Theodor Heinrich Boveri (1862-1915) [1]

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Theodor Heinrich Boveri investigated the mechanisms of heredity. He developed the chromosomal theory of inheritance and the idea of chromosomal individuality. Boveri sought to provide a comprehensive explanation for the hereditary role and behavior of chromosomes. He hoped that his experiments would also help to distinguish the roles of the nucleus [5] and the cytoplasm in embryogenesis [6]. Boveri was particularly interested in how offspring are shaped by the attributes of their parents. His exhaustive studies of chromosomal and cellular behavior during early development paved the way for much of the emerging field of embryology [7].

Born in Bamberg, Germany, on 12 October 1862, Theodor Boveri [8] was the second of four children born to Antonie and Theodor Boveri [8], both of whom were highly creative and fostered their son's remarkable inventive intellect. At a young age, he was encouraged to practice his artistic skills. He was trained in music at the Realgymnasium in Nürnberg, where he also spent much of his spare time drawing and painting. His biographer, Fritz Baltzer, describes Boveri as a man who, throughout his life, was highly creative and intelligent, yet humble and mature beyond his years. Boveri's training in the arts impacted his work ethic in a profound manner, and he always insisted on practicing science both as a natural pursuit and as an art. He had the same expectations of his students.

Boveri graduated from the Realgymnasium in 1881 and entered the University of Munich [9] that same year. Due to the intelligence and motivation he displayed, both at the Realgymnasium and on his university qualification exams, he was awarded residence at the Maximilianeum, the room-and-board subsidized quarters reserved for students showing exceptional merit. After a semester studying history and philosophy, Boveri decided instead to study anatomy and biology. During this time he became an assistant to Carl von Kupffer [10] at the Anatomical Institute [11] at Munich. The aid for both his living situation and his assistantship helped Boveri offset the fact that, by this time, Boveri's father had squandered most of the family's considerable fortune.

In 1885, with von Kupffer as his mentor, Boveri wrote his dissertation Beiträge zur Kenntnis der Nervenfasern for which he was awarded a doctorate. That year he was also awarded a Lamont-Stipendium Fellowship and began working with Richard Hertwig at the Zoological Institute in Munich, which was later extended for an additional two years. During this time, he read Edouard Van Beneden's seminal paper on egg maturation and fertilization [13]. Van Beneden had extensively studied the nematode Ascaris megalocephala because of the small number of chromosomes of this species. His research greatly influenced Boveri, who proceeded to do extensive research on egg maturation and related topics using also Ascaris.
as his model organism [14].

While at the Zoological Institute, Boveri also became lifelong friend with August Pauly who was about ten years Boveri’s senior and an assistant at the Institute. With Pauly’s encouragement, Boveri continued his studies. Between 1887 and 1890, he wrote a series of three Zellenstudien (Cell Studies) that contain his detailed and meticulous observations of chromosomal conduct. In these studies, Boveri described the process of fertilization [13] in Ascaris, especially in comparison to van Beneden’s works. Like van Beneden, Boveri observed equal contribution of genetic material by the sperm [15] and the egg [12], and discovered and named the centrosome, an important structure in cell division. Boveri described the equational and reductional divisions of the germ cell to form the egg [12], making note, for the first time, of the behavior of the tetrads. In the second of his Zellenstudien he also described and expanded upon the individual nature of the chromosomes. Boveri was able to show the individuality of chromosomes by following the lobes that he observed in the nuclei of Ascaris during cleavage. The discovery of chromosomal individuality, repeatedly confirmed by subsequent experiments, represents one of the fundamentals of the study of genetics and provides a basis for understanding embryological and morphological processes.

Work with Hertwig encouraged Boveri to use sea urchin [16] eggs for experimental purposes. The Stazione Zoologica [17] in Naples, Italy, overseen by the German biologist Felix Anton Dohrn [18], provided him with the opportunity to conduct extensive work on sea urchin [16]. As with Ascaris, Boveri was able to make a number of important discoveries using the sea urchin [16] eggs. One of his main findings was the equal importance of both the maternal genetic material and the paternal genetic material to embryonic development. In addition, despite his belief that the nucleic material served as the hereditary substance, he nonetheless continued devising experiments in order to identify the role of the cytoplasm in development as well. From these studies, he made headway into what would later become known as cytoplasmic specification, i.e., the influence that certain cytoplasmic contents have on the behavior of the nucleic material and the differentiation [19] of the cell. During later years, Boveri was also able to demonstrate that each chromosome carried specific hereditary information, and that the chromosomes were not interchangeable—they summed to the total hereditary structure.

In the fall of 1892, shortly after his thirtieth birthday, Boveri received the kind of academic employment opportunity he had been waiting for. Within less than a year, Boveri became a professor of Zoology and Comparative Anatomy at Würzburg, Germany, and was named the director of the Zoological-Zootomical Institute of the same university. This appointment, which lasted him the rest of his life, also made him part of the prestigious list of Würzburg scholars that includes Hans Spemann [20], one of Boveri’s first students, Julius von Sachs and Wilhelm Conrad Röntgen.

Beginning in 1890, however, Boveri began to suffer from severe health issues. He sometimes showed symptoms of influenza, but generally suffered from recurring fatigue and depression, then diagnosed as neurasthenia. His physical condition was exacerbated by his father’s death in 1891, and the severe debts Theodor Sr. had incurred. Though Boveri spent extended periods of time in various sanatoriums, his health was never quite the same again, which considerably taxed his career.

Two major events contributed to Boveri’s continued success during his early years as a professor at Würzburg, one scientific and one personal. In 1900, Correns had rediscovered Mendel’s papers on heredity, which led Boveri to formulate the chromosome theory of
inheritance. He recognized that what Mendel referred to as "factors" were actually the hereditary units found in the chromosomes, and that the individual behavior and assortment of the discrete chromosomes played a crucial role in the inheritance of traits. He determined this by fertilizing an egg with multiple sperm, a technique called dispermy, and observing the anomalies that developed as a result. In the same years, Walter Sutton of Columbia University came up independently from Boveri with a largely identical conclusion. Therefore, the chromosomal theory of inheritance came to be called also the Boveri-Sutton chromosome theory.

The second important event in the early years of Boveri as a professor at Würzburg was his marriage with the Irish-American Marcella O'Grady, a biology professor at Vassar College, on 5 October 1897. The Boveris had one child, Margret, who later became an eminent journalist. Marcella O'Grady was the first woman to be admitted to the sciences at Würzburg. She collaborated with her husband on a series of dispermy experiments which further confirmed the necessary individuality of the chromosomes. While she was an important collaborator and supporter of Boveri, a preponderance of the credit went to him.

During the years following his marriage, Boveri was able to reach two additional, important conclusions about the nature of hereditary processes. First, he found that in most cases, at least in sea urchins, an excess or deficiency of individual chromosomes—aneuploidy—does not disturb normal development. Second, he found that unusual patterns of early cleavage do not cause major changes to the emerging body plan. His research into the subject of chromosomal abnormalities, also led him to publish Zur Frage der Entstehung maligner Tumoren (On the Origin of Malignant Tumors), where he proposed that cancer may result from problems in chromosomal cell-cycle regulatory systems.

Just as he was extremely prolific in his studies of chromosomal function and inheritance, Boveri also devoted time to the study of early embryogenesis, especially in sea urchins and Ascaris. After studying Hans Driesch's work in which Driesch claimed that the sea urchin embryo is unique in its ability to divide an infinite number of times into totipotent cells, Boveri was quickly able to demonstrate that at the 8-cell stage, only half of the cells, when separated, were able to develop into larvae. In his experiments, Boveri was also able to construct a basic fate map for the development of the sea urchin embryo. Boveri also followed the cell fate of Ascaris with great interest, mapping out a lineage tree so replete with information that it took him twelve years to complete. In 1899, he dedicated his work in experimental embryology to von Kupffer, his mentor from Munich. Boveri's work in experimental embryology showed that cytoplasmic determinants are within the egg prior to fertilization in the form of an animal-vegetal gradient. Even before embryogenesis, one pole of the egg cell is designated for more embryonic activity, while the opposite pole is slower, or vegetative.

Theodor Boveri died on 15 October 1915 in Würzburg, Germany, at the age of fifty three. The Theodor Boveri Institute at Würzburg, which encompasses a number of key departments in developmental biology, genetics and other related fields, bears witness to Boveri's profound impact on cytology, embryology and biology at large. His studies of chromosomal behavior paved the way for the current understanding of meiosis and fertilization. His studies of embryology also contributed significantly both to methodology and to ideas regarding the process of early embryogenesis.
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**Subject**

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