

Wilhelm Ludvig Johannsen (1857–1927)

Wilhelm Ludvig Johannsen studied plants and helped found the field of genetics, contributing methods and concepts to the study of heredity around the turn of the twentieth century in Denmark. His experiments on heredity and variation in plants influenced the methods and techniques of geneticists, and his distinction between the genotype of an organism—its hereditary disposition—and its phenotype—its observable characteristics—remains at the core of contemporary biology. Johannsen criticized biological explanations that relied on concepts such as vitalism and teleology. He instead advocated a realist and materialist approach to biology, but one that did not attempt to reduce biological phenomena to the laws of physics and chemistry.

Johannsen was born on 3 February 1857 to Anna Margrethe Dorothea Ebbesen and Otto Julius Georg Johannsen in Copenhagen, Denmark. His father, an officer in the Danish army, could not afford to send Wilhelm to university, his older brother having already attended. After he completed elementary school in 1872, Johannsen was apprenticed to a pharmacist. He taught himself chemistry while working in pharmacies in Denmark and Germany. In 1880, during the final year of his vocational training, Johannsen spent a year at the University of Copenhagen, where he acquired an interest in plant biology while studying with the botanist Eugenius Warming. After passing his examination as a pharmacist in 1879, Johannsen continued to nurture his interests in chemistry and plant biology, and in 1881 accepted a position at the Carlsberg Laboratory in Copenhagen, Denmark as an assistant to chemist Johan Kjeldahl, who developed a quantitative technique for measuring the nitrogen content of organic compounds.

Charged principally with the study of barley while at the Carlsberg Laboratory, Johannsen had the flexibility to investigate metabolic problems concerning the ripening, dormancy, and germination of a wide variety of plants. One of his earliest projects was to search for the causes of mealy and glassy appearances of barley grains—of particular interest to brewers. He published those results in 1884 in his article “Om Frøhviden og dens Udvikling hos Byg” (“About the Endosperm and its Development in Barley”). During his tenure at Carlsberg he further trained in biology at German and French universities, and he developed a quantitative approach to plant physiology. At Carlsberg Johannsen learned of Emil Christian Hansen's work on pure single yeast cell derived cultures, which was based on the techniques of Louis Pasteur, Robert Koch, and Carl Julius Salomonsen. After seven years at the Carlsberg Laboratory, Johannsen resigned as research assistant in 1887, but he continued his own research on barley in Copenhagen and at German universities in Zurich, Darmstadt, and Tübingen, relying on external funding and odd jobs.

Johannsen's career in academia began in 1892, when he was hired as a lecturer of botany and plant physiology at the Royal Veterinary and Agricultural College in Copenhagen, despite his lack of a university degree. About this time his work on barley's commercially important traits transformed into a broader research program concerning the nature of heritable variation. Johannsen set out to identify different kinds of variation in plants. His work on plant variation was influenced and inspired by work from the UK's Charles Darwin and Francis Galton, and from that of the Netherlands' Hugo de Vries and France's Louis de Vilmorin, along with the ongoing mentorship of Eugenius Warming.

At the end of the nineteenth century plant biologists had been grappling with the realization that the kind of continuous heritable variation thought necessary for Darwinian evolution, such as fruit size or yield, was not readily detectable in most plant species. Teasing out the various kinds of variation—particularly heritable from non-heritable variation—and their causes had become a research priority for many. Whereas previous statistical approaches to heredity tended to treat the individuals within groups or populations as having essentially the same hereditary disposition, Johannsen directed

his attention to the various hereditary types that might exist within those groups, and sought to characterize the properties of what he called the pure line, or the progeny of a single self-fertilized individual.

Johannsen's first pure line experiments used both barley and the common bean (*Phaseolus vulgaris*). Cultivating pure lines for barley and for the common bean, Johannsen measured the physical dimensions of the seeds produced in every generation. Johannsen found that he could classify the pure lines in his experimental populations with respect to one of these dimensions, for example bean weight, into what he called types. His analysis suggested that, within a pure line, predictions of an offspring's characteristics were best not when based on the actual characteristics of the mother bean, but instead when based on the type to which the mother bean belonged. If the mother bean belonged to the heavy-bean type, the fact that its own weight might be below average would be inconsequential for the weight of its offspring. Johannsen reported the results of these experiments in 1903 in a book titled *Über Erbllichkeit in Populationen und reinen Linien. Eine Beitrag zur Beleuchtung schwebender Selektionsfragen* (On Heredity in Pure Lines and Populations. A Contribution to Pending Questions of Selection). He argued that variation within each pure line was merely somatic—thereby non-heritable—and that natural selection could only discriminate between those various types that might exist in natural populations. Although he left room for the possibility of mutation, he considered the type of each pure line as unalterable by the environments encountered by its members. That conclusion conflicted with the ideas of his mentor, Warming, who had advocated for the inheritance of acquired characteristics as a source of variation upon which Darwinian selection might act. It also placed Johannsen within the camp of Hugo de Vries, who advocated constancy of type as opposed to continuous heritable variation.

In the same year that his book on pure lines was published, Johannsen was promoted to professor ordinarius at the Royal Agricultural and Veterinary College in Copenhagen. Two years later, in 1905, he accepted a professorship in plant physiology at the university of Copenhagen, where he continued his experiments on pure lines. These experiments and their interpretation formed the basis of his concepts of gene, genotype, and phenotype, which he introduced in his 1909 textbook, *Elemente der exakten Erblchkeitslehre* (The Elements of an Exact Theory of Heredity). For Johannsen, the genotype-phenotype distinction was a strategy for moving genetics away from what he referred to as the transmission concept of heredity, according to which parents transmit their own characteristics directly to their offspring. The genotype referred to the ahistoric factors of heredity—the basis of the hereditary types in his earlier publications—while the phenotype referred to the measurable characteristics of the individual organism, under the control of both the genotype and the environment in which the organism developed. Historian of science Jan Sapp has suggested that the genotype-phenotype distinction was intended as a gate-keeper for the practice of heredity research, excluding morphological-descriptive approaches such as those of the biometricians and practical breeders, and allowing researchers to bypass embryological concerns and methods altogether.

Following his experimental work on heredity Johannsen toured the United States, receiving an honorary degree from Harvard University in 1909, and delivering lectures in 1911 and 1912 at Columbia, Johns Hopkins, Harvard, Cornell, Michigan State, Wisconsin State and Illinois State Universities. The Royal Danish Academy of Science elected him as a member. In the middle of the 1910s Johannsen left laboratory work, and he began writing on the history and philosophy of science. He hoped to purify biology of teleological and vitalistic thinking, a goal advanced in his 1914 book *Falske Analogier med henblik paa Lighed, Slaegtskab, Arv, Tradition og Udvikling* (False Analogies with Respect to Similarity, Kinship, Tradition and Development), in which he criticizes the work of philosopher Henri Bergson of France. In 1917 Johannsen was rector of the University of Copenhagen. He remained at Copenhagen until the end of his career and continued to publish about genetics until his death in 1927.

Sources

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