BOOKS: HUMAN EVOLUTION

# The Context of Our Genetic History

David B. Goldstein

In the first four decades of the 20th century, mathematical geneticists showed how to reconcile Mendelian inheritance with evolution by natural selection. Then, over a short interval, major disciplines within biology were recast in light of the new discoveries through the process termed the evolutionary synthesis. Between 1937 and 1944, Dobzhansky integrated population genetics theory with information on the distribution of variation within populations, Mayr did the same for systematics, and Simpson, for paleontology. But in the study of human evolution, hypotheses flatly incompatible with contemporary evolutionary theory were still being proposed as late as the 1960s. Fortunately, the increasing availability of genetic data in the 1950s and 1960s attracted to the field scientists familiar with population genetics and eventually led to a discipline fully informed by the ideas and techniques of the evolutionary synthesis. A principal architect of this late stage in the evolutionary synthesis was the Italian geneticist Luca Cavalli-Sforza. This synthesis was to prove, however, only the first of many in Cavalli-Sforza's long and astounding career.

**Genes, Peoples, and Languages**
*by Luigi Luca Cavalli-Sforza*

North Point Press (Farrar, Straus and Giroux), New York, 2000. 240 pp. $24, £18.99. ISBN 0-86547-529-6.

It is now universally agreed that the interpretation of genetic variation requires a formal population genetic framework, but population genetics alone cannot tell the story of our history. Few if any important hypotheses about human evolution have been developed solely on genetic data. There are just too many different histories compatible with present-day patterns of genetic variation. After establishing a population-genetic framework for the study of human evolution, Cavalli-Sforza quickly recognized the limitations of a narrow genetic perspective. To provide the necessary context, he and his colleagues have trawled through a stunning range of complementary disciplines including archaeology, linguistics, and physical and cultural anthropology; they have even estimated model parameters from Italian telephone registries.

In short, the synthetic and interdisciplinary nature of current research in human genetic history owes much to Cavalli-Sforza's efforts over the past 40 or so years. Although his most recent book, *Genes, Peoples, and Languages*, will make accessible and lively reading for nonspecialists, its greatest contribution may be the insights it provides into the scientific perspective and intellectual style of one of 20th-century biology's greatest synthesizers. Talented students can be easily taught what they need to know about microsatellites, gene genealogies, and statistical inference. But how does one learn to take an idea or question from archaeology and simplify it sufficiently to formulate a hypothesis testable with genetic data, but not to simplify it so much as to lose the substance of the original question? This may be the most subtle challenge in the field, and the best guidance I can suggest is a careful reading of Cavalli-Sforza's book. Despite this professional utility, outsiders to the field should not be discouraged. Cavalli-Sforza's intent is to describe the fundamental questions and approaches in human evolution, and in the main he achieves his objectives without recourse to highly specialized terminology. In discussions of cultural evolution, he uses a range of everyday examples to illustrate concepts—to make clear, for instance, how and why languages evolve and why their evolution correlates with genetic evolution. Regarding the use of population genetics, the message is often that the technical details must be correct but that the technical details are not the exciting part. This is a message for the specialist audience as well.

The trademark Cavalli-Sforza approach is perhaps most clearly represented in his discussions of gene trees and synthetic maps. Here one should note that it has become fashionable to criticize these and similar methods that rely on statistical summaries of allele-frequency data at multiple loci. Critics argue that the methods require assumptions about human demographic history that are difficult to verify. The debate is well illustrated by population trees. These trees emerge from matrices of pairwise genetic distances between populations. Under the assumption of reproductively isolated populations, branch lengths in the trees correspond to separation times between populations. If there is migration among populations, however, the branch lengths have little biological meaning. In this demographic setting, the branch lengths are determined by a combination of migration rates and separation times, and they are not useful for dissecting these parameters. Because we do not know the level of migration among human populations, some have argued that population trees should not be used and, even more strongly, that allele-frequency approaches should largely be abandoned in favor of analyses of gene genealogies that depict the ancestral relationships among sampled alleles. Unlike trees of populations, which only have biological meaning when populations bifurcate with little subsequent migration, alleles in any population, regardless of the population's demographic complexity, will have a genealogy that can be inferred and interpreted.

Anyone reading this book will realize that these criticisms are technically accurate but substantively wrong. In the author's paradigm, genetic models are never meant to be interpreted in isolation. Cavalli-Sforza does not assume that population trees are appropriate, but rather compares them with archeological data to discriminate among alternative demographic models and to fill in specific details of dates and migration routes where appropriate.

Nongenetic data are even more fundamental in the interpretation of synthetic maps produced by applying data reduction techniques to matrices of multiple allele frequencies in multiple populations. To the extent that differences in allele frequencies are correlated, the entire data set can be reasonably approximated by a much smaller data set representing the positions of the populations along each of several axes (or principal components). In the synthetic maps of Europe, populations are arranged systematically along a southeast to northwest gradient. Cavalli-Sforza and colleagues have demonstrated that population expansions into previously occupied territories can generate exactly these sorts of patterns, and they have suggested that the European pattern resulted from a massive expansion of farmers from the Near East. Critics have argued that the patterns are also consistent with a range of different demographic histories. The synthetic map based on gene frequencies, however, happens to

The author is in the Department of Biology, Galton Lab, University College London, Wolfson House, 4 Stephenson Way, London NW1 2HE, UK. E-mail: d.goldstein@ucl.ac.uk

coincide very well with the spread of farming technologies through Europe as inferred from archaeological evidence. Add linguistic data suggesting that Indo-European languages dispersed into Europe from Anatolia, and a strong case emerges for demographic expansion of Anatolian farmers into Europe. The synthetic maps not only provide support for this idea, but because the first principal component explains 28% of the total variation in sampled allele frequencies, the maps indicate that the expansion of Neolithic farming has had a decisive impact on the genetic composition of Europe.

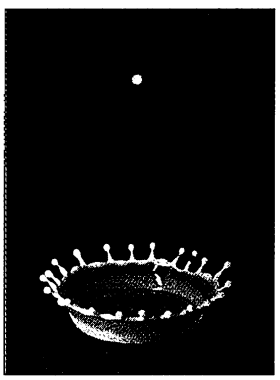
This is not to say that all of Cavalli-Sforza's interpretations are equally persuasive. The weight of evidence supporting a connection between Neolithic farming and the first principal component in Europe is compelling, but his suggestions of historical associations for the second through fifth principal components are less so. For these components, explaining less of the total variation in allele frequencies, the number of alternative historical explanations becomes quite large and the external supporting evidence modest. However, Cavalli-Sforza's aim has never been to be correct in every case, but rather to develop an eye for the subtle and ambiguous clues in genetic data. And some of the clues he sees are breathtaking. Studying synthetic maps of Africa, the author finds indications of an early expansion centered around Mali or Burkina Faso, perhaps near to the time when agriculture was developed. Aware that expansions recorded in synthetic maps would involve settlements on a sufficient scale to leave a material record, he boldly directs archaeologists to search for such settlements. Although he focuses mainly on studies of allele frequency, Cavalli-Sforza also projects infectious excitement about the growing use of high-resolution genealogical inference, which will allow us to chart the movements of individuals with unprecedented accuracy.

One can find minor shortcomings in *Genes, Peoples, and Languages*. The editing is less than attentive in places, there is some repetition, and more attention to heuristics would have helped with some of the tricky concepts. The nonspecialist may not discern the difference between gene genealogies and population trees, and would probably have difficulty defining the former. A more explicit discussion of different demographic models used in human evolution would have also been helpful, and all readers would have benefited from a review of the contexts in which different approaches are most useful: which questions are best addressed with allele-frequency data from unlinked regions, and which with detailed genealogical inference using high-resolution haplotype data from mtDNA, the Y chromosome, or low recombination autosomal regions. These criticisms, however, in no way detract from a highly readable and at times thrilling account of a career that most would consider responsible for how we study human evolution today.

**NOTA BENE: PHOTOGRAPHY**

# Frozen Moments

When visitors dropped in at his lab at the Massachusetts Institute of Technology, Harold Edgerton might hand them a postcard entitled "How to make applesauce at MIT." It was a photograph of a rifle bullet hitting an apple, captured by his electronic strobe light at the moment of impact. Edgerton started out building cameras to study the rotation of electric motors and ended up revolutionizing the art and science of photography with his innovations in electronic flash and strobe lighting. An inspiring teacher, "Doc" even became a character in the comic strip *Doonesbury*. His life and work is now the subject of a CD-ROM from MIT Press.



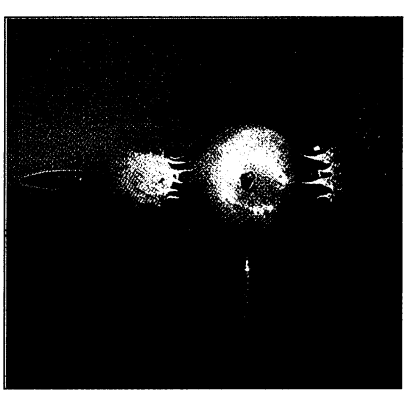
The disc is arranged like a visit to the lab, which was nicknamed "Strobe Alley." The user starts out in a simulated hallway with doors leading to different rooms. One room contains audio and video clips about Edgerton's background. With a click on the notebook, the user sees pages reproduced from his lab notebooks. Another room is an archive of Edgerton's work, arranged in desk drawers with labels such as "Bullets and Blasts" and "Athletes." It is an impressive toy chest of images, which range from the well-known shattering light bulbs and bullets cutting playing cards in half to the other-worldly scenes of atomic explosions captured microseconds after detonation. (During World War II, Edgerton had to develop radically new shutters to handle the quickness and intensity of nuclear blasts.) Also fascinating is Edgerton's undersea work with Jacques Cousteau, for who he developed waterproof strobe lights and imaging sonar equipment.

Still another room is a lab with interactive simulated strobe demonstrations. These are very elementary, but they nicely get their points across. The user can freeze the image of a computer-generated fan blade by adjusting the strobe frequency, or watch as two streams of water drops collide in midair, seemingly defying gravity. Another demonstration shows the innards of a disposable 35-mm camera with its electronic flash circuit made visible. In the same room, one can play with toys like the phenakakistoscope—a crude strobe device that was the 18th-century forerunner of motion pictures.

**Exploring the Art and Science of Stopping Time**
**The Life and Work of Harold E. Edgerton**
***Produced by James Sheldon***

MIT Press, Cambridge, MA, 1999. CD-ROM for Windows and Macintosh. $37.95, £23.50. ISBN 0-262-55031-8.

Although the CD-ROM is well done, the eye hungers for bigger, higher-resolution images of these most visual of records.



One wants to magnify the water drops and bursting bombs again and again to see the detail. And it would be nice to have full-screen video clips rather than the smallish flicker of Quicktime movies. Now that DVD-ROM technology can pack up to 17 gigabytes of info on a single disk (versus the 0.7-gigabyte capacity of CD-ROMs), we can only hope for an updated version 2.0. That could present these images in their fuller glory, possibly with Edgerton's Oscar-winning short film "Quicker 'n a Wink" thrown in as a bonus. —DAVID VOSS

CREDITS: (BOTH) HAROLD E. EDGERTON/HAROLD & ESTHER EDGERTON FOUNDATION/PALM PRESS