Richard Woltereck (1877-1944) [1]

By: Peirson, B. R. Erick Keywords: Biography [2] Heredity [3]

Richard Woltereck studied aquatic animals around Germany in the early twentieth century, and he extended the concept of *Reaktionsnorm* (norm of reaction) to the study of genetics. He also provided some of the first experimental evidence for the early twentieth-century embryological theory of heredity called cytoplasmic inheritance. Through experiments on the water flea, *Daphnia*, Woltereck investigated whether variation produced by environmental impacts on development could play a role in heredity and evolution [4]. Woltereck's research emphasized the importance of environment and development in Wilhelm Johannsen's concepts of genotype and phenotype. Biologists throughout the twentieth century used Woltereck's concept of *Reaktionsnorm* to develop theories and experiments to explain theevolution [4] of adaptive developmental responses to environmental conditions. Later in his career, Woltereck developed a theory of heredity that sought to reconcile embryological concepts, such as regulation [5] and body plans, with Mendelian heredity and Darwinian evolution [4] by natural selection [6].

Woltereck was born on 6 April 1877 in Hanover, Germany, where he attended a classical secondary school. In 1895 he enrolled in the University of Freiburg [7] in Freiburg im Breisgau, Germany, where he studied medicine and zoology, and trained as an embryologist and evolutionary biologist under the supervision of August Weismann [8]. In 1898 Woltereck received his PhD in zoology at Freiburg for his work on the formation and evolution [4] of the eggs of ostracods, a type of small aquatic crustacean. In July 1898 Woltereck joined the zoologist and deep-sea explorer Carl Chun for a nine-month, 32,000 nautical mile voyage aboard the steam ship *Valdivia* collecting plankton for embryological research. That voyage was the first major German deep-sea exploration, spanning the eastern Atlantic and Indian Oceans, and the Mediterranean Sea. After the voyage ended in May 1899, Woltereck continued to work as an assistant to Chun at the University of Leipzig [9] in Leipzig [10], Germany.

In 1901 Woltereck achieved habilitation, a post-doctoral qualification in the German academic system, for his work on the morphology [11] of marine polychaete [12] and annelid worms [13]. He held the position of*Privatdozent* (private lecturer), a pre-tenure position, at Leipzig [10] between 1901 and 1905, where he continued his work onannelids [14] and lectured on marine zoology, embryology [15], and the morphology [11] and physiology of protozoa [16]. Woltereck attempted to reconstruct the evolutionary history of marine annelids through comparisons of their embryological morphology [11] and development. Woltereck ultimately found this comparative approach unsatisfying, however, and he felt increasingly compelled to address questions about the mechanisms of evolutionary change.

Shortly before his habilitation atLeipzig [10], Woltereck became interested in the consequences of Mendelian inheritance for the study of evolution [4]. At the time, zoologists disagreed with each other about whether or not Darwiniannatural selection [6] acting on traits that vary by degrees within populations of organisms— traits such as fruit sizes in plants or statures in animals—sufficiently explained adaptive evolution [4]. The rediscovery of Mendelian heredity fueled the idea among some zoologists that the predominant mode of evolutionary change was saltatory: new adaptations potentially arose only when, across a few generations, organisms greatly differed in their heritable characteristics. Meanwhile, other zoologists advocated Jean-Baptiste Lamarck's suggestion that environmentally induced phenotypic variations could become heritable, and thereby contribute to the process of adaptation. Woltereck inserted himself into this debate by asking whether continuously distributed traits could be permanently altered, either through artificial selection or exposure to different environments.

The opportunity to conduct research on the mechanisms of heredity andevolution [4] came in 1905, when Woltereck became director of a new biological station in Lunz, Austria. The Biologische Station Lunz—founded by the wealthy father of one of Woltereck's graduate students, Hans Kupelwieser—featured not only exceptional equipment for research in the laboratory, but also a variety of natural ponds spread around the Station's property. Under Woltereck's direction, researchers at the Station experimented with aquatic organisms aimed to clarify the mechanistic relationships between heredity, variation, and adaptation. Woltereck turned over directorship of the Station at Lunz to botanist Franz Ruttner in 1908, as Woltereck's ongoing teaching commitments at Leipzig [10] made it difficult for him to also manage the research facility.

At Lunz, Woltereck experimented with freshwater crustaceans, especially the water flea, as had his teacher Weismann in the 1870s. Woltereck designed his experiments to demonstrate the efficacy of selection on continuous variation in producing lasting evolutionary changes. Woltereck found that some of the *Daphnia's* [17] traits, such as the height of their heads, altered in predictable ways when he raised them in different environments. This result led him to articulate the concept of the *Reacktionsnorm*, or norm of reaction, which refers to the complete set of developmental outcomes possible when the same genotype develops in different environments. Nevertheless, he was ultimately unable to substantiate a lasting response to selection on continuous characters.

Woltereck also discovered that when he exposed the*Daphnia* to an extreme environment—such as a highly enriched nutrient medium—for more than forty generations, the resulting changes in head length would be reliably produced in subsequent generations, even after returning the *Daphnia* to a normal environment. He initially interpreted these results to suggest that environmentally invoked changes in phenotype, such as changes in head height, could become incorporated permanently into the genotype, seemingly corroborating the Lamarckian ideas about the inheritance of acquired characteristics. But Woltereck soon found that this effect would wear off after a certain number of generations, and this, combined with a lukewarm response among his peers, led him to retract his support for Lamarckism [18]. Zoologists would later refer to the persistent modifications in phenotype that Woltereck observed as dauermodifications, which were interpreted in later decades as evidence for embryologists' claims that at least some of the causes of heredity were located in the cytoplasms of eggs.

In 1908 Woltereck helped establish the journal *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, and he promoted it. His vision for the journal was that it would help to integrate research from a wide range of biological and hydrographic fields, and encourage communication between researchers working on freshwater and marine systems. The journal was also intended to move hydrobiologists away from mere descriptions of plant and animal life in aquatic environments and towards investigations of the causes of their occurrence in those environments. The *Revue* remained active into the twenty-first century, having modified its title in 1998 to *International Review of Hydrobiology*.

Woltereck was promoted to associate professor at Leipzig [10] in 1910, but his salary remained insufficient to allow him to quit his work under Chun until 1914, when Woltereck renegotiated his contract with the University. The onset of the First World War prompted Woltereck to take a leave of absence from Leipzig [10], and from 1915 to 1919 he worked at the German embassy in Bern, Switzerland. At the embassy he met the writer Hermann Hesse, a pacifist, and together they established an organization [19] to provide books to German prisoners of war. During the war Woltereck became disillusioned with what he saw as increasingly materialistic individualism in European politics, and he developed strong views that emphasized communitarianism and spiritual values.

The war delayed the publication of much of the results that Woltereck and his students had produced in their *Daphnia* experiments between 1911 and 1914. But when these results finally emerged in book-length form in 1919, with the title *Variation und Artbildung* (*Variation and Species-Formation*), its acclaim among Woltereck's peers led Richard Hertwig to recommend him for head of the Department of Experimental Embryology [20] at the Kaiser-Wilhelm Institute for Biology. Due to financial trouble at the Kaiser-Wilhelm Institute, however, Woltereck did not assume that position until 1923.

The years following the end of the war particularly tried Woltereck, as he struggled with severe depression, and his research productivity dwindled. He continued his political and social activism, however, and founded a progressive political magazine titled *Vivos Voco* with Hermann Hesse in 1919. He also worked to establish cooperatives for the employment of students and academics displaced by the post-war economy, and continued to work with the German prisoners' welfare organization [19] through 1921. At about the same time, Woltereck's views shifted radically from a strong materialism [21] to being almost evangelically anti-materialistic. Historian Jonathan Harwood argues that, by the middle of the 1920s, Woltereck had moved toward holism [22] and vitalism [23]. In 1932 Woltereck published *Grundzüge einer allgemeinen Biologie* (*Foundations of General Biology*), a book in which he attempted to restructure biological methodology in an anti-reductionist and anti-materialist framework. In 1926 he developed a lung infection, preventing him from teaching at Leipzig [10] in the spring and summer of 1927, and further compounding the lull in his research publications.

By the middle of the 1920s Woltereck had developed a more sophisticated theory of variation, heredity, and development. He distinguished between what he called exchangeable or accessory traits, which set apart geographic races of a given species, and constitutive traits, which were part of a species' integrated *Bauplan* (body plan). Exchangeable traits were those controlled by Mendelian factors; they were situated in the chromosomes, could mutate reversibly, and were relatively independent of each other. Selection could act on these exchangeable traits, but it was powerless to modify constitutive traits, whose material basis was extra-chromosomal and non-localizable, and whose evolution [4] proceeded in a spontaneous and law-like fashion. These constitutive traits were highly integrated with each other, so that independent changes in a single trait were not possible. Woltereck thought that the distributed nature of the hereditary determinants of constitutive traits enabled them to direct highly coordinated developmental processes, and to thereby account for the phenomenon of regulation [5]. In this way, Woltereck distinguished between microevolution—selection acting on exchangeable traits—and macroevolution—autonomous and integrated changes in a species' body plans. Although critics pointed to the lack of clear mechanisms in Woltereck's account of macroevolution, many of his peers, both inside and outside Germany, took his ideas seriously.

Between 1913 and 1932 Woltereck worked on a long-term ecological experiment, collaborating with zoologists in Denmark and Italy, in which he attempted to induce heritable morphological changes in a particular strain of *Daphnia* by transplanting them from Denmark to ponds and lakes in Italy. By 1922 Woltereck began to observe morphological changes in the transplanted *Daphnia*, but eventually found that the changes were not heritable. These experiments continued into the early 1930s, but the results were never published. In 1931 and 1932 Woltereck spent sixteen months doing field work on species differentiation [24] in ecologically distinct lakes in Southeast Asia and in the US, a trip funded in part by the Rockefeller Foundation [25], in New York City, New York.

In 1932 Woltereck moved to Turkey to take a job as chair of zoology at an agricultural college in Ankara, but he returned to Germany in 1936 to seek medical treatment for injuries sustained in an automobile accident. Upon his return he sought a personal chair at Leipzig [10], but his request was denied on the basis of negative reviews from organizations in the National

Socialist Party that were uncomfortable with his left-liberal politics. Over the next eight years Woltereck continued to write, publishing a philosophical text titled *Ontologie des Lebendigen* (*The Ontology of Life*) in 1940. Woltereck was a member of the Leopoldina at Halle—a prestigious German academy of science—and the Wisconsin Academy of Sciences, Arts and Letters. He died on 23 February 1944 in Seeon, Germany.

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Richard Woltereck was a German zoologist and hydrobiologist who studied aquatic animals and extended the concept of Reaktionsnorm (norm of reaction) to the study of genetics. He also provided some of the first experimental evidence for the early twentieth-century embryological theory of heredity known as cytoplasmic inheritance. Through experiments on the water flea, Daphnia, Woltereck investigated whether variation produced by environmental impacts on development could play a role in heredity and evolution. Woltereck's research emphasized the importance of environment and development in Wilhelm Johannsen's concepts of genotype and phenotype. Biologists throughout the twentieth century used Woltereck's concept of Reaktionsnorm to develop theories and experiments to explain the evolution of adaptive developmental responses to environmental conditions. Later in his career, Woltereck developed a theory of heredity that sought to reconcile embryological concepts, such as regulation and body plans, with Mendelian heredity and Darwinian evolution by natural selection.

Subject

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