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Edited by Lee B. Kass

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Cover Photo

1. Dr. Charles R. Burnham (Ph.D. Wisconsin), National Research Council Fellow, Department of Plant Breeding; 2. Marcus M. Rhoades, graduate student, Department of Plant Breeding; 3. Dr. Rollins A. Emerson, Head, Department of Plant Breeding; 4. Dr. Barbara McClintock, Instructor, Department of Botany; 5. George W. Beadle, graduate student, Department of Plant Breeding. Photo taken at Cornell University, 1929, in the Plant Breeding Garden, outside the Plant Breeding field house (currently fondly called the "McClintock Shed"; see back cover). Beadle shared a Nobel Prize in 1958; McClintock was awarded an unshared Nobel Prize in 1983.

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A COMPANION VOLUME
Volume IV

Barbara McClintock and Harriet Creighton at Cornell University 1929
Stone Hall, Cornell University
(Image used with permission of H. B. Creighton)

Perspectives On
Nobel Laureate Barbara McClintock's Publications
(1926-1984)
A COMPANION VOLUME
Volume IV

Edited by

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The initial release of this Incremental Book of 782 pages, spread over two volumes includes a complete list of the publications of Nobel Laureate Barbara McClintock. In addition, with publisher's permissions, we have reprinted many of McClintock's research articles (45 of 106, or 42%), provided online links for free access to 32 (30%) more, and cited traditional sources for the remaining 29 (27%) articles. Only six (6) of the citations listed in the Contents are not presently accessible online. In this initial release we include fourteen essays ("perspectives"), which are paired with the original scholarship being discussed. Ten more perspectives are forthcoming, and will be offered as additional 'increments' when they become available.

Volume IV is **accessible**, i.e., readable and navigable by users who are visually impaired. If using Adobe Acrobat Reader, this PDF can be read out loud. To activate this capability, choose View > Activate Read Out Loud. Then open the PDF to the desired page and choose View > Read Out Loud > Read This Page Only (or "Read to End of Document"). To end the reading or to deactivate this feature, choose View > Read Out Loud > (either Pause, Stop, or Deactivate Read Out Loud).

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Left to Right, Back Row: Charles Russell Burnham, Marcus M. Rhoades, Rolland A. Emerson, Barbara McClintock;
Front Row: and George Beadle (kneeling with dog).
(Courtesy William B. Provine and Department of Plant Breeding & Genetics, Cornell University)

Plant Breeding Garden, Cornell University, outside the former Department Field Laboratory, now fondly called "The McClintock Shed."

To the memory of Royse P. Murphy,
Mentor, collaborator, and friend
&
To the memory of
William B. Provine,
For inspiring this project
&
My husband, Robert E. Hunt
For his constant encouragement of my efforts

Volume I [The increments appearing in Volumes 3 & 4 are identified by red type.]

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McClintock, B. 1929c. A *2N-1* chromosomal chimera in maize. *Journal of Heredity XX*(5): 218.

Perspective: Identifying the individual chromosomes of maize. by **Randy Wayne**, Cornell University

McClintock, B. 1929d. Chromosome morphology in *Zea mays*. *Science* 69(1798): 629.

1930 **Perspective**: McClintock's presence of mind and forward vision as illustrated in the analysis of an interchange in maize. by **Ron Phillips**, University of Minnesota

McClintock, B. 1930a. A cytological demonstration of the location of an interchange between two non-homologous chromosomes of *Zea mays*. *Proceedings of the National Academy of Sciences* 16(12: 791–796.

McClintock, B. 1930b [ABSTRACT #9] A cytological demonstration of the location of an interchange between two non-homologous chromosomes of *Zea mays*. *Anatomical Record* 47(3): 380.

(**McClintock, B. and H. E. Hill**. 1929 [ABSTRACT #32]. The cytological identification of the chromosomes associated with the '*R-golden*' and '*B-liguleless*' linkage groups in *Zea mays*. *Anatomical Record* 44(3): 291.)

1931 **McClintock, B. and H. E. Hill**. 1931. The cytological identification of the chromosome associated with the *R-G* linkage group in *Zea mays*. *Genetics* 16(2): 175–190.

Perspective: Proof of physical exchange of genes on the chromosomes. by **Edward Coe**, University of Missouri & **Lee B. Kass**, Cornell University

McClintock, B. 1931a. The order of the genes *C*, *Sh*, and *Wx* in *Zea mays* with reference to a cytologically known point in the chromosome. *Proceedings of the National Academy of Sciences* 17(8): 485–491.

Creighton, H. B. and B. McClintock. 1931. A correlation of cytological and genetical crossing-over in *Zea mays*. *Proceedings of the National Academy of Sciences* 17(8): 492–497.

Perspective: **Increment #01 [in Vol. III, page 1.47.1]** by **Lee B. Kass** and **James A. Birchler**

McClintock, B. 1931b. Cytological observations of deficiencies involving known genes, translocations and an inversion in *Zea mays*. *Missouri Agricultural Experiment Station Research Bulletin* 163: 1–30.

1932 **Creighton, H. B. and B. McClintock**. 1932 [EXHIBIT/ABSTRACT]. Cytological evidence for 4-strand crossing over in *Zea mays*. *Proceedings of the International Congress of Genetics II*: 392.

Perspective: An attempt at identifying the position of genes on the chromosomes of maize using X-ray induced chromosome deficiencies. by **Randy Wayne**, Cornell University

McClintock, B. 1932b. A correlation of ring-shaped chromosomes with variegation in *Zea mays*. *Proceedings of the National Academy of Sciences* 18(12): 677–681.

1933 (**McClintock, Barbara**. 1932a [ABSTRACT]. Cytological observations in *Zea* on the intimate association of non-homologous parts of chromosomes in the mid-prophase of meiosis and its relation to diakinesis configurations. *Proceedings of the International Congress of Genetics II*: 126–128.)

McClintock, Barbara. 1933a. The association of non-homologous parts of chromosomes in the mid-prophase of meiosis in *Zea mays*, with 51 figures in the text and plates *VII–XII*. *Zeitschrift für Zellforschung und mikroskopische Anatomie* 19(2): 191–237.

McClintock, Barbara. 1933b. News Items from Ithaca: 11. *Brown midrib1* (*bm1*) … . *Maize Genetics Cooperation News Letter 4* [18 December 1933]: 2.

McClintock, Barbara. 1933c. News Items from Ithaca: 12. A new narrow leafed character is linked with *a1*. *Maize Genetics Cooperation News Letter 4* [18 December 1933]: 2.

1934 **Perspective**: McClintock's pioneering studies of the nucleolar organizer region in maize: exact chromosomal localization and its function. by S**tephen E. Bloom**, Cornell University

McClintock, B. 1934a. The relation of a particular chromosomal element to the development of nucleoli in *Zea mays* with 21 figures in the text and plates *VIII–XIV*. *Zeitschrift für Zellforschung und mikroskopische Anatomie* 21(2): 294–328.

1935 **Perspective**: forthcoming

Creighton, H. B. and B. McClintock. 1935. The correlation of cytological and genetical crossing-over in *Zea mays*. A corroboration. *Proceedings of the National Academy of Sciences* 21(3): 148–150.

Rhoades, M. M. and B. McClintock. 1935. The cytogenetics of maize. *Botanical Review*. 1(8): 292–325

1936 **McClintock, B.** 1936a. Cornell University, Ithaca, N.Y. — 8. Mosaic plants in part heterozygous and in part homozygous for a chromosome 5 deficiency. *Maize Genetics Cooperation News Letter* 10: 5–6.

McClintock, B. and H. Creighton. 1936. Cornell University, Ithaca, N.Y. — 9. Several inversions … chromosome 9 … and chromosome 4,… detected and isolated by Creighton and [McClintock]. *Maize Genetics Cooperation News Letter* 10: 6.

McClintock, B. 1936b. Cornell University, Ithaca, N.Y. — 10. Disjunction studies on interchanges show that sister spindle fiber regions do not separate in I, … . *Maize Genetics Cooperation News Letter* 10: 6

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1938 **McClintock, B.** 1938a. [ABSTRACT] A method for detecting potential mutations of a specific chromosomal region. *Genetics* 23(1): 159. [2.3][1]

(**McClintock, B.** 1937a. [ABSTRACT] The production of maize plants mosaic for homozygous deficiencies: Simulation of the *bm1* phenotype through loss of the *Bm1* locus. *Genetics* 22(1): 200.)

McClintock, B. 1938b. The production of homozygous deficient tissues with mutant characteristics by means of the aberrant mitotic behavior of ring-shaped chromosomes. *Genetics* 23(4): 315–376.

Perspective: forthcoming [2.69]

*[2]**McClintock, B.** 1938c. The fusion of broken ends of sister half-chromatids following breakage at meiotic anaphase. *Missouri Agricultural Experiment Station Research Bulletin* 290: 1-48.

1939 ***McClintock, B.** 1939. The behavior in successive nuclear divisions of a chromosome broken at meiosis. *Proceedings of the National Academy of Sciences* 25(8): 405–416. [2.71]

1 Page numbers in brackets take readers to sections in these volumes where perspectives, with links and/or relevant reprinted publications originate.

2 References preceeded by an asterisk (*) are not reprinted herein, but were collected and published previously in McClintock, B. 1987a. In most instances, we've provided an Internet link to the original article.

1941 **Perspective**: forthcoming [2.73]

*__McClintock, B.__ 1941a. The stability of broken ends of chromosomes in *Zea mays*. *Genetics* 26(2): 234–282.

McClintock, B. 1941b. The association of mutants with homozygous deficiencies in *Zea mays*. *Genetics* 26(5): 542–571. [2.75]

McClintock, B. 1941c. Spontaneous alterations in chromosome size and form in *Zea mays*. pp. 72–80. In: *Genes and Chromosomes - Structure and Organization. Cold Spring Harbor Symposia on Quantitative Biology, Volume IX*. Katherine S. Brehme, ed, The Biological Laboratory, Cold Spring Harbor, Long Island, New York. [2.113]

1942 **Perspective**: forthcoming [2.125]

*__McClintock, B.__ 1942a. The fusion of broken ends of chromosomes following nuclear fusion. *Proceedings of the National Academy of Sciences* 28(11): 458–463.

*__McClintock, B.__ 1942b. Maize genetics: The behavior of "unsaturated" broken ends of chromosomes. Phenotypic effects of homozygous deficiencies of distal segments of the short arm of chromosome 9. *Carnegie Institution of Washington Year Book No. 41*, 1941-1942: 181–186. [2.127]

1943 *__McClintock, B.__ 1943. Maize genetics: Studies with broken chromosomes. Tests of the amount of crossing over that may occur within small segments of a chromosome. Deficiency mutations: Progressive deficiency as a cause of allelic series. *Carnegie Institution of Washington Year Book No. 42*, 1942-1943: 148–152. [2.129]

1944 **McClintock, B.** 1944a. Carnegie Institution of Washington, Department of Genetics, Cold Spring Harbor [sic], Long Island, N.Y. *Maize Genetics Cooperation News Letter*. 18: 24–26. [2.131]

McClintock, B. 1944b. The relation of homozygous deficiencies to mutations and allelic series in maize. *Genetics* 29(5): 478–502. [2.135]

*__McClintock, B.__ 1944c. Maize genetics: Completion of the study of the allelic relations of deficiency mutants. The chromosome-breakage mechanism as a means of producing directed mutations. Continuation of the chromatid type of breakage-fusion-bridge cycle in the sporophytic tissues. Homozygous deficiency as a cause of mutation in maize. *Carnegie Institution of Washington Year Book No. 43*, 1943-1944: 127–135. [2.157]

1945 *__McClintock, B__. 1945a. Cytogenetic studies of maize and *Neurospora*: Induction of mutations in the short arm of chromosome 9 in maize. *Carnegie Institution of Washington Year Book No. 44*, 1944-1945: 108–112. [2.159]

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1946 *__McClintock, B.__ 1946. Maize genetics: Continuation of the study of the induction of new mutants in chromosome 9. Modification of mutant expression following chromosomal translocation. The unexpected appearance of a number of unstable mutants. *Carnegie Institution of Washington Year Book No. 45*, 1945-1946: 176–186. [3.3]

1947 **Perspective**: forthcoming [3.5]

*__McClintock, B.__ 1947. Cytogenetic studies of maize and *Neurospora*: The mutable *Ds* locus in maize. *Carnegie Institution of Washington Year Book No. 46*, 1946-1947: 146–152.

1948 ***McClintock, B.** 1948. Mutable loci in maize: Nature of the *Ac* action. The mutable *c* loci. The mutable *wx* loci. Conclusions. *Carnegie Institution of Washington Year Book No. 47*, 1947-1948: 155–169. [3.7]

1949 ***McClintock, B.** 1949. Mutable loci in maize: The mechanism of transposition of the *Ds* locus. The origin of *Ac*-controlled mutable loci. Transposition of the *Ac* locus. The action of *Ac* on the mutable loci it controls. Mutable loci *c m-2* and *wx m-1*. Conclusions. *Carnegie Institution of Washington Year Book No. 48*, 1948-1949: 142–154. [3.9]

1950 **Perspective**: Transposable controlling elements step out onto the broader scientific stage. by **Clifford Weil**, Purdue University [see also Fedoroff *PNAS*, 2012, 109(50): 20200-20203] [3.11]

***McClintock, B.** 1950a. The origin and behavior of mutable loci in maize. *Proceedings of the National Academy of Sciences*. 36(6): 344–355.

***McClintock, B.** 1950b. Mutable loci in maize: Mode of detection of transpositions of *Ds*. Events occurring at the *Ds* locus. The mechanism of transposition of *Ds*. Transposition and change in action of *Ac*. Consideration of the chromosome materials responsible for the origin and behavior of mutable loci. *Carnegie Institution of Washington Year Book No. 49*, 1949-1950: 157–167. [3.23]

1951 **McClintock, Barbara**. 1951a. Mutable loci in maize. *Carnegie Institution of Washington Year Book No. 50*, 1950-1951: 174–181. [3.25]

Perspective: forthcoming [3.27]

McClintock, B. 1951b [©1952]. Chromosome organization and genic expression. Pgs. 13–47. In: *Genes and Mutations. Cold Spring Harbor Symposia on Quantitative Biology, Volume XVI.* Katherine Brehme Warren (ed.), The Biological Laboratory, Cold Spring Harbor, Long Island, New York.

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1952 ***McClintock, B**. 1952. Mutable loci in maize: Origins of instability at the *A1* and *A2* loci. Instability of *Sh1* action induced by *Ds*. Summary. *Carnegie Institution of Washington Year Book No. 51*, 1951-1952: 212–219. [3.29]

1953 ***McClintock, B.** 1953a. Induction of instability at selected loci in maize. *Genetics* 38(6): 579–599. [3.31]

Perspective: McClintock and epigeneitcs: changes in phase of transposition activity. by **Nina V. Fedoroff**, King Abdullah University of Science and Technology & Penn State University [3.33]

***McClintock, B.** 1953b. Mutations in maize: Origin of the mutants. Change in action of genes located to the right of *Ds*. Comparison between *Sh1* mutants. Change in action of genes located to the left of *Ds*. Meiotic segregation and mutation. *Carnegie Institution of Washington Year Book No. 52*, 1952-1953: 227–237.

1954 ***McClintock, B.** 1954. Mutations in maize and chromosomal aberrations in *Neurospora*: Mutations in maize. *Carnegie Institution of Washington Year Book No. 53*, 1953-1954: 254-260.]3.41]

1955 **McClintock, B.** 1955a. Carnegie Institution of Washington, Department of Genetics, Cold Spring Harbor, Long Island, N.Y. 1. Spread of mutational change along the chromosome. 2. A case of *Ac*-induced instability at the *bronze* locus in chromosome 9. 3. Transposition sequences of *Ac*. 4. A *suppressor-mutator* system of control of gene action and mutational change. 5. System responsible for mutations at *a1m-2*. *Maize Genetics Cooperation News Letter* 29: 9–13. [3.43]

***McClintock, B.** 1955b. Controlled mutation in maize: The *a1m-1-Spm* system of control of gene action and mutation. Continued studies of the mode of operation of the controlling elements *Ds* and *Ac*. *Carnegie Institution of Washington Year Book No. 54*, 1954-1955: 245–255. [3.51]

1956 *__McClintock, B.__ 1956a. Intranuclear systems controlling gene action and mutation. p. 58–74. In: *Mutation, Brookhaven Symposia in Biology, No. 8.* Biology Department, Brookhaven National Laboratory, Upton, NY. [R.C. King, Symposium Chairman.] [3.53]

McClintock, B. 1956b. Carnegie Institution of Washington, Department of Genetics, Cold Spring Harbor, Long Island, N.Y. 1. Further study of the *a1m-1-Spm* system. 2. Further study of *Ac* control of mutation at the *bronze* locus in chromosome 9. 3. Degree of spread of mutation along the chromosome induced by *Ds*. 4. Studies of instability of chromosome behavior of components of a modified chromosome 9. *Maize Genetics Cooperation News Letter* 30: 12–20. [3.55]

*__McClintock, B.__ 1956c. Mutation in maize: *Ac* control of mutation at the bronze locus in *a1m-1-Spm* system of control of gene action. Changes in chromosome organization and gene expression produced by a structurally modified chromosome 9. *Carnegie Institution of Washington Year Book No. 55*, 1955-1956: 323–332. [3.65]

Perspective: forthcoming [3.67]

McClintock, B. 1956d [© 1957]. Controlling elements and the gene. Pp. 197–216. In: *Genetic Mechanisms: Structure and Function, Cold Spring Harbor Symposia on Quantitative Biology, Volume XXI*. K. B. Warren (ed.), The Biological Laboratory, Cold Spring Harbor, Long Island, New York.

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1957 **McClintock, B.** 1957a. Carnegie Institution of Washington, Department of Genetics, Cold Spring Harbor, Long Island, N.Y. 1. Continued study of stability of location of *Spm*. 2. Continued study of a structurally modified chromosome 9. *Maize Genetics Cooperation News Letter* 31: 31–39. [3.69]

*__McClintock, B.__ 1957b. Genetic and cytological studies of maize: Types of *Spm* elements. A modifier element within the *Spm* system. The relation between *a1m-1* and *a1m-2*. Aberrant behavior of a fragment chromosome. *Carnegie Institution of Washington Year Book 56*, 1956-1957: 393–401. [3.81]

1958 *__McClintock, B.__ 1958. The suppressor mutator system of control of gene action in maize: The mode of operation of the *Spm* element. A modifier element in the *a1m-1-Spm* system. Continued investigation of transposition of *Spm*. *Carnegie Institution of Washington Year Book 57*, 1957-1958: 415–429. [3.83]

1959 *__McClintock, B.__ 1959. Genetic and cytological studies of maize: Further studies of the *Spm* system. *Carnegie Institution of Washington Year Book 58*, 1958-1959: 452–456. [3.85]

1961 **Perspective**: Comparative studies relevant to transposon function in plant development. by **Allan M. Campbell**, Stanford University [3.87]

*__McClintock, B.__ 1961a. Some parallels between gene control systems in maize and in bacteria. *American Naturalist XCV*(884): 265–277.

*__McClintock, B.__ 1961b. Further studies of the suppressor-mutator system of control of gene action in maize: Control of *a1m-2* by the *Spm* system. A third inception of control of gene action at the *A1* locus by the *Spm* system. Control of gene action at the locus of *Wx* by the *Spm* system. Control of reversals in *Spm* activity phase. Nonrandom selection of genes coming under the control of the *Spm* system. *Carnegie Institution of Washington Year Book 60*, 1960-1961: 469–476. [3.91]

1962 *__McClintock, B.__ 1962. Topographical relations between elements of control systems in maize: Origin from *a1m-5* of a two-element control system. Analysis of *a1m-2*. The derivatives of *bz m-2*. *Carnegie Institution of Washington Year Book, 1961-1962*: 448–461. [3.93]

1963 *__McClintock, B.__ 1963. Further studies of gene-control systems in maize: Modified states of *a1m-2*. Extension of *Spm* control of gene action. Further studies of topographical relations of elements of a control system. *Carnegie Institution of Washington Year Book 62*, 1962-1963: 486–493. [3.95]

1964 *__McClintock, B.__ 1964. Aspects of gene regulation in maize: Parameter of regulation of gene action by the *Spm* system. Cyclical change in phase of activity of *Ac* (*Activator*). *Carnegie Institution of Washington Year Book 63*, 1963-1964: 592–601, plus 2 plates and 2 plate legends. [3.97]

1965 **McClintock, B.** 1965a. Department of Genetics, Carnegie Institution of Washington, Cold Spring Harbor, N.Y.: 1. Restoration of *A1* gene action by crossing over. *Maize Genetics Cooperation News Letter* 39: 42–[45]. [3.99]

McClintock, B. 1965b. Department of Genetics, Carnegie Institution of Washington, Cold Spring Harbor, N.Y.: 2. Attempts to separate *Ds* from neighboring gene loci. *Maize Genetics Cooperation News Letter* 39: [45]–51. [3.105]

*__McClintock, B.__ 1965c. Components of action of the regulators *Spm* and *Ac*: The component of *Spm* responsible for preset patterns of gene expression. Transmission of the preset pattern. Components of action of *Ac*. *Carnegie Institution of Washington Year Book 64*, 1964-1965: 527–534, plus 2 plates and 2 figure legends. [3.115]

*__McClintock, B.__ 1965d. The control of gene action in maize. Pp. 162–184. In: *Genetic Control of Differentiation, Brookhaven Symposia in Biology: No. 18*. Biology Department, Brookhaven National Laboratory, Upton, N.Y. [H. H. Smith Chairman of Symposium Committee.] [3.117]

1967 *__McClintock, B.__ 1967. Regulation of pattern of gene expression by controlling elements in maize: Pigment distribution in parts of the ear. Pigment distribution in the pericarp layer of the kernel. Presetting of the controlling element at the locus of *c2m-2*. Inheritance of modified pigmentation patterns. *Carnegie Institution of Washington Year Book 65*, 1965-1966: 568–576, plus 2 plates and 2 plate legends. [3.119]

1968 *__McClintock, B.__ 1968a. The states of a gene locus in maize: The states of *a1m-1*. The states of *a1m-2*. *Carnegie Institution of Washington Year Book 66, 1966-1967*: 20–28, plus 2 plates and 2 plate legends. [3.121]

*__McClintock, B.__ 1968b. Genetic systems regulating gene expression during development. In: *Control Mechanisms in Developmental Processes, II. The Role of the Nucleus*. Michael Locke, ed. The 26th Symposium of the Society for Developmental Biology (June 1967) [La Jolla, CA, USA]. *Developmental Biology, Supplement 1*: 84–112. Academic Press. New York. [3.123]

1971 *__McClintock, B.__ 1971. The contribution of one component of a control system to versatility of gene expression: Relation of dose of *Spm* to pattern of pigmentation with the class II state of *a2m-1*. Distinctive phenotypes associated with activation of an inactive *Spm*. An example of versatility of control of gene expression associated with component-2 of *Spm*. *Carnegie Institution of Washington Year Book* 70, 1970-1971: 5–17. [3.125]

1978 **Perspective**: forthcoming [3.127]

*__McClintock, B.__ 1978b. Development of the maize endosperm as revealed by clones. Pp. 217–237. In: *The Clonal Basis of Development*. Stephen Subtelny and Ian M. Sussex eds. The 36th Symposium of the Society for Developmental Biology (June 1977) [Raleigh, North Carolina, USA]. Academic Press, Inc., New York.

*__McClintock, B.__ 1978c. Mechanisms that rapidly reorganize the genome. *Stadler Genetics Symposia, vol. 10*, pp. 25–48. University of Missouri, Agricultural Experiment Station, Columbia, Missouri. [3.129]

1980 *__McClintock, B__. 1980. Modified gene expressions induced by transposable elements. In: *Mobilization and Reassembly of Genetic Information. Proceedings of the Miami Winter Symposium*. W. A. Scott, R. Werner, D. R. Joseph, and Julius Schultz eds. *Miami Winter Symposium 17*: 11–19. Academic Press, Inc. New York. [3.131]

1984 **Perspective**: The special character of McClintock's Nobel Prize address. by **James A. Shapiro**, University of Chicago [3.133]

(**McClintock, B.** 1983. [ABSTRACT]. Trauma as a means of initiating change in genome organization and expression. *In vitro 19*(3, Part II) [March 1983]: 283–284.)

***McClintock, B.** 1984a [Nobel lecture]. The significance of responses of the genome to challenge. *Science* 226(4676): 792-801.

McClintock, B. 1984b. The significance of responses of the genome to challenge. Pp. 174– 193. *Les Prix Nobel 1983.*

McClintock, B. 1993. The significance of responses of the genome to challenge. Pp. 180–199. In: Tore Frangsmyr and Jan Lindsten, eds. *Nobel Lectures in Physiology or Medicine 1981–1990*. World Scientific Pub. Co., Singapore, for the Nobel Foundation.

1987 **McClintock, B.** 1987b. Introduction. Pp. vii-xi. In: T*he Discovery and Characterization of Transposable Elements. The Collected Papers of Barbara McClintock. Genes Cells and Organisms; Great Books in Experimental Biology*, J.A. Moore, series editor, Garland Publishing Co. New York. [3.143]

Part IV: ORIGIN AND DIVERSITY OF MAIZE IN THE AMERICAS (1957-1981) [4.1]

Moreno, U., A. Grobman, and B. McClintock. 1959. Escuela Nacional de Agricultura, La Molina, Lima, Peru: 5. Study of chromosome morphology of races of maize in Peru. *Maize Genetics Cooperation News Letter 33*: 27–28. [4.3]

***McClintock, B.** 1959. Genetic and cytological studies of maize: Chromosome constitutions of some South American races of maize. *Carnegie Institution of Washington Year Book 58*, 1958-1959: 452–456. [4.5]

***McClintock, B.** 1960. Chromosome constitutions of Mexican and Guatemalan Races of Maize: General Conclusions. *Carnegie Institution of Washington Year Book 59*, 1959-1960: 461–472.

Perspective: Barbara McClintock's Cytogenetic Studies of Chromosome Constitutions of Races of Maize in the Americas. by **David B. Walden**, The University of Western Ontario [4.7]

McClintock, B. 1978a. Significance of chromosome constitutions in tracing the origin and migration of races of maize in the Americas. Chapter 11, pp. 159–184. In: *Maize Breeding and Genetics*, David B. Walden ed., John Wiley and Sons, Inc., New York.

Perspective: Significance of McClintock's pattern concept in the analysis of chromosome knob distribution in the races of maize. by **T. Angel Kato Y**, Colegio de Postgraduados, Montecillo, Mexico [4.39]

McClintock, B., T. Angel Kato Y. and Almiro Blumenschein. 1981. Chromosome Constitution of Races of Maize. Its Significance in the Interpretation of Relationships Between Races and Varieties in the Americas. *Colegio de Postgraduados, Escuela Nacional de Agricultura, Chapingo, Edo*. Montecillo, Mexico. xxxi, 517 pp.

Perspective/Book Revew: McClintock et al. Chromosome Constitution of Races of Maize. Its Significance in the Interpretation of Relationships Between Races and Varieties in the Americas [1981]. *Theoretical and Applied Genetics* 67(2-3): 130 (1983). by **David H. Timothy**

Part V: CYTOGENETIC STUDIES OF *Neurospora crassa* (1945-1954) [5.1]

McClintock, B. 1945a. Preliminary studies of the chromosomes of the fungus *Neurospora crassa*. *Carnegie Institution of Washington Year Book No. 4*: 108–112. [5.3]

McClintock, B. 1945b. *Neurospora*. I. Preliminary observations of the chromosomes of *Neurospora crassa*. *American Journal of Botany* 32(10): 671–678.

McClintock, B. 1947 [1 July 1946–30 June 1947]. Cytogenetic studies of maize and *Neurospora*: Continuation of studies of the chromosomes of *Neurospora crassa*. *Carnegie Institution of Washington Year Book No. 46*, 1946-1947: 146–152. [5.13]

McClintock, B. 1954. Mutations in maize and chromosomal aberrations in *Neurospora*: Chromosome aberrations in *Neurospora*. *Carnegie Institution of Washington Year Book No. 53*, 1953-1954: 254-260. [5.15]

*Reprinted in McClintock 1987a. The articles in the issues of the *Carnegie Institution of Washington Year Book may be viewed online or downloaded:*

https://carnegiescience.edu/carnegie-institution-year-books-numbers-1-through-99-years-1903-through-2001

Note: The webpage title (Carnegie Institution Year Books Numbers 1 through 99, years 1902 through 2000) differs slightly.

APPENDICES (Volumes I and II) **[Note: The Appendices (included herein) have been updated to include Volumes III and IV.]**

Increments

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1 For cross-reference purposes, this is the publication number in the annotated, chronological list of McClintock's publications (Table I) in the Front Matter.

2 The symbol ① indicates that the McClintock publication is reprinted in this collection..

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edited by Lee B. Kass

Perspective**:** Barbara McClintock, a Pioneer in the Study of Polyploidy

by Mathieu Rousseau-Gueutin, Université de Renne and Jonathan F. Wendel, Iowa State University

Increment #04 [in Vol. IV, page 1.3.1]

Note: To preserve the page numbering in Volumes I & II — despite the insertion of additional content — the page numbering in the increments uses a prefix to identify the location of the related content in the previously-released volume. For example, the page number "1.3.1", contains a prefix "1.3", to refer to Part 1, page 3 and the number following the prefix indicates the page number within the increment, e.g., "1", in this case.

[See Volume I, Part I, page 1.1, for introductory material.]

Reprint: 2. Randolph, L. F. and B. McClintock. 1926. Polyploidy in *Zea mays* L. *American Naturalist* LX(666): 99–102.

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An Incremental Book

1.3.2

Barbara McClintock, a Pioneer in the Study of Polyploidy

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Polyploidy, or whole genome (see Glossary) duplication (WGD), is widely recognized as a prominent force in the evolution, diversification and adaptation of flowering plants (Van de Peer et al., 2017). As elaborated below, this understanding derives from insights accumulated from decades of research in various domains, including cytogenetics, ecology, molecular evolution, genomics, and other fields. Given our current understanding of the prominence and prevalence of polyploidy, it seems particularly poignant that the first word in the title of the very first co-authored publication by plant cytogeneticist Barbara McClintock (Randolph and McClintock, 1926) nearly 100 years ago, was "Polyploidy". Although polyploidy has been understood for more than a century to be important in some angiosperms, only in the last 20 years has it become clear that all flowering plants have genomes that have undergone multiple rounds of genome doubling (The Arabidopsis Genome Initiative, 2000; Jiao et al., 2011; Wendel, 2015). This new understanding represents one of the key realizations about the architecture of modern plant genomes (Wendel et al., 2016).

The first study on polyploidy in plants dates back more than a century ago to the work on *Oenothera lamarckiana* mut. *Gigas* (Lutz, 1907), but the first use of the term polyploidy is credited to Winkler (1916; reviewed in Soltis et al., 2014). By the middle of the 20th century, it was estimated that about 30 to 35% of flowering plants were polyploids (Stebbins, 1950), based mostly on comparative chromosome numbers within and among genera across the angiosperms. By this time, it also was understood that many of our most important crops, including common wheat (*Triticum aestivum* L.), cotton, oilseed rape, coffee, and potato were polyploids, thus increasing interest in the topic (Bennett, 2004; Leitch and Leitch, 2008) and providing some of our best models for polyploidy research. More recently, with the advent of the genomic era and the sequencing of the first plant genome (The *Arabidopsis* Genome Initiative, 2000), it was discovered that *Arabidopsis* had undergone at least two rounds of WGD during its evolution. This was followed by similar observations in many other plant species, culminating in a recent flood of genome and transcriptome sequencing papers that continue to reveal scores of additional episodes of variously ancient and recent WGD events (Cheng et al., 2018; One Thousand Plant Transcriptomes Initiative, 2019; Smith et al., 2018; Van de Peer, et al., 2017). Thus, we now know that all modern plants are appropriately considered to be paleopolyploids (see Glossary).

Given the prevalence of polyploidy in plants, the question has naturally arisen as to the mechanisms by which it contributes to evolutionary innovation and diversification. Polyploidy instantly duplicates all chromosomes and genes, and thus a great deal of attention has been focused on understanding the functional and structural evolutionary dynamics of duplicated genes and genomes (Wendel et al., 2015). Less clear at present is how the myriad responses in this respect propagate up through the various "omics" to ultimately generate phenotypes that are adaptively relevant, notwithstanding the many correlative studies that implicate polyploidy in the emergence of physiological and morphological innovations (Freeling and Thomas, 2006; Soltis and Soltis, 2016)or whole-genome duplication (WGD, and better adaptation to changing and stressful environments (Te Beest et al., 2012; Vanneste et al., 2014; Van de Peer et al., 2017).

It is against this backdrop that we consider the Randolph and McClintock (1926) paper that is now nearly 100 years old. Little did McClintock know that not only was normal "diploid" maize paleopolyploid, but it was discoveries in maize that initially focused attention on the phenomenon of genome fractionation that occurs following ancient cycles of polyploidy (Schnable et al., 2011; Wendel et al., 2018). Moreover, transposable elements, the discovery of which led to McClintock receiving the 1983 Noble Prize (see Shapiro perspective, this volume), are thought to be involved in many aspects of polyploid evolution, including biases in genome fractionation, insertional mutagenesis and regulatory evolution (Vicient and Casacuberta, 2017). But in their 1926 paper, McClintock and her coauthor were referring to a neopolyploidy (see Glossary) event that dates to her PhD work (McClintock, 1927, 1929) in the Department of Botany and the Department of Plant Breeding, at Cornell University (Ithaca, N.Y.). In this paper, they presented results showing the meiotic behavior of a maize plant that appeared in a maize line obtained from Dr. A. C. Fraser (Cornell University), a member of McClintock's doctoral committee. This particular line was chosen for a detailed cytogenetic examination as it was more vigorous than its sibs and because it had a thicker stalk, broader leaves, stouter tillers and larger anthers (Randolph and McClintock, 1926). As a Botany Department graduate student and a research assistant to United States Department of Agriculture (USDA) employee L. F. Randolph (working at Cornell), McClintock expected that her name would appear first on this paper because she believed she had done most of the research (Kass and Bonneuil 2004, p. 103, 105; Kass 2003). Hereafter, we use the singular name/pronoun (she/her) when describing their co-authored study. To investigate the chromosome number and meiotic behavior of this phenotypically different maize line, she first extracted pollen mother cells by squashing anthers in Belling's (1921) aceto-carmine solution. This latter solution can fix and stain the meiotic chromosomes, enabling visualization under a microscope of all the chromosomes within a pollen mother cell. From this experiment, she observed different meiotic stages (Prophase I/Diakinesis, Fig. 1; Metaphase I, Fig. 2; Anaphase I, Fig. 3; Second Meiotic Division, Fig. 4) of this phenotypically different maize line, and found that it had thirty instead of twenty chromosomes (Anaphase II, Fig 5) and thus was triploid ($2n=3x=30$ compared to a normal diploid maize line with $2n=2x=20$). As this triploid line was more vigorous than its parent, it thus had a transgressive phenotype (see Glossary), a phenomenon that has subsequently been understood to be common in polyploids (Müntzing, 1936; Stebbins, 1940; Levin, 1983), and which remains an area of active investigation today (Doyle and Coate, 2019).

At that time, but still today, the study of meiosis and its underlying molecular mechanisms was an important research field, as meiosis is the most important phenomenon that generates genetic diversity. Recombination and the concomitant exchange of genetic material between homologous chromosomes (crossovers) occurs during this fundamental biological process, generating enormous diversity in gametes and hence the zygotes that are produced. The meiotic process, first discovered by Edouard van Beneden (1883), is a complex mechanism characterized by the orderly progression of events such as pairing, recombination, chiasma formation, and disjunction, culminating in a reduction of chromosome number in the gametes (Rhoades and Dempsey, 1966). Meiosis consists of two successive divisions, the first (Meiosis I) corresponding to the separation of the paired homologous chromosomes and the second (Meiosis II) to the separation of the sister chromatids of each chromosome. Thereafter, fertilization will occur and restore the original chromosome number, at least when crossing diploid individuals from the same species. In the case of a triploid individual, meiosis and chromosome pairing may be complicated as sets of three homologous chromosomes may pair with each other (Prophase I/Diakinesis, Fig. 1; Metaphase I, Fig. 2) and must be resolved to two poles during Anaphase I (Fig. 3). Interestingly, she observed that in the triploid maize line, chromosomes were primarily arranged in ten groups of trivalents (i.e., each set of three homologous chromosomes) at diakinesis of prophase I (Fig. 1) or metaphase I (Fig. 2) of a pollen mother cell (Randolph and McClintock, 1926). In a few cases, pollen mother cells of the same preparation did not only show trivalents, but also univalents (figure not shown), and bivalents (as seen in Fig. 6). From these experiments, she notably observed that in many cases, the third member of a trivalent seemed to be only partly attached to the other two homologous chromosomes (Fig 1, Diakinesis of Prophase I). Thereafter, she looked at how these chromosomes were assorted to the two different poles in Anaphase I and found that in most cases the two anaphase groups presented fifteen chromosomes each (Fig. 3). However, she also observed cells in which the distribution of the chromosomes was 14-16, 13-17, and 12-18. Finally, she looked at the second meiotic division of this triploid maize line and found that most sister cells presented fifteen chromosomes each (Fig. 4, Prophase II). At that time, the investigation of the peculiar meiotic behavior of a polyploid plant had been performed in a few other plant species, such as in *Canna* (Belling, 1921), *Crepis* (Navashin, 1925) and tomato (Mann Lesley, 1926). The presence of only trivalents in most cells of her maize line indicated that it is an autopolyploid and specifically an autotriploid individual (with sets of three homologous chromosomes). However, she did not use this term "autopolyploidy" in this first paper as it had been defined the same year by Kihara and Ono (1926) to differentiate polyploid species arising from the genome doubling of individual(s) from the same species (autopolyploidy) compared to those resulting from interspecific hybridization between related species followed by genome doubling (allopolyploidy).

Based on these observations, McClintock suggested that the triploid maize line most likely arose through the fusion of a normal haploid (reduced) gamete (with half the chromosome number of the parental plant) with a diploid (unreduced) gamete (with the same chromosome number as the parental plant). To support this hypothesis, she showed first that a pollen mother cell from the investigated triploid line occasionally presented twice the number of expected chromosomes in the second meiotic division (Anaphase II, Fig. 5), and thus may give rise to unreduced gametes. Secondly, she reported that such unreduced gametes may also be formed occasionally in a diploid maize line as some pollen mother cells may also sometimes present twice the expected number of chromosomes (Metaphase I, Fig. 7; Second Meiotic Division, Fig. 6 and Fig. 8). A few years later, it was shown that such triploid maize can either arise from the fusion of an unreduced diploid egg with a haploid sperm (Rhoades, 1933), or from a reduced egg with a diploid sperm (Rhoades, 1936). Such unreduced gametes could have been produced by three different cytological mechanisms, such as: (1) pre-meiotic genome doubling; (2) post-meiotic genome doubling; and (3) anomalies that occur during meiotic cell division (Bretagnolle and Thomson, 1995; De Storme and Geelen, 2013). The first of these mechanisms, corresponding to pre-meiotic endomitosis, endoreduplication or nuclear fusion generating tetraploid meiocytes, has rarely been documented in plants and thus is not considered as playing an important role in plant polyploid formation. This is also the case for the second mechanism, in which meiotically formed haploid spores undergo an extra round of genome duplication. In contrast, the third mechanism, which corresponds to meiotic defects in cell division, has been shown to be involved in the production of unreduced gametes in many plant species (De Storme et al., 2012).

To better understand the role of meiotic defects in the production of unreduced gametes, it may be worth recalling the different steps of meiosis, as we now understand them at the molecular level. Meiosis is a specialized cell division, which involves a single round of DNA duplication followed by two rounds of chromosome division, thereby producing gametes with half the chromosome number. During prophase I, chromosomes pair and recombination occurs. In the first meiotic division (meiosis I), homologous chromosomes become separated (reductional division), whereas in the second division (Meiosis II), it is the sister chromatids that separate (equational division), producing a tetrad of haploid spores. Occasionally, defects during the first or second meiotic division can generate unreduced gametes (see examples in Fig. 5, Fig. 7 and Fig. 8). Notably, mutants that produce unreduced gametes have been discovered and studied in maize (e.g., Rhoades and Dempsey, 1966). In McClintock's era it was not possible to identify the molecular genetic details of genes involved in generating unreduced gametes, as her 1926 paper was more than a quarter century prior to the report in 1953 of a detailed structure of the DNA molecule, based on x-ray crystallography. But fast-forwarding more than seventy years to the sequencing of the first plant genome (The *Arabidopsis* Genome Initiative, 2000) and then others, including maize (Schnable et al., 2009), several such genes have been identified and molecularly characterized. Even though McClintock's work was many decades prior to the sequencing and genomics era, she and her colleagues were able to use clever cytogenetic and phenotypic analyses combined to physically localize many genes relative to each other and to particular chromosomes (McClintock, 1931a, b; Rhoades and McClintock, 1935; Emerson et al., 1935; Kass and Bonneuil, 2004; Kass et al., 2019).

Contemporary analyses using both forward and reverse genetics experiments in *Arabidopsis* and maize have shed light on the nature of the genes involved in the production of unreduced gametes. Such genes have been discovered by identifying mutants showing reduced fertility or increased pollen size, as pollen grains from unreduced gametes typically are 30 to 40% larger than those from reduced gametes. After identifying mutants and their underlying genes, molecular cytogenetic and molecular biology experiments performed on these mutants have enabled a determination of the step of meiosis each gene was involved in, whether it had an impact on the production of male and/or female unreduced gametes, as well as the level of homozygosity/heterozygosity of the produced gametes. As an example, mutations of genes involved in the progression to meiosis (Omission of Second Division and Tardy Asynchronomous Meiosis or Cyclin A family) were shown to prevent the separation of sister chromatids (equational divisions) and result in the formation of unreduced pollen and eggs (D'Erfurth et al., 2009; 2010). Similarly, the *ameiotic 1* (*am1*) and *argonaute 104* (*ago104*) genes in maize lead to an equational segregation of chromosomes during the first division and transform the meiotic cell cycle into a mitotic cycle (Gobulovskaya et al., 1993; Pawlowski et al., 2009; Singh et al., 2011). In maize, the *elongate* (*el*) mutant, initially discovered by Rhoades and Dempsey (1966), was found to produce viable unreduced eggs due to the omission of the second division in female meiocytes (Barrell and Grossniklaus, 2005). Finally, other meiotic genes that are either involved in the orientation of the spindle (*Jason or ATP1*: D'erfurth et al., 2008; Erilova et al., 2009; De Storme and Geelen, 2011) or sister chromatid cohesion and centromere organization (*Swi1*: Mercier et al., 2001; Ravi et al., 2008) increase the number of unreduced gametes by changing the orientation of the spindles (fused or parallel instead of perpendicular).

As noted above, the foregoing mutant genes and their phenotypes may be classified into one of two different categories, corresponding to defects in meiosis I or II. Within the first category, corresponding to the First Meiotic Division Restitution (also referred as FDR), recombination does not occur and chromosomes undergo an equational division, generating unreduced gametes that fully retain parental heterozygosity. In some instances, FDR type gametes may also be obtained via cytological alterations (e.g., altered orientation of spindles) rather than the complete loss of Meiosis I and are thus not fully heterozygous [retaining homozygosity only from the centromere to the first crossover (CO)] (Ramanna and Jacobsen, 2003). The second category corresponds to the Second Meiotic Division Restitution (SDR). As Meiosis I is normal (with correct pairing and recombination), SDR gametes are homozygous from the centromere to the first CO, but heterozygous on the telomere side (Ramanna and Jacobsen, 2003). Nowadays, it may be determined if unreduced gametes arose via an SDR or FDR mechanism by testing the level of homozygosity versus heterozygosity of molecular markers close to the centromeres.

Remarkably, given the centrality of meiosis to sexual reproduction in all organisms, production of unreduced gametes is far from a rare phenomenon in plants. In 1975, Harlan and deWet listed 85 plant genera (34 plant families) known to produce unreduced gametes. In plants, the rate of 2n gamete production ranges from 0.0 to 81.1% of all gametes produced (Ramsey and Schemske, 1998). This rate may vary between individuals of the same species or even within flowers of the same plant (McCoy, 1982; Bretagnolle and Thomson, 1995; Ramsey, 2007). On average, about 0.1-2% of gametes are expected to be unreduced in natural populations (Kreiner et al., 2017). This rate may be increased in the presence of abiotic stress, such as heat stress (Pécrix, et al., 2011; Negri and Lemmi, 1998; Mason and Pires, 2015; Wang et al., 2017). As an example, studies performed at Cornell while McClintock was there showed that corn plants exposed to a temperature of 40°C approximately 24 hours after pollination produced 1.8% tetraploid and 0.8% octoploid seedlings (Randolph, 1932).

Returning full circle to the first word in McClintock's first paper in 1926, it is breathtaking to consider the remarkable discoveries about polyploidy in the subsequent century. McClintock stated that "*Nothing is known concerning the manner in which triploidy arose*", but presciently also noted that "*Should viable diploid gametes thus arise, their union with normal haploid gametes would result in a triploid plant*". Now we understand that polyploid species may arise via several pathways (Harlan and deWet, 1975; Pelé et al., 2018), and that sexual polyploidization (via the production of unreduced gametes) is a major route for polyploid formation (Ramsey and Schemske, 1998). The latter entails either unilateral sexual polyploidization, where a diploid (unreduced) and a haploid gamete fuse, or bilateral sexual polyploidization, where two diploid gametes fused and directly lead to a tetraploid zygote (Mendiburu and Peloquin, 1976; Comai, 2005). Because the bilateral sexual polyploidization requires the fusion of two unreduced gametes, one from each of the male and female sides, and each produced at a low frequency, this single-step polyploidization is considered less likely than the two-step route involving a triploid bridge (see Glossary) (Harlan and deWet, 1975; Husband, 2004; Ramsey and Schemske, 1998). In the last sentence of McClintock's paper on maize polyploidy, she speculated that the production of unreduced gametes may underlie other forms of polyploidy in *Zea mays*, presumably via a triploid bridge. Indeed, in the publication of her Ph.D. thesis, she showed that triploid maize can be relatively fertile despite producing aneuploid gametes (McClintock, 1929). The importance of the triploid bridge in tetraploid formation was recently experimentally tested in *Arabidopsis* (Henry et al., 2005) by self-pollination of a triploid individual for few generations and observing that it could form tetraploid individuals. In addition to self-pollination, triploids may also produce tetraploids through cross pollination with either a diploid progenitor or another triploid individual (Bergström, 1940; Husband, 2004; Köhler et al., 2010).

Barbara McClintock, the Nobel laureate who is justifiably acclaimed for her discovery of transposable elements, turns out also to have been a pioneer in the study of polyploidy, as illustrated by her 1926 paper and as elucidated here. We hope that this essay helps bring this fact to light.

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References

Barrell, P. J. and U. Grossniklaus. 2005. Confocal microscopy of whole ovules for analysis of reproductive development: the elongate1 mutant affects meiosis II. *The Plant Journal* 43: 309-320.

Belling, J. 1921. The behavior of homologous chromosomes in a triploid *Canna*. *Proceedings of the National Academy of Sciences* 7(7): 197-201.

Bennett, M. D. 2004. Perspectives on polyploidy in plants–ancient and neo. *Biological Journal of the Linnean Society* 82(4): 411-423.

Bergström, I. 1940. On the progeny of diploid × triploid *Populus tremula*. *Hereditas* 26: 191-201.

Bretagnolle, F. and J. D. Thompson. 1995. Gametes with the somatic chromosome number: mechanisms of their formation and role in the evolution of autopolyploid plants. *New Phytologist* 129(1): 1-22.

Cheng, F., J. Wu, X. Cai, J. Liang, M. Freeling and X. Wang. 2018. Gene retention, fractionation and subgenome differences in polyploid plants. *Nature Plants* 4: 258-268.

Comai, L. 2005. The advantages and disadvantages of being polyploid. *Nature Reviews Genetics* 6: 836-846.

D'Erfurth, I., L. Cromer, S. Jolivet, C. Girard, C. Horlow, Y. Sun, J. P. C. To, L. E. Berchowitz, G. P. Copenhaver and R. Mercier. 2010. The Cyclin-Cyca1;2/Tam is required for the meiosis I to meiosis II transition and cooperates with OSD1 for the prophase to first meiotic division transition. *PLoS Genetics* 6(6): e1000989.

D'Erfurth, I., S. Jolivet, N. Froger, O. Catrice, M. Novatchkova, and R. Mercier. 2009. Turning meiosis into mitosis. *PLoS Biology* 7(6): e1000124.

D'Erfurth, I., S. Jolivet, N. Froger, O. Catrice, M. Novatchkova, M. Simon, E. Jenczewski and R. Mercier. 2008. Mutations in AtPS1 (*Arabidopsis thaliana* Parallel Spindle 1) lead to the production of diploid pollen grains. *PLoS Genetics* 4(11): e1000274

De Storme, N. and D. Geelen. 2013. Sexual polyploidization in plants – cytological mechanisms and molecular regulation. *New Phytologist* 198(3): 670-684.

De Storme, N. and D. Geelen. 2011. The *Arabidopsis* mutant *jason* produces unreduced first division restitution male gametes through a parallel/fused spindle mechanism in meiosis II. *Plant Physiology* 155(3): 1403-1415.

De Storme, N., G. P. Copenhaver and D. Geelen. 2012. Production of diploid male gametes in *Arabidopsis* by cold-induced destabilization of postmeiotic radial microtubule arrays. *Plant Physiology* 160(4): 1808-1826.

Doyle, J. J. and J. E. Coate. 2019. Polyploidy, the nucleotype, and novelty: the impact of genome doubling on the biology of the cell. *International Journal of Plant Sciences* 180(1): 1-52.

Erilova, A., L. Brownfield, V. Exner, M. Rosa, D. Twell, O. Mittelsten Scheid, L. Hennig and C. Köhler. 2009. Imprinting of the polycomb group gene MEDEA serves as a ploidy sensor in *Arabidopsis*. *PloS Genetics* 5(9): e1000663.

Emerson, R. A., G. W. Beadle, and A. C. Fraser. 1935. Summary of Linkage Studies in Maize *Cornell University Agricultural Experiment Station Memoir* 180: 1-83.

Freeling, M. and B. C. Thomas. 2006. Gene-balanced duplications, like tetraploidy, provide predictable drive to increase morphological complexity. *Genome Research* 16(7): 805-814.

Golubovskaya, I., Z. K. Grebennikova, N. A. Avalkina and W. F. Sheridan. 1993. The role of the *Ameiotic1* gene in the initiation of meiosis and in subsequent meiotic events in maize. *Genetics* 135(4): 1151-1166.

Harlan, J. R. and J. M. J. deWet. 1975. On Ö. Winge and a prayer: the origins of polyploidy. *The Botanical Review* 41(4): 361-390.

Henry, I. M., B. P. Dilkes, K. Young, B. Watson, H. Wu and L. Comai. 2005. Aneuploidy and genetic variation in the *Arabidopsis thaliana* triploid response. *Genetics* 170(4): 1979-1988.

Husband, B. C. 2004. The role of triploid hybrids in the evolutionary dynamics of mixed-ploidy populations. *Biological Journal of the Linnean Society* 82(4): 537-546.

Jiao, Y., N. J. Wickett, S. Ayyampalayam, A. S. Chanderbali, L. Landherr, P. E. Ralph, L. P. Tomsho, Y. Hu, H. Liang, P. S. Soltis, D. E. Soltis, S. W. Clifton, S. E. Schlarbaum, S. C. Schuster, H. Ma, J. Leebens-Mack and C. W. dePamphilis. 2011. Ancestral polyploidy in seed plants and angiosperms. *Nature* 473: 97-100.

Kass, L. B. 2003. Records and recollections: A new look at Barbara McClintock, Nobel Prize-Winning geneticist. *Genetics* 164 (August): 1251-1260.

Kass, L. B. and C. Bonneuil. 2004. Mapping and seeing: Barbara McClintock and the linking of genetics and cytology in maize genetics, 1928-1935. Chapt. 5: 91-118, *in* Hans-Jörg Rheinberger and Jean-Paul Gaudilliere (eds.), *Classical Genetic Research and its Legacy: The Mapping Cultures of 20th Century Genetics.* London: Routledge.

Kass, L. B., E. H. Coe, M. N. Cook, M. E. Smith and J. L. Singer (Eds.). 2019. *Founding of the Maize Genetics Cooperation News Letter at Cornell University: A 90th Anniversary Tribute.* (Foreword by E. S. Buckler) [e-book] Internet-First University Press, Ithaca, New York. https://ecommons.cornell.edu/handle/1813/66550

Kihara, H. and T. Ono. 1926. Chromosomenzahlen und systematische Gruppierung der Rumex-Arten. *Cell and Tissue Research* 4(3): 475-481.

Köhler, C., O. Mittelsten Scheid and A. Erilova. 2010. The impact of the triploid block on the origin and evolution of polyploid plants. *Trends in Genetics* 26(3): 142-148.

Kreiner, J. M., P. Kron, and B. C. Husband. 2017. Frequency and maintenance of unreduced gametes in natural plant populations: associations with reproductive mode, life history and genome size. *New Phytologist* 214(2): 879-889.

Leitch, A. R. and I. J. Leitch. (2008). Genomic plasticity and the diversity of polyploid plants. *Science* 320(5875): 481-483.

Levin, D. A. 1983. Polyploidy and novelty in flowering plants. *The American Naturalist* 122(1): 1-25.

Lutz, A. M. 1907. A preliminary note on the chromosomes of *Oenothera lamarckiana* and one of its mutants, *O. gigas*. *Science* 26: 151-152.

McClintock, B. 1927. *A Cytological and Genetical Study of Triploid Maize*, PhD thesis, Cornell University, Ithaca, NY.

McClintock, B. 1929. A cytological and genetical study of triploid maize. *Genetics* 14(2): 180-222. [publication of McClintock's Ph.D. thesis] [See Sorrells' perspective this volume]

McClintock, B. 1931a. The order of the genes *C, Sh* and *Wx* in *Zea Mays* with reference to a cytologically known point in the chromosome. *Proceedings of the National Academy of Sciences* 17(8): 485-491. [see Coe and Kass perspective this volume, reprinted from *PNAS* 2005, Vol. 102 (No. 19. May: 6641-6656)]

McClintock, B. 1931b. Cytological observations of deficiencies involving known genes, translocations and an inversion in *Zea mays*. *Missouri Agricultural Experiment Station Research Bulletin*, 163: 1–30. [See Kass and Birchler perspective in this volume]

McCoy, T. J. 1982. The inheritance of 2n pollen formation in diploid alfalfa *Medicago sativa*. *Canadian Journal of Genetics and Cytology* 24(3): 315-323.

Mann Lesley, M. 1926. Maturation in diploid and triploid tomatoes. *Genetics* 11(3): 267-279.

Mason, A. S. and J. C. Pires. 2015. Unreduced gametes: meiotic mishap or evolutionary mechanism? *Trends in Genetics* 31(1): 5-10.

Mendiburu, A. O. and S. J. Peloquin. 1976. Sexual polyploidization and depolyploidization: some terminology and definitions. *Theoretical and Applied Genetics* 48(3): 137-143.

Mercier, R., D. Vezon, E. Bullier, J. C. Motamayor, A. Sellier, F. Lefèvre, G. Pelletier and C. Horlow. 2001. SWITCH1 (SWI1): a novel protein required for the establishment of sister chromatid cohesion and for bivalent formation at meiosis. *Genes and Development* 15(14): 1859-1871.

Müntzing, A. 1936. The evolutionary significance of autopolyploidy. *Hereditas* 21(2-3): 363-378.

Navashin, M. 1925. Polyploid mutations in *Crepis*: Triploid and pentaploid mutants of *Crepis capillaris*. *Genetics* 10: 583–92.

Negri, V. and G. Lemmi. 1998. Effect of selection and temperature stress on the production of 2n gametes in *Lotus tenuis*. *Plant Breeding* 117(4): 345-349.

One Thousand Plant Transcriptomes Initiative. One thousand plant transcriptomes and the phylogenomics of green plants. 2019. *Nature* 574(7780): 679–85.

Pawlowski, W. P., C.-J. R. Wang, I. N. Golubovskaya, J. M. Szymaniak, L. Shi, O. Hamant, T. Zhu, L. Harper, W. F. Sheridan and W. Z. Cande. 2009. Maize *AMEIOTIC1* is essential for multiple early meiotic processes and likely required for the initiation of meiosis. *Proceedings of the National Academy of Sciences* 106(9): 3603-3608.

Pécrix, Y., G. Rallo, H. Folzer, M. Cigna, S. Gudin, and M. Le Bris. 2011. Polyploidization mechanisms: temperature environment can induce diploid gamete formation in *Rosa* sp. *Journal of Experimental Botany* 62(10): 3587-3597.

Pelé, A., M. Rousseau-Gueutin and A.-M. Chèvre. 2018. Speciation success of polyploid plants closely relates to the regulation of meiotic recombination. *Frontiers in Plant Sciences* 9: 907.

Ramanna, M. S. and E. Jacobsen. 2003. Relevance of sexual polyploidization for crop improvement – A review. *Euphytica* 133(1): 3-8.

Ramsey, J. 2007. Unreduced gametes and neopolyploids in natural populations of *Achillea borealis* (Asteraceae). *Heredity* 98(3): 143-150.

Ramsey, J. and D. W. Schemske. 1998. Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Annual Review of Ecology and Systematics* 29: 467-501.

Randolph, L. F. 1932. Some effects of high temperature on polyploidy and other variations in maize. *Proceedings of the National Academy of Sciences* 18(3): 222-229.

Randolph, L. F. and B. McClintock. 1926. Polyploidy in *Zea Mays* L. *The American Naturalist* 60(666): 99-102.

Ravi, M., M. P. A. Marimuthu and I. Siddiqi. 2008. Gamete formation without meiosis in *Arabidopsis*. *Nature* 451: 1121-1124.

Rhoades, M. M. 1933. An experimental and theoretical study of chromatid crossing-over. *Genetics* 18: 535-555.

Rhoades, M. M. 1936. Note on the origin of triploidy in maize. *Journal of Genetics* 33: 355-357.

Rhoades, M. M. and E. Dempsey. 1966. Induction of chromosome doubling at meiosis by the elongate gene in maize. *Genetics* 54(2): 505-522.

Rhoades, M. M. and B. McClintock. 1935. The cytogenetics of maize. *Botanical Review* 1(8): 292-325.

Schnable, P. S. et al. 2009. The B73 maize genome: complexity, diversity, and dynamics. *Science* 326(5956): 1112-1115.

Schnable, J. C., N. M. Springer and M. Freeling. 2011. Differentiation of the maize subgenomes by genome dominance and both ancient and ongoing gene loss. *Proceedings of the National Academy of Sciences* 108(10): 4069-4074.

Singh, M., S. Goel, R. B. Meeley, C. Dantec, H. Parrinello, C. Michaud, O. Leblanc and D. Grimanelli. 2011. Production of viable gametes without meiosis in maize deficient for an ARGONAUTE protein. *Plant Cell* 23(2): 443-458.

Smith, S. A., J. W. Brown, Y. Yang, R. Bruenn, C. P. Drummond, S. F. Brockington, J. F. Walker, N. Last, N. A. Douglas, and M. J. Moore. 2018. Disparity, diversity, and duplications in the Caryophyllales. *New Phytologist* 217(2): 836-854.

Soltis, D. E., C. J. Visger and P. S. Soltis. 2014. The polyploidy revolution then…and now: Stebbins revisited. *American Journal of Botany* 101(7): 1057-1078.

Soltis, P. S. and D. E. Soltis. 2016. Ancient WGD events as drivers of key innovations in angiosperms. *Current Opinion in Plant Biology* 30: 159-165.

Stebbins, G. L. 1940. The significance of polyploidy in plant evolution. *The American Naturalist* 74(750): 54-66.

Stebbins, G. L. 1950. *Variation and Evolution in Plants*. Oxford University Press. London, UK.

Te Beest, M., J. J. Le Roux, D. M. Richardson, A. K. Brysting, J. Suda, M. Kubesová and P. Pysek. 2012. The more the better? The role of polyploidy in facilitating plant invasions. *Annals of Botany* 109(1): 19-45.

The *Arabidopsis* Genome Initiative. 2000. Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana*. *Nature* 408(6814): 796-815.

Van Beneden, E. 1883. Recherches sur la maturation de l'oeuf et la fécondation. In: *Archives de Biologie* (4): 265-640.

Van de Peer, Y., E. Mizrachi and K. Marchal. 2017. The evolutionary significance of polyploidy. *Nature Review Genetics* 18: 411-424.

Vanneste, K., G. Baele, S. Maere and Y. Van de Peer. 2014. Analysis of 41 plant genomes supports a wave of successful genome duplications in association with the Cretaceous–Paleogene boundary. *Genome Research* 24(8): 1334-1347.

Vicient, C. M. and J. M. Casacuberta. 2017. Impact of transposable elements on polyploid plant genomes. *Annals of Botany* 120(2): 195-207.

Wang, J., D. Li, F. Shang and X. Kang. 2017. High temperature-induced production of unreduced pollen and its cytological effects in *Populus*. *Scientific Reports* 7: 5281.

Wendel, J. F. 2015. The wondrous cycles of polyploidy in plants. *American Journal of Botany* 102(11): 1753-1756.

Wendel, J. F., S. A. Jackson, B. C. Meyers and R. A. Wing. 2016. Evolution of plant genome architecture. *Genome Biology* 17: 37.

Wendel, J. F., D. Lisch, G. Hu, A. S. Mason. 2018. The long and short of doubling down: polyploidy, epigenetics, and the temporal dynamics of genome fractionation. *Current Opinion in Genetics and Development* 49: 1-7.

Winkler, H. 1916. Uber die experimentelle Erzeugung von Pflanzen mit abweichenden. Chromosomenzahlen. *Zeitschrift für Botanik* 8: 417-531.

Short explanation of the different figures presented in the manuscript

Figure 1: Pollen mother cell (at diakinesis) of a triploid maize line harboring ten groups of three chromosomes (referred to as trivalents).

Figure 2: Pollen mother cell (metaphase I) of a triploid maize line harboring ten trivalents.

Figure 3: Pollen mother cell (anaphase I) of a triploid maize line showing the presence of two distinct groups with fifteen chromosomes each.

Figure 4: Beginning of the second meiotic division in one sister cell of a triploid maize line. In this figure, fifteen long and slender chromosomes can be seen.

Figure 5: Occasional events of observation of pollen mother cells in second meiotic division that harbor twice the number of chromosomes (thirty instead of fifteen). Such a phenomenon may lead to the formation of a male unreduced gamete.

Figure 6: Binucleate microsporocyte of a diploid plant that harbors, as expected, ten bivalent chromosomes in each nucleus.

Figure 7: Microsporocyte (now referred to as a pollen mother cell) of a diploid plant harboring twice the number of expected chromosomes: twenty instead of ten bivalents in each metaphase I. Such pollen mother cells may lead to the formation of a male unreduced gamete.

Figure 8: Microsporocyte (now referred to as a pollen mother cell) of a diploid plant harboring twice the number of expected chromosomes in prophase II: twenty-four instead of twelve bivalents.

Glossary

Genome: One complete set of chromosomes in a diploid organism.

Neopolyploid: A polyploid species that has been relatively recently formed, as inferred from the contemporaneous existence of putative diploid parents.

Paleopolyploid: A species that has been subjected to a polyploidization event many millions of years ago. Since this polyploidy event, the number of chromosomes and genes have been reduced through a diploidization process. Such species, where only traces remain of ancient polyploidization events, are considered paleopolyploids.

Transgressive phenotype: A phenotype in a hybrid or polyploid that is outside of the ranges of variability of both parents.

Triploid bridge: A triploid plant resulting from the merger of reduced (haploid) and unreduced (diploid) gametes. Such plants can thereafter produce tetraploid individuals through self- pollination or cross pollination with a diploid species, and as such are considered stepping-stones to the production of tetraploids.

Appendices

[Note: Additions in Volume IV are identified by red text.]

Appendix A-1. Contributors Affiliations

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Appendix A-2. Contributors Biographical Sketches

Dr. James A. Birchler is Curators' Professor of Biological Sciences at the University of Missouri, Columbia. After obtaining a B.S. degree from Eastern Illinois University in botany and zoology (1972), he attended graduate school at Indiana University (Ph.D. 1977) majoring in genetics with a minor in biochemistry. Postdoctoral work was performed at Oak Ridge National Laboratory, Tennessee, and the University of California, Berkeley. Appointments as assistant and associate professor followed at Harvard University beginning in 1985 in the Department of Organismic and Evolutionary Biology. Dr. Birchler joined the faculty at the University of Missouri in 1991. He has served on the editorial boards of *Genetics*, *The Plant Cell*, *BioMed Central Plant Biology*, *Tropical Plant Biology*, *McGraw-Hill Yearbook of Science and Technology*, *Genomic Insights, Journal of Genetics and Genomics*, *Journal of Biomedicine and Biotechnology*, *Molecular Biotechnology*, *GM Crops*, *Maydica*, *Frontiers in Plant Genetics and Genomic*s, *Annual Reviews of Plant Biology* and *Annual Reviews of Genetics*. Birchler has served on the Maize Genetics Executive Committee and on the Council of the American Genetics Association. He is a fellow of the American Association for the Advancement of Science and a member of the National Academy of Sciences.

Dr. Stephen E. Bloom is Professor Emeritus in the Department of Microbiology and Immunology, College of Veterinary Medicine, Cornell University. He received a B.S. degree in Biology from Long Island University (1963), and a Ph.D. in Genetics at The Pennsylvania State University (1968). He joined the Cornell University faculty in 1968 (associate professor 1974, full professor in 1981), held appointments as at-large member of the Division of Biological Sciences (1976-1999), and Associate Director for the Institute for Comparative and Environmental Toxicology (1990-2004), and served as Program Director for a National Institutes of Health (NIH) training grant in Molecular and Environmental Toxicology (1978 – 2004). He did sabbatical leaves at the M.D. Anderson Hospital and Tumor Institute, Houston, TX (1975, collaborating with Dr. T.C. Hsu), at the Worcester Foundation for Experimental Biology (1982, collaboration with Dr. H. Robinson). Supported by grants from the NIH, USDA-NRI, and Cornell Biotechnology Institute, Bloom's research program has focused on the development and investigation of genetic models of diseases, such as meiotic alterations leading to cytogenetic abnormalities and birth defects; cytogenetic mapping and studies of genes regulating disease resistance, including the major histocompatibility locus (MHC); and genetic alterations involved in development of lymphoid cancers and drug resistance.
Bloom taught the first Animal Cytogenetics course at Cornell University, and developed a course in Genetic and Molecular Toxicology. He served as an Associate Editor for the *Journal of Heredity* (1990-2000) and was on the Executive Council for the American Genetic Association (1997-2000). He is a member of the American Association for Cancer Research, Society of Toxicology, American Genetic Association, and American Association of University Professors

Dr. Allan M. Campbell graduated from the University of California (Berkeley, 1950), majoring in Chemistry. He received his M.S, (1951) and Ph.D. (1953) under the direction of Sol Spiegelman at the University of Illinois (Urbana) in Bacteriology. He became Instructor in Bacteriology at the University of Michigan Medical School (Ann Arbor). After two years in the U.S. Army (1953-55), he returned to Ann Arbor (through 1957). He spent a year at the Carnegie Institution of Washington in Cold Spring Harbor, NY (1957-58) and at the Institut Pasteur with François Jacob in Paris, France (1958-59). He joined the Biology Department faculty of the University of Rochester (1959-68) then moved to the Biology Department at Stanford University, where he became Professor Emeritus in 2010. His spouse, biochemist Alice del Campillo-Campbell (AB, Columbia University; MS, New York University; PhD, University of Michigan), has been his research collaborator ever since their marriage in 1958. His doctoral research concerned regulation of galactose synthesis in yeast. His best known accomplishments are elucidating the mechanism of specialized transduction by phage lambda and the mode of attachment of lambda prophage to the bacterial chromosome, and the isolation of conditionally lethal phage mutants. His laboratory has also studied the regulation of biosynthesis of the vitamin biotin. He is a Member of the National Academy of Science (1971), Fellow of the American Academy of Arts and Sciences (1971), and Fellow of the American Academy of Microbiology (1986). He received the Abbott/ASM Lifetime Achievement Award in Microbiology in 2004.

Dr. Edward H. Coe Jr. earned a Ph.D. (1954) in botany at the University of Illinois (with John Laughnan) and received his M.S. degree (1951) in plant genetics (with Charlie Burnham), and a B.S. degree (1949) in agronomy and plant genetics from the University of Minnesota. Following a postdoc with Ernest G. Anderson at Caltech (1954-1955), Coe joined the Plant Genetics Unit of the U.S. Department of Agriculture-Agricultural Research Service at the University of Missouri, where he is currently Professor Emeritus of Plant Sciences. His research has contributed to an understanding of anthocyanin biosynthesis, gametophyte functions, non-Mendelian inheritance, and extrachromosomal inheritance. He is author of or co-author of over 100 refereed journal articles, and author or co-editor of two books; most well-known is the co-edited *Mutants of Maize*. Coe is highly appreciated for his 26 years of continuous service as editor of the *Maize Genetics Cooperation Newsletter* (1974-2000). He played a central role in establishing the Maize Genome Database and in the early planning meetings leading to a plant genome initiative, and to sequencing of the first plant genome, and the maize genome. He is a member of various professional organizations, including the Genetics Society of America, the American Genetic Association, and the Crop Science Society of America. In recognition of his "lifetime contributions to the field of genetics," Coe was awarded the prestigious Thomas Hunt Morgan Award by the Genetics Society of America in 1992. The award was presented to him in recognition of the importance of his basic research, his mentorship of students and postdocs, and his extensive and outstanding service to the maize genetics community. Dr. Coe was described as "the glue that holds the maize community together."

Dr. Nina V. Fedoroff received her Ph.D. in Molecular Biology from the Rockefeller University, and has served on the faculties of the Carnegie Institution of Washington, the Johns Hopkins University and the Pennsylvania State University, where she was the Director of the Biotechnology Institute and the founding Director of the Huck Institutes of the Life Sciences. Fedoroff has published three books and more than 150 papers in scientific journals. She is a member of several academies, including the U. S. National Academy of Sciences and the American Academy of Arts and Sciences. Among her awards is a 2006 National Medal of Science, the highest honor awarded to US scientists. Fedoroff served as the Science and Technology Adviser to the Secretary of State and to the Administrator of the US Agency for International Development (USAID) from 2007 to 2010. She is Distinguished Professor of Biosciences at the King Abdullah University of Science and Technology (KAUST) in Saudi Arabia, an Evan Pugh Professor at Penn State, and a member of the External Faculty of the Santa Fe Institute. She was President of the American Association for the Advancement of Science (AAAS) in 2011-12 and AAAS Board Chair in 2013.

Dr. Lee B. Kass received her Ph.D. in Botany, and Genetics from Cornell University (1975), and earned a B.S. in biology at The City College of New York (CUNY, 1969). She did Postdoctoral research at The University of Cambridge (UK) and Vanderbilt University. She has served on the faculties of The University of Cambridge (UK), University of Tennessee (Nashville), Elmira College (New York), The College of the Bahamas (Nassau), Cornell University, and West Virginia University (Morgantown). Kass has authored, edited or co-edited nine books, and authored or co-authored more than 80 book chapters, proceedings papers, and articles in scientific journals. She is a member of the Botanical Society of America, The Bahamas National Trust, and a former member of many botanical organizations. Kass was chair of the Historical Section of the Botanical Society of America for many years. She established the Elmira College Herbarium in 1985, and currently serves on the Science Advisory Committee of the Bahamas National Trust. Among her awards is the Josef Stein Award, for excellence in teaching and scholarly achievement (1985) and a Fulbright Scholar Award (1996), during which time she and her spouse, Dr. Robert E. Hunt, established the National Herbarium of the Bahamas. She is Visiting Professor at Cornell University, and West Virginia University (Morgantown). Her research focuses on history of botany, and biodiversity and reproductive biology of Bahamian plants.

Dr. Takeo Angel Kato-Yamakake received his Ph.D. from the University of Massachusetts (Amherst, 1975), under the mentorship of Walton C. Galinat. He earned an M.S. in genetics from North Carolina State University (Raleigh, 1964, mentored by Barbara McClintock), and received his B.S. (Ingeniero Agrónomo) from Escuela Nacional de Agricultura, Chapingo, Mexico (1961). Kato was Research Assistant (1958-1959) at Escuela Nacional de Agricultura, Chapingo, State of Mexico, and Cytogeneticist (1960-1972) for the Inter-American Maize Program (Rockefeller Foundation) and International Maize and Wheat Improvement Center (CIMMYT) Project on Cytogenetic Studies of Races of Maize in the American Continent, Chapingo and El Batán, State of Mexico. Since 1975 he has been Profesor Investigador Titular, at Colegio de Postgraduados, Postgrado en Recursos Genéticos y Productividad, Orientación Genética, Montecillo, State of Mexico. His research focuses on origin and evolution of maize in the Americas. He has many publications in this research area, and in 1981 he co-authored, with Barbara McClintock and A. Blumenschein, *Chromosome Constitution of Races of Maize. Its Significance in the Interpretation of Relationships between Races and Varieties in the Americas.* His most recent co-authored publication on this subject is *Origen y diversificación del maíz: una revisión analítica.*

Dr. Wojciech (Wojtek) P. Pawlowski received his undergraduate education at the Agricultural University of Krakow, Poland, Ph.D. at the University of Minnesota, and completed postdoctoral training at the University of California at Berkeley. He joined the faculty of the Department of Plant Breeding and Genetics at Cornell University in 2004, and is now Associate Professor of Plant Genetics. His research focuses on investigating molecular mechanisms of chromosome interactions and recombination in meiosis. His lab uses some of the same maize mutants that Barbara McClintock discovered and studied. He also serves on advisory committees of several US and European research consortia that study chromosome biology.

Dr. Ronald L. Phillips is Regents Professor Emeritus and former McKnight Presidential Chair in Genomics, University of Minnesota (UM). He earned B.S. and M.S. degrees from Purdue University and a Ph.D. from the UM; postdoctoral training was at Cornell University. Dr. Phillips advised 55 graduate students and 23 postdoctoral scientists, and taught plant genetics for over 40 years. He received the prestigious Wolf Prize in Agriculture in Israel (2007) for "ground breaking research in service of mankind." He was elected a member of the National Academy of Sciences (1991). He served on the Board of Trustees of the premier International Rice Research Institute in the Philippines (2004-2009), on the Palm Oil Research Institute of Malaysia Program Advisory Committee for nine years (1991-1999), and on the Scientific Advisory Board of the Donald Danforth Plant Science Center from its inception through 2008. He is a Fellow of American Association for the Advancement of Science, American Society of Agronomy, and Crop Science Society of America. Among his awards are the Dekalb Genetics Crop Science Distinguished Career Award, the Crop Science Society of America Research Award, and Crop Science Presidential Award (2010), and the Medal for Science from the University of Bologna (Italy, 2010). Phillips served as Chief Scientist of the USDA (1996-1998) in charge of the National Research Initiative Competitive Grants Program and chaired the Interagency Working Group that wrote the plan for the NSF Plant Genome Research Initiative. He was President of the Crop Science Society of America (2000) and Chair of the Council of Scientific Society Presidents (2006). His research was one of the early programs in modern plant biotechnology related to agriculture. He is a founding member and former Director of both the Plant Molecular Genetics Institute UM and the Microbial and Plant Genomics Institute. He has served on numerous editorial boards, edited six books, and published over 150 refereed journal articles, 75 chapters, and 355 abstracts. Phillips conducted research and teaching in plant genetics applied to plant improvement with an attempt to bridge basic and applied aspects. As Regents Professor Emeritus, he participates in addressing University-wide, national, and international issues. He serves on institutional advisory boards, the panel of judges for the Monsanto Beachell-Borlaug International Scholars Program and the World Food Prize Youth Institute faculty.

Dr. Mathieu Rousseau-Gueutin is a researcher in the Department of Plant Biology and Breeding at INRAE (National Institute of Research for Agriculture, food and Environment), Rennes (France). He received an M.S. in Genetics, Adaptation and Plant Breeding at the University of Rennes (2004) and a Ph.D. in Plant Biology at the University of Bordeaux (France, 2008). He did post-doctoral research at the University of Adelaide with Jeremy Timmis (Australia; 2009-2012) and at the University of Rennes with M. L. Aïnouche (2012-2014). In 2014, he became a permanent scientist at INRA (INRAE since 2020). His research mainly concerns the origin and evolution of duplicated genes and genomes of polyploid plants (studies on oilseed rape, strawberries, tobacco and Spartina species) as well as the regulation of recombination in polyploids (in oilseed rape). He is author or co-author of 35 referred journal articles and book chapters. He is a member of the Scientific Committee of the Plant Genome Dynamics and Evolution workshop held yearly in France.

Dr. James A. Shapiro, author of the recent book *Evolution: A View from the 21st Century*, is Professor of Microbiology at the University of Chicago. He has a B.A. in English Literature from Harvard (1964) and a Ph.D. in Genetics from The University of Cambridge (UK, 1968). Shapiro's thesis, The Structure of the Galactose Operon in Escherichia coli K12, written under the supervision of William Hayes, contains the first suggestion of transposable elements in bacteria. He confirmed this hypothesis in 1968 during his postdoctoral tenure as a Jane Coffin Childs fellow in the laboratory of François Jacob at the Institut Pasteur in Paris. The following year, as an American Cancer Society fellow in Jonathan Beckwith's laboratory at Harvard Medical School, he and his colleagues used *in vivo* genetic manipulations to clone and purify the lac operon of *E. coli*, an accomplishment that received international attention. In 1979, Prof. Shapiro formulated the first precise molecular model for transposition and replication of phage *Mu* and other transposons. In 1984, he published the first case study of what is now called "adaptive mutation." He found that selection stress triggers a tremendous increase in the frequency of *M*u-mediated coding sequence fusions. Since 1992, he has been writing about the importance of biologically regulated natural genetic engineering as a fundamental new concept in evolution science. Together with the late Ahmed Bukhari and Sankhar Adhya, Prof. Shapiro organized the first conference on DNA insertion elements in May, 1976, at Cold Spring Harbor laboratory. He is editor of *DNA Insertion Elements, Episomes and Plasmids* (1977 with Bukhari and Adhya), *Mobile Genetic Elements* (1983), and *Bacteria as Multicellular Organisms* (1997 with Martin Dworkin). From 1980 until her death in 1992, Prof. Shapiro maintained a close scientific and personal friendship with Barbara McClintock, whom he credits with opening his eyes to new ways of thinking about science in general and evolution in particular.

Dr. Mark E. Sorrells received his Ph.D. in Plant Breeding and Plant Genetics from the University of Wisconsin – Madison in 1978. After a short post-doc he joined the faculty at Cornell University in the Department of Plant Breeding & Biometry. Since 1991 Dr. Sorrells has been Professor and since 2006, Chair of the Department of Plant Breeding & Genetics at Cornell University. The primary focus of Dr. Sorrells' research program is breeding methodology with application to wheat breeding for the Northeastern region of the United States. He is also involved in several international projects in Africa, South America, and Europe. During his career Dr. Sorrells has actively developed and evaluated new breeding methods and currently he is integrating genomic selection into his breeding program to reduce pre-harvest sprouting, increase disease resistance and improve yield. Dr. Sorrells has published more than 225 papers in peer-reviewed journals. He has been active in teaching and advising students, serving as major advisor to 36 Ph.D. students, 9 M.S. graduate students and minor advisor to 22 students.

Dr. David B. (Burt) Walden earned his M.Sc. (1958) and Ph.D. (1959) in the Plant Breeding Department at Cornell University (with Herbert Evert & Ronald Anderson), and a B.A. (1954) degree from Wesleyan University (Middletown, Connecticut). Following an NIH post-doc in Genetics at Indiana University, Walden joined the faculty (Assistant Professor 1961, Professor 1971) in the Department of Botany (now Plant Sciences) at University of Western Ontario, London, ON, Canada, where he is currently Distinguished Research Professor Emeritus. As an undergraduate, Walden worked as a summer assistant to the eminent corn geneticist D.F. Jones at the Connecticut Agricultural Research Station. His research has contributed to an understanding of maize fertilization, chromosome staining and breakage patterns, cytogenetic of maize chromosome replication and aberrations, etc. Walden has edited two books, contributed three book chapters, and has published more than 200 articles in the *Maize Genetics Cooperation Newsletter* and many scientific journals. Highly appreciated for his service to genetics, Walden was elected President of the Biological Council of Canada (1976-1980), President of the Genetic Society of Canada (1980-1984), 17th President of the International Genetics Federation (Canadian, 1988-1993), and served as Secretary General of the 16th International Congress of Genetics (Toronto 1988). He is a member of various professional organizations, including the Genetics Society of Canada. In recognition of his outstanding contributions to teaching and research, Walden was honored as outstanding teacher, Faculty of Science (1967), received the U.WO Board of Governors' Award for Excellence in Teaching (1982), and the Award of Excellence from the Genetics Society of Canada (1996)

Dr. Randy Wayne is an Associate Professor in the Department of Plant Biology at Cornell University, where he has taught Plant Cell Biology and Light and Video Microscopy. Wayne completed his undergraduate studies in Botany at the University of Massachusetts. He earned an M.A. in Biology from the University of California at Los Angeles, and a Ph.D. in Plant Cell Biology from the University of Massachusetts (1985) working under Peter K. Hepler. At UM he learned cytogenetics from Carl P. Swanson. He was a post-doc at The University of Texas at Austin and had a Japanese Society for the Promotion of Science Fellowship to work with Masashi Tazawa at the University of Tokyo. Wayne is noted for his work on plant development, establishing the role of calcium in regulating plant growth. He is an acknowledged authority on how plant cells sense light and gravity, on the water permeability of plant membranes and on light microscopy. He has written two textbooks including *Plant Cell Biology: From Astronomy to Zoology* and *Light and Video Microscopy*, soon to be out in its second edition. He is currently working on both light and gravity and in so doing has published alternatives to Einstein's theories of special and general relativity.

Dr. Clifford Weil is a professor of Genetics in the Agronomy Department at Purdue University and a member of the Whistler Center for Carbohydrate Research. He has a B.S. in Genetics from the University of California, Davis and a Ph.D. in Genetics from Cornell University. His connection to transposons and the work of Barbara McClintock is through a postdoctoral fellowship with Susan Wessler, then at the University of Georgia, working on the *Wx-m5* allele and derivatives of it. These studies led to descriptions of the

Ds chromosome breakage mechanism and studies of short range transpositions within the *wx* locus, developmental regulation of *Ac/Ds* activity and the sequence dependence of *Ds* excision footprints and DNA repair genes and mechanisms that are involved in the transposition process. In 2000, Weil and his colleague, Reinhard Kunze were the first to demonstrate that plant transposable elements could transpose in yeast cells, introducing a model system that is still in use. He is an elected fellow of the American Association for the Advancement of Science.

Dr. Jonathan F. Wendel is Distinguished Professor in the Department of Ecology, Evolution, and Organismal Biology at Iowa State University. His research focuses on mechanisms underlying plant genomic and phenotypic diversify, with a special focus on the phenomenon of whole genome doubling, or polyploidy. Most of his ~280 publications focus on the cotton genus (Gossypium), in which two diploid and two polyploid species were each independently domesticated thousands of years ago. This natural evolutionary diversification, followed by parallel strong directional selection under domestication, provide a model framework for exploring the comparative basis of domestication, the origin of form and of diversity in nature, and the evolutionary consequences of genome doubling. His research has helped shape our understanding of the myriad genomic consequences of allopolyploidy, where two diverged diploid genomes become reunited in a common nucleus. His laboratory has illuminated the evolutionary processes of intergenomic gene conversion, homoeolog expression bias, duplicate gene coregulation and expression dominance, biased fractionation, and the evolutionary trajectories of duplicated networks. He has been recognized in all three major domains of professorial life: Master Teacher, for his role as graduate mentor and educator; Distinguished Professor, for national research prominence; and Outstanding Achievement in Departmental Leadership, for leadership excellence during his 15 years (2002-2017) as department chair, His work has garnered national recognition, as evidenced by his election as a AAAS Fellow, Distinguished Fellow of the Botanical Society of America, and Distinguished Scholar, Crop Science Society of America, among other awards. B.S., University of Michigan (1976); M.S., University of North Carolina (1980); Ph.D., University of North Carolina (1983)

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Harriet Creighton and Lee B. Kass
at the Wellesley College Greenhouse in 1994
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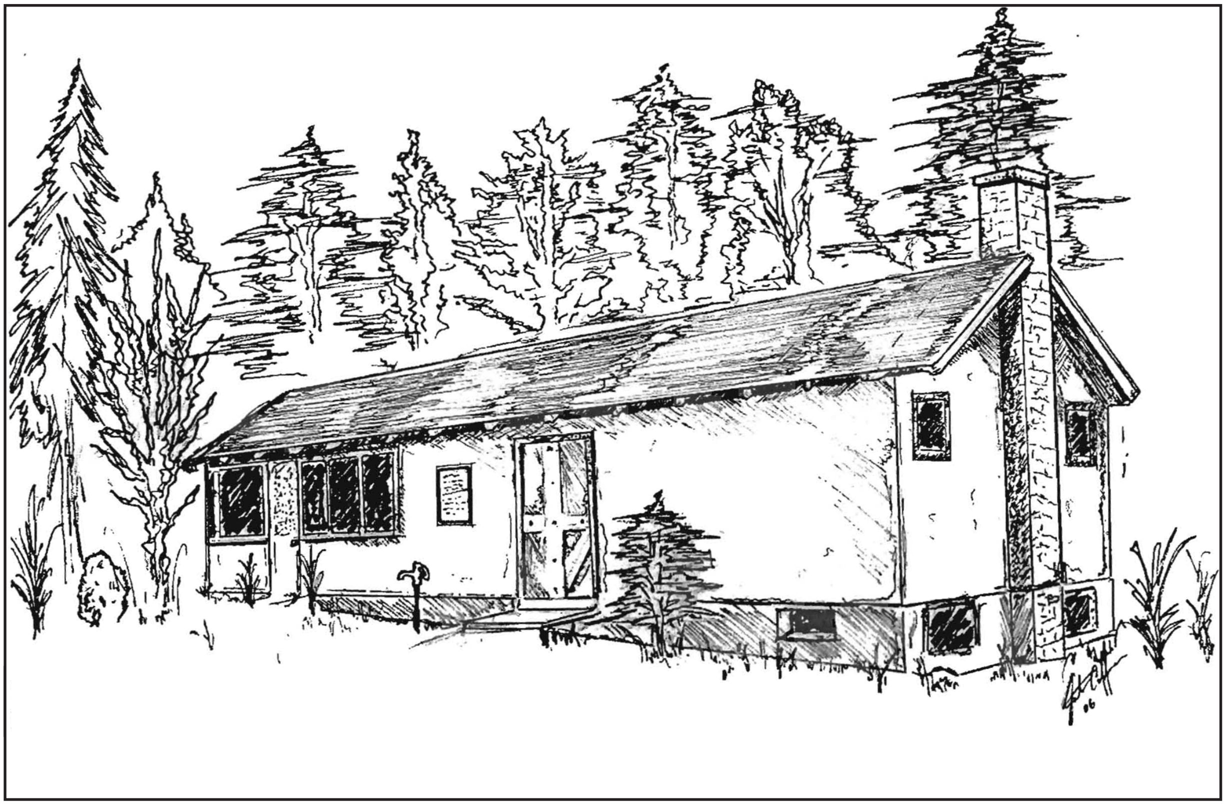
http://botany.org/PlantScienceBulletin/psb-2005-51-4.php#HARRIET

Dr. Lee B. Kass received her Ph.D. in Botany, and Genetics from Cornell University (1975), and earned a B.S. in biology at The City College of New York (CUNY, 1969). She did Postdoctoral research at The University of Cambridge (UK) and Vanderbilt University. She has served on the faculties of The University of Cambridge (UK), University of Tennessee (Nashville), Elmira College (New York), The College of the Bahamas (Nassau), Cornell University, and West Virginia University (Morgantown). Kass has authored, edited or co-edited nine books, and authored or co-authored more than 80 book chapters, proceedings papers, and articles in scientific journals. She is a member of the Botanical Society of America, The Bahamas National Trust, and a former member of many botanical organizations. Kass was chair of the Historical Section of the Botanical Society of America for many years. She established the Elmira College Herbarium in 1985, and currently serves on the Science Advisory Committee of the Bahamas National Trust. Among her awards is the Josef Stein Award, for excellence in teaching and scholarly achievement (1985) and a Fulbright Scholar Award (1996), during which time she and her spouse, Dr. Robert E. Hunt, established the National Herbarium of the Bahamas. She is Visiting Professor at Cornell University, and West Virginia University (Morgantown). Her research focuses on history of botany, and biodiversity and reproductive biology of Bahamian plants.



Justin Coffman

Emerson Garden Field Laboratory
Fondly known as the "McClintock Shed"

Emerson Garden "McClintock Shed" *(Image used with permission of Robert Dirig).*