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CHARLES MADERA RICK
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A Biographical Memoir by

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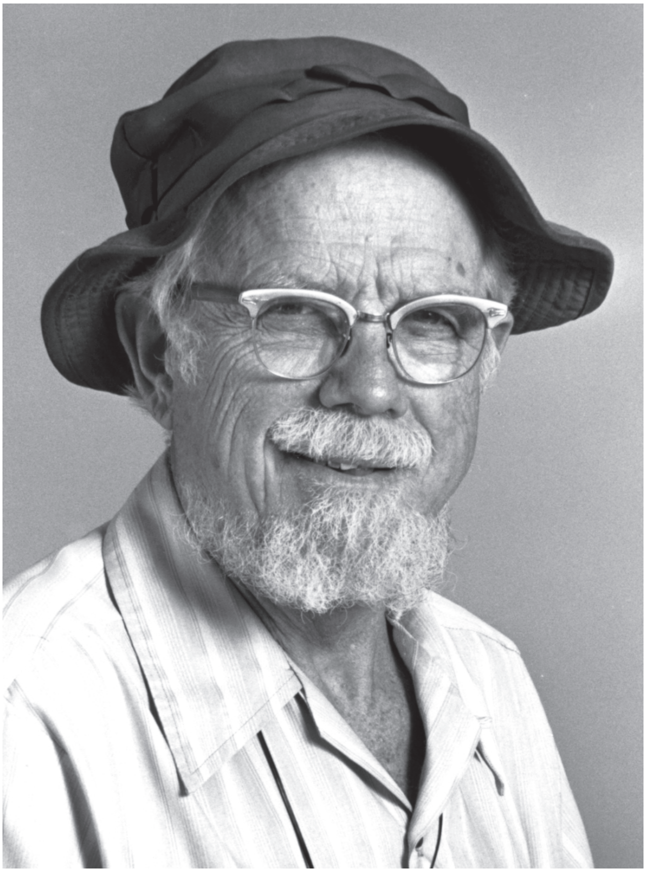

CHARLES MADERA RICK

April 30, 1915–May 5, 2002

BY STEVEN D. TANKSLEY AND GURDEV S. KHUSH

TO CALL CHARLES M. RICK the father of tomato genetics would not be an exaggeration. In the 1940s Rick began a series of studies that transformed tomato from a mere garden vegetable to a model organism. He was adept with the tools of reductionism (e.g., cytology, mutagenesis, biochemical genetics), yet he never succumbed to the reductionist's view of life. Rather, he synthesized all his observations and research into an integrated view of tomato biology, evolution, and biodiversity. Using this comprehensive approach he developed the biology not only of cultivated tomato but also the entire tomato genus, *Lycopersicon*. He was a naturalist and adventurer, once aptly described as Charles Darwin and Indiana Jones rolled into one. Rick traveled extensively throughout the Andean region of western South America collecting the wild relatives of tomato. The result was the development of an invaluable germplasm collection now housed at the C. M. Rick Genetics Resource Center at the University of California at Davis. This collection has become the cornerstone of tomato breeding and genetics and is the source of most of the major disease resistance genes that now characterize modern tomato cultivars. His legacy also includes many seminal papers on topics ranging from the evolution of mating systems to deletion mapping in tomato and a host of scientific protégés (offspring), including the two authors of this tribute, who were influenced by his evolutionary approach to plant genetics and infused with his enthusiasm for biological inquiry and the wonders of the natural world.

THE BEGINNINGS

Charles (or Charley as he was affectionately known) was born in 1915 in Reading, Pennsylvania. He grew up working in his father's peach orchards, and as an active member of the Boy Scouts he engaged in many outdoor activities. These early experiences were to shape Charley's life as a lover of nature, especially plants. Rick began his academic career at Pennsylvania State University, majoring in horticulture and received a bachelor's degree in 1937. It was at Penn State that Charley met and married Martha Overholts, who was to be his life partner and frequent companion on his many expeditions to the Andes and South America. From Penn State Charley matriculated at Harvard University and found a niche working under the advice of professors Karl Sax and M. M. East, pillars in the burgeoning field of cytogenetics and quantitative genetics. Surrounded by Harvard's Arnold Arboretum and embedded in the labs of Sax and East, Charley began to forge the marriage between natural variation and genetics—a theme that would more than anything else characterize the rest of his career.

TOMATO GENETICS—THE EARLY DAYS

Rick received his Ph.D. from Harvard in 1940, just as the United States was beginning to mobilize for war. Finding a limited demand for plant cytogeneticists at this time, Rick took an appointment in the Division of Truck Crops at the University of California at Davis, which had earlier served as the agricultural research station for the University of California at Berkeley. Rick later acknowledged that he was uncertain about the future of a basic plant geneticist in an agricultural setting. Nonetheless he busied himself in exploring a variety of topics including documenting the genetic changes induced by X ray in pollen of *Tradescantia* and the origin of polyembryony in asparagus. It wasn't until a stroll through a nearby tomato field with John MacGillivray, a fellow professor in the department, that Rick fell in love with tomatoes. During this walk MacGillivray intimated to Rick that while pollen irradiation might be of academic interest to some, of greater practical interest was why there were "bull" tomatoes and couldn't Rick "do something about them"? For those readers who are not so familiar with tomato lingo, "bull tomatoes" is not a derogatory term but rather refers to plants that are very large and typically barren of fruit. They occur at a relatively low but consistent frequency in tomato fields. Bull plants produce no useful fruit and because of their large size, they shade adjacent plants. How the skills of a cytogeneticist were relevant to unruly tomato plants was not at all clear to Rick, but he dutifully took on the project. To his surprise he discovered that a large proportion of these unusual plants were spontaneous triploids, hence explaining their reduced fertility. More importantly, these spontaneous triploids provided a ready source of trisomic plants (plants with a single extra chromosome). This eventually led to a comprehensive description of all 12 primary trisomics, which became the cornerstone of tomato cytogenetics and linkage mapping (see next section).

In 1948 Rick began a series of expeditions to South America to seek out the wild relatives of the cultivated tomato. He was a keen observer, and during these seed-collecting trips he took extensive notes on many aspects of population biology (including observations of pollination systems and insect vectors) and geographical and environmental features of the habitats in which the plants were found. He made careful preparations of herbarium specimens and kept notes on each plant in the wild populations from which seed was individually harvested and catalogued. As a result these collections became not only a source of novel germplasm for tomato breeders and geneticists but also provided the basis for subsequent systematic and population biology studies of species and races from the tomato genus, *Lycopersicon,* and its sister genus, *Solanum.* Working with these materials, Rick and colleagues were able to establish the systematic relationships of thousands of wild tomato populations and to group them into species clusters and geographical and compatibility races.

CYTOGENETICS TOUR DE FORCE

From the 1950s through the 1970s Rick was heavily involved with cytogenetic studies of the tomato genome. The beginning of this period can be traced to collaboration with D. W. Barton, a graduate student in the laboratory of S. W. Brown at the University of California at Berkeley. Brown had shown that all the individual chromosome bivalents of tomato could be identified at the pachytene stage of meiosis. He numbered the chromosomes in decreasing order of length. Working together, Rick and Barton applied pachytene analysis to identify the extra chromosome in each of the primary trisomics of tomato. Rick then used these trisomic stocks to associate mutant genes with specific chromosomes by virtue of their modified segregation ratios. In this way 10 of the 12 tomato chromosomes were associated with specific genetic linkage groups represented by mutants; however, a persistent puzzle was that no genes could be assigned to chromosomes 11 or 12.

It was in hopes of solving the chromosome 11 and 12 mystery that Rick invited one of us (G.S.K.) to join his group in the early 1960s for a six-month postdoctoral study. That short-term study eventually turned into a highly productive and very gratifying seven-year stay. In an effort to assign markers to chromosomes 11 and 12 we employed a pollen irradiation technique. Irradiated pollen from wild type plants was used to fertilize genetic stocks homozygous for mutant loci that had hitherto not been assigned to the other 10 chromosomes. Mutant progeny (ostensibly hemizygous for the mutant loci) were selected from these crosses and subjected to pachytene analysis for possible chromosomal deletions. When stocks containing the *a-hl* mutant loci were examined in this manner, we were able to definitively assign them to chromosome 11 by virtue of their association with detectable deletions on this chromosome. (It turned out that the original chromosome 11 trisomic stock was actually a tertiary trisomic involving chromosomes 7 and 10, which explained the original difficulty in assigning genes to this chromosome.) In a similar way we eventually assigned two markers (*alb* and *fd)* to chromosome 12, completing the tomato genetic-linkage map.

These pollen irradiation experiments became a primary source of new stocks for Rick's burgeoning cytogenetics endeavors. Amongst the progenies sired by the irradiated pollen were plant lines with a variety of novel phenotypes. Cytological examination of these stocks revealed three classes of mutant that proved especially interesting: (1) tertiary monosomics in which the short arms of two chromosomes are missing and the long arms of those same chromosomes are fused at the centromere; (2) monoisodisomics, which carry a normal chromosome inherited from female parent but an isochromosome from the male parent; and (3) arm deficiencies, which lack an entire short arm of one chromosome. These stocks in turn gave rise to other cytogenetics stocks (e.g., telotrisomics, secondary trisomics, and tertiary trisomics). Together these lines proved extremely useful for genetic studies. It was during this intense cytogenetic period of Rick's career that he and his students and postdocs used these stocks to pinpoint the physical position of 129 loci, to orient each linkage group with respect to chromosomal orientation, and to localize all of the centromeres of the tomato genome. As a result of these studies tomato became the first dicot in which the genetic linkage map was integrated with the pachytene physical map and thus a model organism for genetics. This integrated genetic-physical map of the tomato genome still guides geneticists and molecular biologists today.

EVOLUTIONARY AND POPULATION GENETIC STUDIES

Rick had a lifelong interest in plant evolution and systematics that was nurtured by the intellectual environment of UC Davis, which boasted many prominent evolutionists. Upon return from his first collecting expedition to South America, Rick embarked on a series of studies aimed at unraveling the systematics of wild tomato species, mapping out the distribution of genetic variation, and determining the biological and geographic factors responsible for these attributes. Rick was both comprehensive and multi-pronged in his approach, using geographic, morphological, cytogenetic, sexual cross-compatibility, and in latter years molecular data to draw inferences. He recognized the importance of mating systems in determining the structure and extent of genetic variation in both wild and cultivated populations of tomato. While a number of wild tomatoes are obligate outcrossers owing to gametophytic self-incompatibility, others, including the cultivated tomato, are facultative outcrossers. Rick discovered that the dominant characteristic determining the degree of cross-fertilization (outcrossing) in these species is the degree to which the stigma surface is exerted beyond the anther cone. He further showed that this method of outcrossing was because of a co-evolution of floral structure and insect vectors found in the native habitats of the wild species.

Rick was in his late fifties when molecular and biochemical genetics were born. Nonetheless he was quick to incorporate molecular techniques in both his evolutionary and genetics research. He used isozymes to quantify and study genetic variation both within and between populations of each wild tomato species. The set of treatises produced during this period (1970s and early 1980s) is now the definitive source of taxonomy and genetic variation for species in the tomato genus. He and his students, including one of the authors of this memoir (S.D.T.), determined the inheritance of and genetically mapped virtually all the isozyme determinates used in these systematics studies. This resulted in the first molecular linkage map and was the predecessor of the DNA linkage maps that are so commonly used in plant genetic, molecular, and breeding studies today. Rick was also one of the first people to recognize the potential of molecular breeding. During one of the systematic studies of genetic variation in cultivated tomato accessions Rick discovered highly significant linkage disequilibrium between a rare isozyme allele and resistance to nematodes. He went on to show that the nematode resistance gene was tightly linked to the isozyme gene and that breeders had introduced the rare allele together with the resistance gene from a wild species. He correctly reasoned that the rare isozyme allele would provide a faster and more accurate screen for resistance than nematode inoculations. This particular assay is still in use by many tomato breeders and was the first example of marker-assisted breeding in plants, which is now the foundation of most crop improvements.

WILD SPECIES AND PLANT BREEDING

While Rick conducted basic studies on the systematics and evolution of the tomato genus, he always had an eye toward the agricultural applications of such research. He was a strong proponent of the use of wild germplasm as a source of novel genes for crop plant improvement. This was somewhat of a radical view as, even today, many plant breeders view wild germplasm as a last resort. As early as 1953 Rick showed that crosses between wild species and their cultivated relatives could reveal novel genetic variation of potential use in agriculture. He promoted the use of geographic and environmental factors as predictors of which wild accessions might contain useful traits. Working with accessions of *L. cheesmanii,* a species endemic to the Galapagos Islands, he discovered a non-abscising pedicel trait and showed that the underlying gene could be transferred to cultivated tomatoes. The result was tomatoes from which the pedicels and calyxes could be easily removed for mechanical harvesting. This trait is now widely used by modern tomato breeders. The list of useful genes that have been transferred from the wild species accessions that Rick collected, studied, maintained, and freely distributed would be much too long to include in this memoir; their impact on tomato breeding has been immeasurable.

Rick also introduced a technique that has had an incredible influence on plant genetics. In the 1970s he began a set of experiments in which he would exchange single chromosomes from a wild species into a cultivated tomato line by backcrossing. This work was made possible by the genetic linkage map that Rick and his colleagues had created. These “introgression lines” could then be used to study the effects of defined segments of wild-species DNA in otherwise isogenic backgrounds. While this work was limited by the resolution of genetic maps available at that time, the concept has proven to be powerful and has been exploited to enormous effect in tomato genetics and molecular biology—most notably by D. Zamir at the Hebrew University in Israel, whose studies are now a model for both plant and animals.

MENTOR, FRIEND, AND STORYTELLER

Charley Rick was advisor to more than 40 students and postdocs, most of whom have gone on to notable careers at major universities and institutions in the United States and several foreign countries. His style of mentoring was largely by example. His enthusiasm for and dedication to his research were contagious. His days started early, by 7:00 a.m. each day, with a bike trip to the office, where he could still be heard typing into the still of the night. Weekends were no exception, excluding time out for gardening, hiking, or weekend trips to his cabin at Bodega Bay. But for Charley this was not work, it was a way of life and a love for the tomato and all that it could reveal.

Rick had an encyclopedic memory and could recall details of almost everything he had read or experienced. A nature walk with Charley would open up your senses and awareness to everything around you, making you wonder how you could have ever missed those things that he so readily saw. He was also a fantastic storyteller: the Mark Twain of plant genetics. Fueled by a lifetime of expeditions and adventures, a wry wit, and an eloquence that is rare among scientists, Charley could keep an audience spellbound. Regardless of the topic he had a knack for taking the ordinary and making it extraordinary and could find the humor in almost every passing moment in life. He was an icon on the UC Davis campus, easily identified by his trademark khaki fishing hat that seldom left his head regardless of whether he was pollinating tomatoes or addressing a group of dignitaries.

Charley was a friend to so many people in so many walks of life. Though his relationship with each person was undoubtedly different, he had a way of making everyone feel special and directly connected to his energy and vitality. He was an avid supporter of the National Academy of Sciences, faithful in attending the annual meeting even when traveling became a physical difficulty, and he gave generously to the Academy to assure its future viability. While Charley's passing was a great loss to the Academy and the plant genetics community, a bit of his spirit is carried by all who had the good fortune of meeting this extraordinary individual.

Charles Rick is survived by his son, John, an eminent archaeologist and a professor at Stanford University; his daughter, Susan Baldi, a professor in both the Life Science and Health Science departments at Santa Rosa Junior College; two grandsons; one granddaughter; and one great-grandson.

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