Victor Jollos (1887-1941) [1]

By: Peirson, B. R. Erick Keywords: Dauermodifikationen [2] pure line experimental technique [3]

Victor Jollos studied fruit flies and microorganisms in Europe and the US, and he introduced the concept of *Dauermodifikationen* in the early 1900s. The concept of *Dauermodifikationen* refers to environmentally-induced traits that are heritable for only a limited number of generations. Some scientists interpreted the results of Jollos's work on *Paramecium* [4] and *Drosophila* [5] as evidence for cytoplasmic inheritance. Jollos was forced to emigrate from Germany to the United States due to anti-semitic government policies in the early 1930s. Nevertheless, his work on *Dauermodifikationen* remained central to theoretical discourse among German zoologists concerning heredity, development, and evolution [6].

Jollos was born on 12 August 1887 in Odessa, Ukraine, then a part of Russia. Jollos's parents, Rosa Jurowsky and Gregor Jollos, emigrated to Germany while he was young, and Jollos attended high-school in Heidelberg and Berlin. As an undergraduate at the University of Berlin [7], Jollos studied with zoologist Max Hartmann, who studied reproduction in unicellular organisms.

Jollos also studied with experimental embryologist and protozoologist Richard von Hertwig at the University of Munich [8] in Munich, Germany, where Jollos received his PhD in zoology in 1910. Jollos pursued protozoology, the study of single-celled eukaryotic organisms called protists, after the first taxonomic system for classifying Protozoa was constructed. Jollos's graduate mentor, Hertwig, founded on of the first German protozoological research institutes in Munich in 1885. While Jollos was a student, protozoologists began to publish in their own journals and train new researchers specifically in the field of protozoology. Protozoologists, including Hertwig, preferred to study the large freshwater protist *Paramecium*. *Paramecium* became Jollos's experimental organism of choice for the next two decades.

From 1912 to 1914 Jollos worked as a research assistant at the Robert Koch Institute (RKI), previously called the Prussian Institute for Infectious Diseases, in Berlin. During this time Jollos reported his first observations of *Dauermodifikationen* in *Paramecium*. Jollos used a technique called the pure line experimental technique to study heredity in *Paramecium*. Wilhelm Ludvig Johannsen in Denmark had developed the pure line method for use in plants in the early 1900s, and microbiologist Herbert Spencer Jennings [9] in the US had adapted the method for use with microorganisms in the 1910s.

For his studies, Jollos induced asexual or parthenogenetic reproduction in *Paramecium* to produce lineages of genetically identical individuals. After exposing *Paramecium* from those lineages to an environmental stressor, such as high levels of toxins or extreme heat, Jollos found that the *Paramecium* exhibited new characteristics, such as resistance to specific toxins, that persisted in the offspring for hundreds of generations, even after Jollos removed the stressor from the environments of those lineages. Jollos called those modifications *Dauermodifikationen*, or permanent modifications.

Although Jollos critiqued theories of cytoplasmic inheritance, some embryologists saw Jollos's *Dauermodifikationen* as evidence that the cytoplasm of germinal cells function in heredity. During this period, biologists debated whether the nucleus [10] or the cytoplasm of germ cells [11] was primarily responsible for transmitting characteristics from parents to their offspring. Geneticists, who largely accepted Gregor Mendel's recently rediscovered principles of heredity, said that the nuclei of germ cells [11] contained hereditary material and produced heritable characteristics in organisms as those organisms developed. Many embryologists resisted these claims, however, and maintained that the cytoplasm, not the nucleus [10], of the germ cell was primarily responsible for heredity, either by controlling the action of nuclear genes [12] or by containing hereditary factors themselves. Plasmon theorists, who claimed that the traits characteristic of taxonomic groups above the rank of species—groups such as genera, classes, and orders—are rooted in cytoplasmic factors rather than nuclear genes [12], also claimed *Dauermodifikationen* as evidence of cytoplasmic inheritance.

With the onset of World War I [13] in 1914, Jollos left his newly-acquired post as acting director of the protozoology department at RKI to pursue medical qualifications for the war effort. Jollos studied medicine at the University of Berlin [7], and he passed his *Medizinisches Staatsexamen* (state medical exams) in 1918. When the war ended, Jollos resumed his experimental work as a research assistant at the Kaiser Wilhelm Institute [14] for Biology (KWI), in the Dahlem district of Berlin, where he remained until 1925. In 1920 Jollos married pianist Ilse Raven, with whom he later had two daughters, Eva and Inge. From 1921 to 1925 Jollos also held the position of *privatdozent* (private lecturer), a pre-tenure position, at the University of Berlin [7].

In 1925 Jollos relocated to Cairo, Egypt, upon the invitation of the Egyptian Government. As a professor at the Egyptian University in Cairo, Jollos organized the new zoology department. Meanwhile, Jollos became special adviser to the Egyptian Ministry of Agriculture in Cairo, concerning sheep [15] and poultry breeding experiments. Jollos also served as president of the Royal Zoological Society of Egypt in Cairo, and he sat on the board of examiners for medical and veterinary schools in Cairo. In 1929 Jollos returned to the KWI in Berlin, where he oversaw a research laboratory in Max Hartmann's Department for

Protistology. Jollos was also reinstated at the University of Berlin [7], where he became an associate professor of zoology.

Jollos saw his experimental work as a contribution to the theory of orthogenetic evolution [6]. Wilhelm Haacke, director of the Natural History Museum in Adelaide, Australia, coined the term orthogenesis [16] in his 1883 book *Gestaltung und Vererbung* (Design and Inheritance). Zoologist Theodor Eimer in Tübingen, Germany, further articulated and promoted the theory of orthogenesis [16] in his 1888 book *Die Entstehung der Arten auf Grund von Vererben erworbener Eigenschaften nach den Gesetzen organischen Waschsens* (Organic Evolution as the Result of the Inheritance of Acquired Characters According to the Laws of Organic Growth). Haacke and Eimer said that natural selection acting on random mutations couldn't explain patterns of directional change in the fossil record, such as the sequential reduction [17] of limbs in the evolution [6] of snakes. Orthogenesists claimed that such directional change involved either an external directive force, or constraints internal to the organism that determined specific directions in which a species could evolve. Jollos theorized that one source of directionality in evolution [6] was directed mutation, the claim that environmental factors, such as high temperature, could elicit specific and predictable heritable mutations.

After returning to Berlin in 1929, Jollos read a report on a new method for producing mutations in fruit flies (*Drosophila melanogaster* [18]) published by geneticist Richard Goldschmidt [19], who was also affiliated with the KWI. Over the next five years Jollos used Goldschmidt's method, which involved exposing *Drosophila* [20] larvae to high temperatures at a key point in their development. That method enabled Jollos to investigate the capacity of environmental factors to produce directional mutations in *Drosophila* [20] for eye color. In the course of those experiments, Jollos generated mutations in what he claimed were orthogenetic series. For example, when Jollos exposed larval flies to high temperatures, those flies developed into adults with light colored eyes, a phenomenon that intensified when he applied the same technique to the flies' offspring. Jollos interpreted these results to corroborate orthogenetic theory, and he thought them consistent with observations from paleontologists, who said that periods of climatic warming correlated with high frequencies of speciation.

Although Jollos was raised as a Protestant, he had Jewish ancestry, and he fell victim to antisemitic policies that took effect with the installation of Adolf Hitler as chancellor of the Third Reich in 1933. Jollos was expelled from his post at the KWI in autumn of that year. Unable to acquire a job in Germany, Jollos and his family emigrated to the UK, where he worked in Francis A. E. Crew's animal breeding lab at the University of Edinburgh [21] in Edinburgh, Scotland, in early 1934. In late 1934 Jollos accepted a fellowship from the Institute of International Education, headquartered in New York, New York, via the Emergency Committee in Aid of Displaced German Scholars, as well as an offer of research facilities at the University of Wisconsin in Madison, Wisconsin.

Jollos lacked incubators for his heat induction [22] experiments for the first six months of his time at the University of Wisconsin. Even with the incubators, Jollos struggled to continue his research given his financial woes. When Jollos's fellowship from the Emergency Committee ended in summer of 1935, he obtained no academic employment, despite the efforts of Goldschmidt and fellow protozoologist Tracy Morton Sonneborn. Jollos and his family were supported financially by temporary funding from the National Coordinating Committee for Aid to Refugees and Emigrants Coming from Germany, honoraria from guest lectures, and a few friends at the university. Jollos's lack of research funding prevented him from continuing the heat induction [22] experiments. With the help of colleagues, Jollos secured limited funding from the National Research Council's Committee on Radiation, headquartered in Washington, D.C., to investigate the mutagenic effects of cosmic radiation [23] in Drosophila [20].

In autumn of 1937 the University of Wisconsin rescinded Jollos's access to laboratory facilities. That year, Jollos suffered two heart attacks. Already suffering from diabetes, his health deteriorated rapidly. In 1937 Jollos completed a lecture tour in the eastern US, visiting Yale Univerity, Johns Hopkins University, the University of Rochester, and Amerherst University. Jollos died on 5 July 1941, at the age of 54, leaving his family in poverty.

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Subject

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