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HISTORY & BIOGRAPHY

The life story of Albert W. Frenkel (1919–2015): a pioneer in photosynthesis research

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Abstract

In this historical perspective, we focus on selected discoveries that Albert Frenkel (1919–2015) made all by himself – single-handedly – which is the discovery of photophosphorylation and NAD reduction in anoxygenic photosynthetic bacteria. Then, we present various aspects of his research life through his unpublished letters with some key scientists in his research field. To give a glimpse of his personal life, we have also provided some photographs.

Keywords: Daniel Arnon; Margareta and Herrick Baltscheffsky; Allan H. Brown; Marie Curie; Robert Emerson; Hans Gaffron; Florence Hellman; Martin Kamen; Fritz Lipmann; Jack Myers; Josephine E. Tilden.

"It seems that the only thing in life which proceeds in linear fashion is time. Everything else seems to move in circles, up and down, or in zig-zags. But I am fortunate that I have friends and family to enjoy."

Albert W. Frenkel (1993)

Introduction

The personal life and research of Albert (Al) W. Frenkel (1919–2015), earlier known as Wolfgang Hans Albert Frenkel, was first described beautifully by Frenkel (1993) himself, and then, by two of us, the authors of this tribute (Govindjee and Frenkel 2015a,b).

Albert Frenkel was born in a German banking family. To carry forth Al Frenkel's personal life, upfront, we show three photographs. Fig. 1 is of Albert Frenkel when he was 12 years old; Fig. 2 shows him in the US Army during World War II; and Fig. 3 shows him at a picnic with a few friends.

Research

In his research, Albert Frenkel focused on anoxygenic photosynthetic bacteria. In contrast to cyanobacteria, algae, and plants, anoxygenic photosynthetic bacteria do not oxidize water to molecular oxygen, but instead, they use different hydrogen donors to fix CO_2 to carbohydrates. Some have Photosystem I-like reactions, whereas others have Photosystem II-like reactions except for the absence of water oxidation (Blankenship 2021). However, all photosynthetic organisms undertake photophosphorylation, *i.e.*, they produce ATP from ADP and Pi in light (Blankenship 2021). In this tribute, we emphasize the work of Albert Frenkel (Frenkel 1954, 1956) for his singular discovery of this phenomenon in anoxygenic photosynthetic bacteria, as well as for his

Highlights

- A. Frenkel discovered photophosphorylation in anoxygenic photosynthetic bacteria
- He was the first to measure NAD reduction in anoxygenic photosynthetic bacteria
- He interacted wonderfully with Robert Emerson, Martin Kamen, and Fritz Lipmann

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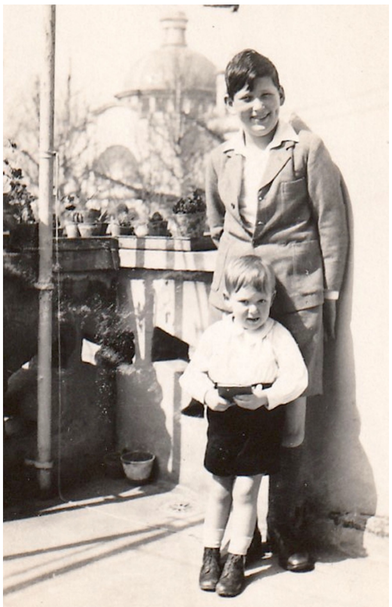

Fig. 1. Albert Frenkel (as a 12–13-year-old boy) with his younger cousin in Milan, Italy, when visiting his aunt's family at the time of his parent's 25th wedding anniversary (~1931). Source: S. Frenkel. From family archives.

Fig. 2. A photograph of Albert Frenkel, during World War II (1944), while serving in the United States Army; at that time, he was associated with the University of Rochester, and his work was related to what was known as the Manhattan Project (led by J. Robert Oppenheimer). Source: S. Frenkel. From family archives.

very first experiments on the reduction of **N**icotinamide **A**denine **D**inucleotide, NAD (then called DPN, **D**iphospho-**P**yridine **N**ucleotide) in these organisms (Frenkel 1958). *See* Appendix 1 for the skepticism of this finding by Martin Kamen. Besides research, Albert was very friendly with his colleagues in the department (*see* Fig. 4). In addition, he was a great family man. Fig. 5 shows him with his wife, Goldie, in the back of their home.

After reminding ourselves a bit about his academic life (*see* below), we will go back in time and emphasize his 1954 discovery of photophosphorylation in anoxygenic photosynthetic bacteria, as well as his 1958 observation of the photoreduction of NAD. We note that before these major discoveries, Frenkel was involved, again, by himself, in one of the very first measurements of carbon fixation in plants (Frenkel 1941), and in showing hydrogen evolution by the green alga *Chlamydomonas* (Frenkel 1952), but we do not discuss them further.

The academic life of Albert Frenkel, and others he met and interacted with

Albert Frenkel was educated in Germany and Switzerland before he immigrated to the USA in 1937. He obtained his Bachelor's (BA; Phi Beta Kappa) and his doctorate (PhD; 'Studies in the enzyme systems in photosynthesis by means of radioactive tracers, carbon monoxide, and ultra-violet light'), at the University of California, Berkeley, in 1939 and 1942, respectively. His PhD was in Plant Physiology, in the Department of Botany, but the work was done under Martin Kamen while working in the world-famous Ernest Lawrence Radiation (Rad) Laboratory (https://en.wikipedia.org/wiki/Lawrence_Berkeley_National_Laboratory).

Fig. 3. A 1949 photograph of Goldie Frenkel (*extreme left*, *top row*) next to Albert Frenkel at a picnic, with friends from the Department of Botany of the University of Minnesota. Source: S. Frenkel. From family archives.

Chronologically, Frenkel's earliest interest in photosynthesis began when he was an undergraduate student at UC Berkeley. He saw flasks with green material being illuminated in Sam Ruben's laboratory, a chemistry

Fig. 4. A 1974 group photograph: Albert Frenkel (who had served as the Head of the Department of Botany at the University of Minneapolis from 1971–1975) is first on the left; the person with the beard is Doug Pratt. We note that administration work was not 'Albert's cup of tea', which was taken over by Ernst Abbe (shown above with a cane) who did it wonderfully well. Source: S. Frenkel. From family archives.

Fig. 5. A 1977 photograph of Albert and Goldie Frenkel in the backyard of their home in Minneapolis, Minnesota. Source: S. Frenkel. From family archives.

instructor at UC Berkeley. For Ruben (1913–1943; born as Charles Rubenstein) *see* Gest (2004). It was during this time that he became acquainted with leaders such as Martin Kamen (1913–2002; Govindjee and Blankenship 2021), and Cornelis (Kees) van Niel (1897–1985; Barker and Hungate 1990). Interestingly, it was during these undergrad days that he had read what Fritz Lipmann (1899–1986; *see* Lipmann 1984, Kresge *et al.* 2005) had written on 'phosphate bond energy' (important for his later work on 'photophosphorylation') as well as what Kees van Niel had written on photosynthesis. This also was the beginning of his friendship with van Niel. In addition, it was at UC Berkeley, that Albert Frenkel met many others including Melvin Calvin (1911–1997; Govindjee *et al.* 2020), Don DeVault (1915–1990; DeVault 1989, Seibert 1991), Andrew A. Benson (1917–2015; Buchanan *et al.* 2016, Nonomura *et al.* 2017), and Sam Aronoff (1915–2010; Govindjee 2010).

Soon thereafter, Albert Frenkel went to California Institute of Technology (Cal Tech) and worked with Robert Emerson (1903–1959; *see* Rabinowitch 1961), from whom he learned how to culture cyanobacteria and measure photosynthesis, as well as how to cultivate the desert rubber plant, guayule (a project of Emerson during World War II). This was followed by being inducted into the US Army and working on the uranium complex and yeast at Rochester, New York (*see* Rothstein *et al.* 1948, and Fig. 2, shown above). Already in 1946, Frenkel was introduced to C. Stacy French (1907–1995; *see* Govindjee and Fork 2006), who was then at the University of Minnesota at Minneapolis.

In 1947, Albert Frenkel was hired as an Assistant Professor in Botany at the University of Minnesota at Minneapolis, and in 1948, he worked with Hans Gaffron (1902–1979; *see* Homann 2003) at Woods Hole, Massachusetts, showing photoreduction of CO_2 with molecular H_2 in algae (Frenkel *et al.* 1950); follow-up studies were published from the University of Minnesota (Frenkel 1952, Frenkel and Lewin 1954).

In addition to the above interactions, we would also like to add Allan H. Brown (1907–2004; *see* Brown and Frenkel 1953, Black and Mayne 2006), who had been chairman of Botany at the University of Minnesota (1957–1960). Albert had great respect for his work and the two discussed regularly the problem of photosynthesis, especially the biological role of oxygen in terrestrial life. Last-but-not-the least was another senior scientist: Josephine Elizabeth Tilden (1869–1957; https://en.wikipedia.org/wiki/Josephine_Tilden) who was an expert on Pacific algae. We note that she was the first woman scientist employed by the University of Minnesota, and Albert had great respect for her work.

1954–1955: Discovery of photophosphorylation in *Rhodospirillum rubrum*

It was during his sabbatical from Minnesota that Albert Frenkel went to Fritz Lipmann's Laboratory, right after Lipmann was awarded the Nobel Prize. It was there that Frenkel (1954) discovered light-induced phosphorylation by cell-free preparations of *Rhodospirillum rubrum*, an anoxygenic photosynthetic bacterium. However, the first detailed research of Al Frenkel on photophosphorylation in this anoxygenic photosynthetic bacterium was presented orally on 28 July 1955, at the Gordon Conference on Agricultural Biochemistry held in Meriden, New Hampshire. The detailed paper on this research by Frenkel (1956) was received by the *Journal of Biological Chemistry* on 17 February 1956. For this research, Frenkel had grown cells of strain S-1 of *R. rubrum*, which was provided to him by Kees van Niel. From these cells, he prepared cell-free extracts and measured phosphorylation under anaerobic conditions, in light, by several methods, both indirect and direct: (*1*) uptake of CO_2 in the bicarbonate-CO_2 system (indirect); (*2*) uptake of Pi; (*3*) increase in acid-labile phosphate; and (*4*) analysis of ATP from the deproteinized mixture, by the method of Fiske and Subbarow (1925). Frenkel had learned not to sonicate his cells, as that clearly led to the loss of phosphorylation. Using 10 μM ADP, 10 μM Pi was shown to be esterified. Further, Mg^{2+} was clearly shown to increase the phosphorylation activity in the above-mentioned paper. However, Frenkel (1954), as noted above, wrote the first paper on 'photophosphorylation' in anoxygenic photosynthesis, as it was published in the *Journal of American Chemical Society*, ~750 pages ahead of the discovery of photophosphorylation in oxygenic photosynthesis by Arnon *et al.* (1954). The rest is history.

1958–1959: Photoreduction of NAD (DPN) by chromatophores from *Rhodospirillum rubrum*

For any organism to be autotrophic, not only ATP is needed, but also reducing power for carbon fixation (Blankenship 2021). It was Albert Frenkel (1958, 1959a) who showed that in *R. rubrum* chromatophores, suspended in glycine-glycine buffer, at pH 7.5, NAD is reduced in light with reduced flavin mononucleotide ($FMNH_2$), and more so, with succinate present.

Frenkel (1958) clearly stated: "*Thus, the simultaneous stoichiometric reduction of DPN and oxidation of $FMNH_2$ in the light represent a reaction in bacterial preparations analogous to the Hill reaction of illuminated chloroplasts.*"

Historically, it is important to point out that Leo Vernon (1958) had independently reported, by adding a plethora of enzymes, the reduction of NADP in *R. rubrum*; to our knowledge, this has not been examined further by others. Soon thereafter, Frenkel (1959b) was invited to write a crucial review of the entire process.

Now, two stories about the above discoveries.

Two stories of serendipity that led Albert Frenkel to go to work with Fritz Lipmann

1. Not getting a Guggenheim fellowship

The first one has to do with not getting a Guggenheim fellowship for work on a different project. It had to do with Frenkel having his sabbatical leave from the University of Minnesota during 1953–1954, and when he was applying for a Guggenheim fellowship to study comparative physiology of photosynthesis (not for 'photophosphorylation'). From information one of us (Govindjee) has from Albert Frenkel: Hans Gaffron (1902–1979; *see* Homann 2003) was consulted by the Fellowship committee and seems to have told Al Frenkel to continue his 'experimental work in the field of photosynthesis'. Indeed, Frenkel did not get the fellowship and wrote a personal note to himself: "*(Gaffron) had informed me of this opinion. I appreciated his honesty and at the time I did not realize that he had done me a favor (I have often thought of writing to the Guggenheim Foundation to thank them for not awarding a fellowship to me)*." It is obvious that if Frenkel had received this fellowship, photophosphorylation experiments would not have been done!

2. Turning down the offer from C.B. van Niel

The second one has to do with Cornelis (Kees) B. van Niel, in whose laboratory at the Hopkins Marine Station, Pacific Grove, California, Frenkel had spent much time, about which he wrote: "*The visits with van Niel and (Lawrence) Blinks were most enjoyable and informative. In fact, van Niel asked me to stay at the Marine Station and do research there. This was tempting and it would have been a valuable experience. However, I had to tell Kees that I had made a commitment to Fritz Lipmann. Van Niel did not seem to be too happy about this. However, nobody at (UC) Berkeley had asked me to stay*." The offer by van Niel was much appreciated by Frenkel, but his commitment to work in Fritz Lipmann's Laboratory won out!

Thus, Frenkel went to Fritz Lipmann (1899–1986; 1953 Nobel laureate in Physiology or Medicine) to do the experiments he wanted to do and was encouraged by Hans Gaffron. He went to Boston, Cambridge, and Revere Beach, where he found the accommodation to stay. During this stay, Frenkel even got sick. Frenkel wrote: "*but Fritz Lipmann was kind enough to activate some young Residents who helped to get me back on my feet. Lipmann also tried to find some financial support for me, but we were not successful; nevertheless, my wife Goldie, our little daughter Susanna and I managed all right. During our stay Bob (Robert) Emerson and family stopped over on there was (way) to (Robin) Hill's(?) lab in Cambridge and we saw them off at their ship.*"

For the sake of 'History of Photosynthesis and its key Discoverers', the above short story on this very personal and wonderful scientist Albert Frenkel – our senior, and the one we admire even today, is very appropriate for the beginners in the field. We will end these stories on the history and biography of Albert Frenkel with the reminiscence of S. Frenkel followed by what Martin Kamen wrote about his work (in Appendix 1). Before we do that, we show in Fig. 6, a group photograph at the Lippman Symposium in Japan, taken in 1988 (as we already know, Lippman was the scientist in whose Laboratory Albert had discovered 'photophosphorylation' in anoxygenic photosynthetic bacteria), and in Fig. 7, a 1996 photograph of Albert Frenkel speaking at a dedication of the Frenkel Reading Room.

Fig. 6. A group photograph at the 1988 Fritz Lippman Memorial Symposium, Japan. Albert Frenkel is in the top row, second on the right. Source: S. Frenkel. From family archives.

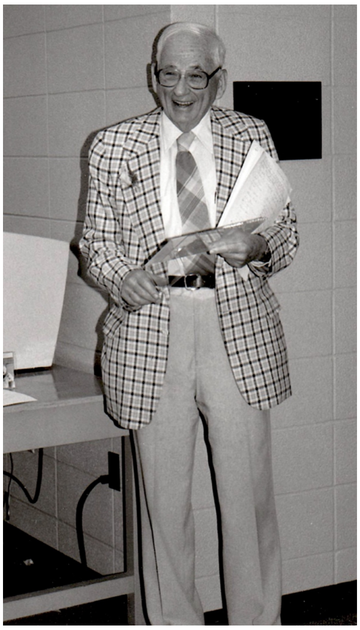

Fig. 7. A 1996 photograph of Albert Frenkel speaking at the dedication of the Albert W. Frenkel Reading Room in the Biological Sciences Building, St. Paul Campus, University of Minnesota. Here, he spoke about his time with Martin Kamen and Sam Ruben (discoverers of carbon-14) while he was at the Radiation Laboratory, University of California, Berkeley. (Note that this room was later changed to be a 'Computer' room.) Source: S. Frenkel. From family archives.

It was during 1988, that Al Frenkel had taken retirement from his Faculty position in Minnesota, yet he continued to remain in contact with one of us (Govindjee) writing and discussing the work of those leaders that both knew quite well, which included Robert Emerson, Hans Gaffron, and Martin Kamen.

We end this Tribute with a personal reminiscence of one of us, the daughter of Albert Frenkel.

Reminiscences of Susanna Frenkel

There was Florence (Jacoby) Hellman (1877–1959) who took my Dad under her wing when he arrived in San Francisco in 1937. When Dad applied to UC Berkeley as a foreign student (our family had emigrated from Germany), he had to go to some little building on the UC Berkeley campus to write an essay to show he was proficient in English! Dad told me that Florence drove him over in her limo along with a couple of her friends. Dad wrote his essay on the Nobel laureate Marie Salomea Sklodowska-Curie (1867–1934). (Interestingly, his later educational and professional life was influenced by radioactivity.) He had just read the new biography of Marie Curie on his train ride from New York City to San Francisco. Although Dad was accepted into UC Berkeley on his merit (receiving two years of college credit for his German Gymnasium education), Florence wanted to be sure that he was accepted! Thus, she suggested that he write the essay. We also know that it was Florence who later gave Dad the money to buy his Gold Phi Beta Kappa key, which is still there, in our family archives.

I would also like everyone to know that Dad's official name on both his bachelor's and doctoral certificates was "*Wolfgang Albert Frenkel; Country: Germany*". It was only in 1944 that he became a citizen of the USA when he was drafted into the US Army.

One personal story – I remember Jack E. Myers (1913–2006) who had done his PhD at the University of Minneapolis, in 1939, visiting our home in Minneapolis. I was impressed to meet him because he wrote articles for the children's Highlights Magazine that I had a subscription to. He was a well-known 'photosynthetiker' (a term he had coined for others doing research in photosynthesis).

Concluding remarks

We now present concluding remarks, basically in Albert Frenkel's own words, since he had said it in the best possible way. The two of us are fortunate to present the above short story on this very personal and wonderful scientist. We both admire Albert Frenkel for the person he was.

Frenkel wrote: "*All I can say is that in 1953, I had a vague notion of learning something about techniques of studying phosphate metabolism. The direction by indirection came from (Fritz) Lipmann and his lab. Later, I heard through the grapevine that Britton Chance (1913–2003) was suspicious (of my 1954 results) and he put Margareta (Yolanda) Baltscheffsky (1932–2009) to work to see if she could repeat my observations. Both she and her husband (Herrick) later published extensively in this area and made many interesting contributions*" (*see e.g.*, Baltscheffsky *et al*. 1966).

We end with a quote that we started this paper with: "So it seems that the only thing in life which proceeds in linear fashion is time. Everything else seems to move in circles, up and down, or in zig-zags. But I am fortunate that I have friends and family to enjoy."

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Appendix 1. Martin D. Kamen wrote (*see* Kamen 1985; p. 267) (italics and bold are by S.F. and G.G.)

Around this time, I received a letter from Albert Frenkel. Albert had worked with Sam Ruben and me back in Berkeley, where he had been a graduate student in plant physiology and had published an article with us on metal exchanges in plant material. He had since taken an appointment in the Middle (Mid) West and now wrote that when he did the simple experiment incubating chromatophores from *R. rubrum* with ADP and inorganic phosphate, he found a vigorous production of ATP when they were illuminated. *I reacted just as all the experts had to us in the past when we had described our results on photoproduction of hydrogen and nitrogen fixation, or the existence of cytochrome c*. Like (C.B.) van Niel, Wilson, and Elsden, I was expertly skeptical and wrote back to Albert that he had probably had some oxygen present in his preparations, *so that what he was seeing was a light stimulation of the ordinary kind of phosphorylation, such as occurred in mitochondria*. Albert replied that he had checked this point and found there was no uptake of oxygen during the light-induced synthesis of ATP in chromatophores. In fact, he could set an upper limit of less than one mole of oxygen used for every ninety or a hundred moles of ATP made. The energy needed to make so much ATP was thousands of times greater than might be available from the minimal amounts of oxygen reduction that I had suggested might be occurring. **This result decisively established that he was seeing the predicted phosphorylation induced by light (subsequently to be called 'photophosphorylation').**

Later, I learned that Albert had been set on the track leading to his discovery of bacterial photophosphorylation by Fritz Lipmann, in whose laboratory he was doing postdoctoral research. Lipmann told me he had suggested to Albert that he repeat some of the experiments Leo (Vernon) and I (Kamen) had reported, remarking something to the effect that "whatever Kamen is doing always has some importance". Essentially (almost) simultaneously with the discovery of photophosphorylation in chromatophores by Frenkel came the announcement of the same process in green plant chloroplasts. Daniel Arnon, working with a young English researcher, F.R. Whatley, and none other than Mary Belle Allen in Berkeley, had done the simple experiment with chloroplasts. And so the basic mechanism of energy transduction in photosynthesis – anaerobic photophosphorylation – was established. I had missed finding it by failing to remember that "**it is best to do the experiment first and think later**".