ERNST Caspari was the first researcher to use methods of developmental biology to analyze the action of a gene. By transplanting larval tissue between the wild type and a red-eyed mutant of the moth, Ephesia, he demonstrated that wild-type larvae produce a diffusible “substance” that is lacking in the mutant and is necessary for the development of eye pigmentation. Further characterization of the substance and an approach to isolate it were interrupted by the Nazi government dismissing Caspari according to the Nuremberg anti-Semitic laws. He escaped to Turkey and later to the United States but did not get a chance to further contribute to the rapid development in the field, which led to the “one-gene-one-enzyme” hypothesis. Caspari’s results, published in 1933, represent the first step toward this hypothesis of gene action.

Seventy-five years ago, the young geneticist Ernst Caspari published some experiments that provided novel insight into a hitherto unsolved basic problem of genetics: How do genes function to produce characters? Both the physical nature of genes and the mechanisms of their action were completely unknown at that time, but were of course the subject of intense speculation. In developmental biology, genetic concepts and methods played no role. In the beginning of the century, Theodor Boveri had performed experiments on the development of the nematode worm, Ascaris, in which he demonstrated that the mode of chromosome distribution in early cleavage was under cytoplasmic control. Somatic nuclei in Ascaris lose considerable numbers of fragments of their chromosomes during the first cleavage mitotic divisions, whereas germ-line nuclei retain the entire genome. This developmental program, Boveri found, depended on the cytoplasmic environment, as experimental relocalizations of the cleavage planes and alterations in the number of blastomeres derived from the animal and the vegetal half of the egg, respectively, yielded corresponding alterations in the numbers of germ-line and somatic blastomeres. These experiments led Boveri to conclude that the developmental fates of the blastomeres were due to extremely small differences within the egg cytoplasm that lead to differences between descendant cells “by repeatedly triggering changes in the nuclei that act back on the cytoplasm” (Boveri 1910, p. 191; I have translated several quotations from German). But even 20 years later, interactions between nucleus and cytoplasm had no place in Spemann’s organizer concept (Spemann 1936), which instead led to laborious efforts in many laboratories to isolate animalizing and vegetalizing factors. Spemann as well as other developmental biologists of the time never considered genetic influences in development, and many decades were to pass until genetic methods were applied to identify the molecular basis of organizer action (e.g., Cho et al. 1991).

Understanding gene action in developmental processes was the aim of a group of zoologists, botanists, and geneticists who worked at the University of Göttingen, Germany, between 1925 and 1935. One of the most successful and most interesting of them was Ernst Caspari (1909–1984). CASPARI (1933) used a novel experimental approach to the problem of gene action, both intellectually and experimentally, the results of which were the first step toward the “one-gene-one-enzyme” hypothesis. Caspari’s pioneering contribution to this field is not often recognized. Today, 75 years later, it deserves our interest, not least because of the social and political context, the sudden interruption of this work by a political catastrophe, the destruction of scientific and intellectual life after 1933 in Germany and the countries...
occupied by it, and Caspari’s personal fate, which he shared with countless other victims.

Ernst Wolfgang Caspari was born on October 24, 1909, in Berlin. His parents were Dr. Wilhelm Caspari, who at that time headed the Department of Animal Physiology at the Royal School of Agriculture, and his wife Gertrud, née Gerschel. The family was Jewish and had lived in Berlin since the 18th century, but both parents as well as Ernst, his brother Fred, and his sister Irene were protestants. Caspari attended two famous grammar schools, the Kaiser-Friedrich-Schule in Berlin and, after his father had been appointed a member of the State Institute for Experimental Therapy in Frankfurt, the Goethe-Gymnasium zu Frankfurt, where he took the high-school leaving examination in the spring of 1928. This education endowed him with a solid knowledge of both Latin and ancient Greek, but he was more influenced by his father talking with him about his research. Eicher (1987) has reported what Caspari told her about his memories of frequent visits to the lab and the experiments with mouse tumors Wilhelm Caspari has become known for. When Ernst Caspari was 14, Eicher reports, he received for Christmas Richard Goldschmidt’s famous introductory book, Ascaris, eine Einführung in die Wissenschaft vom Leben für Jedermann, published in 1921 and later translated under the title Ascaris: The Biologist’s Story of Life. This and other reading so strongly influenced him that he told his father, according to Eicher, that he “wanted to be a geneticist.”

FINDING THE RIGHT PLACE

The young student Ernst Caspari selected not only the field but also the environment he wanted to work in. He had in mind two areas of biological research that were both rapidly growing but were completely separated from each other, genetics and developmental biology. Eicher (1987) reports that his first choice had been Spemann’s laboratory in Freiburg. But, according to his file in the University of Göttingen archive, he stayed there only one semester, which was evidently sufficient to find out that Spemann was not at all interested in genetics. The next semester Caspari spent in Berlin, because his second choices were Richard Goldschmidt and Curt Stern at the Kaiser-Wilhelm-Institut für Biologie. Goldschmidt did not, however, accept graduate students, and Stern was about to leave for the United States, where he had previously worked in Morgan’s laboratory. Caspari then chose Alfred Kühn in Göttingen as his advisor.

Kühn (1885–1968) was a former student of August Weismann with a broad interest in different fields of biology. In Göttingen, he cooperated with the experimental physicist Richard Pohl in investigating color vision in insects, but soon, as he writes in his autobiography, he developed a primary interest in developmental genetics, the goal of which was “to elucidate the way genes act during development” (Kühn 1959, p. 278). His interests were shared by Fritz von Wettstein, who had joined the Faculty of Mathematics and Science in 1925. Whereas Kühn selected as a model the development of the moth, Ephestia kühniella, von Wettstein, a plant physiologist, investigated plasmatic inheritance and the influence of nucleus and cytoplasm in development in mosses by making hybrid crosses between different species (von Wettstein 1926, 1930). The importance of the number of gene copies and the role of the cytoplasm could be studied in such crosses where the parents differed in ploidy levels (von Wettstein 1923, 1924). Notwithstanding the differences between their model systems and the experimental approaches, Kühn and von Wettstein were both interested to find general mechanisms in development and for this purpose applied genetic crosses. They also cooperated by teaching a joint course that they named “Seminar über Probleme der Vererbungsforschung” and in later semesters “Seminar über Probleme der Entwicklungsphysiologie.” In the German university system at that time, it was very unusual for a professor of botany and a professor of zoology to share the teaching of a course. This course was later remembered, indeed, as the first course in a German university on genetics and development in both plants and animals (Melchers 1987). In his obituary for Alfred Kühn, the biochemist Adolf Butenandt (Butenandt 1981, p. 769) 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.” Caspari moved to Göttingen in 1929, the second year of his undergraduate studies. Two years later, he began to do experiments for his doctoral thesis in Kühn’s laboratory (Figure 1).

CASPARI’S EXPERIMENTS

Kühn and his associate Karl Henke had isolated a number of Ephestia mutants that exhibited alterations in the wild-type patterns of wing scale pigmentation. By studying interactions of genes in the formation of the wing pattern, they hoped to gain information on how these genes act in development. Obviously, this system was much too complex for analyzing mechanisms of gene action. Caspari too began to work on a problem in wing pattern formation, but as the results did not satisfy him, he decided to change the field and selected a very different problem, eye color pigmentation. One of the Ephestia mutants isolated in the laboratory was rotläugg (red eyes), which differs from the darkly pigmented wild type by exhibiting red eyes, colorless testicles, and white caterpillar epidermis (Kühn and Henke 1930). The pleiotropic character of the gene made it an attractive candidate for a study of its action, the more so because...
Caspari recognized that variations in the degree of tissue pigmentation occurred between stocks with different alleles and that these variations in color intensity were unidirectional in the different tissues. He estimated pigmentation degrees by comparison with Ostwald's "color body" for a characterization of the different alleles and then devised a technique for transplantation of tissues between genetically different caterpillars.

Transplantation of tissue between developing animals of different genotype was a fascinatingly novel approach at the time. In the introductory segment of his seminal publication, Caspari stated, "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" (Caspari 1933, p. 354). His transplantations showed that the wild-type animals produce a diffusible substance, later identified as kynurenine, that is lacking in the red-eyed mutant and is necessary for the development of wild-type eye color. Caspari also achieved a rescue of the wild phenotype in the mutant by transplanting wild-type tissue into mutant larvae. As a control he proved that the transplanted mutant animals with wild phenotype yielded mutant offspring with red eyes.

Caspari had quite independently chosen the problem and the model system, planned and performed the experiments, and found a convincing interpretation. As Kühn's associate for many years, Viktor Schwartz witnessed, Caspari did not tell his professor about the experiments before they yielded clear results. Today, a graduate student doing experimental research in the lab without her or his supervisor being kept informed is hardly imaginable, but Caspari's behavior was not quite as singular (though rare) at that time as it appears. In a way, it appears complementary to the nowadays similarly unimaginable position and power of a full professor and department head of those days. Alfred Kühn, a very dominant and powerful department head, proved his competence by immediately recognizing the importance of Caspari's results, by supporting him in any way and by redirecting much of the research activities of the laboratory onto the way Caspari had opened. Reviewing the thesis for the Faculty, he wrote, "The work of Mr. Caspari combines, for the first time, frequently used methods of developmental physiology ... with genetic experiments, in order to gain information on the mechanism of action of a gene ... Mr. Caspari has worked very independently, with utmost technical skill and perspicacity" (Promotionsakte Caspari, University of Göttingen archive).

Caspari's article, submitted on August 10, and published on December 20, 1933, in Roux' Archiv für Entwicklungsmechanik, is the beginning of a new era. In a way, it represents the first elements of biochemical and developmental genetics and constituted an important first step toward the one-gene-one-enzyme hypothesis. Several years later, Beadle and Ephrussi (1937) published their elegant work on eye-color mutants in Drosophila, e.g., *vermilion*, which is a homolog of the mutant *rotäugig* in Ephestia and can also be rescued by transplantation of wild-type tissue. But Caspari himself could do very little to contribute to further progress. The year 1933 interrupted scientific life, as it interrupted so many other activities that characterize a free society. On January 30, 1933, the Nazi dictatorship came to power and immediately started to suppress independent intellectual and cultural activities and to dismiss and expel many of the best and most innovative citizens.

Daily life soon became difficult. The small university town of Göttingen had a strong Nazi movement years before the party came to power and saw the first anti-Jewish boycott in March 1933. A new law was enacted on April 7, 1933, that dictated dismissal of "politically unreliable" and, in particular, Jewish employees in the civil service, including all the state universities. In a sympathetic biographical sketch of Caspari, Eicher (1987, p. XXVIII) writes about his situation, "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." In the following, I try to give an impression of the political and academic environment in which Caspari finished and published his experiments, passed his doctoral examination, took his degree, and continued his experimental work (see also Grossbach 1996).

**ACADEMIA DESTROYING ITSELF INTENTIONALLY AND UNDER GOVERNMENTAL DICTATE**

The Faculty of Mathematics and Science at the University of Göttingen had among its members a number of the leading scholars of the time. It is therefore remarkable that several of them were among the first professors at Prussian Universities to be dismissed by the government. By telegraphic order of April 25, 1933, the mathematicians Richard Courant, Felix Bernstein, and Emmy Noether as well as the physicist Max Born (Nobel prize 1954) lost their positions. The psychologist Curt Bondy and the jurist Richard Honigstein, and Emmy Noether as well as the physicist Max Born (Nobel prize 1954) lost their positions. The psychologist Curt Bondy and the jurist Richard Honigstein completed the list. Dismissals of numerous other scholars were performed in parallel at other Prussian universities. A week earlier, physicist James Franck (Nobel prize 1925) had sent a letter of protest against the new anti-Semitic law to the State Secretary of Culture in Berlin in which he asked to be released from his duties as a professor in the civil service and director of his department at the University of Göttingen. In an accompanying letter to the university rector that he released to the press the next day, Franck explained his step by stating, "We Jewish Germans are being treated as foreigners and enemies of our home country" (Göttinger Zeitung, April 18, 1933; documented in Dahms 1987, p. 28). This act of protest, as Franck explained in a letter...
to Kühn on April 24, 1933, had been carefully planned and was aimed to stimulate similar actions of other scholars and a public discussion. Many domestic and foreign newspapers reported on and discussed the case. Still uncensored, the Göttinger Zeitung (see Dahms 1987) stressed professor Franck’s outstanding merits and the severe loss for German and international research his retreat implied, and commented, “Professor Franck’s decision must be seen as a moral act. Let us hope and wish that his step ... will have the sole effect that other scholars who are by the law forced to retreat can remain members of our academic life. Otherwise the loss could become so great as to make recoupment impossible forever or for a long period of time” (documented in Dahms 1987, p. 28).

Franck’s hope to stimulate public protestations was not fulfilled. He received dozens of private letters of support (now in the Franck Papers Collection of the Library of the University of Chicago; see Rosenow 1987). There were, however, almost no supporting public reactions from academia. Instead, there was quite a different local reaction, which must have been entirely unexpected. A group of 42 professors and younger university employees published a declaration in a Göttingen newspaper in which they stated that Franck’s protest was “an act of sabotage” and could “seriously interfere with home and foreign politics of our government of national rise” (Göttinger Tageblatt, April 24, 1933; cited in Dahms 1987, p. 28). The group also expressed their hope “that the government would speed up the necessary purge.” One day later, the new Prussian State Secretary of Culture, Berhard Rust, a high-ranking SA officer and former school teacher, dismissed the first six professors (see above).

Dahms (1987) and Becker (1987) have documented the names of the authors of this incredible declaration. Most of them were in agriculture and in the Medical School. One of them, F. Voß, a faculty member in agriculture, worked in the same building as Ernst Caspari. This must have deeply shocked and alarmed him, as he was busy finishing his experiments and preparing his manuscript for publication, the more as he certainly was informed about the numerous dismissals of Jewish scholars in his home town, Frankfurt, where his father, Wilhelm Caspari, was a professor. Voß, in contrast to outstanding faculty members like Kühn, Franck, and some others, was not supported by the Rockefeller Foundation. Kühn’s group considered Voß to be quite stupid, but the times when stupidity protected against a university career were over. Witnesses had the impression that Voß hoped to get Kühn’s position. This hope was not fulfilled, but he remained a danger.

During the following weeks and months, numerous additional professors and younger employees of the University of Göttingen lost their positions. Full professors were forced to retire but continued to receive a salary, at least in the beginning. Other faculty members were dismissed summarily, at various times, and found themselves without any income. A number of internationally known scholars resigned and accepted positions abroad. The majority of the dismissed were Jewish, and a few others were dismissed because they were considered politically unreliable. This did not necessarily mean that they purposively resisted the ruling powers. For the physicist Kyropoulos (who later moved to Pasadena, CA) to be fired, it was sufficient that his wife had verbally attacked a group of SA soldiers who were being rowdy in the backyard of the Jewish neighbor.

Courant and Born accepted offers from Cambridge in England and Hermann Weyl one from Princeton. Born and his family left Göttingen in May, 1933. Their first stay was in Italy, where Born received a letter from his friend Albert Einstein, who had been director of the Kaiser-Wilhelm-Institut für Physik, and who never returned to his home country after the Nazi party came to power. In his letter of May 30, 1933, Einstein reports on activities at English universities aimed to support the expelled German scholars, and continues, “I am almost convinced that all those who already have a name will be taken care of. But the others, the young, will not have a...
possibility to develop” (Born and Einstein 1969, pp. 120–121). Both Einstein and Born, as their mutual letters show, were very active during the following years trying to find positions for dismissed German physicists. Einstein even played his violin in a beneficent concerto to collect money in support of German scholars. Born, Franck, and Courant also served as advisors to the Turkish government for a modernization of the University of Istanbul (Rosenow 1987), a place where many dismissed intellectuals from Germany, including the young Caspari, were to take refuge (see below). James Franck left Göttingen for Harvard and Johns Hopkins in November 1933. A big crowd of people who followed him in sadness to the railway station must have had a feeling that an era was over.

When Caspari submitted his thesis to the Faculty on July 21, 1933, it was no longer automatically assumed that a Jewish candidate could get a doctoral degree at the University of Göttingen. Caspari did fortunately not meet any difficulties. In contrast, an excellent student at the School of Law, David Daube, at the same time was refused. Daube, who later was professor at the universities in Aberdeen, Oxford, and Berkeley, had submitted a brilliant thesis and had passed the oral examination. The dean then wrote a letter stating that it was solely the new anti-Semitic law that inhibited conferring the degree (Halfmann 1987).

Caspari continued to work in Kühn’s laboratory who somehow managed to employ him. In several publications they demonstrated that the diffusible substance is produced in several tissues of the wild type and is not species-specific, because wild-type pigmentation of the imaginal eyes of Ephestia was also achieved after transplantation into the larva of tissue from other Lepidopteran species. Caspari also began to isolate the substance for further characterization. The project was continuously supported by the Rockefeller Foundation. In 1935, however, the Nazi administration dismissed Caspari from his position as a research associate (wissenschaftlicher Assistent) and thus forced him to interrupt his work. Altogether, the Faculty of Mathematics and Science lost 23 of a total of 82 faculty members. For the entire University of Göttingen, the number was 52 professors and “Privatdozenten.” In addition, numerous young scholars were dismissed (all names are documented in Becker 1987). Among the youngest were Edvard Teller, the astrophysicist Martin Schwarzschild, and Ernst Caspari.

Albert Einstein, in the letter to Max Born cited above, discussed possibilities to help Teller find a place. “My heart bleeds when I think of the young generation” (Born and Einstein 1969, p. 120). Caspari found a place in Turkey at the new University of Istanbul, probably due to Born, Franck, and Courant having been instrumental in the foundation of a science faculty there. “Istanbul Üniversitesi” was founded in 1933 as the country’s first modern university and just now celebrates its 75th anniversary. Many of its first professors were refugees from Germany. Altogether, several hundred German professors and research associates survived the Nazi period in Istanbul and Ankara. Two of them were the jurist Richard Honig, one of the first six scholars dismissed from Göttingen in April 1933, and Ernst Caspari. Caspari worked in Istanbul with the microbiologist Hugo Braun on the transfer of infectious diseases by insects. But, as the conditions for experimental work were restricted, he tried to get to the United States and succeeded, with the help of L. C. Dunn (Columbia University), in 1938. His first job was at Lafayette College. Rheinberger (2000), who read letters of Ephrussi and Caspari to Beadle in the Beadle Collection of the CalTech Archives, reports that Caspari approached both Ephrussi and Beadle, first Ephrussi from Istanbul and then Beadle after he reached the United States, asking whether he could work with them, but was not successful. Rheinberger (2000) also reports that Ephrussi knew of Caspari’s experiments and was in touch with Kühn before the war (see also Hilschmann and Barnikol 2004). Caspari, however, eventually found a new scientific home in the United States, like so many other refugees from Europe, and developed a broad range of interests. At first, he worked with Dunn on closely linked mouse genes with similar effects, and he also to some extent continued experiments with his Ephestia system. Later he worked with Curt Stern at Rochester University on the effects of low-dose irradiation in Drosophila. When working at the Cold Spring Harbor Laboratory, he did extended experiments to isolate the enzyme that is lacking in the red-eyed mutant of Ephestia and is necessary for tryptophan oxidation. This aim was later achieved in collaboration with A. Egelhaaf (see below). Today, Caspari is best known for his contributions to behavioral genetics. During extended periods of time, he also had to manage heavy teaching loads and administrative duties as a professor of biology at Wesleyan University and at Rochester University. He was elected President of the Genetics Society of America and, last but not least, served as Editor of Genetics from 1968 to 1972.

AFTER CASPARI’S DEPARTURE

Caspari and Kühn originally had the idea that the gene rotläugig acted through the production of a hormone (Kühn et al. 1935). After Caspari left, further experiments were performed to characterize the substance lacking in the mutant. In 1937 Kühn and several of his associates moved to the Kaiser-Wilhelm-Institut für Biologie in Berlin-Dahlem where Kühn was appointed director after Richard Goldschmidt, who had been forced to leave and had moved to Berkeley. In Dahlem Kühn and his associate Becker started a collaboration with Adolf Butenandt (Nobel prize 1939) and his graduate student Wolfhard Weidel, which finally resulted in the identification of the substance as
kynurenine, published in January 1940 (Butenandt et al. 1940a,b). Injection of aqueous solutions of kynurenine into pupae of the red-eyed Ephesia mutant resulted in the development of wild-type imaginal eyes (Butenandt et al. 1940a). A year later, Tatum and Haagen-Smit (1941) reported the identification of Drosophila v+ Hormone of Bacterial Origin as kynurenine. As became clear later, mutants in the homologous genes rotäugig and vermilion of Ephesia and Drosophila, respectively, lead to a loss of tryptophan pyrrolase, which catalyzes the synthesis of N-formylkynurenine from tryptophan (Egelhaaf 1958; Egelhaaf and Caspari 1960), a first step in the synthesis of xanthommatin, a brown pigment in the insect eye.

In their earlier work, Beadle and Ephrussi (1937) had already identified a later step in the synthesis of xanthommatin by analyzing the eye-color mutant cinnabar of Drosophila. The development of eye phenotypes in imaginal discs that had been transplanted between vermilion (v) and cinnabar (cn) larvae revealed the sequence of action of the two genes. vermilion imaginal discs transplanted into cinnabar larvae developed to darkly pigmented wild-type eyes. Eye discs of cinnabar larvae, on the other hand, developed eyes with cn phenotype after transplantation into v larvae. The conclusions were that the two genes directed the synthesis of two diffusible substances, the v+ and the cn+ substance, and that the cn+ substance acted on a later step in the process of eye pigmentation. As became clear later, the mutant cinnabar is unable to synthesize 3-hydroxykynurenine from kynurenine because it lacks the necessary enzyme, kynurenine-3 hydroxylase.

These beautiful studies on Drosophila eye-color mutants (Beadle and Ephrussi 1937) opened the way to the first concept of gene action, the one-gene-one-enzyme hypothesis. Drosophila was a model system much superior to Ephesia. The evidence it provided was also soon supported and greatly augmented by the analysis of biochemical pathway mutations in the mold, Neurospora (Beadle and Tatum 1941). This work is widely known and has led to the conclusion “that each gene controls the production, function, and specificity of a particular enzyme” (Tatum 1959, p. 1712), a landmark in the history of genetics. On the other hand, the priority of Caspari’s experiments as a first step toward an understanding of gene action, as well as the priority of Butenandt et al. (1940a) in identifying kynurenine as the rotäugig+/vermilion + substance, should be remembered. We can only guess that Caspari would have continued contributing to the rapidly developing field, had he not been expelled from his home country.

**DID THEY BEHAVE CORRECTLY?**

It is remarkable that the collaboration of the groups of Kühn and Butenandt on the identification of kynurenine was an indirect consequence of the dismissal of two Jewish department directors. Kühn replaced Richard Goldschmidt at the Kaiser-Wilhelm-Institut für Biologie, and Butenandt moved from Danzig to Berlin to replace Carl Neuberg at the Kaiser-Wilhelm-Wilhelm-Institut für Biochemie. The Kaiser-Wilhelm-Gesellschaft being compelled by the government to enforce the anti-Semitic laws, Goldschmidt experienced difficulties from 1933 on and emigrated to Berkeley in 1936. Neuberg (1877–1956), widely respected for his outstanding work on the enzymes and reactions in alcoholic fermentation, was forced to retire in 1934 but managed to remain in charge provisionally until Butenandt was appointed. It has been frequently discussed, both between contemporaries and between members of younger generations, whether it was ethically defensible to accept an academic position from which a Jewish colleague had been dismissed. As to Alfred Kühn, it appears that he hoped to escape from the Nazi environment in the university to create a protected environment for himself, in which he could pursue his research. In Göttingen, he found it impossible to protect Ernst Caspari and a Jewish graduate student in his laboratory. Werner Braun, who left in 1936. Harwood (1993), who has read Kühn’s unpublished letters to colleagues and the Nazi party’s Kühn file in the Berlin Document Center, reports that the Nazis exerted political pressure on him and that he therefore considered emigrating to the United States. When Kühn’s old friend von Wettstein succeeded his former teacher Correns as a director at the Kaiser-Wilhelm-Institut für Biologie, he and others managed to ensure that Goldschmidt’s position was offered to Kühn, an opportunity that obviously was a great relief to him.

Caspari himself, to my knowledge, never criticized Kühn for his behavior. During all the years in America, he had Kühn’s portrait hanging in his office, and he also got in touch with Kühn soon after the war was over.

As to Butenandt, Nordwig (1983) reported that he secretly helped Neuberg to install laboratory facilities in a private food factory and supported him with equipment and chemicals until his emigration to the Netherlands in 1939. Neuberg expressed his gratitude, and also he got in touch soon after the war. Nordwig (1983, p. 53) also cites a letter in which Butenandt later invited Neuberg “to return to the Institute to a position according to his wishes.” Neuberg, however, stayed in the United States.

Kühn and Butenandt, who stayed in Germany and continued to work, like many others, cannot be classified as “Hitler’s professors” (Beyerchen 1977). Did they act ethically defensibly? How could they have been expected to act? If one looks at the country as a whole during those years, most individuals behaved more timidly, less concernedly, and more passively than would have been possible for them without immediately endangering themselves and their families.
The fate of those who could not or did not want to emigrate is known. Victor Klemperer, one of the many witnesses who have documented details from daily life, reports in his famous diary (Klemperer 1995) the stepwise increase of limitations and maltreatments of many kinds: prohibition from visiting the department and other university institutions, prohibition from using the library and to be loaned books, prohibition from being loaned books from private libraries, house searches and arbitrary confiscations of private books, prohibition from owning a typewriter, enforcement to leave the private home and to move to a single room in an apartment building, forced labor, and deportation. Klemperer, a professor of French literature at the Technical University of Dresden, was a “privileged” Jewish citizen because his wife was not Jewish. Therefore he was not deported and murdered but survived as a forced labor convict. Caspari’s father, professor Wilhelm Caspari (1872–1944) did not survive. He died in a ghetto concentration camp in Poland a short time before its liberation by the Soviet army. Having been in charge of the Department of Cancer at the State Institute for Experimental Therapy in Frankfurt since 1920, he was dismissed in 1936 and deported, together with his wife, to Poland in 1941. His merits in medical science and as a physician were later honored by E. Schwartz and R. Chambers in an obituary in Science. Caspari’s mother “was taken from the camp in 1942 and since then has not been heard of, in spite of extended searches made by the Joint Refugee Committee” (Schwartz and Chambers 1947, p. 613). Ernst Caspari had desperately tried to save his parents, but the American visa arrived in Frankfurt shortly after their deportation.

Many of the refugees, including Albert Einstein, never visited their home country again. Others, including Caspari and Curt Stern, got in touch again as soon as possible, the latter by sending CARE packages to his former professor, Max Hartmann (Jaenicke 2006). Caspari paid many visits to Kühn and to former members of the group. He was a visiting professor in the Genetics Department at the University of Giessen, which also awarded the honorary degree of doctor to him, and he enjoyed the symposium by which his old university honored him on the occasion of the 50th anniversary of his doctoral promotion. However, when he was offered the chance to move to the Genetics Department at Giessen, he decided to stay in America. The place he felt he belonged was Rochester.

ENVIOI: ERNST CASPARI’S WORK AND LIFE

Several years before Beadle and Ephrussi (1937) analyzed eye-color mutations in Drosophila and thus laid the foundations for the one-gene-one-enzyme hypothesis of gene action, Ernst Caspari investigated the development of eye pigmentation in the moth, Ephestia. He found that wild-type larvae synthesize a diffusible substance, later identified as kynurenine, that is lacking in a red-eyed mutant and is necessary for the formation of the dark brown pigmentation of the wild-type eye. His seminal experiment was a novel approach, tissue transplantations between organisms with different genotypes. By transplanting wild-type larval tissue into larvae of the red-eyed mutant, he achieved a rescue of the wild-type phenotype. The transplanted mutant animals with wild phenotype yielded, of course, mutant offspring with red eyes. Caspari’s approach to the problem of gene action thus brought together, for the first time as far as I can see, two fields of biology that were strictly separated at his time, genetics and developmental biology. The results, published in 1933, are the beginning of a new era, because they in a way contain the first elements of biochemical as well as developmental genetics, a first step toward the one-gene-one-enzyme hypothesis.

Caspari (Figure 2), working in the laboratory of Alfred Kühn at the University of Göttingen, took up the problem and the model system and performed the experiments quite independently of his supervisor. Kühn immediately recognized the importance of the
results and redirected much of the research activities of the laboratory onto the way Caspari had opened. After the Nazi dictatorship came into power, political suppression rapidly changed the academic environment in which Caspari performed, finished, and published his experiments. He had begun to isolate the substance for characterization, a task later accomplished by the Kühn laboratory in collaboration with A. Butenandt (BUTENANDT et al. 1940a,b), but was dismissed from the university according to the anti-Semitic decrees of the Nazi government. He escaped to Turkey, where he worked at the newly founded Istanbul University, and later found a new scientific home in the United States. He was a professor of biology at Wesleyan University and at Rochester University, was elected President of the Genetics Society of America, and served as Editor of Genetics. His pioneering work on gene action in the pigmentation of insect eyes is not often cited and should be remembered, 75 years after its publication.

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