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'Protoplasm…is soft wax in our hands': Paul Kammerer and the art of biological transformation

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Paul Kammerer's career ended in scandal in 1926 over tampering with his evidence for 'Lamarckian' evolution – the infamous midwife toad. But although Kammerer's conclusions proved false, his evidence was probably genuine. In any case his arguments were not simply for Lamarckism and against Darwinism, as the theories are understood today. If we look beyond the scandal, the Kammerer story shows us a great deal about early 20th-century biology: the range of new ideas about heredity and variation, competing theories of biological and cultural evolution and their applications in eugenics, new kinds of laboratories and professional roles for biologists, and changing standards for documenting experimental results.

Introduction

The 1910s and 1920s were heady times at the 'Vivarium' – or Institute for Experimental Biology – in Vienna. Paul Kammerer (Figure 1) was there reinvigorating the case for the inheritance of acquired characteristics, and Eugen Steinach was conducting his pioneering work on hormones and their effects on body and mind [1]. A charismatic speaker and popularizer, Kammerer wove both lines of research into a vision for controlling human evolution. He explained that dramatic cures of glandular deficiencies had already been achieved:

> A frivolous, mal-gendered or perverse, obese, spineless shirker becomes, with the administration of testicular substance, a serious, determined, hairy, muscular, hard-working and lusty man! A dwarf-like, stunted idiot with wrinkled, scaly skin, brittle nails, open sores, and a stupid, glazed look in the eye is changed by the ingestion of thyroid substance, into a tall, slim, smooth- and light-skinned, sharp-eyed and alert person [2].

Surely, Kammerer argued, it was only a small step from treating pathological cases like these to enhancing the population at large, producing exceptional individuals and making the changes in them hereditary.

Kammerer's evidence that such changes were heritable came from experiments on a variety of animals. The most widely discussed of these was the midwife toad, so named because when it mates normally – on land – the male helpfully takes the eggs from the female and attaches them to his own hind legs for safe brooding (Figure 2). In one experiment, high temperatures induced midwife toad specimens to spend more time in water and even mate there, but this meant that the egg-strands became waterlogged and would not stick to the males. The few eggs that survived the treatment grew into toads that preferred to mate in water, regardless of the temperature of the environment, apparently inheriting the acquired behavior. During the mating season males of this water-breeding line even developed the 'nuptial pads' found in frogs: dark, rough patches on the front legs, which were used to clasp a slippery, wet female.

As Arthur Koestler recounts in *The Case of the Midwife Toad* [3], Kammerer's career ended in scandal in 1926 when it was discovered that his last intact specimen of a midwife toad with a nuptial pad had been artificially darkened with an injection of India ink. The fact that Kammerer committed suicide six weeks later thus looked like an admission of guilt, and his work was discredited. His reputation has never fully recovered, despite Koestler's argument that Kammerer was framed by Darwinians who were desperate to save their theory from his attacks.

Those who know Kammerer from Koestler's account might be surprised to learn that, far from opposing Darwinism, Kammerer counted himself a Darwinian, but in the grand 19th-century style of Ernst Haeckel. Haeckel built his Darwinism into a comprehensive and progressive world-view, an alternative to religion and a force for social change. Darwin himself had assumed that environmentally induced modifications and the effects of using or disusing organs were important sources of favorable and heritable variation, and Haeckel's influential German interpretation of Darwin's work focused on these as the principal causes of Darwinian evolution and cultural progress.

Kammerer aimed to bring Haeckel's brand of Darwinism up to date with 20th-century biology and culture. He provided experimental evidence for the modifying power of the environment, and he outlined a mechanism of heredity that would let acquired characteristics be communicated to genes. Kammerer argued that the hereditary effects of education, practice and artistic achievement assured continual progress in human

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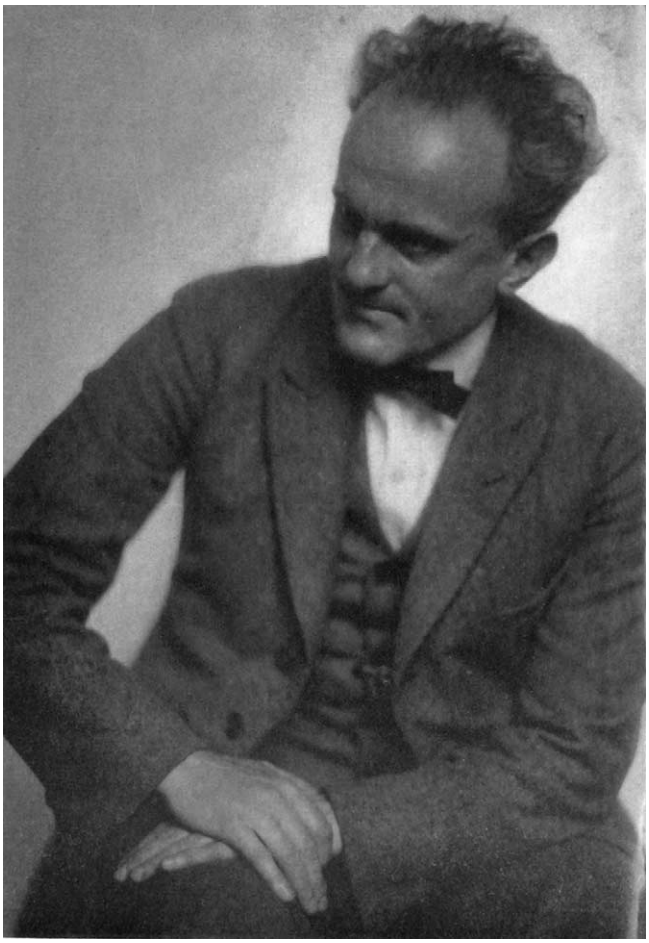

Figure 1. Portrait of Paul Kammerer. Image reproduced from the frontispiece to [3] courtesy of the Herman B. Wells Library, Indiana University, Bloomington, IN, USA, and with permission from Hutchinson.

culture. This became the basis for his alternative eugenics, which proposed to create fit individuals rather than select them.

Kammerer's position at the privately owned Vivarium laboratory – outside of academic biology – gave him the freedom to pursue his dual experimental and cultural projects. He published in both technical journals and the popular press, and he addressed the public directly in what he called his 'big show-lectures'. As we shall see, Kammerer's work at the laboratory and show-lectures also made special demands on him and shaped his research in unexpected ways, which sometimes hurt his scientific credibility [4].

The Vivarium

The Vivarium laboratory was founded in 1902 on the premises of a former zoological exhibit hall in the Prater, the big amusement park on the outskirts of Vienna. Hans Przibram, an aspiring young experimentalist and a man of means, bought the building and retooled it for researching organisms and environments of every description. Modern central heating, supplemented by stoves, provided a range of temperatures for terraria, aquaria and insectaria. A deep cellar provided cold, dark conditions for raising cave animals, and storage space for rainwater and for seawater, which had to be hauled up by train from Trieste. An electric motor circulated the seawater through the aquaria upstairs and back to the cellar. Hothouses and apparatus for manipulating air pressure, photoperiod and the light spectrum, and for simulating gravitational forces were also available, as well as a central aeration system for the fish tanks, and electrical outlets and lights at all the work-tables.

Wilhelm Roux, a leader of the experimental turn in embryology and evolution, arranged in advance to publish all of the research reports that came out of the Vivarium in his journal *Archiv für Entwicklungsmechanik* (Archive for Developmental Mechanics). Meanwhile, other scientists sent specimens of abnormal animals to the Vivarium, which Przibram later exhibited to the public in a 'Museum of *Entwicklungsmechanik*' worthy of the Prater location. Przibram also hired Paul Kammerer, then still a student, to be his first assistant in 1902 or 1903 [5,6].

Kammerer and his experiments

Kammerer was born in Vienna in 1880. His mother was from a converted Jewish family and his father was a factory owner [7]. In his youth he developed the intense devotion to the arts that was typical of his generation and class in Vienna [8]. Kammerer studied music at the Conservatoire, comparative morphology at the University and learned the latest experimental methods from Przibram at the Vivarium.

The results of Kammerer's first experiments were published in 1904. They were performed on a lowland salamander that bears lots of little tadpoles, and an alpine species that bears fewer, but larger, fully metamorphosed land dwellers as offspring. By manipulating temperature and humidity, Kammerer was able to make each species of salamander acquire the reproductive habits of the other. However, to test if this switch was heritable required a three and a half year wait for the offspring to mature. In the meantime, Kammerer launched a staggered series of similar experiments using different species, trying out different Vivarium gadgetry and aiming for ever more striking modifications.

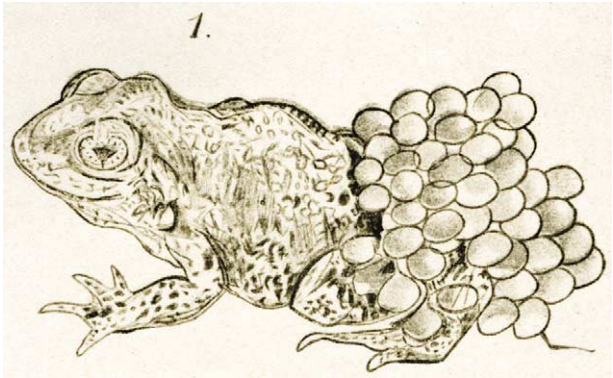

Figure 2. A normal male midwife toad – *Alytes obstetricans* – with egg mass on its hind legs, as drawn by Paul Kammerer's boss Hans Przibram. Przibram was noted for his artwork and his drawings were exhibited at the Secession, Vienna's center for *Jugendstil* art, and printed in the Secession journal: *Ver Sacrum*. Image reproduced from [9] courtesy of the Herman B. Wells Library, Indiana University, Bloomington, IN, USA.

Positive results started spewing out of this pipeline in 1908: the alpine and lowland salamanders bred true and continued to breed in a manner contrary to the norm in their species. Then came the midwife toads with their nuptial pads [9], spotted salamanders that became striped and much more. In backcrosses with unmodified stock, the traits often appeared to follow Mendelian laws thus supporting Kammerer's contention that his treatments induced genes to form [10]. In 1911, these successes earned Kammerer a promotion to the rank of *Privatdozent* – lecturer – at the University [11], which opened doors for him as a popular science writer and public speaker. From then on Kammerer was often on the road, spreading the word about his achievements and their social significance.

The artist and Alma

In parallel to his scientific career, Kammerer also established himself in the music world. By 1910 his musical compositions had been published and performed, and he was socializing with such luminaries as his idol Gustav Mahler and Mahler's wife Alma.

Alma is notorious for the large, yet exclusive, group of artists whom she married or at least graced with the muse's kiss [12]. Her effect on Kammerer was to inspire a lecture and a small book on the inheritance of musical talent and evolutionary progress in the arts, which he dedicated to her and her daughter as living evidence of these phenomena [13]. Kammerer also appears to have been quite smitten by Alma and queued up for her attention around 1912 – somewhere between Mahler and the painter Oskar Kokoschka. He even persuaded her to work at the Vivarium, studying the feeding behavior of praying mantises. In her catty memoirs she recalls her first day on the job, trying to feed mealworms to her experimental subjects:

> I was repelled a little by the giant box full of those squirming worms. Kammerer saw this, took a handful, and stuck the animals in his mouth and ate them up, smacking his lips loudly.

Confident of his charms, Kammerer soon began demanding marriage – or else:

> Every day he would storm out of my apartment, claiming he would surely shoot himself, and he would have to do it upon Gustav Mahler's grave, too, because Mahler had appeared to him in a vision, and so on. I was very frightened at first; eventually I got used to it.

But eventually Alma put an end to it by contacting Kammerer's wife:

> [I] asked her to look after him better, to make herself indispensable to him; most of all to get the pistol away from him, which he was always waving around [14].

It is probably safe to speculate that these antics did not enhance his reputation as a meticulous scientist.

Scientific criticisms

Criticism of Kammerer's experiments was also mounting because, even though he kept producing heritable changes, he never quite pinned down the mechanism that caused them. In retrospect, what was most interesting about Kammerer's work was not that it supported Lamarckism particularly well, but that it challenged biologists to come up with alternative explanations. Genetics was still in its infancy at the time when Kammerer made his claims, and had yet to settle on the modern conception of a random genetic mutation. Therefore, every critic who tried to explain away Kammerer's results went about it differently.

Several prominent authors, such as August Weismann and Ludwig Plate, still thought in terms of an immortal germplasm – resistant to change and containing all kinds of dormant ancestral traits. They suggested that Kammerer's results were 'atavisms' or reversions to old traits, not newly acquired ones. Weismann and others also suggested that selection might be at work, unbeknownst to Kammerer, because when the experiments began the populations of the test subjects were highly variable and mortality was high. In hindsight, inadvertent selection is the most likely explanation, because midwife toads with nuptial pads have occasionally been seen in the wild. This would suggest that variation in the relevant traits probably was present in Kammerer's laboratory stocks, and that he had no need to fabricate the results.

Leading geneticists did not take selection seriously as an explanation, however. Erwin Baur was editor of the first genetics journal: the *Zeitschrift für induktive Abstammungs- und Vererbungslehre* (Journal for Inductive Research on Evolution and Heredity). He argued that Kammerer had produced environmental 'modifications'. In contrast to 'mutations' these were not heritable – except sometimes for a generation or two. Baur's textbook of genetics – the *Einführung in die experimentelle Vererbungslehre* (Introduction to Experimental Heredity) – predicted that the nuptial pads would soon disappear from the midwife toads in Kammerer's stocks [15]. When the traits persisted, a later edition of the book altered the definition of modifications to suggest that they could persist a bit longer than had been previously claimed. Baur also began to cast aspersions on Kammerer's trustworthiness.

Other leading geneticists, such as Richard Goldschmidt and William Bateson, thought that at least some of Kammerer's results might be true mutations, but in an older sense of the term – a 'saltation' or major evolutionary leap. Bateson, who is quite the villain in Koestler's version of the story, focused on the nuptial pads because he considered them Kammerer's only possible example of saltational change. But he could not tell from Kammerer's published documentation if the toads acquired the pads all at once and in every detail, including location, color and texture.

Seeds of the scandal

Kammerer was too careless about documentation to satisfy Bateson. He did not kill and preserve specimens routinely, and the live examples in his stocks did not always display the modifications to good effect. The midwife toads only had nuptial pads during the breeding season, which was not when Bateson came calling.

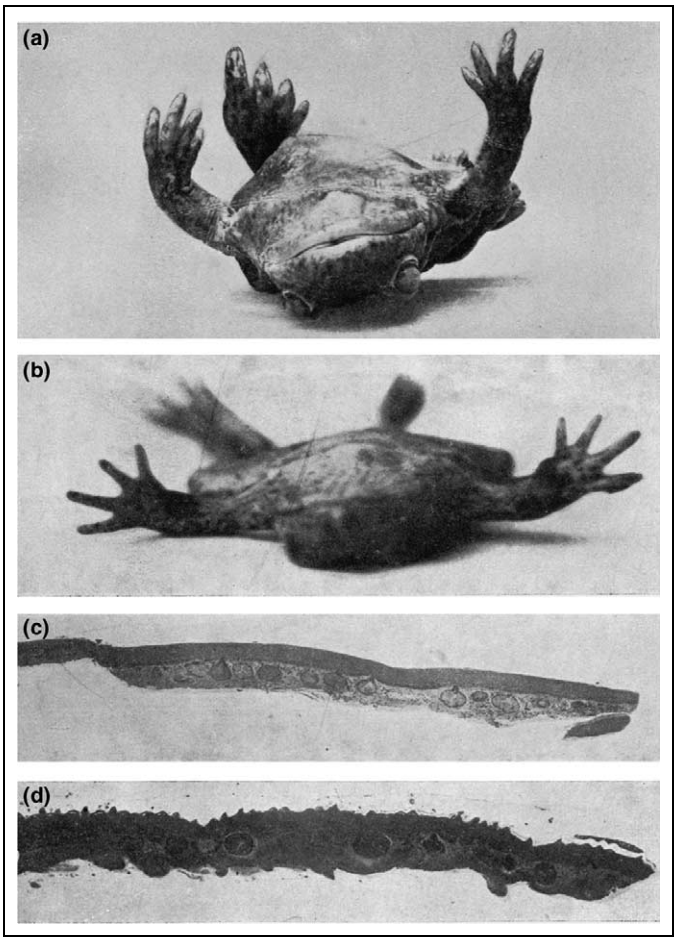

Figure 3. (a) An unmodified male midwife toad. **(b)** The controversial toad from the water-breeding line, with nuptial pads on its front legs. A cross-section of the tissue from the nuptial pad of a female is shown in **(c)**, and from the modified male depicted in **(d)**. **(d)** also shows the characteristic spines and spicules that contribute to the roughness of the nuptial pad. Images reproduced from [23] courtesy of the Herman B. Wells Library, Indiana University, Bloomington, IN, USA.

Kammerer's drawings of the toads and other specimens are very primitive, far below the usual Vivarium standard set by his mentor Przibram (Figure 2).

Kammerer might have compensated for his lack of notes by taking photos, but the Vivarium, despite all its technological sophistication, does not appear to have been equipped for it. Kammerer depended on visiting researchers to photograph specimens, or else he used a commercial portrait studio. Either way, the results were poor. Kammerer's photos of the midwife-toads display little detail (Figure 3) and his salamander photos had to be retouched for publication (Figure 4). Rumors began circulating to the effect that Kammerer's reports were unreliable.

Kammerer's Jewish background made matters worse. One German scientist who was working in Vienna at the time told Goldschmidt that the whole Vivarium was viewed as a snotty, Jewish institution. Weismann's notebooks also record hearsay about Kammerer being both Jewish and unreliable, and Plate's opinion was probably also colored by anti-Semitism [16].

Kammerer's own colleagues at the Vivarium further undermined his reputation. Tensions ran high between him and Franz Megušar, who was also an assistant to Przibram. In 1913, at a meeting of the German Society of Naturalists and Physicians in Vienna, Megušar accused Kammerer of reporting false results. In private, Przibram called Megušar unreliable, insanely jealous and mentally unstable, but publicly he would not criticize either of his assistants. Megušar's accusations were very damaging to Kammerer: particularly in Germany, where Plate repeated them in his two influential books on evolution [17].

Also in 1913, Kammerer made the mistake of picking a fight with Baur. In 1911 one of Kammerer's lectures had been published in Baur's *Zeitschrift für induktive Abstammungs- und Vererbungslehre* [18]. It described how salamander spots merged into stripes and other patterns that were heritable when the salamanders were raised on colored substrates, and was illustrated with retouched photographs (Figure 4). When Kammerer published the formal report on the experiments in Roux's *Archiv* in 1913, he criticized the way Baur had printed his photos [19]. Oddly, Kammerer did not reprint them in the formal report, instead using schematic drawings (Figure 5). He did throw in a few representative photos, for the sake of 'documentary realism', but these were crudely hand-colored in black and yellow (Figure 6).

Baur responded angrily, saying that Kammerer's originals had contained all the defects that Kammerer was trying to blame on the staff at the journal, plus

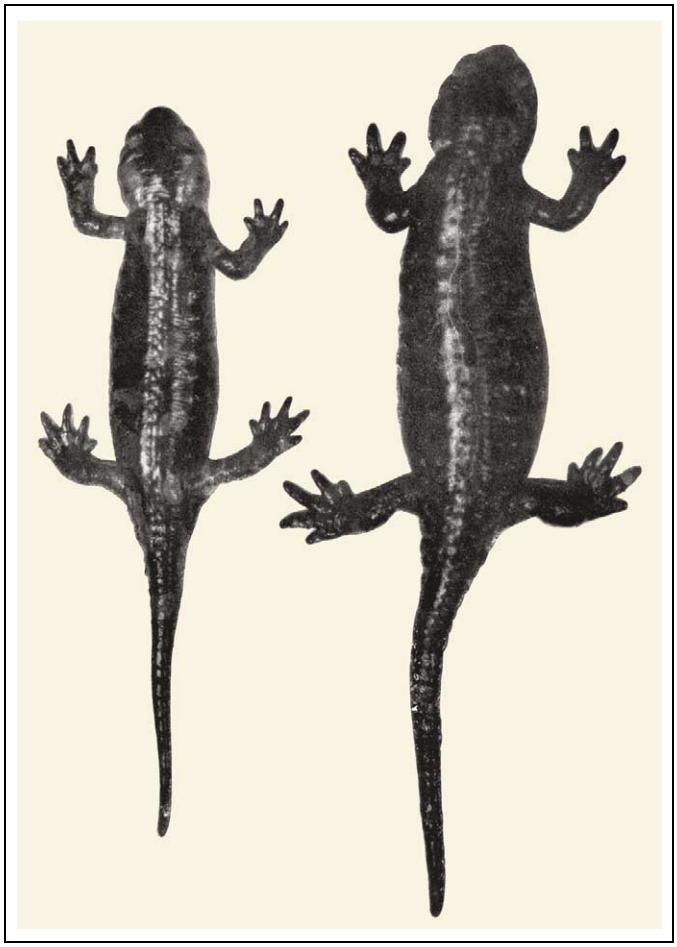

Figure 4. Retouched photos of spotted salamanders – *Salamandra maculosa* – raised on differently colored substrates. On the right, the spots of the salamander have merged into a longitudinal stripe. Image reproduced from [18], courtesy of the Herman B. Wells Library, Indiana University, Bloomington, IN, USA.

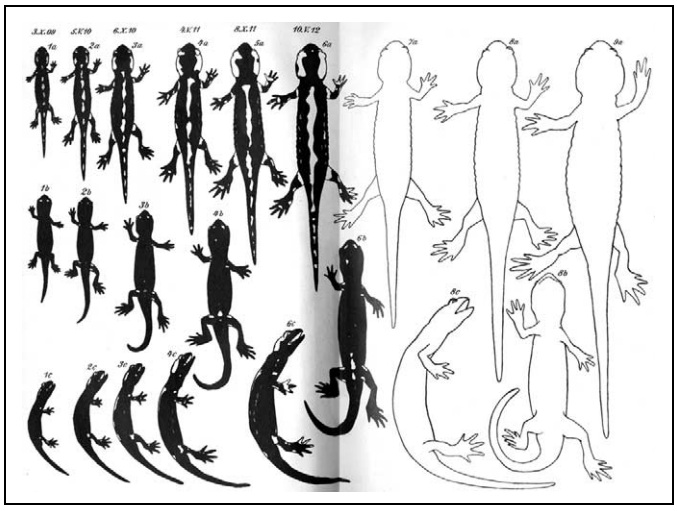

Figure 5. Dorsal, ventral and lateral views of a salamander's changing spots, sketched by hand onto standard salamander outlines. The spots are gradually merging into a longitudinal stripe. Image reproduced from [19], courtesy of the Herman B. Wells Library, Indiana University, Bloomington, IN, USA.

extensive retouching of the spots on the salamanders. Baur had not objected to these alterations in 1911 because the retouching was noted in the caption. However, because these additions were also present in the photos that were printed Roux's *Archiv*, which were only supposed to be 'colorized', Baur suspected they had been painted on and were not actually present on the salamanders [20].

Kammerer's defense was that the slimy creatures were hard to photograph: 'The glare from the skin gave the impression of spots where none was present, and spots that were present were washed out in the glare'. The retouched photos were thus better documentation than unaltered ones, because they gave a more accurate depiction of how the specimens looked in reality. He argued that a retouched photo was no more subjective or unrealistic than the hand-drawings that still were used commonly in scientific journals at that point, and invited skeptics to come and compare the photos to his specimens any time [21].

First World War and postwar career

Unfortunately, by the time the skeptics came to visit the Vivarium Kammerer's collection had dwindled and deteriorated from neglect during World War I. Working for the military censor had kept Kammerer away from the laboratory during the war, but gave him the opportunity to write anti-war essays featuring evolutionary arguments for cooperation and symbiosis.

After World War I, Kammerer was rejected for promotion to the rank of professor. This was partly because of his run-ins with Baur and Megušar, but mostly because of the unseemly hyperbole of his popularizing work – which included a new book on coincidences that the promotion committee considered pseudo-scientific [22]. Kammerer became disgusted with academic science and made little effort to restart his experimental pipeline, although he did write up old results – including one more paper on the midwife toad [23]. He finally quit the Vivarium in 1921 and after that made his living from writing and lecturing, which led to commitments that took him to Britain and the USA in 1923 and 1924.

World War I had disillusioned Kammerer about evolution as well. He could no longer believe that it led inevitably to progress. His postwar show-lectures called on humanity to take charge of its own future and acquire good characteristics deliberately, instead of leaving it to nature: 'Our reason and our will must be able to control organic substance, including that of which our own bodies are composed, just like soft clay in the hands of the modeler or hard steel in the hands of the machinist' [24].

Kammerer touted the 'Steinach operation' to rejuvenate and energize men by conserving their testicular secretions [25]. He also suggested testicle implants to 'cure' homosexuality and radiation treatments to enhance lactation – not only in human mothers, but in dairy cows as well – arguing that the positive effects of such treatments would become hereditary after just a few generations: 'So promptly does living substance react to influences imparted according to plan! So precisely does protoplasm comply with our wishes that it is soft wax in our hands!' [26] Despite the problems Kammerer was facing, these proposals got good coverage in newspapers and magazines.

Figure 6. Colorized photos, which were supposed to improve upon both the retouched ones in Figure 4 and the schematic drawings of Figure 5, but which drew fire from Erwin Baur owing to the spots being changed, not just colored in. Salamander 9 in the upper right is the colorized version of the one on the right in Figure 4. Image reproduced from [19], courtesy of the Herman B. Wells Library, Indiana University, Bloomington, IN, USA.

Bateson and scandal

During a stop in Cambridge, Kammerer exhibited his midwife toad and triggered an exchange with Bateson in *Nature* about whether it had true nuptial pads [27]. This only called more attention to his documentation problems and by this time Kammerer was down to one last travel-worn specimen: it only had one pad left, the other having been used to make microscopic cross-sections.

In contrast to his reception in the West, Kammerer was greeted warmly in the Soviet Union. There his ideas resonated with doctrinaire Marxists, who shared his commitment to the inheritance of acquired characteristics and human improvability. In 1926, the Communist Academy in Moscow offered to build Kammerer a laboratory, and stood by their offer even after the news came out that the last midwife toad had been injected with ink.

The Soviets were willing to accept the story, later picked up by Koestler, that Kammerer had been framed. But I think a more plausible way to solve the case of the midwife toad is by looking to the Baur incident: Kammerer never learned how to photograph a glistening, wet amphibian. Years before the scandal, he probably inked the specimen to enhance the dark nuptial pad for the camera; a suggestion that was also made during the scandal, but summarily discounted [28].

Kammerer might very well have been able to justify using the ink, at least to himself, the same way he justified retouching the salamander photos. Freehand drawing was still quite common in biological journals, so why not freehand corrections to a photo or cosmetic improvement of a specimen? Besides, he still had live specimens to show, and still expected other scientists to take his word for their appearance. However, by 1926 he had no other specimens to corroborate his claims, and scientists had come to mistrust the vague, hard-to-explain results reported by this eccentric improver of humanity, this popularizer, this Jew from an amusement-park laboratory.

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