Curt Stern on Somatic Crossing Over

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Somatic Crossing Over and Segregation in *Drosophila melanogaster*

Curt Stern

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In the mid-1930s, Curt Stern was investigating why certain *Drosophila* mutants develop mosaic patches with different body bristle phenotypes, when he noticed a recurring pattern. In one particular cross, the offspring sometimes carried areas with one recessive phenotype (yellowish-brownish bristles) immediately adjacent to a sector showing a second recessive phenotype (gnarled bristles, known as singed). As he later described in a 106-page stem-winder in *GENETICS*, Stern had accidentally discovered the first example of somatic crossing over and segregation.

Typically, heterozygotes exhibit the dominant form throughout their somatic cells. Calvin Bridges, however, had found dominant mutations that he thought were causing the loss of the chromosome on which they were carried, exposing the recessive phenotype in a mosaic of the somatic cells. These were Minute mutations, which condition smaller bristles and slower development than normal. Stern repeated Bridges' findings and expanded upon them, investigating possible mechanisms by which the carrier chromosome might be eliminated. However, the real explanation came to Stern by chance. He happened to examine flies with heterozygous X chromosomes carrying recessive yellow body (*y*) on one homolog and recessive singed (*sn*) bristles on the other. As in Bridges' Minute flies, Stern found mosaic spots. But often they were present in twin sectors, yellow adjacent to singed. He concluded that an exchange between homologs must have occurred, followed by the distribution of the like chromatids into the same cells that then gave rise to the homozy-

gous sector in the adult. With this "aha" moment, Stern could explain the Minute results: the recessive sector was now homozygous and not hemizygous. Using other mutations and chromosomal aberrations, Stern further demonstrated that somatic crossing over occurred at the four-strand stage of mitosis; that, unlike in meiosis, no reduction of chromatids occurred; that the distribution of somatic and germinal crossing over were quite distinct; and that, as for meiosis, somatic crossing over in inversion heterozygotes led to defective products.

In later years, the use of Minute heterozygotes to expand the size of homozygous normal sectors became a powerful technique to understand developmental patterns of *Drosophila*. Though somatic crossing over occurs rarely compared to germinal crossing over, it has important consequences. It is one mechanism by which loss of heterozygosity can occur in some cells of an organism and is one way loss-of-function tumor-suppressor alleles may become homozygous and lead to the development of cancer.

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