## Calvin Blackman Bridges (1889-1938)

Calvin Blackman Bridges studied chromosomes and heredity in the US throughout the early twentieth century. Bridges performed research with Thomas Hunt Morgan at Columbia University in New York City, New York, and at the California Institute of Technology in Pasadena, California. Bridges and Morgan studied heredity in Drosophila, the common fruit fly. Throughout the early twentieth century, researchers were gathering evidence that genes, or what Gregor Mendel had called the factors that control heredity, are located on chromosomes. At Columbia, Morgan disputed the theory, but in 1916, Calvin Bridges published evidence that, according to Morgan, did much to convince skeptics of that theory. Bridges also established that specific chromosomes function in determining sex in Drosophila.

Bridges was born on 11 January 1889 in Schuyler Falls, New York, to Charlotte Amelia Blackman and Leonard Victor Bridges. When he was two years old his father died. His mother died the following year. After their deaths, his grandmother Anne Eliza Bridges raised him on her farm near Plattsburgh, New York. As a child, Bridges worked on his grandmother's farm and irregularly attended a small primary school nearby. At the age of fourteen, Bridges' grandmother permitted him to go to school in Plattsburgh. Because of his deficient primary school education, Bridges attended a grammar school for two years before attending Plattsburgh High School. In 1909, Bridges graduated from Plattsburgh High School at the age of twenty. Bridges was an honor roll student and received scholarship offers from Cornell University in Ithaca, New York, and Columbia University in New York, New York.

Bridges accepted the scholarship to Columbia University and began his undergraduate degree in 1909. During his first year at Columbia, he took a biology course taught by Morgan. In his sophomore year, Bridges was given a position as an assistant in Morgan's lab at Columbia University. At that time, Morgan studied heredity using Drosophila, which required Morgan to breed flies in milk bottles. Bridges initially cleaned the bottles. In 1912, after three years of school, Bridges graduated from Columbia with a Bachelor of Science degree. Later that year, Bridges married Gertrude Frances Ives, with whom he had three children between 1915 and 1921.

After receiving his undergraduate degree, Bridges began a PhD at Columbia University. He continued working in Morgan's lab, which at that time studied the role that chromosomes play in heredity with Drosophila. Chromosomes are threadlike structures found within cells that scientists later established carried the majority of cells' genetic materials. By the 1900s, researchers had observed that, during sexual reproduction, gamete cells' chromosomes separated to form either sperm or egg cells with half the amount of original chromosomes. They observed that sperm and egg cells combined to form organisms with complete sets of chromosomes.

In 1905, Edmund Beecher Wilson, a researcher at Columbia University, had observed that male Drosophila contained a specific type of sex chromosome, later called the X chromosome, as well as another sex chromosome later called the Y chromosome. Females had two X chromosomes and no Y chromosome. He had asked whether or not the X chromosome played a role in determining sex. Other researchers debated that the Y chromosome determined sex in Drosophila. Though the Y chromosome determines sex in humans, Bridges found that it did not have the same function for Drosophila.

Bridges' sex determination finding was informed by research that Morgan had begun after Wilson's publication. In 1910, Morgan observed the inheritance of a rare trait in Drosophila. The trait was white colored eyes, opposed to typical red colored eyes. For flies to display their traits that develop from factors on their X chromosomes, females often require two copies of that factor to display

it, while males only need one. For that reason, Morgan found that males contained the trait more often than females. Morgan concluded that the genetic factors controlling the white-eyed trait were likely found on the X chromosome, called sex-linked traits. His conclusion provided evidence that chromosomes carry genetic material, a theory that many scientists, including Morgan, had not accepted in the early 1900s. Furthermore, it was used in Bridges' later research. Bridges began studying other traits that Morgan and his lab had identified to be sex-linked, and sought to understand instances in which sex-linked traits did not follow predicted inheritance patterns.

In 1913, Bridges published an article in which he proposed a mechanism explaining unusual inheritance patterns of sex-linked traits that the Morgan lab had identified. He called the process nondisjunction, and he hypothesized that chromosomes were failing to separate during the formation of sperm and egg cells. The resulting sperm and egg cells, when fertilized, produced offspring containing abnormal numbers of sex chromosomes. In 1916, as part of his PhD dissertation, Bridges published an article in which he provided experimental evidence supporting his nondisjunction hypothesis. That article provided further evidence that chromosomes carry genetic material. Additionally, he concluded that, in Drosophila, sex is determined by the X chromosome and not the Y chromosome. He found that the number of X chromosomes, rather than the presence of the Y chromosome, determined sex. For instance, a fly that acquired the chromosomes XXY through nondisjunction would be female because two X chromosomes are sufficient to make a fly female regardless of the presence or absence of a Y chromosome. In humans, the Y chromosome determines sex.

In 1916, Bridges completed his PhD at Columbia University with Morgan as his doctoral advisor. Bridges continued to research in Morgan's laboratory at Columbia University through funds the laboratory had received from the Carnegie Institution of Washington, in Washington, D.C. By 1919, Bridges had become an extramural employee of the Carnegie Institution, which provided Bridges with tenure and a pension. While at Columbia, the Carnegie Institution paid Bridges through Morgan. According to historian of science Robert Kohler, that arrangement resulted in Bridges being dependent on Morgan to fund his research.

Bridges remained at Columbia University until 1928. According to Morgan, Bridges was largely responsible for producing and keeping extensive records of mutants, which were Drosophila that had traits that differed from normal, or wild type, Drosophila. An example of a mutant is the white-eyed mutant that Morgan and Bridges had previously studied. After the Morgan lab found the white-eyed mutant and other mutants, they used that information to create genetic maps, which displayed the positions of factors along the chromosome. Using that information, in 1919 and 1923, Sturtevant and Morgan published genetic maps of entire chromosomes. Those maps informed later Drosophila research on the physical nature of heredity and on the mechanisms that control it.

In 1928, Bridges, Morgan, and other members of the Columbia laboratory moved to the California Institute of Technology in Pasadena, California. Bridges had become estranged from his wife, Bridges and his family did not move to California with him. According to Kohler, Bridges had a promiscuous private lifestyle that complicated his family life and career. Throughout his career, Bridges visited the Cold Spring Harbor Laboratory in Cold Spring, New York. In 1933, prior to one of his visits, the laboratory asked Bridges not to have affairs with any of their staff. He agreed.

At the California Institute of Technology, Bridges continued his work on Drosophila until his death. In 1934, Bridges created genetic maps of oversized chromosomes found in the salivary glands of Drosophila. Because those chromosomes are far larger than normal chromosomes, Bridges was able to visually locate the position of genetic factors. Bridges also edited numerous editions of the Drosophila Information Service, a journal that published information about new mutants and experimental methods. The Drosophila Information Service freely exchanged information amongst Drosophila researchers and standardized practices used by them.

Bridges was recognized for his many contributions to the developing field of genetics. In 1933, Morgan received the Nobel Prize in Physiology or Medicine for his research establishing the chromosome's role in heredity. Morgan acknowledged Bridges's contributions and shared a portion of the prize money with him. In 1936, Bridges was elected to the US National Academy of Sciences.

On 27 December 1938, Bridges died in Los Angeles of complications from syphilis. He was survived

by his two children and wife.

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