

# Perspectives

## Anecdotal, Historical and Critical Commentaries on Genetics

*Edited by James F. Crow and William F. Dove*

### 100 Years Ago: Walter Sutton and the Chromosome Theory of Heredity

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EVERY student of elementary genetics learns of Walter Sutton (1877–1916). Sutton was the first to point out that chromosomes obey Mendel's rules—the first clear argument for the chromosome theory of heredity. This year marks the centennial of SUTTON's (1902) historic paper, surely the most important genetic event in that year. Sutton worked with grasshopper chromosomes, and it was in this paper that he showed that chromosomes occur in distinct pairs, which segregate at meiosis. His concluding statement reads: "I may finally call attention to the probability that the association of paternal and maternal chromosomes in pairs and their subsequent separation during the reducing division . . . may constitute the physical basis of the Mendelian law of heredity" (p. 39).

Sutton, a Kansas farm boy, had been a student of C. E. McClung (1870–1946), a prairie pioneer cytologist at the University of Kansas. McClung took advantage of the great abundance of grasshoppers in that state to make them pivotal for cytological study and to found a school of grasshopper cytologists. In 1912 he moved to the University of Pennsylvania to continue his distinguished career. One of the best known of his students was W. R. B. Robertson, of "Robertsonian translocations."

In a subsequent article, SUTTON (1903) gave a much fuller development of the hypothesis, including the view that the different chromosome pairs orient at random on the spindle, thus giving rise to Mendelian independent assortment. The paper was characterized by clear logic and by beautiful chromosome drawings. As STURTEVANT (1965, p. 38) says of Sutton's work: "With this paper, this phase of the history is finished. The conclusions were not at once generally accepted, but they

could not be disregarded and stand today as essentially correct. At last, cytology and genetics were brought into intimate relation, and the results in each field began to have strong effects on the other." It was not until a decade later, however, that independent assortment was definitively proven. Another McClung student, Eleanor Carothers (1913), found a pair of heteromorphic autosomal homologs in the grasshopper *Brachystola*, in which one homolog was larger than its mate. She showed that these segregated independently of the X chromosome in the meiotic spindle; the large member of the pair went with the X in 154 cases (51.3%) and the small one in 146 cases (48.6%). Later she extended this to more than two chromosomes (CAROTHERS 1917).

In his sophomore year, Sutton became a student of C. E. McClung at the University of Kansas. McCLUNG (1901) had discovered the "accessory chromosome" and correctly concluded that it was related to sex. The X chromosome designation that is now standard grew out of his custom of labeling this chromosome, X, in drawings. But he wrongly concluded that it was male determining. This was a reasonable conclusion, because of an earlier error by none other than his student, Sutton. Sutton had found a species of grasshopper, *Brachystola magna*, in which the male meiotic chromosomes are particularly large and clear. But oogenesis in the female was another story. Cytology was a primitive art in those days and chromosome counts were very uncertain. Consequently, Sutton erroneously reported 22 chromosomes in the female, rather than the correct number, 24. Grasshoppers do not have a Y chromosome and, since the male clearly had 23, McClung's incorrect conclusion was logical enough. The issue was eventually settled by Nettie Stevens (1905), who studied *Tenebrio*, a beetle. In this species, the Y chromosome was small and easily distinguished from the X, and she saw clearly that the female was XX and the male XY.

After two years of graduate work at Kansas and a master's degree (SUTTON 1900), he followed McClung's

**This article is dedicated to the memory of our father, H. E. Crow, who, like Sutton, Robertson, and Carothers, was a student of McClung.**

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Walter S. Sutton (from the Archives of the University of Kansas Medical Center, Kansas City, KS).

advice and moved to Columbia University. His now-famous papers were written there while he was a student of E. B. Wilson. Another student, William A. Cannon, independently reached the same conclusion from his study of cotton chromosomes (WILSON 1902), but Sutton provided the definitive arguments. When Mendel's work was rediscovered in 1900, it must have been apparent to many cytologists and geneticists that the chromosomes in meiosis and fertilization obey Mendel's laws. In fact, several other workers reached very similar conclusions. The German cytologist T. BOVERI (1904) said that he had had the same idea at the same time as Sutton. This did not, however, in the smallest degree detract from Sutton's fine achievement, he said (McKUSICK 1960). WILSON (1925, p. 923) referred to the chromosome theory of heredity as the Sutton-Boveri hypothesis. Boveri's correct insight is not surprising, since he was a leading figure at the time and would be expected to be on top of the subject. But Sutton was a young graduate student, totally unknown to the world of cytology and genetics. A major reason for his success was his discovery of *Brachystola magna*, with its easily visible

meiotic chromosomes. His deep knowledge of cytology is evident in the beautiful, detailed drawings, and the paper is a model of clarity.

Sutton regarded chromosomes as units in inheritance, although he did point out that several alleles must reside in one chromosome and therefore be inherited as a unit. The possibility of recombination within a chromosome was first noted by DeVRIES (1903), foreshadowing the later work on crossing over by the *Drosophila* group. In Wilson's words, "The names of Sutton, Boveri and DeVries will therefore always be closely associated with the cytological interpretation of Mendelism" (WILSON 1925, p. 928).

After this monumental insight, Sutton's name never reappeared in the genetics literature. Whatever happened to him? How could a person of such promise disappear? In brief, he never completed his Ph.D. Instead, he went to medical school, received the M.D., and became a distinguished surgeon.

Walter Stanborough Sutton was born in Utica, New York, the fifth of seven sons. When he was 10 years old, the family moved to a ranch in Russell County, Kansas. The family ranch was noted for breeding high-quality livestock. Sutton showed an early proclivity for gadgeteering and was very skilled in repairing farm equipment. He was also inventive, making his own camera.

On graduation from high school in 1896, he enrolled at the University of Kansas in engineering, a subject he greatly enjoyed. The following summer he returned to his home where the entire family fell ill with typhoid fever. His brother, John, 17 years old at the time, died. John's death affected Walter profoundly and very likely contributed to his decision to switch to medicine.

Sutton returned to the University of Kansas and enrolled in biological sciences in preparation for a career in medicine. He was a well-rounded student. Among other things, he was a member of the basketball team. These were pioneer days of the game. The coach was basketball's inventor, James Naismith. Sutton also distinguished himself as a student and was elected to both Phi Beta Kappa and Sigma Xi. He received a bachelor's degree in 1900 and a master's degree in 1901. He became the first graduate student of C. E. McClung, who was only seven years older. The two developed a close friendship. Here is an illustration of their easy camaraderie (McKUSICK 1960). Reporting his summer discovery of a grasshopper with very large chromosomes, he wrote: "From what you say of the 'immensus' I infer that the gentleman's cells are about the largest that have ever been discovered, and if they are so our department may derive a little fame from the fact." His master's thesis was a study of spermatogenesis in this species (SUTTON 1900).

On McClung's advice, Sutton transferred to the graduate program at Columbia University to study with E. B. Wilson. It was here that he wrote his two monumental papers. All along he had expected to enter medical

school, but he planned to complete his Ph.D. first. CAROTHERS (1913) mentions that he was planning a further paper. For reasons not entirely clear, probably financial, he did not publish the paper and his thesis was never finished; instead he went to work in the summer of 1903 as a foreman in the Kansas oil fields. There he used his inventive powers and mechanical skills to solve a number of technical problems. Continuing for two years, he accumulated enough money to return to medical school. He was able to use his graduate credits to complete medical work at the Columbia College of Physicians and Surgeons in an additional two years.

After receiving his M.D. in 1907, Sutton accepted a two-year fellowship in surgery at Roosevelt Hospital in New York City. He then moved to Kansas City and settled in the home of his parents. He opened an office for private practice and accepted an appointment as Assistant Professor of Surgery at the newly formed four-year medical school at the University of Kansas. Two years later, in 1909, he was appointed Associate Professor of Surgery. He held staff positions at several Kansas City hospitals.

Sutton was held in high regard by colleagues and administrators. He was very productive during his early years in the Surgery Department at the University of Kansas (e.g., SUTTON 1910a,b,c; 1911a,b). He was especially interested in orthopedic and plastic surgery and was noted for his work with children who had congenital anomalies. He continued his interest in photography, begun on his Kansas farm, and several of his reconstructive and orthopedic surgery procedures were documented in photographs.

In 1915 during World War I, he was granted a military leave of absence to accept an invitation to head the surgery staff at an ambulance hospital in Juilly, France. In letters home he wrote about the large number of injured soldiers who came under his care. In 1916 he signed a contract with C. V. Mosby Publishers to produce a book on surgery, and war surgery would no doubt have been included, but his premature death intervened before the work was completed.

Sutton had gained experience on his father's ranch repairing and maintaining farm equipment. These skills were used later in the oil field. According to a fellow worker, Sutton perfected a method for starting large gas engines with high-pressure gas. He also invented a hoisting device for deep well drilling.

He was also inventive in the surgical field. He developed a method for irrigating the abdominal cavity in the treatment of a ruptured appendix. He perfected a method of administering ether anesthesia by rectum, a technique that gained wide acceptance; it was especially useful in head surgery. He invented a "speedometer" for calibrating slow installation of fluids into the rectum. While on hospital duty in France he devised a method for localizing foreign bodies by fluoroscopy.

According to family records, Sutton had several bouts

of appendicitis and on November 6, 1916, he came home early and went to bed. The next day he operated on three cases, but by noon was ill and at 3:30 PM he was himself operated on for a ruptured appendix. He failed to improve and died on November 10, 1916. Ironically, he had studied and written on this very subject.

His death and funeral service received generous news coverage. Deans of four American universities attended, and eulogies were quoted in the newspapers. Many were printed in a small book published by the family and deposited in the Archives of the University of Kansas Medical Center.

Although Sutton became heavily involved in medicine, he did not lose interest in his original field of cytology. According to a fellow medical student, he received reprints from cytologists throughout the world. He would often take out his unpublished thesis and show that he had already worked out the same point. Apparently, he expected to complete and publish the thesis. CAROTHERS (1913) referred to his work with the implication that it was to be published.

At the time of his death, Sutton was 39 years old. Undoubtedly, with his keen powers of observation, cytological skills, inventive turn of mind, and depth of insight, he would have continued to make important contributions had he stayed in cytogenetics. Yet, his great accomplishments in his short career as a surgeon are also a matter of record. In any case, very few scientists who have written only two papers on a subject have made such an important and lasting contribution.

We are greatly indebted to Nancy Hulston, Director of Archives at the University of Kansas Medical Center. The Sutton archives are well organized and extensive, and an exhibit that she prepared was the source of much of the information used in this paper. A book published by the Sutton family following his death was also very useful. Finally, we have also profited by Victor McKusick's article, which reflects a great deal of original research. Some decades ago, we discovered that each of us knew the name, McKusick. One (E.W.C.), a cardiologist, knew of a McKusick who had written an influential book in cardiology (McKUSICK 1958); the other (J.F.C.), a geneticist, knew a leading geneticist with the same name. We two brothers were surprised and delighted to discover that these two McKusicks were, in fact, the same person.

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