Edmund Beecher Wilson (1856-1939) [1]

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Edmund Beecher Wilson [4] contributed to cell biology, the study of cells, in the US during the end of the nineteenth and the beginning of the twentieth centuries. His three editions of *The Cell in Development and Inheritance* [5] *(or Heredity* [6]*)* in 1896, 1900, and 1925 introduced generations of students to cell biology. In *The Cell*, Wilson described the evidence and theories of his time about cells and identified topics for future study. He helped show how each part of the cell works during cell division and in every step of early development of an organism. Developmental biologists trained in the mid-twentieth century reported Wilson's text as their foundation for understanding biology, including about how cells, development, heredity, and evolution [7] interact. Wilson considered cells as the center of all biological phenomena.

Wilson was born in Geneva, Illinois, on 19 October 1856 to Caroline Clarke and Isaac G. Wilson. His father graduated from Brown University [8] in Providence, Rhode Island, and Harvard Law School in Cambridge, Massachusetts. Wilson's mother descended from a New England lineage traced back to the *Mayflower*. When his father became an Illinois circuit court judge in 1859, his parents moved to Chicago and Wilson stayed in Geneva, Illinois, with his aunt and his uncle Charles Patten, who in effect adopted him. What Wilson frequently referred to as his happy life in the country allowed him to discover the natural world, and his family encouraged his interest. Wilson also learned about music early in his life. He later noted the importance of listening to music and his cello playing for his own well-being.

When Wilson turned sixteen, he taught in a nearby country school for a year. After that he took an exam to enter the United States Military Academy at West Point, New York. Although he received the top score, he was too young to enroll and instead began a pattern of following his cousin, Samuel Clarke. Wilson followed Clarke first to Antioch College, a small liberal arts school in Yellow Springs, Ohio, for a year from 1873 to 1874, and then he spent a year studying subjects that he wanted to improve in. He then followed Clarke to the Sheffield Scientific School at Yale University [9] in New Haven, Connecticut, in 1875. There, Wilson learned for the first time about evolution [7], heredity, and natural history [10]. He received his Bachelor's of Philosophy (PhB) degree from Yale in 1878 and remained at Yale briefly as a graduate student.

Wilson again followed Clarke to the newly founded Johns Hopkins University [11] in Baltimore, Maryland. He received a fellowship from Johns Hopkins beginning in 1878 to study primarily with morphologist William Keith Brooks [12]. He received his PhD in biology there in 1881, and he remained at Johns Hopkins as an assistant for another year before going abroad to Europe for further study. In Europe, he visited biologists at universities in Cambridge, UK, and Leipzig [13], Germany, and then he visited the *Stazione Zoologica* [14] (zoological station) in Naples, Italy. He met leaders in biology everywhere he went and his letters from the time show that he especially enjoyed Naples for its mix of music, nature, and science.

Returning to the US in 1883, Wilson replaced his cousin Samuel Clarke as instructor at Williams College [15] in Williamstown, Massachusetts for a year and then he moved to a lectureship at the Massachusetts Institute for Technology in Cambridge, Massachusetts, the following year. In 1885, he moved to Bryn Mawr College [16] in Bryn Mawr, Pennsylvania, which was widely recognized as providing an outstanding and modern education for women, including in the sciences. Wilson left in 1891 to accept a professorship at Columbia University [17] in New York, where he remained until he retired in 1928. Bryn Mawr hired Thomas Hunt Morgan [18] to replace Wilson. Wilson went to Europe again before beginning his Columbia position. He spent time with the cell biologist Theodor Boveri [19] in Munich, Germany, and then he returned to the Naples *Stazione* where he worked with embryologist Hans Driesch [20].

At Columbia, Wilson directed the research of several PhD students and visitors, many of whom went on to prominent careers themselves, such as Albert P. Mathews, Clarence E. McClung, Gary N. Calkins, and Walter S. Sutton. Wilson's students described him as a clear thinker who could present complex ideas straightforwardly. Wilson taught the latest research about cells and also raised questions for students to explore themselves, even in the most introductory courses. He also worked with students pursuing studies down the hall at Columbia with his colleague Thomas Hunt Morgan [18], who in 1904 had also moved to Columbia.

For Wilson, cells brought together the fundamental phenomena of life. His earliest work as a graduate student and young faculty member focused on empirical studies of embryos, including work on what was called cell lineage [21]. He looked at the progression of each cell during early stages of development, starting with the first fertilization [22] of the egg [23] cell by a sperm [24] cell and continuing for as long as he could observe the cell divisions. He followed what happened to each part of the cell during each cell division, including the cytoplasm that fills the cell, and the nucleus [25] with its chromosomes, which are structures in the cell that contain genetic material. Wilson asked what role the cytoplasm, spindle fibers, asters, chromosomes, and every other part of the cell actually play. In his early work, he documented how these roles change in an organism's organization [26] and development, focusing on marine invertebrates such as the *Nereis* worm.

In 1895 Wilson teamed with Columbia photographer Edward Leaming to produce *An Atlas of the Fertilization and Karyokinesis of the Ovum*. The book had the first published photographs to show details of cell division in *Nereis*, including clear images of the dividing chromosomes. A year later in 1896, Wilson published the first edition of *The Cell in Development and Inheritance* [5]. This 371 page volume quickly became a classic, and the second edition in 1900 provided some minor updates and grew to 483 pages. Wilson dedicated *The Cell* to Boveri, the German cytologist. Together, these two books secured Wilson's place as a founder of modern cell biology.

Wilson conducted detailed observations of cells to demonstrate the details of the organization [26] and structure of each cell and its changes during cell division. In his books, Wilson asked about developmental processes in organisms. He looked at the causes of differences among cells as they go through the developmental processes of differentiation [27], where cells take on different roles and become instances of distinct types of cells.

Starting around 1892, Wilson began to pursue what many called experimental embryology [28]. By experimenting with embryos as they developed, researchers went beyond what they could find through observing and documenting cells of normally developing embryos. Wilson's experimental work led him to realize the importance of information inherited from parents to their offspring, through chromosomes and what were later called genes [29], in guiding developmental processes, and the results helped convince Wilson that development closely connects to heredity.

Wilson further investigated the role of chromosomes, partly influenced by Boveri's studies showing that chromosomes are necessary for cells to divide and develop, and partly influenced by the graduate students in his laboratory group. Along with his students, Wilson explored the roles of chromosomes that determine the sex of an individual. As researchers began to discover characteristics consistently linked with sex, Wilson and others asked why such patterns recur in different organisms. Wilson detailed what happens in the different parts of different cells during each developmental stage, studying organisms such as amphioxus, sea urchins, and various worms [30] and molluscs.

Among his publications in specialized and more general journals, Wilson contributed a series of eight "Studies on Chromosomes" that appeared from 1905 to 1912 in the *Journal of Experimental Zoology* [31]. There he detailed what each chromosome was doing in each moment of cell division, and he accumulated evidence about what the chromosomes actually contribute to the developmental process.

Wilson summarized existing knowledge about cells in language that non-specialists could understand, and he also pointed to new research topics. His approach is most obvious in the third edition of what he then called *The Cell in Development and Heredity* [6] in 1925. In its 1232 pages, Wilson detailed how research had progressed since earlier versions of the text, and he showed how the new field of genetics added to what he called the understanding of development and of the cell.

Wilson served in leadership roles and as a member or committee member with many of scientific organizations. Of these, he said that the most important for him was his role as first investigator and later instructor at the Marine Biological Laboratory [32] (MBL) in Woods Hole [33], Massachusetts. After his retirement he became a Trustee at the MBL. In 1904, he married Anne Maynard Kidder after meeting her one summer in Woods Hole [33], and their one daughter Nancy became a professional cellist who played with her father in Woods Hole [33] and in New York.

A member of the National Academy of Sciences [34], Wilson received honorary degrees from Columbia, Harvard, Yale, Johns Hopkins, Chicago, and a number of European universities. He received a gold medal from the Linnean Society in London, the Elliot Medal from the National Academy of Sciences [34], and the National Academy's John J. Carty Medal and Award. Students and colleagues recalled Wilson as a gentleman and expressed sadness when he died in 1939.

In 1981, the American Society for Cell Biology began offering an E. B. Wilson Medal as its highest honor. Many of the recipients have followed in the research directions that Wilson himself began. When then-director of the MBL, Gary Borisy, received the Wilson Medal in 2011, he called Wilson's contributions to cell biology as monumental.

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