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PREBIOTIC CHEMISTRY

Stanley L. Miller (1930–2007): Reflections and Remembrances

Antonio Lazcano · Jeffrey L. Bada

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Abstract An appreciation of Stanley L. Miller, the pioneer prebiotic chemist, who died last year.

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An Earth Made of Glass

"Milk, meat, albumen, bacteria, viruses, lungs, hearts – all are proteins. Wherever there is life there is protein" stated the *New York Times* in its May 15, 1953 issue. "Protein is of fairly recent origin, considering the hot state of the earth in the beginning. How the proteins and therefore life originated has puzzled biologists and chemists for generations. Accepting the speculations of the Russian scientist A. I. Oparin of the Soviet Academy of Science, Prof. Harold C. Urey assumes that in its early days the earth had an atmosphere of methane (marsh gas), ammonia and water. Oparin suggested highly complex but plausible mechanisms for the synthesis of protein and hence of life from such compounds."

"In a communication which he publishes in Science, one of Professor Urey's students, Stanley L. Miller, describes how he tested this hypothesis", continued the New York Times, "A laboratory earth was created. It did not in the least resemble the pristine earth of two or three billion years ago; for it was made of glass. Water boiled in a flask so that the steam mixed with Oparin's gases. This atmosphere was electrified by what engineers call a corona discharge. Miller hoped that in this way he would cause the gases in his artificial atmosphere to form compounds that might be precursors of amino acids, these amino acids being the bricks out of which multifarious kinds of protein are built. He actually

A. Lazcano (✉)
Facultad de Ciencias, UNAM, Apdo. Postal 70-407, Cd. Universitaria, 04150 Mexico D.F., Mexico
e-mail: alar@correo.unam.mx

J. L. Bada
Scripps Institution of Oceanography, University of California at San Diego, La Jolla,
CA 92093-0212, USA
e-mail: jbada@ucsd.edu

synthesized some amino acids and thus made chemical history by taking the first step that may lead a century or so hence to the creation of something chemically like beefsteak or white of egg. Miller is elated, and so is Professor Urey, his mentor."

The media was enticed. The Miller experiment made it to the headlines of all major newspapers and periodicals all around the world, attracting the attention of both researchers and the public. Oparin was attending a meeting in Brussels when Marcel Florkin, the distinguished Belgian biochemist, rushed into the room and showed him a newspaper describing Stanley's results. "I cannot believe it!" said Oparin, whose proposal of a primitive soup and a heterotrophic origin of life were sustained by the evidence of organic compounds in meteorites and by some of the nineteenth century laboratory syntheses of organic compounds. Although he had suggested the possibility of prebiotic synthesis under reducing conditions long before, no one had tried to test his hypothesis under laboratory conditions. With a simple, elegant experiment, Stanley L. Miller had changed single-handed the study of the origin of life by bringing it into the realm of experimental research.

The Chemistry of Life

Although Charles Darwin rarely expressed his ideas on the emergence of life, the widely read books of his follower Ernst Haeckel popularized evolutionary theory and the idea that life was the historical outcome of gradual transformation of lifeless matter. Moreover, towards the end of the nineteenth century the chemical gap separating non-living from living matter had been bridged at least in part by the laboratory syntheses of organic molecules, which for a long time had been considered to be fundamentally different from inorganic compounds.

In 1827 Jöns Jacob Berzelius, probably the most influential chemist of his day, had written that "art cannot combine the elements of inorganic matter in the manner of living nature". However, 1 year later his friend and former student Friedich Wöhler demonstrated that urea could be formed in high yield by heating ammonium cyanate "without the need of an animal kidney", under conditions which would qualify today as prebiotic. It is possible that the laboratory formation of urea may have been preceded by other syntheses relevant to our understanding of the origin of life. In 1807 Joseph Louis Proust, a French chemist who taught in Spain thanks to recommendations provided by Lavoisier himself, reported that under basic conditions hydrogen cyanide produced a complex polymer, together with other uncharacterized compounds which may have included adenine and even amino acids.

Wöhler's work led to a new era in chemical research: in 1850 the distinguished German chemist Adolph Strecker achieved the laboratory synthesis of alanine from a mixture of acetaldehyde, ammonia and hydrogen cyanide. This was followed by the experiments of Alexandr M. Butlerov showing that the treatment of formaldehyde with strong alkaline catalysts, such as calcium oxide-hydroxide, led to the synthesis of sugars. The laboratory synthesis of biochemical monomers soon included more complex experimental settings. Towards the end of the nineteenth century organic synthesis was a solid, well-established field that demonstrated the abiotic formation of numerous organic molecules using electric discharges with various gas mixtures. This work continued in the twentieth century with the work of Walther Löb, Oskar Baudish and others on the synthesis of amino acids by exposing wet formamide [$CHO\text{-}NH_2$] to a silent electrical discharge and to UV light. However, since it was generally assumed that the first lifeforms had been autotrophic, plant-like microorganisms, the abiotic synthesis of organic compounds did not appear to be a necessary prerequisite for the emergence of life. These organic syntheses were not conceived as laboratory simulations of the primitive Earth, but attempts to understand the autotrophic mechanisms of nitrogen assimilation and CO_2 fixation in green plants. The first one to achieve successfully Darwin's warm little pond was Stanley L. Miller (Bada and Lazcano 2003).

Experiments are Messy and Time-Consuming

In 1945 Harold C. Urey moved from Columbia to the University of Chicago, where the faculty included Enrico Fermi, Edward Teller, and other distinguished scientists. These academic luminaries attracted brilliant students, including Lynn Margulis, James Watson, Carl Sagan and Stanley L. Miller, who arrived in the spring of 1951 after graduating from the University of California, Berkeley. At the Department of Chemistry in Chicago Urey soon started to work on cosmochemistry and the origin of life. There is no geological evidence of the environmental conditions on the Earth at the time of the origin of life, nor any fossil register of the evolutionary processes that preceded the appearance of the first cells. Nevertheless, Urey became convinced the Earth's earliest atmosphere was highly reducing, with CH_4 and NH_3 instead of CO_2 and N_2. In 1951 Urey gave a seminar dealing with the origin of the Solar System, and argued that the reducing conditions on the early Earth may have been important to the emergence of life. As Urey wrote in his 1952 book *The Planets: their origin and development*, "if half the present surface carbon existed as soluble organic compounds and only 10 per cent of the water of the present oceans existed on the surface of the primitive earth, the primitive oceans would have been approximately a 10 per cent solution of organic compounds. This would provide a very favorable situation for the origin of life" (Urey 1952).

Stanley attended Urey's lecture, who like Oparin suggested that it would be interesting to simulate the proposed reducing conditions of the primitive Earth to test the feasibility of organic compound synthesis. "Urey's point immediately seemed valid to me", wrote Stanley many years afterward. "After this seminar someone pointed out to Urey that in his book Oparin had discussed the origin of life and the possibility of synthesis of organic compounds in a reducing atmosphere. Urey's discussion of the reducing atmosphere was more thorough and convincing than Oparin's; but it is still surprising that no one had by then done an experiment based on Oparin's ideas" (Miller 1974).

When Stanley arrived to Chicago he had already published two papers on the theory of anesthesia, and was convinced that experiments are "time-consuming, messy and not as important, then I thought, as theoretical work" (Miller 1974). In part to avoid spending time in the laboratory and in part attracted by the scope of the project offered to him, Stanley started to work with Edward Teller, the so-called father of the hydrogen bomb. Stanley began working on how chemical elements might have been formed in the early Universe. A year went by without any major advances, and when Teller told him that he was to set up a laboratory in Livermore, California, Stanley decided to change advisor and approached Urey about the possibility of a prebiotic synthesis experiment to test his model of the atmosphere and Oparin's ideas.

Urey was not very enthusiastic, but Stanley "won a grudging permission to try". When Stanley graduated from high-school in 1947 one of his fellow students had written in his annuary "best luck to a chem whiz". The description was accurate: a month after he had started his experiment Stanley had produced an oily scum and a yellow-brown water solution, which upon analysis showed the presence of glycine, several other amino acids and other compounds of biochemical significance. "Some of us were present at a crowed seminar in which Miller presented his results, with Urey at the front row", wrote a young assistant professor at the time several years later. “By the end of the presentation it was obvious to all that this was an important milestone. In the question period Enrico Fermi turned to Urey and said, “I understand that you and Miller have demonstrated that this is one path by which life might have originated. Harold, do you think it was *the way*?” Urey replied, “Let me put it this way, Enrico. If God didn’t do it this way, he overlooked a good bet!” (Arnold et al. 1995).

Those were the Days, my Friend

When Stanley started to work in the origins of life evolutionary biology was already a well established field of inquiry, but it was believed that emergence of the biosphere been a lengthy process that had required billions of years, that organisms could be divided into plants, animals and microbes, that the oldest fossils were scarcely older than 600 million years, and that space exploration was nothing but a dream that seemed to belong to science fiction.

After encountering some problem with the editorial office of *Science*, Stanley’s article was published in May 1953 (Miller 1974). It followed by about a month the *Nature* paper in which Watson and Crick proposed their model of the DNA double helix. It is probably difficult for us to imagine the intellectual exhilaration of the years that followed, which would lead to the establishment of molecular biology as a major scientific discipline that would soon play a major role in the analysis of evolutionary problems.

With few exceptions, modern attempts to understand the origin of life have been shaped by the unraveling of the details of DNA replication and protein biosynthesis. In Stanley’s case this was shown first by the way in which he and Urey rejected the claim that thermal polypeptides (Fox 1956) were ancestral to DNA-encoded proteins (Miller and Urey 1959). It was followed by his prompt recognition and deep admiration for the work of his longtime friend John Oró on the synthesis of adenine (Oró 1960), and continued until the very end of his life with his staunch support of the RNA world hypothesis and the issues related to its emergence, including the search for laboratory models of the genetic polymers that may have preceded it.

Clathrates: Exploding Ice

Although Stanley is best known for his work in prebiotic chemistry, he also made significant contributions to the field of gas clathrates (hydrates), Clathrates are solids made of water molecules that contain “cages” in which small gas molecules can be contained. They form at a pressure and temperature characteristic of the particular gas.

Stanley became intrigued with clathrates when he read about the problem that methane clathrate formation posed in gas pipelines. The formation of these compounds plugged the pipelines and impeded gas flow. Stanley began investigating their possible geochemical and cosmochemical occurrence. This resulted in a 1961 paper published in *PNAS* (Miller 1961b) on the presence gas clathrates in the solar system that was submitted by Urey.

At about the same time, Stanley became interested in the role of gas clathrates in anesthesia. He noted in a *PNAS* paper (Miller 1961a) also published in 1961 (again submitted by Urey) that several anesthetic gases formed stable clathrates and perhaps these formed under physiological conditions and allowed the anesthetic gases to be transported in the blood stream. Interestingly, Linus Pauling published the same idea in a *Science* paper (Pauling 1961) a couple of months earlier than Stanley’s publication.

Stanley's gas clathrate researches lead him to predict the presence of the clathrate of air in the Antarctic ice sheet at the depth where gas bubbles had been found to disappear (Miller 1969). He named this natural occurring air clathrate "Craigite" in honor of his friend and fellow Urey graduate student Harmon Craig. It was noted that when "Craigite" melts at atmospheric pressure it spontaneously explodes into hot gas and water. Others soon confirmed its presence in Antarctic ice.

Another significant aspect of Stanley's clathrate research dealt with the occurrence of the carbon dioxide clathrate on Mars. The NASA Mariner Mars flybys in the 1960s provided confirmation of the temperature of the Martian ice caps and the partial pressure of carbon dioxide in the atmosphere that previously had been obtained from Earth based observations. Stanley took this information and predicted that the clathrate $CO_2 \cdot 6H_2O$ would be stable under the conditions at the poles of Mars and thus should be a significant component of the Mars polar ices (Miller 1970). Again, this prediction was later confirmed by other observations.

Life on Mars?

It was only logical that with his research in the origin of life that Stanley also was interested in the possibility of life beyond Earth, in particular on Mars. This interest is reflected in the statement below (Miller and Urey 1959):

> Surely one of the most marvelous feats of 20th-century science would be the firm proof that life exists on another planet. All the projected space flights and the high costs of such developments would be fully justified if they were able to establish the existence of life on either Mars or Venus. In that case, the thesis that life develops spontaneously when the conditions are favorable would be far more firmly established, and our whole view of the problem of the origin of life would be confirmed.

Stanley further developed the idea of searching for evidence of life on Mars in a little known paper he published in 1963 where he summarized what was known about the evidence for life on Mars at that time (Miller 1963). He was especially intrigued by the claim of William Sinton (Sinton 1959) who measured the reflectance spectra of Mars and concluded this provided evidence for the presence of vegetation (Stanley corresponded directly with Sinton and stated he disagreed with Sinton's interpretation). He suggested at the end of his summary that the development of a "reliable experiment to determine whether life is actually present on Mars becomes even more urgent". Typically of Stanley, he turned his attention to doing just that.

Stanley considered amino acids to be the best compounds to search for on Mars because of their ubiquitous role in terrestrial biochemistry and the ease with which they could be synthesized under prebiotic conditions. He received a grant from NASA to develop a miniaturized extraction system and amino acid analyzer that could be deployed on future mission to the red planet. Stanley was able to construct a functioning prototype of the instrument that was about the size of a shoebox (compare this to the standard laboratory amino acid analyzer at the time which was about the size of a refrigerator). He also worked with scientists at NASA Ames to construct a complementary gas chromatograph instrument that could separate amino acid enantiomers to help determine the origin of any detected amino acids, the surmise being that life would be based only on one amino acid enantiomer.

With prototype instruments in hand, Stanley decided to try use them to answer the question of the existence of life beyond Earth once and for all – he proposed the amino acid instruments as part of the experimental package for the NASA Viking missions that landed two spacecraft on the surface of Mars in 1976. He was disappointed when he learned that the instrument was not selected and in his final report to NASA Stanley mentioned that he hoped that something along the lines of his proposed design might fly to Mars in the future.

Stanley's dream of searching for amino acids on Mars and determining their chirality does indeed live on. The detection of amino acids and their enantiomers is a central focus of the *Urey* Mars Organic and Oxidant Detector instrument that has been selected as one of the main instruments on the European Space Agency's 2013 ExoMars mission. *Urey* will be able to detect amino acids at the part-per-trillion level, equivalent to the presence of only around 10^3 bacterial cells in a gram of soil (Bada et al. 2008). *Urey* is presently in the Technology and Development phase funded by NASA and with the successful completion of the final design review could be totally funded by NASA for the ExoMars mission in the near future.

Stanley's Steamer

As time went by Stanley stopped one of the customs he had followed his entire scientific career – he ceased to write down his name in his books. The only exceptions were those books about railroad engines and steam powered automobiles. His fascination with steam power took him in several directions, including a trip on the Trans-Siberian railroad pulled by a steam powered locomotive in the early 1970s.

Also about that time, he mentioned his interest in steam power to a graduate student who had an office just down the hall from Stanley's laboratory in Bonner Hall at UCSD. As part of his PhD thesis work, the graduate student, Ray Salemme, had helped set up a machine shop in collaboration with the Physics Department. After discussing their mutual interest in steam power, Stanley and Ray decided to recruit a team (eventually including a Professor of Engineering, Rod Burton and about a half dozen assorted graduate and undergraduate students) to build a steam car to compete in the Intercollegiate Clean Air Car Race. The concept of an automobile powered by an alternative to the internal combustion engine was ahead of its time as were so many of Stanley's research ideas.

After numerous design exercises and experiments (including a few minor explosions), the final design incorporated a Harley Davidson 74 cubic inch V2 motorcycle engine that derived steam pressure from a Doble-inspired coiled monotube steam generator heated by propane. The drive train was mounted in an American Motors Javelin chassis that was donated to the project.

The car was not completely finished in time for the race, so the team trucked the parts to a staging area in a garage in Cambridge to do the final assembly. Owing to a mishap traveling across country, many of the planned automatic control systems were not installed, so that it took two operators to drive the car.

The 1970 Intercollegiate Clean Air Car Race featured 50 zero to low emission vehicles from 40 colleges and universities all over America. Electric Cars, Hybrid Electric Cars, Steam Cars, Propane Cars, and Turbine Cars were placed in five separate race divisions. The race started at the Massachusetts Institute of Technology in Cambridge, Massachusetts on August 24, 1970, and ended at California Institute of Technology in Pasadena, California on September 2, 1970.

The longest run attempted by Stanley's steamer entry was a few miles, which was probably not bad considering the car's early stage of development. After the race, the steam car was shown at several auto shows around the country. The car was ultimately sold at auction to a steam enthusiast a few years later.

It was the Best of Times, it was the Worst of Times

Stanley belonged to a generation of American scientists whose academic life was shaped, in a way we can hardly understand nowadays, by the Cold War atmosphere. The creation of the loyalty-security program in the late 1940's had seriously hindered academic freedom in American universities, by allowing suspects to be fired from their jobs. It was a common practice to smear the innocent by stretching the evidence, or by inventing faults. The toll was awful: incriminating files were kept on the physicist Philip Morrison, the astronomer Harlow Shapley, and the chemist Harold C. Urey while some suspects, like Linus Pauling lost their passport and the right to travel abroad. When A. I. Oparin, whose reputation had been tarnished by his association with Lysenko, invited the 27-year-old Stanley to visit the Soviet Union and take part in the first international meeting devoted fully to the origin of life, he rapidly wrote to Urey asking for advice. In 1949 there had been unsuccessful attempts to incriminate Urey and other professors with subversive activities, but the Chancellor of The University of Chicago defiantly protected them against any possible harassment. Urey never forgot this sad period. He replied to Stanley with a letter that ends with a very revealing paragraph:

> I do not know how to advise you. I think each of us must make up his own mind about this. The nuclear scientists went some time ago, and if they will let nuclear scientists go in the United States without stigmatizing them, I should think that innocent people like us might also go, but one never knows what a McCarthy will do in the future. It is a very sad situation.

As soon as Stanley accepted Oparin's invitation and started the paperwork to obtain travel funds, he was approached by American intelligence officers and asked to report to them any "interesting information" that he may have the chance to see. When he returned home he was interrogated by the agents and 30 years later he would chuckle describing how he had played the naïve young scientist overwhelmed by the hot weather in Moscow and the lack of air conditioning in Soviet buildings, making fun of enjoying the agents' lack of scientific sophistication, which did not allow them to distinguished the differences between the Strecker synthesis and thermodynamics of open systems.

In spite of the rancid McCarthyist atmosphere, neither then nor afterward did Stanley fail to appreciate and promote Oparin's work. He was a fair and honest man, who publicly admired the scheme proposed by Oparin and his efforts to develop an understanding of the emergence of life. Stanley was, after all, a child of the New Deal, as shown by his deep loathing of racial segregation, his deep sense of justice, his sincere admiration of Eleanor Roosevelt, his outrage against the treatment of illegal immigrants and the construction of a wall at the southern border of the USA, together with his strong belief that science is an intellectual adventure that thrives in cultural plurality. His secular vision of the United States as an open society went along with his concern about the way this country is increasingly closing upon itself.

Conclusions

It must have been hard for a young unassuming graduate student be launched all of a sudden into the spotlight of public fame. Stanley was shy, but would defend his ideas vigorously. He was a generous, loyal friend who knew how to listen to others, especially if he was in the right company. A true scholar, his life was centered in science and the understanding of the origin of life, but he enjoyed conversation about the history of science, French civilization and cuisine, books and Mozart's *Don Giovanni*. Also chemistry, travel, history and a good laugh. He was adapt at listening, discussing, asking intelligent questions and making appropriate remarks and, if the going was good, would chuckle, laugh, and feel at ease.

"I felt very nervous by the way in which John D. Bernal sought me during the 1957 meeting in Moscow" said Stanley. "He had been described as one of the finest scientific minds in the world, was very cosmopolitan, approached all the women, seem to speak all the languages. I was not even thirty and felt very uncultivated. To make matters worse, it was very hot and I was uncomfortable". Bernal thanked Stanley for including him among the three authors he had quoted in his 1953 *Science* paper, and when he returned home, Bernal mailed him a copy of his 1951 book, *The Physical Basis of Life.* Stanley marked with pencil some parts of the volume, including a lengthy paragraph where Bernal wrote:

> "In a letter to Sir J. Hooker, he said: 'It is mere rubbish thinking at present of the origin of life; one might as well think of the origin of matter… this does not mean that we should accept wild hypothesis of the origin of life or of matter, which simply conceal ignorance, but rather that we should attempt almost from the outset to produce careful and logical sequences in which we can hope to demonstrate that certain stages must have preceded certain others, and from these partial sequences gradually built up one coherent history. There are bound to be gaps where this cannot be done, but until the process is attempted these gaps cannot be located, nor can the attempt be made to fill them up..." (Bernal 1951).

We will never know how life actually first appeared on Earth. It is probably true that no single experiment will ever reveal how the first life forms emerged, but then Stanley never claimed to do anything more that describe the way in which some of the first steps could have taken place. He showed that the study of the origin of life could be undertaken under experimental conditions – and was overwhelmed for the rest of his life by the results. "The 1953 paper", he once said, "was a hard act to follow". And indeed it was, and the cruelty of the illness that struck him down did so when he was enjoying a stage of great intellectual excitement and creativity.

In his novel *The Procedure* the Dutch writer Harry Mulisch (2001) describes in a disturbing way the sacrifices and rewards that go along with the pursuit of a scientific career. When he saw the book, Stanley was highly amused to realize that he appeared in it as a character: his work had entered not only popular culture but also contemporary literature. There is a chapter in *The Procedure* in which the biologist Victor Verker, the principal character, describes his own fictional biography:

> "...I was born in 1952, but my philosophical birth therefore took place in 1953: the crucial year in microbiology. It was then that Watson and Crick constructed their model of the DNA molecule, the famous double helix. In my philosophical year of birth another remarkable experiment was conducted, with which I'm also closely connected. In the 1940's, provoked by a Soviet scientist, Oparin, there was a debate

about the origin of life on Earth. His motive of course was – after Darwin –, to eliminate God even more definitively. Everyone agreed that a major role in the origin of life was played by twenty amino acids, the building blocks of proteins, but how had they originated? An impudent student, Stanley Miller, had the kind of brilliant thought that doesn't occur to a sensible person: let's try it, he said. With the kind of chemical equipment that every inquisitive adolescent has in his attic, he simulated the presumed condition of the Earth's atmosphere at the time with hydrogen, methane, ammonia, lightning, et cetera, and he made the sparks fly through his mixture – and what do you think? After just a week he was able to demonstrate the formation of all kinds of essential amino acids. I myself can't complain with my eobiont (after all, even the Pope has warned mankind against me), but that pure, elegant simplicity of Miller's experiment awakes in me a respectful admiration..." As indeed it still does.

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