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HISTORY AND BIOGRAPHY

Martin David Kamen (1913–2002): discoverer of carbon 14, and of new cytochromes in photosynthetic bacteria

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Abstract
Martin Kamen was a giant of twentieth century science. Trained as a physical chemist, he was the co-discoverer of radioactive Carbon 14, which has transformed many areas of science as a tracer and as a way to date artifacts. He later switched to the study of metabolism and biochemistry and made important contributions to the understanding of nitrogen fixation and photosynthesis. Finally, he studied cytochromes, primarily from anoxygenic photosynthetic bacteria.

Keywords Carbon 14 · Cytochrome · Isotope · Cyclotron · Photosynthetic bacteria

Introduction

We celebrate here the life and work of Martin David Kamen (August 27, 1913–August 31, 2002). Many of us fondly remember him as a brilliant, engaging, friendly, cheerful person. He had a wide range of talents and a spark of originality, and was always ahead of his time. His talents as a musician (top viola player and child prodigy in music), a writer (par excellence), and a topmost scientist are known to many of us. We are aware that often great discoveries are made by scientists when they are young. Albert Einstein announced his 'Theory of Relativity' when he was 26, and Kamen discovered Carbon 14 (^{14}C) when he was 27. We first discuss his *Early Life* and then provide an overview of his highly significant discoveries, as well his personal life, as the two are intertwined. (a) The *Cyclotron era* (1939–1944): water, not CO_2, is the source of oxygen in photosynthesis; and the most profound discovery of producing the long-lived ^{14}C; this period was followed by a difficult period for Martin since he was fired from his job at the cyclotron (see later for explanation); (b) *The Metabolism era* (1948–1950): discovery of the photoreduction of molecular hydrogen, as well as the existence of nitrogenase in photosynthetic bacteria; and even a stint on the role of calcium in cancer in mice; and, (c) *The Biochemistry era* (1950–1993): the longest era concerned with the existence, and the biochemical and biophysical properties of new heme proteins, including the many cytochromes in photosynthetic bacteria. However, his entire life was *the Philosophical era:* It started when he was a child until he passed away; he talked freely with everyone that he met, and later wrote about his discoveries and his life.

We refer the readers to Kamen (1963a, 1965) for his ^{14}C work; Kamen (1963b) for the steps in photosynthesis, especially with the concept of pts (negative log of time) scale; Kamen (1978) for the history of ancient proteins; Kamen (1985) about his entire scientific life; and Kamen (1986) and Kamen (1989) for excellent and thoughtful descriptions of his life. Although all of Kamen's research has been outstanding and deep, many think that he deserved the Nobel Prize for his discovery of ^{14}C, first described in 1940, with Samuel (Sam) Ruben (1913–1943): a discovery that led to a Nobel Prize in 1960 to Willard Libby (1908–1980) and another in 1961 to Melvin Calvin (1911–1997).

Early life

Menachem Nathan Kamenetsky (Martin David Kamen) was born on August 27, 1913, to Aaron (later Harry) and Goldie (Achber) Kamenetsky (later Kamen) in Toronto,

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Ontario, where his mother had gone from Chicago to visit relatives. The family returned to Chicago (Illinois) and thus Martin grew up in Chicago. As a child, he was a voracious reader and read, at the age of 8, Tolstoy's *War and Peace*. He had a photographic memory, and he could commit, to memory, entire pages of whatever he read for instant recall! He attended Hyde Park High School, graduating in 1930.

In his youth, he was interested primarily in music; he was really a child prodigy. When he was only a 9-year-old boy, he was already giving full-fledged concerts in the Greater Chicago area, playing violin, his first love. However, he later began to play viola, and that too in the company of the World-famous violinist Isaac Stern (1920–2001; http://en.wikipedia.org/wiki/Isaac_Stern).

As a student, Martin excelled in anything he studied. He entered the University of Chicago in 1930; he first took almost all the available courses in mathematics, and then opted for English (taught under Humanities), but switched quickly to chemistry, obtaining a BS (cum laude) in 1933 with a focus on physical chemistry. He then did graduate work in nuclear chemistry at the same university, receiving, just 3 years after his BS, his doctorate (PhD) in 1936 under William Draper Harkins. Martin's thesis was on "*Neutron Scattering*"; his very first research paper was on "scattering of protons" (see Harkins et al 1935). The exciting drama involved in his PhD Prelims is described in Kamen (1985).

We end this section by mentioning that Martin had a cheerful and friendly personality then and even later, as mentioned by everyone we have talked with, and as known to one of us (Gov) who had met him many times. See Fig. 1 for a portrait of Martin Kamen.

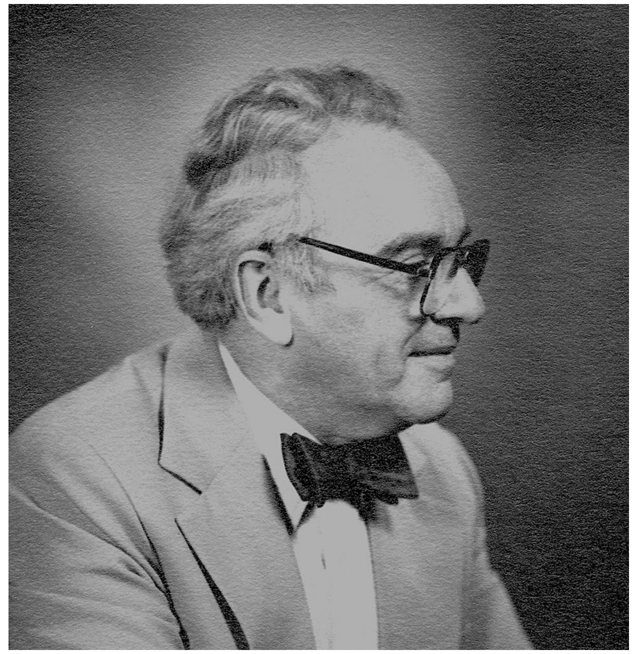

Fig. 1 Martin Kamen (Kamen 1989; photo provided by Martin Kamen to Govindjee)

Research and more

The cyclotron era (1939–1944)

On the path of carbon in photosynthesis: carbon 11 experiments and the discovery of carbon 14

In 1937, right after his PhD, Martin went to work with Ernest O. Lawrence for postdoctoral research at the Radiation Laboratory of the University of California, Berkeley (UC Berkeley). It was there that his fascination with photosynthesis began, and he, with the help of his close colleague Sam Ruben and others, used Carbon 11 (^{11}C), which has a half-life of 21 min (Ruben et al 1939; Kamen 1985).

Although the cyclotron could make a lot of that isotope, it was a frustrating experience because ^{11}C disappeared so quickly. This led to many creative methods to work quickly, including at one point the suggestion to use carrier pigeons to deliver the isotope to a remote laboratory (Kamen 1985). This gave Martin an incentive to work almost day and night to make long-lived ^{14}C. Together with Sam Ruben, he achieved this goal in 1940 (Kamen and Ruben 1940; Ruben and Kamen 1940; Kamen 1963a, 1965). On the day they first made ^{14}C, Kamen was returning home in the early hours wearing a dirty lab coat and with messy hair; at that time, he had an unfortunate encounter with the police, who were looking for a runaway murderer. He had to spend the night in jail and was released the next morning when UC Berkeley vouched for him.

The lifetime of ^{14}C was initially estimated to be 1000–2700 years (it is actually 5730 years). During 1940–1943, there was great excitement as Kamen was making huge quantities of ^{14}C for use in biology and chemistry (working for the Manhattan Project). However, Kamen was unable to reap its benefits, although this discovery was his most important single contribution to science. Edwin M. McMillan (1907–1991); see McMillan (1985), 1951 Nobel laureate in Chemistry, wrote: "It was Kamen who had the spark of originality and the initiative to propose lines of attack, and [it was] Kamen with whom one had the stimulating discussions." Fig. 2 shows Kamen at work at the Lawrence Berkeley Laboratory.

As mentioned above, use of ^{14}C has led not only to the discovery of the path of carbon fixation in photosynthesis by the Calvin–Benson cycle (1961 Nobel Prize to Melvin Calvin; see Benson 2002), but also to a revolution in archeology in dating materials of ancient times up to about 50,000 years old (Arnold and Libby 1949), which led to the 1960 Nobel Prize to Willard Libby.

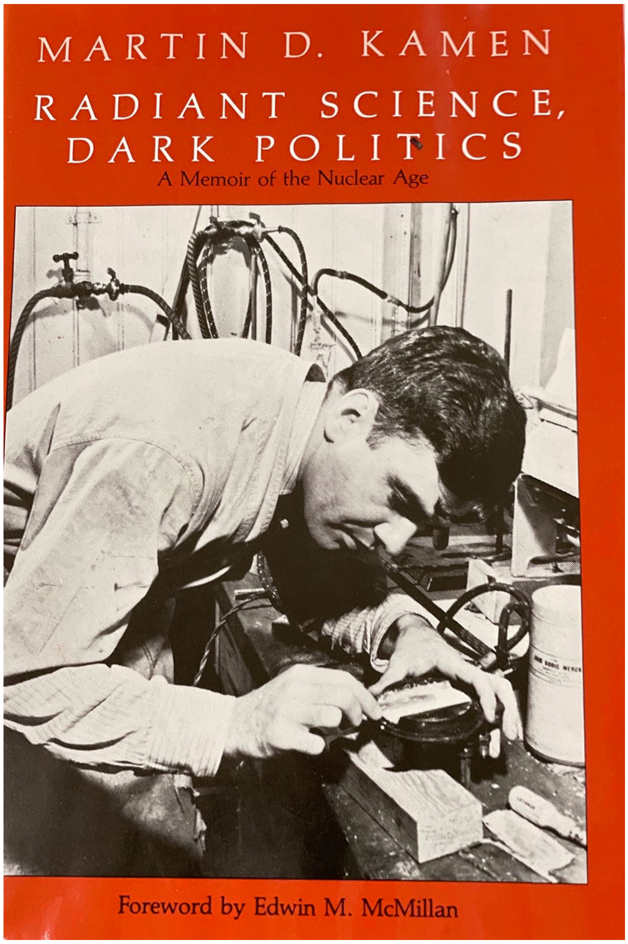

Fig. 2 Martin Kamen at work at Lawrence Berkeley Laboratory in the 1940s. This is the cover of his book *Radiant Science, Dark Politics*, published by the University of California Press in 1985

Oxygen comes from H_2O, not CO_2

Further, during this period, a very important experiment using oxygen 18 water proved that the oxygen evolved in photosynthesis came from water, not CO_2 (Ruben et al 1941). This discovery challenged the earlier views of Nobel laureates Richard Martin Wilstätter (1872–1942; https://www.nobelprize.org/prizes/chemistry/1915/summary/) and Otto Warburg (1883–1970; https://www.nobelprize.org/prizes/medicine/1931/warburg/facts/), who had said that O_2 came from CO_2, not H_2O. The concept that oxygen came from water has been supported by many experiments.

Kamen's difficult period; personal difficulties and his recovery

The years that followed the above research period were a difficult period for Martin, perhaps caused by his passion for music, and his habit of freely communicating with anyone without any hesitation. He was part of a circle of highly talented musicians in the Bay Area, which led him to meet a member of the Soviet Consulate to talk about music (but most likely about a possible cure for leukemia, needed by a close relative of a member of the consulate), which was at a dinner given by the violinist Isaac Stern. Yes, the Soviets were our allies, but not for nuclear weapons. We speculate that perhaps the exchange of music notes (but most probably information on the possible cure of leukemia) between the two was mistaken by FBI agents sitting close by as the passing of atomic secrets. One thought is that Martin, being a brilliant thinker, had earlier interpreted some results of a colleague at Oak Ridge as if his sample had been exposed to a radiation source. Existence of such a facility at Oak Ridge was then a secret, and the colleague was investigated for leaking information. It is considered highly likely that the FBI was already watching him. See below for details.

Kamen was immediately fired from the Lawrence Lab at UC Berkeley, with no notice or chance of appeal or hearing. Roth (2004) describes the day: "It was in 1944, when he had been declared a security risk and was being fired. He was told that the government suspected someone of leaking information about "fusion" and the development of the atomic bomb to him, information which he was not entitled to know, and also that he had met with two officials from the Soviet Consulate in San Francisco and had handed them certain papers". It seems, from Roth's account, that Martin had told many that he had himself deduced the idea of "fusion" from his own analysis of available data, and that it were the Soviet diplomats (Gregory Kheifetz and Gregory Kasparov), who had approached him, at a party, to know about a "product" that could be helpful to a friend of one of the diplomats, who was suffering from leukemia (see above); it seems that it was this information that was passed when Martin was invited to dinner at Bernstein's Fish Grotto in San Francisco.

After this, Kamen could not get any academic job and finally ended up working as an inspector in a San Francisco shipyard. Indeed, it was a shock–a violent one–for one whose discovery deserved, in the opinion of many, a Nobel Prize. Finally, in 1945 he was offered a faculty position at Washington University in St. Louis, with the unwavering and strong support of the university Chancellor, the Nobel Prize-winning physicist Arthur Holly Compton. Figures 3 and 4 show typical laboratory photos from his lab at Washington University in St. Louis.

The worst period for Martin came in the early 1950s: his passport was canceled, and the *Chicago Tribune* declared, in front-page news, "Kamen, a Traitor." Martin suffered mentally, morally, and monetarily. As far as we know, the events were as follows. He had been invited to a symposium on isotopes in Paris and another symposium in Israel. While a travel agency was preparing his air tickets, U.S. federal agents, acting on orders from the State Department,

Fig. 3 Typical scene in the Kamen laboratory at Washington University in St. Louis. Left to right: Herta Bregoff (graduate student), Martin Kamen, and Stanley Hanson (from Durham University, U.K.), Metabolism Laboratory, Mallinckrodt Institute of Radiology, Washington University Medical Center. (Photo taken in 1950; courtesy of Washington University Photographic Services Collection, Washington University Libraries, Department of Special Collections)

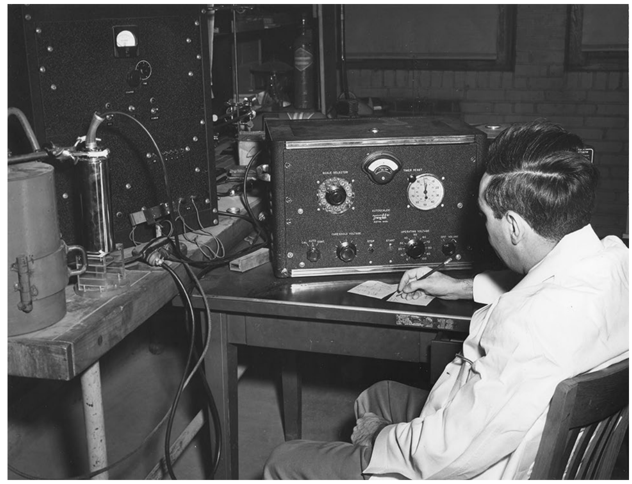

Fig. 4 Martin Kamen (then associate professor of chemistry at Washington University and chemist at the Mallinckrodt Institute) sitting in front of an instrument to record radioactivity from various materials. At the extreme left is a lead-shielded container (~600 lb) in which radioisotopes were delivered from Oak Ridge, Tennessee. Also seen are various types of Geiger counters to record the presence of radioactive materials. (Photo taken in 1950; courtesy of Washington University Photographic Services Collection, Washington University Libraries, Department of Special Collections)

canceled his passport. It was the beginning of the McCarthy Era (https://en.wikipedia.org/wiki/McCarthyism). In addition to the front-page title, the *Chicago Tribune* published, with pictures, unsubstantiated stories on Martin about his passing secret documents to Soviet agents. With time, many individuals and organizations (including the American Civil Liberties Union and the Federation of American Scientists) came forward in his defense and support.

After seven years, the courts ruled in favor of Martin Kamen. It was a day of rejoicing when he had a new passport. Soon thereafter he served exceptionally well at two universities: Brandeis University (1957–1961) and the University of California San Diego, UCSD (1961–1978). During this period, he also served as director of a laboratory in Gif-sur-Yvette, France (1967–1970), and taught at the University of Southern California (1974–1978).

The metabolism era (1945–1950)

At Washington University in St. Louis, Martin was charged with overseeing the university cyclotron. During this period, Martin visited Robert (Bob) Emerson (1903–1959); see e.g., Govindjee (2018) at the University of Illinois at Urbana–Champaign, where he also met Robert (Robin) Hill (1899–1991); https://en.wikipedia.org/wiki/Robin_Hill_(biochemist), who was visiting Emerson's laboratory. Martin came to learn from Bob Emerson how to do specific measurements in photosynthesis (see Fig. 5).

Martin was joined by his first graduate student Howard Gest (1922–2012); see Bauer et al 2012) and the two made

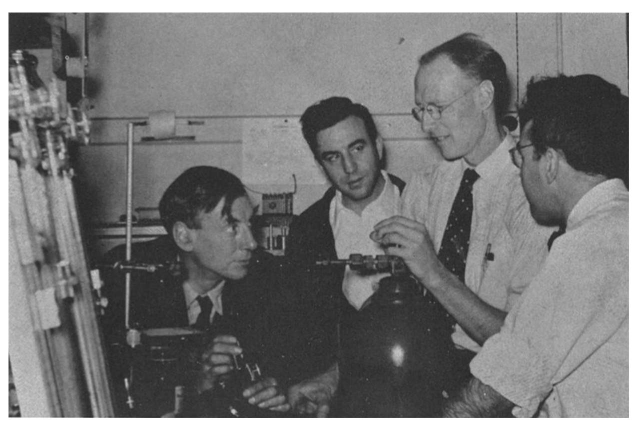

Fig. 5 Martin Kamen (extreme right), Robert (Bob) Emerson, A. Stanley Holt (discoverer of chlorophyll *d* structure), and Robert (Robin) Hill (discoverer of the Hill reaction and cytochrome *f*), visiting Emerson's lab at the University of Illinois. (Photo taken in 1952; from Kamen, 1985, facing p. 213)

two major discoveries: photoproduction of molecular hydrogen by anoxygenic photosynthetic bacteria (Gest and Kamen 1949; Gest et al 1950), and of the ability of a photosynthetic bacterium to fix nitrogen, using its nitrogenase system (Kamen and Gest 1949). These findings led to a new way of looking at the physiological capabilities of anoxygenic photosynthetic bacteria (see Gest et al 1950; Gest 1999; Ludden and Roberts 2002). These discoveries have been pursued by others, and today they are being vigorously studied by many.

Biochemistry era (1950–1993): a tryst with the cytochromes

Meyer and Kamen (1982) wrote: "To allude again to Greek mythology, the extension of studies on cytochromes to prokaryotic systems, after so many years of comparative neglect, seems like the opening of Pandora's box, liberating a horde of creatures strange and wonderful. The effort to isolate and identify the present inchoate mass of prokaryotic *c*-type cytochromes, not to mention those still to be observed, may be likened to putting all these creatures back in the box."

Kamen made major discoveries on haematin compounds, particularly cytochromes in anoxygenic photosynthetic bacteria; this era consumed his scientific acumen in biochemistry, biophysics, and molecular biology of these compounds, for many years beginning from mid 1950s till mid 1990s – almost 5 decades. During this period, several scientists were trained by him, and/or worked with him. This list includes several top scientists in the field, who are also deceased: Richard Penry Ambler (1933–2013; https://www.scotsman.com/news/obituaries/obituary-professor-richard-penry-ambler-ma-phdscientist-2001554); Robert (Bob) G. Bartsch (1922–2019; <https://www.semanticscholar.org/author/Robert-G.-Bartsch/87269753>); Michael (Mike) A. Cussanovich (1940–2010); (Meyer 2011); Takekazu Horio (1928–2003; <https://www.researchgate.net/scientific-contributions/Takekazu-HORIO-67868498>); Francis Raymond Salemme (1945–2020; https://en.everybodywiki.com/Francis_Raymond_Salemme); and Leo P. Vernon (1925–2010; https://www.legacy.com/obituaries/saltlaketribune/obituary.aspx?n=leo-vernon&pid=143464844).

We note that the work by Martin on the discovery of a cytochrome with Leo Vernon (Vernon and Kamen 1954) was very important for understanding the mechanism of bacterial photosynthesis. We provide below, in chronological order, a glimpse of Martin's work on the cytochromes in photosynthetic bacteria.

1950s: The early period

It was Leo Vernon who was the first one to initiate the work on the existence of heme proteins in photosynthetic bacteria (Kamen and Vernon 1954; Vernon and Kamen 1954; reviewed soon thereafter by Kamen 1955). This was followed by comparative studies on all the known cytochromes in bacteria and in mammals (Kamen and Vernon 1955; Kamen and Takeda 1956). Robert Bartsch joined the Kamen Lab and presented detailed data on all the new heme proteins in facultative heterotrophs (Bartsch and Kamen 1958).

1960s and 1970s: a highly prolific period, at university of California San Diego (UCSD)

Bartsch continued digging into the heme proteins, and Kamen's group was joined, in this period by many, including Takekazu Horio, Henk deKlerk (later to work with Martin in France); S. Taniguchi; Q.H. Gibson; Karl Dus; T. Yamanaka; T., Michael Cussanovich; and K. Sletten. During this period, about 20 papers, all on the biochemistry of heme proteins (especially cytochromes) were published in *Biochimica et Biophysica Acta; Journal of Biological Chemistry; Proceedings of the National Academy of Sciences USA*, and in *Biochemistry*. The organisms studied included: *Chromatium* (Bartsch and Kamen 1960; Bartsch et al 1961; Cussanovich and Kamen 1968a; Cusanovich and Kamen 1968b); *Rhodospirillum* (Taniguchi and Kamen 1963, 1965; Dus et al 1968; Sletten et al 1968); *Rhodopseudomonas* (Dus et al 1967; deKlerk et al 1965); and even a diatom *Navicula* (Yamanaka et al 1967). There was a focus on cytochromes of the *c*-type (see e.g., Gibson and Kamen 1966; Yamanaka et al 1967; Bartsch et al 1968; Sletten et al 1968). Further, structural, optical, and redox properties of these (and other) bacterial cytochromes were painstakingly measured by Horio and Kamen (1961), Horio et al (1961), and Ehrenberg and Kamen (1965). All this was followed by a major authoritative review on the structure and function of cytochromes (see Okunuki et al 1968).

Bartsch, Cussanovich, and Horio continued to dig deeper into the understanding of how cytochromes function in photosynthetic bacteria. Kamen's group was joined, in this period by many others, including S.J. Kennel, F.R. Salemme, G.W. Pettigrew, as well as by two highly active scientists R.P. Ambler and T.E. Meyer. Kamen and his team published 20 more research papers on the cytochromes in anoxygenic photosynthetic bacteria, including those in *Nature (London); Biophysical Journal, Archives of Biochemistry and Biophysics,* and *Biochemical and Biophysical Research Communication*. See authoritative reviews by Horio and Kamen (1970), Kamen and Horio (1970) and Kamen (1973) just about the time this period began. Further, the organisms used included, besides various species of *Rhodospirillum* (Dus et al 1970; Flatmark et al 1970; Bartsch et al. 1971; Smith and Kamen 1974), and *Chromatium* (Kennel and Kamen 1971; Kennel et al 1972), used before, *Pseudomonas* sp.

(Cusanovich et al 1970) and *Chlorobium* (Van Beeumen et al 1976). Much deeper understanding of the structure and function of various cytochromes in photosynthetic bacteria was obtained during this period: mostly of cytochromes of *c*-type see e.g., Dus et al 1970; Davis et al 1972; Salemme et al 1973; Errede and Kamen 1978; Ambler et al 1979b), including cytochrome c_2, cc', and even a *b*-type ($b_{557.4}$) (Bartsch et al 1971), cytochrome c' (Kamen et al 1973; Rawlings et al 1977; Ambler et al 1979c), cytochrome c_2 (Smith and Kamen 1974; Pettigrew et al 1975, 1978; Ambler et al 1976, 1979a). It is obvious to us that Martin and his research team dug deeply into the biochemistry and biophysics of cytochromes. His lab was clearly the "*Mecca*" for the structure and function of cytochromes of anoxygenic photosynthetic bacteria.

Kamen's work during the 1980s and the 1990s

Martin Kamen retired in 1978 from UCSD, but continued research on cytochromes, although at a slower pace. He continued to collaborate on cytochromes with R.G. Bartsch, R.P. Ambler and T.E. Meyer during this period. A chronological glimpse of this work follows: Weber et al. (1980) published in Nature (London) structure of cytochrome c', at atomic level showing its dimeric nature. Ambler et al (1981a; 1981b) and Moore et al. (1982) provided new structural and biochemical information on various *c*-type cytochromes (*c*-550; c'; and *c*-556), and of class II cytochromes *c*, respectively. Ambler et al (1993) added two species of halophilic purple bacteria *Ectothiorhodospira* and provided amino acid sequence of their cytochromes *c*. We recommend to all a remarkable perspective on all *c*-type cytochromes by Meyer and Kamen (1982) and the review by Meyer and Cusanovich (2003).

Figure 6 shows a photo of Martin taken shortly before his death. Martin is survived by his son David Kamen and his grandson Alexander Kamen.

Martin Kamen's contribution to teaching photosynthesis

For a concise and complete picture of photosynthesis, àla Kamen, see Martin's elegant book *Primary Processes in Photosynthesis* (Kamen 1963b), in which he used the pts scale for the negative log time (in seconds) of photosynthesis from a femtosecond (pts = 15) to a second (pts = 1). To get a complete and authentic picture of Martin Kamen, his life, and his achievements in chemistry, physics, biology, biochemistry, and medicine, we recommend Kamen's own wonderful descriptions of his life and work (Kamen, 1963a, 1985, 1986, 1989).

Fig. 6 Photograph of Martin Kamen, taken by Howard Gest in 2000

Awards and honors

Kamen received many honorary degrees, including those from the University of Chicago (1969), Sorbonne University, Paris, France (1969), Washington University in St Louis (1977), University of Illinois, Chicago Circle (1978), University of Freiburg (Germany, 1979), Weizmann Institute of Science (Rehovot, Israel, 1987), and Brandeis University (1988).

Kamen's awards include, in chronological order: John Simon Guggenheim Fellow (1956); Fellow of the American Academy of Arts and Sciences (1958); Member, American Philosophical Society (1974); Member of the National Academy of Sciences, USA (1962); Charles F. Kettering Award for Excellence in Photosynthesis (1968); Merck Award of the American Society of Biological Chemists (1982); Albert Einstein World Award of Science, World Cultural Council (1989) and Enrico Fermi Award (1996).

Several articles have been written on Martin's work and life, including a Wikipedia article (https://en.wikipedia.org/wiki/Martin_Kamen); see also, for example, Arnold (2003), Doolittle (2004), and Kauffman (2000, 2002). An outstanding review of a book published in Martin's honor was written by Sable (1983).

Reminiscences

We end this brief memorial to Martin Kamen with selected quotes from others.

Leo Vernon

This is the Martin Kamen I know: kind, gentle, enthusiastic about life, creative, perceptive, and talkative. He has broad knowledge of atomic physics, music, biochemistry, politics, and baseball. He even knows who played first base for the Yankees after Lou Gehrig. (Vernon 1985).

Robert S. Knox (email: rknox@ur.rochester.edu)

I was attending a Gordon Conference on solid state physics in the mid 1960s. Academic Press had a "booth", with their latest books lying on a table. One was Martin Kamen's "*Primary Processes in Photosynthesis*". I was impressed with it–especially some of the problems he brought up that were physics-related. For me Kamen's book was a major reason why I began doing research in the photo-physics of photosynthesis.

Govindjee Govindjee (email: gov@illinois.edu)

I became closely associated with Martin Kamen when he was in Gif-sur- Yvette (France), which resulted in the publication of a paper on the fluorescence characteristics of photosynthetic bacteria of different ages (deKlerk et al 1969); it was a natural collaboration since I was in the business of what fluorescence can tell us about photosynthesis, and Martin was an authority on the biology of anoxygenic photosynthetic bacteria. Besides, we both enjoyed eating "sea food", and Martin knew each and every good restaurant in Paris. He knew each turn in the narrow lanes of Paris to escort us to the best fish restaurant there. Further, my wife Rajni and I enjoyed the wonderful stories he knew about the past "photosynthetikers". My sense of history & biography of the past was served well with our friendship in France. Rajni and I miss him dearly.

David Kamen (email: dkamen5@gmail.com)

Thank you for sending me the text of your tribute to my father. I have read it with pleasure, and greatly appreciate your and your colleagues' dedicated efforts to create a fitting monument to my father's memory and contributions to science. Regarding Fig. 2 (see above): This photo best encapsulates Martin Kamen's personality and dedication to science, at least inasmuch as any single photo can capture an entire lifetime of involvement in that endeavor.

I [refer to] an article jointly authored by Martin and Beka [Doherty] in the *Bulletin of the Atomic Scientists* in 1959, on the need to address, and ultimately to heal, the supposed 'contradiction' between the artistic and the scientific 'sides' of human nature (Kamen and Doherty 1959). It reflects, at the very least, Martin's sensitivity to this contradiction and his interest in resolving it, in the external world and by implication, if I may psychologize, also in the internal one. Devoted to the scientific endeavor as he was, Martin was well aware of the importance of the humanistic side as well, and of the often-dire consequences of its denial (remember that his love of music had been frustrated early on, and that he had lived through depression and war only to arrive at the dawn of what the press referred to as the 'Atomic Age', a time of intense self-examination and re-evaluation culture-wide but especially profound in the sciences).

William Parson (email: parsonb@uw.edu)

Martin Kamen's small book *Primary Processes in Photosynthesis* (Kamen 1963b) was extremely stimulating for many of us who began work in this area in the 1960s. Its influence came back to mind some years later when I reviewed a much weightier compendium with the same name (Parson 1978).

'Softbound, Kamen's book cost only $2.45, but it was a treasure chest of insight and humor. To appreciate the sweep and grandeur of photosynthesis, Kamen said, one must think of time in exponential units, so that the interval of time between, say, 10^{-15} and 10^{-14} second is just as significant as the interval between 1 and 10 seconds. From the absorption of a quantum of light, which takes about 10^{-15} second, to the growth of a field of beans, there are more than 20 orders of magnitude of time—a greater span than the age of the universe measured in years. Kamen argued that the really interesting intervals of time, however, were the ones between 10^{-9} and 10^{-4} second. He called this the era of photochemistry, the time when photosynthetic systems capture the energy of the quantum in the first, fleeting products of a chemical reaction .... As Kamen put it, the photochemical era marked a strong maximum in the spectrum of our ignorance.'

In addition to being an imaginative scientist and a clear and colorful writer, Kamen was a skilled musician with an impressively detailed knowledge of baroque string instruments. Asked why he had set the violin aside in favor of the viola, he modestly explained that people who play the viola are constantly in demand to join string quartets.

Acknowledgements We thank Nancy Winchester for her encouragement and for editing an earlier version of this tribute (Govindjee and Blankenship 2018) to Martin Kamen which is available by writing to one of us (Govindjee) by email (gov@illinois.edu). We thank Rajni Govindjee (for helping us collect information on Kamen's awards and his honorary degrees, and in reading its text before its submission); Teruo Ogawa (for help in locating the Kamen (1973) paper); Arthur Nonomura (for helpful suggestions); and David Kamen (for suggesting the use of the cover photo of Martin's book as Figure 2).

References

Ambler RP, Bartsch RG, Daniel M, Kamen MD, McLellan L, Meyer TE, Van Beeumen J (1981b) Amino acid sequences of bacterial cytochromes *c*' and *c*-556. Proc Natl Acad Sci 78:6854–6857

Ambler RP, Daniel M, Hermoso J, Meyer TE, Bartsch RG, Kamen MD (1979a) Cytochrome c_2 sequence variation among the recognized species of purple non-sulfur photosynthetic bacteria. Nature (london) 278:659–660

Ambler RP, Daniel M, Meyer TE, Bartsch RG, Kamen MD (1979c) The amino acid sequence of cytochrome *c*' from the purple photosynthetic bacterium, *Chromatium vinosum*. Biochem J 177:819–823

Ambler RP, Meyer TE, Kamen MD (1976) Primary structure determination of two cytochromes c_2: close similarity to functionally unrelated mitochondrial cytochrome *c*. Proc Natl Acad Sci 73:472–475

Ambler RP, Meyer TE, Kamen MD (1979b) Anomalies in amino acid sequences of small cytochromes *c* and cytochromes *c* from two species of purple photosynthetic bacteria. Nature (london) 278:661–662

Ambler RP, Meyer TE, Kamen MD, Schichman SA, Sawyer L (1981a) A reassessment of the structure of *Paracoccus* cytochrome *c*-550. J Mol Biol 147:351–356

Ambler RP, Meyer TE, Kamen MD (1993) Amino acid sequences of cytochromes *c*-551 from the halophilic purple phototrophic bacteria *Ectothiorhodospira halophila* and *E. halochloris*. Arch Biochem Biophys 306:83–93

Arnold J (2003) Obituary: Martin David Kamen. Phys Today 56:74–75

Arnold JR, Libby WF (1949) Age determinations by radiocarbon content: checks with samples of known age. Science 110:678–680

Bartsch RG, Coval ML, Kamen MD (1961) The amino acid composition of the soluble *Chromatium* haem proteins. Biochim Biophys Acta 51:241–245

Bartsch RG, Kamen MD (1958) On the new heme protein of facultative photoheterotrophs. J Biol Chem 230:41–63

Bartsch RG, Kamen MD (1960) Isolation and properties of two soluble heme proteins in extracts of the photoanaerobe *Chromatium*. J Biol Chem 235:825–831

Bartsch RG, Meyer TE, Robinson AB (1968) Complex *c*-type cytochromes with bound flavin. In: Okunuki K, Sekuzu I, Kamen MD (eds) Structure and Function of Cytochromes. University of Tokyo Press, Japan, pp 443–451

Bartsch RG, Kakuno T, Horio T, Kamen MD (1971) Preparation and properties of *Rhodospirillum rubrum* cytochromes c_2, *cc*′, and $b_{557.4}$, and flavin mononucleotide protein. J Biol Chem 246:4489–4496

Bauer C, Gest T, Fuqua C (2012) Obituary of Dr Howard Gest. Photosynth Res 112:151–152

Benson AA (2002) Following the path of carbon in photosynthesis: a personal story. Photosynth Res 73:29–49

Cusanovich MA, Kamen MD (1968a) Light-induced electron transport in *Chromatium* strain D I. Isolation and characterization of *Chromatium* chromatophores. Biochim Biophys Acta 153:376–396

Cusanovich MA, Kamen MD (1968b) Light-induced electron transfer in *Chromatium* strain D III. Photophosphorylation by *Chromatium* chromatophores. Biochim Biophys Acta 153:418–426

Cusanovich MA, Tedro SM, Kamen MD (1970) *Pseudomonas denitrificans* cytochrome *cc*′. Arch Biochem Biophys 141:557–570

Davis KA, Hatefi Y, Salemme FR, Kamen MD (1972) Enzymic redox reactions of cytochromes *c*. Biochem Biophys Res Commun 49:1328–1335

deKlerk H, Bartsch RG, Kamen MD (1965) A typical soluble haem proteins from a strain of *Rhodopseudomonas palustris* sp. Biochim Biophys Acta 97:275–280

deKlerk H, Govindjee G, Kamen MD, Lavorel J (1969) Age and fluorescence characteristics in some species of *Athiorhodacea*e. Proc Natl Acad Sci 62:972–978

Doolittle RF (2004) Martin David Kamen. Proc Am Philos Soc 148:499–503

Dus K, deKlerk H, Bartsch RG, Horio T, Kamen MD (1967) On the monoheme nature of cytochrome *c*' (*Rhodopseudomonas palustris*). Proc Natl Acad Sci 57:367–370

Dus K, Flatmark T, deKlerk H, Kamen MD (1970) Comparative study of physiochemical properties of two *c*-type cytochromes of *Rhodosprillum molischianum*. Biochemistry 9:1984–1990

Dus K, Sletten K, Kamen MD (1968) Cytochrome c_2 of *Rhodospirillum rubrum* II. Complete amino acid sequence and phylogenetic relationships. J Biol Chem 243:5507–5518

Ehrenberg A, Kamen MD (1965) Magnetic and optical properties of some bacterial haem proteins. Biochim Biophys Acta 102:333–340

Errede B, Kamen MD (1978) Comparative kinetic studies of cytochromes c in reactions with mitochondrial cytochrome *c* oxidase and reductase. Biochemistry 17:1015–1027

Flatmark T, Dus K, deKlerk H, Kamen MD (1970) Comparative study of physicochemical properties of two *c*-type cytochromes of *Rhodospirillum molischianum*. Biochemistry 9:1991–1996

Gest H (1999) Memoir of a 1949 railway journey with photosynthetic bacteria. Photosynth Res 61:91–96

Gest H, Kamen MD (1949) Photoproduction of molecular hydrogen by *Rhodospirillum rubrum*. Science 109:558–559

Gest H, Kamen MD, Bregoff HM (1950) Studies on the metabolism of photosynthetic bacteria: V. Photoproduction of hydrogen and nitrogen fixation by *Rhodospirillum rubrum*. J Biol Chem 182:153–170

Gibson QH, Kamen MD (1966) Kinetic analysis of the reaction of cytochrome *cc*' with Carbon Monoxide. J Biol Chem 241:1969–1976

Govindjee, (2018) Robert Emerson's 1949 Stephen Hales Prize Lecture: "photosynthesis and the World." Journal of Plant Science Research 34:119–125

Govindjee G, Blankenship RE (2018) Martin D. Kamen, whose discovery of 14-C changed plant biology well as archaeology. available online: Plantae; Historical Perspectives on Plant Science, and at < http://www.life.illinois.edu/govindjee/recent_papers.html>

Harkins WD, Gans DW, Kamen M, Newson HW (1935) The scattering of protons in collisions with neutrons. Phys Rev 47:511–512

Horio T, Kamen MD (1961) Preparation and properties of three pure crystalline bacterial haem proteins. Biochim Biophys Acta 48:266–286

Horio T, Kamen MD, deKlerk H (1961) Relative oxidation-reduction potentials of heme groups in two soluble double-heme proteins. J Biol Chem 236:2783–2787

Horio T, Kamen MD, English E (1962) Optimal oxidation-reduction potentials and endogenous co-factors in bacterial photophosphorylation. Biochemistry 1:144–153

Horio T, Kamen MD (1970) Bacterial cytochromes II functional aspects. Annu Rev Microbiol 24:399–428

Kamen MD (1955) Bacterial Heme Proteins. Bacteriol Rev 19:250–262

Kamen MD (1963a) The early history of carbon-14. Science 140:584–590

Kamen MD (1963b) Primary processes in photosynthesis. Academic Press, New York

Kamen MD (1965) Early history of carbon-14. Adv Tracer Methodol. https://doi.org/10.1007/978-1-4684-8622-3_1

Kamen MD (1973) Toward a comparative biochemistry of the cytochromes. Tanpahshitsu Kukusan Koso 18:753–773

Kamen MD (1978) The natural history of an ancient protein. Proc Am Phil Soc 122:214–221

Kamen MD (1985) Radiant science, dark politics: a memoir of the nuclear age. University of California Press, Berkeley, p 348

Kamen MD (1986) A cupful of luck, a pinch of sagacity. Annu Rev Biochem 55:1–34

Kamen MD (1989) Onward into a fabulous half-century. Photosynth Res 21:139–144

Kamen MD, Doherty B (1959) Some new cliches about an old argument. Bull Atomic Sci 15:89–91

Kamen MD, Gest H (1949) Evidence for a nitrogenase system in the photosynthetic bacterium *Rhodospirillum rubrum*. Science 109:560

Kamen MD, Horio T (1970) Bacterial cytochromes I structural aspects. Annu Rev Biochem 39:673–700

Kamen MD, Kakuno T, Bartsch RG, Hannon S (1973) Spin-state correlations in near infrared spectroscopy of cytochrome *c*′. Proc Natl Acad Sci 70:1851–1854

Kamen MD, Ruben S (1940) Production and properties of carbon 14. Phys Rev 58:194

Kamen MD, Takeda Y (1956) A comparative study of bacterial and mammalian cytochrome *c*. Biochim Biophys Acta 21:518–523

Kamen MD, Vernon LP (1954) Existence of haem compounds in a photosynthetic obligate anaerobe. J Bacteriol 67:617–618

Kamen MD, Vernon LP (1955) Comparative studies on bacterial cytochromes. Biophys Acta 17:10–22

Kauffman GB (2000) Martin D. Kamen: an interview with a nuclear and biochemical pioneer. Chem Educ 5:252–262

Kauffman GB (2002) In memoriam: Martin D. Kamen (1913–2002), nuclear scientist and biochemist. Chem Educ 7:304–308

Kennel SJ, Bartsch RG, Kamen MD (1972) Observations on light-induced oxidation reactions in the electron transfer system of *Chromatium*. Biophys J 12:882–896

Kennel SJ, Kamen MD (1971) Iron-containing proteins in *Chromatium* II. Purification and properties of cholate-solubilized cytochrome complex. Biochim Biophys Acta 234:458–467

Ludden PW, Roberts GP (2002) Nitrogen fixation by photosynthetic bacteria. Photosynth Res 73:115–118

McMillan ED (1985) Foreword. In: Kamen MD (ed) radiant science, dark politics- a memoir of the nuclear age. University of California Press, Berkeley

Meyer T (2011) Michael Cusanovich: a man of many talents and interests. Photosynth Res 108:1–4

Meyer TE, Cusanovich MA (2003) Discovery and characterization of electron transfer proteins in the photosynthetic bacteria. Photosynth Res 76:111–126

Meyer TE, Kamen MD (1982) New perspectives on *c*-type cytochromes. Adv Protein Res 35:105–212

Moore GR, McClune GJ, Clayden NJ, Williams RJP, Alsaadi BM, Angstrom J, Ambler RP, Van Beeumen J, Tempst P, Bartsch RG, Meyer TE, Kamen MD (1982) Metal coordination centres of class II cytochromes *c*. Eur J Biochem 123:73–80

Okunuki K, Kamen MD, Sekuzu I (1968) Structure and function of cytochromes. University of Tokyo Press, Tokyo

Parson WW (1978) A review of primary processes of photosynthesis. In: Barber J (ed) Science. Elsevier, Amsterdam, pp 756–757

Pettigrew GW, Meyer TE, Bartsch RG, Kamen MD (1975) pH dependence of the oxidation-reduction potential of cytochrome c_2. Biochim Biophys Acta 430:197–208

Pettigrew GW, Meyer TE, Bartsch RG, Kamen MD (1978) Redox potentials of the photosynthetic bacterial cytochromes c_2 and the structural bases for variability. Biochim Biophys Acta 503:509–523

Rawlings J, Stephens PJ, Nafie LA, Kamen MD (1977) Near-infrared magnetic circular dichroism of cytochrome *c*'. Biochemistry 16:1725–1729

Roth W (2004) Martin D. Kamen: science and politics in the nuclear age. Chicago Jewish history. Chic Jew Hist Soc 28:4–7

Ruben S, Kamen MD, Hassid WZ, DeVault DC (1939) Photosynthesis with radio-carbon-11. Science 90:510–511

Ruben S, Kamen MD (1940) Radioactive carbon of long half-life. Phys Rev 57:549

Ruben S, Randall M, Kamen M, Hyde JL (1941) Heavy oxygen (O^{18}) as a tracer in the study of photosynthesis. J Am Chem Soc 63:877–879

Sable HZ (1983) Honoring Kamen [review of "From cyclotrons to cytochromes: essays in molecular biology and chemistry. In: Kaplan NO, Robinson A (eds) Science. Academic Press, New York, pp 707–708

Salemme FR, Kraut J, Kamen MD (1973) Structural basis for function in cytochrome *c*. J Biol Chem 248:7701–7716

Sletten K, Dus K, deKlerk H, Kamen MD (1968) Cytochrome c_2 of *Rhodospirillum rubrum.* I. Molecular properties of the protein and amino acid sequences of its peptides derived by the action of trypsin and thermolysin. J Biol Chem 243:5492–5506

Smith GM, Kamen MD (1974) Proton magnetic resonance spectra of *Rhodospirillum rubrum* cytochrome c_2. Proc Natl Acad Sci 71:4303–4306

Taniguchi S, Kamen MD (1963) On the anomalous interactions of ligands with *Rhodospirillum* haem protein. Biochim Biophys Acta 74:438–455

Taniguchi S, Kamen MD (1965) The oxidase system of heterotrophically grown *Rhodospirillum rubrum*. Biochim Biophys Acta 96:395–428

Van Beeumen J, Ambler RP, Meyer TE, Kamen MD, Olson JM, Shaw EK (1976) The amino acid sequences of the cytochromes *c*-555 from two green sulphur bacteria of the genus *Chlorobium*. Biochem J 159:757–774

Vernon LP (1985) Triumph and disaster. In: Kamen MD (ed) Chemical & engineering news. University of California Press, Berkeley, pp 49–50

Vernon LP, Kamen MD (1954) Hematin compounds in photosynthetic bacteria. J Biol Chem 211:643–662

Weber PC, Bartsch RG, Cusanovich MA, Hamlin RC, Howard A, Jordan SR, Kamen MD, Meyer TE, Weatherford DW, Xuong NH, Salemme FR (1980) Structure of cytochrome *c*':a dimeric, high-spin haem protein. Nature 286:302–304

Yamanaka T, deKlerk H, Kamen MD (1967) Highly purified cytochromes *c* derived from the diatom *Navicula pelliculosa*. Biochim Biophys Acta 143:416–424