George Feher (1924 – 2017)

On November 28, 2017 George Feher passed away at the age of 93 in his home in La Jolla, California (USA), where he has lived for more than 50 years, very close to the University of California San Diego (UCSD). He has been one of the first Professors at the Physics Department of the newly founded campus in the early sixties and helped to make UCSD one of the leading research schools in the country.

George Feher was born (29 May 1924) into a Jewish family in Bratislava, Czechoslovakia. In 1938 he was expelled from high school as a Jew – a year before the Nazi occupation. With a group of teenage friends from the swimming club he finally left the country in 1941 over land to Palestine that was under British Mandate at this time. There he first worked in a kibbutz for about one year before he moved to Haifa, where his elder sister Erika lived and where he found a job as radio repairman, which was nicely fitting his technical interests. In Haifa he also took technical courses at a trade school, and in 1943 he became a lab assistant with Franz Ollendorf, then professor at the Technion. During this time he also intensively worked on a descrambling device for the Haganah, the Jewish paramilitary organization in the British Mandate. His device was then successfully used by the Haganah to tap into the encoded communication between the British Commissioner in Jerusalem and the Prime Minister in London. It was only five decades later that George learned about the positive outcome of his highly confidential work at the Technion before the foundation of the state of Israel in 1948.

In 1944 George Feher applied to study at the Technion but failed to be accepted as a student since he was not well-versed in the bible. Subsequently, he applied at a large number of universities in USA – and only two (Harvard and UC Berkeley) were willing to accept him without high school diploma. It took almost two years before he had acquired sufficient money to travel to California, where he took up his studies at UC Berkeley in 1947 under difficult financial circumstances – and finally obtained his B.S. (1950) in engineering physics, his M.S. (1951) in electrical engineering, and his Ph.D. (1954) in physics with Arthur F. Kip and Charles Kittel as supervisors. During his graduate studies he built an EPR spectrometer and applied the at this time rather new technique to study conduction electrons in metals. During these early years he furtively looked also at some biological systems using EPR in the Berkeley laboratory and found signals in blood and illuminated plant material, topics that he later picked up again in his research as biophysicist.

After his Ph.D. he joined Bell Laboratories at Murray Hill (New Jersey) where he had the freedom to develop and explore his own technical ideas. Using his expertise in EPR spectroscopy, he decided to work on semiconductors, which resulted in a series of exciting publications. A seminal paper on sensitivity considerations of EPR (G. Feher, *Bell Sys. Tech. J.*, 36, 449, 1957) laid the groundwork for the theory and design principles of EPR spectrometers. This was before commercial spectrometers became available. His ideas were subsequently used by Varian and others to design their instruments. In 1956 George Feher performed an entirely new, history-making experiment in the field of magnetic resonance. He combined EPR and NMR spectroscopy (G. Feher, *Phys. Rev.* 103, 834, 1956) and actually performed the first double resonance experiment – that paved the way for many more to come in magnetic resonance and other spectroscopies. He called it ENDOR (Electron Nuclear DOuble Resonance) – with reminiscence to the witch of Endor, a village in Israel, where a story of prophecy happened that is told in the Bible (1 Samuel 28:3 - 25). ENDOR combines the high sensitivity of EPR and the high spectral resolution of NMR in an elegant way and allows measuring nuclear magnetic moments and the interactions of the unpaired electron with the magnetic nuclei, the hyperfine couplings, even in complex systems for which the EPR spectrum is completely unresolved. The technique, first applied in solid-state physics, was later extended to study radicals in solution (J. Hyde and A. Maki, 1964), to triple resonance (K. Möbius, 1974/75) and to versions with pulsed microwave and radiofrequency excitations (W. Mims, 1965). ENDOR is now one of the most employed methods in the suite of EPR techniques and applied to answer questions in physics, chemistry and biology alike. During his time at Bell Labs, George Feher performed several other novel experiments that should be mentioned, e.g. the generation of nuclear polarization via "hot" conduction electrons by D.C. electric fields (1959), the formation and detection of short-lived muonium atoms μ^+e^- as donors in silicon (1960), and the construction of the first solid-state MASER (1957), the forerunner of the LASER. This MASER was used on the first US satellite. In later years George continued his strong interest to develop new techniques resulting in such fascinating methods as paraelectric resonance (1965/66) and fluctuation spectroscopy (1973/75).

In 1959/60 George Feher accepted a position as visiting associate professor at Columbia University (New York) as successor of Charles H. Townes. There he met Elsa, his later wife (marriage 1961) who worked in the lab as a PhD student from Argentina. The joint appointment at Bell Labs and Columbia did not last long, and in 1960 he followed the call of Roger Revelle, who was establishing the new campus of UC San Diego in La Jolla. George became one of the first professors at the physics department, where he was given the opportunity to expand his research activities into the field of biophysics that he had always dreamed of. After a transition period of several years, many discussions with biologists and biochemists, and after a sabbatical he spend in a biology lab at MIT and Cold Spring Harbor he decided to work on the primary processes of bacterial photosynthesis. At this time very little was known about the structure and function of the photosynthetic unit and only a few scientists worked in this field. The idea of studying the initial steps of light-induced charge separation in photosynthesis was an obvious extension of his earlier work on electrons in silicon, the material used in solar cells. EPR and ENDOR could be used to follow the electron-transfer reactions in the reaction center (RC) of photosynthetic organisms, i.e. to study and characterize the nature of the primary reaction products which all contain unpaired electrons from the transfer of a single electron from the primary donor to a series of acceptor molecules.

At UCSD George Feher started to grow purple bacteria (*Rhodobacter sphaeroides,* carotenoid-less strain R-26) and soon, using a new detergent (LDAO), succeeded to isolate the RC in highest possible quality as minimal unit capable of light-induced charge separation (G. Feher, *Photochem. Photobiol.*, 1971). This key development allowed the determination of the cofactors: 4 bacteriochlorophylls (BChl), 2 bacteriopheophytins (BPh), 2 ubiquinones (UQ) and one non-heme Fe^{2+} and the characterization of the 3 protein subunits (L, M and H). Using EPR and ENDOR he was able to help identify the primary electron donor as a BChl dimer (1975), which was proposed earlier by J. Norris (1971), and identified an iron-bound quinone as subsequent acceptor (1971/72). To detect broad EPR signals he used light-modulation, and for better Zeeman resolution and assignments he expanded his repertoire from X- (9 GHz) to Q-band (35 GHz) EPR. An important step was the manipulation of the RC, i.e. to remove and exchange the quinones and also the high-spin Fe^{2+} and exchange it with other metal ions, e.g. diamagnetic Zn^{2+} (R. Debus et al., *Biochemistry* 1986). This opened the possibility to study the radical anions of both ubiquinones by EPR and ENDOR in great detail (W. Lubitz and G. Feher, 1999; Flores et al., 2007). As intermediate acceptor the BPh radical anion could be stabilized and studied. Furthermore the magnetic exchange interaction between the paramagnets was investigated and gave information on the electronic tunneling mechanism between these species. In this endeavor EPR/ENDOR was also performed on RC single crystals, the ultimate experiment to obtain the full information on the g, hyperfine and quadrupole tensors (F. Lendzian et al., 1993; R. Isaacson et al., 1995). In the following this finally led to a comprehensive characterization of the electronic structure of all the reactants of light-induced charge separation and helped enormously to better understand the functional details of the RC. These results have been obtained with a large number of students, postdocs and collaborators at UCSD (see G. Feher, *Photosyn. Res.* 55, 1-40, 1998). In the EPR laboratory Roger Isaacson´s expertise was indispensable who worked with George Feher at UCSD since the early sixties. Of equal importance were the excellent biological preparations (Edward Abresch) und the expert help of Melvin Okamura.

George Feher was always aware of the power of X-ray crystallography; consequently he started a program to understand the crystallization process of proteins – namely nucleation, growth and cessation - by using lysozyme as simple model (Z. Kham et al., 1978; S. Durbin et al., 1996). In the seventies it was still considered impossible to crystallize integral membrane proteins like the RC. This was proven incorrect in the early eighties, when bacteriorhodopsin was crystallized (H. Michel and D.

Oesterhelt, 1980) and soon after a bacterial RC could be crystallized from the purple bacterium *Rhodopseudomonas viridis* (H. Michel, 1982) and the structure solved by J. Deisenhofer, H. Michel, R. Huber (J. Deisenhofer et al., *JMB*, 1984) who received the 1988 Nobel Prize in Chemistry for this achievement. Stimulated by this success Feher´s group tried to crystallize the RC of *Rb. sphaeroides* and a first paper was published soon (J. Allen and G. Feher, *PNAS*, 1984) followed by a series of six publications in the same journal (1987/88) in collaboration with the crystallographer D. Rees (CalTech) detailing the cofactors, the protein subunits, the membrane-protein interactions, the carotenoids, the specific iron side and a species comparison. A summary of this comprehensive work appeared in *Nature* (G. Feher et al., *Nature,* 1989). This was all made possible by the excellent RC preparations, the choice of the right crystallization conditions and a careful biochemical characterization, including the determination of the amino acid sequences of the protein subunits, a difficult time consuming task in the early eighties (J. Williams et al., *Proteins* 1986). In later years several other important papers were published by the Feher group, including an attempt to detect light-induced structural changes (M. Stowell et al., *Science*, 1997) that were earlier proposed (D. Kleinfeld et al., *Biochemistry*, 1984) - and a first co-crystallization structure of the bacterial RC with its natural electron donor cytochrome c_2 (H. Axelrod et al., *JMB*, 2002).

Through his work George Feher has greatly contributed to an understanding of electron transfer in the photosynthetic RC, a topic of great general interest. These results have also been important for the much more complex plant reaction centers and for the development of theoretical concept like the Marcus theory employed to biological ET. Even more so, George and his group contributed to an understanding of the protonation of the RC (M. Okamura et al. *BBA*, 2000), from a biochemical point of view the more important process since it drives the formation of ATP. Many of these results were obtained on genetically modified RCs – a system for mutagenesis of the *Rb. sphaeroides* RC was developed and extensively used in the Feher laboratory (M. Paddock et al., *FEBS Lett.*, 2003).

George Feher has been a pioneer not only in the development of EPR and ENDOR techniques but also in biological electron and proton transfer, the understanding of membrane proteins and the primary processes of bacterial photosynthesis – radiating into many other fields of biophysics. He recognized early on that a single technique can rarely solve a complex problem in biology and started to develop and employ numerous methods appropriate to solve the relevant questions in his laboratory. He was also convinced that it is necessary to produce all samples wherever possible in your own laboratory, which required a massive but worthwhile effort moving into different fields of microbiology, molecular biology and biochemistry. To work in such an environment was a great challenge for all his students and postdocs – but the benefits were enormous. I personally owe George a lot for the opportunity to work and learn in such an interdisciplinary environment, which was crucial for my later career.

George Feher was honored by many prizes and awards that are too numerous to be all mentioned here. In particular for his development of EPR and the invention of ENDOR he received the Zavoisky Award, the Bruker Prize, the Gold Medal of the International EPR Society (IES), and became Fellow of the IES and of the International Society of Magnetic Resonance, ISMAR. He has been a member of the National Academy of Sciences, USA, the American Academy of Arts and Sciences and the American Association for the Advancement of Science. All his life George retained an intimate relationship with Israel and often went to visit friends and family and served on several committees. His original idea to return to Israel was abandoned already quite early – but he never made peace with not living in Israel. His 70th birthday was celebrated at the Hebrew University of Jerusalem, the university from which he also received an honorary doctorate in 1994. In 2006 he was awarded the prestigious Wolf Prize at the Knesset in Jerusalem together with Ada Yonath for his life achievements.

Since his early childhood George Feher loved tinkering and later continued to do things with his own hands. At UCSD he kept a small laboratory – that nobody was allowed to enter – where he performed experiments, often off the beaten path, which led to new ideas and the development of novel techniques, e.g. "fluctuation spectroscopy" (G. Feher and M. Weissman, *PNAS* 1973; M. Weissman et al., *PNAS* 1976). Discussions with his students and postdocs about problems and scientific progress in the lab were on his daily agenda. In the department he successfully avoided committee work and found more time to plan new experiments, write successful grants and excellent publications. Many of his papers became citation classics – not only for their scientific content but also for the excellent and clear style of writing. Many of his students profited a lot from his insistence of good writing and to explain the results as simple as possible (but not simpler).

In his private life George Feher was a great sportsman. Since his childhood he liked swimming and even was member of a swimming club in Bratislava. In discussions he vividly remembered the 1936 Olympics in Berlin and the film about it by Leni Riefenstahl, but this event happened at a place that became the center of evil for many Jews. During his whole life George was haunted by the holocaust that affected his family and many of his friends. He wrote a book about it during the last years of his life – that was never published – with fairly dark and negative conclusions about the human nature.

During later years he often visited the UCSD swimming pool together with me providing ample opportunities for scientific and personal exchange afterwards in the sauna or Jacuzzi. Until recent years he was still playing tennis with his colleagues and friends in La Jolla. Dating back to his time as a student in Berkeley, he developed a passion for poker playing – and actually became a dedicated world class poker player who even participated in the world championships in Las Vegas. He also regularly played poker with colleagues at UCSD – and usually won. He had a wonderful sense of humor and was a great story teller – many of the best jokes I know came from him. His "after dinner speeches" are legend – some have even been published, e.g. in the Proceedings of the three Symposia on Photosynthetic Reaction Centers in Cadarache, France, 1987, 1992 and 1997 ("Light Reflections I, II, III").

George is leaving behind his wife Elsa and his two daughters Shoshanah and Paola and three grandchildren. We have lost an outstanding scientist, a great person and a dear friend. With his family we share the mourning for him. George will be sorely missed; he will remain on our memory!

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