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The Midwife Toad Challenge After (Half) a Century

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The evolutionary biologist Paul Kammerer (1880–1926) purportedly demonstrated that environmentally induced character states are carried over to the next generation(s), therewith providing evidence for Lamarckian evolution. Kammerer's work is generally seen as contentious but has also been valued as daring and insightful, and Kammerer has been heralded as an academic forebear of epigenetics. Most of the more pertinent of Kammerer's experiments on amphibians and the sea squirt have either been invalidated by replications that failed, or have been dismissed as virtually impossible. An experiment on color pattern change in the fire salamander stands out because it has been confirmed, but only with data for within a generation, so that Kammerer's claim concerning the inheritance of acquired character states still awaits confirmation. To facilitate and encourage replicate studies, I draw attention to species and populations that would be most practical and promising to work with, for those that are into the challenge.

Keywords: epigenetics, fire salamander, Paul Kammerer, phenotypic plasticity, Arthur Koestler

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THE INHERITANCE OF ACQUIRED CHARACTER STATES AND PAUL KAMMERER

The Lamarckian oriented experiments of the Austrian evolutionary biologist Paul Kammerer (1880–1926) continue to raise debate, with their performer alternatively portrayed as an outstanding scientist ahead of his time (Sermonti, 2000; Vargas, 2009; Vargas et al., 2017) or a highly strung perpetrator of fraud (Whittaker, 1985; van Alphen and Arntzen, 2016, 2017; see also Parnes, 2006; Senglaub, 2006), while others give him both some benefit and some doubt (Gliboff, 2005, 2006, 2010; Taschwer, 2016; Nahm, 2021). After a long period of silence following Kammerer's suicide, science writer Arthur Koestler placed Kammerer and his experiments back in the spotlight (Koestler, 1971) and, with that, the pertinent question of whether organismal evolution might, at least in part, proceed through the inheritance of acquired character states. Over the recent decades, this topic has gained in importance, with a refreshed attention on epigenetic modes of inheritance (Deichmann, 2016; Adrian-Kalchhauser et al., 2020; Anastasiadi et al., 2021). At the heart of the discourse is the discovery that animal cells fated for reproduction (the germ line) are already set apart during early development from other cells that form the body (the soma) (Weismann, 1892). On the basis of this separation, Weismann reasoned that new genetic properties acquired by somatic cells cannot be transmitted to the offspring — the “Weismann barrier.” Kammerer's opponents were neo-Darwinians and argued fiercely against Lamarckian evolution based on Weismann's (and also Mendel's) theories in an acrimonious debate that lasted until after

Kammerer's untimely death. For a gentle introduction to this early twentieth century dispute and to Kammerer, see Sir David Attenborough's "A curious hoax?" (Attenborough, 2013).

Kammerer's most notorious experiments concerned the sea squirt, *Ciona intestinalis*, as well as amphibian species in the genera *Proteus* (the blind cave salamander), *Salamandra* (fire salamanders) and *Alytes* (midwife toads). The call for replication of Kammerer's work has never dissipated (E. W. MacBride in Bateson, 1919; Svoldal, 2010; Nahm, 2021, to name a few). It is, however, not always appreciated that the straightforward experiment on the sea squirt—purportedly demonstrating the inheritance of an acquired character state—was repeated three times, all with negative results (Fox, 1924; Wermel and Lopaschov, 1930; Whittaker, 1975; see also Weissmann, 2012; Jeffery, 2015). Even though this particular study was seen as most pertinent and crucial by Kammerer himself, it was never published other than in summary mode (Kammerer, 1915, 1923, 1924). For a description of the experiment on this deceptively simple looking organism and the different outcomes see **Figure 1**.

Kammerer's amphibian studies are briefly laid out below. I go through the works that put Kammerer's accomplishments to the test and comment upon the feasibility and relevance to further replicate these experiments. I do not focus on the possible wrongdoings of Kammerer, his victimhood from antisemitism or on his position as an early epigeneticist, because these topics distract from the main issue on the inheritance of acquired character states and, moreover, have been evaluated at length elsewhere (Gliboff, 2010; van Alphen and Arntzen, 2016, 2017; Taschwer, 2016).

THE AMPHIBIAN EXPERIMENTS

Color Change and Eye Regeneration

Kammerer observed that the blind cave salamander (*Proteus anguinus*) turned from the pigment-less coloration occurring in wild subterranean populations to a dark color if exposed to daylight and that darkened animals often produced dark offspring, irrespective of whether they were laid as eggs or born as metamorphosed young. He also showed that the salamanders developed relatively large, functional eyes if kept under some particular conditions of light (Kammerer, 1912, 1923).

Mode of Reproduction

Salamandra salamanders come in two different reproductive modes. The Alpine salamander (*S. atra*) produces on land two young that resemble their parents. The offspring pass through embryonic and larval stages, but these occur unobserved inside the mother's uterus, where metamorphosis takes place before they are born (pueriparity). In the fire salamander (*S. salamandra*) the offspring also partially develop inside the uterus, but these are many and are generally deposited as aquatic larvae that have yet to undergo transformation (larviparity). Kammerer kept both species under environmental conditions typical for their counterpart species and noted that over their lifetime the individuals switched from a larviparous

to a pueriparous mode of reproduction, and *vice versa*. The induced reversals of reproductive modes were subsequently observed in the next generation and considered to be inherited (Kammerer, 1904, 1907, 1923).

Color Pattern Change

The fire salamander is secretive yet conspicuous, with sulfur yellow spots or stripes on an intense black background. Kammerer kept metamorphosed fire salamanders in terraria furnished with yellow or black backgrounds and noted that the differential treatment had the effect that the salamanders turned increasingly yellow and black, respectively. The acquired character states were shown to be inherited in experiments covering three generations (Kammerer, 1910, 1913, 1923).

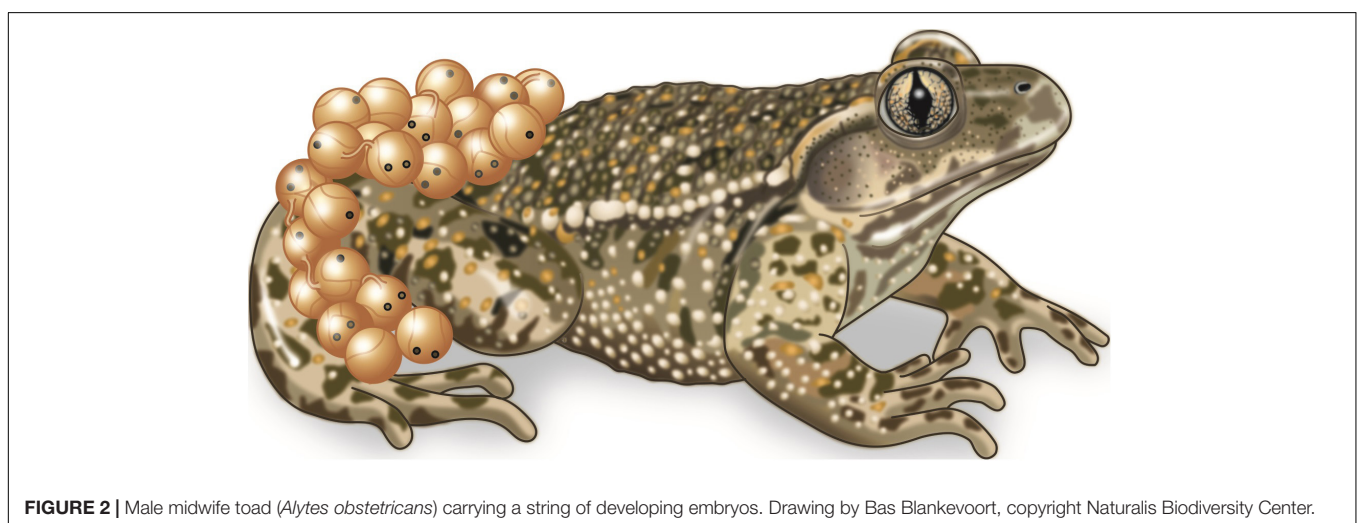
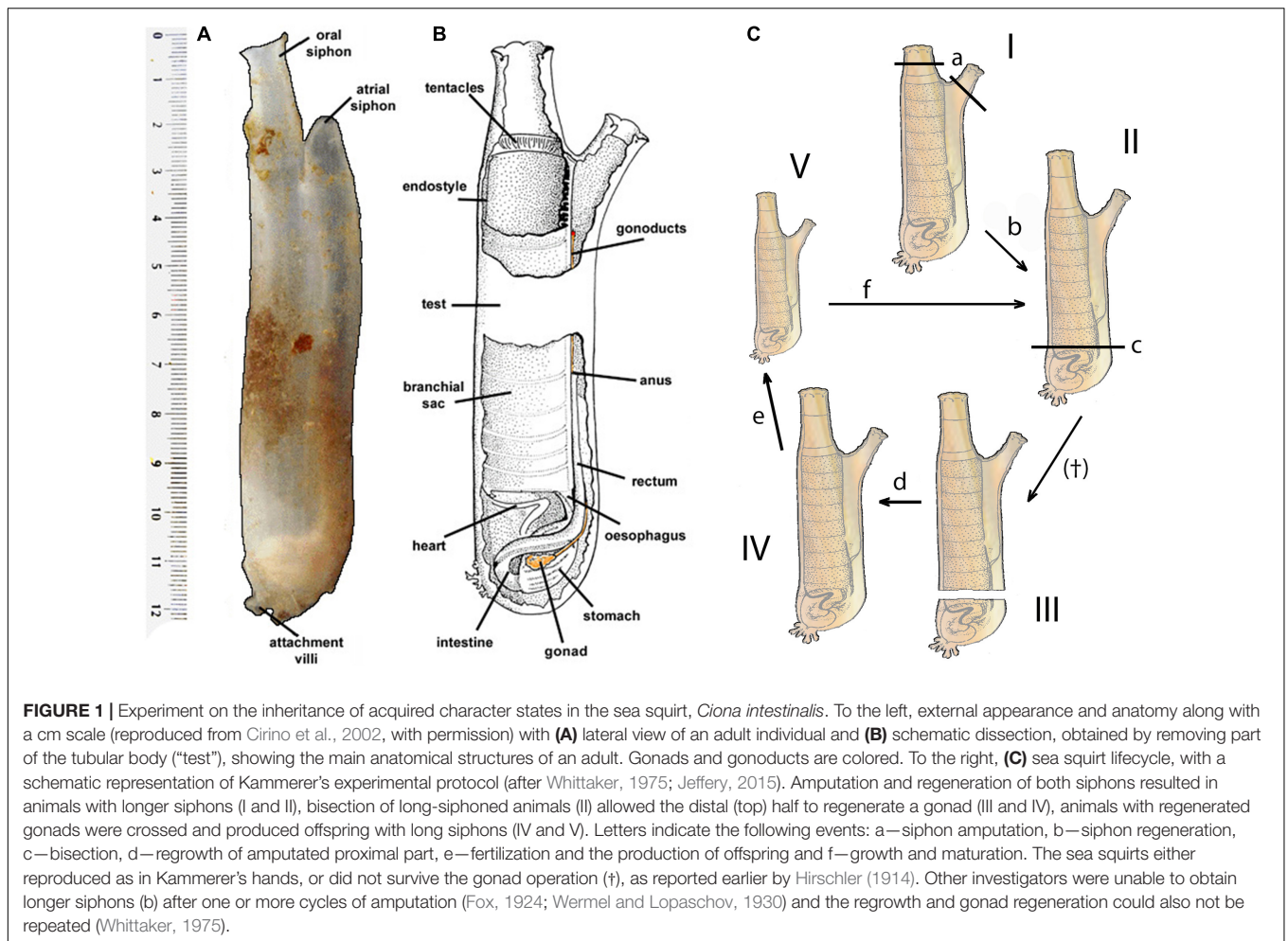
Aquatic Breeding

Midwife toads (genus *Alytes*) are terrestrial breeders in which the male carries the fertilized eggs in a string wrapped around its ankles (**Figure 2**). For excellent footage on the mating behavior of *Alytes obstetricans* see Redondo (2012). In an experiment covering six generations, Kammerer managed to make midwife toads reproduce in water, with male offspring developing seasonal nuptial pads in adulthood and with female fecundity increasing dramatically, which was associated with smaller egg sizes. These are features that are typical of aquatic breeders (Kammerer, 1906, 1909, 1919, 1923).

REPLICATION

The experiment on eye development in *Proteus anguinus* has been attempted by Jacques Durand, who remained more than a little doubtful of Kammerer's results. He reports: "Experiments were designed to find out if the presence of light will actually permit regeneration of eyes. Young specimens of *Proteus* were exposed to the action of daylight for 6.5 years. Others were exposed to artificial light of wave-lengths between 600 and 1,200 nm (i.e., within the red and infrared range of the spectrum). This continued for the first 10 years of age. After several years, individuals exposed to light become bluish-black. Over the same time, even if the eye is initially relatively well developed, the corneal ectoderm thickens, the lens diminishes in size and eventually disappears." (Durand, 1976, p. 462). It is widely known that *P. anguinus* may turn dark under conditions of light (e.g., von Chauvin, 1883; Schreiber, 1912), but a hereditary effect of such a treatment as reported by Kammerer remains to be confirmed. Moreover, Kammerer's observation that *P. anguinus* is facultatively life bearing has not been confirmed (Blackburn, 2019).

As for the fire salamander experiments, Kammerer's early work on a change in reproductive mode is said to have been confirmed (Koestler, 1971). This effort, however, only dealt with the raising of larvae that had been excised from gravid Alpine salamanders (Knoblauch, 1904), as had been previously shown to be tricky, but not impossible (von Chauvin, 1876, 1877). Experiments on color pattern change in the fire salamander are manifold, before as well as after Kammerer, inspired by his work or independently, but three stand out (von Frisch,



1920; Herbst, 1924; Sanchez et al., 2019). These three all reached the same general conclusion that larval and freshly metamorphosed fire salamanders *do* develop slightly different ratios of yellow and black coloration, depending on the color

of the background at which they are raised. The question whether these experiments classify as genuine replicates is addressed by Nahm (2021). Either way, because observations are so far limited to within a generation, the crucial finding

by Kammerer on the heritability of the induced color change awaits confirmation.

Among the wide variety of Kammerer's experiments, those dealing with the common midwife toad (*Alytes obstetricans*) attracted most attention, but as yet efforts to replicate this work did not proceed beyond the early stages (see e.g., "The unrepeatable experiment," Appendix 3 in Koestler, 1971). From a personal involvement, I present the outcome of a humble, serendipitous experiment. Back in the summer of 1977 I placed a small plastic bucket over a toad carrying developing embryos with the aim of photographing it in daylight. By morning this male had shed its egg-string, even though it had not even been touched. I later repeated the experiment to illuminate my MSc-supervisor, Dr. D. Hillenius, who had a keen interest in the Kammerer and Koestler debate and was thrilled by the thought that Kammerer might have secured some groundbreaking results. This time we used a plastic kitchen strainer instead of a bucket, to allow a little wind, moisture and light to pass through, but the result was the same, upon which Hillenius and myself agreed that carrying midwife toads are prone to stress, that *Alytes obstetricans* is not quite the laboratory animal one would choose and that replication of Kammerer's study would be a delicate, if not impossible, undertaking. It almost goes without saying that midwife toad "water eggs" or nuptial pads have not been experimentally produced, other than by Kammerer.

Critique on Kammerer's work took off in 1913, by one of his direct colleagues at the "Biologische Versuchsanstalt" research institution in Vienna (Megušar, 1914; see also Schultschik et al., 2017) and by geneticists abroad, such as Wilhelm Johannsen, who observed: "It is very characteristic for this researcher, that he always obtains so many positive results and that further testing provides nothing." (Johannsen, 1913, p. 449) and William Bateson who noted: "If we had certain assurance that even a single unimpeachable case could be repeated at will, the whole matter would assume a more serious aspect." (Bateson, 1913, p. 210). The most frequently suggested *modus operandi* for a mistaken or cheating Kammerer is that he presented individuals collected from nature as the result of his experiments, such as on the fire salamander by E. G. Boulenger in Bateson (1913, p. 208), on the sea squirt by Whittaker (1975) and van Alphen and Arntzen (2016, 2017) on the whole lot.

PERSPECTIVES

After more than a century of debate, most herpetologists and evolutionary biologists would accord with Bateson who, when provoked to replicate Kammerer's work, commented: "We, however, are likely to leave that task to those who regard it as a promising line of inquiry." (Bateson, 1919, p. 345). To "those" that are into the challenge nevertheless, it would seem ill-advised to put effort in experiments that have already been invalidated (*Ciona*, *Proteus*). Moreover, to extend the work on *Proteus* into the rearing and breeding of offspring would be a demanding undertaking due to the species' exceptionally long generation

time and intermittent breeding (Voituron et al., 2011), launching a venture of several decades.

Replication of Kammerer's *Salamandra* experiments stands out as feasible and not quite inauspicious. Testing for the reversal of reproductive modes among fire and Alpine salamanders presents a blank canvas. With future experimental crosses among individuals that are genetically modified by environmental imprinting in mind, researchers may wish to divert their attention from *S. atra* to some recently discovered Iberian pueriparous lineages of the otherwise larviparous *S. salamandra*. Whereas hybridization of *S. atra* and *S. salamandra* is unlikely on account of their long-term evolutionary independence (since the Miocene; Burgon et al., 2021), the cross-breeding of larviparous and pueriparous forms of *S. salamandra* would seem feasible, considering that they have a most recent common ancestor at just ca. 10,000 years before present, as inferred from biogeographic and molecular genetic data (Velo-Antón et al., 2007, 2012; Lourenço et al., 2018). Another promising model is the larviparous/pueriparous *S. salamandra fastuosa*, also from the Iberian peninsula. This subspecies can alternatively bear numerous larvae or few metamorphosed young (Greven, 2003; Buckley et al., 2007) and, possessing a wider geographical range, may be easier to get hold of than the localized lineages mentioned above. It should yet be kept in mind though that Kammerer's own material was from central Europe (Kammerer, 1904, p. 170–173) where *S. salamandra* is larviparous, as it is all over the species range, except for some lineages in the north of Spain.

The fire salamander color pattern change experiment also qualifies, but before embarking on this endeavor one might wish to take note of Richard Goldschmidt who, upon visiting Kammerer's laboratory, noted that "... the backgrounds of both types, supposed to be yellow and black, were in no way different from one another; both were a filthy, neglected gray!" (Goldschmidt, 1956, p. 166–167). Another word of caution comes from Kammerer himself who stated that the experiment would take one or two decades (Kammerer, 1913, p. 6–7), in a detailed protocol that by a contemporary colleague herpetologist was seen as designed to deter, rather than encourage replication (Werner, 1915). It may be concluded that an experimenter wishing to find a tractable model system to study transgenerational epigenetic effects would probably do better elsewhere. An alternative hypothesis is that Kammerer combined material from different subspecies to make his case, as by Boulenger's opinion mentioned above. Modern molecular genetic techniques would allow to disentangle salamander family relationships and geographical variation but, unfortunately, Kammerer's collection appears not to have survived the turbulences of twentieth century Europe, as indeed the author was not able to retrieve any of it (see section "Acknowledgments"). Finally, the midwife toad challenge seems awkward, unwieldy and altogether impossible. If taken forward nevertheless, it may be beneficial to turn to the species *Alytes muletensis* from Mallorca that breeds well in captivity (Tonge and Bloxam, 1989; Buley and Gonzalez-Villavicencio, 2000).

With one century passed since Kammerer's experiments, and half a century since Koestler's booklet, no data have come to

light to support the inheritance of acquired character states as reported by Kammerer. His findings on color pattern change in the fire salamander have to some degree been confirmed, but a transgenerational experiment to show that they result from a fixed genetic alteration is lacking. To support Kammerer's inferences, data on geographical variation and phenotypic plasticity will not qualify, because it is the inheritance of acquired character states, as directly tractable from morphology and behavior, that is at stake. Accordingly, the "midwife toad challenge" is still out, in particular of course to those who see value in Kammerer's work.

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The author confirms being the sole contributor of this work and has approved it for publication.

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