



Seeing Patterns: Models, Visual Evidence and Pictorial Communication in the Work of Barbara McClintock¹

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Abstract. Barbara McClintock won the Nobel Prize in 1983 for her discovery of mobile genetic elements. Her Nobel work began in 1944, and by 1950 McClintock began presenting her work on “controlling elements.” McClintock performed her studies through the use of controlled breeding experiments with known mutant stocks, and read the action of controlling elements (transposons) in visible patterns of pigment and starch distribution. She taught close colleagues to “read” the patterns in her maize kernels, “seeing” pigment and starch genes turning on and off. McClintock illustrated her talks and papers on controlling elements or transposons with photographs of the spotted and streaked maize kernels which were both her evidence and the key to her explanations. Transposon action could be read in the patterns by the initiated, but those without step by step instruction by McClintock or experience in maize often found her presentations confusing. The photographs she displayed became both McClintock’s means of communication, and a barrier to successful presentation of her results. The photographs also had a second and more subtle effect. As images of patterns arrived at through growth and development of the kernel, they highlight what McClintock believed to be the developmental consequences of transposition, which in McClintock’s view was her central contribution, over the mechanism of transposition, for which she was eventually recognized by others. Scientific activities are extremely visual, both at the sites of investigation and in communication through drawings, photographs, and movies. Those visual messages deserve greater scrutiny by historians of science.

Keywords: cytogenetics, diagrams, genetics, illustrations, McClintock, models, molecular biology, photographs, twentieth-century, United States

... a single color photograph [was] more illuminating than all her papers put together.²

The discovery of mobile genetic elements by McClintock is of profound importance for our understanding of the organization and function of genes. She carried out this research alone and at a time when her contemporaries were not yet able to realize the generality and significance of her findings. In this respect, there are several similarities between her

situation and that of another great geneticist active 100 years ago, Gregor Mendel, who, studying the garden pea, discovered other basic principles of genetics.³

In the announcement of her Nobel Prize, the Swedish Academy of Sciences compared Barbara McClintock to Gregor Mendel. Like Mendel, McClintock is portrayed as a forgotten genius, ignored by colleagues for decades until her insights were uncovered by a new generation. Recent scholarship on Mendel, however, challenges the myth of the martyr to science, suggesting that Mendel's work was known among elite and scientific breeders like Karl Nageli, that his paper was widely disseminated in breeding circles, and that his work was rejected for its lack of relevance to contemporary scientific questions and for lack of confirmation of the pea findings in hawkweed – not because the brilliant experimentalist published in the wrong journal.⁴ In this revised picture of the Austrian monk, he is indeed a great deal like Barbara McClintock as her life and work are being reinterpreted.⁵ Both were well known in their communities of naturalists and breeders and participated in exchanges with leading figures. It was a change of questions, and the attendant change in the form of the acceptable answers, that led to the rediscoveries of both Mendel and McClintock.⁶

In her book, *A Feeling for the Organism*, Evelyn Fox Keller outlines Barbara McClintock's life in science and the difficulties she faced in the 1950s and 1960s in communicating with the growing circle of molecular biologists who met at Cold Spring Harbor every summer. Keller argues that transposition was rediscovered in the 1970s, with credit finally given to McClintock for decades of research.⁷ Characterizing the problem in linguistic and empathic terms, Keller argues that McClintock's "different language" and "feeling for the organism" blocked communication between McClintock and this audience. Building on Keller's work, I argue that molecular biologists were not McClintock's natural community since they did not share her technique or question. McClintock was concerned, fundamentally, with development and gene regulation – issues that were not on the agenda of microbial geneticists in the 1950s when she began presenting her work on transposition and controlling elements.

Unlike Keller, I frame the problem of communication between McClintock and the molecular biologists in the late 1960s, 1970s, and 1980s primarily in terms of scientific communities, organisms, and use of visual evidence. These three aspects illustrate that McClintock's purported isolation is a result of viewing her work only in comparison with molecular biology – and of gauging the reception of her work only in that community – and community boundaries are defined in part by organisms and visual traditions.⁸ Most of the data that McClintock collected on her "controlling elements"



Figure 1. Barbara McClintock in her Corn Fields, circa 1960. [Courtesy of the Library of the American Philosophical Society.]

was never published, though brief analyses appeared in the *Yearbook of the Carnegie Institution of Washington*.⁹ Visual patterns in maize kernels were crucial to McClintock's analyses, and were the main form of illustration in what she did publish, but the understanding of these patterns was confined to a small community of initiates. In McClintock's view, the particular suitability of the photographs of kernels as illustrations had to do with their value in illustrating developmental patterns – not the mechanism of transposition at the level of the base pair.

After François Jacob and Jacques Monod's publication of the operon as a simple regulatory system in 1961, when the growing community of molecular biologists became more interested in gene regulation, they had a regulatory model *which had been articulated and illustrated at the level of the gene* rather than inferred from its phenotypic (and therefore partly developmental) effects.¹⁰ The question of whether regulatory mechanisms in more complex organisms were different in kind or scale – more operons or another system entirely – was left for later researchers. Jacob and Monod's model, and other schematic diagrams and models used in molecular biology, was easy to "see" and comprehend as a *mechanism*. By comparison, McClintock's choice of the kernels to illustrate her *theoretical* arguments in both papers and talks emphasized the developmental arguments she was making, and followed a visual tradition that, by the 1970s, likely made her work seem more obscure and irrelevant rather than clearer and more convincing. Whether one was interested in transposition or developmental control, McClintock's methods and level of explanation separated her from the molecular biologists. Her use of visual evidence reified this separation, making communication with molecular biologists even more difficult.

The Structure of Scientific Communities: Or Building an Audience

Barbara McClintock was well respected for her early cytogenetic studies. Though she had problems securing a job, her experimental work earned the respect of her peers and by 1945 both membership in the National Academy of Sciences and the presidency of the Genetics Society of America.¹¹ The unexpected appearance in 1944 of a number of spontaneously mutating genes set her on a new line of research that led ultimately to transposition (1948) and the Nobel Prize (1983).¹² Transposition – the movement of a gene or chromosomal element from one location on the chromosome to another – is the discovery for which McClintock is famous. This work grew out of her experiments on ring chromosomes, chromosome breakage and fusion, and spontaneous mutations.¹³ When researchers began to find moveable elements in bacteria, yeast, and higher organisms, McClintock was retrospectively

credited with the discovery of the general phenomenon of movement of DNA native to the organism in question, whether as plasmids,¹⁴ transposons, or by other means.¹⁵ The fact that transposition was secondary to McClintock, for whom it represented only a mechanism of developmental regulation, is less well-known.¹⁶

McClintock, Models, and Molecular Biology

McClintock and the Molecular Biologists

The molecular biologists were not McClintock's natural community – sharing neither her organism nor cytogenetic techniques – nonetheless she was determined to gain their respect and following. McClintock's repeated attempts to convince or convert this subcommunity is one of the enduring paradoxes of her career. Whether McClintock's desire to engage with the molecular community was a result of her respect for their intelligence, their proximity to her laboratory during summer meetings at Cold Spring Harbor, or her hope that they would extend her work into other organisms and to molecular-level explanations, she continued to speak to – and increasingly about – this group in the late 1960s, 1970s and 1980s. Her sense that they understood theoretical issues and by the 1970s were interested in gene regulation provides a partial answer.¹⁷ The clash between McClintock and the molecular biologists provides a window into the relationship between the development and perpetuation of conceptual models, scientific illustration and epistemology.¹⁸

When McClintock began to present her work on controlling elements in 1951, she faced an audience which included maize geneticists and many scientists who had worked with maize some time during their careers, but few of whom were working on development or regulation.¹⁹ As she continued to present her work over the ensuing decades, the situation reversed. By the 1970s, maize had become a far less common organism for genetic studies, and by the 1980s, complex developmental questions were beginning to be addressed as new theories and molecular tools were developed.²⁰

McClintock's project dealt with regulation and control in higher organisms, for which transposition was simply one possible mechanism.²¹ The isolation of genetics from embryology (later called development) in the Morgan school of the 1910s and 1920s, and many later attempts to bridge the gap with hybrid work in "developmental genetics" has recently been the subject of historical analysis.²² The direct effect of this split, solidified in Morgan's fly room, was ironically to make all of McClintock's experimental work possible. The Morgan group's pioneering work linking cytology and breeding analysis in *Drosophila* was the counterpart to McClintock's work in

the 1920s linking cytology and breeding analysis in maize.²³ The productivity of transmission genetics, freed in the 1920s from the traditional concerns of evolution and development, allowed new understanding of heredity – precisely as McClintock was beginning her career in genetics. McClintock's control theory brought the problem of development back into her genetics, giving it a complex, theoretical flavor.

"Seeing the Patterns": McClintock's Visual Style

In her discussion of McClintock's career, Evelyn Fox Keller uses the linguistic metaphor of a "different language" to explain the lack of communication between McClintock and the molecular biologists. Keller shows that McClintock's genius lay partly in her observational skill. Understanding her work required a bit of that same skill. As molecular biology matured, it developed its own, tightly stylized and schematic visual language – a language McClintock read, but did not write. Writing at least two decades after the visual language of molecular biology had matured, in their 1992 *festschrift* for McClintock, Nina Fedoroff and David Botstein explain that

... both Barbara's contemporaries and those who came later often criticized her sharply for what they saw as her unwillingness to communicate. By this, they mostly meant she had not made cartoons to reify the genetic abstractions from which she inferred the existence of controlling elements that transpose from place to place in the genome. Indeed, although Barbara often diagrammed chromosomes, she never drew cartoons, and she readily admits frustration with her failure to communicate. [p. 2]

Such criticisms presume that the mechanism of transposition was the most important message that McClintock had to communicate, and fail to address the forms of illustration she did use in her papers and presentations.

Differences between McClintock and molecular biologists in the use and content of models, diagrams, and illustrations highlight the issue of developmental control theory and its concern with patterns of expression and molecular biology's concern with molecular mechanisms. A biologist who studied McClintock's work remarked that after learning to "see the patterns," "a single color photograph [was] more illuminating than all her papers put together."²⁴

McClintock illustrated the papers in her transposition and control work with diagrams of chromosomes and images of maize kernels, following the cytogenetic tradition of displaying the mutant under study.²⁵ In broad outline, the growth of cytology is tied to incremental improvements in laboratory microscopes, the dissemination of instruments, and numerous technical improvements in microscopic technique.²⁶ Cytogenetics also owes a debt to

the growth of the German dye industry in the late nineteenth century, whose products gave us the name “chromosome” or “colored body” due to the fact that these cellular structures selectively absorbed many of the new dyes.²⁷ The precise history of chromosome spreads and karyotyping, which was and remains a skilled empirical field, has not been written. It is clear, however, that the generic problem of preparing cells to obtain a clear spread chromosomes of visible and distinct chromosomes had to be modified according to the details of each organism.²⁸ Breeding experiments which compared chromosome size, shape, and banding pattern in parents and offspring to the traits expressed was the basis for the Morgan school’s claims about the physical basis of heredity.²⁹ McClintock learned and developed techniques of cytogenetics in maize starting in the early 1920s as a graduate student at Cornell University. Shortly after Barbara McClintock completed her Ph.D. at Cornell in 1927, she won the attention of geneticists worldwide with her conclusive demonstration of the correlation between genetic crossing-over, detected statistically, and physical crossing-over of chromosomes observed under a microscope. This provided a key confirmation of the chromosomal theory of heredity, a cornerstone of twentieth-century genetics.³⁰

Careful breeding experiments and cytological techniques permit observations of chromosomes, expressed and visible mutant traits (phenotypes), but not – as molecular biologists would like – detailed articulation of molecular mechanisms. Reconstructions and cinematic animations of cell division (mitosis) and gamete production (meiosis) have been made for demonstration purposes, but the destructive nature of most methods of karyotype preparation make it impossible to follow the same cell through the process either in still photographs or movies.

Figure 2, one of the illustrations to McClintock’s 1951 *Cold Spring Harbor Symposium* paper, shows the knot of chromosomes that the cytogeneticist had to be able to interpret, recognizing individual chromosomes by size and shape. In McClintock’s early maize work at Cornell, she pioneered the study of maize chromosomes in the “pachytene” stage, the stage shown here. In the pachytene stage, when crossing-over occurs in maize, chromosomes are condensed, but stretched out into linear chromatids for crossing-over. Pachytene chromosomes are easier to identify than they are in other stages, but they are also tangled together, so a discriminating eye and long experience are still necessary to interpret the chromosome spreads. The line tracings beside the photograph are camera lucida images, drawn from the microscopic images, which permitted a clearer separation than seen in the photograph. McClintock’s caption read in part, “In Figure 4, a break at *Ds* occurred in a premeiotic mitosis. The acentric fragment, from *Ds* to the end of the arm, was lost to the nucleus. Consequently, this segment is missing in the bivalent.”³¹ Trans-

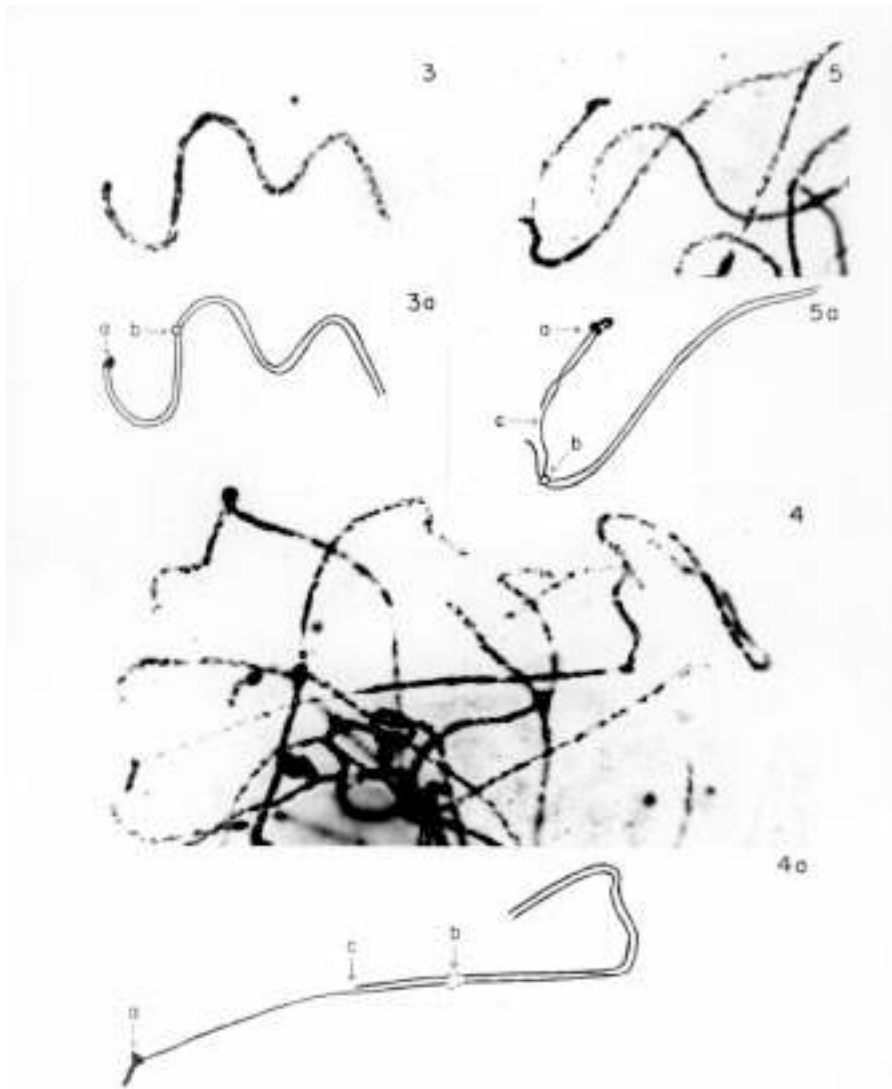


Figure 2. Maize chromosomes in pachytene stage from Barbara McClintock, "Chromosome Organization and Genic Expression," *Cold Spring Harbor Symposium on Quantitative Biology*, **16** (1951), p. 18. [Courtesy Library of the American Philosophical Society and Cold Spring Harbor Laboratory.]

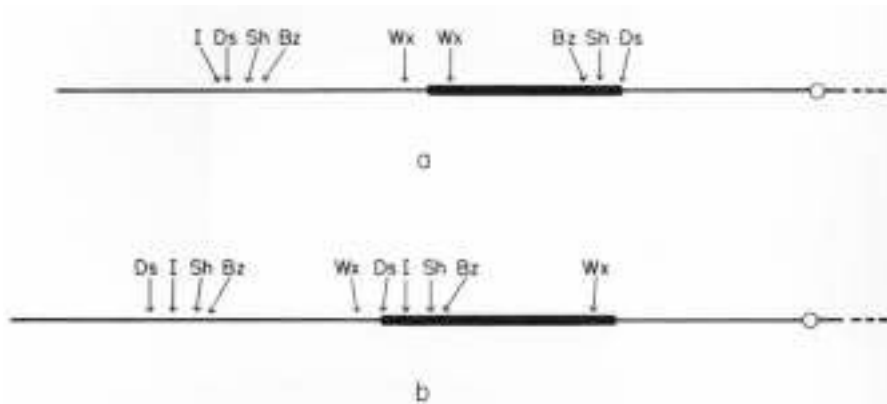


Figure 3. Chromosome map showing *Ds* movement from Barbara McClintock, "Mutable Loci in Maize," *Carnegie Institution of Washington Year Book*, **49**, (1949–50), p. 162; and Barbara McClintock, "Chromosome Organization and Genic Expression," *Cold Spring Harbor Symposium on Quantitative Biology*, **16** (1951), p. 22. [Courtesy Library of the American Philosophical Society, Cold Spring Harbor Laboratory Press, and the Carnegie Institution of Washington.]

position had caused chromosome breakage and loss of the loose end of the chromosome. Figure 3 displays a schematic chromosome map in what had become the conventional form for presenting the relative order and position of genes on a chromosome, with distances determined by frequency of crossing-over in breeding experiments.³² The genes are indicated by the letters next to the chromosomes, and the change in the sequence of genes is the key observation. McClintock explained that these were "diagrams illustrating the constitution of two chromosomes 9, each of which carries a duplicated segment (heavy line). A transposition of *Ds* accompanied the formation of the duplication in each case."³³ McClintock had been able to use what were by the 1940s standard conventions of chromosome mapping to show breakage of chromosomes and migration of traits.³⁴

McClintock presented some of the developmental patterns which had initially drawn her attention, and which suggested developmental changes to her for others to inspect. In Figure 4, one can see the dark wedge of stained cells against the background of light-colored cells. This kernel, McClintock's *Wx* mutation, was stained with an iodine-potassium iodide (I-KI) solution which reacts with starch to produce the dark patches visible in the kernel. Knowing that the kernel grows out from the center, McClintock concluded from the background that the kernel was programmed at fertilization to produce relatively little starch, and therefore absorb little I-KI stain.³⁵ Then at some early stage in the development of the kernel, a transposition event occurred in one cell turning on the gene for starch, and all subsequent divisions from that

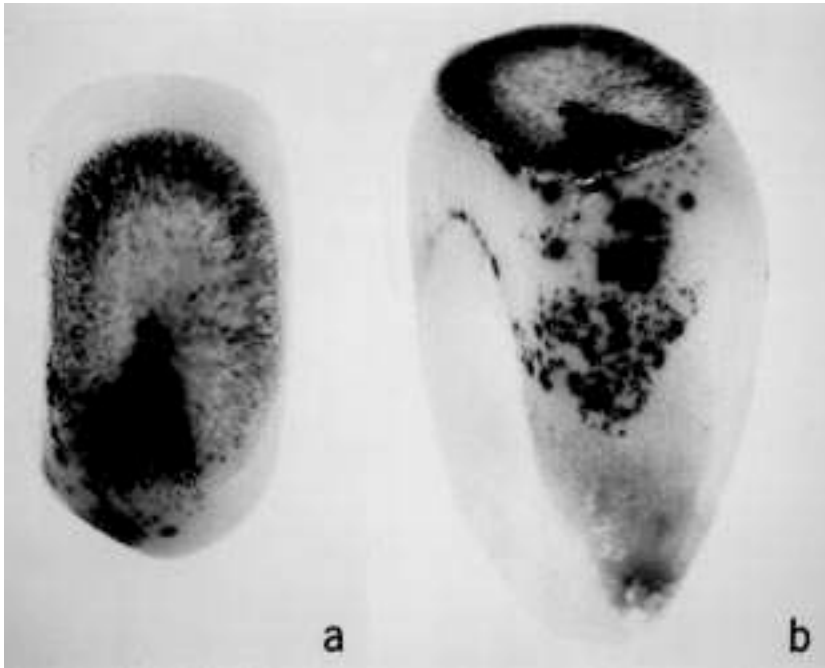


Figure 4. Kernel showing one early and many late transposition events from Barbara McClintock, “The Control of Gene Action in Maize,” *Brookhaven Symposia in Biology*, **18** (1965), p. 167; and Barbara McClintock, “Development of the Maize Endosperm as Revealed by Clones,” in *The Clonal Basis of Development, 36th Symposium of the Society for Developmental Biology* (June 1977) (New York: Academic Press, 1978), p. 229. [Courtesy of the Library of the American Philosophical Society, Brookhaven National Laboratory, and Academic Press, Inc.]

lineage took up the I-KI stain, producing the darkened wedge. In 1965, when McClintock first published this image, the caption read, in part: “Reactivation of the inactive *Ac* occurred in an individual cell early in endosperm development. Response of the operator element at the a_1^{m-3} locus to this reactivation produced the area in the aleurone layer that exhibits many pigmented spots, each spot arising from an individual response of the operator.”³⁶ Note both McClintock’s explanation of the v-shaped section as a question of developmental timing – the *Ac* transposon moved early in this lineage, and with it the character for starch production – and her use of the “operator” language from Jacob and Monod. When McClintock republished this image in 1978, the caption read in part,

From the ear parent the kernel received *a-m3* in chromosome 3 and *wx-m7* in chromosome 9 whose associated *Ac* [transposon] had an *m* component [starch gene] that initially was completely silent. *In a cell, early*

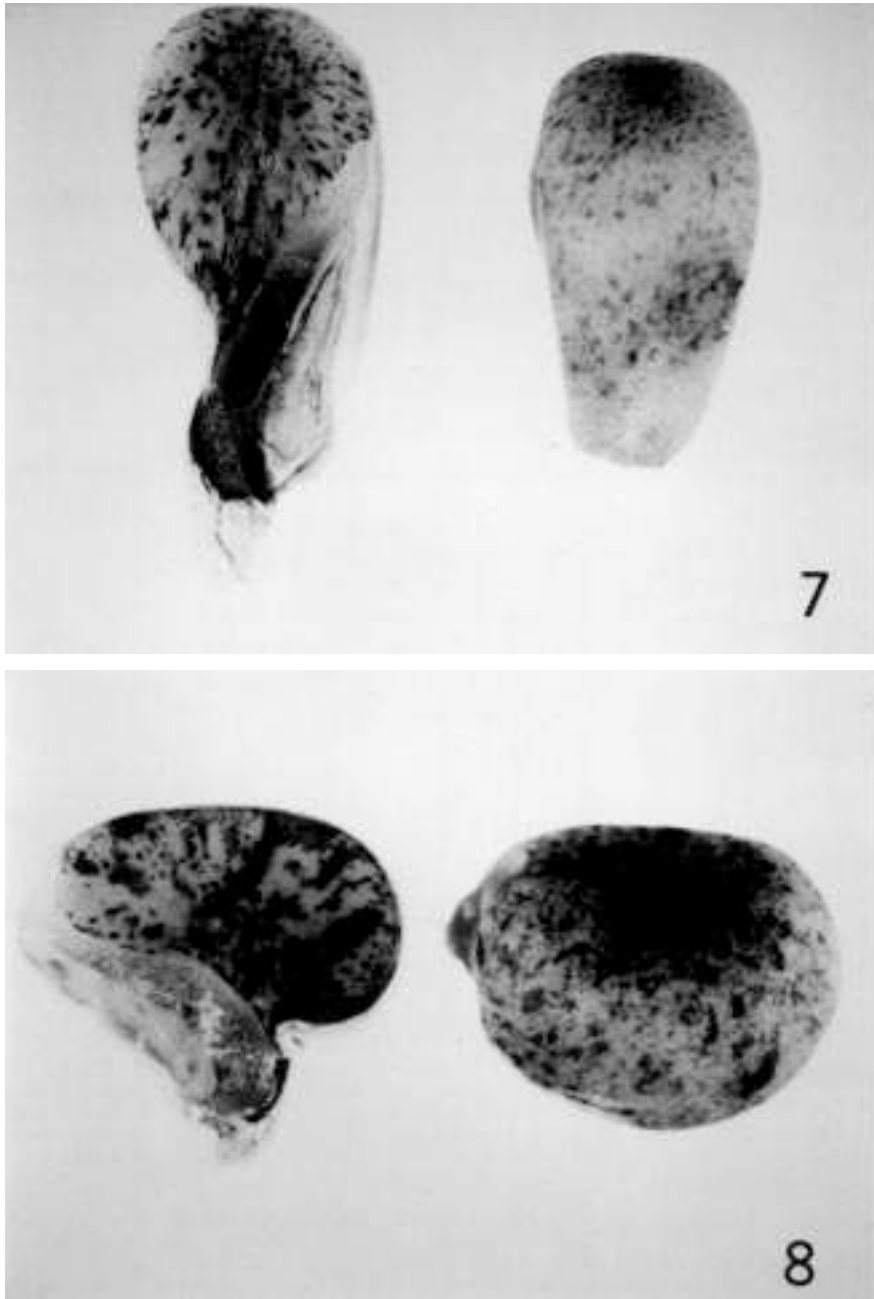


Figure 5. Kernels showing late transposition events. Barbara McClintock, "Development of the Maize Endosperm as Revealed by Clones," in *The Clonal Basis of Development*, 36th Symposium of the Society for Developmental Biology (June 1977) (New York: Academic Press, 1978), p. 232. [Courtesy of the Library of the American Philosophical Society and Academic Press, Inc.]

in endosperm development, it became capable of acting. The V-shaped sector within the endosperm composed of a dark and some lightly stained cells represents the progeny of this cell as does the area with dark spots of anthocyanin pigment in the outermost layer of the endosperm (the aleurone layer) [emphasis added].³⁷

Kernels like Figure 5, showing more diffuse spots made visible with I-KI stain further from the center of the kernel represent transposition events in the starch gene later in the development of the kernel than that in Figure 4. McClintock explained that:

The aleurone layer of the kernel in Figure 7 [in Figure 5] has many closely spaced spots of anthocyanin, and these represent mutations at the locus of *c-m5* The evident mutations are spaced as individual cells or arranged in small clones. This pattern suggests that mutations were not occurring in the leading cambium-like layer of cells, but rather in the cells of the layers just below it that also undergo some divisions.³⁸

That is to say, the transposition events that led to small, widely dispersed darkly staining spots occurred late in the development of the kernel and independently in many different cells. To explain the larger and more concentrated dark patches in her Figure 8 [in Figure 5], McClintock explained, “It is evident in this instance that mutations at *wx-m8* occurred in cells of the leading cambium-like layer as well as in some cells of the underlying layers.”³⁹ The next image (Figure 6), showing darkly staining cells interrupted by wedges of lightly-pigmented (unstained) cells, demonstrates that the gene can be turned off as well as on. McClintock told her readers to “note focal location, close to the crown of the kernel, from which diverge two large sectors composed of deeply stained cells and two composed of near colorless cells, and from which all other rows of cells likewise diverge.”⁴⁰ Developmental patterns were crucial to McClintock’s analysis. They were also dependent on a knowledge of maize development to interpret. Then, even if they were understood, the link to genetic mechanisms was through classical breeding, analysis of mutants, and mapping of traits onto chromosomes. The pictures do not speak for itself, but instead stands for the systematically created mutant stocks, the careful breeding experiments, and the staining and other techniques necessary to render both chromosomes and developmental patterns visible.

McClintock’s explanations relied upon the display of patterns. Images of kernels in papers and public presentations visualized the phenomena she described; patterns in her pictures were the realized evidence for transposition and gene control in development themselves. But McClintock did not draw a mechanism for transposition or a version of the operon at the level of the gene – the molecular mechanisms of transposition and development in maize were

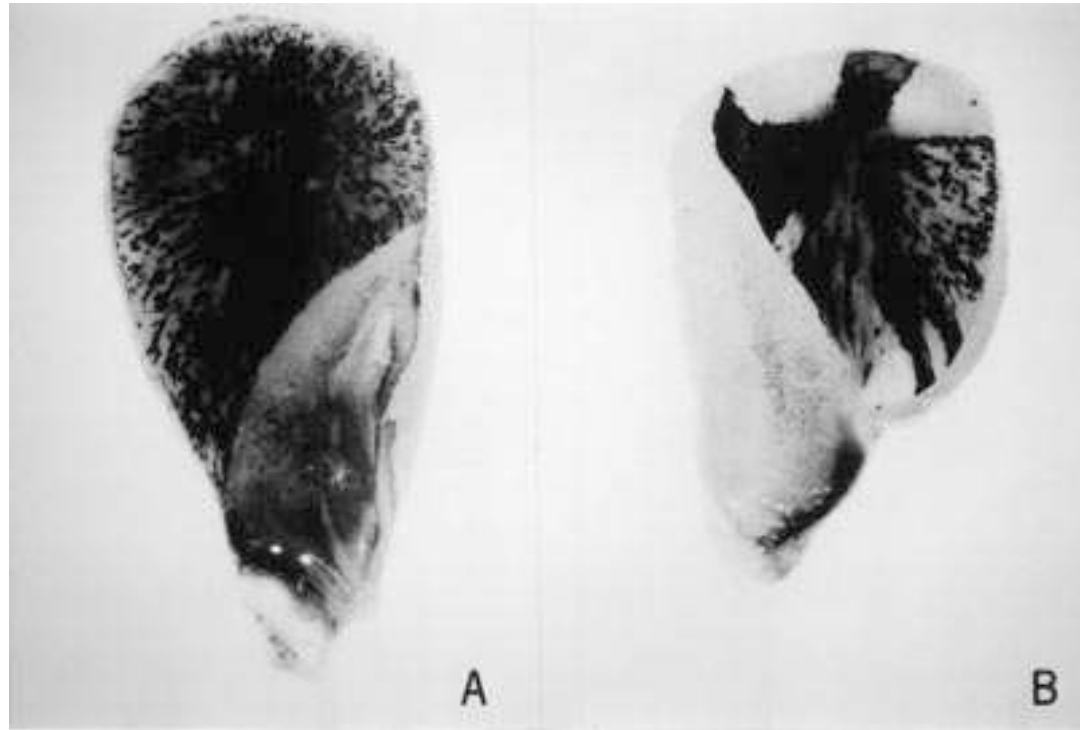


Figure 6. Kernels showing late (a) and early (b) transposition events. Barbara McClintock, "Development of the Maize Endosperm as Revealed by Clones," in *The Clonal Basis of Development*, 36th Symposium of the Society for Developmental Biology (June 1977), (New York: Academic Press, 1978), p. 225. [Courtesy of the Library of the American Philosophical Society and Academic Press, Inc.]

unknown. Lacking visual productions that were recognizable to molecular biologists, who could not make an independent judgment of patterns and their likely meaning because of their lack of familiarity with maize and its developmental pathways, her work was much less illuminating to those who could not “see the patterns.”

The Molecular Alternative

While McClintock continued through the 1970s to present her data primarily in the form of photographs, molecular biologists developed a new visual language. Molecular models to illustrate molecular structures, and “cartoons” to illustrate mechanisms and genetic structures became crucial to both hypothesis generation and dissemination of results in the molecular community.⁴¹ As in chemistry, a convention had to be established for illustrating and discussing genetic structures at the molecular level.⁴² Molecular scale made intervening representations inevitable. Since human beings cannot discern structures smaller than the wavelength of visible light with their own eyes or with light microscopes, tools such as the electron microscope and X-ray diffraction, as well as older methods of chemical analysis, have been necessary to analyze structures of molecular scale. Conventions to represent these structures then become necessary. After all, there is no such thing as “what it really looks like” for structures smaller than the smallest wavelength of visible light.⁴³

The visual language of molecular biology resulted from a blending of the representational traditions of chemistry through biochemistry and microbiology through cytogenetics. Physicists and chemists had played a central role in the introduction of new instruments, simplification of experimental systems, and the search for universal laws that had been part of the program of molecular biology since the 1930s. Following physicist Erwin Schrödinger’s call to search for new physical laws in biology, and foundation officer Warren Weaver’s vision of a biological science transformed by instruments and methods from the physical sciences, many chemists and physicists, some of whom were already working on biological molecules or structures, came together in the 1930s and 1940s to try to articulate biological structures and mechanisms at the molecular level.⁴⁴

The boundaries between biochemistry, biophysics, and protein chemistry – with which molecular biology shared tools and techniques – were perhaps more permeable to both personnel and techniques than were those with classical genetics. A series of discoveries in biochemistry and biophysics was rebuilding the concept of the gene and the basis of genetics at the level of molecules. This work was dependent upon classical genetics for theoretical foundations and on chemistry and physics for methods and instruments. Beadle and Tatum’s “one gene, one enzyme” hypothesis

(1941), Oswald T. Avery's 1944 demonstration that DNA – not protein – was the hereditary material, Watson and Crick's 1953 publication of the double-helix structure for DNA, ribonucleic acid (RNA) and its role as intermediary between DNA and proteins (1958), provided a vision of genes as a series of base pairs at the molecular level.⁴⁵ In the 1960s the molecular understanding was further refined by Jacob and Monod's (1961) the model of gene regulation and Marshall W. Nirenberg's elucidation of the genetic code (1966).⁴⁶ When plasmids (replicating circles of DNA separate from the chromosome), restriction enzymes (which cut DNA at specified base-sequences), and recombinant DNA (segments cut with restriction enzymes and "pasted" with ligase enzymes to form new and "artificial" sequences) completed the revolution in the early 1970s, molecular biology was a science that analyzed and manipulated genetic material chemically at the molecular level rather than manipulation by breeding and evaluation of phenotype.⁴⁷

Much like a microscopist who has to adjust her thinking and find the object of interest again when changing from a lower to a higher-power microscope objective, the turn to molecular methods which analyzed genes at the molecular level permitted gene action to be studied at a new level of explanation – and adjustments would have to be made to both theory and method to coordinate the classical and molecular views of transposition, gene control, and development. At the Brookhaven Symposium on gene control in 1965, McClintock was asked about the molecular mechanisms underlying her developmental patterns. McClintock's response highlights the difference in levels of analysis and explanation between her work and that of the molecular biologists:

I believe that we are not yet ready to construct any model at the molecular level to account for the modes of operation of the gene-control systems that have been discussed. We are still too ignorant of the composition, at the molecular level, of chromosomes in higher organisms and also of the various types of gene-control mechanisms that may operate in these organisms. In view of our ignorance, I believe it would not be profitable to attempt to construct a model at the molecular level.⁴⁸

Even her critics might agree with McClintock here.

"Good to Think With" or Final Products: Models, Line Drawings, Photographs, and the Approximation of Reality

Molecular biologists, like many other scientific communities, used representations in multiple ways. The most interesting of these uses was as hypothesis generators – tools that were "good to think with." The three distinct uses of visual representations in genetics and molecular biology: (1) as evidence; (2)

as hypothesis generators – use of molecular models to construct hypothetical structures is in this vein; (3) purely instructional or designed for dissemination and communication. Particular diagrams can transcend the categories in both directions. An image may be reproduced from laboratory notebook to research publication to textbook, but images or models may be useful in hypothesis formulation or in discussing material among scientists in the same laboratory. Molecular models and diagrams of mechanisms are partially a tradition borrowed from chemistry, the diagrams simultaneously represented summaries of data and hypotheses about mechanism.

The visual conventions of molecular biology, in fact, have two distinct lineages: one from the physical sciences – formulae and structural theory of molecules from chemistry and schematic mechanisms from physics; the other in cytology and microphotography through cytogenetics and microbiology.⁴⁹ The fusion of these two traditions was not complete, and individuals and subgroups generally maintained visual standards more closely allied with their disciplinary origins. Thus McClintock was closer to the traditions of cytology in which one drew what one saw, and Max Delbrück, Salvador Luria, James D. Watson, Francis H. Crick, and other founders of molecular biology, following the chemical and physical traditions, drew what they could infer or reconstruct. Each tradition, though, depended upon a complex set of standardized tools, experimental practices, and visual conventions to see and describe the invisible structures and processes.

Chemists had moved from an understanding of nomenclature and formulas as convention (useful fictions for thinking and communication) to formulas as *hypotheses* about chemical valence and three-dimensional structure or actual microstructure during the nineteenth and early twentieth centuries.⁵⁰ The epistemological debates between chemical formulas as summaries of experimental data and as diagrams of some real microstructure were fierce, with the atomists arguing for a structural reality to the atom, and the anti-atomists arguing that the evidence for such a claim was weak. Mid-nineteenth century atomists finally claimed agnosticism on the question of microstructure of the atom, a bit like McClintock did on the mechanism of transposition, concentrating instead on the value of their notation in expressing and predicting the results of experiments.⁵¹ The concept of the atom formed a valuable idea around which to organize experimental data, even though its literal existence was in question. Similarly, the idea of the transposon explained experimental results which were otherwise difficult to account for, even if its exact mechanism could not be explained yet. The formal end of the debate between the atomists and the anti-atomists came much later, ending in the early twentieth century with victory for the realists over the skeptics.⁵² In the end, the chemical substance *was* the structural formula.⁵³ With the movement

of chemists, physicists, and their instruments into biology, and the extension of the cytological tradition, the progression from notation as summary of data to formulas and diagrams as representations of actual microstructure became possible in biology.

Through the 1950s and 1960s, molecular biologists became ever more interested in models to illustrate the mechanisms and molecular structures they were elucidating, and following the visual traditions of chemistry, results were more and more frequently demonstrated with schematic diagrams rather than photographs or naturalistic images. Though we usually understand photographs to be more objective than drawings, in which details have been selected by the drafter, a photograph always has a photographer – who chooses which images to record on film and which to display or further disseminate, thereby selecting the most important details no less than the sketch artist.⁵⁴ The methods for crossing, selecting mutants, and preparing both karyotypes for the analysis of chromosomes and stained kernels which rendered developmental patterns visible constitute a complex system of experimental practice which highlights certain details at the expense of others. Those patterns represent a construction of scientific evidence different from diagrams of molecular mechanisms, but equally complex. Also, the high level of detail itself is both an analytical and aesthetic choice.

Different uses of visual representations can conflict, and the lines between them can blur. When do images cease being data and begin being hypotheses? When do they shift from hypothesis to assumption? Ambiguity may be necessary – even productive – but the possibility of reifying assumptions and data together in a seamless package is a risk. Schematic images began as necessary tools for illustrating phenomena too small to be photographed. But they fit well with the strongly reductionist tradition of molecular biology. Soon “cartoons” became indispensable tools for molecular biologists. Young scientists trained in this tradition – those who came up in the 1970s and after – learned not only to see but to think in cartoons.

Rollin D. Hotchkiss, in his introduction to the second edition of Evelyn Fox Keller’s biography of McClintock touches on the problem McClintock had in communicating with molecular biologists: “Characteristically, her descriptions remained verbal; I do not recall her ever stopping to draw for us a sketch or diagram of what she was talking about. Small wonder that most of us were ill prepared – and, I think, too lazy – to work hard enough to master the data as it poured forth.”⁵⁵ Hotchkiss implies that McClintock did not think to draw them a sketch or diagram because she didn’t want to stop to explain it. The mechanistic diagram of transposition that Hotchkiss and many of his colleagues hoped for was secondary for McClintock. To her, controlling development was the most important purpose served by transposition.

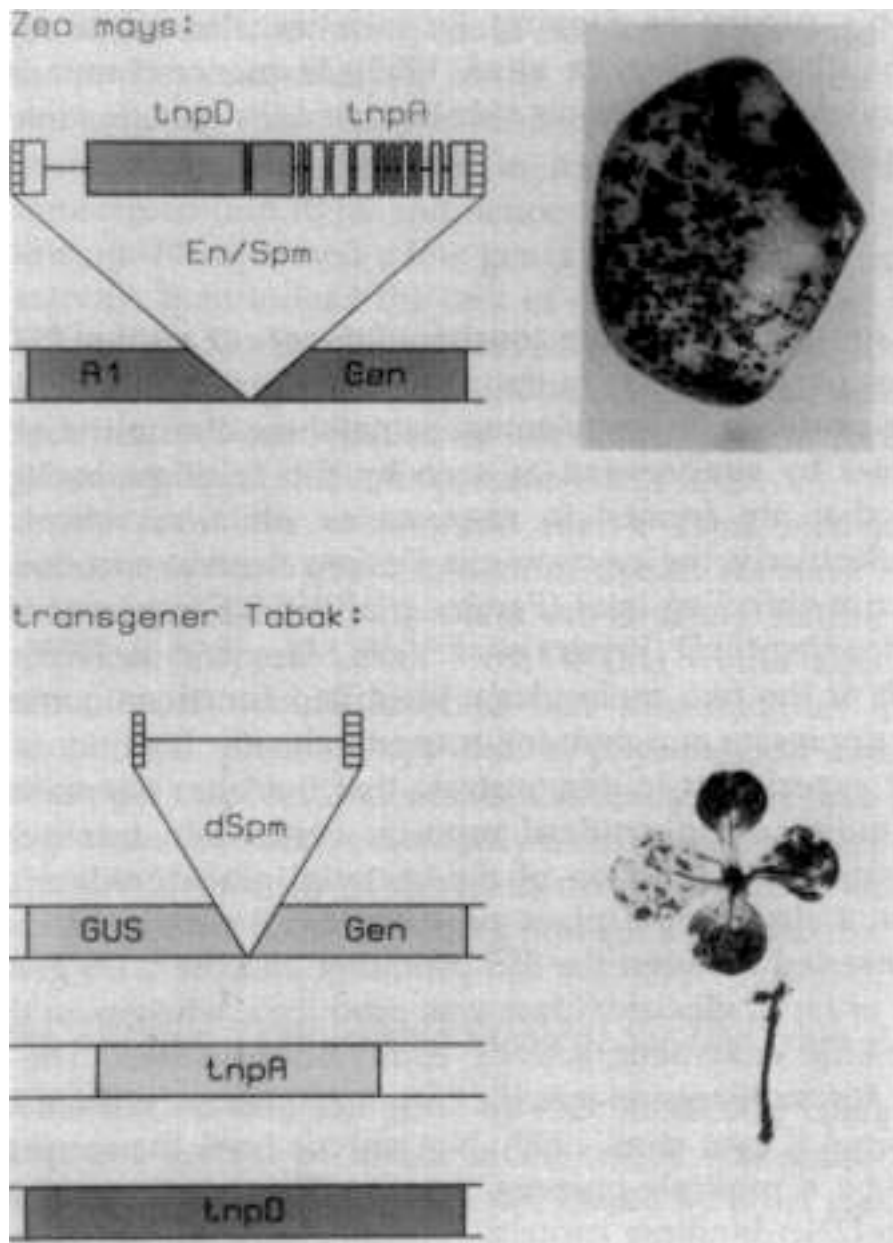


Figure 7. Kernel from McClintock compared to “cartoon” of transposon from Heinz Saedler and Peter Starlinger, “Twenty-Five Years of Transposable Element Research in Köln,” in *The Dynamic Genome: Barbara McClintock’s Ideas in the Century of Genetics*, ed., Nina Fedoroff and David Botstein (Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press, 1992), p. 256. [Courtesy Heinz Saedler, Peter Starlinger, and Cold Spring Harbor Laboratory Press.]

Figure 7 shows the translation of McClintock's controlling elements into conformation with the visual language of molecular biology. This comparison cannot represent what McClintock should have done in the 1960s, since this diagram – showing details of gene structure – could not have been drawn until the 1980s. Instead, it demonstrates the translation and reinterpretation of McClintock's work starting in the 1970s. Translation required both a zooming in from the chromosomal level to the DNA level of explanation (like switching to a higher-powered microscope objective), but, more importantly, an emphasis of mechanism over pattern. Like many translations, the new language alters the meaning. The kernel displays a developmental pattern – the diagram a simple movement of a gene.

The greater ease that visitors to McClintock's laboratory experienced in understanding her work is explained by a variety of factors. Naturally, one is that those likely to visit, and then to write about it, are generally self-selected fans. A second explanation is found in the personal attention given a single visitor and the interactive exchange permitted in that setting. The last is a more theoretical point about static (two-dimensional) illustration of four-dimensional phenomena. Illustration of movement, growth, development, and other forms of change over time (four-dimensional phenomena) present special problems for illustration in two dimensions, problems particularly common in geology and embryology.⁵⁶ McClintock understood that, and her descriptions of the point of origin of new pigment spots in Figures 4–6 highlight her understanding of the time-axis represented by growth and visible through the outward expansion of patterns in kernels over time. How well her illustrations conveyed that to readers and listeners would have depended on the background and experience of each audience member. An alternative approach to change over time is found in cinematic representation change over time, a difficult proposition with living organisms, and almost impossible with destructive analysis techniques which prevent one from following the same individual (kernel in her case) through the process under study.

Through their interaction with McClintock in the laboratory, visitors had an interactive, time-bound experience that assisted them in seeing the element of change over time in McClintock's developmental view. Her photographs of developmental patterns showed change over time implicitly, but one had to be primed in maize development to see it. Time-lapse photography and cinematography have been used by other investigators to show time-bound processes like growth and development, demanding less imagination from the audience, but presenting sometimes insuperable technical barriers to investigators seeking to create films. The cinematic work of Etienne-Jules Marey was influential in bringing time-lapse photography and microcinematography into the study of growth and movement in biology. Marey's photographs of

movement were also an inspiration for cubism – a more symbolic representation of movement. Historian James Strick’s work on Adrianus Pijper presents an analysis of the use of cinematography in the study of movement, and his challenge to the destructive and static methods of electron microscopy in studying movement.⁵⁷

On a scale of exposure from passive to active, those who listened to a talk or read a paper, and saw the static images, were at a disadvantage when compared to those who visited the laboratory. Another group also found McClintock’s work more comprehensible than molecular biologists – maize geneticists and cytogeneticists who shared her methods, organism, or both. It is perhaps trivial to remark that sharing techniques makes it easier to share results because some of the layers of interpretation required to understand the images were already shared – explanations of maize development, cytological techniques, or other aspects of the experimental practice form part of a common vocabulary – and maize workers share a kind of language through their experimental practice.⁵⁸ Organisms and the experimental techniques that are linked to them become the basis of shared skills, vocabulary, and experience. Transposition was first replicated by maize geneticists.⁵⁹

If the molecular biologists of the 1970s could not understand McClintock, as many said they could not, their lack of familiarity with maize genetics may have been part of the reason. The index to James D. Watson’s 1965 edition of *The Molecular Biology of the Gene* lists 25 separate entries and numerous subheadings for *Escherichia coli*, but none for maize or corn.⁶⁰ In a letter to McClintock in 1965, maize geneticist M.G. Neuffer explained his attempts to translate her control work: “You recognized immediately the over simplification in my description of the control systems. I had intended it to be as simple as possible because I find so many good biologists who have great difficulty comprehending these systems.”⁶¹ When Jacob and Monod first published the operon model, McClintock published a review comparing her work to theirs.⁶² In an extended correspondence with Ernst Caspari, who attempted to convince McClintock to write another review, McClintock and Caspari discussed the challenge of communicating her work. In their view, there were two groups: maize geneticists, who often understood transposition and her work in maize, but did not “quite see all the implications”,⁶³ and molecular biologists, who understood the theoretical aspects of gene regulation, but had difficulty integrating her work into what they knew about *E. coli*, plasmids, and mutagenic bacteriophages.⁶⁴ McClintock confided to Caspari that: “I suspect that geneticists, embryologists, and molecular biologists have not known how to incorporate the maize evidence into their thought systems.”⁶⁵ J.R.S. Fincham, later in 1973, tried to convince McClintock that her work was slowly becoming more integrated into the mainstream of genetic research,

tried to explain the “blindness” of his colleagues, but counseled patience: “Something that can’t be fitted into any existing framework of knowledge and ideas tends to get pushed out of mind, even if it isn’t actually disbelieved I think the maize phenomena are no longer so difficult to comprehend in principle, though of course obtaining evidence on detailed molecular mechanisms is a more formidable challenge than it is in a simpler prokaryotic system.”⁶⁶

Maize, after all, was a terrible organism for early molecular biology. Maize had a long generation cycle, was difficult to manipulate biochemically during its growth, had a complex genetic organization, and had intricate developmental patterns. In short – almost everything about maize made it hopelessly complex for molecular manipulation in the 1960s. These characteristics of the organism ensured that McClintock’s audiences in maize and molecular biology would not overlap until decades later.

Simplicity and Universal Mechanisms Versus Complexity and Orchestrated Systems

The simplicity of bacterial genetics offered a major theoretical advantage for molecular biology. It enabled workers to feel they were discovering fundamental properties of genes, enzymes, and cellular structures. The simpler the system in which a given gene or enzyme could be found, the more likely that molecule was fundamental to all life. This sort of universal mechanism suited the converted physicists who dominated the earliest stages of molecular biology. Universalism was bolstered when molecular biologists branched out into other model organisms such as yeast and animal viruses. A basic principle of evolutionary biology states that the simplest explanation for a shared trait is that it was present in a common ancestor. The more species that share the trait, the more likely that trait evolved once and is now universal. By the 1970s universalism was both an analytical tool and an aesthetic of the maturing molecular biology.

McClintock’s 1960s and 1970s reviews, papers, and talks explicitly comparing her work on maize controlling elements to the rising concern in molecular biology over gene regulation was an effort to enlist molecular biologists in her program of developmental genetics.⁶⁷ McClintock hoped to convince her colleagues to expand their interest from transmission genetics to development, and to help them to understand that the genome is not static, but a dynamic “tool” crucial to the adaptation of the organism. The patterns and developmental effects were the important issue to McClintock, and the articulation at the level of the gene that would have made McClintock’s work more easily comparable to Jacob and Monod’s operon or other molecular mechanisms could not be done with cytogenetic techniques and had not yet

been done in maize. Nina Fedoroff, among others, would be responsible for articulating the molecular mechanisms of transposition in maize, in the 1980s.⁶⁸

McClintock argued repeatedly that the operon did not explain everything about gene regulation, a charge her colleagues in molecular biology could not deny.⁶⁹ But for the molecular biologists, if the operon was a universal mechanism, it had brought them one step closer to the secret of life – simplicity itself. McClintock's vision of life was in layers of complexity, so even if the operon were present in every organism, it did not begin to explain evolution, development, or organismal complexity.⁷⁰

McClintock sought a new synthesis. By 1980 McClintock rejected the universalizing tendency of models and diagrams *as they were used in molecular biology*. She felt that the search for universal mechanisms in molecular biology and genetics was limiting scientific imagination. McClintock explained that: "I think once you realize that there is not just one kind of mechanism, there are various ways in which a particular problem is solved by organisms, and anything you think of you will find. There's no question about that. Any kind of strange situation you will find, because it's there."⁷¹ The molecular mechanisms of molecular biology were important to McClintock because she felt that they would be the basis of a new science of cytology and of a new genetics. She hoped to apply that new science to the problem of evolution, and development was the key. In a 1980 interview McClintock discussed the "knitters" who are able to work within a sense of "the now," but who are unable to move beyond that understanding, to see their tacit assumptions, and to view matters with a fresh eye:

It's not just one change, two changes [evolution]; it's innumerable changes. And they all have to be integrated. The consequences of this – the whole period of evolution as considered earlier and the attempts here for instance to have the department – it was all right for the thinking of the time, but really had not been, I think, carefully analyzed. It had been over enthusiastic. Just like DNA. People thought the type of controls that Jacob and Monod came out with – that everything was solved . . . it's so blinding. And this is what I fear all the time, that people just go on. The thing they do as a consequence lots is what I call knitting. There were loads and loads of knitters. They give us loads and loads of information. They just knit, knit – which is necessary. And I'm glad they get this enthusiasm that they have, because they think they have half solved something very definite. They have given the needed information with which to make the next steps. If you don't get caught in the times and trying to explain everything on what I call the "now basis," on the basis of what we know now, I believe that that isn't the way to solve things. The way to solve

things is to have anything that you see change your thoughts in such a way that you take a new direction and you allow yourself to take a new direction, because you see something that doesn't belong to the now.⁷²

Visual Evidence in Science and the History of Science

The history of science, like most fields of history, has been shy of exploring material and visual culture in favor of the seemingly less problematic textual records.⁷³ Yet the wider issues of modeling, representation, visual communication, and scientific illustrations have recently begun to receive attention. Recent interest in natural history and medical museums like that in Renato Mazzolini's 1993 edited volume complements work in history of science and sociology of science on visual language and pictorial representation.⁷⁴ Scientists, who for centuries had been forced to develop methods for illustrating the natural world, have faced the problem of conveying visual information to each other. Art historian William Ivins has argued that woodcuts, engraving, and other means of reproducing pictorial images were the basis of the Renaissance, Scientific Revolution, and Industrial Revolution.⁷⁵ Histories of scientific illustration and advice manuals written to teach young scientists the conventions and techniques of illustration stand as testaments to the importance of illustration in conveying crucial information in scientific texts, and of the role of changing technologies of visual reproduction in determining the form of those illustrations.⁷⁶ The importance of illustration in teaching, learning, and communicating scientific knowledge means that visual materials were produced in great quantity, and survive in museums, archives, and libraries. More study is needed, however, in how they were and are used, and even historians whose subject is not an obviously "visual" topic will likely find these images and objects valuable. Those interested in reconstructing practice (scientific, medical, or technological) will find them essential. How images were used – as evidence, as aids to hypothesis generation or as illustration for dissemination – may present important clues to historians trying to understand the picture or model at hand *and* the theory or practice it was intended to bolster.

Mechanisms, Patterns, and Theories

In McClintock's case, studying her visual evidence highlights the importance of pattern, complexity, and development in her work. Bringing development to the forefront of her work clarifies her vision of developmental timing and gene regulation. Divergent visual traditions help to explain why McClintock and the growing community of molecular biologists in the 1970s and 1980s

had such difficulty understanding each other, and the required vocabulary for reading her visual language explains why those who knew her well and visited her laboratory found her illustrations more informative than did casual observers. Even if McClintock could have drawn cartoons of the mechanism of transposition – which was not known – that was hardly the only obstacle to the acceptance of her theories about transposition and development. Naturally, the images can only tell part of the story, but one that has been less discussed than the clear conceptual problems transposition posed.⁷⁷ The images highlight something else important, the patterns. McClintock's emphasis on development, her agnosticism about the mechanism of transposition, and the secondary place of the mechanism in her work is apparent in her choice of images.

Conclusion

In McClintock's case the structured lack of communication grew out of moral, epistemological, and pragmatic factors. Organisms, schematic models, and the relevance of development to transmission genetics stood between McClintock and the colleagues who later said they always believed her, even when they didn't understand her.⁷⁸ Claims that "I always knew she would make good" are suspect, particularly when applied retrospectively to a Nobel laureate. Ultimately, the acceptance and integration of McClintock's work in the scientific mainstream in the 1960s and 1970s was due to confirmation of transposition in other organisms, notably in *E. coli*, and to the crucial importance of moveable DNA to the problem of drug resistance in bacteria.⁷⁹ If McClintock's Nobel Prize was based on the public health importance of her work, as is suggested in the Nobel Prize announcement, it was its extrapolation to bacteria and drug resistance that drew attention to her work in maize. The problems of development that had so fascinated McClintock, and inspired her work on transposition, remained opaque to most geneticists as late as the 1980s.

Notes

1. Thanks to the following individuals who have read drafts or otherwise shared their insights (none of whom are responsible for any errors that remain): Elizabeth Armstrong, Peter J. Bruns, Eve Buckley, Joshua Buhs, Lena Chen, Nathaniel Comfort, John Dettloff, Thomas Haigh, Donna Cassidy Hanley, Sally Smith Hughes, Susan D. Jones, Robert Kohler, M. Susan Lindee, Erin McLeary, Chris Ritter, Charles Rosenberg, Peter Schwartz, Geert Somsen, Jeffrey Tang, Audra Wolfe, and an audience at the Joint Atlantic Seminar for the History of Biology, Johns Hopkins University, Baltimore, Maryland, April 4, 1998.

2. "A biologist" quoted in Evelyn Fox Keller, *A Feeling for the Organism: The Life and Work of Barbara McClintock* (San Francisco: W.H. Freeman, 1983), p. 149.
3. Last paragraph of press release announcing the 1983 Nobel Prize in Physiology or Medicine from the webpage of the Nobel Foundation: <http://www.nobel.se/laureates/medicine-1983-press.html>, last updated July 23, 1997, accessed and printed December 15, 1997. See also: *Les Prix Nobel 1983: Nobel Prizes, Presentations, Biographies and Lectures* (Stockholm, Sweden: Almqvist & Wiksell International, 1984).
4. On the neglect or reputed neglect of Gregor Mendel: Augustine Brannigan. "The Reification of Mendel," *Social Studies of Science*, **9** (1979), 423–454. Augustine Brannigan and Richard A. Wanner, and James M. White, "The Phenomenon of Multiple Discoveries and the Re-publication of Mendel's Work in 1900," *Philosophy of the Social Sciences*, **11** (1981), 263–276. Alain F. Corcos and Floyd V. Monaghan. "Was Nageli to Blame for Mendel's Choice to Work with Hawkweeds?" *Michigan Academician: Papers of the Michigan Academy of Science, Arts, and Letters*, **20** (1988), 221–223. Michael H. MacRoberts, "Was Mendel's Paper on 'Pisum' Neglected or Unknown?," *Annals of Science*, **42** (1985), 339–345. Robert C. Olby, *Origins of Mendelism*, 2nd ed. (Chicago: University of Chicago Press, 1985). Hans-Jorg Rheinberger, "When Did Carl Correns Read Gregor Mendel's Paper? A Research Note," *Isis*, **86** (1995), 612–616. Jan Sapp, "The Nine Lives of Gregor Mendel," in *Experimental Inquiries: Historical, Philosophical, and Social Studies of Experimentation in Science*, ed. H.E. Le Grand (Dordrecht: Kluwer Academic, 1990), pp. 137–166. Federico Di Trocchio, "Mendel's Experiments: A Reinterpretation," *Journal of the History of Biology*, **24** (1991), 485–519. Alexander Weinstein, "How Unknown Was Mendel's Paper?," *Journal of the History of Biology*, **10** (1977), 341–364.
5. See especially Nathaniel Comfort, *"Breakage, Fusion, Bridge": The Discovery and Reception of Barbara McClintock's Controlling Elements* (Ph.D. Dissertation, State University of New York at Stony Brook, 1997).
6. Rediscovery as a concept has recently received some much-needed analysis. R.C. Olby, "Rediscovery as an Historical Concept," in *New Trends in the History of Science*, ed. R.P.W. Visser, H.J.M. Bos, L.C. Palm and H.A.M. Snelders (Amsterdam: Rodopi, 1989), pp. 197–208. Andrew F. Huxley, "Discovery and Forgetting in Science," *Proceedings of the American Philosophical Society*, **130** (1986), 475–481.
7. See especially Keller, *A Feeling for the Organism*, pp. 153–195. On the career of Barbara McClintock, see also: Ana Barahona and Francisco J. Ayala. "La Importancia del Contexto y el Trabajo de Barbara McClintock," *Arbor: Ciencia, Pensamiento y Cultura*, **598–99** (1995), 9–26. Nathaniel C. Comfort, "Two Genes, No Enzyme: A Second Look at Barbara McClintock and the 1951 Cold Spring Harbor Symposium," *Genetics*, **140** (1995), 1161–6. *The Dynamic Genome: Barbara McClintock's Ideas in the Century of Genetics*, ed. Nina Fedoroff and David Botstein (Cold Spring Harbor, N.Y.: Cold Spring Harbor Laboratory Press, 1992). Evelyn Fox Keller, *Reflections on Gender and Science* (New Haven: Yale University Press, 1985), pp. 115–26. Barbara McClintock, *The Discovery and Characterization of Transposable Elements: The Collected Papers of Barbara McClintock* (New York & London: Garland Publishing, 1987). San MacColl, "Intimate Observation," *Metascience: An International Review Journal for the History, Philosophy and Social Studies of Science*, **7** (1989), 90–98. Sharon Bertsch McGrayne, *Nobel Prize Women in Science: Their Lives, Struggles, and Momentous Discoveries* (Secaucus, N.J.: Carol Publishing Group, 1993). Jan Sapp presents an important parallel case for a mechanism of inheritance that was difficult to integrate into most contemporary genetic theory and practice and the importance of developmental biology in inspiring this line of work,

Beyond the Gene: Cytoplasmic Inheritance and the Struggle for Authority in Genetics (New York: Oxford University Press, 1987).

8. My concern here is with the communication, dissemination, and acceptance of McClintock's work in wider scientific communities, not the issue of discovery and its attendant questions of reason versus intuition at the level of the individual. Keller's discussion of McClintock's "different language" is quite thoughtful, and to the extent that she discusses communication with others, I find her account compelling. See esp. pp. 139–151. I do not take issue directly with Keller's feminist epistemology except to suggest that the differences between intuition, unarticulated reasoning, and experience (which may contain aspects of both) are difficult to document historically. My discussion of epistemology, standards of proof and argument is at the level of communication in the scientific community. There is a large philosophical literature on the subject of discovery, and interested readers are referred especially to the work of Kenneth F. Schaffner, *Discovery and Explanation in Biology and Medicine* (Chicago: University of Chicago Press, 1993). See also: Mirko D. Grmek, "A Plea for Freeing the History of Scientific Discoveries from Myth," in *On Scientific Discovery: The Erice Lectures 1977*, ed. Mirko Drazen Grmek, Robert S. Cohen, and Guido Cimino (Dordrecht, London, and Boston: D. Reidel Publishing Company, 1981), pp. 9–42. For a presentation of feminist epistemology of science, see Helen E. Longino, *Science as Social Knowledge: Values and Objectivity in Scientific Inquiry* (Princeton and London: Princeton University Press, 1990).
9. McClintock's published papers on transposition appear in: Barbara McClintock, *The Discovery and Characterization of Transposable Elements: The Collected Papers of Barbara McClintock* (New York: Garland Publishers, 1987). McClintock wrote a much fuller account, supported by extensive presentations of the data, which was never published. See McClintock Papers, Series III, Boxes 1 and 2. Comfort presents an account of the creation of these reports in *Breakage, Fusion, Bridge*, p. 201.
10. François Jacob and Jacques Monod, "Genetic Regulatory Mechanisms in the Synthesis of Proteins," *Journal of Molecular Biology*, 3 (1961), 318–358.
11. On women scientists and the institutional problems they faced in building scientific careers see: *Creative Couples in the Sciences*, eds. Helena M. Pycior, Nancy G. Slack, and Pnina G. Abir-Am (New Brunswick, N.J.: Rutgers University Press, 1996). Margaret W. Rossiter, *Women Scientists in America: Struggles and Strategies to 1940* (Baltimore: Johns Hopkins University Press, 1982). Margaret W. Rossiter, *Women Scientists in America: Before Affirmative Action, 1940–1972* (Baltimore: Johns Hopkins University Press, 1995). *Uneasy Careers and Intimate Lives: Women in Science, 1789–1979*, eds. Pnina G. Abir-Am and Dorinda Outram (New Brunswick: Rutgers University Press, 1987).
12. Nathaniel Comfort, *Breakage, Fusion, Bridge*, pp. 69–172.
13. This work is discussed in detail in Keller, *A Feeling for the Organism*; Keller, *Reflections on Gender and Science*; Comfort, "Two genes, no enzyme"; Comfort, *Breakage, Fusion, Bridge*. The relevant papers were reprinted together McClintock, *Discovery and Characterization of Transposable Elements*.
14. A plasmid is a small piece of DNA present in a cell separate from its chromosome or chromosomes. Plasmids replicate independently of the chromosome and can be passed from one species of bacteria to another.
15. For an example of the meanings and usages that have come to be associated with it, see: Douglas E. Berg, and Martha M. Howe, eds., *Mobile DNA* (Washington, DC: American Society for Microbiology, 1989).
16. Comfort, *Breakage, Fusion, Bridge*, pp. 230–289.

17. McClintock to Caspari, Caspari Papers, September 27, 1972.
18. I use epistemology here as an actors' category, following what McClintock and the scientists with whom she was working felt could be extrapolated from what kind of evidence rather than an external philosophical standard of proof. In that sense, my work falls into the tradition of "epistemic sociology" rather than philosophical epistemology.
19. Comfort, *Breakage, Fusion, Bridge*, pp. 230–289.
20. Jan Sapp, *Beyond the Gene*. Evelyn Fox Keller, *Refiguring Life: Metaphors of Twentieth-Century Biology* (New York: Columbia University Press, 1995), esp. pp. 1–42.
21. Comfort, *Breakage, Fusion, Bridge*, pp. 118–72.
22. On the history of embryology and development, see: Alice Levine Baxter, *Edmund Beecher Wilson and the Problem of Development: From the Germ Layer Theory to the Chromosome Theory of Inheritance* (Ph.D. Thesis, Yale University, 1974). Philippe Caspar, *Penser l'Embryon, d'Hippocrate à Nos Jours* (Paris: Editions Universitaires, 1991). *A Conceptual History of Modern Embryology*, ed. Scott F. Gilbert (New York: Plenum Press, 1991). *A History of Embryology: The Eighth Symposium of the British Society for Developmental Biology*, ed. T. J. Horder, J. A. Witkowski, C. C. Wylie (Cambridge: Cambridge University Press, 1986). Evelyn Fox Keller, "Developmental Biology as a Feminist Cause?" *Osiris: Second Series*, 12 (1997), 16–28. *Histoire du Concept de Récapitulation: Ontogenèse et Phylogenèse en Biologie et Sciences Humaines*, ed. Paul Mengal (Paris: Masson, 1993). John A. Moore, "Science as a Way of Knowing: Developmental Biology," *American Zoologist*, 27 (1987), 415–573. Alain Prochiantz, *Les Stratégies de l'Embryon: Embryons, Gènes, Évolution* (Paris: Presses Universitaires de France, 1988).
On the creation of "developmental genetics": Garland E. Allen, "T. H. Morgan and the Split Between Embryology and Genetics, 1910–35," in *A History of Embryology: The Eighth Symposium of the British Society for Developmental Biology*, eds. T. J. Horder, J. A. Witkowski, C. C. Wylie (Cambridge: Cambridge University Press, 1986), pp. 113–46. Richard M. Burian, Jean Gayon, and Doris Zallen, "Boris Ephrussi and the Synthesis of Genetics and Embryology," in *A Conceptual History of Modern Embryology*, ed. Scott F. Gilbert (New York: Plenum Press, 1991), pp. 207–227. Scott F. 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 R. Benson and Jane Maienschein (Philadelphia: University of Pennsylvania Press, 1988), pp. 311–46. Scott F. Gilbert, "Induction and the Origins of Developmental Genetics," in *A Conceptual History of Modern Embryology*, ed. Scott F. Gilbert (New York: Plenum Press, 1991), pp. 181–205. Evelyn Fox Keller, "Language and Science: Genetics, Embryology, and the Discourse of Gene Action," *Great Ideas Today* (1994), 2–29. Evelyn Fox Keller, *Refiguring Life*.
23. On the Morgan group's linkage of cytology and breeding experiments, see: Garland E. Allen, *Thomas Hunt Morgan: The Man and His Science* (Princeton, N.J.: Princeton University Press, 1978); Robert E. Kohler, *Lords of the Fly: Drosophila Genetics and the Experimental Life* (Chicago: University of Chicago Press, 1994), esp. pp. 53–90. On McClintock's parallel work, see: Keller, *A Feeling for the Organism*, pp. 39–61; Comfort, *Breakage, Fusion, Bridge*, pp. 70–78.
24. Keller, *A Feeling for the Organism*, p. 149.
25. A history of cytogenetic practice, particularly one focused on the experimental techniques and visual representation of results, would be necessary to answer definitively the question of how much of McClintock's technique and visual practice is idiosyncratic and how much is part of a shared culture. Unfortunately, such a history has not yet been written. The history of cytology, though, is relevant. See: Augustín Albarracín

- Teulón, *La Teoría Celular: Historia de un Paradigma* (Madrid: Alianza Editorial, 1983). John Randal Baker, "The Cell Theory: A Restatement, History, and Critique." *Quarterly Review of Microscopical Science*. Part I, **89** (1949), 103–125; Part II, **90** (1949), 87–108; Part III, **93** (1952), 157–190; Part IV, **94** (1953), 407–440; Part V, **96** (1955), 449–481 [republished as: John Randal Baker, *The Cell Theory: A Restatement, History, and Critique* (New York: Garland, 1988)]. William Coleman, "Cell, Nucleus and Inheritance: An Historical Study," *Proceedings of the American Philosophical Society*, **109** (1965), 124–158. François Duchesneau, *Genèse de la Théorie Cellulaire* (Montreal: Bellarmin; Paris: Vrin, 1987). Arthur Frederick William Hughes, *A History of Cytology* (London; New York: Abelard-Schuman, 1959). Marc Klein, *A la Recherche de l'Unité Élémentaire des Organismes Vivants; Histoire de la Théorie Cellulaire* (Paris: Librairie du Palais de la Decouverte, 1960).
26. On the history of microscopy and microtechnique: Brian Bracegirdle, *A History of Microtechnique* (Ithaca: Cornell University Press, 1978). Gerard L'E. Turner, "'Some Curious Old Instruments': The Assembly of the Royal Microscopical Society's Collection of Microscopes," *Journal of the History of Collections*, **1** (1989), 149–166. Royal Microscopical Society (Great Britain), *The Great Age of the Microscope: The Collection of the Royal Microscopical Society through 150 Years* (Bristol, England and Philadelphia, Hilger, 1989).
 27. See: Anthony S. Travis, *The Rainbow Makers: The Origins of the Synthetic Dyestuffs Industry in Western Europe* (Bethlehem: Lehigh University Press; London: Associated University Presses, 1993).
 28. For details of *Drosophila* and salivary chromosome preparations, see Allen, *Thomas Hunt Morgan*, 154–213; and Kohler, *Lords of the Fly*, 53–90. For George Beadle's experience with *Neurospora* cytogenetics and McClintock's role in it, see Keller, *A Feeling for the Organism*, 113–118.
 29. Thomas Hunt Morgan, *The Physical Basis of Heredity* (Philadelphia: Lippincott, 1920).
 30. Harriet B. Creighton and Barbara McClintock, "A Correlation of Cytological and Genetical Crossing-Over in *Zea mays*," *Proceedings of the National Academy of Sciences*, **17** (1931), 492–427.
 31. Barbara McClintock, "Chromosome Organization and Genic Expression," *Cold Spring Harbor Symposium on Quantitative Biology*, **16** (1951), 13–47, 18.
 32. Though Allen, *Thomas Hunt Morgan*, and Kohler, *Lords of the Fly*, present the origins of this experimental practice and its visual representation, a systematic study of its dissemination remains to be done.
 33. *Ibid.*, 22.
 34. For the development of chromosome mapping in Thomas Hunt Morgan's laboratory, see Robert E. Kohler, *Lords of the Fly: Drosophila Genetics and the Experimental Life* (Chicago: University of Chicago Press, 1994).
 35. The trait whose expression was affected was not important except that it had to be visible to McClintock on analysis. The first transposons McClintock identified changed the expression of pigment genes, and led to the spotted and speckled kernels she went on to analyze. Figure 4 shows a change in carbohydrate metabolism in which starch becomes visible when the kernel is stained with iodine. This image was published twice: Barbara McClintock, "The Control of Gene Action in Maize," 167; and Barbara McClintock, "Development of the Maize Endosperm as Revealed by Clones," in *The Clonal Basis of Development, 36th Symposium of the Society for Developmental Biology* (June 1977) (New York: Academic Press, 1978), pp. 217–237, 229.
 36. Barbara McClintock, "The Control of Gene Action in Maize," p. 167.

37. McClintock, "Development of the Maize Endosperm as Revealed by Clones," p. 229.
38. *Ibid.*, p. 233.
39. *Ibid.*, p. 234.
40. *Ibid.*, p. 225.
41. For a discussion of three-dimensional molecular models made of wood, plastic, and metal that became a hallmark of molecular biology, see: Eric Francoeur, "The Forgotten Tool: The Design and Use of Molecular Models," *Social Studies of Science*, 27 (1997), 7–40.
42. The history of molecular biology cannot be adequately summarized here, but see, eg.: Pnina G. Abir-Am, "The Politics of Macromolecules: Molecular Biologists, Biochemists, and Rhetoric," *Osiris: Second Series*, 7 (1992), 164–191. Soraya De Chadarevian and Jean-Paul Gaudilliere, "The Tools of the Discipline: Biochemists and Molecular Biologists [Introduction to a special issue on this topic]," *Journal of the History of Biology*, 29 (1996), 327–330. Horace Freeland Judson, *The Eighth Day of Creation*. Lily E. Kay, *The Molecular Vision of Life*. Robert E. Kohler, *Partners in Science*. Robert Olby, *The Path to the Double Helix*.
43. This observation, and a great many other thoughtful analyses of scale, method, and epistemology appear in Nicolas Rasmussen, *Picture Control: The Electron Microscope and the Transformation of Biology in America, 1940–1960* (Stanford: Stanford University Press, 1997).
44. Erwin Schrödinger, *What is Life? The Physical Aspect of the Living Cell, Based on Lectures Delivered under the Auspices of the Institute at Trinity College, Dublin, In February 1943* (Cambridge: Cambridge University Press, 1944). Gunther Stent argues that the core of this group was Alfred D. Hershey, Salvador Luria, and Max Delbrück. *Phage and the Origins of Molecular Biology*, ed. John Cairns, Gunther S. Stent, and James D. Watson (Cold Spring Harbor, N.Y.: Cold Spring Harbor Laboratory, 1966), p. 5. See also William C. Summers, "How Bacteriophage Came to Be Used by the Phage Group," *Journal of the History of Biology*, 26 (1993), 255–67. See also: Evelyn Fox Keller, "Physics and the Emergence of Molecular Biology," *Journal of the History of Biology*, 23 (1990), 389–409. Approaching from a different angle, protein chemist Linus Pauling would also have to be included in the founding generation, along with a number of X-ray crystallographers working on biologically-active molecules. On Pauling, see: Thomas Hager, *Force of Nature: The Life of Linus Pauling* (New York: Simon & Schuster, 1995). Ted and Ben Goertzel, *Linus Pauling: A Life in Science and Politics* (New York: Basic Books, 1995). *The Pauling Symposium: A Discourse on the Art of Biography. Proceedings of the conference on the life and work of Linus Pauling (1901–1994): February 28–March 2, 1995, Corvallis, Oregon*, ed. Ramesh S. Krishnamurthy, Clifford S. Mead, Mary Jo Nye (Corvallis: Oregon State University Libraries, 1996). Anthony Serafini, *Linus Pauling: A Man and His Science* (New York: Paragon House, 1989).
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55. In Keller, *A Feeling for the Organism*, p. xv. For other perspectives on miscommunication, see: "In this sense, McClintock's presentation in 1951 was well timed, and, had less been packed into the brief time available, or had her presentation been more clearly articulated, it might well have succeeded in capturing her audience's imagination." Keller, *A Feeling for the Organism*, p. 157. "There was Barbara McClintock, a tiny but formidable scientist, speaking as fast as anyone I knew and packing years of work into a one-hour lecture. Her discoveries in maize genetics had to wait decades before being appreciated as opening new paths in biology." Salvador Luria, *A Slot Machine, A Broken Test Tube: An Autobiography* (New York: Harper Colophon Books, 1984), p. 34.

56. See, for example: Martin J.S. Rudwick, *Scenes from Deep Time*. James Strick, "Swimming Against the Tide: Adrianus Pijper and the Debate over Bacterial Flagella, 1946–1956," *Isis*, **87** (1996), 274–305. More symbolic work by artists in the early twentieth century attempting to illustrate the fourth dimension (whether construed in space or time) is fascinating, but the semiotics of that community were difficult to translate into the realistic images demanded by scientific communities. On symbolic renderings of a temporal fourth dimension in two-dimensional art see: George Kluber, *La Configuración del Tiempo: Observaciones Sobre la Historia de las Cosas* (Madrid: Nerea, 1988). M. Baudson, *L'Art et le Temps: Regards sur la Quatrième Dimension* (Paris: A. Michel, 1985). J. McClain, "Time in the Visual Arts: Lessing and Modern Criticism," *Journal of Aesthetics and Art Criticism* Baltimore, **44** (1985–1986), 41–58.
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72. Transcript of interview of Barbara McClintock, August 21, 1980 by Dr. Franklin H. Portugal, p. 3. Keller describes McClintock's concern with the tendency of scientists to see their models as reality, explaining that "That's why models, when they first begin to be promulgated, are so bothersome to me." Keller, *A Feeling for the Organism*, p. 174. Georges Cuvier was similarly concerned with contaminating his drawings and reconstructions with unproven hypotheses, refusing to permit drawings that he considered too "speculative" to appear in his publications. Martin J.S. Rudwick, *Scenes from Deep Time*, pp. 36–7.
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