

# Joining forces to uncover human evolutionary history

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A meeting on Genes, Peoples and Languages, in honor of the 80th birthday of L. Luca Cavalli-Sforza, was held at the Institute for Pure and Applied Mathematics, University of California, Los Angeles, CA, USA, from 11 to 15 February 2002.

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The discovery of blood-group polymorphisms in the early 1900s provided the first anthropological markers that were easily measured, genetically simple and constant throughout individual lifetimes. Moreover, they had multiple frequent types, most of which had worldwide distributions, but whose frequencies differed among human populations [1,2]. Could it be possible to infer the history of human migrations using this genetic variation, and that of the new markers that were continually being identified? Geneticist L. Luca Cavalli-Sforza (Stanford University, Stanford, CA, USA) answered 'yes,' integrating genetics with knowledge about climate, culture, geography, language and skeletal morphology [3]. With the inherent difficulty in reconciling these diverse sources of data, reconstructing what actually happened in recent human evolution remains a challenge. The Institute for Pure and Applied Mathematics (IPAM) meeting was designed to foster discussion among the several research communities interested in this same endeavor.

Cavalli-Sforza's wide-ranging keynote address included a retrospective on his famous comparison of genes and languages, which found that trees of human populations and trees of languages can be surprisingly concordant [4,5]. One of us (D.N.) noted that, although genetic variation might be largest among Africans, the Americas, which have less genetic diversity, contain many more language families. This apparent anomaly arises from the fact that genes and languages provide different information about the past, as a result of the different forces that operate on them. For example, recent cultural

assimilation in Africa could have caused linguistic extinctions without purging genetic variability, whereas geographical fragmentation in the Americas might have led to linguistic expansions in a group that was genetically relatively homogeneous [6].

## Population genetics and archaeology

The interdisciplinary exchange at the meeting highlighted the benefits of communication between geneticists and anthropologists. As data accumulate, geneticists can develop ever more sophisticated models, constrained by archaeological results on population-size fluctuations and spatiotemporal locations of ancient peoples. Joanna Mountain's (Stanford University) work with Alec Knight demonstrated the utility of informed interdisciplinary dialogue: her description of extreme genetic distances between click-speaking Hadzabe of Tanzania and speakers of click languages in southwest Africa revives a hypothesis that clicks might have been part of a language spoken by a population ancestral to all extant humans.

Analysis of complex genetic models requires assistance from mathematics and computational statistics. Henry Harpending (University of Utah, Salt Lake City, UT, USA), Magnus Nordborg (University of Southern California, Los Angeles, CA, USA), and Charles Oxnard (University of Western Australia, Perth, Australia) showed how simulation of diverse scenarios consistent with known human history can be accomplished. However, the more difficult problem of statistical inference about what actually did happen is another matter. Because individual genomes are related through genealogical trees that arose during the stochastic process of evolution, genotypes of different individuals are inherently correlated, producing data that is not suited to standard statistical approaches. Thus, coalescent theory, specially designed for such data, will acquire a greater role [7]. Numerous subtleties in evolutionary data were presented: Susan Holmes

(Stanford University) described a novel approach to measuring distances between phylogenetic trees; one of us (N.A.R.) discussed that the time to the most recent common ancestor of a genetic sample is only weakly related to the separation time of two populations from which the sample was taken; Robert Martin (Field Museum of Natural History, Chicago, IL, USA) showed that the most ancient fossil from a group can be considerably more recent than the origin of the group itself. For the primates, this gap might be tens of millions of years [8].

## The importance of multiple markers

A key insight from the coalescent approach is that multilocus data are needed for comparing likelihoods of demographic scenarios. More generally, Marta Mirazón Lahr (Cambridge University, UK) pointed out that signals of different characters dissipate at varying rates, with linguistic change being most rapid, genetic change somewhat slower, and change of major 'morphological complexes' even slower. Thus, studies of events on a particular timescale should use markers that would have evolved on that scale. For example, Jean-Jacques Hublin (Université Bordeaux, France) and Alan Walker (Pennsylvania State University, University Park, PA, USA) showed that slowly changing allometric relationships that vary relatively little within groups are appropriate for comparisons of fossils. Walker found that slower rates of dental development, which correlate with extended life histories, might reflect the cognitive breakthroughs of modern humans; interestingly, the dental development pattern of modern humans was shared by a Neanderthal but not by apes, Australopithecines, or other species of the genus *Homo* [9].

The meeting provided a glimpse into issues that are imminent with the forthcoming glut of human genomic polymorphism data. Daniel Falush (Max Planck Institute, Berlin, Germany) presented a new algorithm

for inference of population relationships using data from many loci, demonstrating the method on the human parasite *Helicobacter pylori*, for which suitable data are already available. Multilocus studies of human populations presented by Anna Di Rienzo and Wen-Hsiung Li (both from the University of Chicago), as well as primate microarray comparisons discussed by Joseph Hacia (University of Southern California), suggest that we might soon be able to identify the loci that have undergone selection during the history of the human lineage. Whereas neutral loci can be used to help reconstruct demographic histories, selected genes, together with temporal changes in morphology and behavior, can help determine what characters led to proliferation of anatomically modern humans. Whether Richard Klein's (Stanford University) scenario of a rapid positively selected genetic change ~50 000 years ago is supported, the

linking of genomic and anthropological data, as proposed by Cavalli-Sforza, is sure to provide years of exciting work for us all.

#### Acknowledgments

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## Birds of two worlds: temperate–tropical migration systems

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The Birds of Two Worlds symposium was held at the US Fish and Wildlife Service's National Conservation Training Center, Shepherdstown, WV, USA, from 6 to 10 March 2002.

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Each spring, billions of birds begin their northward migration to summer breeding grounds. Recently, 150 biologists converged somewhat ahead of the spring migrants to discuss the ecology and evolution of these migration systems. The topics at this symposium ranged from the evolution of migration to adaptations of migrants to their summer and winter environments, constraints imposed on annual cycles by migration, and genetic and geochemical markers used to localize the origins of migrant individuals. Recent findings based on new technologies complemented the deepening insights into ecology and behavior developed through more traditional approaches.

Character mapping of migration on molecular phylogenetic trees indicates

that migratory behavior is extremely labile (A. Helbig, University of Greifswald, Germany; L. Joseph, Philadelphia Academy of Natural Sciences, PA, USA) with losses exceeding gains in North American warblers by 15 to 2 transitions (I. Lovette, Cornell University, NY, USA). Migrating species or clades of songbirds have their ancestral roots predominantly in tropical rather than temperate residents. In several groups, some nonmigratory species are derived from populations of migrants that remained in their winter quarters to form isolated breeding populations in the West Indies, southern Europe, the Indian Ocean and Australasia.

Postnatal dispersal by migrants tends to homogenize genetic variation within populations, seemingly reducing the potential of migrant species to diversify (D. Winkler, Cornell University). On a larger scale, however, migration divides between adjacent breeding populations that take alternative migration routes to disjunct wintering areas strongly inhibit mixing owing to the low fitness of hybrids that set off on inappropriate headings

(D.E. Irwin and J.H. Irwin, Lund University, Sweden). Such divides, associated for example with routes to the east and west of the Himalayan Mountains, often coincide with species boundaries. Sister-taxon relationships in clades with migrants nonetheless tend to follow north–south axes between migrants and nonmigrants, rather than east–west axes between migrant populations.

Ecological relationships of long-distance migrants differ dramatically between North America, where most species spend the winter in forested regions of the wet tropics, and the Western Palearctic, where destinations are primarily the drier, savanna and woodland habitats of tropical Africa (P. Hockey, University of Cape Town, South Africa; K. Böhning-Gaese, Universität Mainz, Germany; F. Bairlein, Institut für Vogelforschung, Germany). The habitat differences among winter migrants are paralleled in some cases by habitat preferences on the breeding grounds (T. Price, UC San Diego, CA, USA), and also appear to influence social