BOOK REVIEWS

McClintock Myths

The Dynamic Genome. Barbara McClintock's Ideas in the Century of Genetics. NINA FEDOROFF and DAVID BOTSTEIN, Eds. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY, 1992. viii, 422 pp., illus. $65.

Barbara McClintock's extraordinary contributions to genetics during a 70-year career inspired many myths among her colleagues, and after her belated Nobel Prize in 1983 among the wider scientific community and even the public at large. As a Cornell graduate student and instructor she engendered "the golden age of maize cytogenetics" and reputedly "always did everything better than anyone else, and was always right." In Ithaca, and later at the University of Missouri, her discovery that a particular chromosomal segment "organizes" nucleoli and that chromosome tips (telomeres) have special properties that broken chromosome ends can acquire by "healing" reinforced speculation that she had a mysterious "feeling for the organism" that conferred insights not available from coldly rational, deductive, "masculine" reasoning. Shortly after finally achieving a permanent position with the Carnegie Institution of Washington's Genetics Department at Cold Spring Harbor, McClintock discovered that the beautiful patterns on the kernels of Indian corn were caused by tiny controlling elements, now known as transposable elements, that moved from place to place on chromosomes according to an intricate logic she insisted was related to processes controlling embryonic development. At a time when many viewed genomic stability as the cornerstone of genetics, her work was reputedly misunderstood and ignored, becoming widely believed only after 1975 when transposable elements were rediscovered in bacteria by practitioners of the now dominant field of molecular biology. This book is a celebration of McClintock's career that was presented to her on the occasion of her 90th birthday. In it readers can examine for themselves these McClintock myths and become better acquainted with the real McClintock through a few of her most famous papers and the reminiscences of many whom she influenced personally and intellectually.

We learn repeatedly of the extraordinary effect McClintock had on those who knew her. McClintock thought deeply about topics ranging from the working of the human mind, the process of evolution, weather forecasting, and acupuncture, to the migrations of indigenous peoples as deduced from their maize strains. Her filing cabinets were filled not only with detailed records, summaries, figures, and conclusions from her maize research. They overflowed with observations from nature, including the developmental genetics of the Queen Anne's lace and touch-me-nots she observed on regular excursions near Cold Spring Harbor. A spur-of-the moment visit to her laboratory would frequently lead to a four- or five-hour, intensely intellectual conversation on science, art, politics, and their practitioners. Bruce Alberts, Oscar Miller, and Evelyn Witkin speak for many in describing a feeling of exhilaration following such conversations, a feeling of having experienced a unique personality, a pure intellect devoid of any pretension. Guenter Albrecht-Buehler compares her in her desire to impress to "a Bengal tiger stirred up by a photo safari." To Alberts she showed it was possible to maintain the "pure curiosity and excitement about science we experienced as young students." She was repelled by attempts to find in her life and work anything more or less than a search for scientific truth as close as the human mind can ever know it.

A display at the DNA Learning Center, 1989. [From *The Dynamic Genome*; Cold Spring Harbor Laboratory Archives]

McClintock encouraged innumerable young scientists who sought her counsel, and she generously provided them with advice, unique genetic stocks, and, in Elizabeth Blackburn's case, pages of detailed handwritten summaries "to save . . . the trouble of reading these long papers." However, she could be daunting as well. Harriet Creighton, who collaborated with McClintock to demonstrate that recombination is accompanied by a physical interchange of chromosomal material, describes McClintock's competitive nature on the tennis court and the near impossibility of adjusting a microscope to her exacting specifications. Beginning with her first resolution of the individual maize chromosomes, McClintock's abilities as a cytologist were unsurpassed. Helen Crouse, one of McClintock's few graduate students, describes calling her to the microscope to look at a new translocation she had painstakingly identified. After only an instant McClintock nodded and also pointed out a second rearrangement she had overlooked. Similar casual examination of George Beadle's slides led to her addition as a co-author when she rapidly interpreted his data. Charles Burnham admits to arriving in the laboratory very early to have enough time to analyze new chromosomal preparations before McClintock would get so much as a glance. David Perkins describes how in a ten-week visit to Stanford, McClintock revolutionized the cytogenetics of *Neurospora*, accomplishing more than in all previous study of this and related fungi. Following an intricate description of chromosome movements, Gerald Fink describes her response to his hopeful "I think I understand": "You think you do—but you don't," she winked.

The papers that resulted from McClintock's cytogenetic research have a timeless quality. Joseph Gall and Helen Crouse describe the simplicity and power of her analysis of the nucleolus organizer. Her papers on the fate of broken chromosomes, mostly in *Genetics*, and her narrative culminating in the discovery of transposition published in the Carnegie Institution Yearbooks between 1944 and 1950 represent two of the best detective stories in the biological literature. We learn from Nancy Kleckner's discussion of meiotic pairing and Elizabeth Blackburn's molecular studies of telomeres that after 50 years McClintock's work continues to inspire advances on the frontiers of chromosome research. The breakage-fusion-bridge cycle she discovered in the late '30s has recently been implicated in producing gene amplifications such as those commonly found in human cancers.

Was Barbara McClintock's discovery of transposable elements unappreciated? McClintock herself describes the reaction to her 1951 Cold Spring Harbor symposium presentation and the accompanying 35-page article (reprinted in this volume) as one of "puzzlement and, in some instances, hostility." We learn from Mel Green and Ira Herskowitz that this common view is only partly true. Most geneticists understood the existence of transposable elements; indeed, a small group of maize workers in addition to McClintock continued to analyze their properties. But most scientists, including even H. J. Muller, simply didn't know what to make of them. Meanwhile, the intellectual and generational landscape of genetics was undergoing revolutionary change. Young molecular biologists possessed a new confidence, bordering on arrogance, that they could learn everything of significance by studying a few prokaryotic organisms and their viruses. "You are wasting your time with *Drosophila* genetics," Harriet Ephrussi Taylor told Mel Green in 1953, and plant genetics probably ranked even lower. Nevertheless, McClintock's ideas remained known and were influential. Controlling elements were invoked to explain the properties of phase variation in *Salmonella* by Lederberg in 1956, the properties of bacteriophage mu by Taylor in 1963, the mammalian X inactivation center by Cattanach in 1967, the unstable *Drosophila* white-crimson mutation by Green in 1969, and yeast mating-type interconversion by Oshima in 1971. Science knows no truer measure of appreciation. Although many prokaryotic geneticists became aware of McClintock's work only after the rediscovery of transposable elements in bacteria around 1975, others discussed their research with her regularly. Allan Campbell recounts McClintock's influence on his seminal model of prophage integration and remarks on the similarity between his reasoning and her earlier studies of ring chromosomes. David Botstein describes her detailed critique, prior to publication, of his important 1975 manuscript on Tn*10* transposition. Despite the generally narrow purview and frenzied competition of the brash young biologists, so different from the outlook of maize researchers, they rapidly characterized transposition as a cutting and pasting of DNA molecules, opening the only path to further advances. Nina Fedoroff, Heinz Saedler, and Peter Starlinger tell the story of how McClintock's elements were molecularly characterized and provide simple models to explain many of the genetic properties they display.

Wasn't McClintock right about transposable elements, but wrong to claim they are related to developmental control mechanisms? Autonomous transposable elements frequently regulate their defective cousins using an element-encoded DNA-binding protein, a common developmental mechanism. Furthermore, autonomous elements themselves appear to be controlled by methylation, a frequently postulated regulatory strategy for host genes and chromosomes. But what about transposition itself? The movement of transposable elements or the action of their protein products has yet to be associated with the development of most organisms. However, the function of transposable elements remains very difficult to test critically, because it has not been possible to simultaneously modify all their dispersed copies to learn of any consequences. Furthermore, McClintock suggested that transposons could serve their hosts in an evolutionary role, by providing the genome with an ability to respond constructively to challenges from the environment. Mary Lou Pardue describes recent work on the repair of broken chromosomes in *Drosophila* that suggests a simple mechanism for telomere healing. Newly broken chromosome ends produced by certain methods do not undergo fusions as in maize but remain unstable and lose DNA sequences each time the chromosome replicates. However, a specific family of DNA sequences appears to recognize such ends and frequently transposes onto them, replacing the lost material. In conjunction with other insertionally specific transposons, this accumulation of new sequences may, over the course of a few organismal generations, regenerate a newly functional telomere. Clearly, much remains to be learned about the multitude of transposable elements swarming within apparently all genomes. However, it would not be too surprising to see yet another of McClintock's ideas vindicated when the necessary experiments can actually be carried out.

Was Barbara McClintock able to see so much further than most of her contemporaries because she possessed special powers derived from a mysterious, holistic approach? If so, they were certainly not the warm, fuzzy, "put your brain in neutral" kind of analysis widely shilled today as

Vignettes: Anthropobotany

The tragic ballad of the woodbine that falls in love with a morning glory ("but she twines to the left and he to the right") is evidence that non-scientists [have been] fascinated by the mechanics of twining (note: according to the bard, the offspring of this unnatural union grew straight up and fell over).

—*F. E. Putz* and *N. Michele Holbrook*, in *The Biology of Vines* (Francis E. Putz and Harold A. Mooney, Eds.; Cambridge University Press)

If asked what gardening and horticulture are all about, we might quickly respond—plants! But think about it: For whose benefit are horticultural books written, botanical societies, plant societies, and garden clubs established? Were Latin plant names invented so that plants would know who they were . . .?

—*Charles Lewis*, in the foreword to *The Role of Horticulture in Human Well-Being and Social Development: A National Symposium* (Diane Relf, Ed.; Timber Press)

Plants are downright dangerous. Try to think of any food that makes eating irresistible which is not derived from plants! And as if plant inventions like chocolate (Ah, chocolate!), coffee, wine, and spices would not do enough damage to the neat and trim appearance of human bodies, the plants provide us with addictive substances, too. Keep in mind who seduces our brains with tricky substances like nicotine, cocaine, or morphine! So, let us not be too sentimental about some other slightly beneficial plant products like digitalis, aspirin, and five million other pharmaceuticals. Look at the inner city problems all over the United States and tell me that these problems were not caused by plants!

—*Guenter Albrecht-Buehler*, in *The Dynamic Genome: Barbara McClintock's Ideas in the Century of Genetics* (Nina Federoff and David Botstein, Eds.; Cold Spring Harbor Laboratory Press) providing deep insight. McClintock's powers derived from reasoning so well developed that the therefores and QEDs of her papers and conversations left others straining to catch up. Could it be that the information available from manipulating maize chromosomes and studying effects on kernel and plant development was simply underestimated by those who decided the system had outlived its usefulness? Even today, maize chromosomes remain arguably the best material for the analysis of heterochromatic chromosome regions, a prime residence of transposable elements. Could it be that to such a gifted mind knowledge of the emergent properties of the biological world's higher organizational levels—the plant galls and the patterns on beetles' wings—provided valuable insights into its lower levels, rather than just vice versa? Perhaps, to those recently entering biology, to those working primarily at a single level, or to those still recovering from self-inflicted wounds with Occam's razor, this could seem like vitalism resurgent.

Barbara McClintock's life and the issues she addressed are too large to be fully encompassed by this volume. But it is a pure pleasure for anyone interested in the history of genetics and the life of one of its greatest exponents. James Shapiro suggests that McClintock may eventually be seen as the "central figure in 20th century biology." Perhaps Allan Campbell best summarizes the lessons we can learn from her life: "Throughout her career she has shown that true originality has no need to fear competition, that a first-rate intellect can set its own criteria for self-esteem, and that the joy of discovery can be given precedence over all else."

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Insects Recaptured

The Treatise on Invertebrate Paleontology. Part R, Arthropoda 4. Vols. 3 and 4, Superclass Hexapoda. F. M. CARPENTER. Geological Society of America, Boulder, CO (distributor), and University of Kansas, Lawrence, 1992. xxiv, 655 pp., illus. $87.50.

Insects are the most abundant animals on earth, in terms both of species and of individuals. About a million extant species have been described, but students of tropical forest canopies are finding so many previously unknown species that they suggest that there may be as many as 30 million species when all have been described. One estimate of the number of individuals present at one point in time puts it at 10^{18}. Study of the evolution of this exceedingly successful group of organisms has challenged biologists for many years. Unfortunately, the fossil record is not as helpful as we would like it to be. For most animal phyla (such as the Chordata and Mollusca) at least a third of the total known species are represented as fossils, but for insects the figure is more like 1 percent. Insects do not occur in marine sediments, and their delicate forms are preserved only in certain fine-grained terrestrial sediments and in amber—and even then often only as tantalizing fragments.

Nevertheless there is much to be learned from Frank M. Carpenter's long-awaited two volumes on Hexapoda in the *Treatise on Invertebrate Paleontology*. Carpenter's first paper on fossil insects was published in 1928, his latest in 1992—a span of 64 years. He explains that teaching and administrative duties prevented him from devoting full time to this project until he retired in 1974. We may feel fortunate that he has enjoyed such a long retirement, for the labor of synthesizing the scattered literature was enormous, and there is no one else who could have done it and done it so well. A great deal of research on fossil insects has been conducted in Russia, and having the results of this research made available to those of us who do not read Russian is a special reward from these volumes. All groups of insects (and the few non-insectan hexapods) that are represented in the fossil record are reviewed, although the Blattaria (cockroaches) are not covered as to families and genera, in deference to the ongoing studies of Jörg Schneider on the rich fossil record of that group.

Fifty-five orders of insects known only from fossils have been described, many of these on the basis of small fragments. Carpenter reduces these to ten, either by placing taxa in other, more inclusive orders or by simply listing them as "order unknown." Eleven orders were already present in the Upper Carboniferous; most were already fully winged, and two are still with us (mayflies and cockroaches). Yet the Lower Carboniferous is a void, and the Devonian contains only a few fragments of springtails (wingless hexapods, not here considered insects). Much obviously occurred in the Lower Carboniferous, including the origin of wings. Insects were on the wing long before birds and bats, and they are the only organisms that did not sacrifice their forelimbs when they acquired flight (aside, some wag has said, from angels). Carpenter briefly reviews some of the hypotheses that have been proposed concerning the origin of wings, but the secrets remain locked in the Lower Carboniferous.

For persons not well acquainted with the insect fossil record, there are many surprises in these volumes. Who would have supposed that the Mecoptera (scorpion flies), now a minor group, were represented by 24 families in the Mesozoic? Or that the Psocoptera (book and bark lice), hardly a significant component of contemporary ecosystems, had a diverse assemblage in the Permian (20 genera in seven families)? The Palaeodictyoptera, an order of over 100 genera occurring in the late Paleozoic, all possessed stout beaks that they may have used to extract juices from Cordaitales (forerunners of modern conifers). The Titanoptera had large stridulatory areas on their wings; they were large insects, and one can imagine *Mesotitan giganteus* resounding through Triassic forests, long before there were birds to join in the chorus. Many, but not all, early groups of insects were large, one of the largest being a dragonfly-like insect with a wingspan of 70 centimeters. Persons addicted to attributing the demise of the dinosaurs to a comet from space at the end of the Cretaceous will find little evidence to support their beliefs here; many groups of insects flourished and expanded through the Cretaceous-Tertiary interface.

Special bonuses in these volumes include a preliminary section on nomenclature by the editor of the *Treatise*, Roger Kaesler, and several useful stratigraphic range charts. Many genera are illustrated by line drawings, and there are several excellent photographs, taken by the author. Altogether these are extremely useful volumes that will not be rivaled for many years to come.

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Progress in Physiology

A History of Gastric Secretion and Digestion. Experimental Studies to 1975. HORACE W. DAVENPORT. Oxford University Press, New York, 1992. xviii, 414 pp., illus. $75.

Gastric secretion and digestion haven't been the same since the farmer's son from Lebanon, Connecticut, set out from home with a new mare and a hundred dollars. Who cares why? Horace W. Davenport, one of the deans of gastrointestinal physiology. Davenport, who occupied the