BACTERIOPHAGE
2016, VOL. 6, NO. 2, e1173168 (12 pages)
http://dx.doi.org/10.1080/21597081.2016.1173168

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LIFE IN SCIENCE

OPEN ACCESS

# Grete Kellenberger-Gujer: Molecular biology research pioneer

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**ABSTRACT**

Grete Kellenberger-Gujer was a Swiss molecular biologist who pioneered fundamental studies of bacteriophage in the mid-20th century at the University of Geneva. Her life and career stories are reviewed here, focusing on her fundamental contributions to our early understanding of phage biology via her insightful analyses of phenomena such as the lysogenic state of a temperate phage ($\lambda$), genetic recombination, radiation's in vivo consequences, and DNA restriction-modification; on her creative personality and interactions with peers; and how her academic advancement was affected by gender, societal conditions and cultural attitudes of the time. Her story is important scientifically, putting into perspective features of the scientific community from just before the molecular biology era started through its early years, and also sociologically, in illustrating the numerous "glass ceilings" that, especially then, often hampered the advancement of creative women.

**ARTICLE HISTORY**
Received 17 February 2016
Revised 17 March 2016
Accepted 23 March 2016

**KEYWORDS**
gender; glass-ceiling; lysogeny; phage genetics; recombination; restriction-modification; science history

## Introduction

Grete Kellenberger(-Gujer) was born Margaretha Gujer on November 12, 1919 in the village of Rümlang near Zürich.[1] In the 1950s and 60s, she contributed importantly to establishing the international reputation of the University of Geneva as one of the first European Universities to develop research programs in the new field of molecular biology.[2] She is renowned for studies of lysogeny, genetic recombination and DNA restriction-modification, in collaboration with Jean Weigle and Werner Arber (Nobel Prize 1978).[3-5] Her formidable scientific acumen and achievements did not, however, result in her establishing a traditional academic career, nor did they result in a position that matched her scientific creativity and contributions. Rather, for most of her career she was paid only as a laboratory technician or research associate, often part-time and on soft money, and intermittently for a number of reasons, as summarized below.[1] She died on March 13, 2011.

Her story is important scientifically, one of creativity and productivity during the early and middle years of modern microbial and molecular genetics. It is similarly important sociologically, illustrating the numerous "glass ceilings" that confronted even the most creative women in western democracies in the mid-twentieth century, a history that is not sufficiently known among the far more empowered young women of today.[6]

## Family and education

Grete was raised in Rümlang, a small village near Zürich, the youngest of 3 children. Her father ran the local village post office. Her mother became ill with cancer, was bedridden for several years and died when Grete was 17. Grete attended elementary school in the village, and then, unlike most young villagers (and in general most Swiss contemporaries during those years), went on to higher studies. She enrolled in a classical humanist curriculum in the Girl's Gymnasium (Töchterschule, or high school) in Zürich, and graduated in 1939, shortly before the start of the Second World War in Europe, with a "maturity" diploma and the rank of best in class. She had dreamed of further literary studies, but could not pursue them because of limited family resources. Rather, she started work in an insurance company, Rentenanstalt, but enrolled a few years later (1942) in the Federal Polytechnic of Zürich (ETH) (Chemistry Section). She

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dropped out after 4 semesters, due in large part to wartime economic difficulties, and perhaps also to a lack of self-confidence. She then started work at the Lohnausgleichkasse (wage equalization fund) of Zurich, and in the following year (1945) married Eduard Kellenberger, a physics student whom she had met at the ETH.

Grete and Eduard moved to Geneva in 1946, where he started PhD studies under the direction of Professor Jean Weigle, who had studied X-ray diffraction of mineral crystals, had helped design the first Swiss-manufactured electron microscope, and was Director of the University's Institute of Physics. Also in 1946 Grete (Fig. 1) gave birth to their only child, Elisabeth, who would later become a molecular biologist, and publish under the name of Elisabeth DiCapua,[1] once in collaboration with her father.[7]

Grete carried out innovative microbial genetic research at the University of Geneva during 2 periods: during her marriage to Eduard (1948-1965) (Fig. 2), and after their divorce (1971-1980). In the second period, she published using the name Kellenberger-Gujer. Interestingly, in retrospect, she had to obtain special permission from Eduard's second wife to keep using the name Kellenberger for social identification

**Figure 1.** Grete Kellenberger in 1946. © Elisabeth DiCapua. Reproduced by permission of Elisabeth DiCapua. Permission to reuse must be obtained from the rightsholder.

**Figure 2.** Eduard and Grete Kellenberger, Naples 1963. © Elisabeth DiCapua. Reproduced by permission of Elisabeth DiCapua. Permission to reuse must be obtained from the rightsholder.

(and for publications).[1] This, because the Swiss Consulate in the US and the US tribunal that settled the divorce decreed that Grete's name after the divorce was to be Gujer,[1] since Swiss law at the time obliged divorced women to switch back to their maiden names – after having obliged them to lose their maiden names upon marriage.

## First period in Geneva, 1948-1965, and pioneering phage studies: Collaborations with Eduard Kellenberger, Jean Weigle, Maria Zichichi

During their first years in Geneva Grete helped Eduard with his PhD project, which was to improve new, Swiss-made electron microscopes and to develop methods for examining structures of diverse types of living matter.[2] They focused, in particular, on methods for preparing and photographing biological samples of many types, including bacterial cells and nucleoids (Eduard's PhD thesis).[8,9] Grete was a co-author on several of the resulting publications.[10-12] Life was exciting but also complicated professionally, in that, as Grete recalled, most physicists had little interest in electron microscopy[13] and their EM group was consigned to one of the University's oldest buildings. Sample preparation was in a room next to the lab of botany professor Fernand Chodat, who had research interests in bacterial physiology, and who was the son of Robert Hippolyte Chodat, formerly Director of the

University's Institute of Botany and a Rector of the University. The room for electron microscopy was several floors below the lab.[14,15] Eduard wrote "*In the darkness of the night we both*" (himself and his technician Andrea de Stoutz) "*were frequently frightened by the busts of the famous late professors placed along the staircase*!"[16] – perhaps in jest, but illustrating the hiatus between post-war biophysicists such as himself and their "new biology" *vs*. the University's tradition-bound senior faculty.

Weigle suffered a heart attack in 1946, resigned his physics professorship in Geneva in 1948, moved to California, and joined the phage group of the great physicist-turned-biologist, Max Delbrück, at the California Institute of Technology. He returned to Geneva each summer to collaborate with Grete and other group members. In his first summer back (1949) he brought an idea from Caltech for a new research project: the genetic analysis of bacteriophages, especially $\lambda$, recently discovered by Esther Lederberg. Grete embraced this idea with passion and dedication, and in pursuing it, rapidly achieved scientific independence and creativity, as seen in her correspondence with Weigle, stored at Caltech (http://archives.caltech.edu). Based on their collaborative studies, Eduard was promoted to Group Leader of the University's new Institute of Biophysics and Director of the Center for Electron Microscopy. The Institute was housed from 1953 onward in the basement of the School of Physics, near the Arve river. Eduard and Institute members (Fig. 3) had numerous scientific interactions with bacteriologists at the Geneva-based World Heath Organization such as Ole Maaloe, an early member of the phage group and pioneer of quantitative bacterial physiology[17] and also collaborated with biologists and physicians in the Faculties of Science and Medicine, using electron microscopy to better characterize their samples.[18,19] That said, Grete recalled feeling that the University's biologists did not fully understand or perhaps respect the group's "new biology" (in translation) "*thinking that the physicists know no biology, because they do not know the names either of plants, or animals*," and further wrote "*We were something strange. And me, I was nothing, as I had never finished my studies.*"[13]

Grete's hand-written financial reports showed that funds in the Kellenberger group were very limited. Eduard's salary was extremely small, and there was little financial support for research from the University.[13] They lacked funds to purchase chemicals such as cesium chloride for ultracentrifugation, and even the breakage of a glass Petri dish significantly impacted on the lab's budget.[13,14] Visitors were often invited to the Kellenberger home to save on costs of restaurant meals, and Ingeborg ("Isambour") Hösterey, hired in 1956 as a German "au pair" to take care of Elisabeth, was soon switched to secretary and general help in the group, with a salary of 3 Swiss francs per hour.[14] Isambour would later marry Eduard's EM and photography assistant, Edouard Boy de la Tour.

Each summer Weigle (Fig. 4) brought new phage and bacterial strains and ideas to Geneva, collected from Caltech, the Institut Pasteur (Paris) and other labs visited en route. His and Grete's collaboration intensified, as shown by their resultant publications and her letters in the Caltech archives.[2] Grete's intellect was stimulated in particular by the challenge of decrypting unexpected and complicated phage and *E. coli* mutants and their phenotypes.[15,20-25]


**Figure 3.** Eduard Kellenberger's group at the "Institut de Physique", Genève, 1958. From left to right: George Streisinger (invited Professor, he came to Geneva from Cold Spring Harbor for a few weeks to give a series of graduate seminars, shortly before joining the University of Oregon faculty), Janine Séchaud (PhD student and soon thereafter Postdoc with Streisinger), Naomi Franklin (Postdoc), Werner Arber (PhD student), Grete Kellenberger (Researcher), Antoinette Ryter (Assistant), Eduard Kellenberger (Director of the Laboratory of Biophysics), and Antoinette Bolle (Researcher). © Unknown. Reproduced by permission of Edouard Boy de la Tour (source). Permission to reuse must be obtained from the rightsholder.

**Figure 4.** Jean Weigle in the basement of the "École de Physique", early 1960s. © Unknown. Reproduced by permission of Edouard Boy de la Tour (source). Permission to reuse must be obtained from the rightsholder.

Thanks to the collaboration between Grete and Jean Weigle, and their and Eduard's electron microscope images of wild type and mutant phage, Geneva became world-renowned as a major center of electron microscopy studies, and also particularly well known for molecular genetic analyses in the small phage research community. The Institute's productivity was further enhanced by researchers coming variously for postdoc training, sabbaticals, to give seminars, or simply discussion – a stream of colleagues, collaborators and friends often further attracted by the region's exquisite mountains and cultural environment.

Eduard and Weigle, as laboratory heads, were the ones invited to present findings at international meetings. So, Grete may have received less credit than deserved for her insights, experimental design and results.[1,26] Her remaining in the shadows can be ascribed to several factors including not speaking English fluently at the time, and her modesty, which contrasted with Eduard's own outgoing, magnetic personality. In a letter of January 1966 to Maria Ludovica Zichichi, she half-jokingly admitted this: (in translation) " …*I would have been happy to receive the honorariums and travel reimbursements of these speakers, and give a talk about lysogeny myself, but you know very well that I am not capable of speaking in public, and this is the only reason why we did not get the Nobel Prize for our works.*"[27]

In 1954, Grete convinced Werner Arber, whose one year contract as electron microscopy technician, focused especially on phage T4 structure,[28] was finishing, to stay as a graduate student, despite lack of funds. This was accomplished in part by introducing him to the intriguing phenomenon of sudden and complete lysis of bacterial cultures after $\lambda$ prophage induction.[13] Officially Arber's thesis directors were Weigle and Fernand Chodat, but it was Grete who taught him conceptual and practical phage genetics, and who guided his work closely in Geneva, especially while Weigle was abroad.[2,15,20,29,30] After Arber obtained his PhD (1958) and left for a postdoc in the USA, Grete often suffered from a lack of collaborators, noting that "*they just give me people who stay in the lab for too little time.*"[13] As one prominent exception, however, between 1960 and 1962 Grete had an excellent collaboration with Maria Ludovica Zichichi, who had studied biology and genetics at the Universities of Illinois and of California, Berkeley (receiving BS and MS degrees, respectively) (Fig. 5). Zichichi is the daughter of the noted Florentine physicist, Gilberto Bernardini, who had served as visiting and research professor at Columbia University and the University of Illinois from 1949-1956, and then as Director of Research of CERN's proton synchrotron, near Geneva (1957-1964). Through her father, she met the Sicilian nuclear physicist Antonino Zichichi, and married him soon thereafter.

**Figure 5.** Part of the "Groupe de Biophysique" in 1963. From top to bottom, from left to right: Dave Pratt (Postdoc), Dick Epstein (Research Associate), Lucienne Roth (Secretary), Anna Reale (Postdoc), Werner Arber (Assistant Professor), Benigna Blondel (Assistant), Ingeborg Boy de la Tour (Secretary), Antoinette Bolle (Research Associate), Eduard Kellenberger (Professor), Jacques Bron (Workshop Assistant), Edouard Boy de la Tour (Photography Assistant), Maria Zichichi (Master Graduate Assistant), and Grete Kellenberger (Researcher). 

Grete's collaboration with Maria Zichichi was very productive, resulting in 4 prominent publications.[24,25,31,32] In one they (i) showed that a λ variant called "b2" had about 18% less DNA than λ wild type by buoyant density analyses in CsCl gradients and direct DNA measurements, (ii) mapped b2 by genetic crosses, and (iii) noted that λb2 formed turbid plaques that, like λ wild type plaques, contained cells immune to superinfection, and (iv) showed that λb2 formed "abortive lysogens" whose prophages are not chromosome-associated (integrated), and are inherited by only one of 2 daughter cells at cell division, but that can be induced to grow lytically by UV radiation. They suggested that the b2 deletion removes (part of) the site λ uses for chromosomal "attachment,"[24] an interpretation subsequently shown to be correct. This first detailed analysis of a λ deletion mutation was also important in providing some of the first evidence that prophage repression and attachment (integration), although well coordinated during lysogenization, are separate processes.

As a second seminal example they demonstrated recombination by direct DNA exchange between interacting λ genomes, using the b2 deletion and another size variant, "b5," which was allelic with "c" plaque morphology mutants and is now known to correspond to lambdoid phage 21′s smaller immunity region.[25]

Zichichi decided to leave research at the end of 1962, however, after the birth of her third child, a decision that left Grete distressed, again without good collaborators. In an April 1963 letter to Zichichi, Grete wrote her (in translation) "*nobody manages to get as high rate of transfer as you used to*" and confessed her solitude "*I am sad to be working alone.*"[27]

Arber returned in 1960 from his postdoc to a faculty position in the University's Institute of Biophysics. Grete continued to share her ideas with and suggest experiments to him and his PhD student Daisy Dussoix (https://fr.wikipedia.org/wiki/Daisy_Dussoix). For example, she suggested that Dussoix test if UV irradiation caused DNA degradation,[13,26] and proposed to Arber that 2 different enzymes are involved in restriction-modification: one would cause DNA degradation, as does UV irradiation (Grete's project with Weigle), and a second would protect DNA from such degradation.[33] In a 1960 letter to Arber, Grete wrote (in translation): "*There was a seminar by somebody called […] Lehman from Stanford*" (i.e., Robert Lehman, who years later was one of the

postdoc advisors of Arber's PhD student Daisy Dussoix), *"about the intracellular E. coli DNAses, it would have been very interesting for you, and I think this is the direction to take for the phenomena you are studying. To devote 3 months to that would be nothing, one should rather forecast at least 3 years, don't worry about that […]. I think that with the UV, there are some initial points of attack, and then this continues for a certain time [under the action of the DNAses], but at high doses almost everything is destroyed because the distances between the points of attack become shorter and shorter. For phage P1 it would be something similar. There would be a DNAse that can attack normal DNA (λ and Hfr bacteria for example) but there would also be a phage P1 enzyme that would render the DNA resistant. […] It's hard to approach this without chemistry*." Arber eventually adopted Grete's idea of host-specific restriction as an enzymatic property,[2,34] although enzymatic mechanisms were not suggested in his first (1962) papers on DNA restriction and host-controlled modification.[35,36] Arber received the Nobel Prize in 1978[3] (shared with Dan Nathans and Hamilton Smith) for showing that restriction involves degradation of DNA by a specific enzyme.

## The USA (1965-1970) and in Geneva again (1971-1980)

Grete's professional and personal trajectory was dramatically altered in the mid-1960s. In 1965 Eduard started a sabbatical year as a "Regent" Invited Distinguished Professor at Kansas State University, in the lab of K. Gordon Lark (previously Eduard's Postdoc in Geneva).[1,14] Eduard brought with him several group members (Fig. 6), including Grete, PhD student Uli Laemmli, and Edouard Boy de la Tour (nicknamed "Nadar" to distinguish him from Eduard Kellenberger, and in reference to the great nineteenth century French photographer Gaspard Félix Tournachon – initially called "Tournadar," then Nadar). In January 1966, Grete wrote Zichichi that (in translation) "*Eduard once asked me if I wanted to stay here while he "settles things in Geneva*,"" and that "*Gordon Lark wrote a grant application for "67 in which I am listed*," and "*therefore, the future is as wide as the horizon of Kansas*." In reality, the marriage between Grete and Eduard had been in crisis for several years. It ended suddenly in the fall of 1966, with Eduard leaving Grete in Kansas and returning to Geneva. Grete was deeply wounded, and wrote Zichichi about her pain, and also about the possibility of leaving science: (in translation) "*I am thinking about changing professions, to go to Sweden to learn embroidery. I also thought of going to New York to learn photography…in the end I thought that with the little money I have I could try to write theater for 2 or 3 years, this is what I really love*."[27] But Grete was highly respected in the scientific community and received 3 job offers (letter to Zichichi of March 5, 1967[27]): one in Dallas (attractive economically: $12,000 per year, with insurance, moving expense, supplements, etc., paid), one at the International Laboratory of Genetics and Biophysics in Naples (300,000 liras per month, an excellent salary at that time in Italy), and one from Lucien Caro, a French scientist with close ties to Geneva, for an independent position in his biophysics group at Oak Ridge National Laboratory in Tennessee. Grete considered going to Naples, since she loved Italy and Italians, had fond memories of Naples, and by then had an Italian son-in-law (Nicola DiCapua). However, in the end

**Figure 6.** Kansas, 1965: the three cars. From left to right: the Rambler, with Ingeborg and Edouard Boy de la Tour; the Cadillac, with Cornelia van der Kamp and Uli Laemmli; and the red Ford, with Grete and Eduard Kellenberger. © Unknown. Reproduced by permission of Edouard Boy de la Tour (source). Permission to reuse must be obtained from the rightsholder.

she accepted Caro's offer. Laemmli and Grete remained in Kansas for another 8 months and together analyzed T4 phage head assembly.[14,37,38] Although Laemmli spent many hours with Grete as friend and collaborator, providing moral support, he did not then know that Grete did not have a doctorate nor even a University diploma (nor did Zichichi, despite their closeness,[27,38] although Janine Séchaud and other group members in the 1950s were aware of this[15]). After their final 8 months in Kansas Laemmli drove Grete and her possessions to Oak Ridge in his old Cadillac (Fig. 6), where she joined Caro's group, while Laemmli returned to Geneva.[1,14,38]

Jean Weigle's death in 1968 was another big scientific and personal blow for Grete. This she illustrated with modesty and grace in the acknowledgments of her 1971 article[39]: "*The discussion may appear somewhat disproportionate with respect to the few new results given in this paper but it was my intention to bring some order in my thoughts to the memory of Jean Weigle, who patiently and kindly disciplined my imagination for so many years.*"

Grete returned to Geneva in 1971 along with Caro, who had been recruited to the University's Institute of Molecular Biology (created in 1963 by fusing the Laboratory of Biophysics with Alfred Tissières' Laboratory of Biochemical Genetics) following Kellenberger's and Arber's move to the Biozentrum in Basel.[1,14,15,38] In Geneva once again, Grete finally received a relatively good salary, paid from Caro's Swiss National Science Foundation grant. For several years, also starting in 1971 she had fruitful collaborations with one of us (DB), who had come to Geneva as a Chargé de Recherche (Postdoc) in Caro's laboratory. They shared a passion for λ and the λdv plasmids derived from it.[40-42] The stimulating atmosphere created by interactions with her and with Caro encouraged many innovative experimental adventures, including those that, during Berg's last year in Geneva, culminated in the serendipitous discovery of drug resistance transposon Tn5 as a DNA segment that could insert into phage λ DNA and transpose from λ to the *E. coli* chromosome.[43] For a few years following Berg's return to the US, Grete continued her mutational and molecular analyses of intriguing λdv plasmid - *E. coli* host chromosome replication interactions.[44,45] However, the principal interests in the Department shifted increasingly from microbial genetics to eukaryotic studies during these years, and Grete took early retirement in 1980[1] (Fig. 7).

**Figure 7.** Grete Kellenberger in the 1980s. © Edouard Boy de la Tour. Reproduced by permission of Edouard Boy de la Tour. Permission to reuse must be obtained from the rightsholder.

## Scientific legacy and academic recognition

In addition to Grete's collaborative articles with Eduard Kellenberger and Jean Weigle cited above, several other works also stand out, in particular those from her collaboration with Arber,[30,46–48] Robert Weisberg,[39,49] Berg,[40-42,49] the Polish microbiologist Anna Podhajska[44,45,50] (who had spent a year with Grete in the early 1970s) and Lucien Caro.[44]

Overall, Grete's greatest fundamental contributions in molecular biology included early evidence (using λb2) that prophage repression, induction and chromosome association (integration) involved separate physiologic events, and her demonstration of genetic recombination by DNA breakage and rejoining, rather than by the alternative and then popular replicative mechanism.[24,25,49,51] Her 1961 article on recombination with Weigle[25] was accompanied in PNAS by one with the same conclusions from Matthew Meselson and Jean Weigle.[52] It is sad that although Grete's approach was more original and elegant,[51] Weigle delayed Grete's completed manuscript while waiting for Meselson to finish his experiments, which confirmed what she had already shown.[1] In the end, Meselson's article appeared just before Grete's, and is most cited in genetics textbooks.[51] This may illustrate how a politico-academic editorial attitude could relegate contributions of women to the second level.

But what to say of Grete's academic recognition? Grete had been offered the possibility of doing a PhD while she was in the US. But she was already 50, not particularly interested in a teaching position for which this degree would have been essential, and much preferred continuing with important experiments, rather

than interrupting them to focus on course work and exams.[1] Arber estimates that Grete certainly deserved a doctorate *honoris causa*,[29] an idea that had circulated at the University of Geneva in the 1970s,[26,51] and that Grete remembered as the initiative of Professors Alfred Tissières and Roger Weil.[1] However, this was not followed through in the Faculty of Sciences, where Grete worked,[26,51] although Laemmli says that he would have supported this idea, had somebody told him of it.[38] It is good that the University's separate Faculty of Medicine clearly recognized Grete's major contributions to biomedical science and awarded her the "Prix Mondial Nessim-Habif" in 1979, shortly before her retirement.[1,51]

## Recognition and advancement: A gender perspective

Grete provided an example of a brilliant, productive female scientist who did not receive the career recognition (post, salary, independence) that her competencies, skills, and achievements deserved. Why? Can one blame her for limited self-esteem, academic ambition and leadership? Arber suggested that technically yes, it was "her fault" that she interrupted and never resumed her studies, and did not strive for the kind of independent academic career that was so typical of her male counterparts.[29] How much did this stem: from the decision to help her husband early during their careers, especially for economic reasons? from the then-prevalent view in Swiss and other societies that submission to one's husband's needs was expected, especially of women from her working class socioeconomic background? and/or from her dream of (also) doing other things such as writing poetry and for the theater? It is important to frame Grete's life and career decisions in the context of her cultural and family background. Patriarchal stereotypes were extremely strong in Swiss culture and society, and may have had an important role in the choices that Grete made. Societal pressures and expectations that women should assume subordinate roles provided a strong implicit bias in determining the options that Grete considered, and in the attitudes of her contemporaries toward her career progression.[53-56] Grete's department colleague Jean-David Rochaix, who came to know her in the mid-70s, noted that "*one should not forget that it was very difficult at that time for a woman in science to be recognized, especially in Switzerland, where women did not obtain the right to vote at the federal level until the early 70s.*"[57] Obtaining a PhD for a woman would not necessarily lead to a professorial position either: for example, Janine Séchaud went to the US in 1960 for a successful postdoc with Streisinger, but upon her return to Geneva was happy to become a research associate and instructor ("Chargée de Cours") until her retirement. [15] So, the idea of an independent academic career may have looked too hard, or simply inappropriate, to Grete. Ironically, such a career probably would not have been so much easier had she sought to lead her own research group in a non-Swiss society. In the US before the 1972 passage of "Title IX" anti-discrimination legislation, for example, it was not uncommon for brilliant young science-oriented women to be discouraged from entering PhD programs; and for excellent, accomplished female PhD scientists to be passed over for academic jobs that would have been offered to them had they only been men. It is important to remember that this pattern, in turn, led to a paucity of role-models that would encourage young women to pursue academic careers. Furthermore, obtaining tenure for female junior faculty and staff scientists was also excessively difficult because they were asked to do much better than men of equivalent standing. Fortunately this pattern began changing in the US with "Title IX" legislation passage in 1972, which mandated that no federal funds could be awarded to institutions with patterns of anti-female discrimination. Despite such legislation there is still much gender-inequality in many countries, including Switzerland, and also the US, which ranked 26th and 19th, respectively, in the 2015 "glass ceiling index" of the quality of working women's environments in 29 countries.[58]

As additional illustration, at the University of Geneva, the first female Professor in a scientific discipline in the post-World-War-II period was Kitty Ponse, a brilliant endocrinologist, appointed in 1961. However, until 1967 Ponse and the philosopher Jeanne Hersch were the University's only female full professors.[51] By the time of Grete's retirement (1980), the University of Geneva had only 8 female full Professors, and in 2016 there were 69 (18% of a total of 379), of which only 6 (7% of 83) were in the Faculty of Sciences.

Given societal patterns and attitudes at the time, we can well imagine that Grete's choice to work modestly in her husband's shadow was considered appropriate,

almost obligatory: to help her husband and thereby family, despite limiting her own advancement, and to continue in the stimulating collaboration with Weigle, who Grete admired for his French-style brilliance and flirtatious wit.[1] Collectively, the intellectual challenge, the pleasure of identifying and solving puzzling and important problems, and the increasing international recognition (despite her reserve and her discomfort speaking in English) must have been enough to keep her going.[1,14,15,38] Laemmli pointed out what an extraordinary and positive thing it was for a woman with no university degree to be accepted, recognized and treated as a peer by colleagues.[38] However, this does not offset the fact that she had a far lower and less secure salary than her skills and competence deserved, and lacked independent access to the resources, students and other associates that would have more rapidly advanced her projects and ideas. So, one can only imagine what Grete would have accomplished had her great creativity been matched by great ambition, the unwavering support of her colleagues in promoting her advancement, and a post and resources that she so deserved – support that was, with only few exceptions, given automatically to her male peers.

## Grete's personality and creativity

Grete (Fig. 7) was an exceptional woman: a complex personality, and above all very intelligent and creative, with a deeply developed critical thought, great imagination, and exceptional intuition.[1,15,26,38] She was also kind and generous, and had a wonderful sense of humor.[1,14,27] She nurtured team work in every sense during the early years of the Institute of Biophysics: scientifically, by freely sharing her ideas and skills with colleagues; and also socially, by organizing, for example, productive cake-and-croissant-coffee-breaks[29] in which science was much discussed, and Christmas party shows with humorous satirical sketches.[14]

She made the lab atmosphere interesting, lively, exciting and happy for all.[1,14,27,29,57] Two of her inventive, good-humored jokes illustrate this: in one Institute Christmas party, Nadar (Edouard Boy de la Tour), inspired by Grete, depicted a physics professor who was thin and tall in a photo-montage with his head attached to the body of a flying heron – to the delight of all, except perhaps the professor[14]! Another time, Grete convinced a student to dress solely in black during experiments, lest reflections (radiation) from the white lab coat induce new unwanted mutations in the bacteria under study.[14]

Grete was reserved and discrete, and could appear shy, but also had great courage and asked pointed questions at seminars.[1,14,26,27,51] She rarely displayed strong emotions. But Jean-David Rochaix remembers vividly her great joy and radiant smile when she learned that Werner Arber had received the Nobel Prize: it was one of the rare times that he remembered seeing Grete give free rein to her strong emotions.[57] Her creativity was not limited to scientific research and the lab environment. Until age 30, she was recognized as a skilled pianist, but her piano was sold to finance a trip to a scientific meeting at Royaumont Abbey, north of Paris, for Eduard and herself. At age 50 she learned to play the guitar, and throughout her life she produced a large variety of creative works: her own clothes, letters full of humor, fictional stories (that she kept secret), original embroideries (Fig. 8), an illustrated story ("Bourribang," with 24 watercolors), and a tape of songs for her grandchildren.[1]

During breaks in scientific meetings in the Alps, when the men went for hard walks or mountain climbing, Grete would typically sit quietly in a meadow writing poetry that she would then read to everyone's delight at the evening banquet.[1] Zichichi recalled the adorable personality of "Greta" and her generosity in naming Zichichi first author in their last collaborative paper, although Grete had done most of the experimental work after Zichichi's departure from the lab.[27]

**Figure 8.** Embroidery by Grete Kellenberger. © Elisabeth DiCapua. Reproduced by permission of Elisabeth DiCapua. Permission to reuse must be obtained from the rightsholder.

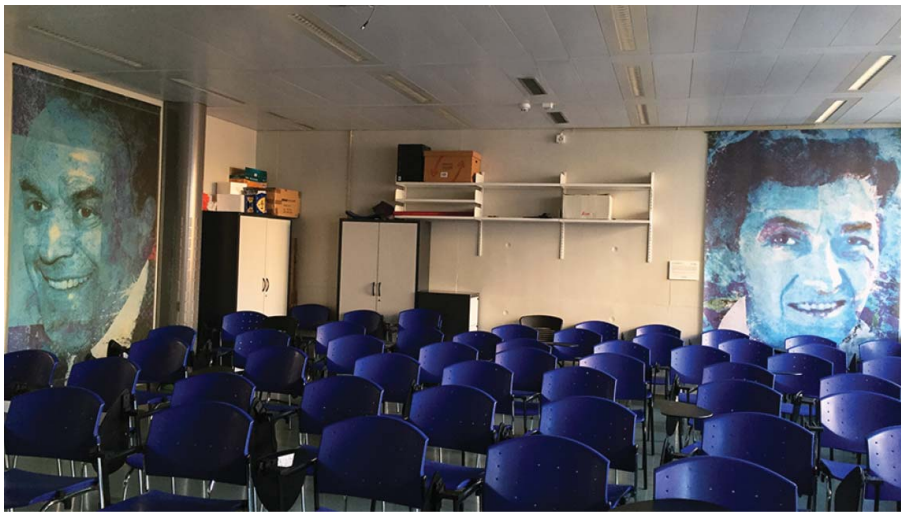

**Figure 9.** Canvases depicting Werner Arber (left) and Grete Kellenberger-Gujer (right) in the seminar room of the Department of Molecular Biology of the University of Geneva. The text of the commemorative plaque was written by DB and Jean-David Rochaix. © Sandra Citi and (for canvases) Atelier Roger Pfund Communication Visuelle SA. Reproduced by permission of Atelier Roger Pfund Communication Visuelle SA. Permission to reuse must be obtained from the rightsholders.

Raised as a protestant, Grete became an atheist and relinquished her affiliation to the Church, but respected believers. She thought that religion was about the mysteries of nature, and that for scientists it was enough to study nature itself. In society, she did not like competition, stupidity, and selfish capitalism, and in her last years she became more and more disillusioned and isolated.[1]

## Recognition, "*enfin*"

Salvador Luria (Nobel Prize 1968) said of her (31.5.1967): "*She is well known and well appreciated for her contributions to molecular genetics and in fact one may say that she has exerted significant leadership in this field. Her more important contributions were those related to the analysis of deletion mutants of bacteriophage λ, which lead to one of the proofs of the physical basis of genetic recombination at the molecular level. […] She was responsible for training in bacteriophage research some of the best European geneticists.*"[26]

In 2009, on the occasion of the 450th anniversary of the University of Geneva's founding, Grete was honored in the exhibition "Faces à Faces," a project conceived and organized by Brigitte Mantilleri (Director of the University's Equal Opportunity Office) in close collaboration with Juliette Labarthe, to commemorate the personalities who contributed to its fame. The exhibition featured portraits on canvas by the Roger Pfund Workshop, that were placed in front of the windows of the University's Le Corbusier-inspired Uni-Dufour central administration building.[59] Three canvases depicted Grete, as suggested by Pierre Spierer (former PhD student with Alfred Tissières, and later Professor, Dean of the Faculty of Sciences, and Vice-Rector of the University). In 2010 one of us (SC) suggested that the Department of Molecular Biology purchase one of Grete's canvases. That canvas now decorates the Department's seminar room in the building Sciences III, "face to face" with a canvas from the same exhibition depicting her former student and collaborator Werner Arber (Fig. 9): an artistic tribute to encourage women scientists of today and tomorrow!

## Acknowledgments

We are immensely grateful to Elisabeth DiCapua for sharing memories, documents and photographs related to her late mother, and comments on the manuscript, and to Edouard Boy de la Tour for providing documents and many original photographs with precise identification of scientists, and for his delightful sense of humor in recollecting funny events and quotes. Our deepest gratitude also goes to Maria Ludovica Zichichi, for sharing her memories, and the content of some of Grete's letters to her; to Werner Arber, for recollecting their time in Geneva and kindly providing publications related to that period; to Uli Laemmli, for his memories of their time in Kansas; to Janine Séchaud, for information about the Biophysics Group and comments on the manuscript; to Bruno Strasser, for information critical to understanding the historical context and comments on the manuscript; to Dominique Belin and Jean-David Rochaix, for their insight, comments and suggestions of people to contact; to the late Lucien Caro, for inviting one of us (DB) to Geneva and his (LC's) generous support of the resulting collaboration and friendship with Grete, the memories of which continue to influence and enrich his (DB's)

life to this day; and finally to the late Claire M. Berg, DB's sibling and research collaborator, discussions with whom increased his sensitivity to some of the issues discussed here. The research into Grete's life and work would not have been possible without the initiative of the Equal Opportunity Office of the University of Geneva and the Emilie Gourd Foundation, who sponsored the establishment of a project "Biography of women in Switzerland" to address the Wikimedia Gender Gap (https://fr.wikipedia.org/wiki/Projet:Suisse/Biographies_des_femmes_en_Suisse): SC thanks Brigitte Mantilleri for encouragement, Natacha Rault, Gabrielle Marie and Marie Pierre Vidonne for guidance in the Wikipedia project, and Lorena Parini for comments on gender issues.

## Funding

SC is a member of the Equal Opportunity Committee of the Faculty of Sciences of the University of Geneva, and her research in the University's Department of Cell Biology is funded by the Swiss National Foundation, the Swiss Cancer League and the State of Geneva. DB's research in the United States has been supported by the National Institutes of Health and by the National Science Foundation. SC and DB thank Thanos Halazonetis and the Department of Molecular Biology, and Brigitte Mantilleri and the Service de l'Egalité of the University of Geneva for graciously supporting the Open Access publication option for the article.

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