floating elements that bind to the chromosomes. This "episome" model later became a popular interpretation of controlling elements, and one McClintock never liked.¹¹⁹ Between 1960 and 1965 she adopted the terms "operator" (for *Ds*) and "regulator" (for *Ac*) from the bacterial geneticists. What did not change was McClintock's commitment to the idea that genes were controlled, that control was a normal trait of organisms, and that it determined the growth and differentiation of the plant.

McClintock disliked attending meetings and publishing papers. Her favored means of scientific communication was through an energetically maintained informal network. Her reputation was such, however, that when she did speak, others scientists attended. Her mutable gene work was cited in textbooks and review chapters. At least four textbooks from the 1950s and 1960s discuss her work; among these is that of Adrian Srb, Ray Owen, and Robert Edgar, which was widely used in genetics courses across the country.¹²⁰ Her research was also cited in major review articles by leaders in the field.¹²¹ It was described as "spectacular" and "striking."¹²² Already by 1959, J.A. Peters counted her 1950 *PNAS* article in the rank of the classics of Mendel, Morgan, and Watson and Crick.¹²³ Yet her work was often relegated to sections on poorly understood or anomalous phenomena, reflecting the feeling that the findings were important but the interpretation did not quite fit. A McClintock admirer, Guido Pontecorvo, seems to have summed up many geneticists' views when he wrote, "The outstanding work in maize (review: McClintock, 1956) . . . is probably very relevant here. Unfortunately I do not understand the details of this work well enough to put my finger on what may be particularly significant."¹²⁴

In the 1950s geneticists held McClintock's controller argument judiciously at arm's length. In the 1960s they rejected it. The reason was the operon. In 1961, François Jacob and Jacques Monod published a model of genetic control for the bacterial gene called *lac Z*.¹²⁵ In it, a "structural gene" (i.e., a gene that produces a protein) is flanked by regulatory regions. Molecules bind to the regulatory sites to turn the gene on and off. The operon model has no transposition. Because of its simplicity, its elegance, and its applicability to other problems in bacterial genetics, the operon was accepted immediately: Jacob and Monod won the Nobel Prize in Physiology or Medicine in 1965.

McClintock considered this the rediscovery by bacterial geneticists. In 1956 she had argued that transposition was not a good diagnostic feature of controlling elements, that controlling elements could affect more than one

gene, and that they likely occurred in many organisms.¹²⁶ After Jacob and Monod's paper appeared, McClintock published an article in *American Naturalist* comparing bacterial operons with maize controlling elements.¹²⁷ The parallels had nothing to do with transposition. In 1961 she wrote, "Recently, ...controlling elements have been identified in bacteria."¹²⁸ "There wasn't any transposition" in the operon, she acknowledged later in an interview: "The main thing was control.... They showed that there was a control."¹²⁹ A few of her close colleagues recognized this as her major contribution. Yet McClintock was not – and still is not – widely acknowledged as having discovered genetic regulation. Bacterial geneticists of the 1970s, hailed in the standard McClintock narrative as her rediscoverers and legitimators, brushed aside her sweeping theory as another idea in the history of science that had once been plausible but could now be seen to be wrong. Indeed, one bacterial geneticist recalled her telling him that she had been irritated at them for exactly that.¹³⁰

Conclusion

The modern view of mobile genetic elements is, ironically, closer to Brink's view than McClintock's. When, in the late 1960s and early 1970s, mobile elements were discovered in bacteria and viruses, they were renamed "transposons." A group of senior and junior bacterial geneticists demonstrated their respect for McClintock when they attributed to her the term "transposable element" – the phrase Brink used to emphasize his view that transposition did not demonstrate control.¹³¹ Most molecular geneticists today believe transposons to be genetic parasites, possibly related to viruses, that replicate and spread themselves around the genome.¹³² Transposons' most likely evolutionary function is in generating genetic variation. Even some of McClintock's staunchest advocates today invert her argument, saying that she showed the developmental control of transposition, or argue that she'd have been better off if she had omitted argument and "left it at transposition."¹³³

The mechanism of transposition turned out to be quite general, used by many species for diverse purposes. McClintock's theoretical argument was discarded as a dead end. By the late 1970s, then, to talk about McClintock's work since 1948 was to talk about "transposition." She adopted this language, as did everyone else. But for her, "transposition" always meant "control." As late as 1980, however, she still differentiated between the two. In an interview with historians Will Provine and Paul Sisco, she remarked about the new publicity she had been receiving, and said that the focus was wrong: "People have said how pleased I must be that all of this transposition is going on and I said, 'Don't take that for granted'. The real point is control. The real

secret of all of this is control. It is *not* transposition" (emphasis in original transcript).¹³⁴

If the real point is control, McClintock should be viewed not only in the context of the history of genetics, but also in that of the history of developmental biology. The question she sought to answer after 1944 was essentially an embryological one. Because her answer to the paradox of nuclear equivalence was intranuclear rather than cytoplasmic, few embryologists attended to her work; they recognized the problem but could not hear her solution. Geneticists understood her answer, more or less, but could not see that transpositions implied control. Keller has discussed the historical moment – in the mid-1960s, just when transposition was found in bacteria – that embryology and genetics met and became developmental biology.¹³⁵ Goldschmidt and McClintock had been attempting a developmental genetics with a small set of blunt tools.

If the real point is control, the language of gender no longer helps in describing McClintock's work on mobile genetic elements. The reception of controlling elements is a poor model for gendered discrimination in science. Transposition was accepted; control was greeted skeptically. There is nothing insidious about this skepticism; separation of speculation from evidence is a sign of healthy science. Though McClintock, like nearly all women at the time, was subject to entrenched, cultural gender discrimination, she seems to have been treated "like a man" much more than most women.¹³⁶ Science is more gender-blind at the top than in the middle ranks. Sentimental portraits of her feminine style of science also no longer stand up. Control is hardly a nurturing concept – at one point she even contemplated "master-slave possibilities" of control.¹³⁷ She worked violence on her plants' chromosomes as much as any X-ray-blasting geneticist. She saw her plants as instruments, which she manipulated to get information: "It looks like I have an affection for it, but it isn't that."¹³⁸ She seems indeed to have solved problems intuitively, but the most famous examples of that style of science – Einstein, Richard Feynman, the mathematician John Nash – are men.¹³⁹ McClintock's example supports the argument that good science has no gender.

If the real point is control, McClintock regains agency. She chose to publish a speculative paper, her "dive into the deep." She chose not to publish most of her data. She chose to publish what she did mainly in review articles and non-peer-reviewed sources. She chose to remain at Cold Spring Harbor, where she had ample funding and no restrictions, where she was unencumbered by administration and teaching, where the summers bustled with molecular biologists and the winters were full of solitude. She did not cast transposition, like some perfect, fragile bubble, to the winds of scientific opinion. Evidence and interpretation were tangled and there was tugging and

tweezing by many individuals, including her, to extract what was useful. She was not a simple victim, but part of a complex social process.

If the real point is control, McClintock's example enriches our understanding of scientific reputation. Science builds on past results, but not straightforwardly. Later scientists have taken from her work that which has suggested new experiments. They credited her with the results they found useful, even while stripping away her grand biological vision. Her recognition for transposition was a high compliment, if backhanded. Younger scientists went to great lengths to give her credit, even attributing to her the phrase of her competitor. Practitioners are sometimes forced to bend their internal history in order to assure it conforms with what is believed to be right.

If the real point is control, McClintock's historiographical significance is altered. Her example reminds us not to fall prey to stereotypes or essentialist arguments. It shows that there can be no avoiding careful study of the scientist's science; it informs even meta-historical questions about the subject. It shows that scientists' personal histories construct the past and cannot always be taken at face value. McClintock's guiding principle was to embrace and investigate the complexity of nature. As with her science, so with her. In her case, focusing on the individual in all her complexity is an antidote to "great man" history of science. Not because she wasn't great (she was); not because she wasn't a man (though she wasn't). But because she fits no pedestal. Great men must be monolithic. The fact that her story is not seamless, has no heroes or villains or moral, does not work as an allegory, suggests a reconsideration of pat narratives. Of McClintock's much-vaunted interest in the paranormal, her friend Evelyn Witkin said it wasn't belief, but that "she just felt we were at a point of profound ignorance, that we were overestimating our understanding of the way things worked."¹⁴⁰ The reference was to nature, but it might have been to the nature of science.

Notes

1. This work was supported in part by research grants from the American Philosophical Society, Philadelphia, the Lilly Library, Indiana University, and the Carnegie Institution of Washington, as well as a Dissertation Improvement Grant from the National Science Foundation. Carl-Henry Geschwind, Carol Greider, Horace Freeland Judson, Carla Keirns, Mark Lesney, Steve Weiss, and two anonymous reviewers gave valuable comments during preparation of this manuscript. The title for this paper is taken from a comment McClintock made in an interview with me while access to it was still restricted. The "maize genetics cooperation," begun in the 1920s, is extended to a maize genetics history cooperation.
2. Evelyn Fox Keller's biography of McClintock, *A Feeling for the Organism* (New York: Freeman, 1983), is now in a "Tenth Anniversary Edition." McClintock is featured in nearly every recent biographical volume on women scientists: Joan Dash, *The Triumph*

- of Discovery: Women Scientists Who Won the Nobel Prize* (Englewood Cliffs, NJ: Julian Messner, 1991); Deborah Felder, "Barbara McClintock," in *The 100 Most Influential Women of All Time* (New York: Citadel Press, 1996), 185–187; Sharon Bertsch McGrayne, "Barbara McClintock," in *Nobel Women in Science* (New York: Birch Lane, 1993), 144–175; Olga Opfell, *The Lady Laureates: Women Who Have Won the Nobel Prize*, Second edition (Metuchen, NJ: Scarecrow Press, 1986); Margaret Rossiter, *Women Scientists in America: Before Affirmative Action, 1940–1972* (Baltimore: The Johns Hopkins University Press, 1995). She is the subject of at least three children's stories: Edith Hope Fine, *Barbara McClintock, Nobel Prize Geneticist* (Springfield, NJ: Enslow Publishers, 1998); Deborah Heiligman, *Barbara McClintock: Alone in Her Field* (New York: W.H. Freeman, 1994); Mary Kittredge, *Barbara McClintock* (New York: Chelsea House Publisher, 1991).
3. Nathaniel Comfort, *Breakage, Fusion, Bridge: The Discovery and Reception of Barbara McClintock's Controlling Elements*, Ph.D. Dissertation, State University of New York, 1997, pp. 78–102; Ana Barahona and Francisco Ayala, "La importancia del contexto y el trabajo de Barbara McClintock," 1995, *Arbor* **CLII**: 9–26, pp. 19–21; Keller, *A Feeling for the Organism*, Ch. 8.
 4. "Staff meeting – October 28, 1946," folder "Chromosome los[s] unclassified," Box 9, Series V, Barbara McClintock Collection, American Philosophical Society Library, Philadelphia (hereafter "MC").
 5. "Crossing-over and change in Ac location," folder "Ds. To be done for Summer 1948," Box 9; "4/18/48: For change in position of Ac locus," folder "Odd notes – to Sept 1948, Box 9"; "28 April 1948 – 4306: Transposed Ds," Untitled folder, Box 15, Series V, MC; For details, see Comfort, *Breakage, Fusion, Bridge*, pp. 132–154.
 6. Comfort, *Breakage, Fusion, Bridge*, p. 195.
 7. Barbara McClintock, "Cytogenetic studies of maize and Neurospora," 1945, *Carnegie Inst. Wash. Yearbook* **44**: 108–112; McClintock, "Maize genetics," 1946, *Carnegie Inst. Wash. Yearbook* **45**: 176–186; McClintock, "Cytogenetic studies of maize and Neurospora," 1947, *Carnegie Inst. Wash. Yearbook* **46**: 146–152; McClintock, "Mutable loci in maize," 1948, *Carnegie Inst. Wash. Yearbook* **47**: 155–169.
 8. Barbara McClintock, "The origin and behavior of mutable loci in maize," 1950, *Proc. Natl. Acad. Sci. USA* **36**: 344–355; McClintock, "Chromosome organization and gene expression," 1951, *Cold Spring Harbor Symposium on Quantitative Biology* **16**: 13–47.
 9. Keller, *A Feeling for the Organism*.
 10. *Ibid.*, p. 170.
 11. *Ibid.*, p. 139.
 12. Evelyn Fox Keller, *Reflections on Gender and Science* (New Haven: Yale University Press, 1985), p. 158.
 13. Ruth Bleier, *Science and Gender: A Criticism of Biology and Its Theories on Women* (Elmsford, NY: Pergamon, 1984), pp. 204–206; Dash, *The Triumph of Discovery*, p. 92; Mary Frank Fox, "Gender, environmental milieu, and productivity in science," in *The Outer Circle: Women in the Scientific Community*, ed. Harriet Zuckerman, Jonathan Cole and John Bruer (New York: W.W. Norton, 1991), pp. 203–204; Sandra Harding, *The Science Question in Feminism* (Ithaca: Cornell University Press, 1986), p. 122; Hilary Rose, *Love, Power and Knowledge: Towards a Feminist Transformation of the Sciences* (Bloomington: Indiana University Press, 1994), p. 157; Linda Jean Shepherd, *Lifting the Veil: The Feminine Face of Science* (Boston: Shambhala, 1993), pp. xiii, 70, 88.
 14. Dash, *Triumph of Discovery*, p. 92.
 15. Shepherd, *Lifting the Veil*, p. 70.

16. Shepherd, *Lifting the Veil*, p. 88; Felder, *The 100 Most Influential Women of all Time*, pp. 186–187.
17. Fox, “Gender, environmental milieu, and productivity in science,” p. 203.
18. Evelyn Fox Keller, “The gender/science system: or, Is sex to gender as nature is to science?” *Hypatia* 2(3) (1987): 37–49, p. 43; Evelyn Fox Keller, “How gender matters, or, why it’s so hard for us to count past two,” in *Inventing Women: Science, Technology, and Gender*, edited by Gill Kirkup and Laurie Smith Keller (Cambridge: Polity Press/Open University, 1992), p. 50.
19. Keller, “How gender matters,” 188–195.
20. Evelleen Richards, and John Schuster, “The feminine method as myth and accounting resource: A challenge to gender studies and social studies of science,” 1989, *Zygon* 19: 697–720; Evelyn Fox Keller, “Just what *is* so difficult about the concept of gender as a social category? (Response to Richards and Schuster),” 1989, *Zygon* 19: 721–724; Evelleen Richards, and John Schuster, “So what’s not a social category? or You can’t have it both ways (Reply to Keller),” 1989, *Zygon* 19: 725–729; Keller, “How gender matters,” pp. 48–51.
21. Allan Spradling, “McClintock myths: Review of *The Dynamic Genome: Barbara McClintock’s ideas in the century of genetics*,” 1993, *Science* 259: 1206–1208, p. 1208.
22. James D. Watson, Nancy Hopkins, Jeffrey Roberts, Joan Steitz, and Alan Weiner, *Molecular Biology of the Gene*, 4th ed (Menlo Park, CA: Benjamin Cummings Publishing Co., 1987), p. 22.
23. A prime example of the mythologization of McClintock by a scientist is Guenther Albrecht-Buehler, “Revenge of the Mayans,” in Fedoroff and Botstein, *Dynamic Genome*, pp. 273–276. See also Keller’s take on scientists’ reaction to her work in “The gender/science system,” p. 41.
24. Harding, *The Science Question in Feminism*, p. 31.
25. Rossiter, *Women Scientists in America: Before Affirmative Action*.
26. See references in note 2.
27. Opfell, *The Lady Laureates*, p. 265.
28. McGrayne, “Barbara McClintock,” p. 166.
29. Opfell, *The Lady Laureates*, p. 265.
30. Nina Fedoroff, “Two women geneticists,” 1996, *American Scholar* 65: 587–592, p. 590.
31. Fedoroff and Botstein, “Introduction,” *Dynamic Genome*, p. 3.
32. Nobel Foundation database of Nobel laureates, <http://www.nobel.se>
33. McClintock, cited in Keller, *A Feeling for the Organism*, pp. 136, 137, 140.
34. H. Bentley Glass, *A Guide to the Genetics Collections of the American Philosophical Society* (Philadelphia: American Philosophical Society, 1988), p. xvi; Miriam B. Spectre, “The Barbara McClintock papers: A welcome surprise,” 1993, *Mendel Newsletter* 3: 13–17.
35. A 1980 interview with McClintock by William Provine and Paul Sisco has recently been deposited at the Cornell University Archives, Krogh Library, Cornell University, Ithaca, NY (Lee Kass and William Provine, “Formerly restricted interview with Barbara McClintock, now available at Cornell University Archives,” *Maize Genetics Cooperation Newsletter* 73, in press). Franklin Portugal’s August, 1980 interview with McClintock is available at the American Philosophical Society Library under the collection number “rec. 230.” Evelyn Fox Keller has deposited tapes and transcripts of four interviews with McClintock, conducted between 1978 and 1980, as well as tapes of interviews with George Beadle, Marcus Rhoades, and others, at the American Philosophical Society Library in Philadelphia. I have also deposited at APS tapes and transcripts of interviews

cited in this article. As of this writing, neither the Keller interviews nor mine have received catalog numbers.

36. Keller, *A Feeling for the Organism*. McClintock quoted on control, p. 123; "principal significance of transposition . . .," p. 188.
37. McClintock, "The origin and behavior of mutable loci in maize."
38. Marcus Rhoades, "The effect of varying gene dosage on aleurone color in maize," 1936, *Journal of Genetics* **33**: 347–354; Rhoades, "Effect of the *Dt* gene on mutability of the al allele in maize," 1938, *Genetics* **23**: 377–397.
39. This dialogue was reconstructed from letters found in folder "Marcus Rhoades, 1949–1982," Series I, MC, and folder "f. 21 – Correspondence: 1950," Box 12, "McClintock," Marcus Rhoades Collection, Lilly Library, Indiana University (hereafter, "RC").
40. Jan Sapp, *Beyond the Gene: Cytoplasmic Inheritance and the Struggle for Authority in Genetics* (New York, Oxford: Oxford University Press, 1987), p. 17.
41. Garland Allen, "T.H. Morgan and the split between embryology and genetics, 1910–1935," in *A History of Embryology*, ed. T.J. Horder, J.A. Witkowski and C.C. Wylie (New York, Cambridge: Cambridge University Press, 1985), pp. 113–146; Sapp, *Beyond the Gene*, pp. 34–35.
42. Thomas Hunt Morgan, "Genetics and the physiology of development," *Am. Nat.* **60** (1926), 489–515, quoted in Jan Sapp, "Concepts of organization: the leverage of ciliate protozoa," in *A Conceptual History of Modern Embryology*, p. 231.
43. Position effect was first described by Alfred H. Sturtevant, "The effects of unequal crossing over at the *Bar* locus in *Drosophila*," *Genetics* **10**(1925), 117–147; Alfred H. Sturtevant and Thomas Hunt Morgan, "Reverse mutation of the *Bar* gene correlated with crossing over," *Science* **57**(1923), 746–747. On heterochromatin and the position effect, see Elof Axel Carlson, *The Gene: A Critical History* (Philadelphia: W.B. Saunders & Co., 1966), Ch. 13–15; L. C. Dunn, *A Short History of Genetics* (New York: McGraw-Hill, 1965), pp. 162–163.
44. Folder "Thoughts on various genetic and cyt. phenomena. 1945 to 1950 or earlier," Box 9, Series V, MC.
45. McClintock to Marcus Rhoades, 3 April 1950, Box 12 ("McClintock"), folder 21, RC.
46. McClintock to Rhoades, 30 March 1950, Box 12, folder 21, RC.
47. *Ibid.*
48. Curriculum vitae, folder "Curriculum vitae," Box "A–G," Series II, MC.
49. McClintock to Rhoades, 6 July 1950, Box 12, folder 21, RC.
50. McClintock, "The origin and behavior of mutable loci in maize," p. 355, footnote 4.
51. *Ibid.*, p. 347.
52. *Ibid.*
53. These reports may be found in Box 14, Series V, Boxes 1 and 2, Series III, MC, and in folders 28 and 31, Box 12, RC.
54. McClintock, "The origin and behavior of mutable loci in maize," p. 353.
55. All quotes in this paragraph from McClintock, "The origin and behavior of mutable loci in maize," p. 355.
56. Richard Goldschmidt, *Physiological Genetics*, Reprint. Originally published: 1st ed. New York: McGraw-Hill, 1938. *Genes, Cells, and Organisms* Series (New York: Garland, 1988); Goldschmidt, *The Material Basis of Evolution* (New Haven: Yale University Press, 1940); Scott Gilbert, "Cellular politics: Ernest Everett Just, Richard B. Goldschmidt, and the attempt to reconcile embryology and genetics," in *The American Development of Biology*, ed. Ronald Rainger, Keith Benson and Jane Maienschein (New Brunswick, NJ: Rutgers University Press, 1988), 311–346, pp. 320–321.

57. Richard Goldschmidt, "Marginalia to McClintock's work on mutable loci in maize," 1950, *Am. Nat.* **84**: 437–455.
58. *Ibid.*, p. 437.
59. *Ibid.*, p. 446.
60. On Goldschmidt's ideas, see: Michael Dietrich, "From gene to genetic hierarchy: Richard Goldschmidt and the problem of the gene," [unpublished]; Gilbert, "Cellular politics," pp. 334–339; Evelyn Fox Keller, *Refiguring Life: Metaphors of Twentieth Century Biology* (New York: Columbia University Press, 1995), p. 16.
61. McClintock to Beadle, January 28, 1951, folder 5.26, George Beadle Collection, California Institute of Technology Archives (hereafter "BC").
62. *Ibid.*
63. McGrayne, "Barbara McClintock," p. 168.
64. Barbara McClintock, "Introduction," in *The Discovery and Characterization of Transposable Elements: The Collected Papers of Barbara McClintock*, ed., John A. Moore (New York: Garland, 1987), vii–xi, p. x.
65. Keller, *A Feeling for the Organism*, p. 139. See also McGrayne, "Barbara McClintock," p. 168; Dash, *The Triumph of Discovery*, p. 92.
66. Barbara McClintock, interviewed by Neville Symonds, [undated], Cold Spring Harbor, NY, tape recording, transcribed by the author.
67. Nathaniel Comfort and Bentley Glass, *Building Arcadia: A History of Cold Spring Harbor Laboratory* (Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press, in press); Horace Freeland Judson, *The Eighth Day of Creation: Makers of the Revolution in Biology* (New York: Simon and Schuster, 1979), p. 67; Norton Zinder, "Forty years ago: The discovery of bacterial transduction," 1992, *Genetics* **132**: 291–294. The standard romance version of Cold Spring Harbor in the 1940s and 1950s is laid out in the essays in John Cairns, Gunther Stent, and James D. Watson, eds., *Phage and the Origins of Molecular Biology*. Expanded Edition (1992) (Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press, 1966).
68. The published papers are thus a rough guide to the meeting. The printed discussion of the Symposium volumes must be treated skeptically, since the editors selected from transcripts the comments they felt were relevant, and sometimes moved comments and questions around to improve logic and readability. One thing we probably can take literally is that the published comments were actually made at the meeting; with rare exceptions of invited speakers who were not able to attend meetings in the 1930s, the comments were not submitted *post hoc*. For further description and analysis of the Cold Spring Harbor Symposium, see Nathaniel C. Comfort, "Arc of a paradigm: The Cold Spring Harbor Symposium on Quantitative Biology, 1933–1953," Paper presented at the Joint Atlantic Seminar on the History of Biology, Cold Spring Harbor, NY, March 25, 1995; Comfort, *Breakage, Fusion, Bridge*, pp. 239–254; Nathaniel C. Comfort, "Two genes, no enzyme: a second look at Barbara McClintock and the 1951 Cold Spring Harbor Symposium," *Genetics* **140**(1995), 1161–1166, *passim*; Zinder, "Forty years ago," *passim*.
69. Alfred Hershey and Martha Chase, "Independent functions of viral protein and nucleic acid in growth of bacteriophage," 1952, *Journal of General Physiology* **36**: 39–56. See also Alfred Hershey, "The injection of DNA into cells by phage," in *Phage and the Origins of Molecular Biology* pp. 100–108 and Judson, *The Eighth Day of Creation*, pp. 130–31.
70. James D. Watson and Francis H.C. Crick, "Molecular structure of nucleic acids: A structure for deoxyribose nucleic acid," 1953, *Nature* **171** (25 April 1953): 737–738; Watson and Crick, "The structure of DNA," in *Cold Spring Harbor Symposia on Quantitative*

- Biology*, ed. Milislav Demerec (Cold Spring Harbor, NY: The Biological Laboratory, 1953), 123–131; Judson, *The Eighth Day of Creation*, Ch. 1–3; Robert Olby, *Origins of Mendelism* 2nd edition (Chicago: University of Chicago Press, 1985), Ch. 18, 21.
71. George Beadle and Edward Tatum, "Genetic control of biochemical reactions in *Neurospora*," *PNAS* **27** (1941), 494–506; Lily Kay, *The Molecular Vision of Life: Caltech, the Rockefeller Foundation, and the Rise of the New Biology* (New York: Oxford University Press, 1993), pp. 126–32, 195–208. See also Keller, *Refiguring Life*, pp. 16–17.
 72. See, for example, Zinder, "Forty years ago," p. 292.
 73. Milislav Demerec, "Foreword," 1951, *Cold Spring Harbor Symposia on Quantitative Biology* **16**: v.
 74. Richard Goldschmidt, "Chromosomes and genes," 1951, *Cold Spring Harbor Symposia on Quantitative Biology* **16**: 1–11, p. 7.
 75. Goldschmidt, "Chromosomes and genes," p. 3.
 76. Several interview subjects recalled this as the length of McClintock's paper. Though long, it was by no means the longest paper of the meeting: by Norton Zinder's 1996 account, Joshua Lederberg's lasted six hours. Talks at Cold Spring Harbor are now regulated with lab timers.
 77. McClintock, "Chromosome organization and gene expression," p. 36.
 78. *Ibid.*
 79. McClintock, "Chromosome organization and gene expression," p. 46; Comfort, "Two genes, no enzyme," p. 1163.
 80. McClintock, "Chromosome organization and gene expression," p. 17.
 81. William B. Provine and Paul Sisco, 1980. Interview with Barbara McClintock. 28 August 1980. Cold Spring Harbor, NY, transcript. Deposited at Division of Rare and Manuscript Collections, Carl A. Kroch Library, Cornell University, Ithaca, NY.
 82. Ernst Caspari, "Quantitative biology (Editorial)," 1951, *Science* **114** (Sept. 7): 3.
 83. Several interview subjects said they recalled no discussion after the paper; among these was Wacław Szybalski, who claims to have been responsible for transcribing comments for the printed discussion. For a more detailed discussion of the citations of McClintock's work elsewhere in the 1951 Symposium volume, see Comfort, "Two genes, no enzyme," p. 1165.
 84. Norton Zinder, Interview with Nathaniel Comfort, 12 March 1996, New York, NY, tape recording, deposited at American Philosophical Society Library.
 85. Joshua Lederberg, interviewed by Nathaniel Comfort, 12 March 1996, New York, NY, tape recording, deposited at American Philosophical Society Library.
 86. Wacław Szybalski, interviewed by Nathaniel Comfort, 14 October 1996, Madison, WI, tape recording, deposited at American Philosophical Society Library.
 87. See for examples, Comfort, *Breakage, Fusion, Bridge*, pp. 140–141, 264–267.
 88. Demerec to Beadle, 2 June 1953, folder 5.26, BC.
 89. One interview subject, who wished not to be named, said that "Goldschmidt had a nearly perfect scientific record: He was almost always wrong."
 90. Barbara McClintock, "Mutable loci in maize," *Carnegie Inst. Wash. Yearbook* **49** (1950), 157–167, pp. 161–163.
 91. Comfort, *Breakage, Fusion, Bridge*, pp. 249–250.
 92. Robert A. Nilan, telephone interview, May 11, 1998.
 93. *Ibid.*
 94. R.A. Brink and R.A. Nilan, "Studies on variegated pericarp," 1951, *Maize Genetics Cooperation News Letter* **25**: 42–47.

95. R.A. Brink and R.A. Nilan, "The relation between light variegated and medium variegated pericarp in maize," 1952, *Genetics* **37**: 518–544, p. 537.
96. Norton Zinder interview with Nathaniel Comfort.
97. Jerry Kermicle, interviewed by Nathaniel Comfort, October 15, 1996, Madison, WI, tape recording, deposited at American Philosophical Society Library.
98. James F. Crow, interviewed by Nathaniel Comfort, October 13, 1996, Madison, WI, tape recording, deposited at American Philosophical Society Library.
99. Jerry Kermicle interview.
100. R.A. Brink, "Paramutation and chromosome organization," 1960, *Quarterly Review of Biology* **35**(2): 120–137, p. 132.
101. Brink, "Paramutation and chromosome organization," p. 132.
102. Peter A. Peterson, "A mutable pale green locus in maize," 1953, *Genetics* **38**: 682–683; Peter A. Peterson, "6. The mutable pale green locus," 1953, *Maize Genetics Cooperation News Letter* **27**: 58–60.
103. Brink and Nilan, "The relation between light variegated and medium variegated pericarp in maize," p. 538; Peterson, "A mutable pale green locus in maize," p. 682–3; Peterson, "6. The mutable pale green locus," p. 59.
104. Peter A. Peterson, "The pale green mutable system in maize," 1960, *Genetics* **45**: 115–133; Brink and Nilan, "The relation between light variegated and medium variegated pericarp in maize," p. 541. Brink continued to use "transposition" in subsequent papers, e.g.: Peter C. Barclay and R.A. Brink, "The relation between Modulator and Activator in maize," 1954, *Proc. Natl. Acad. Sci. U.S.A.* **40**: 1118–1126; Cheng-Mei W. Fradkin and R.A. Brink, "Crossing over in maize in the presence of the transposable factors Activator and Modulator," 1956, *Genetics* **41**: 901–906.
105. Barbara McClintock, "Mutations in maize and chromosomal aberrations in *Neurospora*," 1954, *Carnegie Inst. Wash. Yearbook* **53**: 254–260.
106. *En* later turned out to be *Spm*. This, however, was not suspected at the time.
107. M. Gerald Neuffer, "1. Additional *Dt* loci. 2. A new pale aleurone gene," 1953, *Maize Genetics Cooperation News Letter* **27**: 67–68; M. Gerald Neuffer, "1. Redesignation of *pa*. 2. Activator of *bz-m2* mutability. 3. Location of *Dt2*, *Dt3*, and *bz2*: X-ray deficiency method. 4. Modifiers of *Dt* activity," 1954, *Maize Genetics Cooperation News Letter* **28**: 63–65; M. Gerald Neuffer, "3. Similarity of *M* and *Ac* mutator systems. 4. The effect of *Dt* on mutations of *A1* to *al*. 5. Dosage effect of multiple *Dt* loci. 6. Peculiar mutational behavior at the *A1* locus," 1955, *Maize Genetics Cooperation News Letter* **28**: 59–61; M. Gerald Neuffer, "Dosage effect of multiple *Dt* loci on mutation of *a* in the maize endosperm," 1955, *Science* **121**: 399.
108. Barbara McClintock, "Intranuclear systems controlling gene action and mutation," 1956, *Mutation (Brookhaven Symposia in Biology)* **8**: 58–74, pp. 64–65.
109. Barbara McClintock, "Induction of instability at selected loci in maize," 1953, *Genetics* **38**: 579–599.
110. McClintock to Edgar Altenburg, January 22, 1953, McClintock correspondence, Edgar Altenburg Collection, Lilly Library, Indiana University.
111. Keller (*A Feeling for the Organism*, p. 140) writes that McClintock received only two requests; McClintock herself (Introduction, *The Discovery and Characterization of Transposable Elements: The Collected papers of Barbara McClintock*, Edited by John A. Moore, *Genes, Cells, and Organisms: Great Books in Experimental Biology* [New York: Garland, 1987], p. x) wrote that she received three. McGrayne ("Barbara McClintock," p. 168), wrote that "only three scientists outside her field" requested the article.
112. "California Institute of Technology Lectures," Box "Ac – Chromosome," Series III, MC.

113. Lecture notes are located in Series III, MC.
114. McClintock, "Intranuclear systems controlling gene action and mutation," p. 64.
115. *Ibid.*, p. 67.
116. Barbara McClintock, "Controlling elements and the gene," 1956, *Cold Spring Harbor Symposium on Quantitative Biology* **21**: 197–216.
117. These included: John Laughnan at the University of Illinois; Drew Schwartz, a former Rhoades student who moved to Oak Ridge National Laboratory; E.J. Dollinger, of Brookhaven National Laboratory, Paul Mangelsdorf of Harvard, and Oliver Nelson at Purdue and later Wisconsin. McClintock mentioned several of these projects in McClintock, "Intranuclear systems controlling gene action and mutation," p. 67. For more detail, see Comfort, *Breakage, Fusion, Bridge*, pp. 277–280.
118. Among the attendees working with the material and/or concepts of controlling elements were A.H. Ar-Rushdi, of the Scripps Institution of Oceanography, Seaward Sand, of the Connecticut Agricultural Experiment Station, and Drew Schwartz, who had done his degree with Rhoades and gone on to Oak Ridge National Laboratory. The McClintock correspondence (Series I, MC) contains many other examples of young scientists who wrote to her for samples and scientific advice.
119. According to Jerry Kermicle, Brink entertained this idea. François Jacob later likened her elements to episomes (François Jacob, "Genetic control of viral functions," 1959, *Harvey Lectures* **1959** (1): 1–39, p. 32).
120. Robert King, *Genetics* (New York: Oxford University Press, 1962), pp. 187–188; Ruth Sager and Francis Ryan, *Cell Heredity* (New York: John Wiley & Sons, 1961), pp. 341–349; J.A. Serra, *Modern Genetics*, Vol. 1 (New York: Academic Press, 1965), p. 454; Adrian Srb, Ray Owen, and Robert Edgar, *General Genetics*, 2nd ed. (San Francisco: W.H. Freeman, 1965), p. 341.
121. For example, L.J. Stadler, "The gene," 1954, *Science* **120**: 811–819, p. 818.
122. "Spectacular": Torbjorn Caspersson and Jack Schultz, "Cytochemical measurements in the study of the gene," in *Genetics in the Twentieth Century*, ed. L.C. Dunn (New York: MacMillan, 1951), 155–171, p. 168; "Striking": George Beadle, "Chemical genetics," in *Genetics in the Twentieth Century*, 221–239, p. 235.
123. James A. Peters, ed., *Classic Papers in Genetics* (Englewood Cliffs, NJ: Prentice-Hall, 1959).
124. Guido Pontecorvo, *Trends in Genetic Analysis*, (New York, Columbia University Press, 1958), p. 66.
125. François Jacob and Jacques Monod, "Genetic regulatory mechanisms in the synthesis of proteins," 1961, *J. Molecular Biology* **3**: 318–356.
126. McClintock, "Intranuclear systems controlling gene action and mutation," pp. 215–216.
127. Barbara McClintock, "Some parallels between gene control systems in maize and in bacteria," *Am. Nat.* **95** (1961), 469–476, p. 469.
128. Barbara McClintock, "Further studies of the suppressor-mutator system of control of gene action in maize," *Carnegie Inst. Wash. Yearbook* **60** (1962), 469–476. p. 469.
129. Barbara McClintock interview with Provine and Sisco, 1980.
130. David Botstein, interviewed by Nathaniel Comfort, December 23, 1996, Belmont, CA, tape recording, deposited at American Philosophical Society Library.
131. A. Campbell, D.E. Berg, D. Botstein, E.M. Lederberg, R.P. Novick, P. Starlinger, and W. Szybalski, "Nomenclature of transposable elements in prokaryotes," in *DNA Insertion Elements, Plasmids, and Episomes*, ed. J.A. Shapiro, A.I. Bukhari and S.L. Adhya (Cold Spring Harbor: Cold Spring Harbor Laboratory Press, 1977), pp. 15–22, p. 16.

132. J.D. Boeke and J.P. Stoye, "Retrotransposons, endogenous retroviruses, and the evolution of retroelements," in *Retroviruses*, ed. H. Varmus, S. Hughes and J. Coffin (Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press, 1997), pp. 343–435; D.R. Edgell, N.M. Fast, and W.F. Doolittle, "Selfish DNA: the best defense is a good offense," *Curr. Biol.* **6** (1996), pp. 385–388; J.A. Yoder, C.P. Walsh, and T.H. Bestor, "Cytosine methylation and the ecology of intragenomic parasites," *Trends Genet* **13** (1997), 335–340.
133. James Shapiro, interview with Nathaniel Comfort, 27–28 January, Chicago, IL, tape recording; Nina Fedoroff, interview with Nathaniel Comfort, 3 February 1997, telephone interview.
134. Barbara McClintock interview with Provine and Sisco, 1980.
135. Keller, *Refiguring Life*, pp. 24–25, 103.
136. See examples in Comfort, *Breakage, Fusion, Bridge*, Ch. 6.
137. McClintock to Oliver Nelson, 28 March 1968, Folder "Nelson, Oliver E," Series I, MC.
138. Barbara McClintock, Interview with Evelyn Fox Keller, 13 January 1979, Cold Spring Harbor, NY, transcript, deposited at American Philosophical Society Library.
139. Abraham Pais, *Subtle Is the Lord: The Science and the Life of Albert Einstein* (Oxford, England: Oxford University Press, 1982); James Gleick, *Genius: The Life and Science and Richard Feynman* (New York: Pantheon, 1992); Sylvia Nasar, *A Beautiful Mind* (New York: Simon & Schuster, 1998).
140. Evelyn Witkin, Interview with Nathaniel Comfort, March 19, 1996, Princeton, NJ, tape recording, deposited at American Philosophical Society Library.