William Bateson (1861-1926)

At the turn of the twentieth century, William Bateson studied organismal variation and heredity of traits within the framework of evolutionary theory in England. Bateson applied Gregor Mendel's work to Charles Darwin's theory of evolution and coined the term genetics for a new biological discipline. By studying variation and advocating Mendelian genetics, Bateson furthered the field of genetics, encouraged the use of experimental methodology to study heredity, and contributed to later theories of genetic inheritance.

Bateson was born in Whitby, England on 8 August 1861 to parents Anna Aiken Bateson and William Henry Bateson, who was a classics scholar and Master of St. John's College at the University of Cambridge in Cambridge, England. Bateson had five siblings. Despite being described as vague and aimless by his grammar school headmaster at Rugby School in Rugby, England, Bateson entered St. John's College at Cambridge in 1879. Cambridge professors Adam Sedgwick and Walter Frank Raphael Weldon influenced Bateson as he studied embryology and anatomy. Bateson took first-class honors in the first part of the Cambridge final honors degree examination, the Natural Sciences Tripos, in 1882. A year later, Bateson sat the second part of the exam in zoology and received a first-class honors degree.

During the summers of 1883 and 1884, Bateson, on the advice of Sedgwick and Weldon, worked on a vertebrate ancestry project in the US. Bateson studied the morphology and embryology of the acorn worm Balanoglossus kowalevskii, (later called Saccoglossus kowalevskii), under Johns Hopkins University zoologist William Keith Brooks at the Chesapeake Zoological Laboratory, which was located in Hampton, Virginia. Throughout their time together, Bateson observed Brooks's rejection of the traditional methods of comparative embryology and morphology to derive phylogenies, the evolutionary histories of a group of organisms. Brooks advocated that embryologists and morphologists who studied variation should use rigorous experimental methods. Influenced by Brooks's ideas, Bateson left embryological research and focused on the experimental study of variation and heredity.

After he returned to Cambridge in 1884, Bateson began publishing his research on Balanoglossus and was elected Fellow of St. John's College in 1885. He continued to examine variation of organismal traits as part of the link between environment and adaptation, and he spent more than a year conducting related fieldwork in Russia, Turkistan, and Egypt. Overall, Bateson spent much of his time at Cambridge, where he collected, organized, and analyzed organisms with abnormalities as well as species that exhibited discontinuities in variation, or did not show a continuous gradient of change between organisms within the species.

In 1894 Bateson published the findings in his first book, Materials for the Study of Variation Treated with Especial Regard to Discontinuity in the Origin of Species. Bateson's book outlined discontinuities in variation that he had observed between species. For example, he explains that the male Lamellicorn beetle, Xylotrupes gideon, is found in two forms, long-horned or short-horned. The absence of males with horns of medium length meant that variation within that species was not continuous. In Materials for the Study of Variation, Bateson also debuted terms such as meristic to describe variation in the number of body parts, and homeotic to describe variation in the arrangement of body parts, after which scientists later named homeotic genes. Bateson's book also challenged Charles Darwin's theory of natural selection. Bateson argued that natural selection could not fully explain the origin of species. According to Darwin, natural selection caused species to evolve from other species via the gradual accumulation of small advantageous characters within the organisms of the evolving species. However, Bateson noted instances of discontinuous varia-

tion within species, an observation that strengthened his support of saltationism, as he argued that evolution may sometimes occur in large jumps, rather than through the gradual accumulation of differences.

Initially, Materials for the Study of Variation received criticism. Bateson's critics included his former mentor Weldon, who disagreed with the qualitative methods that Bateson had used to study variation. Further criticism came from those in the discipline of biometry, a school of thought that sought to explain evolution through statistical methods, and that relied upon the conception of continuous variation among organisms within a species. Despite the lack of support from biometricians, geneticist Reginald Crundall Punnett, who created the Punnett square and collaborated with Bateson at Cambridge, later deemed Bateson's book as a landmark in biological thought. After it was published in 1894, Bateson was elected as Fellow of the Royal Society in London, England. Bateson was involved with the Royal Society throughout the rest of his life, and he earned the Royal Society's Darwin Medal in 1904 and the Royal Medal in 1920.

With the rise of biometry, Bateson did not abandon his investigation of discontinuous variation, but he shifted his methodology from observational to laboratory experimentation. Many morphologists did not support Bateson's transition, so he turned to an underutilized resource for research assistance: women. Bateson initially worked with his sister, Anna Bateson, and later, Dorothea Pertz, both botanists trained at Newnham College, one of Cambridge's colleges for women. In 1895 Bateson began a series of cross-breeding and hybridization experiments with botanist Edith Rebecca Saunders. Bateson and Saunders's crosses of the flowering plant Biscutella laevigata exhibited discontinuous variation in the smoothness of leaves, so they expanded their work to include four other flowering plant species from genera Matthiola, Lychnis, Atropa, and Datura. Despite their extensive experiments, they could not distinguish any consistent pattern or mechanism of inheritance. Bateson expanded his work to include butterflies and poultry, but still could not fathom a mechanism until 1900, when Bateson and Saunders learned of Mendel's 1866 pea inheritance paper, which Mendel had written while in Austria.

Bateson adopted Mendel's work, and he advocated for others to do so. The majority of Bateson and Saunders's results from flowering plant crosses fit Mendel's laws of inheritance. In 1902 Bateson published Mendel's Principles of Heredity: A Defence, and Bateson's support of Mendelism rather than of biometry started an argument between Bateson and Weldon. This argument culminated in a debate in 1904, known as the biometric-Mendelian controversy, at the British Association for the Advancement of Science meeting at Cambridge. The debate involved Bateson and Karl Pearson, a colleague of Weldon's. Even though many scientists supported biometry rather than Mendelism, Bateson advocated for Mendel's theories, and he sought to expand upon Mendel's work through his own research.

During the first decade of the twentieth century, Bateson assembled a research group that included Punnett, who co-founded the Journal of Genetics with Bateson in 1910. Beatrice Durham, whom Bateson married in 1896, also assisted in the research, caring for research organisms and recording data. Bateson's team persisted even when Bateson left a genetics professorship at Cambridge in 1910 to be the first director of the John Innes Horticultural Institute in Merton, England. Throughout this time, Bateson and his colleagues made several discoveries in genetics and described various genetic phenomena. These included Bateson's definition of linkage, the tendency of genes that are located near each other to be inherited together; and epistasis, a type of gene interaction in which the expression of one gene can be activated or suppressed by another gene, though epistasis was first extensively described in 1907 by Muriel Wheldale Onslow, a member of Bateson's research group. Using crossbreeding and hybridization experiments, Bateson demonstrated that both plant and animal populations exhibit Mendelian principles. Bateson and Punnett also researched plant chimeras, single organisms that have two distinct genotypes.

In 1913 Bateson published his final book, Problems of Genetics, which discussed genetic phenomena and speciation. Bateson continued to study organisms with abnormalities and the problems of variation within the context of the origin of species. By this time, many biologists had accepted Mendel's theories. Bateson opposed chromosome theory, however, which held that genes were located on chromosomes. Chromosome theory had gained scientific support by 1910, yet Bateson found it difficult to reconcile Mendelian segregation and genetic linkage with the chromosome theory of inheritance. Toward the end of his life, Bateson came to partially accept chromosome theory, but he criticized what he perceived to be its inability to completely explain inheritance. Bateson remained director at the Horticultural Institute until his death at age sixty-four in 1926.

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