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HISTORY AND BIOGRAPHY

Remembering George Feher (1924–2017)

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Abstract
We provide a tribute to George Feher, one of the founding scientists in the use of biophysical techniques to probe photosynthetic complexes, especially the bacterial reaction center. His early life is briefly reviewed followed by a description of the impact of his 30 years of photosynthesis research. We describe his pioneering work in bacterial photosynthesis that helped to provide a detailed picture of the molecular events responsible for light energy capture and the subsequent electron and proton transfer events in photosynthetic organisms. These studies had a profound and lasting impact on our understanding of the molecular mechanisms of photosynthesis. We also include some personal comments from his former students and colleagues.

Keywords Photosynthetic bacteria · Reaction centers · *Rhodobacter sphaeroides* · Electron paramagnetic resonance · Electron-nuclear double resonance · Electron transfer · Proton transfer

Introduction

George Feher was born on May 29, 1924 in Bratislava, Czechoslovakia (now in Slovakia) and died in La Jolla, California on November 28, 2017. He was a remarkable scientist who made important discoveries in solid-state physics, biophysics, and spectroscopy. Quite notable were his contributions to the early development of electron paramagnetic resonance (EPR) and his invention of the first double resonance technique, ENDOR (electron-nuclear double resonance) (Feher 1956, 1957a). When he started his work in photosynthesis, little was known about the first light-induced photochemical step except that this process involved the transfer of an electron from an excited donor chlorophyll to an unknown acceptor in a pigment-protein complex called the reaction center (RC) located in cell membranes. In a seminal work, presented at a meeting in Gatlinburg in 1970, he reported the detergent isolation of a pure active RC complex and the discovery of the EPR signal of the acceptor (Feher 1971). This initial work was followed in the next 3 decades by a multitude of studies on the RC, in his laboratory and many others, that revealed the structure and function of the RC using a staggering array of techniques including EPR, ENDOR, Mössbauer, extended X-ray absorption fine structure (EXAFS), Stark effect, and transient optical spectroscopies, as well as amino acid analysis, gene sequencing, antibody labeling, site-directed mutagenesis, protein crystallization and X-ray crystallography. At the end of his career, he saw the RC as the intricate molecular machine that we know today. Throughout his life, George was at the forefront of research in the field, asking important—the right—questions and pointing the way to their solution (Feher et al. 1989). This paper presents a brief summary of his work, as detailed accounts of his research along with complete references can be found in earlier articles (Feher 1998a, 2002; Okamura 2014).

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Early life

As a young man in Czechoslovakia, George took an interest in electronics and growing crystals to be used in radio receivers. These interests would resurface in his research later in life. After Germany invaded and occupied

Czechoslovakia, George, being Jewish, was not allowed to continue his education in high school. At the age of 17, he escaped with a group of friends to Israel (then Palestine, a British mandate). He joined a kibbutz, and later went to Haifa where he worked as an electronics technician for Franz Ollendorff at the Israel Institute of Technology (Technion). At that time Israel was struggling for independence. George used his skills in electronics to help the Israeli underground, the Haganah, including successfully unscrambling the coded telephone line between the British High Commissioner in Jerusalem and the British Prime Minister in London.

After independence, George applied for admission to the Technion, but was required to take a special exam since he had no high school diploma. He was not allowed admission because he failed one part of the exam, dealing with the Old Testament. Fortunately, he was admitted to the University of California at Berkeley, which had a more enlightened admission standard. There he obtained his BS in Engineering Physics and MS in Electrical Engineering, followed by his PhD in Physics in 1954.

After his PhD, George went to Bell Laboratories, making use of his training as a physicist and using EPR spectroscopy to study free electrons in solids. He helped to develop a solid-state version of the MASER, a device invented in 1953 and now used in microwave communications, and he invented the ENDOR technique (Feher 1956), a sensitive spectroscopic method used to determine interactions between electron and nuclear spins in materials. With ENDOR, George obtained detailed information about the electronic structure of silicon, a material found in electronic devices and in solar cells (Feher 1959). ENDOR spectroscopy later was shown to be very useful in his studies of photosynthesis and became an established tool in the study of metalloproteins. After Bell Labs, George went briefly to Columbia University to help set up a program in solid-state physics, where he also met his wife Elsa; then in 1960 moved to the University of California, San Diego (UCSD) in La Jolla as one of the first faculty members of the Department of Physics.

Biophysics at UCSD

Initially, George performed research on solid-state materials at UCSD with the intent of moving into the field of biophysics (Fig. 1). Before starting his biophysics program, George took a sabbatical at MIT in 1967–1968 to learn how research in biology was done. There he worked with Lisa Steiner, a protein biochemist, who taught him biology and started a long collaboration. At MIT, he saw a difference between research in biology and physics. George said, "Biology is a 'doers' field. You have to run centrifuges and gels and not spend time in deep thought, as physicists are prone to do. The challenge of biophysicists is to effectively synthesize

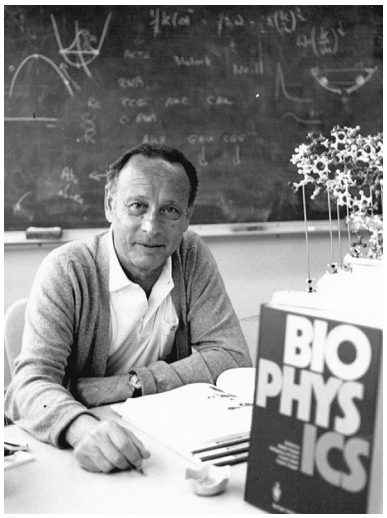

Fig. 1 George Feher founded the biophysics program at the University of California San Diego and excelled at methodologies and approaches to biophysical problems

the approaches from both disciplines." This insight would serve him well in his research in photosynthesis where he strove to utilize the best available methods in both biology and physics to understand the primary events in light capture and charge separation.

Back at UCSD in 1968, George started working on photosynthetic bacteria aided by Martin Kamen, whose laboratory was involved in isolating cytochromes from a variety of bacterial species. Roderick Clayton (1963) had made the first steps in characterizing the RC from the purple bacterium *Rhodopseudomonas sphaeroides* (now *Rhodobacter sphaeroides*). By using optical spectroscopy, he was able to identify the initial primary photochemical event as oxidation of the primary donor species (D also called P for pigment) due to light-induced electron transfer to the primary acceptor (X), $DX + h\nu \rightarrow D^+ X^-$. This reaction occurred even at cryogenic temperatures, and the light-induced spectral changes were found to be reversible (Arnold and Clayton 1960). Reed and Clayton (1968) had used the detergent Triton X-100 to isolate an RC particle from photosynthetic membranes. For membrane proteins, the choice of detergent is critical to the quality of the preparation and within a few years, George's laboratory had developed an improved protocol using a different detergent, lauryl dimethylamine oxide (LDAO), to solubilize the RC from the membrane, and was able to isolate a pure RC protein from *R. sphaeroides*, containing three protein subunits (L, M, and H) (Feher 1971).

Identification of the primary reactants

George used the isolated RC preparation to search for the electron acceptor signal with two students, Jim McElroy and

Roger Isaacson, performing EPR measurements at cryogenic temperatures to reduce the spin relaxation and using a sensitive light modulation to separate the EPR signal from ambient noise (Fig. 2). With this approach, a broad light-induced EPR signal assigned to the primary acceptor was observed for the first time (Feher 1971). Subsequent work by many researchers revealed that X is not a "primary" acceptor at all but that the initial charge separation occurs from D through a series of intermediate acceptor species, and finally to X.

The chemical identity of the acceptor species X was a puzzle. Initially X was thought to be a bound Fe atom due to the observation of a very broad EPR signal. However, Paul Loach's lab showed that removal of Fe from RC particles did not block the light-induced electron transfer, as reduction of the acceptor was still observed (Loach and Hall 1972). George's work with Mel Okamura at UCSD, along with that of other groups, showed that X was part of a quinone-Fe complex, containing two quinones, Q_A and Q_B, bridged by a Fe atom. At physiological temperatures, an electron is transferred from D, transiently through bacteriochlorophyll (BChl) and bacteriopheophytin (Bphe) acceptors, then to Q_A acting as the primary acceptor followed by transfer of the electron to the secondary acceptor Q_B. After receiving a second electron and binding two protons, Q_B leaves the RC and serves as a mobile proton carrier to pump protons across the membrane, driving the synthesis of ATP in the cell.

Another early focus was the elucidation of the nature of the primary donor by comparing the signal of the radical cation $D^{\cdot+}$ with that of model compounds. As observed earlier by James Norris and coworkers (Norris et al. 1971), George found that the electronic *g*-value of the $D^{\cdot+}$ EPR signal and its saturation behavior was the same as that of an oxidized BChl radical ($BChl^{\cdot+}$) in solution, but the linewidth of the signal was narrower by a factor of 1.4 (McElroy et al. 1972). Norris explained the narrowing by arguing that the linewidth would decrease by $\sqrt{2}$ if the unpaired spin was delocalized over two BChl molecules. This prediction was independently verified by Norris and coworkers (Norris et al. 1973) and by George with a postdoc, Arnold Hoff (Feher et al. 1975). This assignment demonstrated the power of the ENDOR technique that George had developed, as these measurements showed pronounced spectral shifts that were directly interpreted in terms of the hyperfine couplings in $D^{\cdot+}$ being reduced—on the average—by a factor of two relative to those of monomeric $BChl^{\cdot+}$. Strong support for this electronic dimer model was provided later from different ENDOR studies, e.g., of $D^{\cdot+}$ in RC single crystals (Lendzian et al. 1993). On the acceptor side, the iron-quinone complex was characterized using multifrequency EPR and ENDOR leading to a full characterization of the spin distribution and electronic structure of the radical ions of the quinone acceptors (Lubitz and Feher 1999) in samples with removed or replaced non-heme iron, a method that was developed by a graduate student, Richard Debus (Debus et al. 1986). Iron replacement (by Zn^{2+}), quinone removal/replacement (Okamura et al. 1975), and selective isotope labeling combined with Q-band EPR and ENDOR enabled the determination of the hydrogen bonding interactions to the quinones that are responsible for the different functional properties of the quinone acceptors in the RC. This comprehensive work was finalized by a postdoc from Peru, Marco Flores, more than 20 years after it had been started by Wolfgang Lubitz as a postdoc in George's lab (Flores et al. 2007).

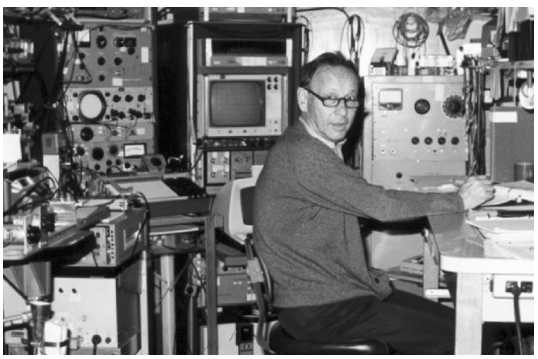

Fig. 2 George Feher next to one of the electron paramagnetic resonance spectrometers at UCSD in the mid-1980's

Determination of the protein structure

George did not confine his work to spectroscopic measurements, as he realized the importance of determining the structural properties of the RC. He collaborated with Lisa Steiner in determining the amino acid composition (Steiner et al. 1974) and then the amino-terminal partial sequences of the three protein subunits (Sutton et al. 1982). These efforts were made difficult due to the hydrophobic nature of the proteins, consistent with the location of the RC in the interior of the membrane. The topography of the RC as an integral membrane protein was established by antibody labeling studies done by his student, Gunars Valkirs, who showed that the RC proteins spanned the membrane (Valkirs and Feher 1982). The amino-terminal sequencing laid the foundation for the full sequencing of the subunits using the then new techniques for DNA sequencing. JoAnn Williams, a student in George's lab, in collaboration with Mel Simon, isolated the genes and determined the sequences for the three subunits (Williams et al. 1986). The results showed that the two subunits, L and M, each contain five continuous hydrophobic stretches separated by hydrophilic residues, while the H subunit had only one continuous hydrophobic stretch, giving an early picture of the RC as containing eleven transmembrane helices. The sequencing also revealed the homology among the L and M subunits and the D1 and D2 subunits of photosystem II.

The breakthrough in RC structure work came from the determination of the three-dimensional structure using protein crystallography. George had a continuing interest in crystals and had a research program in crystallization of proteins including membrane proteins, even though some grant reviewers thought that the crystallization of a membrane protein was impossible. The feasibility was demonstrated by the crystallization of the RC protein from *Rhodopseudomonas viridis* (now *Blastochloris viridis*) and determination of its X-ray crystal structure by Hartmut Michel, Johann Deisenhofer and Robert Huber (Deisenhofer et al. 1984). George worked with Jim Allen at UCSD and Doug Rees at UCLA to crystallize the RC protein from *R. sphaeroides* and determined its structure a short time later (Allen et al. 1987).

George was pleased that the structures provided a framework for the interpretation of the spectroscopic data (Feher et al. 1989). The structure corroborated many of his key spectroscopic findings, such as the presence of the BChl dimer as the primary electron donor, and the BChl dimer and two quinones serving as bookends for a line of cofactors across the membrane (Feher 1998a). One of the unexpected features was the twofold symmetry of the RC, with two branches of cofactors being related by an approximate twofold symmetry axis, which also relates the L and M subunits. George was struck by the beauty of this symmetry and framed one of the figures of the three-dimensional structure of the RC as a keepsake in his home.

The arrival of the RC structures set the stage for new directions of spectroscopic experiments. The structure led to many questions concerning the role of each cofactor, and calculations of molecular orbitals were now possible. Several laboratories investigated features that controlled the transfer of electrons along only one of the branches despite the division into two branches of cofactors, one from D to Q_A and the second from D to Q_B. With a postdoc, Herb Axelrod, George and Doug Rees extended the crystallographic studies by determining the structure of the RC co-crystallized with cytochrome c_2, its mobile electron transfer partner, revealing the interactions responsible for binding and inter-protein transfer (Axelrod et al. 2002). Being the first structures of membrane proteins, the RC structures became a well-recognized template for modeling other proteins present in cell membranes. In particular, these bacterial RC structures were critical references for the interpretation of spectroscopic data of photosystems I and II located in cyanobacteria, algae, and plants, until the determination of those structures a decade later.

Characterization of electron and proton transfer

The RC was an ideal system for studying electron transfer reactions. The timescales for transfer between components range from femtoseconds to milliseconds involving distances from 0.3 to 2.2 nm. To test the theories and models that had been presented to explain these data, George devised new experiments involving varying the free energy dependences of the electron transfer rates. For example, one way to change the energy difference, using a physicist's approach to change the energy for charge recombination from $Q_A^{\cdot -}$ to $D^{\cdot +}$, was by applying an electric field across the RC embedded in a monolayer film. The change in rate as a function of energy agreed with theory (Gopher et al. 1985). Another way, using a chemical approach, was to change the energy for the electron transfer from $Q_A^{\cdot -}$ to Q_B by substituting quinones with different redox potentials for Q_A. A PhD student, Michael Graige, found the rate of this reaction was independent of the energy difference, indicating that electron transfer did not limit the observed rate. This supported a model called conformational gating, where the rate was determined by a conformational change in the protein (Graige et al. 1998). This conformational change explained earlier results by a PhD student, David Kleinfeld, who found that this reaction rate was greatly changed in RCs frozen in the light (in the charge-separated state) or frozen in the dark (Kleinfeld et al. 1984). The importance of protein dynamics in electron transfer was underscored by observation of different conformations of Q_B in RC crystals frozen under different conditions (Stowell et al. 1997).

Proton transfer across the cell membrane plays an essential role in the formation of ATP in cells according to the chemiosmotic theory first proposed by Peter Mitchell (1966). The uptake of protons from the cytoplasm by the RC occurs at the point where Q_B binds two protons upon full reduction. Proton transfer requires a series of tightly connected protonatable residues forming a pathway, which presented a problem since Q_B is bound in the hydrophobic protein interior away from the aqueous surface. George's student, Mark Paddock attacked this problem using site-directed mutagenesis to modify protonatable residues in the RC near Q_B and determined the effect on the electron transfer and proton-binding rates. A significant cluster of acidic and hydroxylic residues near Q_B identified specific pathways for proton transfer (Paddock et al. 2003). These results defined the sequence of proton and electron transfer steps and helped demonstrate how the coupling of proton and electron transfer is crucial for redox reactions in proteins.

George received many awards for his research in Physics and Biophysics. These include: the American Physical Society Prize in 1960, election to the National Academy of Sciences in 1975, the Oliver Buckley Solid State Physics Prize in 1976, National Lecturer of the Biophysical Society in 1983, the Rumford Prize from the American Society of Arts and Sciences in 1992, the Gold Medal of the International EPR/ESR Society in 1992, the Zavoisky Award in 1996, and the Wolf Foundation Prize in Chemistry in 2007 (Fig. 3).

Fig. 3 George Feher receiving the 2007 Wolf Prize, being congratulated by Professor Hanoch Gutfreund

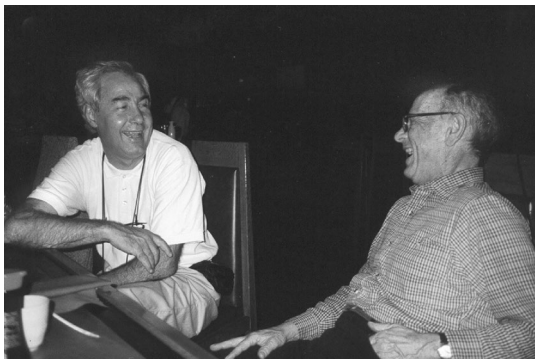

Fig. 4 George Feher, known for telling jokes and stories, shares a laugh with Rafael Calvo

George's approach to life and science

One key to George's success in research was his insistence on clarity. He was critical of fuzzy interpretations and theories based upon noisy EPR spectra. He would identify the most important problems and make use of the best experimental techniques to answer those questions. When he started work on photosynthesis, EPR and ENDOR spectroscopies were ideal for identifying the primary reactants created by single electron transfer reactions. He realized that the protein structure was a critical component and was fearless in making use of different biophysical and biochemical approaches as a means to address this end. He believed that new ideas and imagination were necessary and had a practice called the "Friday afternoon experiment" where one could try out a new idea with a short experiment. Another key was his tenacity in pursuing his goals as evident in the work on crystallization of membrane proteins, which required pursuing a research direction that many thought to be not feasible.

George was a skilled communicator in person and in print. He was a welcomed speaker at meetings as his incisive comments carried full weight and were well respected. His papers are a paradigm of clear scientific writing. George stressed to all of his students and postdocs that they needed to develop the skill of good writing. After a careful read of a new manuscript, George would return it, suggesting he had made just "a few small changes" while presenting a heavily marked copy, and ask for another draft. This editing would continue through numerous revisions until finally the "n–1" draft was ready for proofreading. He did not publish a large volume of papers but each paper reported a well-presented, significant finding.

George was a wonderful teller of stories and jokes (Fig. 4). A serious discussion at a laboratory meeting would often be punctuated by George telling a new joke. At a meeting about RCs organized by Jacques Breton in Cadarache France, George was asked to give a light after-dinner talk that he filled with humorous stories (Feher 1988). This talk was so well received that he was asked to do it again at two subsequent meetings (Feher 1992, 1998b). These three talks, called Light Reflections I, II, and III, were filled with George's wit and wisdom. For example: "Most of our students are great, only occasionally one turns out badly even after years of training. Then one feels like Aaron when he told Moses: 'I poured in gold and out came a calf'. Unfortunately, the problem is not over with graduation. What kind of recommendation can one give? After all you don't want to ruin the fellow's career. The best I could come up with was something like: 'He worked for 5 years in our group and when he left we were perfectly satisfied!'."

George's drive for excellence in research was also exhibited in his love of challenges outside of science. He was a competitive swimmer in his youth and continued swimming throughout his life. He won medals for swimming in Senior Olympics competitions up into his 80s. He was an enthusiastic tennis player, self-taught with deficiencies in technique, but ran after every ball with fierce determination. He was an avid poker player who would sometimes participate in tournaments in Las Vegas. He not only understood the probabilities of drawing a winning card but also was a keen observer of people and could judge whether a player was bluffing or had a winning hand. He enjoyed a long-standing bimonthly poker game in La Jolla with a group of friends and colleagues that continued until his last days.

George had a full, rich life, overcoming more than his share of adversity to achieve major advances in science. When he died at the age of 93, he suffered from a variety of debilitating physical ailments but his mind was clear as ever. He is survived by his wife Elsa and two daughters, Shoshanah and Paola; Shoshanah's husband, Geoff Sternlieb, and Paola's partner, Joe Josephson; and three grandchildren: Avi, Sylvie, and Joshie Sternlieb. His wisdom, high principles, keen sense of humor, as well as his legacy of scientific accomplishments, serve as inspiration for all who knew him.

Reminiscences from students and colleagues

Ed Abresch, research associate (1976–2011)

I first met George Feher in 1976 when I began working for him as a laboratory technician. My primary responsibility was to provide his students and postdocs with the bacterial RCs they needed for their experiments. Larry Ackerson, a senior technician, told me that only "Cadillac" work was done in the Feher lab. Because I was not very familiar with George's research history when I began working for him, this sounded somewhat pretentious to me. Nevertheless, I was very happy to be paid to do research. Over the years I worked in George's lab, I came to accept Larry's characterization of the research. The quality of work in the lab was directly attributable to George and his ability to demand and inspire excellence in his students, postdocs and technicians, and to focus on the most crucial questions. George met with each of his students and postdocs on a weekly basis, where they would have to explain their experiments and data. At times the meetings could be harrowing because George would not accept incomplete or sloppy explanations of results. His protégés would alternate between depression and elation depending on how well their weekly meetings went. Furthermore, George kept up with the smallest details in everyone's work. I also had sporadic meetings with him and I was often surprised when he brought up a detail I had forgotten but had told him at a previous meeting—and I was only one of about ten different people he met with. I was amazed how he could stay on top of everyone's work down to the smallest details.

George was relentless in his search for accurately understanding the results of the experiments we were doing. And his mannerisms helped convey the force with which he was determined to get to the facts. His lightly accented English and perfect grammar only increased the effectiveness of his words. Even though he was not a native English speaker, his English was more correct and precise than most of us who grew up in America. If you unintelligibly described something or didn't make good sense, he would often peer over the top of his reading glasses and say with a slight accent, "I don't understand what you're talking about." He insisted that you understand and accurately describe your results.

In my particular case, I owe George for giving me the opportunity to do original research in bacterial photosynthesis. Although I was first hired on to provide support for his students and postdocs, over time he encouraged and guided me in research in various areas including studies in the crystallization of photosynthetic RCs. I will always treasure the opportunity he gave me, and all that he tried to teach me.

Noam Adir, postdoctoral scientist (1990–1995)

I first heard George lecture in Jerusalem in 1989. Quickly, I realized that the science that he and his group were doing was exactly what I was looking to do as a postdoc, and would eventually lead to a university position in Israel. To my joy, George indeed accepted me, and we made plans that I would come to the lab in June 1990, to join the group that was already hard at work on mapping out the residues involved in proton uptake by the RC from *R. sphaeroides*. When I arrived in La Jolla, we had our first meeting and out of the blue, George said, "why don't you try to crystallize Photosystem II"? A seemingly simple question—but one that turned out to be life changing. During the next 5 years, we indeed developed the methodologies needed to crystallize photosystem II from plants. While the structure could not be determined from these crystals, I believe that our work was an essential first step towards the eventual determination of the cyanobacterial photosystem II complex by groups in Germany, the UK and Japan.

An off-shoot of the photosystem II project was that we started a second project, the co-crystallization of the cytochrome c_2:RC complex from *R. sphaeroides*. In this project, I had an opportunity to work with almost the entire group of the time: Mel Okamura, Ed Abresch, Herb Axelrod, Scott Rongey, Paul Beroza, Roger Isaacson, Mark Paddock as well as Doug Rees's group at Caltech. This was the first successful crystallization of a soluble protein with a membrane protein complex, and was very exciting. The merging of biochemistry, biophysics, structural biology, molecular biology, and computational chemistry in this project was a wonderful experience, which has guided the way I try to do science, ever since.

I am forever grateful to George for the support he gave during my time in La Jolla. George was a demanding mentor, but his clarity and vision were instrumental in achieving the difficult goals we set for ourselves. He was very supportive during the establishment of my own lab in Israel. I was thus very happy that I had an opportunity to organize a symposium to celebrate his 2007 Wolf Prize in Chemistry. The symposium took place at the Schulich Faculty of Chemistry of the Technion, where George had worked in the mid-1940s, before going to the US to study at UC Berkeley.

Herb Axelrod, assistant project scientist (1989–2004)

In 1989, I joined George's research group as a postdoctoral researcher. I was invited to meet George in La Jolla at the now legendary "Friday-afternoon" seminars. To put it directly, my seminar was a disaster! After the seminar, I sat at a table in the room with George and Jim Allen. I think that we all realized that my performance and interview

were weak. However, we engaged in casual conversation and George shared with me his Jewish heritage. I must now admit that even though I was terribly anxious and insecure about the meeting, those few words enabled me for the first time during the visit to speak meaningfully and coherently. Without hesitation, I described how much I cherish the strength and kindness of my Latvian-Jewish grandmother. A few years later, during a tense research meeting with George, I asked him directly why would he accept me into his laboratory when he seemed less than enchanted with the progress of my research. George told me at the time that he accepted me into his group because he was impressed by the way I described my devotion to my Jewish grandmother! Yes, George was as genuine as you can get. He did not shy away from the fact that we are all human with a complex interplay of emotions, relationships, and commitment.

I entered George's group to determine the crystal structure of cytochrome c_2, the physiological electron donor to the photosynthetic RC. Completion of the structure required more than a decade of work and at no point did George disengage from the goal of the structure determination. George's tenacity and dedication to the project served as an inspiration to continue. In a sense, the fact that George would not give up on the project indicated that he had faith in my ability to bring the project to fruition even though it was a gamble. Since George was a successful gambler and a poker champion, I figured that I could win at the project if I had him on my team.

Although George had a reputation for being demanding, this was only his outer shell. At his core, George was the kindest, most generous and forgiving person that I have ever known, even though I am sure he would have disagreed. I now realize that on some occasions, I was taxing George with my own personal complaints, but he transcended his role as supervisor and truly showed a tremendous degree of empathy for not only challenges in the lab but also my own personal struggles, even though he was facing his own personal health challenges. While most other supervisors would have been dismissive, I am fortunate that George chose a higher pathway. On my last visit with George in La Jolla in December 2016, it was important to me to let George know how deeply I valued his guidance, mentorship, and friendship. His response was gentle and will always soothe me when I am in times of personal and career distress. George told me "Herb, you turned out well." I am fortunate that he left me that simple, profound statement.

Kim Bagley, postdoctoral scientist (1986–1989)

Ubiquinones and Hungarian pancakes—each brings back memories of my time in George's lab. I joined his lab as a postdoc in 1986 with the intention of using light-induced Fourier transform infrared difference spectroscopy to examine the changes that occur at the quinone binding sites following light absorption. The original plan was that I would use an older instrument owned by a faculty member in the chemistry department at UCSD for the experiments. However, it was ultimately determined that a better instrument was required. So, arrangements were made for me to perform the experiments in the laboratories of Jacques Breton and Eliane Nabedryk at CEN Saclay near Paris. I note that, prior to my time in the Feher/Okamura lab, I had never done any wet bench biochemistry, instead relying on my collaborators to supply the necessary samples for my research. However, in the Feher/Okamura lab, that was not how science was done. I therefore set out, with the patient help of Ed Abresch, to produce a series of isotopically labeled RCs for my project. Among the samples required were RCs containing ^{13}C labeled ubiquinone-10. This required growing *R. sphaeroides* on ^{13}C labeled sources and then isolating the ^{13}C-labeled ubiquinone. It was a time-consuming and expensive process and I was quite proud of myself when I had a few milligrams of ^{13}C-labeled ubiquinone in hand. To determine the infrared spectrum of the labeled ubiquinone, I happily took my sample over to the adjacent chemistry building and the spectrum was beautiful! Unfortunately, on my way back from the chemistry building, I stumbled on the stairs and dropped the glass vial containing all of my labeled ubiquinone, now dissolved in a solvent, at the top of a flight of concrete stairs of the chemistry building. Needless to say, my ^{13}C-labeled ubiquinone sample did not survive the experience, and I was left with the unwelcome task of explaining what had happened to George, who, I knew, did not suffer fools gladly when it came to mistakes in the lab. This disaster occurred quite late in the day, and so, after a sleepless night I made my way to see George and meekly explained what had happened. George looked at me calmly, sighed, and after what seemed like an eternity asked, "How long will it take you to make another sample?" I did indeed make another sample, nothing more was ever said about the episode, and the biochemical techniques I learned in his lab have served me well over the years. In fact, I was ultimately hired at SUNY Buffalo State to teach their biochemistry sequence, which includes a laboratory on biochemical techniques, and of course, a discussion of the role of quinones in photosynthesis.

In addition to talking science with George, we often talked about the time I spent in Szeged, Hungary as a graduate student. From those chats, I learned that his last name stems from the Hungarian word fehér, which translates as 'white.' I also learned that he and I shared a fondness for Hungarian crepes filled with melted chocolate and walnuts. He introduced me to a wonderful little Hungarian restaurant near the university, in Del Mar, where we enjoyed some Hungarian crepes together on several occasions. I now make those crepes every Mardi Gras for my family and friends,

and each time I think of George, his zest for life, his kindness about my disastrous first attempt at making isotopically labeled ubiquinones, and, of course, the many things I learned from him while I was a postdoc in his lab.

Steve Boxer, research colleague

I first encountered George's work as a beginning graduate student when I used a technique called INDOR, the nuclear magnetic resonance analog of ENDOR, to assign the ^{13}C and ^{15}N spectra of chlorophyll and pheophytin. George invented ENDOR to study the unpaired spin in Si, a towering conceptual and methods development that also yielded results of huge importance in the early days of the semi-conductor industry. Quoting Slichter (1990) "A double resonance experiment of great historical importance was performed by George Feher" (referring to Feher 1957b). This is not an overstatement because ENDOR really established all flavors of double resonance. While INDOR was replaced by 2D nuclear magnetic resonance, ENDOR (including pulsed versions) continues to be a core tool for studying free radicals and proved essential for George's huge body of work on free radicals in photosynthetic RCs.

When the X-ray structure of the bacterial RC was just emerging, a group of us were summoned by Maibi Michel-Beyerle to the first Feldafing meeting on Starnberger See in Bavaria. My mother, who with my father had escaped from Vienna in 1939, was horrified as this was where many Nazis had their summer homes. George knew this well and talking about this became an important non-scientific connection. After the meeting, he and I visited Hans Deisenhofer at the Max Planck Institute in Martinsried, Germany. The RC structure from *R. viridis* was still being refined, and we spent 5 h in the dark in front of an Evans and Sutherland Graphics workstation (the state-of-the-art at the time) with Hans listening to and absorbing every detail of what we knew, so much based on experiments from George's group. It was the high point of my scientific career, a total revelation to see the structure unfolding, with Hans, the master of the structure, absorbing all this information that his and Hartmut Michel's work provided a new framework for understanding. It must have been bittersweet for George who had spent so much effort in his own lab trying to crystallize the RC.

A last recollection was from a meeting in Jerusalem in 1989. As part of the meeting, we visited the newly opened Tower of David museum. It was my first visit to Jerusalem, and I lingered behind the rest, as did George. Pointing to photos, he recalled his experiences as a refugee, in particular, with some glee, going after the British occupiers. We had a complex relationship—it was impossible not to be a competitor because he was fiercely competitive, but there was a common bond from our personal and professional backgrounds. His papers were masterpieces of clarity and insight, and his guidelines on how to write a paper, presented during after-dinner comments at a Cadarache meeting, are posted above every desk in my lab (1992). I feel very lucky to have known this great scientist.

Frank (Bud) Bridges, PhD student and postdoctoral researcher (1964–1970)

In the early 1960s, George Feher was studying polarized nuclei, and together with postdoc Gil Clark, monitored the nuclear polarization using nuclear magnetic resonance. I was introduced to and became excited about this work when Gil Clark gave a talk at the University of British Columbia in 1963, where I was finishing my Masters thesis using nuclear magnetic resonance to study deuterated methane. I decided to apply to the new UCSD campus in La Jolla and joined the Feher group in September 1964, jumping quickly into the experiments. Shortly after arriving, I was told was that George had decided to move into biophysics and I was his last solid-state physics student.

In 1966 Feher and another graduate student, Ian Shepherd, discovered paraelectric resonance of OH^- dipoles in potassium chloride. This phenomenon is the electrical analog of the well-known magnetic resonances of EPR and nuclear magnetic resonance. In this case, the energy levels of oriented electric dipoles are split by the application of a direct current electric field. I became interested, particularly because some off-center defects also showed similar behavior, and spent the end of my last year as a graduate student and also a short postdoc (1969) in the Feher group learning to do microwave experiments (thanks to Roger Isaacson and Mickey Shanabarger). In early 1970, I joined UC Santa Cruz as an Assistant Professor and set up a laboratory to do these experiments on a range of systems. One of the crucial issues for such studies was the need to be able to do paraelectric resonance experiments over a wide range of frequencies, and the eventual system we developed covered the range from 4 to 200 GHz. The training I received in George's group was crucial for my success in setting up this lab that operated for 2 decades.

Peter Brzezinski, postdoctoral scientist (1989–1991)

Soon after arriving as a postdoc in George's lab, a fellow colleague showed me referee comments that he and George had received on a manuscript that they had submitted for publication in a scientific journal. I don't remember the exact wording, but the general spirit of the short message was: "I studied the manuscript very carefully and tried to find something that would be missing, inconsistent or perhaps even wrong, but couldn't. This is a piece of scientific art that presents important data interpreted and discussed by a sharp intellect. It should be published as is." Although I

could not fully grasp the meaning then, I later came to realize that these comments signified the essence of the way George approached scientific problems. They also reflected his scientific integrity and his performance as a role model for those of us who had the privilege of working in his lab. Undoubtedly, this was the most important period of my scientific life, not only considering the acquired knowledge, but also learning about and reflecting on the way to do science. We miss you George, and we will always remember you as a humanist with the sharpest of intellects and a warm sense of humor.

Rafael Calvo, PhD student and postdoctoral researcher (1966–1968)

I met George and Elsa in Buenos Aires in 1964, when they came to start a research group and design a new EPR spectrometer. This marked the start of a relationship that would last over 50 years. Over the next 5 decades, he was first my PhD thesis advisor, and then during many unforgettable stays in La Jolla, I became George's postdoc and eventually his collaborator. We used to speak in English when we discussed science but spoke in Spanish for everything else (i.e., family, politics, poker). Whatever the language, every meeting with George was a joy. Writing or discussing a paper with him was a privilege. He was meticulous when it came to experiments, was always full of questions as well as answers, had remarkable scientific insight and clarity, and had an impeccable "gut instinct." But it is not just his skill, dedication and achievements that will be remembered, for he also had a famous sense of humor and great generosity. George was a great mentor and scientist, but most importantly, a great friend, and his legacy is palpable in the lives of those who were fortunate enough to share in his work and life.

Richard Cogdell, research colleague

I first met George Feher in 1975 at Rod Clayton's Photosynthesis Gordon Conference. We had a conversation about my new picosecond data on the electron transfer pathway in purple bacterial RCs. I was a young, long-haired postdoc working with Bill Parson and Rod Clayton and George was already a 'big cheese.' He was really rather scary. Over the next few years I got to know him rather well as we often went to the same conferences. It seemed always to be my misfortune to have to speak after George. He gave immaculate and highly amusing talks. His data always seemed to be so perfect. It made me feel quite small and inadequate to follow on from such a consummate performer. For years at the beginning of conferences I always looked first to see if there was a suitable gap between when he and I were scheduled to speak.

As time went by we became good friends and enjoyed many great discussions. He was critical in the best sense and very supportive. I was deeply honored that he invited me to be one of the speakers at his special symposium when in 2007 he was awarded the Wolf Prize in Israel. I will miss him. There is not much to recommend in getting old, especially when you start to lose good friends such as George.

Marco Flores, postdoctoral scientist (2000–2004)

The first time I heard about George Feher was during my graduate studies in Rio de Janeiro, Brazil. My PhD adviser, George Bemski, was a dear friend of George and told me many stories about his achievements as well as his strong personality and his systematic manner of doing research. A few years later, when George Feher hired me as a Postdoctoral Scientist, I was thrilled and afraid at the same time. I moved to San Diego in 2000 and took over a project that had been started by Wolfgang Lubitz in the early 1980s, dealing with the electronic structure of the primary acceptor Q_A. It took me a few weeks to adapt to the Feher lab, since bacterial photosynthesis was a completely new subject for me, and my English at that time was deficient. Communicating with George was never a problem because he was fluent in Spanish, but I also needed to interact with the other members of the group. George offered to pay for an intensive 30-day English course at UCSD. After I registered for the course, he told me: "There are two kinds of immigrants in the United States, those that study English for 30 days and learn and those that study English all their life and never learn." Later, I told this story to Mark Paddock, and he told me that George's statement probably applied to US citizens too.

The goal of my project was to investigate the physical properties of Q_A using ENDOR spectroscopy. We wanted to show that hydrogen bonds tune the electronic structure of $Q_A^{\cdot-}$ and therefore define its function as a one-electron transfer gate. We knew from previous experiments that the two protons that are hydrogen-bonded to $Q_A^{\cdot-}$ exchange with deuterons, but the rates were unknown. After determining these rates, we were able to prepare samples in which each hydrogen-bonded proton was preferentially deuterated, allowing the identification and assignment of the ENDOR signals corresponding to each hydrogen bond. I enjoyed these experiments as they were well planned with the touch of George. On the day that I finished the ^2H ENDOR experiments, he came to my office to congratulate me and told me: "Marco, we have finally done it."

Before I left to accept a job offer from Wolfgang Lubitz to work at the Max Planck Institute in Mülheim an der Ruhr, Germany, we decided to write two papers. The preparation of the first manuscript—a short one—was smooth and ready after a few rounds with George. However, the second

one did not follow the same fate. George wrote to me after reading the first draft: "Marco, I do not want written on my tombstone: He was a great scientist but his last paper was a disaster." Only then did I realize that I was the last postdoc of George. Anyway, the second manuscript was very much improved, mainly with the help of Wolfgang Lubitz, and both papers were finally published in the Biophysical Journal. A few weeks after the publication of the second one, Wolfgang and I received in Mülheim a package with a good bottle of Champagne delivered as a present from George to celebrate the conclusion of our project and his last scientific paper.

In 2008, I began serving as the Lead Research Scientist of the EPR facility at Arizona State University. This position was very convenient because it allowed me to frequently visit San Diego—where my long-time girlfriend Shawn used to live. It also gave me the opportunity to visit George in La Jolla. We had our informal chats until recent years. I am convinced that George during his long lifespan greatly impacted the lives of many scientists, including mine. George was very gifted in designing the proper experiments, and he was demanding but at the same time very supportive and loyal to his people. I am glad that I have known him and his family. George, I am going to miss visiting you in La Jolla!!!

Michael Graige, PhD student (1995–2000)

It was an honor and privilege to grow-up scientifically in the labs of George Feher and Mel Okamura. As I look back years later, I appreciate the amazing training I received. George always held the highest scientific standards, and was an excellent teacher and communicator. He exemplified the values of understanding science at the detailed level, a dedicated work ethic, and integrity in drawing conclusions. I have shared with many younger scientists George's wisdom through his quotes that are now part of my vocabulary. For example, it is important to provide the proper level of confidence, when drawing conclusions from data. So, from least to most confidence, George would say the data were: "consistent with, suggests, indicates, shows, or proves" the conclusion. And he would never actually use "proves." Other of George's informal quips often pops into mind—great reminders of important concepts he taught me. For example, related to the value of hard work, when I asked if we were having our recurring Monday meeting on Labor Day, he replied, "Science knows no holidays." I took that as a yes. It was George who provided the first true feedback to me; it was timely and direct, and helped me to increase self-awareness in the professional environment. It also provided a great example for giving feedback to others.

I am glad that I joined the lab when I did. Midway through my graduate career George became professor emeritus, and mellowed somewhat, compared to the stories I heard about his earlier years. Still, it was the hardest 5 years of my life! He was happy for my success. He was visibly disappointed when I did not do my best, which made me strive harder the next time. I clearly remember the nicest compliment that I received from George. It was during a conversation we had discussing the great contributions from his past postdocs and grad students. At the end of it he smiled and said of the recent group, "I can't complain." Thanks to George for believing in me, and investing in me. I hope that I have been able to repay a fraction of my indebtedness by striving to practice science with integrity and passing along bits of his wisdom to the next generation of scientists. He did not just advance the fields of solid-state physics and biophysics. Rather, he touched several other fields through his mentorship and by sharing his wisdom. My formation enabled my contributions to the development of DNA array and sequencing technologies, and I appreciate the contributions of his other students in the fields of biotechnology, physics, and biochemistry.

If these two paragraphs were not clear, and simply understandable, my apologies. Unfortunately, George was not available to provide his masterful editing to improve the clarity. I will always remember his words of wisdom, including when he said, "Great writing cannot save poor science, but poor writing can ruin good science." As I look back, my only regret was not bugging him more.

Marilyn Gunner, research colleague

In my scientific career, I was lucky to have George Feher as someone who I never directly worked for, yet always felt like a mentor. Much of my early work was in an area, the study of quinone reduction in bacterial reactions, where George's lab was preeminent. It could be frustrating since what George said was the gold standard, irrespective of what might be measured elsewhere. But it was also wonderful meeting George at conferences, since he always showed a real interest in swapping what was new each time we met. I as an eager student wanted to share all my results, while George the older poker player would always be more circumspect choosing what to share and what to withhold. I can remember the clarity of these meetings with real pleasure.

As I got to know George better I learned and appreciated his personal story of change and survival. As he told his stories I would listen to learn how he could know when it was time to make changes. His ability to find the next chance in science and in life was inspiring to watch. The few times I saw him after his leaving active science reinforced my sense of his knack for change. He moved on to write a memoir. Now when I saw him the sometimes scary, competitive persona was no longer needed, and we moved to the pleasures of discussing simple things and how his life continued to evolve.

Roger Isaacson, research specialist (1961–2004)

In my senior year (1959–1960) at Pomona College, California, I had hopes of entering graduate school in the new field of radio astronomy but was turned down by several universities due to low grades. I did not do well in classes, spending too much time as the technical director of the campus radio station. My physics professor told me that a graduate school in physics had just opened up in La Jolla and I should apply, in spite of my grades. Maybe being such a new grad school, there would not be too much competition.

Fortunately, George Feher noticed my resume, with electronics experience and a hobby as an amateur radio (ham) operator (since age 12). He contacted me saying he could hire me as an electronic technician, but encouraged me to spend an extra year at Pomona, retaking several physics classes. What George did for me, going out of his way to jump-start my career, was typical of what he did over the years for so many people. His support was the only reason I was accepted as a physics graduate student at UCSD. After getting an MS in Physics in 1964, George hired me as a Research Specialist, a non-PhD academic position.

Newly arrived at UC San Diego, George was just starting solid-state physics research projects in NMR and EPR, methods completely unfamiliar to me. I still recall my pleasant surprise on how closely related both NMR and EPR were to my hobby involving radio transmitters and microwave equipment. In particular my skills building homemade radio transmitters that would not interfere with neighbors' TV reception really helped. At Pomona College, I had taken a microwave laboratory course that applied directly to building our own X-band EPR spectrometer, patterned after the one George used at Bell Labs. It was very fortunate that I had the opportunity to work with designs he had developed, such as wide gap (10 cm) magnets, immersion dewars for (very) low-temperature work, and various EPR/ENDOR cavities. Eventually, when working on protein single crystals, we found dielectric resonators to be ideal at X-band for high sensitivity ENDOR (CW) angular studies. A Q-band ENDOR cavity resonator was built, modeled after one from the lab of Charles Scholes (Sienkiewicz et al. 1996). These systems were our workhorses until George retired in 2004. EPR and ENDOR were instrumental in elucidating the electronic structure of the radical ions created in the charge separation processes in RCs.

Early on, even at Bell Labs in the fifties, George realized how computers (main frames then) could become nonproductive time wasters. The slide rule was a different story. He was enamored with the HP 35 pocket calculator when it was introduced in 1972, and we immediately incorporated it into the EPR lab to calculate *g*-values. However, he made sure we still kept a conveniently located slide rule in every room in the lab and were not distracted by inappropriate "new technologies." For years (when we still made graphs on paper) he would proudly show how much quicker he could reduce and plot data with a slide rule. Furthermore, you had an inherently rounded-off answer that was closer to the actual accuracy of the experiment instead of a misleading 8-digit readout.

For 40 years, I had the most fulfilling job I could have asked for. I had the opportunity to work with students and post docs from around the world in fields of material science, chemistry, and biology. George's legendary skills in grant writing supported all of us continuously for decades. He positively affected the careers of so many with his ground-breaking and imaginative scientific work. We all miss George, and I am grateful to him for teaching us the value of striving for the highest scientific and personal standards.

Rachel Nechushtai, research colleague

I first met George as a graduate student in the Technion in the laboratory of Prof. Nathan Nelson. George was a member of the Technion Board of Directors and used to come every year for the annual meetings, and would give a talk on the advancements in characterizing the bacterial RCs in his UCSD laboratory. As a graduate student, I attended all of his lectures since they brought to Israel the state-of-the-art, often unpublished news from the "Mecca" of photosynthesis. My PhD advisor highly admired George and used to tell me again and again that "if my performance in my PhD research was good enough he may consider recommending me to Professor George Feher for a postdoctoral position." After one of George's talks in the Technion, I told him that by chance I found out that he was the uncle of my best friend and classmate who sat next to me for our 4 years of high school—Dalia Zohar. What a small world.

We became very close colleagues after a conference held in 1983 in Zurich, Switzerland on RCs. I gave a talk on my results on Photosystem I, and afterwards George invited me to join him on a train journey from Zurich to Basel, where he was going to check about a possible collaboration for the crystallization of his RCs. It was on this trip that we discussed the possibility that I would join his laboratory as a postdoc, which never happened because UCSD in those days did not have a good PhD program in History for my husband. Instead, I performed my postdoc training at UCLA in the laboratory of the late Philip Thornber, who also highly admired George's laboratory. Since UCLA is in Los Angeles and about a 3-h drive from La Jolla, I used to visit the UCSD lab at least once a year.

In 1987, I went back to Israel, as a Faculty member of the Hebrew University, and established close collaborative research with George's lab. We were awarded a joint grant from the United States-Israel Binational Science Foundation

(BSF) and the visits to UCSD became a routine. In a way, I became part of the lab and became friends with the members of the laboratory—Mel Okamura, Roger Isaacson, Ed Abresch, Mark Paddock, Herb Axelrod, Mike Graige, Simone Powell, and many others. The Feher-Okamura lab became my second scientific home—I loved coming twice a year for extended periods of time (the month of February and often for the 2–3 months of summer sabbaticals). I learned so much there, wrote some joint papers and was very lucky to spend long talks with George.

On May 13, 2007, the Israeli Knesset (Parliament) awarded George the Wolf Foundation Prize for his work on RC structure–function. For me, it was a very emotional event. After thanking everyone in English, George gave a speech in fluent Hebrew about what such an award means for someone who could not be admitted to the Technion in 1946 because he flunked the test on the Bible. After the speech, the spokeswoman of the Knesset (Mrs. Dalia Itzik) stood up and clapped hands for a long time.

I miss you George. You were my greatest teacher and friend. I miss our endless talks about Israel past and present, our scientific talks and how much I learned from you. You were a role model to me. As close to perfect as possible, you hated when I described you in these words. I miss when you got mad that I am not capable of drawing straight-enough lines or write good-enough English or when I could not estimate precisely the length of time it will take me to finish to write/correct a draft of a paper. I can only say; "what can I do that I am not a George Feher."

Bill Parson, research colleague

When he wanted to make a point, George would tell a story, and he always seemed to have one at hand. One that struck home with me when I was beginning to enjoy the luster of theoretical work concerned an experimentalist who found that *A* was greater than *B* and asked a theoretician colleague whether the finding agreed with the colleague's theory. His colleague replied that, yes, the results agreed perfectly with the theory. A few days later, the experimentalist returned to apologize that there had been an error in his measurements, and that in fact *B* was greater than *A*. "Good," said the theoretician, "that agrees even better!".

George also told of two young men who had a disagreement about whether they should bother to learn a foreign language. As they were discussing the question, a stranger lugging a suitcase walked up and asked, "Excuse me, but can you tell me where the train station is?" When it was evident that they had not understood his question, he tried again, "Entschuldigen Sie bitte. Wo ist die Bahn?" Again, there was no answer, so he tried "Excusez moi, si vous plais. Ou est la gare?" Then "Permiso. ¿Donde está el estación?" When that still drew a blank, the stranger sighed glumly and walked off. "You see what a waste of time it would be to study another language," remarked one of the young men, "that poor fellow speaks four languages, and still nobody understands a word he says!".

George could have stretched that story out to quite a length if he had wanted to, because I think he spoke almost every known language. Some of his most compelling stories were his modest accounts of how he and a few other teenagers on his high school swimming team escaped from the Nazi Slovak state by swimming across the Danube at night, about his internment by British military forces in Israel, the difficulty of adjusting to life on a kibbutz, and about his learning electronics by building a radio and later working as a radio repairman. He was a remarkable person in many ways, and we'll miss him.

Doug Rees, collaborator

George Feher changed my life on January 5, 1984 when he sent a letter to David Eisenberg and me inquiring whether we would like to get together at UCLA to discuss his work with Jim Allen crystallizing the photosynthetic RC from *R. sphaeroides*. Would we? I could not believe this stroke of good fortune to have an opportunity to work on the crystal structure of a membrane protein, especially one as interesting as a photosynthetic RC. Even as a graduate student, I had been interested in membrane protein structure, but given all the difficulties with their preparation, this area of research seemed impossibly remote. And here, out of the blue, it was going to happen! Dave and I met with Jim and George and launched our collaboration, which Dave graciously let me pursue. The next few years were some of the most intense, exhilarating and challenging I have experienced, working closely with Jim, George and my graduate student Todd Yeates. Jim frequently made the drive from UCSD to UCLA delivering crystals, which we then mounted in the X-ray beam and collected the diffraction data under green illumination, to minimize potential light-induced damage. The resolutions of the structural analyses improved from 5 Å in 1986 to 2.8 Å in 1987, ultimately achieving 2.2 Å in 1997 (Allen et al. 1987; Stowell et al. 1997), which seemed inconceivable when we started and impressed upon me the progress that could be made on a project given enough time and dedicated effort. Our final paper with George was published in 2002, and described Herb Axelrod's work on the RC—cytochrome c_2 complex, a fitting culmination to nearly 2 decades of collaboration (Axelrod et al. 2002).

I was most impressed by George's clarity of thought and precision—I had never had such an experience writing papers where every word and thought was so carefully considered. This was an invaluable and enlightening experience, but also occasionally nerve-wracking. I recall that during one structural study, a histidine ligand moved ~ 4 Å away

from a bacteriochlorophyll magnesium during refinement—at the resolution we were working, it was likely an artifact of the refinement and so I didn't discuss this explicitly with George before publication. He was caught off guard by a question at a meeting about this interaction and I clearly remember his phone call asking me about this, and especially how I felt afterwards (and to this day) by not keeping him informed about this matter. George was passionately interested in all the details and needed to understand every facet of a project—he was an incredible role model for me in this regard.

Of course, as important as science was to George, there was much more to his life, but for many years, I was only vaguely aware of his life story and interests in poker and other activities. It was only after his passing that I learned he had recently written "Thoughts on the Holocaust," and reading this book reminded me of how much more there was to learn from him. Thank you, George, for sending that letter and allowing me to work with you on one of the most exciting scientific projects I can imagine, with one of the most remarkable individuals I can imagine.

Scott Rongey, BS and PhD student (1987–1998)

I had the privilege of working with George over a span of 10 years through my journey from an undergraduate, to graduate, to postdoctoral student. While it isn't common to attend the same school for undergraduate and graduate studies, my experience as an undergraduate working in the lab gave me the opportunity to see the special environment that George, along with Mel Okamura, had created. In an effort to understand structure–function relationships for the photosynthetic RC, they created an environment that attracted people with a diverse set of skills. The group was comprised of students from different departments (Biology, Chemistry and Physics), postdocs from around the world, full-time technical staff, and visiting faculty from other institutions. Their group used a variety of methods to study a single system, which was in contrast to many other groups that studied a variety of systems with a single method (e.g., X-ray crystallography, specific spectroscopy techniques). While there are pros and cons to both approaches, their approach of using several methods to study a system resonated with me and I realized that I wanted to learn in that environment.

During my time with the group I learned many things from George and gained a better appreciation of many facets of his life. In particular, I realized how many people he had helped, taken risks on, and advocated for over the years; I'm thankful that I was one of the people that benefited from his efforts. Even years after leaving the lab I often think about George, the training he helped instill in me, and how fortunate I am to have worked with him. I also think about, and use, some of his idioms such as "nature doesn't have corners" to explain that there are always regions of transitions between things, and "truth times simplicity equals a constant" when considering the amount of detail to provide for an explanation.

Lisa Steiner, collaborator

I met George at MIT in the academic year 1967–1968. He and Elsa were friends of Anne Good, whom I knew from the MD program at Yale. In 1967, Anne was a postdoc with Jon Singer at UCSD. She knew I was going to MIT, and told Elsa and George (who were headed to MIT for a year's visit) to look me up, which happened. I believe George came to a lecture I gave about antibodies. Since I knew something about proteins, George told me about RCs, which he then learned how to purify after returning to UCSD. At about this time, Mike Jacobson, a graduate student with David Baltimore, showed me how to run sodium dodecyl sulfate polyacrylamide gels, a technique I soon applied to RCs as well as to antibodies. It was clear that we needed to obtain more information about the three bands that we observed on the gels. When I was a postdoc with Rod Porter in London (1965–1967), I had met Ieuan Harris and I thought a visit to his lab at the Medical Research Council in Cambridge, England, might bring us closer to this goal and, of course, also get me back to England. Such a visit was arranged and I turned up in early May of 1976, found a flat, and settled in. Of course, a bike was necessary for survival in Cambridge and I bought a well-used one. In the lab, Ieuan turned me over to John Walker, who had arrived quite recently from France. I did some sequencer runs (probably of intact RCs) but I was in a rush before leaving at end of summer and did not bring the data home. In the end, Mick Sutton came to my lab and repeated those runs, leading to the determination of the N-terminal sequences of the three subunits, as finally published in 1982 (Sutton et al. 1982). The partial sequences of the polypeptides obtained by protein chemical methods were then used to validate the derived amino acid sequences of the genes.

Massimo Trotta, postdoctoral researcher (1991–1992)

Next to talking with Mel and George, the most instructive moment of any given week was the Friday afternoon seminar where you could throw in ideas, and discussion would sparkle freely. I was always eager to be present and missed very few of them. Sometimes the discussion was shorter; I have the feeling that it happened when the Los Angeles Lakers, led by Magic Johnson at the time, would play a basketball game on Friday afternoon. I must say I have no scientific proof of that being more than a fortuitous coincidence of events, but if it was true, it was never in George's or Mel's

intention. After one of those—very few indeed—shorter Friday afternoon discussions, George was heading back to his office and saw me in the office I shared in the Physics Department (Mayer Hall) with two other postdoctoral scientists, Herb Axelrod and Noam Adir. I have a sharp recollection of this meeting as it marked a very confidential moment I shared with him.

We dangled on some ideas for further nuclear magnetic resonance experiments involving the quinone exchange at the Q_B-binding site, but he ended up asking about my story and my original family. I told him I was the seventh of eight children and that immediately drew his attention. I went further in telling anecdotes until he discovered that my mother was roughly his same age while my father was 10 years older than her. He was a soldier of the Italian army in the Second War World and had been wounded and taken prisoner by the British army in North Africa. George kindly asked me my recollection of stories about my father but unfortunately, being an orphan since the age of nine, I had very few things to tell him besides the fact that I had learned from my mother that my father always mentioned that he had been treated well by the English troops during his long imprisonment. George, at that point, started telling me his personal story about how he fled from Slovakia to Palestine to escape the inhuman treatment of Jews in his country. This conversation impressed me very much as it showed the unsettled feeling he still had and that there were questions he wanted to ask concerning the war and the holocaust.

When I was invited to contribute to this article, I googled through George's publications and learned that in September 2017, 2 months before leaving this world, he had published the book "Thoughts on the Holocaust" (Feher 2017) that I immediately ordered and eagerly read. I suddenly knew that I had to share that confidential moment to show once more how interesting was George's personality. Too bad I could not congratulate—nor discuss—with him for the book. However, he is now in a place where Planck's constant is much smaller than anywhere else in the universe (Feher 1988).

Neal Woodbury, research colleague

In the late 1970s, I spent part of my undergraduate career at UCSD. I was a biochemistry major with an interest in physics, and there was a new class being offered in the emerging field of biophysics. It sounded like something I should find out about, so I signed up for the course. The primary lecturer was George Feher. He was a soft-spoken, but extremely engaging professor, and he proceeded to tell us about things that I never imagined existed. I was particularly interested in the interaction between light and biology. The concept that light both damaged DNA and was directly involved in repairing it was eye opening, but what really caught my attention was the notion that biology had built molecular devices that used light to move electrons from one place to another and generate chemical energy during the process of photosynthesis. It was George's passion for the subject and his exciting description of what was then NOT understood that captured my interest. There are a few defining points in one's life and career, and this was definitely such a point for me, initiating a decades long quest to understand photosynthetic energy and electron transfer and what it tells us about the underlying workings of biology.

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