

# Re-examination suggests Paul Kammerer's scientific 'fraud' was a genuine discovery of epigenetic inheritance

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At left, the controversial scientist Paul Kammerer. Upper right: An image of the fingers of an experimental male midwife toad, showing a rugose nuptial pad (red arrow). Lower right: A schematic illustration from a paper by Kammerer of an

experimental water-breeding male midwife toad. Credit: Universidad de Chile

Paul Kammerer committed suicide in 1926 after being accused of fraud in his famous experiments of "inheritance of acquired traits" with the midwife toad. A new study shows how recent advances in molecular epigenetics and re-examination of his descriptions suggest the experiments were actually authentic.

The alleged scientific fraud by Paul Kammerer is perhaps one of the most controversial mysteries in the history of biology. In the early 20th century, he was a famous evolutionary scientist, hailed as a "new Darwin" in the pages of the *New York Times*. His experiments provided impressive evidence that environmental life experiences could have a direct, inheritable effect on progeny, as maintained by his intellectual predecessor Lamarck, and by Darwin himself. In one of his most famous experiments, Kammerer had shown how a normally terrestrial species, the midwife toad, could be made to live and mate in water when kept in an artificially heated environment. These modified "water" toads laid eggs that grew into toads with an innate preference to live and mate in water, even when raised in normal, unheated environments. In successive generations of water toads, Kammerer reported that male toads developed nuptial pads on their fingers. These are rough, dark-colored thickenings of skin that are usually absent in midwife toads, but present in other water-loving species, which use them to grasp females during copulation. Additionally, Kammerer crossed one of his modified "water" males with a normal, untreated land female, obtaining 100% water toads in the first generation, and about three-quarters water toads in the second generation. Thus, modified traits were being inherited according to Mendel's rules of genetics, the same that most of us were taught in high school.

In 1926, fellow scientist G.K. Noble examined a fixed and worn-out specimen of an experimental "water" toad. Noble found that the fingers had been injected with india ink to create an artificial resemblance to nuptial pads. A huge scandal ensued, placing Kammerer's entire scientific legacy into question. Kammerer committed suicide shortly after, and although he left letters maintaining that his results were authentic, many interpreted the suicide as an admission of guilt. Thus, Paul Kammerer became a symbol of scientific fraud, as well as a powerful story about the ultimate failure and scientific invalidity of studies in the "inheritance of acquired traits." This view of Kammerer has continued to be the mainstream opinion, although some voices have defended his innocence. Soviet contemporaries did not accept the fraud accusations, and even made a popular propaganda film, "Salamandra" (1928), that narrated how Kammerer (who was a leftist jew) had been framed by his enemies in the wake of Austrian Nazism. In the 1970's, the renowned journalist Arthur Koestler wrote a famous book, "The case of the midwife toad," which pointed out several problems with the fraud accusations, including the fact that the specimens had been observed by several experts, who should not have been easily fooled by crude ink injections.

It is no secret that even today, the "inheritance of acquired characteristics" is often treated as an impossibility, supposedly discarded by experiments such as the amputation of the tail of mice during successive generations, which never leads to mice being born without tails. It was argued that no special mechanism existed by which environmental change could directly modify inheritance, and that every apparent case could be ultimately explained by indirect effects of natural selection and conventional genetics. But these views started to change drastically since the 1990's, along with the progress in techniques to study molecular genetics. These uncovered several molecular mechanisms, such as DNA methylation, that could directly change inheritance in response to the environment. The modern field of

epigenetics studies those changes in gene expression that do not involve a mutation, but are nevertheless inherited in absence of the signal or event that initiated the change. During the 21st century, experiments in mice have reported such inheritable modifications, identifying the relevant genes that have been altered by epigenetic mechanisms.

In light of these recent ground-breaking discoveries, a team of scientists from the University of Chile (Alexander Vargas), the Technical University of Munich (Quirin Krabichler) , and Linköping University (Carlos Guerrero-Bosagna) have re-examined Kammerer's descriptions of the midwife toad experiments, and have published their conclusions yesterday in the Journal of Experimental Zoology. The situation is perhaps analogous to detectives analysing a journal that describes numerous murders in great detail: There are many opportunities to find out whether it fits with reality, or is merely a work of fantasy. If some of the alleged data in Kammerer's papers were entirely extraordinary, beyond known phenomena or explanatory mechanisms, we should remain cautious. If, in turn, science offers experimental evidence that matches Kammerer's reports down to specific details, we may consider a greater likelihood of their authenticity.

The team concluded that Kammerer's descriptions are completely within the realm of possibilities uncovered by modern epigenetics. This in itself is an important alternative to fraud and the alleged impossibility of the experiments. However, they additionally confirmed a very special detail about the experiments: Dominance in hybrid crosses would depend on the sex of the toads, such that if Kammerer now crossed a land male with a water female, the first generation would be 100% land toads, and the next,  $\frac{3}{4}$  land toads. Such switches in dominance according to sex (also known as "parent of origin effects") have been known to scientists for a long time, but have only recently been understood to result from epigenetic mechanisms. Kammerer and other Lamarckians never placed any importance on this detail, which was mentioned as little more than a

curiosity. However, since epigenetic mechanisms produce these effects in several modern experiments, it provides a very specific resemblance, that strongly suggests the authenticity of the midwife toad experiments. There is no good reason why Kammerer would invent such a detail if his descriptions were a mere work of fantasy.

The new in-depth study of Kammerer's descriptions has also clarified several important details about the experiments, which are shown to favor an epigenetic mechanism over other discussed alternatives. Recent claims that Kammerer would provide changing and unreliable accounts of his experiments are also conclusively discarded by the new study. Gunter Wagner, an evolutionary geneticist and professor at Yale University, calls the new study an "exciting read" and "the most in depth analysis of Paul Kammerer's primary publications to date, and the only one that has been performed in the light of recent biological knowledge on epigenetics."

Why did so many of Kammerer's contemporaries disbelieve the experiments? Most likely, they were conceptually unprepared to understand the results, many of which are puzzling and hard to make sense of without a modern knowledge of epigenetic molecular mechanisms. An especially important contemporary of Kammerer was William Bateson, who coined the word "genetics." Bateson described the results of Kammerer's hybrid crosses as "most astounding," but doubted their reality, arguing that until they were clearly demonstrated and confirmed, "we are absolved from basing broad conclusions on his testimony."

Indeed, Kammerer had a unique way of thinking for his time. While most of his contemporaries would split into opposite "Mendelian" and "Lamarckian" bands, he combined the experimental principles of both schools of thought. He was also unusual among Lamarckians in that he did not believe that the inheritance of acquired traits was necessarily

progressive or beneficial, but could also produce neutral or detrimental traits.

The new paper by Vargas, Krabichler and Guerrero-Bosagna coincides with the very recent publication of a new book in German, "Der Fall Paul Kammerer" ("The case of Paul Kammerer") by journalist Klaus Taschwer. This book provides abundant new historical data on the strange circumstances surrounding the discovery of the ink-injected nuptial pads, strongly suggesting that Kammerer was indeed framed. Combined with the scientific approach of Vargas et al., there is now more evidence than ever that suggests the authenticity of the midwife toad experiments. Conclusive evidence, however, can only come from renewed experimentation with the midwife toad. New molecular techniques would allow a quick assessment of epigenetic mechanisms, and important advances have already been made that demonstrate epigenetic inheritance and parent of origin effects in other amphibians. To further encourage new research in the midwife toad, Vargas et al have included a model of epigenetic mechanisms that can explain Kammerer's results through specific assumptions, that can be experimentally tested. Renewed research in the [midwife toad](#) may not only give closure to one of the most intriguing mysteries in the history of biology, but it is also likely to generate important scientific advances on how epigenetic mechanisms work in evolution and adaptation.

Modern epigenetics may clear Kammerer's name, and is already carrying out what is likely to be his unfulfilled contribution to science. In an ironic final paragraph of his paper on hybrid crosses, Kammerer alludes to the fact that Mendel himself was overlooked in his lifetime: "May my work fare better than its great predecessor written by Mendel; may it find its useful application in science and economy before the author's death and before the passing of many decades!"

**More information:** ALEXANDER O. VARGAS et al. An Epigenetic

Perspective on the Midwife Toad Experiments of Paul Kammerer (1880-1926), *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* (2016). [DOI: 10.1002/jez.b.22708](https://doi.org/10.1002/jez.b.22708)

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