Francesco Cavalli-Sforza

LUIGI LUCA CAVALLI-SFORZA,A PIONEER IN THE RECONSTRUCTION OF HUMAN EVOLUTION

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SOMMARIO

Presentazione . . . . . p. 9
Presentation . . . . . » 11

Parte prima
SAGGI

Nicolette Mout, *«And New Philosophy Calls All in Doubt». Paolo Rossi and the History of Early Modern Science* . . . . . » 15
Carlo Ginzburg, *Schemi, preconcetti, esperimenti a doppio cieco. Riflessioni di uno storico* . . . . . » 29
Peter R. Grant – B. Rosemary Grant, *Population Biology and Speciation* . . . . . » 51
Anthony Thomas Grafton, *The Republic of Letters: the European Intellectual Community in an Age of Religious War (1500-1700) and its Relevance Today* . . . . . » 65
Dominique Schnapper, *L'utopia repubblicana* . . . . . » 77
Francesco Cavalli-Sforza, *Luigi Luca Cavalli-Sforza, a Pioneer in the Reconstruction of Human Evolution* . . . . . » 83
Luigi Luca Cavalli-Sforza, *A Comprehensive Outline of My Research: Drift vs. Natural Selection as Factors of Evolution and the Importance of Demography* . . . . . » 89
György Ligeti, *Rapsodische, Unausgewogene Gedanken über Musik, Besonders über Meine Eigenen Kompositionen* . . . . . » 101

Parte seconda

INTERVISTE E RECENSIONI

Understanding Plant Ecology, an interview with David Tilman by Charles Godfray . . . . . p. 117

«Sono sempre stato comparatista...», intervista a Piero Boitani di Peter Kuon . . . . . » 127

Storia e storie della musica, intervista a Reinhard Strohm di Walter Rauhe . . . . . » 139

Looking for the Lights of the Enlightenment, an interview with Bronisław Baczko by Frédéric Le Bihan, Olivier Mongin, Michel Porret and Eric Vigne . . . . . » 147

Parte terza

IINTER-LA^{+}B, INTERNATIONAL INTERDISCIPLINARY RESEARCH LABORATORY

Utopian Thinking: Past, Present and Future (2015) . . . . . » 169

Markus Zürcher, *Introduction* . . . . . » 171

Marie Capel, *Une mauvaise langue pour que vive l'utopie* . . . . . » 175

Ugo Bellagamba, *Des villes ideales aux villes futures ou la science-fiction comme continuité de l'utopie* . . . . . » 179

François Rosset, *Dialogue avec Bronisław Baczko: autour de la notion du mal en utopie* . . . . . » 199

Roberto Scazzieri, *Dominique Schnapper,* L'utopia repubblicana*: Comment* . . . . . » 203

Parte quarta

FORUM INTERDISCIPLINARE DELLA FONDAZIONE

Balzan Prizewinners 2017; Interdisciplinary Forum . . . . . » 209

Peter Suter, *Presentation of James P. Allison and Robert D. Schreiber* » 211

James P. Allison, *Descriptive Resume* . . . . . » 215

Robert D. Schreiber, *Establishing a Role for Immunity in the Control and Shaping of Cancer* . . . . . p. 225
Bengt Gustafsson, *Presentation of Michaël Gillon* . . . . . » 229
Michaël Gillon, *En quête d'autres mondes* . . . . . » 233
Marjan Schwegman, *Presentation of Bina Agarwal* . . . . . » 247
Bina Agarwal, *The Challenge of Gender Inequality* . . . . . » 251
Thomas Maissen, *Presentation of Aleida and Jan Assmann* . . . . . » 263
Aleida und Jan Assman, *Forum-Vorträge* . . . . . » 267
Research Projects 2017 . . . . . » 275

Parte quinta

EVENTI E NOTIZIE DALLA FONDAZIONE

Al Premio Balzan James Allison anche il Nobel . . . . . » 291
Marino Viganò, *Renata Broggini: le attività per la Fondazione* . . . . . » 295
Salvatore Veca, *Presentazione del volume I di* Balzan Papers . . . . . » 305

Architettura: una storia. In ricordo di James S. Ackerman (1919-2016) » 307
Howard Burns, *James S. Ackerman: storia e valori* . . . . . » 309
Guido Beltramini, *James Sloss Ackerman, 1919-2016* . . . . . » 315
Leo Schubert, *In ricordo di James Ackerman: le ville di Le Corbusier e la villa antica* . . . . . » 319
Federica Rossi, *Dall'Europa dei Lumi alla Russia degli Zar: Nikolaj L'vov traduttore di forme e parole* . . . . . » 323
Valeria Cafà, *In memoria di James Sloss Ackerman: Palazzo Massimo alle Colonne di Baldassarre Peruzzi* . . . . . » 335

Utopia e Lumi. La lezione di Bronisław Baczko (1924-2016) . . . . . » 345
François Rosset – Michel Porret, *With Bronisław Baczko: from Utopia to the* Dictionnaire critique de l'utopie au temps des Lumières . . . . . » 347
Carlo Capra, *Note a margine del* Dictionnaire critique de l'utopie au temps des Lumières . . . . . » 357

Gianni Francioni, *Appunti su Baczko, Venturi e l'utopia* . . . . . p. 365

La Fondazione Internazionale Balzan . . . . . » 381
Organi della Fondazione Internazionale Balzan . . . . . » 383
Premi Balzan per le Lettere, Scienze Morali, Arti; per le Scienze Fisiche, Matematiche, Naturali e Medicina . . . . . » 391
Premi Balzan per l'Umanità, la Pace e la Fratellanza fra i popoli . » 397

Francesco Cavalli-Sforza *

LUIGI LUCA CAVALLI-SFORZA, A PIONEER IN THE RECONSTRUCTION OF HUMAN EVOLUTION

Luigi Luca Cavalli-Sforza (Genoa 1922 – Belluno 2018) was a founder of the field of human population genetics, and the very first scientist to reconstruct the genealogical trees of humankind. He is internationally recognized as one of the leading geneticists of the twentieth century. The range of his research works extends from bacterial recombination to evolutionary trees to cultural transmission. He has shown how historical research can benefit from cooperation between different disciplines, actually providing new tools to understand our own past.

Luigi (Gigi) Cavalli was born in Genoa on 25 January 1922, but grew up in Turin. His father, Pio Cavalli, was an early advertising agent who traveled extensively. He published the first Italian book on the subject, *La spada dell'America* (*America's Sword*, 1919). His mother, Attilia Manacorda, of an old family from Monferrato, was among the first Italian women to graduate from university, with a degree in the Humanities. In an intellectually stimulating family environment, Luigi, the only son, grew up to detest the limited outlook of school learning under the Fascist regime, and with his family's support, stopped attending high school, studied at home, and took the exit exam as a private student. He turned out to be the youngest to pass it at sixteen, and with the best marks in town.

In 1938, Luigi enrolled in the Faculty of Medicine at Turin, but transferred the following year to the University of Pavia, meanwhile having earned a full scholarship to the local Collegio Ghislieri, thanks to his excellent grades. Although his interests later shifted towards biology, being a second-year medical student turned out to be a stroke of luck for him when Italy entered the Second World War, as doctors in training were exempted from the draft.

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* Università Vita-Salute San Raffaele, Milan; Marradi, February 2019.

At Pavia, Luigi met his mentor, Adriano Buzzati-Traverso, assistant professor at the time, who introduced him to genetics and laboratory experimentation, with microbes, drosophilae, mice. Luigi graduated at the end of the war, and in the years that followed he managed to work first as a doctor in a hospital, then as a researcher in the preparation of serums, all the while conducting research in genetics and broadening his knowledge of statistics, also thanks to scholarships from abroad.

Meanwhile, he became engaged to, and later married, Alba Ramazzotti, Adriano's great-niece, whom he had met when the small research lab moved out of town to avoid bombings. They had four children: Matteo, Francesco, Luca Tommaso and Violetta. Luigi's name changed in those years: his friends dubbed him Luca (putting together the first syllables of his first name and surname). His surname changed too, to Cavalli-Sforza, when after his father's death he was adopted by Francesco Sforza, the second husband to his maternal grandmother.

At the first International Congress of Genetics in Stockholm, 1948, Luca introduced himself to Ronald Fisher, the great statistician and geneticist (later Sir Ronald), who knew of his early research and invited him to work in Cambridge. In the two following years, Luca completed his scientific training under Fisher's guidance, and upon his request he developed the experiments on bacterial recombination that Joshua Lederberg had begun to publish in the U.S. Working in cooperation with the Lederbergs and the Irish geneticist William Hayes, they eventually demonstrated that DNA exchanges between bacteria did take place. In 1958, Lederberg was awarded the Nobel Prize for this discovery, which would pave the way to genetic engineering twenty years later.

Back in Italy in 1950, Luca taught statistics and genetics at the Universities of Parma and of Pavia while cooperating with Buzzati-Traverso to establish molecular biology in Italy. Luca was eager to contribute to the development of Italian science after twenty years of isolation imposed by Fascism, yet was aware that it was highly unlikely that Italian research could compete with advanced research abroad. He resolved to explore a field of study, the genetics of human populations, that researchers had thus far shunned, discouraged by the length of time our species takes to reproduce. He obtained a grant from the Rockefeller Foundation to study the genetics of people in the valley of the Parma River. With the help of fellow students, among them Don Antonio Moroni, a Catholic priest and biologist, Luca was able to collect blood samples from 75 parishes in the high, middle and low Parma Valley. The genetic variation between villages could thus be examined through a handful of genetic markers, and furthermore checked against the genealogies provided by church records from the pre-

vious 400 years. The results were the first experimental evidence showing the huge importance of random genetic drift in human evolution, a factor hitherto underestimated but which in later years was shown to account for the majority of all molecular evolution. Cavalli-Sforza devoted most of his acceptance speech of the Balzan Prize in 1999 to this fundamental discovery.

The Parma Valley research also proved the usefulness of statistical tools in dealing with chance factors, and in the early Sixties Luca started – in Pavia where, by that time, he had become full professor – collecting all data on genetic markers available in the literature all over the world. He recruited the help of Anthony Edwards, a fellow disciple of Fisher's, and as soon as the first computer became available, they began feeding it the data and analysing it with programs Edwards expressly created. The result was the first evolutionary tree of humanity: published in 1963, it still holds today, with a million times more data available.

Using the tools gradually made available by the development of molecular biology and twenty years later by DNA analysis, in the mid-Sixties Luca embarked on a full-fledged attempt to reconstruct the genealogy and dispersion of humanity, based on genetic analysis, demography, and the parallel study of cultural evolution. In 1966, he embarked on the first of what turned out to be, over the twenty following years, ten expeditions among Central African pygmies, collecting blood samples along with anthropometric and anthropological data, later to be compared with the genetic makeup of more recent populations. Many more trips brought Luca to visit aboriginal peoples and the anthropologists working with them all over the planet.

In 1968, Luca accepted an offer from Stanford University for a long-term teaching position in the Department of Genetics at Stanford Medical School. The amount of bureaucracy needed to manage research and institutional duties in Italy had begun to take too much of his time, and he knew he would find more room and support for research in the U.S. After a one-year trial to see how his family would react to the change, Luca and Alba moved permanently to Stanford in 1971. In 1976, *The Genetics of Human Populations* appeared: written with Walter Bodmer (later Sir Walter), another fellow disciple of Fisher, who had preceded him in Stanford, the volume established a new discipline, also laying the foundations for the genetic reconstruction of human history.

The Stanford years lasted until 2008, and brought Luca's project to maturity, combining different branches of learning to shed light on the human past and present. In cooperation with archaeologist Albert Ammerman, they examined the Neolithic spread of farming in Europe, and checked it

against genetic data on present-day European peoples, showing how the spread of agriculture had largely been a demic diffusion, of people rather than of technology. Parallel research involved Luca in strictly medical fields, tackling epidemiological issues and investigating consanguinity as well as the genetic bases of schizophrenia, cystic fibrosis, neurofibromatosis, Wilson disease, autism.

His inquiry into the mechanisms of cultural evolution, traditionally disregarded by anthropologists, carried out in collaboration with Marcus Feldman, an Australian mathematician and geneticist also working at Stanford, resulted in the publication of *Cultural Transmission and Evolution: a Quantitative Approach* (1981), the first text to approach the study of cultural evolution with quantitative methods. The study of linguistic change over space and time accompanied this line of inquiry, through cooperation with linguists in different parts of the world.

Almost forty years of research on the reconstruction of human evolution eventually bore fruit in a monumental work, *The History and Geography of Human Genes* (1994). Written with the Italian geneticists and statisticians Paolo Menozzi and Alberto Piazza, it portrays the diffusion of modern humans in the world, reconstructed through genetic data, checked against data provided by paleontology, archaeology, demography, and other sciences that inquire into the past. The evolutionary tree based on genetic genealogies turned out to match closely the evolutionary tree of world languages, as reconstructed by linguist Joseph Greenberg. Biology and culture confirmed each other.

In the early Nineties, as the Human Genome Project (HGP) began to take shape, Luca proposed the Human Genome Diversity Project (HGDP) aimed at collecting and analysing variation between different peoples in the world. The HGP would yield a single individual genome; the HGDP would examine differences worldwide. Although the project had a strictly scientific scope, backed by a strong ethical statute to protect donors and prevent all commercial exploitation of their DNA, it met strong and rather specious political opposition. Still, it managed to gather a collection of over 1000 blood samples from 52 aboriginal populations and to make it available to hundreds of researchers, as it has been for over twenty years now.

In the Twenty Hundreds, Luca's research on population genetics produced the first genealogical tree of human males, based on Y chromosome heredity. It also showed that loss of diversity in human populations strictly correlates with distance from our common African origin, due to the impact of genetic drift. His inquiries into cultural evolution produced the twelve-volume *La cultura italiana*, a research encyclopedia investigating the whole landscape of the history of Italy and the Italians, from land and

people to languages, to building and technology, economy, communication, food and play, down to science and all arts. Luca also wrote much to further the public understanding of evolution, often in collaboration with his son Francesco: popular science books as well as science textbooks for high school students.

Luca and Alba moved back to Italy in 2008. They spent fall, winter and spring in Milan and summer in Alba's family villa in Belluno, where they had met in 1943 and where Luca died, aged 96, on August 31, 2018. Alba had passed away three years earlier. They were together for over 70 years.

Luca Cavalli-Sforza's legacy goes beyond the creation of a new discipline and the many discoveries he made. It lives on in the work of thousands of researchers exploring the directions he set out. He is often quoted for having provided the final refutation of the concept of human «races»: a milestone, yes, yet a mere step on the road he paved with his work, showing how an understanding of evolutionary processes and cooperation between different sciences can help us to illuminate our own past in unprecedented ways.

Abstract – Francesco Cavalli-Sforza writes a memoir of Luigi Luca Cavalli-Sforza (1999 Balzan Prizewinner for the Science of Human Origins), one of the leading geneticists of the twentieth century, and founder of the field of human population genetics. What emerges is an account of the geneticist's prodigious pioneering work, that not only reached across continents and disciplinary boundaries, but also revolutionized research methodologies in exploring human evolution.

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