The Germ-Plasm: a Theory of Heredity (1893), by August Weismann [1]

By: Zou, Yawen

Friedrich Leopold August Weismann [3] published *Das Keimplasma: eine Theorie der Vererbung* (*The Germ-Plasm: a Theory of Heredity* [2], hereafter *The Germ-Plasm*) while working at the University of Freiburg [4] in Freiburg, Germany in 1892. William N. Parker, a professor in the University College [5] of South Wales and Monmouthshire in Cardiff, UK, translated *The Germ-Plasm* into English in 1893. In *The Germ-Plasm*, Weismann proposed a theory of heredity based on the concept of the germ plasm, a substance in the germ cell that carries hereditary information. *The Germ-Plasm* compiled Weismann's theoretical work and analyses of other biologists' experimental work in the 1880s, and it provided a framework to study development, evolution [6] and heredity. Weismann anticipated that the germ-plasm theory would enable researchers to investigate the functions and material of hereditary substances.

Prior to publishing *The Germ-Plasm*, in 1885 Weismann had published "The Continuity of the Germ-Plasm as the Foundation of a Theory of Heredity [2]." In that essay, Weismann argued that only the hereditary substance of the germ cells [7] was inheritable, and that cells that derive from all other parts of parents' bodies (soma cells), could not transmit from parents to offspring. Compared with the 1885 essay, *The Germ-Plasm* provided hereditary explanations for developmental and evolutionary phenomena. *The Germ-Plasm* has an introduction and four parts, divided into fourteen chapters.

In the Introduction of *The Germ-Plasm*, Weismann provides a brief history of hereditary theories before the germ-plasm theory. Weismann also gave an account for biologists who had influenced him. Before the germ-plasm theory, Herbert Spencer and Charles Darwin [8], both in the UK, had proposed their own theories of heredity. Weismann argues that all the previous theories of heredity, including Darwin's theory of pangenesis [9], were unsatisfactory. In his 1868 book *The Variation of Animals and Plants under Domestication*, Darwin elaborated the theory of pangenesis [9] based on the concept of the gemmules, atomic inheritable substances that body cells emit. Darwin stated that gemmules could circulate through blood and aggregate into germ cells [7], but Weismann disagreed with Darwin's claim.

In the 1880s, Francis Galton [10] in London modified the pangenesis [9] theory, arguing that the circulation of gemmules happened not as Darwin had claimed, but rather on a small scale. Then, in 1884, Carl W.von Nägeli in Munich, Germany, postulated the concept of idioplasm in his book *Mechanico-Physiological Theory of Descent*. According to Nägeli, idioplasm was a reproductive substance located in the plasm of all cells, not just in germ cells [7]. Weismann later said that germ-plasm was the idioplasm of the germ cell.

In part one of *The Germ-Plasm*, "The Material Basis of Heredity [2]," Weismann describes the constitution and structure of the germ-plasm. Weismann postulates that there are four hierarchical levels of substances in the cell, and he coins four terms to name them. The four levels, from the lowest to the highest one, are biophors, determinants, ids, and idants. At the first level are biophors, minute units that collectively make up the whole cell, and Weismann postulated that they directed the cell's metabolism and growth. Biophors referred to various kinds of chemical molecules. At the second level are determinants, which are the primary constituents of the hereditary substances, and the biophors determined the particular phenotype and variability of a cell. At the third level are ids, or aggregates of many determinants. At the highest level are idants, which are aggregates of ids. The concept of idants corresponded to the concept of chromosomes. During an organism's development, ids reduce their number through cell division, so the new cells contain fewer ids and determinants than the old ones. Weismann claims that only one determinant is active in a body cell, and that the other determinants remained inactive, so a cell develops to have only one phenotype. Later in his book, Weismann uses those four concepts of biophors, determinants, ids, and idants to explain the hereditary and developmental phenomena in various sexual and asexual organisms.

In part two of the book, "Heredity [2] in Its Relation to Monogonic Reproduction," Weismann explains phenomena associated with monogenic reproduction, or asexual reproduction, which referred to the reproduction of a new organism from a single parent. Weismann discusses how some asexual organisms can regenerate lost parts, as when some animals regrow body parts bitten off by a predator. Weismann states that the regeneration of an entire body part has two possible causes: either cells regenerate lost parts because the cells remain young, or they regenerate those parts because they were inactive before the bite. Weismann classes those causes as due to supplementary determinants, which he says are contained in a developed cell.

Weismann next discusses fission and gemmation, both of which were cellular processes. Fission is a process through which a parent cell divides into two or more parts, whereas gemmation is a process during which a new part buds from a parent organism, and eventually leaves the parent organism as a new organism. Although Weismann concedes that fission and gemmation may both arise from regeneration, he postulates that they are distinct processes. Weismann argues that fission is due to the doubling of determinants. In contrast, gemmation is caused when the germ-plasm in particular doubles in a fertilized egg [11]. Additionally, Weismann argues that one germ-plasm then remains inactive and moves to the bud. The last phenomenon Weismann addresses is the formation of germ-cells in asexual reproduction, which for Weismann is a process similar to gemmation.

In part three of the book, "The Phenomena of Heredity [2] Resulting from Sexual Reproduction," Weismann addresses sexual reproduction, or reproduction from two parents. Weismann defines the process of amphimixis as the fusion of the germ-plasms from two parents. Weismann claims that each sex cell only carries half of the idants of a parent, and due to the fusion of idants during amphimixis, the idants of germ-plasm in the zygote [12] doubles. In his 1885 essay, Weismann had predicted the halving of sexual cells, and Theodor Boveri [13]'s and Eduard Strasburger's 1888 experiments supported Weismann's claim. Boveri and Strasburger, in Germany, showed that the number of chromosomes of primitive sperm [14] cells reduced to half in sperm [14] cells. For Weismann, an offspring's hereditary substances carry half of the ids from a paternal cell and the other half from maternal cell, and the collection of both partly explains why offspring have traits from each parent. Weismann notes that sometimes the offspring resemble traits of one parent more than the other, a phenomenon due, according to Weismann, to the competition of ids from the two parents during development.

Weismann says that hereditary phenomena are more complicated in sexual organisms than in asexual ones, and he devotes much of his text to sexual organisms. For example, Weismann describes reversion as a phenomenon according to which an offspring's characteristics resemble those of the grandparents, or remote ancestors, but are absent in the parents. Weismann argues that reversion happens because of unequal allocations of hereditary materials across generations. In reversions, the majority of a grandparent's or a remote ancestor's ids pass on to the offspring and become prominent in the offspring.

Additionally, Weismann discusses the mechanism for dimorphism, the phenomenon of two distinct phenotypes in members of the same species. One form of dimorphism Weismann discusses is sexual dimorphism, or distinct characteristics in individuals of different sexes in the same species. For instance, in tapeworms females are bigger than males and look quite different from males. Weismann postulates that cells of tapeworms carry both spermatogenetic (male) determinants and oogenetic (female) determinants. According to Weismann, in male tapeworms, spermatogenetic determinants are active whereas oogenetic determinants are inactive, whereas the converse held for female tapeworms. Weismann also discusses polymorphism, or triple or plural dissimilar phenotypes coexisting within the same species, such as in butterflies.

In the fourth part of the book, "The Transformation of Species: Its Origin in the Idioplasm," Weismann addresses the issue of inheritance of acquired characteristics, and he provides a theory of variation. Earlier, Weismann had supported, but later rejected the hypothesis that organisms inherit the characteristics that their parents' had acquired during their own lifetimes. Acquired characteristics are defined as traits acquired through environmental factors, disease, or training during the life time of an organism. Earlier scholars such as Jean-Baptiste Lamarck, who lived in France in the early nineteenth century, proposed that such traits could transmit to the offspring. In *The Germ Plasm*, Weismann rejects the theory and argues that acquired characteristics are traits of the soma cells, and the hereditary substances of soma cells cannot transmit to the next generation. However, Weismann says that environments can influence the process of inheritance by modifying the germ-plasm, for example, temperatures can influence butterflies' traits.

Additionally, Weismann elaborates a theory for variation within a group of related organisms, claiming that variations in germ-plasm cause those groups to evolve. He hypothesizes two causes of variations, the first relies on environmental factors, such as nutrients, the second on the multiplication of determinants. Weismann further argues that external factors are the major causes for variation.

After he published his theories, Weismann modified his theory to respond to critiques. In the 1900s, biologist Hugo de Vries [15] in Amsterdam, Netherlands, supported Weismann's distinction of soma cells from germ cells [7], but de Vries defended the theory of pangenesis [9] and proposed the theory of intracellular pangenesis [9]. According to the intracellular pangenesis [9] theory, the hereditary material can only move inside cells, instead of circulating in the blood. De Vries engaged a two decades debate with Weismann, who had to constantly re-examine his own theory. Nevertheless, *The Germ-Plasm* triggered debates among and influenced twentieth century researchers, and Weismann's distinction between germ cells [7] and soma cells became called the Weismann barrier.

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