

Edmund Beecher Wilson [5] experimented with Amphioxus (Branchiostoma [6]) embryos in 1892 to identify what caused their cells to differentiate into new types of cells during the process of development. Wilson shook apart the cells at early stages of embryonic development, and he observed the development of the isolated cells. He observed that in the normal development of Amphioxus, all three main types of symmetry, or cleavage patterns observed in embryos, could be found. Wilson proposed a hypothesis that reformed the Mosaic Theory associated with Wilhelm Roux [7] in Germany. Wilson suggested that cells differentiated into other cells when influenced by physiological (dynamic) changes in the hereditary substance contained in cells, and not because of the qualitative division, or parcelling out, of the substance into daughter cells. Wilson published his results in August 1893.

The experiment came at the end of Wilson's trip to Europe from 1891 to 1892, which included encounters with Theodor Boveri [8] and Hans Driesch [9], researchers from Germany. Embryologists such as Roux and Driesch were at the forefront of a movement in experimental embryology [10] called Entwicklungsmechanik [11] or developmental mechanics. They sought to find out the mechanistic causes of generation and the formation of developing organisms, through controlled, analytical experiments. Roux and Driesch studied the physiology rather than comparative morphology [12], which was the predominant method for embryologists at the time. Wilson did not meet Roux, but he became friends with Driesch, at the Stazione Zoologica [13] in Naples, Italy.

Wilson observed that early embryos from different species of annelids, such as Nereis [14], varied in their cleavage forms. Wilson designed his experiment to try to explain the formation of particular forms of cleavage, the process by which the egg [15] divides without increasing in size. Aside from the rotational cleavage exhibited by mammals, embryologists observed spiral, bilateral, and radial forms of symmetry in embryos, which undergo full cleavage. Wilson also sought to resolve perceived contradictions in the experimental results of Roux and Driesch.

Driesch had worked on sea urchins at the Stazione Zoologica [13]. He built on results obtained by Roux with frogs from the species Rana esculenta [16] in 1888. Roux had killed one of the cells of the frog [17] embryo early in development, and he found that the remaining live portion of the embryo would only form part of an organism, rather than a whole. Those results led Roux to formulate the Mosaic Theory of development, or the theory that the cell separated hereditary materials in different amounts to daughter cells at cell division, a process called qualitative division.

Driesch had expected to find the Mosaic pattern of development that Roux had observed, in which the ability of cells to form various cell and tissue types diminished with every division. However, when Driesch shook apart the cells at various early stages of cleavage, he found that separated cells developed into normal, though smaller than normal, adults. He classified the ability of a cell to develop into a whole organism from only part of an embryo as regulatory development. In that type of development, the fate of a cell changes if its context changes, meaning that the cell only becomes part of an organism if it remains part of the embryo, but the cell gives rise to a whole organism if it becomes separated from the rest of the embryo early in development.

Wilson conducted his work at Faro, on the island of Sicily, Italy, in June and July of 1892. He worked with an organism that showed a great deal of variability, and was amenable to experimental manipulation. He chose the marine invertebrate Amphioxus, also called Branchiostoma lanceolatum [18]. Amphioxus possesses a notochord [19], a rod-like structure that helps provide structure in embryos and some adult organisms. All vertebrates develop a notochord [19] at some stage of their development, but few invertebrates do. Alexander Kovalevsky had observed that Amphioxus had a notochord [19] in the late nineteenth century, which was a result pursued by morphologists of the time because many of them studied the evolutionary origins and ancestry of vertebrates. Wilson wanted to study the causes of the different forms of cleavage found in early development, and he was interested in evolutionary relationships found in Amphioxus.

Wilson collected adult organisms at sunrise from the surface of what he called a pantano, a lagoon that was connected to the sea by a canal. He placed those specimens in glass vessels that contained regularly refreshed water, which enabled the organisms to spawn. When they did, Wilson placed the eggs into smaller vessels, and he added fresh sperm [20] to fertilize them. Wilson
Wilson suggested that *Amphioxus* behaved so differently from Roux's frogs because of different timings in their respective processes of differentiation [25] and change. Wilson proposed that embryos take on more of a mosaic character as development proceeds. Wilson suggested that in different species, that process might take a longer or shorter amount of time, so at any one stage of development, one organism may appear to show mosaic development [28], and another regulative. However, Wilson considered that in the developmental processes of all organisms, regulative patterns of development turn into mosaic patterns as development proceeds.
Wilson published the results and interpretation in August 1893. The results of his experiment formed a key part of his theories about the different possible causes in differentiation and development. For example, in 1896 he revisited his experimental themes, and he recalled his experiment with Amphioxus in a paper discussing cleavage and mosaicism, as well as in his textbook *The Cell in Development and Inheritance*.

Wilson's experiment with Amphioxus raised questions as to the usefulness of investigations of early development for the determination of evolutionary ancestry and relationships. His experiments contributed to the debate among scientists about the causes of the generation of differentiation and form in development. In a lecture delivered at the Marine Biological Laboratory at Woods Hole, Massachusetts, in 1893, Wilson spoke about the role of the environment of the organism in development. While he acknowledged that the environment was important, he also described how the activity of the idioplasm in the cells might help to create the environment within the organism, which then influences the future activities of the idioplasm. He also proposed a hierarchical view of development, in which early differentiation sets the pattern for future differentiation.

Wilson continued to study the themes raised by his Amphioxus experiment. In particular, he engaged with the theory of germinal localization, or that unequal distribution of certain form-generating substances in the egg causes differentiation through the distribution of those substances into different cells upon cleavage and division. In 1904, he published experiments that he conducted with the marine mollusc Dentalium, which confirmed his germinal localization hypothesis. In the twentieth-century, however, Wilson studied the role of the nucleus in development. In particular, he focused on chromosomes, and his work helped to develop the theory that the chromosomes were the material bearers in cells of hereditary characteristics.

Many scientists have cited Wilson's 1893 experiment, and many historians regard it as an important work. The editor of the *American Naturalist* recognized Wilson's work with Amphioxus in both 1893 and 1894. Wilson's colleagues at the Marine Biological Laboratory incorporated information derived from his work concerning the process and variation of cleavage, on the mosaic theory, and on the significance of his findings about cleavage for aspects of Roux's theory into their summer lectures. Wilson corresponded with Driesch during and after his experimental work, and the two discussed the significance of their respective findings. At the *Stazione Zoologica*, Thomas Hunt Morgan added to Wilson's experiment and methods in Morgan's 1895 work with Amphioxus in an early investigation of regeneration. Later scientists such as Scott F. Gilbert cited Wilson's experiment as an attempt to bring together mosaic and regulatory development under one common explanation.

With the 1892 experiment with Amphioxus, Wilson entered the debates about the cause of differentiation in development, a key question in experimental embryology. He developed his hypothesis in experiments, lectures, and published works over the following decade. Wilson's theory shifted in the following years, when it was incorporated with the findings of Theodor Boveri, who studied chromosomes at the University of Munich, Germany. The change in Wilson's theory led to a theory of differentiation based on the role of chromosomes in cells by the end of the 1890s. Eventually, Wilson considered the role of inherited materials in the nucleus as central in development. He also studied chromosomes, and his acceptance of Gregor Mendel's theories of heredity. Mendel's theories and methods involved the study of the transmission of traits between generations. Wilson's acceptance of those theories led to work in the first decade of the twentieth century, when he independently discovered the role of chromosomes in the determination of sex in insects, as did Nettie Marie Stevens.

**Sources**


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