Expanded version of a talk given at the Symposium & 9th Altenberg Workshop in Theoretical Biology, sponsored by the Konrad Lorenz Institute and the Austrian Academy of Sciences, Vienna and Altenberg, Austria, 2002.

The Spoiler: Paul Kammerer's Fight for the Inheritance of Acquired Characteristics

SANDER GLIBOFF
Indiana University

Abstract. In scientific controversy, as in sports, there are winners and losers, but sometimes also spoilers—unheralded outsiders, who defy convention and change the terms, the style, and the outcome of the competition, even if they cannot win it themselves. In the fight over the inheritance of acquired characteristics in the 1910s and 1920s, Paul Kammerer was the spoiler. His dramatic experimental results and provocative arguments surprised the established stars of genetics and evolution and exposed their weaknesses, particularly their inability to agree on the nature and causes of variation or on a better explanation of Kammerer's results than Kammerer's own "Lamarckian" one.

Keywords: Genetics, Evolution, Variation, Mutation, Lamarckism, Old-School Darwinism, Paul Kammerer, Midwife Toad, Germany, Austria, Early 20th Century.

Introduction

In scientific controversy, as in sports, there are usually winners and losers, but in Paul Kammerer's fight for the inheritance of acquired characteristics in the 1910s and 1920s, the outcome was not so simple. To be sure, Kammerer's precise ideas about the inheritance of acquired characteristics never were born out and had little support, even among avowed "Lamarckians" at the time. Even worse, his suicide in 1926, following the midwife-toad scandal, silenced the few allies still with him, and sealed his posthumous reputation as a fraud. Yet Kammerer's work had caused repeated uproars in the scientific literature and elicited vehement, but contradictory rebuttals from the champions of Darwinism, neo-Darwinism, and Mendelism. Especially when it came to accounting for the nature and origin of heritable variations, Kammerer's opponents were in disarray and had a hard time defeating him.

In this paper, I treat Kammerer as that special kind of loser, known to sports fans as the "spoiler": the unheralded outsider, whose unconventional tactics allow him to surprise and embarrass the established stars of his discipline and expose their weaknesses. I retell the story of Kammerer's life and work, showing how he used his outsider's position and unique laboratory results to provoke the experts and sow confusion in their ranks.

By this interpretation, the Kammerer controversy was not simply about Kammerer's results or his specific hypotheses, or even the inheritance of acquired characteristics more generally, but also about *how else* heritable variation might be produced, if not by Kammerer's preferred mechanisms. The only thing Kammerer's opponents could agree on, was that Kammerer could not be right.

Protoplasm was "soft wax in our hands," according to Paul Kammerer, or like "hard steel in the hands of the machinist,"[1] and he knew how to effect changes in animal form and behavior. From around 1904 until the outbreak of the First World War, Kammerer's skilled hands made spotted salamanders became striped; land salamanders produce larvae with gills and water-breeders skip their aquatic larval stages. He made blind cave salamanders develop functional eyes; sea squirts dramatically increase the length of their siphons; mural lizards change their colors; tree frogs and midwife toads change their reproductive behaviors.[2]

Kammerer's best-remembered transformation was one of several on the midwife toad.[3] The toad normally mates on land, where the male first coaxes the strand of eggs from the female in a manner reminiscent of a midwife, then attaches the strand to his own hind legs for brooding. At a later stage, the male takes the eggs to the water, where the larvae hatch and swim away, breathing through external gills.

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1. Paul Kammerer, *Das biologische Zeitalter: Fortschritte der organischen Technik* (Vienna: Verein Freie Schule, [1920]), 8 & 1.

2. Paul Kammerer, "Adaptation and Inheritance in the Light of Modern Experimental Investigation," *Annual Report of the Board of Regents of the Smithsonian Institution* (1912): 421–441 + 8 plates, provides an overview in English.

3. Paul Kammerer, "Experimentelle Veränderung der Fortpflanzungstätigkeit bei Geburtshelferkröte (Alytes obstetricans) und Laubfrosch (Hyla arborea)," *Archiv für Entwicklungsmechanik der Organismen* 22 (1906): 48–140 + Taf. V; Paul Kammerer, "Vererbung erzwungener Fortpflanzungsanpassungen, III. Mitteilung: Die Nachkommen der nicht brutpflegenden Alytes obstetricans," *Archiv für Entwicklungsmechanik der Organismen* 28 (1909): 447–545 + Taf. XVI–XVII; Paul Kammerer, "Vererbung erzwungener Formveränderungen, I. Mitteilung: Brunftschwiele der Alytes-Männchen aus 'Wassereiern,'" (Zugleich "Vererbung erzwungener Fortpflanzungsanpassungen, V. Mitteilung"), *Archiv für Entwicklungsmechanik der Organismen* 45 (1919): 323–370.

In the most controversial experiment, Kammerer subjected midwife toads to elevated temperatures that compelled them to spend more and more of their time in the water, until they even began mating there. But then the egg strands would not stick to the male's hind legs any more. They swelled with excess water and drifted away.

The few eggs that survived under these conditions grew into a second generation of toads that again mated in the water and failed to brood their eggs, regardless of whether they had been raised at the elevated temperature or at normal room temperature. It appeared, then, that the water-breeding behavior had been inherited. Even more remarkable, from the third generation on, males of the water-breeding line developed an anatomical feature resembling the "nuptial pads" of related species of frogs: dark, rough patches that appear on the front legs of the male during the breeding season, with which they grasp slippery females.

According to Kammerer, these and other comparable results demonstrated, first, that environmental factors induced behavioral and morphological changes in the animal body, or somatoplasm; and, second, that these changes could become hereditary after being communicated somehow to the hereditary material, or germplasm. This general view of the origin of variation was sometimes called "somatic induction," a form of Lamarckianism or inheritance of acquired characteristics. Kammerer also claimed more specifically that the somatic change was communicated to the chromosomes and caused new Mendelian genes to form. That made him one of the first "Lamarckians" to embrace the chromosome theory and attempt an evolutionary synthesis with genetics.

As is well known, Kammerer's career ended in scandal and suicide in 1926, when it was revealed that his last intact specimen of a modified midwife-toad had been injected with India ink where the nuptial pads were supposed to be.[4] Kammerer's opponents interpreted his suicide as an admission of guilt and claimed that he had not only tampered with that specimen, but had fabricated most or all of his other results as well.

In the Whig history of science, Paul Kammerer has therefore gone down as a two-time loser: once for being on the wrong side—the Lamarckian side—of the fight over the inheritance of acquired characteristics, and again for using dubious, if not fraudulent methods to support his false ideas.

There is also an anti-Whig version of the story, written by Arthur Koestler

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4. G. Kingsley Noble, "Kammerer's Alytes (1)," *Nature* 118, no. 2962 (Aug. 7, 1926): 209–210.

in The Case of the Midwife Toad.[5] There the roles are reversed: the Darwinian side was doubly in the wrong. They used dubious, if not fraudulent methods to discredit Kammerer, and they never answered the challenge that his work represented. They never really disproved the inheritance of acquired characteristics and never came up with anything better than blind chance to explain the origin of favorable variations.

Although the Whig- and anti-Whig stories are ostensibly polar opposites, they agree on several historical points, on which, as I shall argue, they are both wrong. They assume that there were—and still are—only two sides in the controversy, the "Lamarckian" and the "Darwinian," that one side's loss was automatically the other's gain, and that Kammerer was the champion of the Lamarckian side.

The Field and the Fight

In the early twentieth-century context, the sides were not drawn so clearly, especially since Kammerer counted himself as a good Darwinian, despite his belief in the inheritance of acquired characteristics. He was not a neo-Darwinian, of course, but from the earlier German school of Ernst Haeckel, for whom Lamarckian environmental effects were a necessary source of heritable variation, as they had been for Darwin himself.

Furthermore, there were multiple Lamarckian factions in the early 20th century, most of whom rejected Kammerer's results and conclusions, despite their general agreement on the heritability of acquired characteristics. They objected variously to his experimental approach, his assumptions about genes and chromosomes, or his strict materialism that denied a role for the mind and the perceived needs of the organism in guiding evolution.

The rest of Kammerer's opponents were also a diverse group, consisting of Darwinians, neo-Darwinians, Mendelians and other saltationists, and orthogenecists. There was no unified Darwinian side that was vindicated by Kammerer's downfall, any more than there was a Lamarckian side that stood and fell with him.

One important anti-Kammerer group were the neo-Darwinians, followers of August Weismann, who denied the possibility of any mode of inheritance of acquired characteristics. Weismann argued for a strict isolation of the germplasm. No matter what somatic changes the environment might effect,

5. Arthur Koestler, *The Case of the Midwife Toad* (London: Hutchinson, 1971).

they could not be communicated even in principle to the hereditary material..[6] Weismann himself took a stand against Kammerer, as did his student Heinrich Ziegler.

Within the Darwinian camp, but opposed to Weismann were Kammerer's most likely potential allies, the "old-school Darwinians," as I shall call them, including Ernst Haeckel, Richard Semon, and Ludwig Plate. (There does not seem to be a good term in English for Darwinians of the non-neo persuasion.) They criticized Weismann for failing to provide a satisfactory explanation of variation. How were new and timely adaptive variations supposed to arise in an isolated germplasm? Weismann's system seemed to them to require vitalism or predestination.[7]

Yet even among the old-school Darwinians, opinions diverged on the mechanisms by which characteristics might be acquired and inherited. Haeckel and Semon favored the idea of a kind of protoplasmic memory that allowed the developing embryo to "remember" and recreate the sequence of changes that its ancestors underwent. Environmental effects could become heritable by causing new developmental steps to be inserted into the memorized sequence. Semon in particular elaborated the memory analogy into a full-fledged theory of heredity and development and an alternative to both Weismannism and Mendelism.[8]

Other old-school Darwinians were more open to the new genetics and looked for ways of reconciling it with the inheritance of acquired characteristics.

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6. August Weismann, "Zur Frage nach der Vererbung erworbener Eigenschaften," *Biologisches Centralblatt* 6 (1886): 33–48; August Weismann, *Das Keimplasma: Eine Theorie der Vererbung* (Jena: Gustav Fischer, 1892).

7. Ernst Haeckel, "Zur Phylogenie der australischen Fauna: Systematische Einleitung," introduction to *Zoologische Forschungsreisen in Australien und dem malayischen Archipel: Mit Unterstützung des Herrn Dr. Paul von Ritter, ausgeführt in den Jahren 1891–1893*, by Richard Semon (Jena: Gustav Fischer, 1893); Ludwig Plate, *Selektionsprinzip und Probleme der Artbildung: Ein Handbuch des Darwinismus*, 4th ed. (Leipzig and Berlin: Wilhelm Engelmann, 1913).

8. Ernst Haeckel, *Die Perigenesis der Plastidule: Oder die Wellenzeugung der Lebenstheilchen: Ein Versuch zur mechanischen Erklärung der elementaren Entwickelungs-Vorgänge* (Berlin: Georg Reimer, 1876); Richard Semon, *Die Mneme als erhaltendes Prinzip im Wechsel des organischen Geschehens*, 2nd ed. (Leipzig: Wilhelm Engelmann, 1908); Richard Semon, "Die somatogene Vererbung im Lichte der Bastard- und Variationsforschung," *Verhandlungen des naturforschenden Vereines in Brünn* 49 (1911): 241–265.

Plate pursued a dual strategy of accepting genes and chromosomes, while maintaining that there also had to be additional, non-genic mechanisms of heredity.[9] Kammerer, in contrast to Plate, Semon, and even some of the Mendelians, was willing to embrace the gene concept and chromosome theory as sufficient to account for all of heredity, as long as there was room for environmental effects to produce new genes.[10]

Challenges to Darwinians of all stripes, came from the saltational theories that were on a roll after 1900. They drew support from the success of Mendelism, which they interpreted as requiring evolution to proceed by discrete jumps from one stable hereditary form to another. Saltational theories minimized or eliminated the roles of both natural selection and of gradual, incremental environmental effects. As discussed in detail below, Kammerer's most vocal critics, including William Bateson and Erwin Baur, along with more moderate voices such as Richard Goldschmidt, came from the Mendelian-saltationist camp. The saltationists had a conception of variation by "mutation," but there was no consensus on the physical nature and causes of such a thing, as the Kammerer controversy revealed.

Lamarckism was also flourishing, but the term meant different things to different people. Some stressed the direct effects of the physical environment;[11] the modifying effect of the organism's needs, either with[12] or without[13] a mediating role for the psyche; or the natural tendency to rise up the animal scale or at least to progress in certain directions.[14] Lamarckian ideas on

9. Plate, *Selektionsprinzip und Probleme der Artbildung.*

10. Paul Kammerer, "Mendelsche Regeln und Vererbung erworbener Eigenschaften," *Verhandlungen des naturforschenden Vereines in Brünn* 49 (1911): 72–110.

11. J. T. Cunningham, "The Evolution of Flat-Fishes," *Natural Science: A Monthly Review of Scientific Progress* 1 (1892): 191–199.

12. August Pauly, *Darwinismus und Lamarckismus: Entwurf einer psychophysischen Teleologie* (Munich: Ernst Reinhardt, 1905).

13. H. Graham Cannon, *Lamarck and Modern Genetics* (Manchester: Manchester University Press, 1959).

14. Carl Nägeli, *Mechanisch-physiologische Theorie der Abstammungslehre* (Munich: R. Oldenbourg, 1884); to some extent also [Gustav Heinrich] Theodor Eimer, *Die Entstehung der Arten auf Grund von Vererben erworbener Eigenschaften, nach den Gesetzen organischen Wachsens*, 3 vols. (Jena: Gustav Fischer, 1888–1901).

hereditary mechanisms and responses to genetics and experimental approaches like Kammerer's were also many and varied.

Anyone who thinks science makes progress by falsifying and eliminating theories would have to be dismayed by the state of evolutionary biology in the early twentieth century. The theories had been proliferating for decades and there seemed to be no prospect of knocking any of them out, without opening new lines of experimental inquiry.

The Vivarium

Calls for experimentation and for the building of new kinds of biological laboratories (i.e., not designed for physiology and medicine) could be heard from various evolutionary factions in Britain, France, and the U. S.[15] The Station for Experimental Evolution at Cold Spring Harbor was an important product of these efforts in 1904. In Germany, the cytologist Theodor Boveri gave voice to similar aspirations in a 1906 call, with a Lamarckian slant, for the a state-supported laboratory for the study of evolution and heredity.[16] He eventually got his wish when he was entrusted with planning and recruiting for the genetics department at the Kaiser-Wilhelm-Institut (forerunner of the "Max-Planck") in Berlin-Dahlem.

One more place where the call to experimentalism was heeded, was in the Prater, the big amusement park at the outskirts of Vienna. There, in 1902, an exotic-animal exhibit was going out of business. The "Vivarium," as the exhibit hall was called, had been built in grand pseudo-Renaissance style for the World's Fair of 1872, but could no longer compete with the zoological gardens at Schönbrunn. The young zoologist Hans Przibram, who had poor job prospects, but a rich family, bought the Vivarium, converted it into a laboratory, and set himself up as its director, with two botanists as partners.

15. Sharon E. Kingsland, "The Battling Botanist: Daniel Trembly MacDougal, Mutation Theory, and the Rise of Experimental Evolutionary Biology in America, 1900–1912," *Isis* 82 (1991): 479–509; George M. Cook, "Neo-Lamarckian Experimentalism in America: Origins and Consequences," *Quarterly Review of Biology* 74 (1999): 417–437.

16. Theodor Boveri, *Die Organismen als historische Wesen*, Festrede zur Feier des dreihundertvierundzwanzigjährigen Bestehens der Königl. Julius-Maximilians-Universität zu Würzburg. Gehalten an 11. Mai 1906 (Würzburg: Königliche Universitätsdruckerei von H. Stürtz, 1906).

Przibram's goal, as he later explained, was to establish a fundamentally new type of research institution, one devoted to the experimental method, rather than to any particular subject area:

> Its main purpose is not the investigation of a narrow group of organisms. . . . Its activities should not be limited to specific problems, instead it should draw all the big questions of biology into its purview. Not specialization, but generalization from the experiences we gain is our goal: the favoring of a certain methodology and technology alone sets our Institute apart from earlier biological research facilities.[17]

In practice, however, the Vivarium was not open to every possible subject of experimental study. Przibram ruled out physiology, for example, because he thought it was already well established as an experimental science, with its own laboratories, and because generally it did not study the whole organism through its entire life-cycle, as the Vivarium would. He wanted the Vivarium to develop new equipment and techniques for breeding a wide variety of organisms and studying development, growth, regeneration, and reproduction under experimental conditions. The young discipline of genetics might have fit his requirements and found an institutional home at the Vivarium, but Przibram made an executive decision not to include it in his program.

Przibram hired Paul Kammerer, then still a student, but already with publications to his credit on the building and maintaining of terraria and aquaria, to be his first assistant.

Kammerer and his Experiments

Kammerer was born in Vienna in 1880. He studied music at the Conservatory and comparative morphology at the University, under Berthold Hatschek, a Haeckel-protégé. He was unhappy with the Haeckelian approach, working with preserved specimens and constructing evolutionary relationships within an established theoretical and methodological framework.[18] When the opportunity

17. Hans Przibram, "Die biologische Versuchsanstalt in Wien: Zweck, Einrichtung und Tätigkeit während der ersten fünf Jahre ihres Bestehens (1902–1907)," Bericht der zoologischen, botanischen, und physikalisch-chemischen Abteilung, *Zeitschrift für biologische Technik und Methodik* 1 (1908–1909): 234.

18. Paul Kammerer, curriculum vitae, typewritten manuscript (photocopy), [ca. 1910], Paul Kammerer Papers, American Philosophical Society, Philadelphia, Mss.B.K128 (henceforth cited as Kammerer Papers).

arose, he moved his work to the Vivarium and added an experimental component to his dissertation, comparing two species of salamander, the spotted, lowland *Salamandra maculosa*, and the black, alpine *S. atra*.

Kammerer's first experiments focused on the reproductive adaptations of the two species. The lowland *S. maculosa* typically produces around forty small eggs that hatch into aquatic larvae with gills, while the alpine *S. atra* carries its eggs for a longer period and produces just two fully metamorphosed offspring, with legs and lungs. Kammerer was able to reverse those reproductive strategies. By manipulating temperature and humidity, he got the alpine salamanders to produce a larger number of small, aquatic larvae and the lowland salamanders just two fully developed young.[19]

Kammerer's next project at the Vivarium was a test of whether those changes were heritable. He raised the offspring of the modified salamanders both with and without the modifying environmental conditions, and waited to see what kind of offspring they would produce. Unfortunately, Kammerer's model organism took three and a half years to mature. While he was waiting, he launched a staggered series of very similar experiments with other organisms, aiming for more dramatic transformations in behavior and morphology.

In 1908, the first positive results came out of the pipeline. The salamanders' modified reproductive habits was inherited, he reported,[20] in a paper that won him a prize in Germany and his *Habilitation* and promotion to the rank of instructor (*Privatdozent*) in Austria. Further experiments coming out of his pipeline included the ones on the midwife toad in 1909, on the coloration of lizards in 1910, on the spotted and striped salamanders in 1911, and on the development of eyes in the blind cave salamander, Proteus in 1912.[21]

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19. Paul Kammerer, "Beitrag zur Erkenntnis der Verwandtschaftsverhältnisse von Salamandra atra und maculosa: Experimentelle und statistische Studie," *Archiv für Entwicklungsmechanik der Organismen* 17 (1904): 165–264 + Taf. XIII.

20. Paul Kammerer, "Vererbung erzwungener Fortpflanzungsanpassungen, I. und II. Mitteilung: Die Nachkommen der spätgeborenen Salamandra maculosa und der frühgeborenen Salamandra atra," *Archiv für Entwicklungsmechanik der Organismen* 25 (1908): 7–51 + Taf. I.

21. Kammerer, "Vererbung erzwungener Fortpflanzungsanpassungen, III. Mitteilung"; Paul Kammerer, "Vererbung erzwungener Farbveränderungen, I. und II. Mitteilung: Induktion von weiblichem Dimorphismus bei Lacerta muralis, von männlichem Dimorphismus bei Lacerta fiumana," *Archiv für Entwicklungsmechanik der Organismen* 29 (1910): 456–498; Paul Kammerer,

Methodological Critique

The same basic experimental design appeared in every one of Kammerer's transformation experiments. Kammerer raised groups of animals under various conditions, until he found an environment in which a morphological or behavioral change occurred. If the change occurred under one set of conditions and no others, he could reasonably argue that, in some sense, those conditions had caused the change.

In cases where Kammerer did follow-up experiments to test for heritability of the new characteristics, he reused the same experimental design and apparatus for raising the offspring of his modified organisms. If the new characteristic re-appeared in all environments, and not just the one that had caused the change in the first place, then he could reasonably argue that the change no longer depended on the presence of the environmental stimulus, but must be hereditary.

Here Kammerer was borrowing standard methods from *Entwicklungsmechanik*, or developmental mechanics, as envisioned by Wilhelm Roux, one of the leading spokesmen for the new wave of experimentalism. Kammerer followed Roux's prescription for the "analytical experiment," designed to identify causal agents in development. The idea was to observe a developmental step in the presence and absence of suspected causal agents, to see which of those agents actually did affect the course of the process.[22]

Where Kammerer ran into trouble was in drawing inferences about how, and through what intermediate mechanisms, his environmental agents caused new characteristics to be acquired and inherited. Kammerer's favored hypothesis of somatic induction, under which somatic changes were communicated to the chromosomes, was certainly consistent with his results and capable of explaining them. Unfortunately for Kammerer, the same could be said for several competing hypotheses as well.

Rival theoreticians were able to exploit Kammerer's results in order to try and support their own hypotheses. This was indeed the most frequent kind of response early on, from about 1909 to 1914. An analysis of the alternative hypotheses that were put forward reveals a great deal about the intellectual context of the time, particularly the lack of consensus on the causes of heritable

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"Direkt induzierte Farbanpassungen und deren Vererbung," *Zeitschrift für induktive Abstammungs- und Vererbungslehre* 4 (1911): 279–288 + Taf. III–V; Kammerer, "Adaptation and Inheritance."

22. Wilhelm Roux, "Einleitung," *Archiv für Entwicklungsmechanik der Organismen* 1, no. 1 (1894): 18.

variation and the lack of a well-defined alternative to the inheritance of acquired characteristics.

For Kammerer

The only writer I can find who backed Kammerer on every point was Hugo Iltis, the maize specialist, Mendel biographer, and early promoter of Mendelism. A socialist, he considered the inheritance of acquired characteristics a necessary antidote to racism and selectionist eugenics, and he valued Kammerer's work as a means of reconciling soft heredity and an environment-oriented eugenics with Mendelism.[23]

Kammerer's most effective ally before the First World War was Richard Semon, a personal friend and a mentor in theoretical matters as well. A Haeckel student and a tropical explorer and collector in his younger days,[24] Semon later turned more to theory following a sex scandal, tame by today's standards, which nonetheless spoiled his chances for a respectable university position. Today, Semon is remembered mostly for his ideas on organic memory, his *Mneme* theory.[25]

Kammerer's results became one of the mainstays of Semon's spirited defenses of the inheritance of acquired characteristics,[26] but Semon was not a friend of somatic induction, genes on chromosomes, or for that matter the experimental methods of *Entwicklungsmechanik*. He had his own unified theory of heredity, development, and evolution to promote, and to use as an explanation of Kammerer's results.

Kammerer's mentor in matters methodological was Przibram at the Vivarium, but these too disagreed on matters of theory as well. Przibram accepted

23. Hugo Iltis, "Rassenwissenschaft und Rassenwahn," *Die Gesellschaft. Internationale Revue für Sozialismus und Politik* 4, no. 1 (1927): 97–114.

24. Richard Semon, *Zoologische Forschungsreisen in Australien und dem malayischen Archipel: Mit Unterstützung des Herrn Dr. Paul von Ritter, ausgeführt in den Jahren 1891–1893*, 6 vols. (Jena: Gustav Fischer, 1893–1913).

25. Paul Kammerer, "Richard Semon: Zur Wiederkehr seines Todestages," newspaper clipping from *Der Abend* (Vienna), Dec. 27, 1920, Kammerer Papers; Daniel L. Schacter, *Stranger Behind the Engram: Theories of Memory and the Psychology of Science* (Hillsdale, NJ: Lawrence Erlbaum, 1982).

26. Semon, *Die Mneme als erhaltendes Prinzip im Wechsel des organischen Geschehens*; Semon, "Die somatogene Vererbung"; Richard Semon, *Das Problem der Vererbung "erworbener Eigenschaften"* (Leipzig: Wilhelm Engelmann, 1912).

the Weismannian barrier between germ- and somatoplasm and doubted that somatic changes could be communicated to the germ. Instead he favored the theory of "parallel induction," according to which, an environmental influence could affect soma and germ simultaneously and equivalently, giving the appearance of inheritance of acquired characteristics, while maintaining the isolation of the germplasm. He was undecided about whether the chromosomes were the physical bearers of heredity.[27]

After the First World War and the death of Semon, Kammerer's most important ally was probably the embryologist Ernest W. MacBride in Britain. But like Semon and Przibram, MacBride, too, disagreed with some of Kammerer's specific claims. MacBride's Lamarckism was much closer to the original in its assumption of extreme gradualism. The dramatic transformations that Kammerer was able to effect in a single generation did not fit his conception of Lamarckian evolution.[28] Several other critics also questioned whether any trait that could be changed so quickly was stable enough to count as hereditary or to play a significant role in evolution.[29]

Some other avowed Lamarckians rejected Kammerer's results altogether. In Britain, H. Graham Cannon attacked somatic induction, genetics and for that matter most other forms of "heredity" as the term is commonly understood. Instead, he thought the form of the organism was re-created in every generation from the dynamic interactions of the parts of the organism with each other and with the environment. It did not depend so much on transmission of a hereditary substance from the previous generation. In a stable environment, similar characteristics were produced anew in succeeding generations, which gave the appearance of heredity. Contrary to Cannon's expectations, Kammerer's experiments showed an environmentally induced characteristic persisting even after the organism was returned to its original environment. He concluded, therefore, that there must be something wrong with Kammerer's experiments

27. Hans Przibram to Hugo Iltis, July 23, 1923, Kammerer Papers.

28. Peter J. Bowler, "E. W. MacBride's Lamarckian Eugenics and its Implications for the Social Construction of Scientific Knowledge," *Annals of Science* 41 (1984): 245–260.

29. August Weismann, *Vorträge über Deszendenztheorie: Gehalten an der Universität zu Freiburg im Briesgau*, 2 vols., 3rd ed. (Jena: Gustav Fischer, 1913), 2:74–75; Franz Megušar, "Über den Einfluß äußerer Faktoren und über Vererbung bei Krustazeen, Insekten, Mollusken, und Amphibien," mit Demonstrationen und Lichtbildern, *Verhandlungen der Gesellschaft deutscher Naturforscher und Ärzte* 85, pt. II/1 (1914): 717–719.

and the whole experimental approach.[30]

Another potential "Lamarckian" ally whom Kammerer could not win over was J. T. Cunningham in Britain, an accomplished experimentalist, whose studies of fish coloration and the development of flounders' eyes were among the most commonly cited pieces of experimental evidence in favor of the inheritance of acquired characteristics. Cunningham even agreed with Kammerer in principle on somatic induction,[31] but did not think Kammerer's experiments supported the hypothesis very well. He called Kammerer a victim of self-deception and lamented that, "Lamarckian doctrine has often suffered more from the indiscretion of its advocates than from the attacks of its enemies."[32]

. . . And Against

According to the Whig and anti-Whig histories, those were supposed to be his "Lamarckian" allies. Now let us consider what his real opponents had to say.

Ludwig Plate, Haeckel's successor at Jena, was one of the most powerful editorial voices in the fields of heredity and evolution, thanks to his position at the *Archiv für Rassen- und Gesellschaftsbiologie* (Archive for Racial- and Social Biologie) and to his critical reviews of the field in book form. On the whole, he was an old-school Darwinian like Kammerer and desired to find experimental support for the inheritance of environmentally induced variations, but he worried about alternative explanations of Kammerer's results.

At first, Plate favored atavism—reversion to an ancestral condition—as the best explanation. That meant that Kammerer had activated some ancient hereditary potential that was still present in the germplasm of his experimental animals. Applying this to Kammerer's dissertation work, Plate thought both reproductive strategies were evolutionarily old within the salamander lineage. The switch from one to the other should therefore not count as acquiring new characteristics.[33]

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30. Cannon.

31. J. T. Cunningham, "Breeding Experiments on the Inheritance of Acquired Characteristics," *Nature* 111, no. 2795 (May 26, 1923): 702.

32. J. T. Cunningham, "Dr. Kammerer's Lecture to the Linnean Society," *Nature* 112, no. 2804 (July 28, 1923): 133.

33. Ludwig Plate, Review of "Vererbung erzwungener Fortpflanzungsanpassungen, I. u. II. Mitteilung," by Paul Kammerer, *Archiv für Rassen- und Gesellschafts-Biologie* 5 (1908): 118–120.

Kammerer's repeat performance on the midwife toad changed Plate's mind for a time, and in his 1913 book he took a clear, though cautious, stand in Kammerer's favor.[34] In later writings, however, Plate rejected Kammerer's evidence and spread allegations about poor laboratory practices and dishonesty on Kammerer's part.[35]

On the neo-Darwinian side, August Weismann's notebooks contain several discussions of Kammerer. However, Weismann was reluctant to discuss Kammerer in print. As a rule, he did not like to give unworthy opponents the satisfaction of a response. Finally, in the third edition of his *Vorträge über Deszendenztheorie* (Lectures on the theory of descent), in 1913, he entered the fray with two brief alternative explanations of Kammerer's results. First and foremost was the atavism objection, which he formulated in his own terms as the reactivation of ancestral "determinants" that had lain dormant in the immortal germplasm. In second place came the possibility of selection having acted upon pre-existing variation not noticed by Kammerer.[36] Either way, Kammerer's results, if they proved to be trustworthy, were not threats to Weismann's germplasm theory, but illustrations of it.

Curiously, from a present-day point of view, natural selection was not highly favored as an alternative explanation, not even among the neo-Darwinians, although Weismann student Heinrich Ziegler listed selection ahead of atavism among his explanations of Kammerer.[37] Some Mendelians, too, complained that Kammerer had not experimented on inbred "pure lines," an omission that would have made a limited amount of selection possible.[38] Nonetheless, atavism and saltation were the alternatives that Kammerer had to rebut most

34. Plate, *Selektionsprinzip und Probleme der Artbildung*, ix & 468–478.

35. Ludwig Plate, *Allgemeine Zoologie und Abstammungslehre*, 2 vols. (Jena: Gustav Fischer, 1922–1924), 1:9; Ludwig Plate, *Die Abstammungslehre: Tatsachen, Theorien, Einwände und Folgerungen in kurzer Darstellung*, 2nd ed. (Jena: Gustav Fischer, 1925), 119.

36. Weismann, *Vorträge über Deszendenztheorie*, 2:74–75.

37. Heinrich E. Ziegler, "Die Streitfrage der Vererbungslehre (Lamarckismus oder Weismannismus)," *Naturwissenschaftliche Wochenschrift* NF 9, no. 13 (1910): 193–202 + Taf.

38. R. von Hanstein, "Experimente über Erblichkeit von Abänderungen," *Naturwissenschaftliche Rundschau*: *Wöchentliche Berichte über die Fortschritte auf dem Gesamtgebiete der Naturwissenschaften* 26, nos. 1–2 (1911): 6–8 & 20–21.

frequently.

Among the Mendelians, Richard Goldschmidt and William Bateson saw evidence in Kammerer's results for a theory of evolution by means of fortuitous, large-scale mutations. In the second edition of his genetics textbook (1913), Goldschmidt discussed Kammerer's experiments sympathetically and at length, and even refrained from rejecting the heritability of acquired characteristics outright. He did point out, however, that Kammerer's experiments were also consistent with saltational evolution.

Goldschmidt was most intrigued by one of the lesser-known midwife-toad experiments, in which Kammerer had tried to prolong the aquatic stage until the larvae, like the axolotl, became sexually mature without metamorphosing. A single larva out of a large starting population survived Kammerer's treatments and matured, and Goldschmidt thought that such a unique individual might have represented a mutation in the saltationist sense.[39]

Bateson's marginal notes and underlining in his copies of Kammerer's articles indicate that, like Goldschmidt, he was most interested in those experiments that yielded the fewest transformed individuals, as if he, too, were looking for saltations. Bateson focused on the nuptial pads of the midwife toad because, as he explained, that was the only trait in all of Kammerer's experiments that fit his conception of a mutation. Everything else he dismissed as only "a matter of more or less,"[40] and therefore not a mutation, not significant in evolution, and probably not even heritable.

Bateson later pressed Kammerer for further anatomical details and for specimens to examine, but was never quite satisfied that there was a discrete nuptial pad, rather than a more-or-less dark, more-or-less rough patch of skin. If it were a discrete characteristic, then it would support Bateson's conception of evolution, not Kammerer's, and if it were not, then the experiment was irrelevant. Bateson is quite the villain in Koestler's version of the Kammerer controversy, spearheading the "Darwinian" attack on Kammerer's "Lamarckism," but in fact he makes a very poor Darwinian. He was only scrutinizing Kammerer's data for its relevance to his saltationism.

In contrast to Bateson and Goldschmidt, geneticist Erwin Baur did not see

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39. Richard Goldschmidt, *Einführung in die Vererbungswissenschaft*, 2nd ed. (Leipzig: Wilhelm Engelmann, 1913), 456–469.

40. William Bateson to J. H. Quastel, letter draft, Apr. 24, 1923, William Bateson Papers, American Philosophical Society Library, History of Science Collection, Philadelphia, microfilm, film no. 26 (henceforth cited as APS Bateson Papers), Reel E, Section Balto #32, Index 5.

any potential mutations in Kammerer's experiments. In his 1911 textbook of genetics, Baur classified the changes Kammerer obtained as fleeting, environmentally induced "modifications." Modifications were not truly heritable. If they appeared in two generations in a row, that was because embryos, eggs, or germ-line cells had been exposed inadvertently to Kammerer's treatments while they were still within the parental body. In other words, both generations had been modified simultaneously by the one experimental treatment, without heredity being involved. Baur was even prepared to make the same claim if Kammerer produced a third modified generation, under the assumption that as many as three generations of protoplasm, nested one within the other, might have experienced Kammerer's treatments at the same time, but that was his limit.[41]

Unfortunately for Baur, Kammerer had reported a fourth generation of water-breeding midwife toads by the time Baur published the second edition of his textbook in 1914. Baur chose to stand by his mutation-modification distinction and even the three-generation limit. He then had to reject Kammerer's report of a fourth generation as vague and unreliable.[42]

The Spoiler

Early on, Kammerer took these kinds of criticisms and alternative interpretations in stride. He thought he could still claim to have established at least a weak version of somatic induction, that is, that environmental stimuli caused hereditary changes to appear:

> . . . I maintain that no matter whence the ability to react purposefully derives, whether it is atavism or selection, one thing remains unaffected: changes have arisen under the influence of external factors, and those changes have appeared again in subsequent generations, despite the absence of these factors.[43]

In other words, he thought that all he needed to demonstrate was that some heritable change had occurred, and that his environmental manipulations had caused that change.

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41. Erwin Baur, *Einführung in die experimentelle Vererbungslehre* (Berlin: Gebrüder Borntraeger, 1911), 37 & 260.

42. Erwin Baur, *Einführung in die experimentelle Vererbungslehre*, 2nd ed. (Berlin: Gebrüder Borntraeger, 1914), 55.

43. Kammerer, "Vererbung erzwungener Fortpflanzungsanpassungen, I. und II. Mitteilung," 42–43, emphasis original.

Despite this concession, Kammerer argued steadfastly for his more specific claims about somatic induction and, with time, he lost patience with all the counterarguments and alternative explanations. All together they seemed to him to add up to nothing but sophistry, and he complained his opponents were trying to place an unreasonably high burden of proof upon him. Any time he could produce a new trait easily, his opponents said it was unstable, a mere "modification," or not truly heritable. And any time he could demonstrate heritability, they said the had not truly produced the trait, that it was an atavism or pre-existing variation or mutation: "Whatever is altered, one [critic] says it is an acquired characteristic and therefore not heritable; the other says it is heritable and therefore not an acquired characteristic."[44]

One solution to this problem might have been for Kammerer to follow up one of his animal transformations with further experiments that might have ruled out one or more of the alternative explanations. That might seem like an obvious strategy for skilled experimenter like Kammerer, working at a well-equipped and innovative institution like the Vivarium, but it ran counter to the stated goals and priorities of the laboratory.

Przibram had specifically ruled out specialization on a narrow group of organisms, problems, or theories. As a young researcher, Kammerer was not encouraged to study any model organism in depth, or to explore the heredity, physiology, and variability of the characteristics he produced, or even to keep abreast of the burgeoning field of genetics. The laboratory was devoted to the technology and methodology of experiment, and Kammerer served its interests best when his research showed off its material capabilities: the wide range of its animal stocks and manipulable environments, and its potential for bringing evolution under experimental control.

Kammerer did not fight the fight in a conventional way. Instead of refining his case for somatic induction, he piled on new, dramatic, and equally ambiguous demonstrations of evolution in the laboratory. He left himself open to repeated disparagement of his idea of somatic induction, and to appropriation of his results to support other theories. But even though they had Kammerer on the ropes, opponents were forced to reveal their disagreements with each other and their collective inability to explain the nature and causes of variation.

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44. Paul Kammerer, "Dunkeltiere im Licht und Lichttiere im Dunkel," *Die Naturwissenschaften*, Heft 2 (1920): 32.

Conclusion

So who was the winner in Kammerer's fight for the inheritance of acquired characteristics? Well, it wasn't Kammerer, that's for sure. In his own lifetime he seems to have converted hardly anyone of note to his specific views on somatic induction and incipient genes. And in the long run, the midwife-toad scandal and the evolutionary synthesis sealed his reputation as the loser.

Kammerer did have two things in his favor, though. One was his move to embrace genetics and the chromosome theory. On that score, at least he had the last laugh on Bateson, who, notoriously, rejected the chromosome theory.[45] The other was the fact that he offered a concrete, mechanistic, and environmentally driven explanation for the origin of variation. His version of somatic induction dispensed with the needs and psyche of the organism, with teleological, internally driven changes, drives to perfection, and "spontaneous" reconfigurations of the organism. Its end-products were up-to-date genes on chromosomes, instead of old-fashioned determinants in the germplasm or protoplasmic memories.

If it weren't for the midwife-toad scandal, Kammerer's version of somatic induction would probably have fared no worse than his opponents' theories. By the 1930s, the inheritance of acquired characteristics in all of its guises became redundant. So did the idea of parallel induction. With the rapid rise of genetics, Weismann's and Plate's assertions about atavisms and ancestral determinants in the germplasm were already becoming historical curiosities, even as they were made. Likewise, the saltationism of Bateson and Goldschmidt was giving way to a concept of discrete, but smaller, genetic changes that could be reconciled with continuous variation and gradual evolution. And Baur's distinction between genetic mutations and environmental modifications that could persist up to three generations without being heritable, could not be maintained.

In the long run, of course, the genetics-based selection of the modern evolutionary synthesis, together with the modern conception of the physically caused, but adaptively "random" genetic mutation[46] have won general acceptance, and have the potential to explain most of Kammerer's results. However, these ideas were not available in time to play a role in the Kammerer controversy.

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45. William Coleman, "Bateson and Chromosomes: Conservative Thought in Science," *Centaurus* 15, nos. 3–4 (1970): 228–314.

46. I date the modern mutation concept to Muller's report on the effects of X-rays: Hermann J. Muller, "Artificial Transmutation of the Gene," *Science* 66 (1927): 84–87.

Kammerer's fight was not against the evolutionary synthesis, but against older conceptions of evolution.

In the short run, however, the winner in the Kammerer controversy as it played out until 1926 was—nobody. Not one of the active contenders was able to advance his program decisively. None could disprove somatic induction, either. Labeling Kammerer a fraud was the easiest way to reach a consensus and to get rid of him and the unpleasant questions he raised about the origin of variation. This is not intended as an apology for the scandal, but rather as an explanation for the intense and widespread interest in it.

As for the Whig and anti-Whig histories: the one celebrates the victory of a selectionism that was not really involved in the fight, while the other makes Kammerer into a martyr for a vague "Lamarckism" that he did not really champion. Both stories oversimplify the factional struggles within evolutionary biology, and obscure Kammerer's ability to spoil a good fight.

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