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Perspectives

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Marcus Rhoades, Preferential Segregation and Meiotic Drive

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LONG before microarray biologists coined and promoted the term "discovery science," maize geneticists were avid practitioners of this mode of investigation. In fact, one might say that for a number of years, the field of maize genetics basically operated as discovery science. Many have speculated about why maize remains a model organism for genetic analysis, given its long life cycle relative to other species. It has many virtues, sometimes little understood or appreciated by outsiders, but the maize geneticist's style of science devoted to discovery and an unusually strong commitment to cooperation probably contributes to this trend. One of the great practitioners of this style of science was Marcus Rhoades (Figure 1), who often advised beginning graduate students: "Just get in the lab and start to work; you can't help but find something." "What are the facts?" was his common refrain to model building and theorizing. Along with his penchant for discovery was a dogged experimentalist attack to explore the parameters and dimensions of a new finding.

Rhoades discovered the first case of cytoplasmic male sterility in maize; the independence of the plastid from nuclear control by the action of the *iojap* mutation; the Dotted "mutator" system that was later found to be a transposable element (see Fedoroff 1998); many features of chromosomal behavior; the "duplicate" nature of the maize genome; effects of supernumerary chromosomes on the normal set; and preferential segregation resulting from neocentromere formation caused by abnormal chromosome 10 (Dempsey 1973, 1983, 1994; Peterson and Peterson 1973). This last topic maintained Rhoades's interest until the end of his career. It is, in fact, a rather astounding phenomenon: a variant of chromosome 10 will cause blocks of heterochromatin on all chromosomes to proceed to the poles of meiosis ahead of the normal centromeres (Figure 2). For anyone familiar with the usual course of events, the sight of this progression is indeed fascinating.

Rhoades was born in Missouri and raised in Kansas (Dempsey 1973, 1983, 1994). Eventually he found his way to the University of Michigan, where he encountered E. G. Anderson "of attached-X fame" (Rhoades's own phrase). Anderson had just demonstrated, using attached-X females of Drosophila, that crossing over occurred at the four-strand stage of meiosis. Rhoades's introduction to genetics was a seminar on this topic conducted by Anderson (Dempsey 1994). Rhoades was reportedly befuddled by this topic, but determined to understand it. Under Anderson's tutelage, Rhoades went on to receive a master's degree in genetics from Michigan, at which time he was encouraged to enter the Ph.D. program at Cornell to work with R. A. Emerson. Emerson had been Anderson's own Ph.D. advisor. It was at Cornell that the stellar group of Rhoades, George Beadle, Charles Burnham, Barbara McClintock, and Emerson coalesced to elucidate many features of maize genetics and cytogenetics in general. A photo of this group, together with Beadle's dog, taken during pollination season has been widely reprinted (*e.g.*, Sheridan 1982; Dempsey 1983; Keller 1983), and many have commented upon the collection of talent that was present at Cornell at that time (see also Nelson 1993). Rhoades showed this picture to his cytogenetics class at Indiana University in 1974 and remarked in an uncharacteristic lapse of modesty, but with characteristic wit, "Even the dog was smart!"

It was at Cornell that Rhoades began an enduring friendship with Barbara McClintock (Rhoades 1984). He was a strong advocate of her work and an admirer of her abilities both in terms of cytological technique and interpretation. Rhoades (1984) recalled his role in getting her to apply her cytological skills to the research problems of the Cornell maize genetics group (see Kass and Bonneuil 2003 for a detailed account of all the factors involved). His course material covered all of her studies, and the laboratory instruction included advice

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FIGURE 1.—Marcus Morton Rhoades in his laboratory at the University of Illinois. (From University of Illinois Bulletin, Vol. 46, No. 63, April 1949. Photo supplied by Ellen Dempsey.)

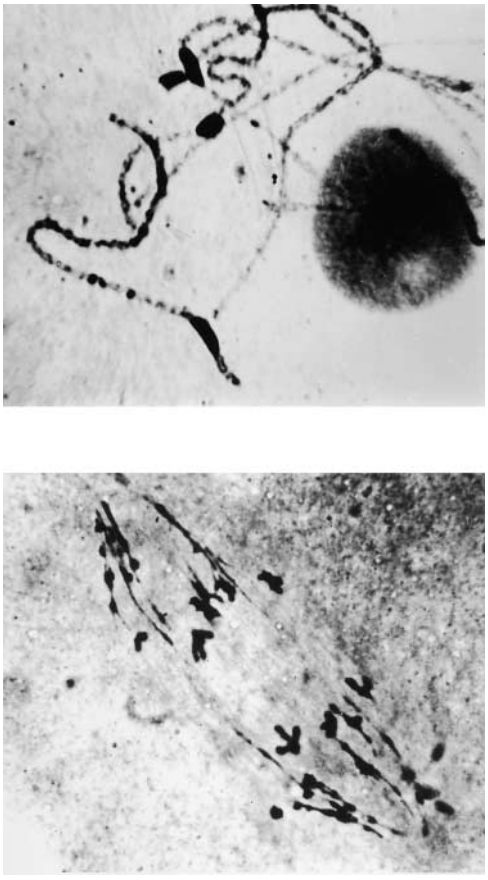

FIGURE 2.—Abnormal chromosome 10 and its effect on segregation. (Top) A pachytene smear of abnormal chromosome 10 (on the left). The deeply staining block of heterochromatin near the end of the long arm is unique to this version of the chromosome. The three deeply staining chromomeres proximal to the Ab10 knob are also specific to this chromosome. (Bottom) A smear preparation of anaphase I in microsporocytes homozygous for Ab10. Note the greatly stretched chromatin fibers proceeding to the poles ahead of the normal centromeres. A chromosome pair without knobs is near the center of the image. In this case the homologs are separating normally and do not have extensions toward the poles. (Photos were first published by RHOADES 1952 and were generously supplied by Ellen Dempsey.)

handed along from McClintock on how to analyze meiotic chromosome spreads, for example, "to focus up and down through the nucleus to follow the chromosomes along." It was a rare visit to Rhoades's lab in which McClintock's name was not mentioned in the most glowing terms. McClintock shared with Rhoades a penchant for discovery that no doubt contributed to their lasting scientific bond.

During his time at Cornell, Rhoades made many contributions to maize genetics and wrote his thesis on the first case of cytoplasmic male sterility found in maize. Rhoades regularly recalled his thesis defense. A chemist unfamiliar with the details of genetics was on his committee. After Rhoades was asked to leave the room at the end of the presentation, an innocent set of questions by this outside member to the committee on why cytoplasmic inheritance might be considered unusual led to an extended educational discussion. Time slipped by without the committee realizing that Rhoades was awaiting a decision in the hallway. Friends of Rhoades, seeing him pace back and forth, speculated that he was "in trouble." As a consequence of this experience, Rhoades always made certain that such discussions in which he took part were kept short.

While at Cornell, Rhoades played an important role in the 1932 International Congress of Genetics by preparing a "living chromosome map" in which mutant plants were planted in rows corresponding to their position on the chromosomes (CROW 1992).

The discovery of preferential segregation: From Cornell, Rhoades accepted a position with the United States Department of Agriculture (USDA), first in Iowa and then in Arlington, Virginia. It was in this position that Rhoades discovered the phenomenon of preferential segregation. Albert LONGLEY (1937, 1938) had described an "abnormal chromosome 10" (Ab10) that was present in populations of Native American varieties and in teosinte, the wild progenitor to maize. This chromosome was characterized by Longley as possessing extra blocks of heterochromatin near the end of the long arm of the chromosome. In a simple experiment to test the effect of this chromosome on recombination,

Rhoades (1942) crossed a stock carrying Ab10 to a tester line and backcrossed the hybrid. A deviation from a normal 1:1 ratio for the *R* locus (an anthocyanin pigment marker closely linked to the knob) was observed. Rhoades coined the phrase *preferential segregation* to describe this phenomenon. In his class he related that his first reaction to seeing those ears was that the off ratio was due to pollen contamination from an unwanted male parent. Then, with an impish smile, he added that his pollination technique could not have been that bad and that there must be a process operating that affected the relative transmission of the two alleles. He was also known to ask, "What famous government building now stands on the field in which preferential segregation was discovered?" Rhoades was an employee of the USDA at the time and his experimental fields were in Arlington. These plots were later abandoned by the USDA and have since become the site of the Pentagon.

In the hybrid mentioned above, Ab10 was carrying the recessive allele of *r*, and the normal chromosome 10 had the dominant allele. A testcross to the recessive *r* tester line produced an excess of colorless kernels in a 70:30 ratio instead of the expected 50:50 ratio. The altered ratio occurred on the heterozygous ears, but not when the plants were used as a pollen parent. When Rhoades swapped the *R* alleles so that the dominant marker was linked to Ab10, the majority of kernels were colored. In maize, as in most plants, megasporogenesis produces four cells, but three degenerate and do not develop into ovules. The basal megaspore differentiates into the megagametophyte via a few mitoses to produce the egg, polar nuclei, and associated cells. It was concluded that Ab10 must find its way into the basal megaspore more often than at random. A cytological examination of anaphase in the male flowers of plants with Ab10 (Rhoades and Vilkomerson 1942; Rhoades 1952) showed that parts of the chromosomes other than the centromere proceeded to the poles ahead of the normal spindle attachment sites. Heterochromatic knobs, of which the one on Ab10 is the largest, were good candidates for the regions responsible for this behavior.

Albert Longley (1945) tested this proposition using different lines of maize that varied in the position or size of these knobs. Longley had characterized the cytology of many accessions and had a ready knowledge of the appropriate stocks to use. He found that preferential segregation occurred for the knobbed homolog for every one tested, but only in the presence of a copy of Ab10. Thus, any site on a chromosome that has a knob where there is none on the homolog [or a larger version than on the homolog (Kikudome 1959)] will be preferentially segregated to the basal megaspore in the presence of Ab10. As a result, knobs would continue to be selected for greater size when Ab10 is part of the genome.

Rhoades's 1942 article on preferential segregation is an interesting study in objective detachment leading to a logical conclusion. He systematically covers the data that falsify one trivial explanation after another in an asymptotic approach to the conclusion of altered segregation. He even hung plants upside down in the greenhouse to see if the extra chromatin on Ab10 made it heavier and thus more prone to be present in the basal megaspore (there was no effect). There is a tone of disbelief throughout the article, but having disproved the alternatives, he concluded that preferential segregation must be occurring.

The receipt date on the preferential segregation article is listed as December 25, 1941. In 1940 Rhoades had accepted a position in the Department of Botany at Columbia University in New York City. One wonders how an article could possibly be received on Christmas Day? The answer lies in the fact that Rhoades was the Managing Editor of Genetics at the time. The completed manuscript and its submission were apparently a gift to himself.

Interestingly, the tone of disbelief in his 1942 article continues even to the Rhoades and Dempsey (1966) article on the topic. One source of concern to Rhoades came from studies of inversion heterozygotes conducted with his long-time research associate Ellen Dempsey (Rhoades and Dempsey 1953). Rhoades had studied Drosophila for a year at Caltech (1929–1930) during his graduate student years under the guidance of Alfred Sturtevant and Theodosius Dobzhansky. He therefore had an appreciation for Drosophila genetics and grasped the implications of the fact that paracentric inversion heterozygotes in Drosophila show little sterility. The basis of this phenomenon is thought to be that the bridge formed by recombination within the inversion loop orients the tetrad of chromatids so that the intact noncrossover chromatid remains in the egg and the abnormal crossover chromatids go to the polar bodies (Sturtevant and Beadle 1936). Rhoades and Dempsey conducted extensive work on inversion heterozygotes in maize and found that a similar orientation of chromatids does not occur. Bridge formation results in broken chromatids that can become included in the basal megaspore at frequencies predicted from random distribution. This dichotomy of results, in that there is an apparent orientation with Ab10 but none with inversion heterozygotes, appeared to plague Rhoades's thinking on the interpretation for many years. Subsequent studies of megasporogenesis in Ab10 material clearly showed that preferential segregation results from an orientation of knobbed chromatids toward the outer poles of female meiosis (I. Golubovskaya, personal communication).

Many of Rhoades and Dempsey's later studies on Ab10 were included as notes in the Maize Genetics Cooperation Newsletter under some version of the title "Further studies on preferential segregation," describing work conducted during his tenure at the University of Illinois

FIGURE 3.—The maize genetics group at Illinois (early 1950s). Front row: Marcus Rhoades, Dwayne Richardson, Mei Lin, S. H. Tulpule. Back row: Ellen Dempsey, John Laughnan, George Ziska, Edward H. Coe. When Rhoades moved to the University of Illinois from Columbia University in 1948, Laughnan was also recruited to the Illinois faculty from Princeton. Dempsey was a research associate with Rhoades. Richardson, Lin, and Tulpule received Ph.D.'s under the direction of Rhoades. Coe was a graduate student with Laughnan. Both Rhoades and Coe were later named recipients of the Thomas Hunt Morgan award from the Genetics Society of America for lifetime contributions to genetics. (Photo courtesy of Susan Gabay-Laughnan.)

(1948–1958; Figure 3) and at Indiana University (1958–1974; Figure 4). Rhoades served two terms as the editor of the newsletter, from 1932 to 1935 and again from 1956 to 1974. Ellen Dempsey played a pivotal role in the assembly of the newsletter during the latter period. An offhand comment in Rhoades's presence about a "little" note in the newsletter was met with the friendly retort that "for Miss Dempsey, the Newsletter is a *big* publication," no doubt in honor of her substantial contributions to its yearly production. Rhoades also served on several editorial boards (DEMPSEY 1973, 1983, 1994). As noted above, he was Managing Editor of GENETICS from 1940 until 1948, but continued with service on the editorial board and as an active reviewer of manuscripts until 1966. He served a term as the president of the Genetics Society of America (1943) and of the American Genetics Association (1950–1953). Among the many honors he received, Rhoades shared the first Thomas Hunt Morgan award from the Genetics Society of America in 1981 with Barbara McClintock.

In his many service activities, Rhoades no doubt made a tremendous impact on the field of genetics. Many wished for his approbation. An attendee at the annual maize genetics meeting once commented, "Rhoades sits in the front row and passes judgment on all the talks." A more accurate interpretation is that Rhoades had a voracious appetite for maize genetics and high standards as an experimentalist. Rhoades was the perfect gentleman and would break up any heated scientific discussion by commenting, "This is good clean fun, but . . . ." At his last presentation at the maize meetings in 1987 at the age of 83, Rhoades talked on preferential segregation. In his conclusion, he said: "I know this may seem old fashioned to some of you, but it's the kind of thing that keeps an old maize geneticist like me going."

Preferential segregation, segregation distortion, and meiotic drive: Seventeen years after Rhoades defined preferential segregation, SANDLER *et al.* (1959) described an apparently analogous phenomenon in Drosophila caused by a locus they named *Segregation distorter* or *Sd* (see GANETZKY 1999). These authors cited RHOADES (1942) but did not use his terminology (preferential segregation), introducing instead the phrase *segregation distortion.* Their phrase has largely replaced Rhoades's in the literature, as revealed by a database search of several journals that found 234 articles using "segregation distortion," but only 22 using "preferential segregation."

The phenomenon of meiotic drive refers to the situation in which one member of a pair of homologs is preferentially recovered in the progeny of a heterozygote. Such a situation will dramatically alter allele frequencies in a population, thereby affecting the evolution of the genome and the species by means independent of allele fitness. SANDLER and NOVITSKI (1957), who first defined meiotic drive (see CROW 1988), cite Rhoades's work on Ab10 as one example. They drew the distinction between gametic selection (the superiority of gametes carrying the favored allele) and meiotic drive, which depends on the manner of meiotic division. At that time, *Sd* became the favorite model system for the study of meiotic drive, but then it was learned that heterozygous *Sd* males have a normal meiosis, and *Sd* better fits the definition of gametic selection (PEACOCK and ERICKSON

Figure 4.—Attired in pollination regalia, Marcus Rhoades works in the maize nursery at Indiana University. (Photo courtesy of Ellen Dempsey.)

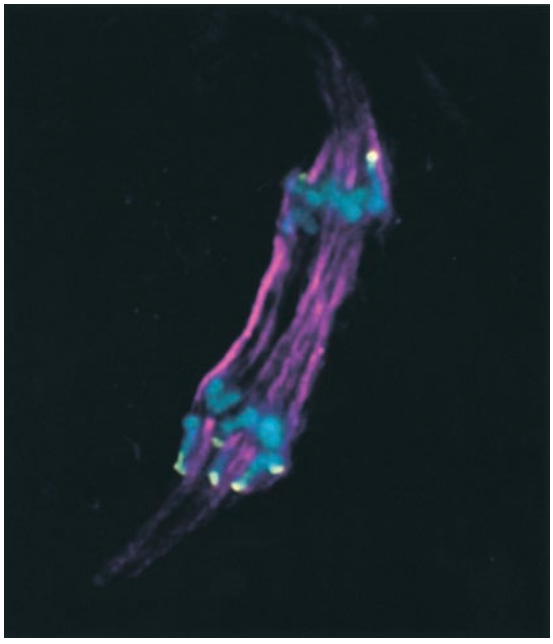

Figure 5.—Neocentromere activity at anaphase II. Neocentromeres (yellow, labeled with the 180-bp repeat) pull chromosome arms (blue) poleward by interacting laterally with spindle fibers (purple). (Photo by Hong-Gu Yu and R.K.D.)

1965). This revelation required that the definition of meiotic drive be enlarged to include defects in gamete production. The case of Ab10, which was discovered first, remains true to the original definition.

Ab10 and preferential segregation today: Maize knobs were among the first loci to draw the attention of plant molecular biologists. The laboratory of Jim Peacock in Canberra, Australia, cloned a 180-bp repeat that is present in most knobs and especially on Ab10 (Peacock *et al.* 1981). These cytological features were found to be composed of small repeats that are present thousands of times at any one site. Rhoades spent two sabbaticals in the Peacock lab and was pleased to learn the molecular nature of the heterochromatin of Ab10 and the knobs. However, correspondence to R.K.D. from Rhoades and Dempsey in early 1991 clearly indicated a concern that no one would continue working on their favorite chromosome. They need not have worried; the number of articles on Ab10 and references to their work on preferential segregation have only increased in the last decade.

Rhoades viewed neocentromeres as a form of centromere and was particularly interested in how they move on the spindle (Rhoades 1952). In recent years, fluorescence microscopy has highlighted a variety of new and interesting details about the mechanism of neocentromere motility in maize. Time-lapse 3D microscopy demonstrated that neocentromeres are active throughout prometaphase, metaphase, and anaphase and that their rates of movement can be as much as 50% faster than normal chromosome movement. Observations of cells triply stained for chromosomes, tubulin, and the 180-bp repeat revealed that neocentromeres interact with kinetochore fibers laterally, instead of end-on as is typical of true centromeres (Yu *et al.* 1997) (see Figure 5). This novel interaction with microtubules is probably responsible in part for their accelerated rates of movement. Major structural and regulatory components of the kinetochore, such as centromere protein C (CENP C) and mitotic arrest-deficient 2 (MAD2), do not localize to neocentromeres, suggesting that they are minimal centromeres specialized for poleward movement (Dawe *et al.* 1999; Yu and Dawe 2000). Neocentromere-like phenomena have been extensively studied in other organisms as well. In humans, neocentromeres have proven to be very similar to true centromeres and have provided an important framework for interpreting the structure and function of centromeric DNA (Choo 2001). The term neocentromere, once relegated to cytogenetics textbooks, has gained widespread acceptance.

Rhoades and his students also took a strong interest in dissecting the various functions associated with Ab10, using deficiencies affecting the size of the knob (Emmerling 1959; Kikudome 1961; Miles 1970; Rhoades and Dempsey 1985, 1986, 1988, 1989), and many were ana-

lyzed with respect to their effects on meiotic drive, neocentromere activity, and another unusual property of Ab10—its capacity to increase recombination throughout the genome. A variety of new deficiencies have been identified in the last decade, as well as at least two mutations, which abolish meiotic drive but have no discernible cytological abnormalities (Dawe and Cande 1996; Hiatt and Dawe, 2003a,b). Taken together, the data suggest that at least four different loci are required for meiotic drive, two more than originally envisioned by Rhoades (Hiatt and Dawe 2003b).

A surprising discovery from recent deficiency studies was the demonstration that there are two independent neocentromere "systems" on Ab10 (Hiatt *et al.* 2002). Previous data had shown that a second repeat, known as TR-1, coexists with the 180-bp sequence in many knobs (Ananiev *et al.* 1998). Hiatt and colleagues used *in situ* hybridization to show that three novel chromomeres on Ab10 are composed in large measure by this 350-bp TR-1 repeat. Remarkably, the TR-1 repeats have even more pronounced neocentromeric activity than the 180-bp clusters and often extend well ahead of the knobs in thin threads that appear to run alongside the microtubules. Using deficiencies generated by Rhoades and Dempsey (1985), the authors demonstrated that TR-1 repeats are sufficient to move knobs poleward, that a gene(s) required for TR-1-mediated neocentromere activity maps to a proximal portion of Ab10, and that a gene(s) required for 180-bp neocentromere activity maps to a more distal site (Hiatt *et al.* 2002). These data suggest that the interaction between neocentromeres and the spindle is sequence specific, rather than simply an outcome of the repetitive nature of the DNA in knobs.

Ab10 has also piqued the interest of evolutionary biologists. As an example of meiotic drive, one must wonder why Ab10 and the knobs it affects have not been swept to fixation in maize and teosinte populations. Despite being under meiotic drive, Ab10 has an average frequency of only 14% in those teosinte populations in which it occurs, and the knobs remain similarly polymorphic in the presence of Ab10. Buckler *et al.* (1999) modeled the dynamics of Ab10 and knob frequencies in teosinte populations. Their analyses confirm Rhoades's inference (1942) that Ab10 has a deleterious male gametic effect, allowing an evolutionarily stable polymorphism as a balance between meiotic drive and gametic selection. Their analyses also imply that knobs arose in response to meiotic drive imposed by Ab10 and, remarkably, that knob size, frequency, and chromosomal position are all effects of Ab10. Rhoades might have enjoyed the thought that Ab10 was a major force in the evolution and structure of the maize genome.

Another recent development is a meiotic-drive-based model for the rapid evolution of centromeric repeats (Henikoff *et al.* 2001). According to this model, there is an "arms race" between selfish centromeres competing for access to the reproductive cells (by interacting more efficiently with the kinetochore) and a variant of histone 3 (CenH3) that associates with the centromeric DNA. CenH3 appears to be a critical molecule in determining the site of the kinetochore on the chromosome. CenH3 is postulated to adapt rapidly to weaker centromeres, imparting equality to opposing centromeres and restoring organismal fitness. The ideas in this model are based in many ways on the mechanism of meiotic drive in maize as worked out by Rhoades.

No hypothesis could have predicted the behavior of abnormal chromosome 10 and the phenomenon of preferential segregation/meiotic drive. It required a mind open to the unusual, a strict adherence to the facts over dogma, and, once discovered, rigorous hypothesis testing to define the details. For Rhoades, the framework of facts became the model. Much remains to be learned about what makes a centromere, a neocentromere, and the role of meiotic drive in shaping the genome. The answers to these questions will be found by emulating Rhoades's spirit of discovery, his dogged persistence, and his intellectual honesty and by heeding his advice to "Just get in the lab and start to work."

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