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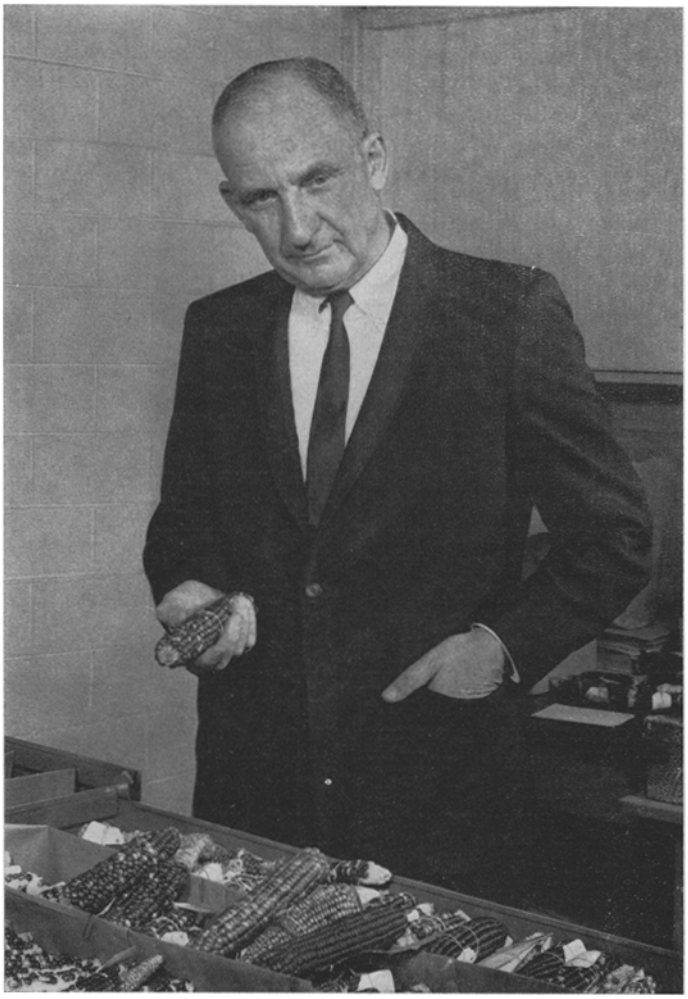
Marcus M. Rhoades

The papers in this volume of Theoretical and Applied Genetics are a tribute to Professor Marcus M. Rhoades from some of his former students and from various associates on the occasion of his seventieth birthday. Up to the present and for more than four decades, Rhoades has played a vital role in the development of Genetics, particularly maize Cytogenetics. His personality and genius have inspired those who have worked with him, attended his classes, or benefited from his research.



A scientist's legacy may be hard to define. In Dr. Rhoades' case there is no such difficulty. His legacy is surely the endowment of a competent and enthusiastic generation of students who continue to make significant contributions to the field of Genetics. Marcus Rhoades possesses a number of skills which together have made this endowment possible. First among such skills is the ability to recognize problems that are susceptible to scientific manipulation. Further, the tactical and technical ability to conceive and conduct experiments is needed. In addition, the ability to see how the results relate and contribute to other bits of information is essential. These combined skills are rarely found in one individual but when they are, quality research results.

Over the years Rhoades has continued to set an example of excellence in his varied research efforts. His work has spanned three eras in Genetics; the

Emerson period of post-Mendelism, the pre-DNA period when the basic axioms were established (from recombination to the discovery of DNA), and the post-"DNA-operon" period which encompasses developmental and organismal studies. Throughout, maize genetics has benefited enormously from Rhoades' research. At the same time his other attributes as a stimulating teacher and an individual of unusual friendliness and warmth, have endeared him to a wide set of acquaintances throughout the world.

Marcus M. Rhoades was born on July 24, 1903 in Graham, Missouri. He attended the University of Michigan and earned a B.S. in 1927 and an M.S. in 1928. From there, he proceeded to Cornell College in Ithaca, New York, where he joined Professor R. A. Emerson's group. This exciting group included L. F. Randolph, Barbara McClintock, George Beadle, Charlie Burnham, George Sprague, H. S. Perry, H. W. Li, A. C. Fraser, and a number of others. A synergistic atmosphere was generated at Cornell — the Genetics under Emerson and the Cytology under Sharp — that could be rivaled only in the Morgan "flyroom". Before completing his Ph. D. in Genetics in 1932, Rhoades spent a year (1929—1930) as a fellow at the California Institute of Technology working with *Drosophila*. His thesis was on "the cytoplasmic inheritance of male-sterility in *Zea mays*".

In 1935, he joined the United States Department of Agriculture as a Research Geneticist in the Division of Cereal Crops and Diseases, Bureau of Plant Industry at Ames, Iowa, where he participated in setting up the Iowa Corn Yield Test in addition to doing basic cytogenetic work. This sojourn in the Midwest's Corn Belt must have been revealing to the young Cornell trained geneticist who could see how little maize genetics was influencing breeding technology at the time. Following this experience with the USDA at Iowa State, Rhoades continued his work over a period of years at three different universities: Columbia (1940), Illinois, and Indiana. Certainly, he must have felt the receptive climate emanating from the Columbia group, which included T. Dobzhansky, F. Schrader, A. W. Pollister, L. C. Dunn, and F. Ryan and which was closely associated with the Department of Genetics at Cold Spring Harbor that included M. Demerec, B. McClintock, B. P. Kaufmann, and M. McDonald. At these institutions, which were also meccas for visiting foreign geneticists, searching questions were being posed about chromosome content, characteristics, and chemistry. In retrospect, the mystery surrounding the exact nature of hereditary material at that time seems actually to have been a blessing, since it reserved the 1940s for consideration of certain problems that an earlier discovery of DNA would have diverted and thus retarded.

During his stay at Columbia, numerous students enrolled in Marcus Rhoades' Cytogenetics classes, and a number of them subsequently went on to further explore the potential of this discipline professionally (D. Perkins, P. T. Morgan, M. Shaw, R. Sager, C. Pittendrigh, B. Wallace, M. Lieb, E. Witkin, W. Maas in addition to many contributing to this volume). His course in Cytogenetics at Columbia included topics such as meiosis, chromosome aberrations, somatic crossing over, balanced lethals, position effects, and ploidy, and these were illustrated with examples from maize, *Drosophila*, *Oenothera* and *Datura*. During this period, the Columbia group heard the first rumbles of major break-throughs in Genetics when Beadle and Tatum reported on gene enzyme relations in *Neurospora* and sex was discovered in bacteria by Lederberg and Tatum. At the same time, the first suggestions of control and regulation of gene output were promulgated, and Barbara McClintock reported that particular phenotypes in maize were being modified by elements unassociated with the modified genes.

Marcus Rhoades' Cytogenetics course has for years received much approbation. It is rich in information and moves at a brisk pace from basic facts to more complex and challenging aspects. Current problems are always considered in historical perspective when a relationship exists. Emphasis is placed on deducing as many valid conclusions to an experiment as possible. Then uncertainties and ramifications in need of solution are discussed.

Marcus Rhoades returned to the Midwest in 1948 when the Botany Department at the University of Illinois convinced him to join them. There he established an active laboratory for the training of plant cytogeneticists which so few of the major land-grant agricultural colleges in the 1940s possessed. Among students who received training in Marcus Rhoades' Cytogenetics classes at Illinois, were some of today's leaders in cytogenetic investigations of soybeans, wheat, sorghum, as well as corn. They in turn are now training another generation of students. An additional result of Marcus Rhoades' Illinois sojourn was the relocation from Cornell of the Maize Cooperative Seed Center for the purposes of distributing information informally and developing and distributing corn mutants. So it can easily be understood why it is that even today, fifteen years later, the impact of Marcus Rhoades' presence at the University of Illinois is so strongly felt.

In 1958 Marcus Rhoades assumed the Chairmanship of the Department of Botany at the University of Indiana. Those were busy times with departmental responsibilities, active research programs, graduate student training, and teaching. Throughout four decades of research activity, Marcus Rhoades has collaborated with numerous colleagues and, most significantly, from the Columbia days to the present with Ellen Dempsey. She has assumed many tasks and performed them with unexcelled skill, aided Rhoades' research programs in numerous ways, helped in the training of many graduate students, and

assumed much responsibility for the "Maize Genetics Cooperative Newsletter".

One of the most intriguing problems that Marcus Rhoades has attacked from combined cytological and genetical viewpoints is that which deals with chromosome behavior during meiosis. He has judiciously used genetic data to confirm cytological observations, and cytological observations have been used to verify genetic anomalies. His detailed study of "Abnormal 10" confirms the hypothesis of neocentromere formation and preferential fertilization. Observation of neocentric fiber emanation from chromosome knobs provides a new concept about the origin of centromere fibers. "Abnormal 10" was used as a tool to explore basic questions about the relationship of observable chromosome pairing and the time of crossing over. Rhoades accumulated strong evidence and arguments in favor of the hypothesis that the time of crossing over is midprophase of meiosis and that the process is accomplished by a breakage-rejoining mechanism. He has always been mindful of the potential pragmatic value of certain cytogenetic anomalies and suggested using "Abnormal 10" to break up linkage blocks, since its presence enhances proximal crossing over.

The mechanism of meiosis was further probed through the use of the "elongate" gene. In this case, Rhoades carefully tested alternative hypotheses to explain the origin of diploid eggs. Recovery of unreduced gametes provided an opportunity to map centromeres, a most difficult determination in higher plants. Like the "Abnormal 10" and "elongate" research, earlier work with telocentrics and centromeres also helped clarify meiotic mechanisms.

A classic example in genetic literature of the assiduous pursuit of data to extract the maximum amount of evidence is the 1953 study of Inversion 3a. Careful observation of the data illustrates Rhoades' method of critical analysis and precise correlation of genetic information and chromosome behavior. Rhoades and Dempsey were not content to accept previous dogma dealing with inversion behavior and non-transmissibility of broken chromosomes in plants. When a discrepancy was found, an explanation was sought. They subsequently uncovered the reason for the survival of deficient-duplicate chromosomes. This inversion paper is one all Genetics graduate students should read but, as one recently remarked, "it isn't a paper that you would read with your feet up on the desk. You must read it like a dictionary."

During the middle 1930s while perusing the corn collections in Randolph's laboratory, Marcus Rhoades became curious about some colored dots on certain kernels. A study of the *Dt* gene followed and introduced the concept of gene control of specific mutability. The work was a forerunner of Barbara McClintock's elegant studies involving controlling elements. Although much has been elucidated about these elements, the intriguing question about their exact mode of operation remains unsolved.

Marcus Rhoades' early research on cytoplasmic male sterility pointed the way to some future concerns. His analysis of the role of the cytoplasm in male sterility exhibited his thoroughness in exploring various possibilities. Although abundant ancillary information has since been accumulated about male sterility in corn, the mechanism leading to pollen abortion is still a mystery. (Of course, the use of the cytoplasmic male sterile was to have a massive impact on American corn production, and it eventually became the best illustration of the practical utilization of modern Genetics.) Rhoades continued his cytoplasmic investigations with a study of the *iojap* gene that affects the formation of plastids. In summation of the *iojap* case, he states, "Although induced by a nuclear factor, the *ij* gene, the mutated plastid, like a Frankenstein monster, is no longer under the control of its master."

Where applicable, Marcus Rhoades continuously considers the evolutionary aspects of corn. In the case of duplicate genes or of B chromosomes, he has underscored the roles they undoubtedly played in the evolution of races of maize. In relating knobs to B chromosomes, he posed precise and crisp questions: Do A chromosome knobs interact with B chromosomes? Is the rate of loss of B's in a genome stabilized when a certain balance is attained? What is the relationship of knob size, position, and number to rate of loss? As one admirer of Rhoades' work has expressed it, "It is difficult to find within all of contemporary genetics a set of questions more precisely framed in operational terms ... the compelling zest of an experimentalist extraordinaire is strikingly clear."

Many honors have come to Marcus Rhoades in recognition of his scientific stature. He was elected to the National Academy of Sciences in 1946 and to the American Philosophical Society in 1962. He has received the Botanical Society of America Award for "Outstanding Contributions to American Botany." He has been a Visiting Professor at numerous institutions: the University of Sao Paulo, Brazil (1947 to 1948), North Carolina State College (1953), Cornell University (1956), Jessup Lecturer at Columbia University (1958), and lecturer at the Universities of Texas and California. He has been a member of numerous editorial boards: the Columbia Biological Sciences (1941—1948), the National Research Council Fellowship Committee, the New York Botanical Garden, the American Journal of Botany (1939—1940), the Botanical Review, the American Genetics Association, and the Annual Review of Genetics.

He has served as President and Vice-President of the Genetics Society of America, President of both the Botanical Society of America and the American Genetics Association. Rhoades has also served on the Educational Advisory Board of the John Simon

Guggenheim Memorial Foundation, and on the Foundation's Committee of Selection, which screens fellowship applicants.

Rhoades was the editor of "Genetics" for several years. Frequently his students at Columbia were the beneficiaries of his efforts at deciphering and analyzing submitted papers, and they learned immediately about new concepts emerging in Genetics during this period of concentrated research activity with x-rays, ultraviolet, and fast neutrons. In addition, *Neurospora* and *Paramecium* genetic studies were developing, mutation in bacteria was described (Luria and Delbruck), as was the tactical ability to handle bacteriophage (Hershey).

Rhoades' involvement in the progressive development of maize genetics is evidenced by his activity with the "Maize Cooperative" from its beginning at Cornell as a "clearing house" for information and a distribution relay point for genetic stocks. The two services, the "Letter" and the stock collection, have significantly facilitated corn genetics research. The "Maize Genetics Cooperative Newsletter" moved with Dr. Rhoades to Indiana where it continues to be produced with Ellen Dempsey's assistance.

Those colleagues who have known Marcus Rhoades' strenuous research, teaching, and administrative commitments find his devotion to competitive sports something of a surprise. At both the Universities of Illinois and Indiana, he was an active and enthusiastic football and basketball fan and became a member of the Athletic Council at each institution. Those of us in his first Cytogenetics course at Illinois remember his controlled patience as the Saturday class extended beyond noon and closer and closer to kickoff time. As a sports booster he shows the same excitement and enthusiasm expressed in classroom and laboratory. Nor does he limit his interest in sports to that of a spectator. Both at Illinois and Indiana he has been an active bowler.

Persons coming in contact with Marcus Rhoades find him unassuming and modest in manner, a model of integrity. He possesses a wry and dry sense of humor. He shows an abundance of patience and understanding with students. As evident in his writings and reviews, he corals razor-edged arguments which are clearly and incisively expressed. He applies extreme objectivity in handling data. One of his contemporaries calls him a "scientific puritan — one who collects and publishes hard facts."

Rhoades has been known to search out young scientists who have presented short papers at meetings and warmly convey his thoughts about why the work seemed to him to be significant and what bearing it might have on related issues. Those who have been fortunate enough to receive his gracious encomium will continue to relish the memory indefinitely.

Former students look back with fondness to Professor and Mrs. Rhoades' generosity and hospitality. The Rhoadeses hosted a generation of students at Thanksgiving and Christmas holidays as well as on numerous other occasions.

Marcus Rhoades' handling of graduate students is somewhat unique. He considers graduate students mature individuals who learn from their own mistakes. He encourages independent thinking and excellence in performance. His students are given the freedom to envelop themselves in a significant research problem. For some this freedom has proved difficult and frustrating at times, but in the end all his students grow to admire, respect, and appreciate Dr. Rhoades' indirect leadership and great strength.

As indicated previously, outstanding scientists leave a lasting legacy. Probably no greater legacy exists than the endowment of a generation of students with zeal, enthusiasm, and perseverance in pursuit of quality performance. Rhoades' competence, warmth, and friendliness have encompassed many, many students and associates, a number of whom join in presenting this volume of contributed papers to him on the occasion of his 70th birthday.

This issue is dedicated with admiration and affection.

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