

August Friedrich Leopold Weismann (1834-1914)

August Friedrich Leopold Weismann studied how the traits of organisms developed and evolved in a variety of organisms, mostly insects and aquatic animals, in Germany in the late nineteenth and early twentieth centuries. Weismann proposed the theory of the continuity of germ-plasm, a theory of heredity. Weismann postulated that germ-plasm was the hereditary material in cells, and parents transmitted to their offspring only the germ-plasm present in germ-cells (sperm and egg cells) rather than somatic or body cells. Weismann also promoted Charles Darwin's 1859 theory of the evolution of species. Weismann argued that only changes to the germ cells, and not body cells, could be inherited, a theory that influenced theories of heredity throughout later centuries.

Weismann was born on 17 January 1834 in Frankfurt am Main, in the German Confederation. His mother, Elise Eleanore Lübbren, was a musician and painter, and his father, Johann Konrad August Weismann, was a classics professor. Weismann studied music, particularly the works of Beethoven, and he studied nature, from which he collected butterflies. He noted diverse patterns and colors of butterflies, information that later informed his research on the development and evolution of butterflies and caterpillars.

In 1856 Weismann got his medical degree from the University of Göttingen in Göttingen, in the German Confederation. After graduation, Weismann worked as an assistant in a hospital for three years in Rostock, in the German Confederation, before becoming a physician in Frankfurt am Main in 1859. From 1861 to 1863, Weismann was the private physician for Archduke Stephen of Austria. In 1861, Weismann studied at the University of Giessen in Giessen in the German Confederation, with Rudolf Leuckart for two months, working on the ontogeny (development) and morphology (form) of animals, insects in particular. That year, Weismann read Charles Darwin's *On the Origin of Species* two years after it was published in 1859, after which he adopted evolutionary theory. Weismann studied different factors he thought might cause morphological transformations in insects, including natural selection.

In 1863, Weismann became a docent in zoology and comparative anatomy, a mid-ranking academic position, in the University of Freiburg in Freiburg im Breisgau, also in the German Confederation. In 1864, Weismann's eyesight declined, which left him partially blind and limited his ability to use microscopes. Nonetheless, he studied the metamorphosis and development of butterflies.

Weismann became the founding director of the Zoological Institute at the University of Freiburg in 1867. That year, he married Marie Dorothea Gruber from Genoa, Italy. The couple had at least five children. Along with his students and assistants, Marie aided his experimental and observational studies after his eyesight failed. Marie died in 1886, but Weismann remarried at the age of sixty in the mid-1890s to Willemina Tesse from the Netherlands, a marriage that lasted six years.

In 1868, Weismann delivered a lecture: "Über die Berechtigung der Darwin'schen Theorie" ("On the Validity of the Darwinian Theory"), in which he argued that the evolution of new species occurred by natural selection. From 1868 to 1872, he debated with Moritz Wagner of the University of Munich in Munich, Germany, about the role of geographic isolation in speciation. Weismann agreed with Darwin that natural selection and sexual selection alone could explain how species diverged from one another, whereas Wagner argued that geographical isolation of populations was necessary for speciation. That debate was one of Weismann's earliest public debates about the theory of natural selection.

In 1872, that debate culminated in a monograph by Weismann on Wagner's theories, called *Über den Einfluss der Isolierung auf die Artbildung* (On the Influence of Isolation on Speciation). Weismann

argued that natural selection played a significant role in the development of organisms. Edwin G. Conklin, a biologist who studied evolution and development in the US, said in 1895 that Weismann appeared more Darwinian than Darwin about natural selection. Weismann taught evolutionary theory for more than forty years, and he published books on evolutionary theory.

Weismann's eyesight improved after 1871, so he resumed his microscopic studies. He studied the metamorphosis of butterflies, especially how changes in environmental conditions such as temperature caused variations in the wings of butterflies. Other studies dealt with the markings of caterpillars and the metamorphosis of Axolotl, also known as the Mexican salamander. These works culminated in a two-volume account published in 1875 and 1876 titled *Studien zur Descendenz-Theorie* (Studies on the Theory of Descent). From 1878 to 1883, he investigated how sex cells were generated in *Hydromedusae*, a small jellyfish-like marine invertebrate. He also studied parthenogenesis, a form of asexual reproduction that allows the egg to develop into a new organism without fertilization, in *Cladocera*, a type of water flea.

From 1881 onwards, Weismann published a series of essays about heredity. Those essays were collated in English in 1889's *Essays upon Heredity and Kindred Biological Problems*. The essays discussed topics including senescence, acquired characteristics, and the germ-plasm theory. For example, in the first chapter, "The Duration of Life," a translation of an essay originally published in German in 1881, Weismann detailed his evolutionary theory of senescence, the name given to the gradual deterioration of function of most life forms after they mature to adults. Weismann argued against theories that associated the length of an organism's life with the size or complexity of its body, or with how active it appears to be. Instead, he appealed to natural selection, arguing that it adapted organisms to reach reproductive maturity, and that it would not select for the capacity of the organism to live any longer once it was past reproductive age. He further argued that the death of male bees after they reproduced was selected for by nature to save nutrition for the colony, a phenomenon that precluded those organisms that had already reproduced from consuming resources.

In 1884, Weismann quit microscopic study again due to the deterioration of his eyesight and instead focused on theoretical questions in biology. The following year, Weismann published an essay titled "Die Continuität des Keimplasmas als Grundlage einer Theorie der Vererbung" ("The Continuity of the Germ-plasm as the Foundation of a Theory of Heredity"). The English translation of it comprised the fourth chapter of *Essays on Heredity*. Inspired by his work on the generation of sex cells and parthenogenesis, Weismann hypothesized that the germ-plasm, which he now argued was a substance in the nucleus of a germ cell, had a highly complex structure. Germ cells are reproductive cells that produce egg and sperm cells, as opposed to somatic cells, which are body cells such as skin or liver cells. In this essay, Weismann theorized that the germ-plasm in germ-cells alone, rather than the somatoplasm contained in somatic cells, was transmissible from parents to offspring. Weismann distinguished somatic cells from germ cells in multi-cellular organisms, and he proposed that changes made to somatic cells cannot be passed to germ cells or to the next generation, a theory later called the Weismann Barrier.

Weismann therefore rejected the possibility of the inheritance of acquired characteristics, if those characteristics were changes which occurred in somatic cells. The theory of the inheritance of acquired characteristics derived from work published by Jean-Baptiste Lamarck in France in 1809. Lamarck and his adherents argued that characteristics acquired during the lifetime of an organism could be transmitted to that organism's offspring. For example, according to Lamarckism, the long neck of a giraffe evolved because changes to the length of the neck resulted from the giraffe's use in straining to reach leaves on tall trees, and those changes were passed on to the next generation. As this straining continued over many generations, the length of the giraffe necks kept increasing. In 1888, Weismann delivered a lecture at the meeting of the Association of German Naturalists at Cologne, Germany, in which he described the results of an experiment that he said contradicted Lamarck's theory and supported the theory of the Weismann Barrier. The lecture became the eighth chapter of *Essays on Heredity* titled "The Supposed Transmission of Mutilations". In the experiment, Weismann cut off the tails of 901 mice and their offspring for five generations. If acquired characteristics were heritable, Weismann reasoned, the experimental mice should eventually produce offspring with no tails. Yet, as Weismann had predicted, the descendants of those amputee mice still grew tails like normal mice. He used his experimental results to frame a comprehensive

argument against the possibility of the inheritance of acquired characteristics.

In Weismann's 1892 monograph *Das Keimplasma. Eine Theorie der Vererbung* (The Germ-Plasm. A Theory of Heredity), he propounded a theoretical system of heredity and development. He coined four terms, biophors, determinants, ids, and idants, to represent the constituents of germ-plasm at four hierarchical levels. At the first level, biophors were the fundamental and smallest units of hereditary factors. At the second level were determinants, comprising combined biophors. A determinant was conceived to be a unit of hereditary substance initially in the germ cells, which could transmit to body cells and determine the structure and function of a body cell. At the third level Weismann posited ids, groups of determinants. Weismann proposed that ids derived from germ cells that carried the entire complement of determinants, but that the ids were scattered during development into different cells. At the highest level were idants, which carried ids, and which corresponded to chromosomes.

Weismann predicted that in sexual reproduction, a form of reproduction involving two parents, the number of idants normally present in cells must reduce to half, so that, of the idants in the cells of an offspring, half came from the mother's germ cell and half came from the father's germ cell. That theory explained why the offspring had traits that resembled those in the mother and those in the father.

In 1896, based on his germ-plasm theory, Weismann proposed the theory of germinal selection as an extension to the theory of evolution by natural selection in *Über Germinal-Selection: eine Quelle bestimmt gerichteter Variation* (On Germinal Selection as a Source of Definite Variation). Weismann proposed that germinal selection applied to the biophors and determinants in the germ cells even before those cells joined to form a zygote. At that time, biologists debated what caused the traits in one organism to vary from those in another and whether or not such variation was random or generated in a definite direction. Weismann postulated that variations resulted from different combinations of determinants in germ cells. The stronger determinants outcompeted the weaker determinants, and germinal selection therefore kept the stronger determinants in the germ cells and eliminated weaker ones from the germ cells. Weismann argued that the germinal selection created adaptive rather than simply random variations. Weismann used his theory to explain the loss of useless organs, such as the eyes of blind cave fish, during development, by suggesting that germinal selection eliminated the determinants for those organs. Weismann acknowledged that external factors, such as environmental factors, could play a role in development of organisms. But his theory of germinal selection enabled him to explain how new variations of traits in organisms arose even when changes to determinants did not pass from parents to offspring. Only variations to the determinants housed in the germ cells, affected by changes in nutrition, could be passed on to the next generation.

Weismann received numerous awards, including the Linnaean Society of London's Darwin-Wallace Medal in 1908, and the Darwin Medal from the Royal Society of London in 1909. Weismann died on 5 November 1914.

Sources

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