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STERLING HOWARD EMERSON

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A Biographical Memoir by

JOHN R. S. FINCHAM

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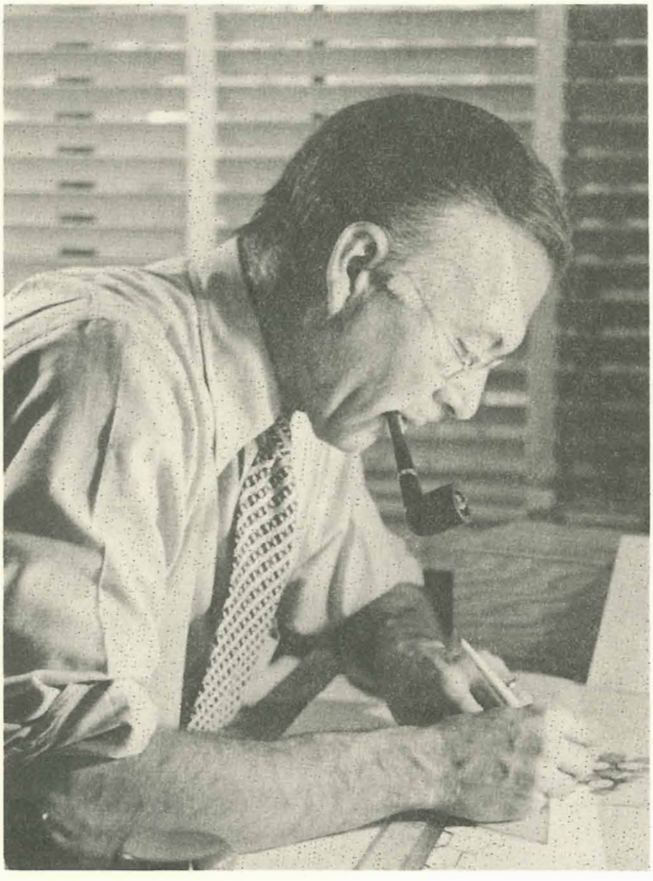

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Sterling Emerson

STERLING HOWARD EMERSON

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BY JOHN R. S. FINCHAM

STERLING EMERSON was born in Lincoln, Nebraska, the son of R. A. Emerson, the main pioneer of corn genetics. In 1914 his father was appointed head of the Department of Plant Breeding at Cornell, and the family moved to Ithaca. Sterling himself graduated from Cornell University in 1922. The same year saw his first scientific publication, a long paper in *Genetics* under the names of R. A. and S. H. Emerson on the genetic relationships of andromonoecious mutants in maize. Following graduation he undertook postgraduate work in the field of plant cytology in the University of Michigan under the supervision of Bartlett. He obtained a fellowship to work between 1925 and 1926 in Scandinavia, first in Lund and then Copenhagen. This visit was not as fruitful as it should have been because he had the misfortune to contract tuberculosis and had to go to a Swiss clinic to recover. But he was able to spend at least some time in the laboratory of O. Winge, later to become the main pioneer of yeast genetics.

Sterling's postgraduate work at Michigan was on the genus *Oenothera,* and his earlier papers contributed to the understanding of the *Oenothera* system of balanced segmental interchanges and its genetic consequences. This line of

work gave scope for his talent for solving logical puzzles as well as to his skill as a microscopitst. In 1928, the same year he obtained his Ph.D., he was appointed to an assistant professorship in genetics under T. H. Morgan at the California Institute of Technology, where except for two sabbatical years and a secondment, he remained throughout his career.

During his long period at Caltech, Sterling's interests extended into several distinct areas of genetics. He continued work on *Oenothera* until 1941 and, around 1937, started an investigation of the self-incompatibility system of *Oenothera organensis,* a plant that existed in the wild only in a few locations in the Organ Mountains of New Mexico. He worked out the genetic basis of the pollen-style reaction and showed that it conformed to the *Nicotiana* one locus–multiple allele gametophytic system. He developed the method for observing the growth of individual pollen tubes down styles and was thus able to distinguish the 50 percent pollen function characteristic of crosses between plants with one allele in common. By skillful grafting experiments he was able to show that pollen rejection was an autonomous function of the style. The culmination of this work was a population survey that led to a fairly complete description of the number, distribution, and spread of the self-incompatibility alleles within the small population. This was one of the classic analyses of a plant outbreeding system—a system that unhappily now exists only in the archives, since *O. organensis* is probably extinct in its natural habitat.

After G. W. Beadle moved to Caltech from Stanford to take up the chairmanship of the Biology Division, Sterling Emerson joined enthusiastically in the new work on the biochemical genetics of *Neurospora crassa.* He was attracted

by the elegance of the genetic system as well as by the prospect of finding out more about how genes work. In particular, he became fascinated with the complexity of metabolic pathways and the explanation that they gave of how genes could interact. He always loved making elegant diagrams, and the *Cold Spring Harbor Symposium* volume of 1950 contained one of his more ambitious efforts, presenting a synoptic view of competitive reactions and antagonisms in amino acid biosynthesis as revealed by studies of mutants. His own contribution in this area had a characteristically genetical angle. In collaboration with Marko Zalokar, he had discovered a mutant that was not only resistant to sulfanilamide but even required the drug for growth. He found that certain revertants were heterocaryons with a proportion of the nuclei carrying a mutation that blocked the biosynethesis of *p*-aminobenzoic acid. The explanation was that the original mutant required sulfanilamide in order to counteract *p*-aminobenzoate acid, to which it was hypersensitive, and that the new mutation suppressed the phenotype simply by reducing *p*-aminobenzoate to a nontoxic level. This suggested a new and delightfully simple explanation for the classical genetical phenomenon of heterosis, which had hitherto been explained as due to complementary action, either of different genes or of different alleles of the same gene (overdominance). The *Neurospora* example demonstrated the possibility of heterosis resulting from combinations of alleles that were not complementary in action but merely additive, the average of the activities of two different alleles being just what the situation demanded.

Another of Sterling Emerson's interests in *Neurospora* can be seen as an extension of his early interest in cytology. For several years, in collaboration with his wife, Mary, he

experimented with ways of obtaining viable protoplasts from mycelium. Their best success was with a morphological osmotically sensitive mutant (*os*), which, through a process of selective breeding, eventually yielded a stable plasmodial strain called "slime." This strain, totally unrecognizable as the derivative of a filamentous fungus, turned out to carry two other mutations as well as *os*. It has never been easy to recover anew from crosses but it can nevertheless be maintained vegetatively and has been used in a number of laboratories for a variety of experimental purposes. Sterling himself used it to study mitotic nuclear division under the microscope *in vivo*. Meiosis and the immediate postmeiotic mitotic divisions in the *Neurospora ascus* had been described and photographed by Jesse Singleton and Barbara McClintock, but vegetative nuclear division had always been very obscure. The live plasmodium, however, could be prepared for microscopy as a very thin layer and, with the oil immersion lens and phase contrast, nuclei could then be seen dividing with unprecedented clarity. Chromosomes appeared only as dots appearing fleetingly on the spindle, but the behavior of the nucleolus and the nuclear membrane was particularly clear. Sterling took his microscope kit and slime culture to the first Neurospora Information Conference, held in La Jolla in 1958, and demonstrated the system to an admiring audience. Unfortunately, a proper photographic record was difficult to obtain, and no publication ever emerged from this highly original work.

Undoubtedly, Sterling Emerson's most constant scientific interest throughout his career was in genetic recombination. This interest was fostered by his early work on the *Oenothera* balanced translocation system and it took a new turn in 1933–35 with his collaboration with G. W. Beadle (then in his first Caltech phase) on the analysis of cross-

over relationships in *Drosophila* using attached-X chromosomes. Emerson and Beadle were able to show that each cross-over between chromosomes at the first division of meiosis could, with equal likelihood, involve either one of the two chromatids into which each chromosome was divided. The particular advantage of attached-X chromosomes was that they permitted the recovery together of two of the four X chromosomes emerging from a single oocyte meiosis. This half-tetrad analysis, however, was still second-best to whole tetrad analysis, which was achievable in *Neurospora* and other Ascomycete fungi.

Fungal tetrad analysis fascinated Emerson for most of the rest of his life. His contributions in the area were both theoretical and practical. He became the author of a number of definitive reviews of the use of fungi for formal genetics, with special emphasis on the analysis of crossing-over. He was naturally extremely interested in the early reports by C. C. and G. Lindegren on gene conversion in yeast meiotic tetrads, and was initially very skeptical about them. His thorough understanding of the possibilities of aberrant chromosome behavior enabled him to suggest a number of alternative explanations that, in his view, had to be rigorously ruled out before one could admit exceptions to Mendel's First Law. However, as the further evidence accumulated during the 1950s, not only from yeast but from *Neurospora* and other fungi as well, Emerson incorporated gene conversion into his own thinking about recombination mechanisms. Taking up the heteroduplex/mismatch correction model of Robin Holliday, he was the first to attempt an algebraic formulation that would predict the frequencies of different patterns of conversion and crossing-over in terms of heteroduplex formation and correction parameters. He was probably the first to point out

that, on the Holliday model, the correction frequencies on the two participating chromatids need not necessarily be the same, and his analysis of the available data indicated that in general they were not the same. Unfortunately, this left the formula with as many parameters as observable quantities, but it nevertheless served as a useful framework for thinking for a decade or more.

When approaching retirement, Sterling Emerson decided that it was time for him to make his own contribution to the fungal recombination data. He decided on the Ascomycete species *Ascobolus immersus*, which had the great advantage of providing spore color markers that could be scored visually in the meiotic tetrad (actually an octad, with a further mitotic division affording the opportunity of detecting postmeiotic segregation). A French strain of the species had already been extensively investigated in the University of Paris at Orsay, but Sterling isolated his own strain from the environs of Pasadena. The Pasadena strain turned out to have markedly higher conversion frequencies than the French, but with considerable variation in this respect. In collaboration with Clare Yu-Sun and Bernard Lamb (a visitor from England), some of this variation was identified as due to differences in *cis*-acting conversion-promoting sequences, closely linked to the segregating markers. These studies, now carried considerably further by Lamb, are still highly relevant to the whole question of how meiotic recombination is initiated, and foreshadowed current research that has just recently penetrated to the molecular level.

Throughout his research career, Sterling Emerson did what interested him, and his interests were, by modern standards, exceptionally broad. He combined the skills of the analytical geneticist and chromosome cytologist with a

naturalist's knowledge of plants and animals. He acquired an excellent knowledge of biochemistry and, for a time, became quite deeply involved in immunology. His excursion into the latter area resulted in only one publication, and that one fell by the wayside. It is nevertheless worth recalling as an example of his bold thinking. In the early 1940s biochemical genetics was getting under way, and, while there was no clear idea about the nature of the gene or of how it replicated itself, there was speculation about template models for gene replication and expression. Emerson, following an idea of A. H. Sturtevant, thought it possible that a protein might mirror the unique surface shape of the gene that specified it, and hence that an antibody formed against the protein might also interfere with the replication of the gene. Accordingly, he tried out rabbit anti-*Neurospora* antibodies as mutagens on *Neurospora.* Some mutants were indeed recovered, and they seemed to be sufficiently numerous to be significant. Unfortunately, the evidence never got any stronger. Had nature been ordered differently, that work might have won a Nobel Prize.

Emerson spent only two extended periods away from Caltech after his appointment in 1928. In 1951-52 he spent most of the academic year in Cambridge, England, where he took over the supervision of the graduate student of his friend (a colleague on *Oenothera* expeditions) David Catcheside, who was himself on sabbatical. He is still remembered by those students for his sympathetic help and friendship. He moved in summer 1952 to the Pasteur Institute, Paris, where he worked for a few months in the laboratory of Boris Ephrussi. His other absence from Caltech was a more radical break. Between August 1955 and September 1957 he served a geneticist in the biology branch of the Atomic Energy Commission in Washington. In this capacity he spent much

time assessing applications for funding, and he had to exercise judgment over virtually the whole range of the genetics and molecular biology of the day. Few could have been better prepared for the job or more conscientious about mastering the detail involved. I believe that he enjoyed the broad scientific interest of the post—probably more than he did the Washington environment.

Sterling Emerson lived a simple and unpretentious life. His relaxations were often linked to his work, to which he was always devoted. He liked algebraic problems and playing with numbers. He loved making pictures and diagrams. Some of his early representations of hypothetical DNA structures in recombinations conveyed real insights. A striking painting of a canyon in the Organ Mountains, one of the *Oenothera organensis* sites, hung over his fireplace. His artistic urge also found an outlet in making ornaments, some of them marvels of craftsmanship, out of wood obtained from his garden. He was always ready to relax socially, and liked drinking beer; a very extensive and varied collection of beer cans filled part of his garage. In personality he was dignified, humorous, and considerate. In later years he took great pleasure in his grandchildren. As his son-in-law, I found him an unfailingly helpful and sympathetic friend.

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