

## Genes and development: an early chapter in German developmental biology

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Gene action and its spatial and temporal control is a crucial constituent of development. From a modern point of view, it is therefore surprising that genetic concepts and methods were of no importance in the work of the outstanding German developmental biologists Hans Driesch and Hans Spemann. Both were apparently not interested in genetics. The dramatic progress in classical genetics cannot have escaped Driesch's attention, especially as T.H. Morgan had worked in his laboratory, but it is easy to see that it had no place in his "vitalistic" biology. Much less obvious is that Spemann's critical and open mind should have never led him to consider genetic influences in development. Theodor Boveri had interpreted the decisive influence of cytoplasm onto the fate of the blastomeres in *Ascaris* development as a "simple paradigm" for the interactions of cytoplasm and nucleus during ontogenesis and "for the way by which extremely small differences within the egg cytoplasm, by repeatedly triggering changes in the nuclei that act back on the cytoplasm, finally lead to the dramatic differences between newly formed cells" (Boveri, 1910). For us, it would appear natural to envisage the formation and inductive action of Spemann's organizer in terms of nuclear-cytoplasmic interactions. But Spemann, as his students have witnessed, did not even like to teach genetics, and many decades were to pass till the task was undertaken to identify the organizer by genetic methods (Cho *et al.*, 1991).

I do not know whether Spemann paid attention to an experiment that brought together, for the first time as far as I can see, the analysis of gene action in a mutant and the classical transplantation used in developmental physiology. According to a statement Erik Nordenskiöld made in his History of Biology (the German edition of which was published 1926), genetics appeared to him the most popular biological discipline of the

time. However, the physical nature of the genes and the mechanisms of gene action were completely unknown. To elucidate such mechanisms in developmental processes was the aim of a group of biologists who worked at the University of Göttingen in the decade from 1925 to 1935.

In these years, Göttingen was a world centre of mathematics. The physics and chemistry departments also belonged to the leading institutions in their field. Biology was very small. There were two chairs of botany and one of zoology. Alfred Kühn, a student of August Weismann, became director of the Zoology Department in 1920. He started a cooperation with the physicist Pohl on color vision in insects but went soon over to development and genetics. In his autobiography he writes about these years that his primary interest was in the field of developmental genetics. "The goal was to elucidate the way genes act during development" (Kühn, 1959). Kühn found a colleague with similar interests, the plant physiologist Fritz von Wettstein who came to Göttingen in 1925. Kühn had been instrumental in von Wettstein being offered a chair of botany, and from Wettstein's appointment on they cooperated in teaching a joint course that was repeated in many semesters and was first named "Seminar über Probleme der Vererbungsforschung", later "Seminar über Probleme der Entwicklungsphysiologie". In the German university system of these years it was very unusual that the director of a botany department and the director of a zoology department together taught a course. This course is still remembered by former students as the first course in a German university on genetics and development in both plants and animals (Melchers, 1987). It attracted physicists, chemists, and mathematicians who wanted to learn about the progress in general biology. Also other courses were novel. The young student Adolf Butenandt made a new experience when he moved from Marburg to

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Göttingen for the summer semester 1924. In an obituary for Alfred Kühn, he writes: "Whereas biology at almost all German universities of the time was taught - strictly separated into botany and zoology - as a descriptive science, Alfred Kühn ... lectured for his students on general problems of biology. With these lectures ... Alfred Kühn opened the way for a general biology that nowadays is a natural subject matter of teaching and research at our universities" (Butenandt, 1969).

Its quality and stimulating scientific atmosphere attracted students and scholars from many countries to the Faculty of Mathematics and Science. The departments of mathematics, physics, and zoology were supported by the Rockefeller Foundation. When the economic depression caused the Prussian government to cut the funds and to reduce the number of positions of research assistants, the Faculty established a committee to work out suggestions for a solution that would avoid the dismissal of young scientists. The names of the committee members illustrate the scientific rank of the Faculty in 1931. Max Born, who was the dean, Richard Courant, James Franck, Alfred Kühn, Richard Pohl, and Adolf Windaus made a detailed plan for funding the salaries of research assistants by private money from the pockets of the full professors and got their colleagues to accept it (Born, 1969; Becker, 1987). The funding worked until the Nazi government came into power and the Faculty's destruction began.

Kühn and von Wettstein investigated aspects of development in very different model organisms. Crosses between different genera and species of mosses revealed the importance of "plasmatic inheritance" and the influences of nucleus and cytoplasm onto the development of a plant phenotype (Wettstein, 1926, 1930). The degree of ploidy was changed experimentally to study its influence on moss development (Wettstein, 1923, 1924). Whereas the influence of cytoplasm and of the number of gene copies was evident from the plant model in von Wettstein's and his students' work, Kühn and his associate Karl Henke used an insect, the moth *Ephestia*, to study the cooperation of specific genes in the development of a phenotype. The common interest of both groups, gene action in development, induced them to look at plant and animal development from the same point of view. This approach became very successful and led into the new field of biochemical genetics.

Kühn and Henke had isolated a number of *Ephestia* mutants. One of them (Kühn and Henke, 1930) is "*rotäugig*" (red eyes). They named the mutant allele *a* and the wild-type allele *A*. Heterozygous hybrids have the same dark eyes as the wild type. Homozygous mutants cannot develop the dark eye pigment and exhibit a red eye colour, due to another type of pigment that in the wild type eyes is covered by the dark pigment. Not only the eye color is changed. The reddish larval epidermis and the brownish mauve testes of the wild phenotype contain little or no pigment in the mutant *a*. A young graduate student, Ernst Caspari, tried to analyze the action of *rotäugig*. In his *Ephestia* cultures, external influences like temperature appeared to cause a certain extent of variation in the degree of pigmentation (Fig. 1). The variation in color intensity was always equidirectional in the larval epidermis, testes, and imaginal eyes. This observation led Caspari to suspect that pigmentation in these different tissues is caused by the same developmental process. "*Rotäugig*" must exert its action repeatedly in different developmental

stages: the pigmentation of the larval epidermis occurs during embryonic development, that of the testes within the last larval instar, and that of the complex eyes during metamorphosis of the pupa. In his doctoral thesis, Caspari did then a novel experiment. "It has not been tried yet to approach the problem of the mechanism of gene action by the method that is very frequently used in developmental physiology, operative experiments", he writes (Caspari, 1933). Transplantation of tissue between animals of different genotype, he hoped, would elucidate the mechanism of action of *A* and *a*. Transplantations of testes or ovaries from wild-type animals into homozygous red-eye larvae caused the differentiating host testes and imaginal eyes to develop the dark pigmentation typical for the wild phenotype. Caspari concluded that the allele *A* acts through synthesis of a substance that is lacking in *a/a* animals. This substance is present in testes from wild-type animals and after transplantation enables larvae of the mutant genotype to acquire a normal pigmentation. Caspari proved that the dark-eyed moths developing from *a/a* larvae after implantation of wild-type tissue were not genetically changed. In crosses with *a/a* animals he obtained exclusively red-eyed offspring.

The mutation of *A* thus had the effect that a substance necessary for pigmentation in different tissues was no longer produced. Therefore, Caspari concluded, was the normal function of gene *A* to control the synthesis of a substance. Transplantation experiments, a classical tool of developmental physiology, had enabled him to identify a biochemical mutant. Caspari's thesis work was not published in a genetics journal but in Roux' *Archiv für Entwicklungsmechanik* (Caspari, 1933). It appeared 1933, several years earlier than Beadle, Ephrussi, and Tatum published their classical work on eye colours in *Drosophila* and the genetic control of biochemical reactions in *Neurospora*, and can therefore be considered the origin of biochemical genetics.

In further experiments Caspari and Plagge found that several tissues other than the gonads also synthesized the substance and that tissue from many other Lepidopteran species caused eye pigmentation in the *Ephestia* mutant subsequent to implantation (Kühn *et al.*, 1935; Plagge, 1936).

Of the mutant animals that survived the implantation of testes or ovaries and underwent metamorphosis, 10.3% developed brown and 89.7% developed black eyes (Caspari, 1933). Caspari concluded that a certain quantity of the substance lacking in the *a/a* genotype was necessary to accomplish full pigmentation. The substance was identified by Butenandt and Weidel in collaboration with Kühn's associate Becker (Butenandt *et al.*, 1940): it is kynurenine, synthesized in wild-type animals from tryptophan, that is a necessary metabolite within the pathway for the synthesis of the dark pigments of the insect eye, the ommochromes. Injection of kynurenine into *a/a* larvae resulted in normal pigmentation; below a certain level, the amount of pigment synthesized was directly proportional to the amount of kynurenine applied (Kühn and Becker, 1942). Finally, Kühn's associate Egelhaaf showed that the red-eyed mutant of *Ephestia* cannot synthesize formyl kynurenine from tryptophan and lacks the enzyme tryptophan pyrrolase necessary for this step (Egelhaaf, 1958, 1963). Caspari's analysis of an eye-color mutant in *Ephestia* had thus revealed the first case for a "one gene - one enzyme" relation, several years before the beautiful studies of Beadle and Ephrussi (1937) on the development of eye colors in *Drosophila* and Beadle and Tatum (1941) on bio-

chemical effects of genes in *Neurospora* led to the one-gene one-enzyme hypothesis.

Several other genes were later found to be necessary in *Ephestia* for further steps in ommochrome synthesis by enzymes. In *Drosophila* the gene corresponding to *rotäugig* is *vermilion* (*v*). The enzyme tryptophan pyrrolase is lacking in *vermilion* flies. By transplanting eye imaginal discs between *vermilion* and *cinnabar* (*cn*) larvae and studying the development of eye phenotypes, Beadle and Ephrussi (1937) found that the gene action of *cinnabar* is on a further step in ommochrome synthesis. From their results they concluded that the two genes direct the synthesis of two diffusible substances, the *v*<sup>+</sup> and the *cn*<sup>+</sup> substance. *Vermilion* imaginal discs transplanted into *cinnabar* larvae developed into pigmented wild-type eyes, indicating that the *v*<sup>+</sup> substance had been provided by the *cn* hosts. Eye discs from *cn* larvae, on the other hand, upon transplantation in *v* larvae yielded eyes with *cn* phenotype. The *cn*<sup>+</sup> substance was later identified as 3-hydroxykynurenine that is synthesized from kynurenine by kynurenine-3-hydroxylase, an enzyme lacking in *cn* animals.

A remarkable feature of scientific life in a German university of the time was the extent of freedom graduate students had in organizing and performing their work. Caspari selected even himself the problem he so successfully worked on. Kühn and his group were analyzing the formation of the *Ephestia* wing pattern and the genes involved in it. As Eicher (1987) reports, Kühn gave Caspari a problem to investigate in this field, but when it did not work Caspari decided to change to the eye pigmentation mutant, and, after discussing the method with Karl Henke, he began his transplantation experiments. He told Kühn about these experiments first when he had achieved clear and exciting results, and both agreed about the importance of the findings. Much of the work of the group in the following was based on Caspari's breakthrough. But its influence was much broader. To give an example, Georg Melchers, then an associate of von Wettstein, considered his own transplantation experiments between biennial and annual plant races by which he could analyze the development of flower formation (Melchers, 1936) to be influenced rather by Caspari's work than by any earlier approach in botany (Melchers 1987).

While the priority of the results of Caspari and the Göttingen group is clear, the wealth of information and conceptual progress achieved with *Drosophila* eye color mutants and especially with biochemical pathway mutants in *Neurospora* is convincing and classifies the work of Beadle, Ephrussi, and Tatum as a milestone in the history of biology. Why is it that progress in the *Ephestia* system was comparatively slow? And why was Caspari to become best known for his work in behavioral genetics?

Answers to these questions shed light on the political situation in Germany and in the University of Göttingen at that time. This situation is part of our history and of the history of science, but it is not only of historical interest. Plagge and Becker, two excellent young scientists, were killed in the war. Caspari, the most innovative of the younger generation in Kühn's laboratory, suffered the same fate as so many scientists who were expelled from their home-country, if their lot was not even worse, after the Nazi government had come to power. Science in Germany, let alone the humanities, literature and the arts, intellectual and social life, has never recovered from the enormous loss of many of the best

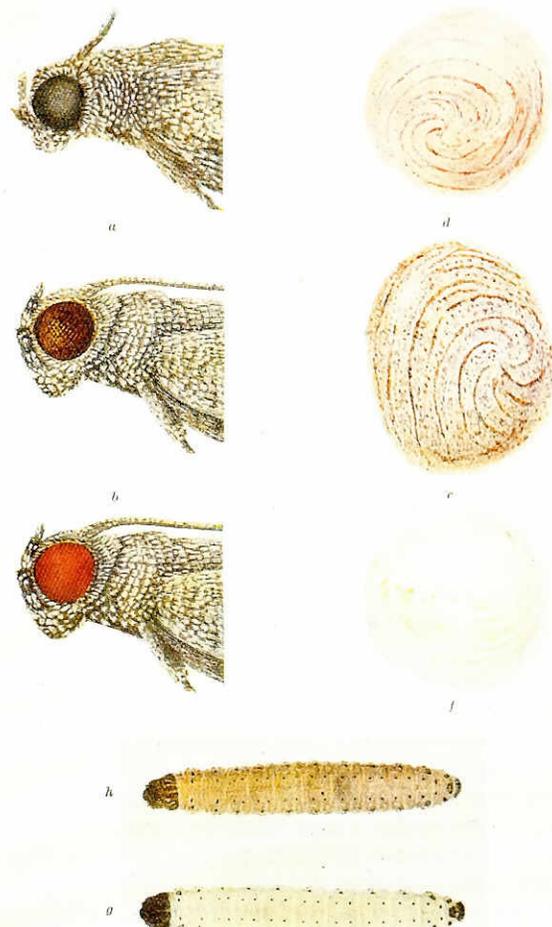


Abb. 2a–h. a Falter der schwarzäugigen Rasse AA. b Falter mit kaffeebraunen Augen der aa-Rasse. c Rotäugiger Falter der aa-Rasse. d und e Imaginale Hoden von Mehlmotten der AA-Rasse. f Imaginaler Hoden der aa-Rasse. g Ausgewachsene Raupe der aa-Rasse. h Ausgewachsene Raupe der AA-Rasse mit durchscheinendem Hoden.

**Fig. 1.** Color plate from Caspari (1933) shows the pigmentation of imaginal eyes (left), adult testes (right), and last instar larvae (below) of homozygous A/A and a/a animals, respectively. (a and b) illustrate variations in eye color intensity, and d and e variations in testis pigmentation, respectively, in the A/A genotype. These variations, Caspari observed, were due to external influences and were always equidirectional in the different tissues of an animal. With permission from Springer-Verlag.

and most innovative citizens. In an obituary article, Eva M. Eicher (1987) writes about Caspari: "Certainly it was not the right time to be a young intellectual in Germany when the Nazi regime came to power, especially a young intellectual Jew."

The first anti-Jewish boycott in Göttingen was in March 1933. In April the Prussian government, according to a new antisemitic law, began to suspend and dismiss Jewish university professors and other employees from the civil service. It was aimed, as a local newspaper put it, "to finish most of the shake-up before the first of May, in order to avoid riots at the beginning of the summer semester" (Göttinger Tageblatt, April 15, 1933, cited after Dahms, 1987). It was in this semester Caspari took his doctor's degree.

The law did not apply to veterans of the First World War. One of them, the Nobel Prize winner James Franck, as a protest against the discrimination of Jewish citizens, asked to be released from his duties. "We Jewish Germans are being treated as foreigners and enemies of our home country", he wrote in his public protest note that was published and discussed in many German and international newspapers. Franck had hoped to initiate a wave of protest all over the country. He received very many private letters of support from people from all classes, e.g. a letter signed by all officers of his former regiment who expressed their everlasting friendship for him. However, few colleagues reacted, and there was no public protest from individuals or scientific organizations (Dahms, 1987; Rosenow, 1987). A local newspaper commented that Franck's resignation was a severe loss for German and international research and expressed the hope that Franck's step would have the effect to prevent dismissal of other scientists to whom the new law applied. "Otherwise the loss could become so great as to make recouplement impossible forever or for a long period of time" (*Göttinger Zeitung*, April 18, 1933; cited after Dahms (1987). A prophecy that was to be fulfilled!- Most remarkable is a reaction Franck's public protest evoked in a group of 42 professors and other university employees in Göttingen. In a newspaper advertisement they expressed their conviction that Franck's protest was "an act of sabotage" and could "seriously interfere with the home and foreign politics of our government of national rise" (*Göttinger Tageblatt*, April 24, 1933; cited after Dahms, 1987). They also expressed their hope that the government would speed up the necessary purge. Göttingen is the only German university where a group of professors and other teachers voluntarily demanded the dismissal of their Jewish colleagues and called it "the necessary purge". According to Dahms (1987), most of the signers were at departments of agriculture, at the Medical School, and at the department of orientalism. Five were in the Faculty of Mathematics and Science; they were "Privatdozenten" who possibly hoped for a free position.

According to the university calendar for the summer semester 1933, the number of professors of mathematics and sciences who taught courses had already decreased considerably. It was the semester when Caspari took his doctoral degree. His thesis was submitted to Roux' Archiv for publication on August 10. Somehow Kühn managed to employ him. Caspari's list of publications (see Eicher, 1987) contains four additional papers from Göttingen in the years 1934 to 1936. However, when Kühn obtained a grant from the Rockefeller Foundation, primarily based on Caspari's results, he was not allowed to hire him (Eicher, 1987).

Becker (1987) has documented the names, positions, and fate of all persons that were dismissed from the University of Göttingen or were forced to retire. In the Faculty of Mathematics and Science, 23 professors and "Dozenten" (of a total of 82), and many young scientists too, left. Among them is an almost incredible number of world-famous scholars. Three of the youngest are Edvard Teller, the astrophysicist Martin Schwarzschild, and Ernst Caspari. Caspari was dismissed in 1935.

Many of the professors accepted offers from abroad, Hermann Weyl from Princeton, Richard Courant and Max Born from Cambridge, England. James Franck left Göttingen for Harvard and Johns Hopkins University in November 1933, followed to the railway station by a big crowd of people. Ernst

Caspari had no offer from one of the centres of science. He could emigrate to Turkey where he worked with a microbiologist, Hugo Braun, until he obtained a fellowship at Lafayette College and went to the U.S. in 1938.

When trying to characterize that productive period of developmental biology in Göttingen, one could say that the right people were in the right place. German university departments being small at this time, it was important that cooperation worked beyond department borders. Kühn and von Wettstein shared a deep interest in development and genetics, and they both had in mind to unravel general laws of biology rather than restricting themselves to botany and zoology. For many students, it was the rise of a new era in biology that they remember with enthusiasm (Butenandt, 1969; Melchers, 1987). Ernst Caspari moved to Göttingen because he wanted to work in genetics. Eicher reports in her inspired and sympathetic biographical sketch of Caspari (Eicher, 1987) that he first went to Freiburg to study with Spemann but moved to Berlin when he realized that Spemann was not fond of genetics. In Berlin, his first choice was Goldschmidt, who unfortunately did not take graduate students. As he could not work for Curt Stern either, because Stern had already moved to the United States, Caspari's next choice was Alfred Kühn in Göttingen.

The period that was so productive lasted only for a short time. 1931 von Wettstein accepted an offer from the University of München, and he and his group moved there. In 1933 the time of tolerance and scientific freedom was over. The Faculty of Mathematics and Science lost many of its best members and students. Kühn found it increasingly difficult to protect Caspari and a Jewish graduate student in his laboratory, Werner Braun. Caspari left in 1935, Braun in 1936. Harwood (1993) who has read the Nazi party's Kühn file in the Berlin Document Center and Kühn's (unpublished) letters to colleagues reports that the Nazis exerted increasing political pressure on him and that he was prepared to emigrate to the United States. In 1934 von Wettstein succeeded his teacher Correns as a director at the Kaiser Wilhelm Institut in Berlin-Dahlem. The institute lost two outstanding scholars, Richard Goldschmidt and Curt Stern, who both emigrated to the United States. Goldschmidt's position was offered to Kühn, and he and his group moved to Dahlem in 1937. What is listed in the Göttingen University calendar under the heading General Biology after Kühn left is something quite different: the pseudo-science "racial biology". The place had changed, the right people had left.

Harwood (1993) has described differences between German and American interests and approaches in genetics and developmental biology during the twenties and thirties. His comparative view suggests that German biologists at that time were far more concerned in developmental genetics than was the case in America. This would have been a good basis for modern genetics. However, the political situation being as it was, scholars and students were dismissed and persecuted, institutions were destructed and biological evidence abused in a racialist pseudo-science. Modern genetics was shaped elsewhere.

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and events in 1933 is based on the detailed and extensively documented reports of Dahms (1987) and Rosenow (1987). I am grateful to the late Erich Freiberg (Tübingen) who shared his memories from the Göttingen of his youth. Some of the material of this article was included in a talk (*Der Weg zur allgemeinen Biologie: Entwicklungsbiologie und Genetik in Göttingen*) held on the occasion of the 250th anniversary of the University of Göttingen (published in *Naturwissenschaften in Göttingen*, Ed. H.-H. Voigt. Vandenhoeck and Ruprecht, Göttingen 1988).

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