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One of molecular biology's founders, and humanist

An obituary of Salvador E. Luria

The movement towards the unification of modern biology, which came to be known as molecular biology, began in the early forties. At the heart of this movement was the realization that the nature of the gene and of gene action is the central problem of all biology. Microbial genetics, in particular the genetics of enteric bacteria and their viruses, called bacteriophage or simply phage, became the vehicle of a great intellectual revolution which led to the confluence of genetics and biochemistry. The phage group in the US, whose founders Salvador Luria, Max Delbrück and Alfred Hershey shared the Nobel prize for physiology or medicine in 1969, played a crucial role in the evolution of molecular biology. Luria died on 6 February 1991.

Salva Luria was born in a middle-class Jewish family of Turin in 1912. His father, David Luria, managed a printing business. At the high school in Turin, Luria was influenced by the anti-Fascist and socialist inclinations of his teachers, who included the Marxist philosopher Antonio Gramsci and the liberal socialist and novelist Augusto Monti. From his teachers Luria acquired a liking for the academic life and a preference for intellectual pursuits over economic pursuits. His close friendship with Ugo Fano, who later became a professor of physics at Chicago, inculcated in Luria a liking for mathematics and physics. Fano introduced Luria to the exciting new ideas of Bohr, Heisenberg, Schrödinger and Fermi.

Luria joined the medical school at the University of Turin and graduated in 1935 with high honours. He was not inclined to practise medicine and was attracted by research. He tried radiology in the hope that it would bring him closer to biophysics but radiotherapy and diagnostic radiology turned out to be the 'dullest of subjects'. Finally, at the suggestion of his friend Ugo Fano, Luria transferred to Rome, where Fermi and his colleagues were active. Luria came to know Franco Rasetti and Eduardo Amaldi. The year in Rome among physicists was a critical point in Luria's career. It taught him to 'think a bit in the way the physicists do'. Rasetti introduced Luria to radiation biology and gave him a set of papers by the German physicist Max Delbrück. In these papers Delbrück had explored the

question of the gene as a molecule. The seeds of the seminal collaboration that was to follow a few years later were thus sown in Rome. In the meanwhile, Luria met the bacteriologist Geo Rita. Rita introduced Luria to the world of bacteriophage, how to grow these invisible particles and how to enumerate them by counting plaques. Luria was greatly excited, for bacteriophages seemed to be objects with which one could do precise and quantitative experiments. Who knows, Luria wondered, these tiny objects could open the way to the holy grail of genetics that Delbrück was pursuing. The bacteriophage, the gene and Delbrück thus came together in Luria's mind by a remarkable coincidence of circumstances. Independently Delbrück had arrived at the same idea and was working at Caltech with phages.

In July of 1938 Luria received a fellowship from the Italian government to study radiation biology at Berkeley in the US. He immediately decided to change his plans and go to Pasadena to work with Delbrück. That, however, was not yet to be. On the 18th of July, Mussolini issued his 'racial manifesto', aligning Italy with Fascist Germany and excluding Jews from the 'pure Italian race'. Luria lost his fellowship and left Rome for Paris, where he worked for a short period with Fernand Holweck, an expert in high-vaccum physics and radiation biology. When the German armies entered France, Luria managed to escape on a bicycle 'just ahead of the Germans'. In September 1941 he landed in New York.

On Enrico Fermi's laconic recommendation 'I believe he will make good use of whatever help you may give him', Luria received a fellowship from the Rockefeller Foundation and joined a biophysics laboratory in the College of Physicians and Surgeons at Columbia University In December 1940 Luria finally met Delbruck. They made plans for experiments, which began almost immediately, in January 1941, at Columbia and were continued the following summer at Cold Spring Harbor. During 1942 Luria joined Delbrück at Vanderbilt University where Delbrück was now teaching physics. In 1943 Luria was appointed to Indiana University, where he carried out his most significant piece of work, which appeared as the famous Luria-Delbrück paper of 1943.

The Luria Delbruck paper had to do with gene mutations in bacteria. When cultures of bacteria are exposed to phage, most of the bacterial cells are killed. But a few phage-resistant cells survive. It was believed by many microbiologists that the exposure to phage induced some of the bacteria to become resistant. An alternative explanation was that phage resistance was due to spontaneous gene mutations that arose before exposure to phage. Luria argued that if a number of parallel cultures, each containing the same number of bacteria, were exposed to phage, the number of survivors in the cultures was expected to vary somewhat differently on the basis of the two hypotheses. If resistant variants were induced by the virus, the probability of finding a resistant survivor remained the same in all cultures. On the other hand, if the variants arose by spontaneous gene mutation prior to exposure, their numbers were likely to depend upon the number of cell divisions the mutants had undergone before encountering the phage. The experimental results fitted the latter hypothesis and showed that the mutations of bacteria were, in principle, the same as gene mutations in classical genetics. Later Luria was able to show that bacteriophages also mutate spontaneously to produce stable genetic variants.

The years 1943–45 were remarkable years. Delbrück and Hershey independently demonstrated genetic recombination in phage, and in the same year Lederberg and Tatum discovered recombination in *Escherichia coli*. Bacteria and their viruses thus came to occupy the centre of biological research and the stage was set for the dramatic progress in genetics that was to follow. In later years Luria made other important contributions, among which the discovery of host-induced modification stands out. The study of this phenomenon ten years later by Werner Arber led to the discovery of restriction enzymes, which are the principal tools of recombinant-DNA research.

In 1950 Luria moved to the University of Illinois and in 1958 to the Massachusetts Institute of Technology where he remained till the end. Luria, together with Cyrus Levinthal (who also died recently) and the biochemist Boris Magasanik, attracted a host of brilliant scientists to MIT, which became one of world's leading centres in molecular biology. In later years Luria directed MIT's new Cancer Research Center, although he himself did not do any cancer-related work and kept his laboratory in the biology building intact. His role as director of the Cancer Center was to attract the most talented scientists to the centre and enable them to flourish with minimal hindrance.

Luria was a superb teacher and his lectures to undergraduates, published by the MIT Press as *36 Lectures in Biology*, have inspired and attracted many generations of physics and engineering students to biology. Luria's first graduate student at Bloomington was James Watson, who worked with him on reactivation of irradiated phages. Luria encouraged and helped Watson to go to Cambridge to work with John Kendrew. The outcome is too well-known to need recounting. Another prominent early associate was the virologist Renato Dulbecco who shared the 1975 Nobel prize for physiology or medicine with David Baltimore and Howard Temin, yet others who made their mark were Edwin Lennox and the late George Streisinger. Luria knew how to pick and nurture talent.

Luria wrote with literary finesse and verve. His book *General Virology* has remained a standard text on the subject for four decades and has seen two revised editions, coauthored, first with J. Darnell in 1967 and then with Baltimore and Campbell in 1977. The popular book *Life: The Unfinished Experiment* won the National Book Award for science, and Luria and Stephen Jay Gould jointly wrote *A View of Life*. Luria's autobiography *A Slot Machine, A Broken Test Tube* provides an insightful account of the intellectual and emotional development of this remarkable man and the turbulent times in which he lived and worked.

Luria was committed to Left-wing and socialist beliefs and retained his commitments till the end. He firmly believed in the necessity of political action against injustice and oppression. I have a vivid recollection of Luria and Noam Chomsky leading the demonstrations on Massachusetts Avenue against the Vietnam War. Luria made a distinction between personal commitment and group loyalty. He was free of prejudice and spoke out against all injustice, be it against the Russian Jews, the African Blacks or the Palestinian Arabs. The world of science is poorer for having lost a man like him.

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