Experimental Studies on Germinal Localization (1904), by Edmund B. Wilson

By: Lowe, James Keywords: Germinal Localization [1] mosaic theory

At the turn of the twentieth century, Edmund B. Wilson performed experiments to show where germinal matter was located in mollusks. At Columbia University [2], in New York City, New York, Wilson studied what causes cells to differentiate during development. In 1904 he conducted his experiments on mollusks, and he modified the theory about the location of germinal matter in the succeeding years. Wilson and others modified the theory of germinal localization to accommodate results that showed the significance of chromosomes in development and heredity.

Wilhelm Hiss [3] at the University of Leipzig [4] in Leipzig [5], Germany, proposed the theory of germinal localization in 1874. His theory proposed that certain materials present in the egg [6] during fertilization [7] were responsible for the differential development that occurred after cell division. Biologists proposed various versions of the theory of germinal localization in the decades following Hiss's work. His argument was that substances are unequally distributed throughout the cytoplasm of the egg [8], and that the eventual production of tissues and organs can be traced back to those distributions.

Wilson debated these theories with Charles O. Whitman, the director of the Marine Biological Laboratory (MBL) in Woods Hole [9], Massachusetts. Whitman proposed a theory of cytoplasmic localization according to which the future organization [10] of the organism was already present in the egg [11] before it divided, a view Wilson rejected. Wilson conducted his experiments, and he analyzed the theory from the 1890s onwards.

However, studies by biologists such as Eduard van Beneden at the University of Liège in Liège, Belgium, and Theodor Boveri [12] at the University of Munich [13] in Munich, Germany, had demonstrated that in the process of cell division, the daughter of the nucleus [14] into daughter cells occurred with more precision than did the division of the cytoplasm. This resulted in theorists such as August Weismann [15] at the University of Freiburg [16] in Freiburg, Germany, and Wilhelm Roux [17] at the Anatomi Institute [18] in Breslau, Germany, to propose theories of germinal localization that addressed the nucleus [19] as the cause of cell differentiation [20] during development.

The theories of germinal localization were associated with the mosaic theory proposed by Weismann and Roux. They argued that the inherited substance contained in the nucleus [21] of the fertilized egg [22], or egg yolk [23], was distributed unequally when the egg yolk [24] divided, and it remained unequal in all subsequent cell divisions. This substance would cause cells to differentiate. Hans Driesch [25] and Oskar Hertwig, both in Germany, rejected the mosaic theory. In the early 1890s, Driesch found that the cells separated from the embryo at an early stage could still produce a whole embryo, indicating that the isolated cell still had all the materials needed for the production of the different cell types. Hertwig also argued that, in growth and development, there was not a qualitative division of the nuclear material, with some of it going to one daughter cell and the rest to the other. Instead, he proposed a quantitative division, where the materials in the nucleus [26] were divided equally between daughter cells, having increased in number beforehand.

Wilson began to engage in these debates in 1893 when he published the results of his 1892 experiment with the marine invertebrate Amphioxus [27]. Like Hertwig, Wilson argued that evidence indicated a quantitative division of inherited substance, rather than a qualitative division, throughout the daughters of dividing cells. He developed his argument in his 1896 textbook The Cell in Development and Inheritance. Towards the end of the book, Wilson discussed these theories, assessed them in the light of recent experimental evidence, and proposed his version of the germinal localization theory. He argued that the egg might be initially isometric, meaning that it did not have internal differences corresponding to later portions of the organism. Wilson claimed that from its formation to fertilization [8], the egg yolk became less isometric. He proposed that the pre-embryonic stages of an egg yolk [28] established the basic plan of the organism, the organism's anterior-posterior and left-right axes, and its type of symmetry. In 1896, Wilson stressed the role of conditions external to the cell, such as relations with other cells and nutrition, in these continuing arrangements of material. He argued that these external conditions accounted for the effects produced when experimenters changed the fates of embryonic cells by removing them from the embryo.

Wilson designed his experiments in 1903 and 1904 with the mollusk Dentalium [29] to test the theory of germinal localization. In these experiments, he focused on what he called pre-localization, a process occurring before segmentation [30] or cleavage of a fertilized egg [31]. Wilson claimed that if he could establish the process of pre-localization before the embryo segmented, that he would demonstrate that the localization was a progressive, epigenetic phenomenon driven by the nucleus [14]. In his view, pre-localization would disprove the theories of cytoplasmic preformation [32], according to which the egg yolk was already organized at fertilization with the formative materials for later parts already distributed to particular parts of the egg yolk [33].

Wilson's experiment followed the method of Yves Delage [34], who worked at the Sorbonne in Paris, France, and who cut fertilized eggs with a scalpel. Wilson cut single cells of fertilized mollusc embryos into fragments, and then he tracked the development of the cell fragments. As with his experiment with Amphioxus in 1893, Wilson established the normal development of Dentalium. He prepared, stained, and sectioned the samples and then observed them with a camera lucida [35]. Wilson used different stains to identify the presence of different substances in different areas of the egg yolk. Wilson observed that, in normal eggs, the materials were unequally distributed, and that those materials moved within the eggs. These observations indicated that the material distributed through the egg yolk [8] before the egg yolk [31] segmented.

Wilson used his scalpel to make precise cuts of the egg yolk [31] prior to cleavage, when the egg yolk [31] rapidly divides to produce smaller daughter cells or called blastomeres. Wilson used the scalpel to remove the polar lobe, a protrusion of the cell that contains white matter at the vegetal or lower pole which, after the first cleavage division, is attached by a tube to only one blastomere [36]. After the second cleavage, it is attached to one of the cells, which result from the division of that blastomere [37], and it is then absorbed by the cell.

When Wilson removed the polar body at the two-cell stage, also called the trefoil stage because the polar body appears like a third cell, the resulting larvae lacked any of the tissues and organs which derive from the mesoderm [38] germ layer in normal embryos. Wilson found the same result when he removed the cell that absorbed the polar body. The abnormal embryos therefore contained no shell gland, muscles, mouth, or foot. Wilson concluded that the polar lobe must contain certain materials, which help form the mesoderm [39], and he used examples from experiments with isolated blastomeres to support his case. When he observed the egg yolk [31] before cleavage, Wilson noted that the materials that went into the polar body were already visible in a particular part of the egg yolk [31].

Wilson conducted more precise experiments to further explore these results. He cut horizontal sections through an area that contained the specific polar material. As a result, most embryos failed to develop, whereas some did. Wilson remarked that the ones that did develop into larvae ranged from normal size to one-fourth of the normal size. However, he noted that, despite the change in size, they were otherwise normal in form and possessed the structures developed from the mesoderm [39], while the lobe-less larvae did not. Wilson described this result as the post-material spreading in the egg yolk [31], so even if much of it is excluded by one of his cuts, enough remained to predetermine the mesodermal fate of the particular blastomeres [40] in which it was found.

When Wilson cut sections vertically through the polar area, he observed that the formative materials were stratified horizontally in the polar area. In a number of cases, Wilson's vertical sections yielded two smaller than normal larvae, each with all the normal structures, including those Wilson associated with the polar material.

Wilson concluded that the development of Dentalium was mosaic in character. He hypothesized that the prelocalized materials in cells determined particular cell types, tissues, and structures in the later embryo and larva. Wilson noted that although the different outcomes of vertical and horizontal cuts indicated that the polar materials were stratified in a particular way in the egg yolk [31], their position in the egg yolk [31] did not correspond to the position of the structures they would determine in the embryo.

Wilson's results helped him to develop the hypothesis he had proposed in 1893. He argued that the pattern of mosaic development was explained by the movement of different formative materials into different parts of the egg yolk [31] before cleavage separated out those materials into different cells. According to this scheme, these materials would be distributed differentially to the daughter cells, explaining the process of differentiation [41]. Thus, Wilson rejected the theory of cytoplasmic precocitalization and claimed that, as the localization process continued after fertilization [42] and beyond the first cleavage stage in some organisms, localization could not account for the observed results. Wilson proposed that, instead, the segregation of materials into different regions of the fertilized egg yolk [31] must be a result of the activity of the nucleus [14].

In 1925, in the third and final edition of his textbook The Cell in Development and Heredity [43], Wilson discussed germinal localization, and he situated his work of 1903 and 1904 in a series of experiments ranging from the 1890s to the second decade of the twentieth century. Wilson showed that these experiments demonstrated the ability of cells to self-differentiate even when isolated, with developmental potency distributed along the lineages of cells produced by the cleavage divisions.

Wilson's account of these issues indicated that, by 1904, he had completed much of his theory of differentiation [41] and progressive development. His theory stated that cytoplasmic localization resulted from the activities of the nucleus [14] or nuclei. He proposed that the different modes of development, including the mosaic and regulative modes, could be explained by a difference in timing of the progressive formation of different organ-forming germ regions in the egg yolk[31] and embryo. This theory enabled him to explain how isolated blastomeres could be totipotent, even after the division of the egg yolk [31] cytoplasm into different cells after the cleavage divisions.

Thomas H. Morgan, in his 1934 book Embryology and Genetics, acknowledged Wilson's work on germinal localization, and advocated a similar approach. Morgan argued for an integrated study of the problems of development, centered on the interaction between the cell's cytoplasm and the products of nuclear activity, associated with genes [44] on the chromosomes.

Sources

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