Genetic Variation in Africa

The demic expansion models outlined by Luigi L. Cavalli-Sforza *et al.* (Articles, 29 Jan., p. 639) provide a welcome empirical expansion of our understanding of the forms of genic exchange that linked human populations in the past. We originally used theoretical models of genic exchange, balanced against local selection and drift, as the basis for understanding the processes unifying *Homo* populations over long periods (*1*), and those of Cavalli-Sforza *et al.* confirm and extend such concepts. Genic exchange is fundamental to the multiregional evolution hypothesis, and we are not aware of any living workers who see the "parallel" emergence of modern forms that Cavalli-Sforza *et al.* describe. Far from parallelism, we see human evolution happening everywhere because every area has always been part of the whole.

Cavalli-Sforza *et al.* assert, however, as have others, that there is greater genetic diversity in Africa, both nuclear and mitochondrial, which they see as evidence for recent modern human origins on that continent. Such assertions may be misleading, as it is our expectation that Africa *should* have greater genetic diversity, whatever the source of human modernity. We see five reasons for this.

1) *Size*. Africa is huge, 35 times the size of New Guinea, where it is argued that a third of all human mitochrondrial DNA variability is to be found (*2*).

2) *Environmental diversity*. Africa is the only Old World landmass that straddles the Equator, producing two dynamic latitudinal environmental clines. Cavalli-Sforza *et al.* compare its genetic variation with that of New Guinea without compensating for the fact that Africa spans more than seven times that island's single latitudinal range. Moreover, Africa encompasses an exceptional variety of environments and geographic barriers conducive to genetic drift and relative isolation. Thus its potential for both adaptive and nonadaptive genetic variation is enormous.

3) *Time depth*. In both currently competing views of our origins, Africa has been occupied longer than any other region. Other things being equal it should have developed greater diversity in its nuclear and mitochrondrial genomes.

4) *Central place*. For much of the Pleistocene, phenotypic skeletal variability in polytypic *Homo* was greater at its African center of origin (*1, 3*). This corresponds to the expectations of central and peripheral population concepts, and we assume the phenotypic variation observed in fossil samples reflects these geographic patterns of genetic variation.

5) *Genic exchange*. There has been a tacit assumption that while Africa has been the source of genic exchange of all kinds to other areas, it has somehow remained genetically pristine and isolated. Yet genic exchange involving northern Africa, certainly in Holocene times, across the Straits of Gibraltar and from the Levant, has modified gene pools over much of northern and eastern Africa. To the southeast, Madagascar was settled by sea from Indonesia some 1000 years ago, and there is evidence that this migratory process was reflected in landings on the east African coast, yet another influence on African genomes.

For all these reasons we expect that Africa will have great, even the greatest, diversity at any time in the human past. As both the "out of Africa" and the multiregional hypotheses of modern human origins place the source of those origins in Africa, greater diversity there does not solely support either concept. Only hominid fossil and archaeological data can do that.

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2. A. C. Wilson and R. L. Cann, *Sci. Am.* **266**, 68 (April 1992).
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Response: Thorne *et al.* discuss genetic diversity in Africa and the reasons for it, a subject we only touched upon in our article. We do expect greater diversity in Africa than in the rest of the world because this continent has been occupied by modern humans and their immediate ancestors for a longer time. Thorne *et al.* give *time depth* of human occupation as the third of five reasons for this expectation, but give four other reasons, of which the first (*size*), second (*environmental diversity*), and fifth (*genetic exchange*) are unconvincing: Asia tends to come before, or to be comparable with, Africa for these three reasons; comparison with New Guinea is not taken from our article. Reason four (*central place*) is really another facet of reason three (*time depth*). The real issue, however, is the relevance of our observations to the multiregional evolution hypothesis, which these authors espouse.

This hypothesis was inspired by claims of regional continuity of cranial morphology, which are, however, far from being accepted unanimously by paleoanthropologists. Several articles in (*1*) have reexamined them independently, and there is a roughly one-to-one split among "pro" and "con" discussants. A recent, thorough reanalysis (*2*) uses a new morphological approach, reaching conclusions that disagree with the multiregional hypothesis.

What is the relevance of our observations to this hypothesis? Can one, should one, integrate it with that of demic expansions? This would involve *Homo sapiens sapiens* expanding from Africa and admixing with descendants of *H. erectus* or archaic *H. sapiens* in other parts of the world. The gene frequency data we have presented do not indicate a need to postulate such admixtures; but at the same time, they do not exclude them, as we mentioned in our article and explain in more detail (*3*). Because of the absence of recombination, mitochondrial DNA data are more informative on this issue and have so far not given evidence in favor of the participation of older local inhabitants in the European, East-Asian, or Oceanian gene pools. One cannot, however, say that this did not happen infrequently (*4*).

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4. R. L. Cann, in *The Human Revolution*, P. Mellows and C. Stringer, Eds. (Princeton Univ. Press, Princeton, NJ, 1989), pp. 17–30.

Corrections and Clarifications

Reference 4 in the article "Demic expansions and human evolution" by L. L. Cavalli-Sforza *et al.* (29 Jan., p. 639) was incorrect. It should have read as follows: "F. Weidenreich, *Evolution* **1**, 221 (1947); C. Coon, *The Living Races of Man* (Knopf, New York, 1965); M. H. Wolpoff, in (*2*), pp. 62–108."