The Inheritance of Acquired Characteristics (1924), by Paul Kammerer [1]

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The Inheritance of Acquired Characteristics is a book published in 1924, written by Paul Kammerer, who studied developmental biology in Vienna, Austria, in the early twentieth century. *The Inheritance of Acquired Characteristics* summarizes Kammerer's experiments, and explains their significance. In his book, Kammerer aims to explain how offspring inherit traits from their parents. Some scholars criticized Kammerer's reports and interpretations, arguing that they were inaccurate and misleading, while others supported Kammerer's work. Kammerer said that the results of his experiments demonstrated that organisms could adapt to different environments by acquiring new features during the course of their lifetimes, and that they transmitted those acquired features to their offspring.

Boni and Liveright, Incorporated published *The Inheritance of Acquired Characteristics* in New York in 1924. Although the book appeared in English, the author wrote the manuscript in German, and Albrecht P. Maerker-Branden translated it into English. Kammerer dedicated his book to Ernest W. MacBride, a colleague and scholar in London, UK.

In *Inheritance*, Kammerer compiles the results of his lifelong experiments on development and inheritance, which he had presented in a series of conferences while traveling in the US and Britain in 1923 and 1924. When Kammerer conducted his experiments during the first two decades of the twentieth century while in Europe, Charles Darwin [2]'s 1859 theory of evolution [3] lacked evidence to explain how offspring inherited traits from their parents. Scholars in the early 1920s attempted to complement the theory of evolution [3] with Gregor Mendel's laws on inheritance. In Europe in 1865, Mendel identified discrete features in organisms, and he observed the rate and frequency that individuals transmitted those particular features to offspring. Naturalists interpreted Mendel's laws as about innate, rather than acquired, features.

Other naturalists suggested a different explanation for the mechanics of inheritance. Kammerer refers to Jean-Baptiste Lamarck's 1809 work, which suggested that living beings could inherit the features their parents or ancestors acquired throughout those ancestors' lives. In his 1924 book, Kammerer claims that organisms inherit their parents' acquired features. Additionally, Kammerer argues that through the inheritance of acquired features, it is possible to improve human society by manipulating developmental processes and producing better individuals.

Inheritance consists of two sections, titled "Biological Part" and "Eugenical Part." The first section includes chapters one to forty-one, and the second section includes chapters forty-two to fifty-four. The "Biological Part" provides evidence for the hypothesis that organisms transmit to their offspring the features they acquired as adaptations to their environments. In the "Eugenical Part," Kammerer compares Darwin's theory of evolution [3] to socialism, an ideology emphasizing the role of the community rather than individuals in economic and social processes. Kammerer claims that the inheritance of acquired features could enable people to improve their fitness, or the ability to survive and reproduce, and to produce better-adapted offspring.

In chapters one to two, the author introduces the theoretical framework for the inheritance of acquired features. Kammerer highlights the way humans [4] learn a language as an example to show that individuals are not born with the all the features they display in life, but that they have to acquire some of those features. Kammerer claims that if individuals can inherit their parents' acquired features, humans [4] do not have to depend on the traits they're born with, but can increase the number of favorable traits for future generations.

In chapter three, the author discusses the breeding experiments he had conducted on different organisms, including salamanders, owls, midwife toads, and sea-squirts. He had conducted the breeding experiments to demonstrate the possibility that acquired characteristics could be inherited. Kammerer argues that the results show that animals can transmit their acquired features to their offspring and that the theory could also apply to humans [4]. In chapters four to seven, the author reviews some breeding experiments that other scholars had conducted on butterflies and beetles to also support the hypothesis of the inheritance of acquired characteristics.

In chapter eight, Kammerer addresses the question of whether the acquired characteristics that organisms display are new characteristics or are retrogressions to ancient features (atavisms). According to the author, if acquired features are retrogressions to earlier stages, then it is unclear how individuals within species evolve to fit their environments better than their ancestors did. Kammerer claims that the retrogression hypothesis does not explain individuals' adaptations to particular environments. Many scholars had criticized Kammerer's earlier interpretation of his own results. They argued that the acquired features he described as new characteristics were in fact a retrogression to features previously apparent in the species' ancestries that had disappeared. Kammerer reports that he wanted his experiments to show that, by transmitting favorable

features they acquired to their offspring, parents can produce fitter individuals. He also claims that through this process, humans [4] can therefore improve societies.

In chapters nine to ten, Kammerer reports the results of his breeding experiments on the midwife toad (*Alytes obstetricans* [5]), which he had conducted in the early 1900s in the Institute for Experimental Biology located at the Vivarium in Vienna, Austria. The midwife toad typically lives in a dry environment and deposits eggs on the land. Then, it moves to the water to enable the eggs to hatch and the offspring live in the water as tadpoles. Once the tadpoles develop into adults, they move to land. Kammerer conducted two series of experiments on the midwife toad.

In the first series of experiments, he eliminated the midwife toads' tendencies to lay eggs in water. To do so, he bred the toads in a dry environment, and over several generations, they adapted to live and reproduce on land. Also after a few generations, the toads bore fully developed offspring, capable of living outside of the water immediately from birth. From these results, Kammerer argued that the capability of bearing fully developed organisms was an evolutionary novelty, or new characteristic, for the toads.

In the second series of experiments, Kammerer tried to induce the males of the midwife toad to develop nuptial pads or blackish swellings between the forearm and the thumb. Nuptial pads help male toads of other species grasp female toads during the mating process, which often takes place in water. Midwife toads do not have nuptial pads in their natural environment. Kammerer heated the environment where the experimental midwife toads lived, causing them to move to water. After a few generations, Kammerer said that the males had developed nuptial pads to grasp the females while mating. As other frogs and toads have nuptial pads, Kammerer interpreted the fact that the experimental midwife toad had acquired nuptial pads as a retrogression to an ancient characteristic.

In chapters eleven to fifteen, Kammerer refers to some of the controversies that arose over the hypothesis of the inheritance of acquired characteristics. One of the critiques against Kammerer's experiments came from Erwin Baur, who studied plants in Germany in the early twentieth century. Baur claimed that an acquired feature in a parent does not necessarily transmit to the offspring. He noted that the given characteristic could disappear in descendants. According to Kammerer, natural selection [6], or the process by which certain individuals survive over others to pass traits to the next generation, only has a secondary role in evolution [3]. He claims that natural selection [6] does not produce new variations, but could only explain why unfit individuals disappeared. Kammerer emphasizes the role of the environment in generating variety through individuals' development. In contrast, many others, later called neo-Darwinians, considered variations as randomly happening in nature.

In chapters sixteen to seventeen, Kammerer details the experiments he conducted on salamanders, beginning in 1903. These experiments contributed to the disagreements between Kammerer and others over the mechanics of inheritance. Kammerer conducted two series of experiments on fire salamanders (*Salamandra maculosa* [7]) at the Vivarium. Kammerer induced salamanders to adopt a different reproductive habit by breeding them in a different than normal environment. After inducing the salamanders to breed outside of the water, Kammerer observed that the offspring could fully develop within the mother. From those experiments, Kammerer concluded that the salamanders had developed new features as adaptations to the new environment, and that they had transmitted those acquired characteristics to their offspring.

In chapter eighteen, Kammerer argues that organisms are able to transmit acquired features according to Mendel's laws of inheritance. To do so, Kammerer refers to August Weismann [8]'s 1893 germ plasm theory. Weismann, who studied plants in Germany, distinguished between somatic cells, or body cells, and germ cells [9], or reproductive cells, and he argued that only germ cells [9] could transmit particular features from parents to the offspring. Using Weismann's theory, Kammerer claims that the changes that occur during one organism's life are able to pass from somatic cells to germ cells [9], thus enabling offspring to inherit acquired features from their parents.

In chapters nineteen to twenty-one, the author addresses some of his peers' objections to his interpretations of the results from his experiments. For example, many had criticized Kammerer's experiments on salamanders, arguing that those organisms' skin colors did not change completely when the salamanders were forced to breed and live on different colored soils. According to Kammerer's critics, one could not claim that the changed features were acquired characteristics; rather they were just natural variations. Kammerer responds to those critiques and says that organisms could acquire new features as those features passed from somatic cells, such as skin cells of the salamander [10], to reproductive cells, thereby allowing those traits to be passed to offspring.

In chapters twenty-two to twenty-four, Kammerer reports his experiments on sea-quirts (*Ciona intestinalis* [11]), experiments that focused on regeneration and inheritance. Sea-squirts have a cylindrical body, and two tubes or siphons extend from their heads, the longer being the inhalant or oral tube, the shorter being the exhalant or anal tube. After cutting off both siphons, Kammerer observed that both siphons regenerated and became longer than the original siphons. Additionally, the offspring of parents whose siphons had been cut off showed longer siphons than the offspring of parents who had not had their siphons cut off. Kammerer says that acquired characteristics,in this case longer siphons, could be transmitted from parents to the offspring.

In chapter twenty-five, the author comments on some of his peers' research on hybrid plants in which the offspring are hybrids of parents who belong to different species. According to Kammerer, scientists had argued that hybrid plants derived from one parent plant, the female, but carried a recessive trait that resulted in a physical appearance unlike that parent plant. Other researchers demonstrated that hybrid plants derived from two parents, a male and a female, that both contributed to the

offspring's features. Kammerer says that hybrid plants indicated that organisms could acquire their parents' acquired traits.

In chapters twenty-six and twenty-seven, Kammerer discusses why organisms do not inherit mutilations, or damaged body parts. According to Kammerer, mutilations are not acquired features, but are lost or damaged features, and for this reason they do not transmit to the offspring. Moreover, he argues that mutilation is not a genuine characteristic. Kammerer claims that a genuine characteristic results when organism reacts to an outside influence. He uses the example of when a part of the body regenerates after mutilation. He says only regenerated parts can transmit to the offspring, not mutilated, or missing parts.

In chapter twenty-eight, Kammerer reports the experiments on plants that Adolf Cieslar in Germany had conducted in the early 1920s. Cieslar planted seeds from the pine (*Picea excelsa*[12]) in different locations: the crest of a mountain, a mild climate, a cold climate, and an experimentally controlled botanical garden. Cieslar observed that those pines grew at different rates, even if they were planted at the same time. From this evidence, Kammerer argues that the environment directly affects organisms' growth and development.

In chapter twenty-nine, Kammerer discusses inheritance experiments on protists, which he calls the lowest living beings. Kammerer claims that it would be inappropriate to attribute the inheritance of acquired features to protists, as protists do not reproduce sexually and only consist of one cell. Kammerer acknowledges that many factors, both chemical and mechanical, can influence protists' development, but that protists do not transmit traits like other organisms.

In chapter thirty to thirty-three, Kammerer claims that the inheritance of acquired features causes species to evolve. Kammerer describes multicellularity, or the property of organisms composed of multiple cells, as an evolutionary phenomenon deriving from multitudes of single celled organisms combining. He claims that this phenomenon transmitted to offspring for numerous generations, producing multicellular organisms. Kammerer also contends that organisms can inherit behaviors and psychological characteristics. He refers to Ivan Pavlov's 1923 work completed in Russia, in which Pavlov conducted experiments to test mice's inheritance of parents' behavior. From Pavlov's and others' experiments, Kammerer concludes that inheritance of behaviors is an additional aspect of the inheritance of acquired features.

In chapters thirty-four to thirty-six, Kammerer analyzes the ways that organisms inherit diseases, immunity, and alcoholism. Kammerer claims that parents who became immune to a particular disease often transmit that immunity to their offspring. Kammerer also reviews experiments that demonstrate the numerous mental and physical traits that offspring can inherit through alcoholic parents.

In chapter thirty-seven, Kammerer discusses the phenomenon of the thickening of the skin on the sole of the human foot. He describes this process as taking place over the course of a life time. Kammerer reports on microscopic investigations that indicated that the soles of human fetuses' feet have developed pads, or horny pads. Kammerer says that while the thickened sole is apparent in an embryo, the entire foot undergoes accelerated growth in the womb [13]. Newborn humans [4] have remnants of horny pads, but they are not completely visible. According to Kammerer, this phenomenon shows that the feature parents acquired passes to the offspring, though the horny pads remain small until more weight is put on them by years of walking.

In chapters thirty-eight to forty-one, Kammerer summarizes various experiments and evidence for and against the theory of the inheritance of acquired characteristics. To do so, he first cites experimental evidence in work completed by himself or by others that supports the theory of the inheritance of acquired characteristics. He then cites what he calls indirect or non-experimental proofs in favor of the inheritance of acquired characteristics. Kammerer references phenomena such as adapted immunity against poisonous venom of predators, and as adaptations in response to different geological locations. He then provides examples of traits and adaptations to which the inheritance of acquired characteristics does not apply. Kammerer also reviews Darwin's theory of evolution [3] in light of those experiments. He suggests that, in emphasizing natural selection [6] on populations of individuals, Darwin under-estimated the impact of acquired adaptations in inheritance. Kammerer argues for more focus on adaptations, with natural selection [6] as a secondary factor, in shaping evolution [3].

The second section of *The Inheritance of Acquired Characteristics* is titled "Eugenical Part," and it spans chapter forty-two to the end of the book. In chapter forty-two, Kammerer addresses the social implications of Darwin's theory of evolution [3]. In this section, the author provides evidence for how evolutionary biology can improve society. He proposes that people can improve their communities by encouraging fit individuals to reproduce more than less fit individuals. Kammerer argues that Darwin's evolutionary theory impacts populations and that humans [4] should attempt focused, progressive development in societies rather than waiting for selective processes.

In chapters forty-three to forty-four, Kammerer writes about race theory. Race theory says that there are differences between races and people from different nations. Kammerer claims that that those differences result from the process of inheritance of acquired features. Kammerer also discusses the theory of mutual aid, proposed by Petr Kropotkin in Russia during the early twentieth century. The theory of mutual aid states that cooperation, both in animal and in human populations, is essential to evolution [3] as it facilitates individuals to survive by helping each other and building communities. Kammerer uses the theory of mutual aid to account for how altruistic behavior in social organisms could evolve. By stressing the role of mutual aid in evolutionary mechanics, Kammerer argues that socialism was consistent with the Darwin's theory of evolution [3].

In chapters forty-six to forty-eight, Kammerer discusses the ways in which the inheritance of acquired features impacts how

societies function. He explains how purpose-driven breeding increases production in domestic animals and other factions of agriculture. He also discusses how adopting children can be risky, in light of those children having inherited what Kammerer deemed as undesirable traits that may become apparent. He stresses the importance of raising those children in environments in which they acquire new and favorable traits to pass on to their offspring. He further emphasizes the effects of pregnant women's environments. He says that children who developed *in utero* while their mother was incarcerated are more apt to have criminal tendencies themselves.

In chapters forty-nine to fifty-one, the author analyzes the way time impacts evolution [3]. Kammerer discusses inheritance as it relates to old age. For example, he argues that people born from old parents are sometimes clever due to the fact that their parents had the opportunity of accumulating and transmitting experiences to their offspring. Kammerer reviews some of his colleagues' experiments on the evolutionary effects of rejuvenation. Rejuvenation is the phenomenon of species retaining favorable features associated with youth, such as the capacity to breed longer into their lifespans than their parents. Kammerer argues that rejuvenation plays a role in evolution [3] and that there should be more experiments on artificial rejuvenation.

In chapters fifty-two to fifty-four, Kammerer argues for productive eugenics [14], or a way to produce a more fit population by enhancing the production of variable traits and selecting those variations that are beneficial. In his book, Kammerer criticizes standard eugenic practices, which relied on sterilization [15] and other methods to remove un-desirable traits from a population. Kammerer proposes that evolutionary biologists should work to increase beneficial variation throughout a population, and that they should select favorable individuals to produce offspring with favorable traits.

In 1926, two years after the publication of *The Inheritance of Acquired Characteristics*, Gladwyn K. Noble, the curator of reptiles at the American Museum of Natural History in New York, New York, published a letter in *Nature* criticizing many of Kammerer's experimental results. Noble had analyzed Kammerer's midwife toad specimens and claimed that they were fakes. Noble's letter diminished Kammerer's reputation within the scientific community. A few months later, Kammerer's corpse was found on the top of a mountain in Puchberg am Schneeberg, Austria. Newspapers reported that Kammerer had committed suicide.

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Kammerer, Paul, 1880-1926. Inheritance of acquired characteristics[28] Kammerer, Paul, 1880-1926 [29] Inheritance of acquired characters [30] Evolution (Biology) [31] Adaptations [32] Laboratory animals--Breeding--Experiments [33] Theoretical and experimental biology [34] Midwife toads [35] Heredity [36] Darwinism, Social [37]

Topic

Publications [38] Theories [39]

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