Paul Kammerer (1880-1926) [1]

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Paul Kammerer conducted experiments on amphibians [3] and marine animals at the Vivarium, a research institute in Vienna, Austria, in the early twentieth century. Kammerer bred organisms in captivity, and he induced them to develop particular adaptations, which Kammerer claimed the organism's offspring would inherit. Kammerer argued that his results demonstrated the inheritance of acquired characteristics, or Lamarckian inheritance. The Lamarckian theory of inheritance posits that individuals transmit acquired traits to their offspring. Kammerer worked during a period in which scientists debated how variation between organisms and within species was caused, and how organisms could inherit that variation from their parents. Kammerer contended that the inheritance of acquired characteristics occurs during embryological development, but several scientists argued that he provided poor evidence for his claims.

Kammerer was born to Sofie Kammerer and Karl Kammerer in Vienna, Austria, on 17 August 1880. Sofie Kammerer, a pianist from Hungary, had two sons from a previous marriage, while Karl Kammerer, the founder and co-proprietor of a factory for optical instruments in Vienna, had one son from a previous marriage. During his childhood, Kammerer studied music and nature. Kammerer started his academic career studying music at the Vienna Academy in Vienna, Austria. He later pursued science, as well as music, at the University of Vienna, Austria.

When he was twenty-two, in 1902, Kammerer joined the Institute for Experimental Biology at the Vivarium in Vienna, Austria, as an assistant. He worked with zoologist Hans Przibram and soon began dissertation work. His initial experiments including breeding salamanders (Salamandra maculosa [4] and Salamandra atra [5])in captivity to record any physiological adaptations they developed in response to the changing environment. While researching at the Vivarium, Kammerer received a doctorate in zoology from the University of Vienna in 1904.

In 1905, Kammerer met the Baroness Felicita Maria Theodora von Wiedersperg, whom he married in 1906. The two had a daughter, Lacerta, one year later. Throughout his life, Kammerer had several affairs, including liaisons with dancer Grete Wiesenthal, painter Anna Walt, and musician Alma Malher. In 1906, Kammerer became a lecturer at the University of Vienna.

In his first series of experiments at the Vivarium, Kammerer took Alpine salamanders (Salamandra atra), which are born fully developed and typically live in a dry environment, and he bred them in a moist environment. Depending on the type of environment in which salamanders live, the offspring are born either fully developed or as tadpoles. Salamanders that live in a moist environment give birth to tadpoles, which develop into adult forms after birth. In Kammerer's experiment, Alpine salamanders bred in a moist environment gave birth to tadpoles capable of living in the water. Additionally, Kammerer bred spotted salamanders (Salamandra maculosa) in a dry environment. Salamanders in this species typically live in a moist environment and are born as tadpoles, before growing into adult form. The bred salamanders had a longer gestation [6] period and gave birth to fully developed individuals. These offspring skipped the tadpole stage that required water.

While conducting breeding experiments between 1902 and 1907, Kammerer claimed that subsequent generations of salamanders had inherited the characteristics previously acquired as adaptations to a new environment. Kammerer published the results of his breeding experiments on salamanders in 1904 and 1907. For his experiments on salamanders, the Natural Science Society of Frankfurt awarded Kammerer the Sömmering Prize for Fundamental Discoveries in Physiology in 1909.

Kammerer later conducted another series of experiments involving the midwife toad (Alytes obstetricans [7]). Whereas toads generally mate in the water, the midwife toad mates on land. Typically, male toads in other species develop black swellings on their palms and fingers to clasp the female during the mating season, called nuptial pads. Due to the dry environment in which they live, female midwife toads generally have dry and course skin, so male midwife toads do not develop such nuptial pads. Kammerer bred midwife toads in a moist environment for several generations. Kammerer found that the offspring developed nuptial pads and also that subsequent offspring seemed to have inherited this characteristic. The results of Kammerer's experiments on the midwife toad were published in 1906.

Scientists debated how to interpret Kammerer's midwife toad results. Scientists from different fields attempted to repeat Kammerer's experiments. William Bateson [8] from the UK visited the Vivarium in 1910, and Kammerer reportedly denied to send specimens for Bateson to observe. At the time of his visit, which occurred in the fall, the toads did not display any nuptial pads, as
the pads generally become apparent in the spring, with mating season. A few months later in the same year, Bateson wrote a letter to Kammerer asking for the original midwife toad specimens, which Kammerer never sent.

Among the experiments Kammerer conducted at the Vivarium, one series involved \textit{Ciona intestinalis}, a species of tunicates, or marine invertebrates called sea squirts. Sea squirts have two tube-like structures protruding from their heads called oral siphons. Kammerer cut away the two siphons on various live specimens and observed that the siphons grew back to be longer than in their original form. Kammerer bred sea squirts with this induced characteristic of longer siphons and recorded that the offspring inherited longer than normal siphons.

During World War I, like many institutions at the time, research and work at the Vivarium was limited. Kammerer served with the military censor department while also working intermittently on articles and various works. During this period, most of Kammerer's animals from his experiments died and he was unable to preserve viable specimens for the many of those he had worked with, save a few. In 1915, Kammerer published a textbook \textit{Allgemeine Biologie} [General Biology], and four years later in 1919 he published the monograph \textit{Das Gesetz der Serie} [The Laws of Series], in which he attempted to explain the phenomenon of coincidence from a scientific perspective. In the same year, critics of Kammerer's work incited another controversy in the journal \textit{Nature}, arguing that they had again repeated Kammerer's midwife toad experiments but obtained different results.

During a 1923 lecture given in Cambridge, England, Kammerer cited the experiments he conducted on \textit{C. intestinalis} before 1914. He claimed that the results of his work demonstrated the hypothesis of the inheritance of acquired characters. A few months after Kammerer's visit to Cambridge, zoologist Harold Munro Fox published a letter arguing that he had repeated the experiments on \textit{C. intestinalis} but did not obtain the same results as Kammerer. Kammerer replied that, after reviewing the literature, he had found that zoologist Pio Mingazzini had conducted the same experiments on sea squirts at the Zoological Station in Naples, Italy, in the 1890s, and had obtained the same results as Kammerer had.

In 1923 and 1924, Kammerer traveled the US and the UK to continue lecturing and writing. During lectures, he displayed specimens that he had managed to preserve, including a midwife toad. In 1924, he published an English translation of his book \textit{The Inheritance of the Acquired Characteristics}. In this book, Kammerer describes the different experiments he conducted. He describes his experiments as substantial evidence to support Jean Baptiste Lamarck's early nineteenth century theory of inheritance, called the inheritance of acquired characteristics. Additionally, in this book Kammerer details the debates surrounding his breeding experiments.

Two years later in 1926, Kammerer left his laboratory space and specimens to the Vivarium and took a position as director of a laboratory to be built by the Communist Academy in Moscow, USSR. In the 1920s and 1930s in Europe and the Soviet Union, some proponents of socialism supported Lamarck's hypothesis of the inheritance of acquired characters, which Kammerer claimed to be able to demonstrate. Proponents of this view also supported scientific research on the impact that environmental factors can have on species, including \textit{humans}. Kammerer left Europe to conduct work in the Soviet Union to avoid some of the controversies created by his experiments.

In the meantime, Gladwyn K. Noble, Curator of Reptiles at the American Museum of Natural History in New York, New York, visited the Vivarium and analyzed Kammerer's preserved midwife toad specimen, as well as photographs from Kammerer's experiments. Noble claimed that Kammerer's specimen was a fake, as the specimen reportedly contained black ink on its fingers and reportedly lacked any indication of pads. Noble claimed that Kammerer had deposited ink, and possibly attached other items on specimens, to create the illusion of nuptial pads.

Hans Przibram, head of the zoological department at the Vivarium, agreed that the specimen could no longer be used as evidence for Kammerer's results. However, he claimed that this specimen, and others that were not preserved, did indeed contain nuptial pads, which had possibly deteriorated with time due to poor preservation techniques. Przibram provided cross sections of several other specimens that appeared to contain nuptial pads. He also contacted individuals and scientists to solicit eye witness accounts of the specimens as Kammerer presented them several years earlier.

On 7 August 1926, Noble published a letter in \textit{Nature} in which he argued that Kammerer had faked his experiments and falsified his results. On 23 September 1926, Kammerer apparently committed suicide. His corpse was found on the top of a mountain in Puchberg am Schneeberg, Austria, and a gun was found in his hand. The controversies surrounding Kammerer's experiments continued after his death. In 1929, the Soviet Union produced a film, titled \textit{Salamandra}, which supported Kammerer's research and attempted to give evidence for the inheritance of acquired characteristics. Historians of science in the twentieth and twenty-first centuries debated Kammerer's results, as well as the claims made by his critics.

Sources
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