NATIONAL ACADEMY OF SCIENCES

MARCUS MORTON RHOADES

1903—1991

A Biographical Memoir by

WAYNE R. CARLSON AND JAMES A. BIRCHLER

Biographical Memoir

National Academies Press
washington d.c.

Courtesy of Indiana University News Bureau

M. M. Rhoades

MARCUS MORTON RHOADES

July 24, 1903–December 30, 1991

BY WAYNE R. CARLSON AND JAMES A. BIRCHLER

THERE ARE MANY ways to characterize scientists. Some could be said to choose a problem and begin to apply various techniques to understand it. Others explore the field with open eyes and open mind, grasping the unexpected for investigation. Marcus M. Rhoades was the latter type. His oft-repeated entreaty to beginning graduate students, "Just get in the lab and start work; you can't help but discover something," gave evidence of his belief in this approach. Certainly his own discoveries were a diverse group of seminal contributions to genetics.

Marcus M. Rhoades was born on July 24, 1903, in Graham, Missouri, and spent his childhood in Downs, Kansas. He developed a strong affinity for the Midwest and often boasted of the fertile fields and wide expanses of that part of the United States. Rhoades attended the University of Michigan, majoring in botany and mathematics. When he was a senior and uncertain of his interests, he was befriended by Prof. E. G. ("Andy") Anderson. Anderson introduced Rhoades to plant genetics and, when Rhoades later wrote a memorial resolution on Anderson, he praised him warmly. After receiving his B. S. and M. S. degrees at Michigan, Rhoades studied for his Ph.D. at Cornell University under

Anderson's major professor, R. A. Emerson, a maize geneticist. During his graduate years Rhoades lived for three years in Emerson's home as "a member of the family" (1984). He was part of a brilliant group of maize cytogeneticists, which included fellow students Barbara McClintock, Charles Burnham, and George Beadle. Rhoades interrupted his Ph.D. work for one year to visit the California Institute of Technology as a teaching fellow. At this time he worked on *Drosophila* under the guidance of A. H. Sturtevant and T. Dobzhansky, with occasional support from T. H. Morgan and C. B. Bridges. By the time he received his Ph.D. Rhoades had written five research papers. During his graduate years Rhoades worked with the best minds in both maize and *Drosophila* genetics. No wonder he frequently advised his graduate students that they would look back on their graduate years as the best years of their lives.

Rhoades met his future wife Virginia at Cornell University, and they were married in 1932. Virginia Hatcher Rhoades was a graduate student in L. F. Randolph's laboratory and she made significant contributions to maize genetics, with work on pollen development and genetic factors of chromosome 10. She subsequently gave up research in favor of raising their two sons, Marcus junior and William.

Following completion of his Ph.D. in 1932 Rhoades stayed at Cornell as an experimentalist in plant breeding until 1935. In that year he joined the U. S. Department of Agriculture as a research geneticist and was stationed at Iowa State University until 1937. While there, he participated in setting up the yearly Iowa corn yield test. In 1937 the USDA transferred him to the Arlington Experimental Farm outside Washington, D.C. At the farm his basic cytogenetic research flourished, with considerable support from both his supervisor M. T. Jenkins and bureau chief F. D. Richey. Rhoades returned to academics in 1940 as associate professor at Columbia University. He was promoted to professor in 1943, and remained at Columbia until 1948, when he was appointed professor at the University of Illinois. He spent ten productive years of teaching and research at Illinois and next served as chairman and professor of the botany department at Indiana University from 1958 to 1968. In 1968 he resigned the chairmanship and was given the rank of distinguished professor at Indiana University. Rhoades retired in 1974, but he continued his research activities at Indiana until shortly before his death in 1991.

During his career Rhoades worked on a wide variety of topics in maize cytogenetics, including crossing over and basic cytogenetic principles; cytoplasmic male sterility; centromeric misdivision; the first transposon-type mutator system; a nuclear gene, *iojap*, that affects the chloroplast genome; meiotic mutations, including *ameiotic 1*; meiotic drive by abnormal chromosome 10; properties of heterochromatin; and the effect of B chromosomes on heterochromatin. The listing of Rhoades's work demonstrates the variety of his interests. It does not, however, reveal the thoroughness with which he approached each topic. One has to examine only a few of his papers to understand the high standard of proof that Rhoades demanded before publication.

Rhoades developed certain friendships and associations during his lifetime that had a far reaching effect on his career. In 1946 he selected a student from his cytogenetics class to help with pollinations in the corn field. Ellen Dempsey was later promoted to research associate. In that position she performed genetic crosses and cytogenetic analyses plus various duties, including the tutoring of graduate students, review of thesis manuscripts, and much of the assembly of the *Maize Genetics Cooperation News Letter*. Rhoades and Dempsey published a number of joint papers from 1953 to 1990. Several reviews of the life of Marcus Rhoades were written by Dempsey, including two Festschrift publications and one memorial resolution (Dempsey, 1973,1983,1994). We have borrowed liberally from these publications, since they come from the person who knew Rhoades's work better than anyone. Peterson and Peterson also wrote an article on the life of Rhoades (Peterson and Peterson, 1973).

Another longtime association for Rhoades was with Drew Schwartz. Rhoades was Schwartz's Ph.D. supervisor at Columbia and later at the University of Illinois. Subsequently, he was instrumental in bringing Schwartz to Indiana University. Schwartz played a major role in developing the area of biochemical genetics in maize. His work was a bridge to the later study of molecular biology in maize, and a number of Schwartz's students went on to become leaders in the field. The synergism between Rhoades and Schwartz carried over to benefit Schwartz's students.

Other important associations were with John Laughnan at the University of Illinois and Jim Peacock at the Commonwealth Scientific and Industrial Research Organization in Canberra, Australia. Rhoades and Laughnan shared field plots at Illinois and gave a joint seminar. They often advised each other's graduate students. Peacock provided Rhoades with a place to work away from the considerable administrative duties of the chairmanship at Indiana University. Two visits to Canberra allowed Rhoades the time to write several papers and to become acquainted with molecular cytogenetic methods.

The honors given Rhoades were numerous. Among the most significant was his election to three prestigious societies: the National Academy of Sciences, American Philosophical Society, and American Academy of Arts and Sciences. In addition, Marcus Rhoades and Barbara McClintock were given the first T. H. Morgan Medal from the Genetics Society of America in 1981. Rhoades was also honored with two

Festschrift publications, on the occasions of his seventieth and eightieth birthdays. Contributions to the publications came from former students and colleagues. At one of the gatherings for presentation of a volume Rhoades stated that his students had made him proud and maintained that some of their research contributions had exceeded his own. We all knew the latter was untrue, but the comment was typical of his modesty.

Following the example of his mentor, R. A. Emerson, Rhoades provided much help to the maize genetics community and the genetics community at large. It was Emerson who began the spirit of cooperation among maize geneticists. He organized the first meeting of maize workers in 1928 during the meetings of the American Association for the Advancement of Science. The cooperation that began in 1928 was formalized at the Sixth International Genetics Meeting in 1932, when a group of maize geneticists formed the Maize Genetics Cooperation. The Cooperation, originally located at Cornell University, established a center for the preservation of seed stocks and published the *Maize Genetics Cooperation News Letter*. At the 1932 meeting Rhoades was asked to take charge of the newsletter. He served as its editor from 1932 to 1935 and again from 1956 to 1974. Rhoades also participated in the collection and maintenance of seed stocks and later was primarily responsible for moving the stock center to its present location at the University of Illinois.

Rhoades was editor of *Genetics* from 1940 to 1948 and was a member of numerous journal editorial boards over the years. He served on the committees of many organizations, including the Guggenheim Memorial Foundation, National Institutes of Health, National Science Foundation and Atomic Energy Commission. Another type of service, performed not infrequently, was the authoring of biographical papers on colleagues. Among these were the National Academy of Sciences' *Biographical Memoir* for R. A. Emerson (1949) and L. J. Stadler (1957) and memorial biographies of E. G. Anderson (1973, Stadler Symposium) and B. McClintock (1986, *Maydica*).

Rhoades was also known for his teaching. As recalled by Ellen Dempsey, Rhoades's two-semester cytogenetics course at Columbia was very popular. By the time Rhoades was teaching at Indiana University and serving as chair of the botany department the course was one semester in length. We (JB and WC) both took the course at Indiana and recall the lectures as well organized, intellectually challenging, and taught with humor and concern for the student. In terms of graduate education Rhoades sponsored twenty-six Ph.D. students during his career, and their names were recorded by Dempsey (1973). In dealing with new graduate students Rhoades would start a student on a project and provide the materials needed. After that he considered that the research belonged to the student and never asked that his name be placed on papers his students wrote. Consequently, he is senior author on almost all the papers in his bibliography.

Formal retirement freed Rhoades for greater interaction with Schwartz's students. One of the authors (JB) recalls that visits to the Rhoades lab were greeted with "Have a seat, young man" and inquiries about the latest experiments. He freely gave advice about available stocks that might be useful. These visits were often characterized by recollections about notable geneticists and their work. It is clear he had some strong favorites. In the field he would wander into one of JB's plots and offer judgment on the corn and weeds and give tips on field work in general.

Rhoades was modest and did not view himself as an extraordinary talent, but more as a gatherer of data. He did not consider himself a gifted theorist, nor did he particularly approve of "theorizing." Rhoades's approach to science was described by Dempsey (1973). He was an acute observer and studied any anomalies in his crosses assiduously until they were explained. This approach led to the discovery of the *Dotted* mutation, the neocentromeres of abnormal chromosome 10, and the high loss phenomenon of B chromosomes. In the last case Rhoades found some recessive kernels on an ear that should have had only the dominant phenotype. The simplest explanation would have been that pollen (self) contamination by the recessive parent occurred. Rhoades would not accept this explanation and one can certainly imagine him confidently dismissing any criticism of his technique. While Rhoades was well known for his modesty, this trait did not extend to his view of his own technical skills, whether they were field techniques, such as pollinating and collecting sporocytes, or laboratory skills, such as staining cells and chromosome analysis.

A brief, but by no means comprehensive, review of research discoveries by Marcus Rhoades follows. Rhoades began his career with a Ph.D. thesis on the topic of cytoplasmic male sterility in maize. This was the first study of its kind on a topic that has been of enormous economic significance in the cultivation of maize.

Rhoades loved to recount the story of his thesis defense. After Rhoades had left the room for the decision a chemist on the committee, who was unfamiliar with genetics but intrigued by Rhoades's work, drew the group into an extended discussion for his own edification, forgetting that Rhoades was waiting in the hallway and enduring the inquiries of fellow graduate students as to whether he was "in trouble." As a result of this experience Rhoades always kept the discussion following student committee meetings to a minimum.

During studies for his Ph.D. Rhoades also worked on some basic principles of crossing over, principles that were just emerging at the time. For example, he demonstrated in maize that crossing over occurs at the four-strand stage (1932). Subsequent work covered a variety of topics, including mutator genes. The *Dotted* mutator was first identified by observation of a variegated endosperm color phenotype (purple dots on a colorless background) on seeds of a single ear (1938). *Dotted* was shown to be an unusual mutator gene because it affects a specific locus, *a1*, and does not have a general effect on other genes. It was later found that the dotted phenotype is due to the movement of a transposable element at *a1* under the influence of *Dt*. A completely different mutator system, affecting plastids, was also discovered by Rhoades. It was one of the first cases of nuclear-cytoplasmic interaction found and one that is often cited in textbooks. In this case a nuclear gene, *iojap*, causes a change in the chloroplast. These alterations are heritable in the cytoplasm, even after the nuclear mutation is replaced.

Few organisms are as well suited to cytogenetic work on meiosis as maize. The combination of excellent meiotic cytology with a strong genetic tradition has produced a long line of cytogenetic studies. Rhoades's focus as a cytogeneticist was very much on meiosis and he often studied mutations that disrupted the process. In addition, he discovered one of the key genes in the switch from a mitotic to a meiotic program, *ameiotic 1*. Another focus of Rhoades's work was the centromere. He discovered a telocentric of the short arm of chromosome 5 (1940) and used it to study centromeric stability.

No mention of the research of Rhoades would be complete without reference to a long commitment to analysis of abnormal chromosome 10, an intrigue that began at the USDA and continued until his death. This chromosome, discovered by A. Longley in 1937, differs from the normal chromosome 10 by the addition of chromatin to 10L. The abnormal chromosome was shown by Rhoades to possess a unique system of meiotic drive. Rhoades delighted in informing students that the meiotic drive aspect was discovered in his Arlington, Virginia, USDA plot "on which the Pentagon now stands." Due to the findings of Rhoades this work remains one of the best explained systems of meiotic drive. It was shown that the abnormal chromosome, when heterozygous with a normal 10, is recovered about 70% of the time in the female gametes versus 30% for the normal chromosome. Transmission through the male is normal (50/50). Cytological studies showed that the abnormal chromosome causes the production of neocentromeres in both the male and female meiosis. These neocentromeres (accessory centromeres) migrate precociously to the poles at the meiotic anaphases. Neocentromeres pull chromatids attached to them to the outer poles of the linear female meiotic quartet. Since the basal product is destined to produce the egg cell, with the other three cells deteriorating, chromatids with neocentromeres are favored for transmission through the female. No advantage to neocentromeric chromatids occurs in the male, because orientation of the meiotic cells is not linear and because all meiotic cells survive. Rhoades also showed that the neocentromeres only form on chromatids that carry chromosomal knobs (i.e., large heterochromatic regions that are separated by some distance from the centromere). Therefore, when a bivalent is heterozygous for one chromosome carrying a knob and one lacking the knob, preferential recovery of knobbed chromatids occurs in the female following a crossover between the centromere and the knob. Abnormal chromosome 10 has a large knob whereas the normal chromosome lacks a knob.

Consequently, abnormal 10 is recovered in excess through the female.

Rhoades and Dempsey discovered a system that could be used for studying the structure of abnormal chromosome 10. While working with the maize B chromosome they found that a certain stock gave frequent chromosome breakage in the presence of B's. The chromosomes being broken were the knobbed chromosomes, with breakage occurring at the second pollen mitosis. According to Rhoades and Dempsey the B chromosomes caused knobs to stick together at the second pollen mitosis, giving bridge formation and bridge breakage. The timing of the breakage was quite useful, because the broken chromosome subsequently enters the zygote. Entry into the zygote "heals" the chromosome presumably by the addition of telomeric DNA to the broken end. Consequently, the breakage-fusion-bridge cycle cannot occur. Therefore, all the deficiencies caused by chromosome breakage in this system are simple terminal deficiencies. Rhoades and Dempsey (1985) used this fact to make terminal deletions of the long arm of abnormal 10. They showed that the additional chromatin of abnormal 10 is interspersed with normal chromatin and is not a simple terminal addition to the chromosome.

Rhoades demonstrated that the system producing the chromosomal breakage contains two components; it requires at least two B chromosomes plus a specific inbred genetic background to be effective. Under these circumstances chromosomes with knobs undergo frequent chromosome breakage in the pollen. The breakage is visualized by the expression of a recessive phenotype in a homozygous recessive x homozygous dominant cross. The system became known as "high loss" due to the frequent elimination of dominant markers from knobbed chromosomes. A further value of this system was the discovery of new transposon systems.

Chromosome breakage in maize seems to stimulate the activation of transposons, and new transposons were reported and analyzed in 1989.

A remarkable aspect of Marcus Rhoades's career was his ability to continue producing imaginative and significant research for more than fifty years. From his first publications in 1931 until his last in the late 1980s Rhoades maintained a standard of quality in his research that was unwavering and was an example to all his students and colleagues.

REFERENCES

Dempsey, E. 1973. Random observations on a distinguished professor. *Theor. Appl. Genet.* 43:97-100.

Dempsey, E. 1983. Marcus M. Rhoades, the later years. *Maydica* 28:203-12.

Dempsey, E. 1994. Marcus Morton Rhoades. *Proc. Am. Phil. Soc.* 138:561-67.

Peterson, P. A. and S. R. Peterson. 1973. Marcus M. Rhoades. *Theor. Appl. Genet.* 43:93-96.

SELECTED BIBLIOGRAPHY

1931

Cytoplasmic inheritance of male sterility in *Zea mays*. *Science* 73:340-41.

1932

The genetic demonstration of double strand crossing-over in *Zea mays*. *Proc. Natl. Acad. Sci. U. S. A.* 18:481-84.

1933

With R. A. Emerson. Relation of chromatid crossing over to the upper limit of recombination percentages. *Am. Nat.* 67:1-4.

An experimental and theoretical study of chromatid crossing over. *Genetics* 18:535-55.

A cytogenetical study of a reciprocal translocation in *Zea mays*. *Proc. Natl. Acad. Sci. U. S. A.* 19:1022-31.

A secondary trisome in maize. *Proc. Natl. Acad. Sci. U. S. A.* 19:1031-38.

1935

With B. McClintock. The cytogenetics of maize. *Bot. Rev.* 1:292-325.

1936

A cytogenetic study of a chromosome fragment in maize. *Genetics* 21:491-502.

The effect of varying gene dosage on aleurone color in maize. *J. Genet.* 33:347-54.

1938

Effect of the *Dt* gene on the mutability of the *a1* allele in maize. *Genetics* 23:377-95.

1939

With V. H. Rhoades. Genetic studies with factors in the tenth chromosome in maize. *Genetics* 24:302-14.

1940

Studies of a telocentric chromosome in maize with reference to the stability of its centromere. *Genetics* 25:483-520.

1941

The genetic control of mutability in maize. *Cold Spring Harbor Symp. Quant. Biol.* 9:138-44.

Different rates of crossing over in male and female gametes of maize. *J. Am. Soc. Agron.* 33:603-15.

1942

Preferential segregation in maize. *Genetics* 27:395-407.

With H. Vilkomerson. On the anaphase movement of chromosomes. *Proc. Natl. Acad. Sci. U. S. A.* 28:433-36.

1945

On the genetic control of mutability in maize. *Proc. Natl. Acad. Sci. U. S. A.* 31:91-95.

1946

Plastid mutations. *Cold Spring Harbor Symp. Quant. Biol.* 11:202-207.

1949

With W. E. Kerr. A note on centromere organization. *Proc. Natl. Acad. Sci. U. S. A.* 35:129-32.

1950

Gene induced mutation of a heritable cytoplasmic factor producing male sterility in maize. *Proc. Natl. Acad. Sci. U. S. A.* 36:634-35.

1951

Duplicate genes in maize. *Am. Nat.* 85:105-10.

1952

Preferential segregation in maize. In *Heterosis*, ed. J. W. Gowen, pp. 66-80. Ames: Iowa State College Press.

1953

With E. Dempsey. Cytogenetic studies of deficient-duplicate chromosomes derived from inversion heterozygotes in maize. *Am. J. Bot.* 40:405-24.

1955

The cytogenetics of maize. In *Corn and Corn Improvement*, ed. G. F. Sprague, pp. 123-219. New York: Academic Press.

1966

With E. Dempsey. The effect of abnormal chromosome 10 on preferential segregation and crossing over in maize. *Genetics* 53:989-1020.

With E. Dempsey. Induction of chromosome doubling at meiosis by the elongate gene in maize. *Genetics* 54:505-22.

1967

With E. Dempsey and A. Ghidoni. Chromosome elimination in maize induced by supernumerary B chromosomes. *Proc. Natl. Acad. Sci. U. S. A.* 57:1626-32.

1968

Studies on the cytological basis of crossing over. In *Replication and Recombination of Genetic Material*, eds. W. J. Peacock and R. D. Brock. Canberra: Australian Academy of Sciences.

1972

With E. Dempsey. On the mechanism of chromatin loss induced by the B chromosome of maize. *Genetics* 71:73-96.

1973

With E. Dempsey. Cytogenetic studies on a transmissible deficiency in chromosome 3 of maize. *J. Hered.* 64:125-28.

With E. Dempsey. Chromatin elimination induced by the B chromosome of maize. I. Mechanism of loss and the pattern of endosperm variegation. *J. Hered.* 64:12-18.

1980

With A. Pryor, K. Faulkner, and W. J. Peacock. Asynchronous replication of heterochromatin in maize. *Proc. Natl. Acad. Sci. U. S. A.* 77:6705-6709.

1981

With W. J. Peacock, E. S. Dennis, and A. J. Pryor. Highly repeated

DNA sequence limited to knob heterochromatin in maize. *Proc. Natl. Acad. Sci. U. S. A.* 78:4490-94.

1984

The early years of maize genetics. *Annu. Rev. Genet.* 18:1-29.

1985

With E. Dempsey. Structural heterogeneity of chromosome 10 in races of maize and teosinte. *Plant Genet. U. C. L. A. Symp.* 35:1-18. M. Freeling, editor. Alan R. Liss, Inc., New York.

1989

With N. S. Shepherd and E. Dempsey. Genetic and molecular characterization of *a-mrh-Mrh*, a new mutable system of *Zea mays. Dev. Genet.* 10:507-19.