

Origins and Affinities of Modern Humans: A Comparison of Mitochondrial and Nuclear Genetic Data

L. B. Jorde,¹ M. J. Bamshad,¹ W. S. Watkins,¹ R. Zenger,¹ A. E. Fraley,¹ P. A. Krakowiak,¹ K. D. Carpenter,¹ H. Soodyall,^{3,4} T. Jenkins,³ and A. R. Rogers²

¹Department of Human Genetics, Eccles Institute of Human Genetics, University of Utah Health Sciences Center, and ²Department of Anthropology, University of Utah, Salt Lake City; ³Department of Human Genetics, School of Pathology, The South African Institute for Medical Research, University of the Witwatersrand, Johannesburg; and ⁴Department of Anthropology, Pennsylvania State University, University Park

Summary

To test hypotheses about the origin of modern humans, we analyzed mtDNA sequences, 30 nuclear restriction-site polymorphisms (RSPs), and 30 tetranucleotide short tandem repeat (STR) polymorphisms in 243 Africans, Asians, and Europeans. An evolutionary tree based on mtDNA displays deep African branches, indicating greater genetic diversity for African populations. This finding, which is consistent with previous mtDNA analyses, has been interpreted as evidence for an African origin of modern humans. Both sets of nuclear polymorphisms, as well as a third set of trinucleotide polymorphisms, are highly consistent with one another but fail to show deep branches for African populations. These results, which represent the first direct comparison of mtDNA and nuclear genetic data in major continental populations, undermine the genetic evidence for an African origin of modern humans.

Introduction

Genetic data can reveal much about human evolution. Earlier genetic studies of human populations were based on blood group and protein polymorphisms (Nei and Roychoudhury 1982; Cavalli-Sforza et al. 1988), but these systems may not be selectively neutral and do not directly reflect variation at the DNA level. MtDNA has been used extensively in studies of human origins (Cann et al. 1987; Vigilant et al. 1991; Rogers and Harpending 1992; Sherry et al. 1994; Horai et al. 1995), and most of these analyses have shown excess genetic diversity in African populations. This result has been interpreted as support for an African origin for modern *Homo sapiens*, although some disagree with this interpretation (Spuhler

1993; Templeton 1993). Drawbacks of mtDNA are that it provides a limited amount of information about genetic variation (Nei and Livshits 1989) and that it may not be selectively neutral (Excoffier 1990). More recently, nuclear DNA polymorphisms, including restriction-site polymorphisms (RSPs) (Bowcock et al. 1991; Kidd et al. 1991) and highly variable minisatellite and microsatellite polymorphisms (Deka et al. 1991, 1995; Edwards et al. 1992; Mountain and Cavalli-Sforza 1994; Bowcock et al. 1994; Di Rienzo et al. 1994), have been used to infer human evolutionary history.

While nuclear and mtDNA data reveal some evolutionary patterns in common (Bowcock et al. 1994), the degree of concordance between these two types of data has not been closely scrutinized. In particular, no study has compared both types of genetic variation in the same individuals across major continental populations. We present the results of a direct comparison of mtDNA and nuclear variation in a series of 243 Africans, Asians, and Europeans. Our analyses show that nuclear and mtDNA data present discordant pictures of human population affinities.

Material and Methods

The study population consists of 75 Africans (22 Sotho-Tswana, 14 Tsonga, 14 Nguni, 15 San, 5 Biaka Pygmies, and 5 Mbuti Pygmies), 78 Asians (12 Cambodians, 17 Chinese, 19 Japanese, 6 Malay, and 9 Vietnamese, 2 Koreans, and 13 individuals of mixed Asian ancestry), and 90 Europeans (20 unrelated French members of the CEPH kindreds and 70 unrelated Utah males whose ancestries are traced almost exclusively to Great Britain, Denmark, Norway, and Sweden [O'Brien et al. 1994]; the latter are consequently termed "northern Europeans"). The Sotho-Tswana, Tsonga, and Nguni are all Bantu speakers who are thought to have diverged from one another during the past 1,000–2,000 years. Informed consent was obtained from all subjects whose blood was drawn at the University of Utah.

African, Asian, and European DNAs were prepared from blood or transformed lymphoblast cell lines. DNA extractions were performed by established methods (Bell et al. 1981; Sykes 1983). Genotypes for 30 tetranucleo-

Received March 8, 1995; accepted for publication June 1, 1995.

Address for correspondence and reprints: Dr. Lynn B. Jorde, Department of Human Genetics, Eccles Institute of Human Genetics, University of Utah Health Sciences Center, Salt Lake City, UT 84112. E-mail: lbj@thor.med.utah.edu

© 1995 by The American Society of Human Genetics. All rights reserved.
0002-9297/95/5703-0001\$02.00

tide short tandem repeats (STRs) and 30 RSPs were analyzed using PCR. Genomic DNA sequences were amplified in 1× buffer (10 mM Tris, pH 8.3; 50 mM KCl; and 1.5 mM MgCl₂) using 20 ng of template genomic DNA, 50 μM dNTPs, 20 pmol of each primer, and 1 U *Taq* DNA polymerase in a total reaction volume of 25 μl. Samples were cycled 30 times in a Perkin-Elmer 9600 PCR machine. For all STR systems, one primer was end-labeled using γ³²P-ATP and polynucleotide kinase. One picomole of radiolabeled primer was added to the standard PCR reaction above. PCR products for the STR systems were separated by denaturing polyacrylamide gel electrophoresis and visualized by autoradiography. PCR-amplified segments for each of the RSPs were digested for 2 h by adding 10 U of the appropriate restriction enzyme in 10 μl of 1× restriction enzyme buffer to each sample. Restriction fragments were separated by agarose gel electrophoresis (3% NuSieve) and visualized by ethidium bromide staining.

The polymorphisms of each major type (RSPs and STRs) are unlinked, and nearly all are located on separate chromosome arms. Genome Data Base (GDB) ID numbers for RSP markers are G00-178-350, G00-181-665, G00-206-704, G00-197-514, G00-180-400, G00-178-648, G00-251-590, G00-185-229, G00-171-808, G00-177-841, G00-177-108, G00-187-676, G00-285-016, G00-181-821, G00-180-411, G00-250-584, G00-178-649, G00-181-402, G00-182-559, G00-180-743, G00-196-856, G00-177-381, G00-210-937, G00-180-968, G00-182-529, G00-192-312, G00-196-905, G00-181-184, G00-182-305, G00-185-174. STR loci used in this analysis are D1S407, D1S399, D2S273, D3S1537, D3S1545, D4S1525, D4S1530, D5S580, D6S400, D6S393, D7S620, D7S623, D8S499, D8S384, D9S249, D9S762, D10S526, D10S516, D10S525, HRAS1 (GDB ID G00-187-026), VWFII (GDB ID G00-177-640), D14S119, D15S195, D16S485, D17S919, D18S390, D19S403, D19S400, D20S161, and D20S428.

The mtDNA region corresponding to hypervariable sequence-2 (HVS-2) in Vigilant et al. (1989) was PCR-amplified as described by Bamshad et al. (in press). After extensive sequencing of HVS-2 in 20 individuals, a 200-bp region corresponding to bases 71–270 of the Cambridge Reference Sequence (Anderson et al. 1981) was found to contain 90% of the polymorphisms in the region and was thus examined in all individuals. The mtDNA sequence and the allele frequencies for the STRs and RSPs are given in the appendix.

Data were analyzed at two levels of population subdivision: major continental populations (African, Asian, and European) and the 13 subpopulations listed within these major populations. Allele frequencies for each RSP and STR system were estimated directly by gene counting. Heterozygosity for each of these systems was estimated as $1 - \sum x_i^2$, where x_i is the estimated frequency of the i th allele in the system.

Standard errors of these estimates were obtained by using equation 8.7 in Nei (1987). Nucleotide diversity for the mitochondrial sequence was measured as $(n/(n-1))\sum x_i x_j \pi_{ij}$, where n is the number of individuals, x_i is the frequency of the i th mtDNA haplotype in the population, and π_{ij} is the proportion of nucleotides that differ between the i th and j th mtDNA haplotypes (Nei 1987). The standard error of this estimate was estimated using equation 10.7 of Nei (1987). The proportion of genetic variance attributable to population subdivision was estimated using the G_{ST} statistic (Wright 1965; Nei 1987). Selective neutrality of the mtDNA data was evaluated using tests devised by Tajima (1989) and Rogers (in press).

For the nuclear polymorphisms, genetic distances between pairs of populations were estimated using Nei's standard distance (Nei 1987). This measure assumes an infinite-alleles model of mutation. Genetic distances for the STRs were also estimated using a new measure formulated by Shriver et al. (1995), which weights distances by the difference in the number of repeat units and thus assumes a stepwise mutation model. For the mtDNA sequence data, Kimura's (1980) two-parameter model was used to estimate nucleotide diversity between each pair of individuals. An empirically derived transition:transversion ratio of 30:1 was used (Bamshad et al., in press). The average diversity within and between populations was then estimated by equation 10.21 of Nei (1987).

The relationships among populations were depicted by neighbor-joining trees (Saitou and Nei 1987), using programs in the PHYLIP package (Felsenstein 1993). The neighbor-joining method tends to provide more accurate estimates of population affinities than some other methods because it does not assume equal evolutionary rates in each branch of the tree (Nei and Roychoudhury 1993). Two other tree-making methods (the Fitch-Margoliash least-squares method and the unweighted pair-group method using arithmetic averages) yielded similar results (data not shown). To assess the reliability of these trees, 1,000 bootstrap replicates were run for each set of systems.

The degree of congruence among the STR, RSP, and mtDNA distance matrices was evaluated using the Mantel matrix comparison test (Mantel 1967; Smouse et al. 1986). This test yields a product-moment correlation coefficient for each pair of distance matrices. An empirical significance level is obtained by repeatedly permuting the columns of one of the distance matrices and comparing the actual correlation coefficient with those generated from the permuted matrices. Each pair of matrices was permuted 10,000 times.

Results and Discussion

Genetic Diversity within Major Populations

The gene diversities for each major population are given in table 1. Europeans exhibit the highest level of

Table 1

Gene Diversity (\pm Standard Error) for Each Major Population

	RSPs	STRs	mtDNA ^a
Africans322 \pm .073	.769 \pm .102	.031 \pm .001
Asians377 \pm .052	.681 \pm .074	.011 \pm .001
Europeans432 \pm .032	.724 \pm .086	.010 \pm .001
Overall377 \pm .018	.725 \pm .020	.020 \pm .001

^a Diversity at the nucleotide level. The standard error estimates include sampling variance only. The standard errors for the mtDNA nucleotide diversity are larger if stochastic variance is also included.

heterozygosity for RSPs, while Africans have the lowest heterozygosity level. This pattern has been seen in other studies of RSPs (Bowcock et al. 1991) and could reflect the fact that most of these polymorphisms were first detected in European populations (Mountain and Cavalli-Sforza 1994). In contrast, the highest STR heterozygosity values are seen in Africans, and the lowest are seen in Asians. The average number of STR alleles per locus is highest in Africans (9.5), intermediate in Europeans (8.2), and lowest in Asians (8.1). These differences are not statistically significant using a one-way analysis of variance, however, and the standard errors of the heterozygosity estimates given in table 1 show that these values are not significantly different.

The gene diversity values based on mtDNA are similar in magnitude to values obtained in other studies (Horai et al. 1993). These diversity values differ significantly, with African diversity approximately three times higher than that of Asians and Europeans.

Application of Tajima's (1989) neutrality test to the mtDNA data shows that gene diversity in Europeans and Asians is considerably lower than predicted by neutral theory ($D = -1.43$ and -1.46 , respectively). The African gene diversity is greater than predicted by neutral theory ($D = 0.60$). However, these values lie within the 90% confidence limits of the neutral prediction, so the neutrality hypothesis is not rejected by this test. Rogers's test, which is based on the distribution of nucleotide differences within populations, rejects the hypothesis of mutation-drift equilibrium. This is consistent either with a rapid expansion of the human population or with a departure from selective neutrality.

Genetic Diversity between Populations

The genetic distances between each pair of continental populations are given in table 2. In each system—RSPs, STRs, and mtDNA—the Asian-European distance is smaller than the African-Asian and African-European distances. The Africans are more divergent for mtDNA sequence than for the two sets of nuclear polymorphisms: the ratio of distances involving Africans to those not involving Africans is approximately 2:1 for nuclear polymorphisms but 9:1 for the mtDNA sequence.

Table 2 also lists the G_{ST} values for each system. The G_{ST} estimate for RSPs, .107, indicates that ~11% of genetic variation can be attributed to subdivision at the level of major continental populations. This value lies within the 10%–15% range seen in other studies of RSPs (Bowcock et al. 1991), protein and blood group polymorphisms (Jorde 1980; Nei 1993; Cavalli-Sforza et al. 1994), and craniometric data (Relethford and Harpending 1994). The G_{ST} value obtained from STRs, .034, is substantially smaller than the value obtained from RSPs and likely reflects the relatively high STR mutation rate. It should be emphasized, however, that this estimate of G_{ST} does not take differences in STR allele sizes into account.

The G_{ST} estimate for mtDNA sequence, .199, is higher than the estimates based on nuclear polymorphisms. This difference may be attributed to the fact that the effective population size of mtDNA is one-fourth that of nuclear DNA (Birky et al. 1983), producing more rapid genetic drift for mtDNA polymorphisms. Previous G_{ST} estimates derived from mtDNA restriction site data range from .31 to .46 and are thus substantially higher than our estimate (Stoneking et al. 1990; Merriwether et al. 1991). In part, this may be because the control region, from which the present G_{ST} estimate was derived, has a much higher mutation rate than the remainder of the mitochondrial genome, from which the previous estimates were derived. In addition, the previous G_{ST} estimates were obtained using the method of Takahata and Palumbi (1985), which appears to yield inflated values (Harpending et al., in press).

Figure 1 displays a neighbor-joining tree based on mtDNA data in 13 subpopulations. All 13 subpopulations cluster into the appropriate major continental groups (Africans, Asians, and Europeans). Long branch lengths are seen for most of the African populations. This pattern has been observed in most other mtDNA analyses and has been a major component of the argument for an African origin of modern humans (Cann et al. 1987; Vigilant et al. 1991; Stoneking 1993). The non-African populations have comparatively short branch lengths, and the nodes separating these populations are very close to one another.

Figure 2, which presents a neighbor-joining tree estimated from RSP data, demonstrates pronounced clustering of each of the three major continental populations. As has been seen in other studies (Bowcock et al. 1994; Cavalli-Sforza et al. 1994), the Mbuti Pygmies have a long branch length; this may be caused by small effective population size. The Malay sample, which was derived from an aboriginal population, also has a long branch length. In contrast to the mtDNA tree, the African populations do not display markedly longer branch lengths in the RSP tree.

A neighbor-joining tree based on STRs is shown in figure 3. The distance measure of Shriver et al. (1995),

Table 2

Genetic Distances between Major Populations for Each Major Genetic System

	RSPs ($G_{ST} = .107$)	STRs ^a ($G_{ST} = .034$)	mtDNA ($G_{ST} = .199$)
African-Asian154	.024	.009
African-European124	.016	.010
Asian-European066	.010	.001

^a The distances reported for STRs were estimated using the method of Shriver et al. (1995).

which assumes a stepwise mutation process, was used in estimating the tree. Figure 3 closely resembles figure 2, with populations clustering into major continental groups. This marked clustering argues against the hypothesis that the low G_{ST} values seen for STRs reflect interpopulation convergence resulting from forward-backward mutation (Bowcock et al. 1994). Instead, the high STR mutation rates produce low G_{ST} values because of a high level of within-group diversity relative to total diversity (Jin and Chakraborty, in press). Genetic

distances, however, can remain large and well defined, as observed in the present analysis.

An STR tree based on Nei's standard distance, which assumes an infinite alleles model, was less similar to the RSP tree and displayed less clear separation of continental population groups. This result provides indirect evidence that STR variation is modeled more accurately by a stepwise mutation process (such as replication slippage) than by an infinite alleles process (such as unequal chromosome exchange) (Shriver et al. 1993; Di Rienzo et al. 1994).

Table 3 contains the Mantel matrix correlations for each pair of distance matrices. These correlations give quantitative support to the visual interpretations of the

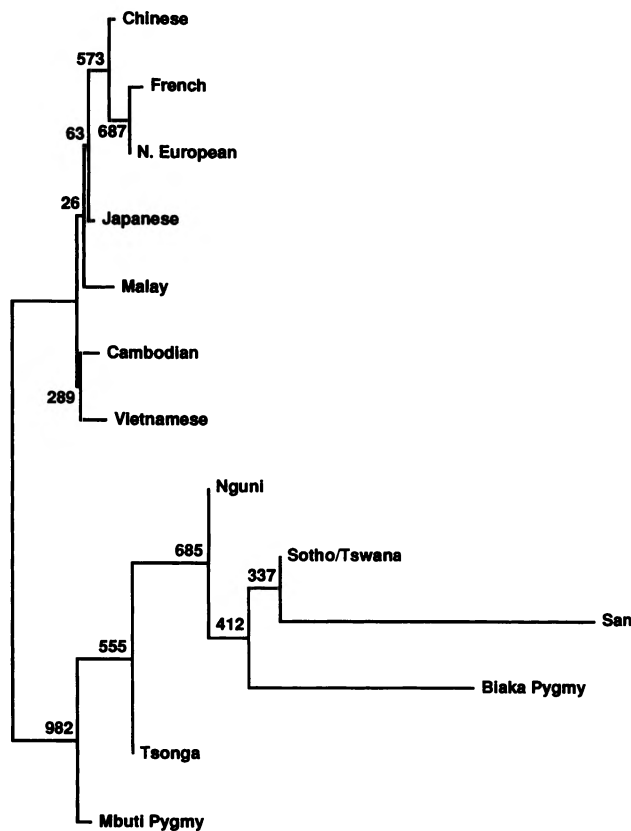


Figure 1 Neighbor-joining tree based on mtDNA sequence data. In this and all subsequent figures, the numbers listed next to branch nodes indicate the no. of times that the bootstrapped replicates supported the branches to the right of the node. Absent numbers indicate that the configuration of the actual tree differed from that of the consensus tree at this node.

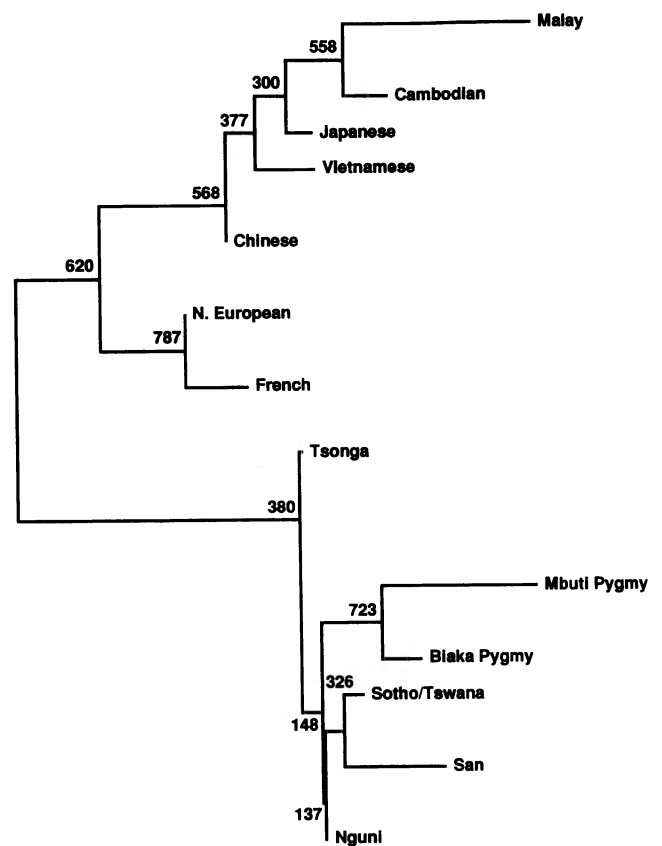


Figure 2 Neighbor-joining tree based on Nei's standard distance for 30 RSPs (Nei 1987). See legend to fig. 1.

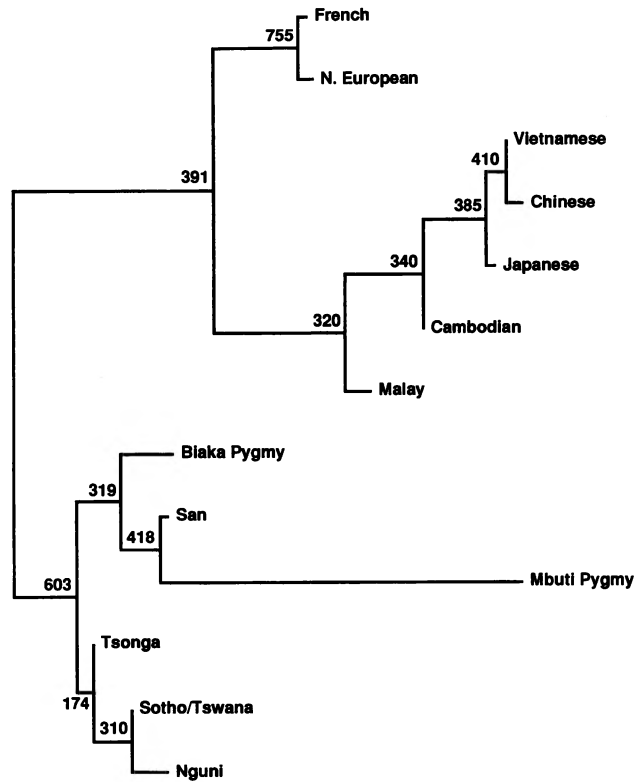


Figure 3 Neighbor-joining tree based on Shriver et al.'s (1995) distance for 30 STRs. Bootstrapping was done using each locus (rather than each allele) as the sampling unit. See legend to fig. 1.

neighbor-joining trees. In addition to the data sets described above, a distance matrix based on five trinucleotide repeat systems (Huntington disease, spinal bulbar muscular atrophy, spinal cerebellar ataxia type 1, myotonic dystrophy, and dentatorubral pallidoluysian atrophy [DRPLA]) is included. These data, which are described fully by Watkins et al. (in press), were generated on the same study population as the RSP, tetranucleotide, and mitochondrial systems. The tetranucleotide

and RSP distances yield a large and highly significant correlation ($P < 10^{-4}$), and the correlation is higher when the distance measure of Shriver et al. (1995) is used for the tetranucleotides. The trinucleotide repeat distances are also highly correlated with both of the other sets of nuclear systems ($P < 10^{-4}$). In contrast, all of the correlations involving mtDNA with nuclear systems are lower and either less significant or nonsignificant. The largest correlation is seen with RSPs ($r = .512, P < .001$), while the correlations with tetranucleotide systems are nonsignificant ($P > .05$) and the correlation with trinucleotide systems is low and marginally significant ($r = .219; .04 < P < .05$).

Implications for Modern Human Origins

Our mtDNA results are consistent with those of most other studies in showing increased gene diversity and long branch lengths for African populations. The nuclear DNA results are also consistent with previous studies of nuclear blood group and protein polymorphisms (Cavalli-Sforza et al. 1988; Nei and Roychoudhury 1993), RSPs (Bowcock et al. 1991), dinucleotide repeat polymorphisms (Bowcock et al. 1994; Di Rienzo et al. 1994; Deka et al. 1995), and a sample of four *Alu* polymorphisms (Batzer et al. 1994) in showing greater divergence for African populations than for other populations.

Although all data types suggest greater African divergence, the degree of divergence is less for the nuclear data than for the mtDNA data. In addition, while the nuclear RSP and STR results are highly concordant, there is less concordance between the mtDNA and nuclear results shown in figures 1–3. This has important implications for genetic inferences about modern human origins, since population history should affect mtDNA and nuclear DNA variation similarly. There are several possible reasons for this discordance:

1. *Ascertainment bias in nuclear polymorphisms.*—The mtDNA polymorphisms cannot be affected by an ascertainment bias, because they were obtained from DNA sequence ascertained uniformly in all populations. The

Table 3

Mantel Matrix Correlations for Each Pair of Genetic Distance Matrices

	RSP	STR (Nei's distance [Nei 1987])	STR (Shriver's distance [Shriver et al. 1995])	Trinucleotides
mtDNA512 ^a	.359	.274	.219 ^b
RSP655 ^c	.769 ^c	.747 ^c
STR (Nei's distance)814 ^c	.555 ^c
STR (Shriver's distance)640 ^c

NOTE.—Other correlations are nonsignificant.

^a $P < .001$.

^b $.04 < P < .05$.

^c $P < 10^{-4}$.

RSPs were detected primarily in Europeans, and the resulting bias may contribute to the excess European heterozygosity in the RSP data. This is unlikely, however, to be the sole cause of increased heterozygosity. A statistical analysis of ascertainment bias in two-allele systems demonstrates that this bias can account for no more than half of the excess European heterozygosity (A. R. Rogers and L. B. Jorde, unpublished information). A parallel analysis of systems with multiple alleles shows that ascertainment bias is negligible for the highly heterozygous STR polymorphisms. If ascertainment bias were responsible for the discordance observed here, one would predict that the RSPs, which presumably have the greatest degree of bias, would have the lowest correlation with mtDNA sequence. Instead, table 3 shows that they have the highest correlation. In addition, one of the expanded trinucleotide repeat polymorphisms, DRPLA, was ascertained in Asians. Yet this polymorphism yields a neighbor-joining tree with the same configuration as the tetranucleotide tree, with roughly equal branch lengths in Africans and Asians (Watkins et al., in press). Given these results, it is unlikely that ascertainment bias alone accounts for the discordance between mtDNA and nuclear DNA results.

2. *Differences in substitution rates.*—The substitution rate in the mtDNA HVS-2 region is estimated to be ~12.5% per nucleotide per million years, or 3×10^{-6} per nucleotide per generation (Sherry et al. 1994). This is considerably higher than that of the RSPs, whose substitution rate is estimated to be 10^{-7} – 10^{-9} per nucleotide per generation (Nei 1987; Bowcock and Cavalli-Sforza 1991). The mutation rates for tetranucleotide repeats are the highest of the three systems, estimated at 10^{-4} – 10^{-3} per generation (Edwards et al. 1992; Weber and Wong 1993). If substitution rates accounted for the discordance observed here, one would expect the two nuclear substitution rates to be most similar to one another. Instead, the mtDNA substitution rate is intermediate between those of the two sets of nuclear polymorphisms.

3. *Inadequate sample sizes.*—All population genetic analyses are necessarily based on a limited collection of individuals and polymorphisms. It is unlikely that the differences observed here are caused by a limited sample size, because all three nuclear data sets produce highly consistent results and the mtDNA results are consistent with those published previously using different population samples and different portions of the mtDNA genome (hypervariable sequence 1 and RSPs outside the *D* loop). Nonetheless, the degree of resolution of the mtDNA data is limited by the fact that the mtDNA molecule is effectively a single locus.

4. *Differences in male-female migration rates or effective population sizes.*—Because mtDNA is maternally inherited while nuclear DNA is biparentally inherited, differences in the two types of data could be produced by differences in male-female migration patterns or effective popula-

tion sizes. Higher mtDNA diversity between African populations would then require that male dispersal has been greater than female dispersal in African populations and/or that fewer females than males contributed to the African gene pool for a long period. Additional light will be shed on these possibilities as more information is gained about genetic variation in human Y chromosome DNA (Spurdle and Jenkins 1992).

5. *Lack of selective neutrality in mtDNA.*—An important assumption in inferring population history from genetic data is that genetic polymorphisms are selectively neutral. The RSPs and STRs used in this study occur primarily in noncoding DNA, and most appear to meet this assumption (Bowcock et al. 1991; Shriver et al. 1993). In contrast, mtDNA polymorphisms outside the noncoding *D* loop show a departure from neutrality (Excoffier 1990; Merriwether et al. 1991; Templeton 1993), with a relative lack of diversity seen in Asians and Europeans. The HVS-2 data analyzed here show a similar departure from neutrality in Asians and Europeans, although it is not statistically significant. These departures may reflect the action of natural selection, or they could be the result of past population expansions (Rogers and Harpending 1992; Rogers, in press). Since there is no recombination in the mitochondrial genome, natural selection on a coding gene will exert a substantial genetic “hitchhiking” effect, even on polymorphisms in the noncoding *D* loop. It is thus possible that the differences seen here in mtDNA and nuclear DNA may be produced by natural selection rather than population history.

Increased mtDNA diversity in Africans has been a linchpin of the argument that modern humans originated in Africa and then replaced existing archaic populations on other continents. Proponents of this view argue that since Africa is more diverse genetically, its population must be older (Stoneking 1993). However, diversity can be strongly affected by events in a population's history, such as the timing of major bottlenecks, and therefore does not necessarily reflect a population's age (Rogers and Jorde 1995). Our findings further compromise the diversity argument by showing that nuclear DNA trees lack the deep branches (and thus the excess genetic diversity) observed in mtDNA trees. These results do not disprove the African replacement hypothesis. However, they weaken the genetic evidence in its favor.

Acknowledgments

We wish to thank Li Jin for providing a computer program that calculates the Shriver et al. (1995) distance and Kenneth and Judith Kidd for providing Asian DNA samples. Elisabeth Manderscheid aided in blood sample collection. This research was supported by NSF grants BNS-8720330 and DBS-9310105, the Clinical Research Center of the University of Utah (NIH RR-00064), the Technology Access Center of the Utah Human Genome Project, and a supplemental equipment grant from the University of Utah.

Appendix

The data in figures A1–A3 are available in computerized format from the authors.

Locus	Allele	SO	TS	NG	BI	SA	CA	CH	JA	MA	VI	NE	FR	MB
D1S407	1	263	0	0	0	0	0	0	0	0	556	0	0	0
	2	0	357	714	0	333	417	294	789	0	0	447	278	1000
	3	1579	3213	3213	1000	2333	1250	2059	1316	1667	2222	1342	2778	1000
	4	4211	4286	2857	4000	2667	3333	4412	3421	833	3889	5299	3889	2000
	5	3158	714	1786	4000	2333	2083	2647	3684	7500	3333	1866	1667	4000
	6	526	1071	1071	0	1000	2917	588	789	0	0	895	833	2000
	7	0	0	0	0	1000	0	0	0	0	0	75	0	0
	8	0	0	0	0	333	0	0	0	0	0	75	556	0
	9	263	357	357	1000	0	0	0	0	0	0	0	0	0
D1S399	1	0	357	0	0	0	0	294	0	556	231	0	0	0
	2	333	357	0	2000	714	417	625	0	0	769	1053	0	0
	3	333	357	0	0	357	0	0	0	0	385	263	0	0
	4	1667	1071	1154	2000	0	0	625	0	0	1111	769	526	0
	5	333	714	1154	0	0	0	0	0	0	231	0	0	0
	6	0	0	0	0	0	1667	0	588	833	0	308	263	0
	7	5000	4286	4615	3000	6429	6667	5938	8529	7500	7778	6308	6579	8750
	8	2000	2143	2692	2000	1786	1250	2500	588	1667	556	769	526	1250
	9	333	0	0	1000	714	0	312	0	0	0	231	789	0
	10	0	714	385	0	0	0	0	0	0	0	0	0	0
D2S273	1	0	0	0	0	0	0	0	0	0	0	250	0	0
	2	526	714	0	0	908	0	0	278	1000	2857	785	750	1000
	3	1316	714	1071	0	908	2083	3235	2222	2000	714	1857	2250	3000
	4	2895	714	2143	3000	1817	833	1764	1667	1000	2143	1786	2000	2000
	5	2105	1786	3571	2000	4545	417	2647	556	3000	2857	2357	2250	2000
	6	1053	2500	1429	0	0	4167	1764	3333	3000	714	1357	1500	2000
	7	1842	3571	1786	5000	1817	2500	588	1667	0	714	1857	1000	0
	8	263	0	0	0	0	0	0	0	0	0	0	0	0
	9	0	0	0	0	0	0	0	278	0	0	0	0	0
D3S1537	1	0	0	0	1000	0	0	0	0	0	0	0	0	0
	2	789	357	0	0	357	1250	588	1764	1000	556	662	0	4000
	3	1316	2857	769	2000	1429	3333	3824	3235	0	3889	3824	3000	0
	4	1053	1071	769	2000	0	2083	1764	1471	1000	1111	956	250	1000
	5	1316	714	2308	0	1786	0	0	0	1000	556	515	1250	0
	6	4737	5000	5385	5000	3571	3333	3824	3529	7000	3333	3676	4250	2000
	7	789	0	769	0	2857	0	0	0	0	556	368	1000	2000
	8	0	0	0	0	0	0	0	0	0	0	0	0	1000
	9	0	0	0	0	0	0	0	0	0	0	0	250	0
D3S1545	1	0	0	0	0	0	417	0	0	0	0	0	0	0
	2	0	0	0	0	333	0	0	0	0	0	72	0	0
	3	526	0	357	0	1000	1667	1250	263	1250	556	362	750	0
	4	1579	1429	714	2500	1667	2917	3438	1842	0	2778	2464	2250	1000

Locus	Allele	SG	TS	NG	BI	SA	CA	CH	JA	MA	VI	NE	FR	MB
D4S1525	5	2632	1071	2500	2500	5000	1667	1875	5263	5000	2778	3477	3250	2000
	6	2368	1429	1786	1250	1000	417	2500	1842	2500	3333	2464	2750	6000
	7	1053	2857	1071	0	666	0	0	263	0	0	72	250	0
	8	0	0	0	3750	0	0	0	0	0	0	145	0	0
	9	263	714	0	0	333	1250	625	263	1250	556	942	750	1000
	10	1579	2500	3571	0	0	1667	312	263	0	0	0	0	0
	1	263	0	0	0	714	0	0	0	0	0	0	0	0
	2	1316	2143	357	2000	2500	0	0	0	0	0	72	0	0
	3	1053	714	357	3000	1071	0	588	278	0	0	507	833	6000
	4	526	1071	714	2000	1071	2083	1176	1111	2000	1667	797	833	0
5	1842	714	1429	2000	714	2083	2940	3889	4000	6667	580	1111	3000	
6	2368	2143	4286	1000	1429	3750	2940	1667	3000	1667	1304	1667	0	
7	1053	1786	1429	0	1071	1667	2059	2500	1000	0	2101	2500	1000	
8	526	1071	1071	0	714	417	294	556	0	0	3841	2222	0	
9	263	357	357	0	357	0	0	0	0	0	362	556	0	
10	789	0	0	0	357	0	0	0	0	0	0	0	0	
11	0	0	0	0	0	0	0	0	0	0	435	278	0	
D4S1530	1	263	0	0	0	714	0	0	0	0	0	72	0	0
	2	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0	0	72	0	0
	4	0	0	0	0	0	0	0	0	1579	0	72	789	0
	5	263	1071	1071	0	0	0	588	0	0	0	145	789	0
	6	263	357	714	0	714	455	882	789	0	1429	217	263	1250
	7	1842	1786	1429	0	357	3635	1764	789	2000	1429	580	526	1250
	8	2105	1071	2857	5000	2500	1364	2647	2105	3000	2857	870	1316	1250
	9	1842	1429	2500	1250	2857	1364	1176	2632	1000	2857	1884	2632	1250
	10	1579	2857	1071	2500	1429	1817	1176	1053	2000	1429	2029	1842	1250
	11	789	714	0	0	714	908	1176	1053	2000	0	2391	1053	2500
	12	263	357	0	1250	357	455	588	0	0	0	1232	526	0
	13	789	357	357	0	357	0	0	0	0	0	217	0	1250
	14	0	0	0	0	0	0	0	0	0	0	217	263	0
D5S580	1	0	0	357	0	0	0	0	0	0	0	0	0	0
	2	0	0	357	2000	0	0	0	0	0	0	72	0	0
	3	0	0	714	0	0	417	0	0	0	0	72	0	0
	4	0	357	0	0	0	0	0	0	0	1111	0	263	0
	5	263	0	0	0	0	833	0	0	0	0	362	263	0
	6	263	357	1071	1000	385	833	0	263	1250	0	362	0	0
	7	526	714	357	0	385	0	294	263	0	0	507	1579	2500
	8	263	714	357	1000	1538	417	0	0	0	0	580	526	0
	9	263	357	0	0	385	0	0	263	0	0	652	526	5000
	10	0	0	357	0	769	417	0	0	0	556	652	0	0
	11	789	1429	0	2000	0	0	882	0	0	0	435	263	0

Locus	Allele	SO	TS	NG	BI	SA	CA	CH	JA	MA	VI	NE	FR	MB
	12	263	0	714	1000	2308	0	588	526	0	0	362	263	2500
	13	1316	714	714	0	769	0	0	526	0	0	290	526	0
	14	1316	1071	357	1000	769	833	0	0	0	0	362	263	0
	15	1842	1429	714	2000	769	417	0	0	0	556	580	1053	0
	16	0	357	0	0	385	0	294	0	1250	556	0	0	0
	17	263	1429	357	0	385	0	0	0	0	0	72	0	0
	18	526	0	357	0	0	0	0	526	0	0	0	0	0
	19	526	714	1071	0	385	417	588	1842	2500	1111	507	526	0
	20	263	0	0	0	0	0	0	0	0	0	0	0	0
	21	1316	357	2143	0	769	5417	7353	5789	5000	6111	3986	3947	0
	22	0	0	0	0	0	0	0	0	0	0	145	0	0
D6S400	1	0	0	0	0	0	0	0	312	0	0	0	0	0
	2	0	0	0	2000	833	417	0	0	0	0	74	0	1000
	3	938	385	1923	0	833	0	0	0	0	0	0	0	4000
	4	938	769	385	1000	417	833	294	0	0	0	294	526	0
	5	938	1538	1923	2000	0	0	0	0	1250	0	147	0	1000
	6	938	385	769	0	1250	0	0	312	0	0	221	789	0
	7	2500	2308	1538	0	1667	833	588	312	3750	556	1103	526	0
	8	625	385	769	1000	2500	0	294	0	0	0	515	1053	1000
	9	312	769	385	0	833	0	0	0	0	0	0	0	1000
	10	625	385	1154	0	833	1667	588	312	0	2778	1324	789	1000
	11	2188	3077	1154	4000	833	6250	8235	8750	5000	6667	6250	6316	1000
	12	0	0	0	0	0	0	0	0	0	0	74	0	0
D6S393	1	263	357	357	0	0	0	312	263	0	556	71	0	0
	2	526	357	0	0	357	0	0	263	3000	556	429	0	1000
	3	526	1071	1429	2000	714	2500	2500	3158	2000	4444	2500	2500	0
	4	0	1786	1429	1000	2143	3750	1250	526	2000	1111	214	500	1000
	5	2105	1071	0	3000	714	833	1562	1053	2000	0	1714	1250	6000
	6	5789	4643	5714	4000	5000	833	938	1842	0	1667	714	1000	0
	7	789	714	1071	0	357	0	0	0	0	0	71	0	0
	8	0	0	0	0	714	2083	3438	2895	1000	1667	4286	4750	2000
D7S620	1	0	0	0	1000	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0	0	0	0	1000
	3	0	0	0	0	0	0	0	0	0	0	147	0	1000
	4	1842	357	2500	1000	1000	417	882	1842	0	2500	1324	1316	2000
	5	2895	3571	1071	1000	3667	4167	5000	4211	4167	4167	4191	3684	1000
	6	3421	2857	3571	3000	1667	3750	3235	3684	2500	2500	3382	4211	4000
	7	526	357	1071	2000	1667	1667	588	263	3333	833	882	526	1000
	8	526	357	1071	2000	1000	0	294	0	0	0	74	263	0
	9	789	1786	714	0	1000	0	0	0	0	0	0	0	0
	10	0	714	0	0	0	0	0	0	0	0	0	0	0
D7S623														

Locus	Allele	SO	TS	NG	BI	SA	CA	CH	JA	MA	VI	NE	FR	MB
	1	0	769	0	0	0	0	294	0	0	0	214	0	0
	2	263	1154	714	0	1071	2083	882	0	0	556	714	1000	0
	3	2895	2692	3571	9000	3213	5000	4706	3684	5000	5556	3786	2750	2000
	4	3684	5000	3213	1000	3929	2917	3824	5263	5000	3333	4143	5750	4000
	5	2368	385	1786	0	1071	0	294	1053	0	0	1000	500	2000
	6	789	0	357	0	357	0	0	0	0	556	143	0	2000
	7	0	0	357	0	357	0	0	0	0	0	0	0	0
D8S499	1	0	385	0	0	0	0	0	0	0	0	0	0	0
	2	0	0	357	0	0	0	0	0	0	0	0	0	0
	3	278	0	0	0	0	0	0	0	0	0	0	0	0
	4	278	385	0	0	0	833	882	0	0	0	357	0	0
	5	833	1154	1071	0	357	0	588	263	2500	714	1214	750	0
	6	1389	769	714	0	714	1250	588	526	833	0	500	1000	2000
	7	1389	1923	2143	5000	714	1250	294	789	0	1429	643	750	1000
	8	833	769	0	0	2500	0	0	0	0	0	286	0	0
	9	833	385	714	1000	714	417	0	526	0	0	0	0	2000
	10	1667	769	1786	1000	2857	0	0	263	0	2143	1000	1750	4000
	11	1667	1154	1429	0	1786	833	588	263	2500	2143	1929	1250	1000
	12	833	2308	1786	3000	0	2500	6765	4474	3333	3571	2071	2000	0
	13	0	0	0	0	357	2083	294	2895	833	0	2000	2500	0
	14	0	0	0	0	0	833	0	0	0	0	0	0	0
D8S384	1	0	0	0	0	0	0	0	0	0	0	214	500	0
	2	263	0	0	0	0	0	0	588	0	0	1357	3500	0
	3	2368	4286	714	2000	0	2273	1562	588	1000	625	2000	3250	0
	4	3684	4643	3929	4000	1786	4091	3125	5294	3000	3125	3856	2250	4000
	5	2895	357	5000	4000	5357	3635	3125	2940	4000	3750	2000	250	5000
	6	526	0	357	0	1429	0	1875	294	2000	2500	429	250	0
	7	0	714	0	0	1071	0	312	294	0	0	143	0	1000
	8	263	0	0	0	357	0	0	0	0	0	0	0	0
D9S249	1	5789	7143	6071	3000	5000	2917	3529	2895	5000	5000	6500	6000	9000
	2	4211	2500	3571	7000	5000	7083	6470	7105	5000	5000	3500	4000	1000
	3	0	357	357	0	0	0	0	0	0	0	0	0	0
D9S762	1	0	0	0	0	0	0	417	0	0	1250	556	0	0
	2	0	0	0	0	357	417	333	0	0	556	0	0	0
	3	0	1154	769	0	357	417	666	1667	1250	0	682	0	0
	4	1429	3077	2308	3000	2857	1250	666	666	0	0	2652	2222	3000
	5	3571	2308	1923	6000	3213	2917	2333	1333	3750	2222	2652	3889	2000
	6	3571	1923	3462	1000	1429	1667	1667	2333	2500	1667	2727	2778	3000
	7	714	1538	1538	0	1429	2917	4333	4000	1250	5000	1136	1111	2000
	8	714	0	0	0	357	0	0	0	0	0	152	0	0
D10S526	1	263	0	0	0	0	0	625	0	0	1111	227	263	0

Locus	Allele	SO	TS	NG	BI	SA	CA	CH	JA	MA	VI	NE	FR	MB
	2	263	0	0	0	833	625	526	1000	1111	682	1842	0	
	3	263	769	0	0	666	417	1250	0	0	682	2105	2000	
	4	263	385	0	1000	1333	417	2188	1053	0	556	1364	526	1000
	5	263	385	1071	1000	333	0	312	0	0	556	908	263	0
	6	0	385	357	0	0	0	0	263	0	1111	1288	526	0
	7	0	0	0	0	0	0	312	789	0	0	379	0	0
	8	0	0	0	0	333	417	0	0	1000	0	152	0	0
	9	0	385	0	0	0	0	0	0	0	0	0	0	0
	10	0	0	0	0	333	417	0	0	0	0	0	263	0
	11	263	0	0	0	666	0	0	0	0	0	0	0	0
	12	526	1538	1786	2000	666	833	938	526	0	1667	227	526	1000
	13	3158	3077	1786	1000	666	1667	1562	2105	6000	0	530	1579	2000
	14	1316	1154	1071	1000	1667	1250	938	1579	1000	0	758	526	2000
	15	2105	769	1429	2000	2333	3333	1250	2368	0	3889	1591	1316	1000
	16	0	0	2143	1000	1000	417	0	789	1000	0	1212	263	0
	17	1053	769	357	1000	0	0	0	0	0	0	0	0	1000
	18	263	385	0	0	0	0	0	0	0	0	0	0	0
D10S516	1	263	385	0	0	357	0	588	278	0	556	145	0	0
	2	263	769	714	2000	0	455	588	556	0	556	362	250	3750
	3	526	1154	357	1000	357	2273	294	1389	0	1667	652	500	2500
	4	0	385	0	1000	714	0	588	1111	1000	0	145	500	0
	5	789	0	0	0	714	0	0	0	0	0	72	0	0
	6	0	0	0	0	0	0	0	0	0	556	507	0	0
	7	0	0	357	0	0	455	0	0	0	0	507	750	0
	8	0	0	357	0	357	0	294	278	0	1111	652	0	0
	9	2105	1538	2143	3000	1429	1817	1764	1944	3000	1111	2029	2000	1250
	10	1053	3077	357	1000	2143	5000	4412	1944	4000	2222	2464	3750	1250
	11	2895	1538	4643	1000	2857	0	1176	1667	2000	1111	1594	2000	1250
	12	1842	1154	1071	1000	357	0	0	833	0	1111	870	250	0
	13	263	0	0	0	714	0	294	0	0	0	0	0	0
D10S525	1	263	714	357	0	0	0	0	0	0	0	0	0	0
	2	0	0	357	0	385	0	0	0	1000	0	76	0	0
	3	1579	0	357	3000	1154	2917	0	1250	3000	2778	833	1111	4000
	4	3158	3571	2857	5000	5000	4583	5667	5000	3000	5000	4091	3889	1000
	5	2895	2500	4643	1000	2308	2083	2333	2500	2000	1111	2955	3055	4000
	6	2105	2857	1429	1000	1154	417	1000	1250	1000	1111	2045	1944	1000
	7	0	357	0	0	0	0	1000	0	0	0	0	0	0
HRAS1	1	7500	6538	7143	6000	5909	9091	7941	7667	7000	8889	6154	5500	8000
	2	556	0	0	0	1817	0	0	0	0	556	1769	1750	0
	3	1944	3462	2857	4000	2273	908	2059	2333	3000	556	2077	2750	2000
VWFI1	1	263	0	0	0	417	0	0	0	0	556	71	0	0

Locus	Allele	SO	TS	NG	BI	SA	CA	CH	JA	MA	VI	NE	FR	MB
	2	263	357	1071	1000	417	5000	2500	1764	1667	3333	1000	500	0
	3	789	2143	1429	2000	1667	500	1250	1176	833	556	429	750	1000
	4	4737	3929	3213	3000	5417	2000	1562	2940	833	1667	3643	3000	6000
	5	2632	2500	2857	4000	1250	1500	3438	3529	4167	1667	3143	4000	3000
	6	789	357	714	0	0	0	625	294	833	0	714	1500	0
	7	0	357	357	0	0	1000	625	294	1667	2222	1000	250	0
	8	263	357	357	0	833	0	0	0	0	0	0	0	0
	9	263	0	0	0	0	0	0	0	0	0	0	0	0
D14S119	1	0	0	0	0	333	0	0	0	0	556	0	0	0
	2	556	0	357	0	0	0	0	0	0	556	286	250	0
	3	278	385	714	1000	0	417	0	263	833	556	571	250	0
	4	1111	769	2143	1000	2000	417	1250	2368	1667	556	785	1000	0
	5	3055	2308	357	3000	1000	3750	2500	1842	833	2222	1643	1000	0
	6	833	769	714	1000	666	1667	938	2632	2500	2222	2786	2250	2000
	7	556	1154	1071	1000	333	1250	938	789	833	1667	1000	1000	0
	8	0	0	0	1000	333	2083	1875	1053	3333	1111	857	1000	0
	9	278	769	0	0	1000	0	625	789	0	556	929	750	0
	10	556	1154	1071	0	666	417	625	0	0	0	643	1750	0
	11	0	769	0	0	666	0	625	0	0	0	357	500	0
	12	0	0	357	0	333	0	625	0	0	0	143	0	0
	13	278	0	0	1000	333	0	0	0	0	0	0	0	1000
	14	556	769	357	0	0	0	0	0	0	0	0	0	0
	15	1389	1154	2143	1000	2333	0	0	263	0	0	0	250	7000
	16	556	0	714	0	0	0	0	0	0	0	0	0	0
D15S195	1	278	0	0	0	0	0	0	312	0	0	217	250	0
	2	833	0	357	0	385	908	1176	1875	1000	556	507	500	0
	3	1111	2500	1786	2000	2692	3182	2647	1875	3000	3333	2609	2750	3000
	4	0	714	0	2000	0	0	0	0	0	1111	0	0	0
	5	3889	3929	2857	3000	3462	3635	3235	4375	5000	3889	3406	3250	3000
	6	0	0	0	0	385	0	0	0	0	0	0	0	2000
	7	3055	2857	1786	1000	1154	2273	2059	1250	1000	1111	2609	2250	1000
	8	0	0	0	0	0	0	0	0	0	0	0	0	1000
	9	278	0	1429	2000	1154	0	882	312	0	0	580	750	0
	10	0	0	357	0	769	0	0	0	0	0	0	250	0
	11	556	0	1429	0	0	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0	0	72	0	0
D16S485	1	0	0	357	0	0	0	294	278	0	0	145	250	0
	2	1053	0	714	0	833	1176	833	0	0	1159	500	0	0
	3	1316	2500	2143	2000	769	3750	3824	2500	4000	3571	2029	250	1000
	4	3684	5000	3571	5000	3846	3333	3235	3889	3000	4286	3406	3500	2000
	5	2105	357	1071	1000	1923	1250	588	2500	2000	2143	2609	3500	2000
	6	1316	1429	2143	2000	3462	833	882	0	0	0	435	2000	2000

Locus	Allele	SO	TS	NG	BI	SA	CA	CH	JA	MA	VI	NE	FR	MB
D17S919	7	526	714	0	0	0	0	0	0	1000	0	0	0	3000
	8	0	0	0	0	0	0	0	0	0	0	145	0	0
	9	0	0	0	0	0	0	0	0	0	0	72	0	0
	1	0	0	357	0	0	0	0	0	0	0	217	0	0
	2	0	0	0	0	0	0	0	833	0	0	0	250	0
	3	526	714	357	0	333	1364	666	833	0	0	1087	1500	0
	4	1579	1071	357	5000	1000	1817	2000	833	3750	1667	1522	2000	1000
	5	526	1429	1071	2000	2667	5455	6333	4167	6250	5556	3913	3500	7000
	6	1053	1429	2143	1000	1000	1364	666	3055	0	2222	2101	1000	2000
	7	5526	5000	4286	0	3667	0	333	278	0	556	1014	1750	0
	8	526	0	714	1000	666	0	0	0	0	0	72	0	0
D18S930	9	0	0	357	0	0	0	0	0	0	0	0	0	0
	10	0	357	0	1000	0	0	0	0	0	0	72	0	0
	11	263	0	357	0	666	0	0	0	0	0	0	0	0
	1	294	0	0	0	0	0	0	263	0	0	0	0	0
	2	588	0	357	0	1364	833	882	0	0	0	214	278	0
	3	588	1667	714	0	2273	2500	3235	3158	0	2222	1143	1944	2000
	4	5588	4167	6786	8000	3182	6250	5588	5526	10000	5556	6071	5000	3000
	5	1471	2500	714	1000	1817	417	294	1053	0	1667	1571	1389	1000
	6	1471	1667	1429	1000	908	0	0	0	0	0	286	278	4000
	7	0	0	0	0	455	0	0	0	0	556	429	556	0
	8	0	0	0	0	0	0	0	0	0	0	286	556	0
D19S403	1	0	0	0	0	0	0	0	0	0	0	286	0	0
	2	0	357	0	0	0	417	312	0	1667	0	714	250	1000
	3	789	357	1429	1000	500	417	0	263	833	0	357	1250	3000
	4	1579	1786	1071	1000	500	0	0	0	833	556	571	750	1000
	5	789	357	714	0	0	0	0	0	0	0	500	750	1000
	6	0	714	357	1000	500	417	0	0	833	0	0	0	2000
	7	1316	714	0	0	1000	0	0	0	0	0	0	0	0
	8	1316	714	1071	3000	500	417	938	526	0	0	0	0	0
	9	2632	4286	1786	2000	5500	8333	8750	9211	5000	8889	6929	6500	1000
	10	1579	714	3571	2000	1000	0	0	0	0	0	571	500	1000
	11	0	0	0	0	500	0	0	0	0	0	71	0	0
	12	0	0	0	0	0	0	0	0	833	556	0	0	0
D19S400	1	263	0	0	0	333	0	0	0	0	0	0	0	0
	2	263	0	357	2000	0	417	312	526	0	0	143	0	3000
	3	3684	3571	3929	3000	666	833	0	0	0	0	785	250	2000
	4	2368	2143	2857	2000	3333	1250	312	526	0	1111	1714	2250	2000
	5	1053	1071	1071	0	666	0	625	1579	0	1667	1786	1000	1000
	6	263	1429	714	1000	2000	1667	1250	1053	1000	1111	929	1750	2000
	7	1579	714	1071	1000	2333	833	2188	1579	2000	0	2357	2000	0
D20S161	8	526	357	0	0	666	833	1875	1053	2000	2222	429	1500	0
	9	0	0	0	0	0	1667	625	1316	1000	1111	429	250	0
	10	0	714	0	0	0	833	1250	1579	0	1111	1143	750	0
	11	0	0	0	1000	0	417	625	0	2000	556	286	250	0
	12	0	0	0	0	0	1250	938	789	2000	1111	0	0	0
	1	263	0	0	0	0	0	312	263	0	0	0	0	0
	2	526	714	1071	0	357	417	0	1053	0	1667	147	500	2000
	3	2632	2500	3213	1000	714	1667	1562	1842	0	1111	735	750	2000
	4	2632	2500	1429	3000	3213	2917	2188	2105	3333	556	1691	2000	1000
	5	2105	1786	2857	2000	2857	3333	2500	3421	6667	5000	5441	4250	1000
	6	1053	1429	714	1000	1786	1250	3125	1053	0	1111	1912	2500	1000
	7	0	0	0	0	0	417	312	263	0	556	74	0	0
8	263	0	0	0	357	0	0	0	0	0	0	0	2000	
9	526	1071	714	3000	714	0	0	0	0	0	0	0	1000	
D20S428	1	263	0	0	0	0	0	0	0	0	0	0	263	0
	2	263	357	714	0	0	833	0	294	0	0	447	0	2000
	3	1579	2857	1786	2000	1500	2500	2940	1764	0	2222	1866	2105	2000
	4	4211	2500	3213	1000	4000	3750	2940	4412	6000	5000	3060	2368	3000
	5	2632	2500	3571	2000	3000	1250	2647	1764	3000	1111	2239	3158	3000
	6	526	714	0	0	1000	833	0	0	0	0	373	526	0
	7	263	357	714	3000	500	0	0	0	0	556	0	0	0
	8	0	357	0	2000	0	833	1471	1764	1000	1111	2015	1579	0
	9	263	0	0	0	0	0	0	0	0	0	0	0	0
	10	0	357	0	0	0	0	0	0	0	0	0	0	0

Figure A1 Allele frequencies ($\times 10,000$) for 30 tetranucleotide repeat polymorphisms. SO = Sotho/Tswana; TS = Tsonga; NG = Nguni; BI = Biaka Pygmy; SA = San; CA = Cambodian; CH = Chinese; JA = Japanese; MA = Malay; VI = Vietnamese; NE = northern European; FR = French; and MB = Mbuti Pygmy.

Locus	SO	TS	NG	BI	SA	CA	CH	JA	MA	VI	NE	FR	MB
178-350	526	0	1071	0	0	8333	5000	5556	6000	7857	4348	4737	0
181-665	7632	7692	7143	8000	8929	6667	7941	8529	4167	5556	8235	7750	8000
206-704	263	714	1071	0	2000	3333	3529	2500	4000	1111	2984	2105	0
197-914	8421	8846	8929	10000	7143	5909	7647	8056	2500	7143	6103	6500	10000
180-400	2778	1071	417	2000	714	455	294	0	1250	0	4766	5881	0
178-648	4211	6154	3846	3000	1429	5833	5294	5000	6000	6667	6118	6316	3000
251-590	556	1250	769	1000	385	1250	1176	1316	5000	625	3529	4062	1250
185-229	6316	4643	6071	8000	5000	1667	5000	5263	4167	2222	4191	3750	9000
171-808	1579	1786	2308	3000	2308	1667	1471	1667	4167	2222	3197	4474	2000
177-841	4737	4231	3929	7000	3462	2500	3125	4167	1667	3889	3712	3000	9000
177-108	3333	5000	4643	5000	3929	6667	7059	7000	7500	7222	5448	5000	3000
187-676	4211	3077	2308	2000	1071	417	0	0	1667	1667	4071	3750	1000
285-016	10000	8846	10000	10000	9615	3333	4062	1944	2500	5556	5149	3333	10000
181-821	3158	3929	3571	4000	5357	5417	5625	5000	5833	3571	4130	3421	5000
180-411	7647	7307	8077	6000	7000	6667	6176	6842	7000	7222	6567	7250	10000
250-584	1316	1071	1786	0	0	2500	294	938	0	0	143	0	0
178-649	4118	3462	3571	5000	4286	5417	5333	3750	4167	5556	6961	6579	3333
181-402	8333	8846	8571	9000	7857	2500	1471	1875	0	0	3551	5278	8750
182-559	2105	3077	2857	3000	1071	8750	7188	8947	9000	6667	6103	6579	7000
180-743	6579	5714	5357	6000	6071	3333	3235	5000	4167	3333	6071	5000	9000
196-856	3158	2143	1429	3000	1429	7500	5294	6176	7500	5556	4000	4750	0
177-381	9722	10000	9286	8750	9667	3750	2812	2632	7500	3889	3043	2000	10000
210-937	789	769	1429	0	0	3750	2059	2647	5000	1875	580	1500	3000
180-968	4722	5000	3462	2000	3571	3750	4062	4375	4000	1667	6562	6176	5000
182-529	1053	1786	1154	3333	1071	3750	3235	2188	0	1250	2357	2632	0
192-312	5263	5000	5000	6250	6429	3750	3824	2222	833	4444	3623	5250	5000
196-905	5000	3462	5000	2000	9000	6250	5881	7500	5000	5625	4776	3684	0
181-184	4722	5769	3846	7000	6538	4583	3438	2940	3000	3750	2077	3421	5000
182-305	10000	10000	9643	10000	10000	9583	10000	9722	9167	10000	5786	5500	10000
185-174	9118	6538	6667	5000	8182	5833	4375	4118	5000	2857	4609	5526	7500

Figure A2 Allele frequencies ($\times 10,000$) for 30 RSPs. Population abbreviations are given in the legend to fig. A1.

References

- Anderson S, Bankier AT, Barrell BG (1981) Sequence and organization of the human mitochondrial genome. *Nature* 290:457–465
- Bamshad M, Fraley AE, Crawford MH, Cann RL, Busi BR, Naidu JM, Jorde LB. MtDNA variation in caste populations of Andhra Pradesh, India. *Hum Biol* (in press)
- Batzler MA, Stoneking M, Alegria-Hartman M, Bazan H, Kass DH, Shaikh TH, Novick GE, et al (1994) African origin of human-specific polymorphic *Alu* insertions. *Proc Natl Acad Sci USA* 91:12288–12292
- Bell GI, Karem JH, Rutter JR (1981) Polymorphic DNA region adjacent to the 5' end of the human insulin gene. *Proc Natl Acad Sci USA* 78:5759–5763
- Birky CW, Maruyama T, Fuerst P (1983) An approach to population and evolutionary genetic theory for genes in mitochondria and chloroplasts, and some results. *Genetics* 103:513–527
- Bowcock A, Cavalli-Sforza LL (1991) The study of variation in the human genome. *Genomics* 11:491–498.
- Bowcock AM, Kidd JR, Mountain JL, Hebert JM, Carotenuto L, Kidd KK, Cavalli-Sforza LL (1991) Drift, admixture, and selection in human evolution: a study with DNA polymorphisms. *Proc Natl Acad Sci USA* 88:839–843
- Bowcock AM, Ruiz-Linares A, Tomfohrde J, Minch E, Kidd JR, Cavalli-Sforza LL (1994) High resolution of human evolutionary trees with polymorphic microsatellites. *Nature* 368:455–457
- Cann RL, Stoneking M, Wilson AC (1987) Mitochondrial DNA and human evolution. *Nature* 325:31–36
- Cavalli-Sforza LL, Menozzi P, Piazza A (1994) The history and geography of human genes. Princeton University Press, Princeton.
- Cavalli-Sforza LL, Piazza A, Menozzi P, Mountain J (1988) Reconstruction of human evolution: bringing together genetic, archaeological, and linguistic data. *Proc Natl Acad Sci USA* 85:6002–6006
- Deka R, Chakraborty R, Ferrell RE (1991) A population genetic study of six VNTR loci in three ethnically defined populations. *Genomics* 11:83–92
- Deka R, Jin L, Shriver MD, Yu LM, DeCruo S, Hundrieser J, Bunker CH, et al (1995) Population genetics of dinucleotide (dC-dA)_n(dG-dT)_n polymorphisms in world populations. *Am J Hum Genet* 56:461–474
- Di Rienzo A, Peterson AC, Garza JC, Valdes AM, Slatkin M, Freimer NB (1994) Mutational processes of simple-sequence repeat loci in human populations. *Proc Natl Acad Sci USA* 91:3166–3170
- Edwards A, Hammond HA, Jin L, Caskey CT, Chakraborty R (1992) Genetic variation at five trimeric and tetrameric tandem repeat loci in four human population groups. *Genomics* 12:241–253
- Excoffier L (1990) Evolution of human mitochondrial DNA: evidence for departure from a pure neutral model of populations at equilibrium. *J Mol Evol* 30:125–139
- Felsenstein J (1993) PHYLIP (Phylogeny Inference Package) version 3.5c. Department of Genetics, University of Washington, Seattle
- Harpending H, Relethford J, Sherry S. Methods and models for understanding human diversity. In: Boyce AJ, Mascie-Taylor CGN (eds) *Molecular Biology and Human Diversity*. Cambridge University Press, London (in press)
- Horai S, Hayasaka K, Kondo R, Tsugane K, Takahata N (1995) Recent African origin of modern humans revealed by complete sequences of hominoid mitochondrial DNAs. *Proc Natl Acad Sci USA* 92:532–536
- Horai S, Kondo R, Nakagawa-Hattori Y, Hayashi W, Sonoda S, Tajima K (1993) Peopling of the Americas, founded by four major lineages of mitochondrial DNA. *Mol Biol Evol* 10:23–47
- Jin L, Chakraborty R. Population structure, stepwise mutations, heterozygote deficiency and their implications in DNA forensics. *Heredity* (in press)
- Jorde LB (1980) The genetic structure of subdivided human populations: a review. In: Mielke JH, Crawford MH (eds) *Current developments in anthropological genetics*, Vol. 1. Plenum, New York, pp 135–208
- Kidd JR, Black FL, Weiss KM, Balazs I, Kidd KK (1991) Studies of three Amerindian populations using nuclear DNA polymorphisms. *Hum Biol* 63:775–794
- Kimura M (1980) A simple model for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *J Mol Evol* 16:111–120
- Mantel N (1967) The detection of disease clustering and a generalized regression approach. *Cancer Res* 27:209–220
- Merriwether DA, Clark AG, Ballinger SW, Schurr TG, Soodyall H, Jenkins T, Sherry ST, et al (1991) The structure of human mitochondrial DNA variation. *J Mol Evol* 33:543–555
- Mountain JL, Cavalli-Sforza LL (1994) Inference of human evolution through cladistic analysis of nuclear DNA restriction polymorphisms. *Proc Natl Acad Sci USA* 91:6515–6519
- Nei M (1987) *Molecular evolutionary genetics*. Columbia University Press, New York
- Nei M, Livshits G (1989) Genetic relationships of Europeans, Asians and Africans and the origin of modern *Homo sapiens*. *Hum Hered* 39:276–281
- Nei M, Livshits G, Ota T (1993) Genetic variation and evolution of human populations. In: Sing CF, Hanis CL (eds) *Genetics of cellular, individual, family, and population variability*. Oxford University Press, New York, pp 239–252
- Nei M, Roychoudhury AK (1982) Genetic relationship and evolution of human races. *Evol Biol* 14:1–59
- (1993) Evolutionary relationships of human populations on a global scale. *Mol Biol Evol* 10:927–943
- O'Brien E, Rogers AR, Beesley J, Jorde LB (1994) Genetic structure of the Utah Mormons: a comparison of results based on DNA, blood groups, migration matrices, isonymy, and pedigrees. *Hum Biol* 66:743–759
- Relethford JH, Harpending HC (1994) Craniometric variation, genetic theory, and modern human origins. *Am J Phys Anthropol* 95:249–270
- Rogers AR. Genetic evidence for a Pleistocene population explosion. *Evolution* (in press)
- Rogers AR, Harpending HC (1992) Population growth makes waves in the distribution of pairwise genetic differences. *Mol Biol Evol* 9:552–569
- Rogers AR, Jorde LB (1995) Genetic evidence on the origin of modern humans. *Hum Biol* 67:1–36
- Saitou N, Nei M (1987) The neighbor-joining method: a new

- method for reconstructing phylogenetic trees. *Mol Biol Evol* 4:406-425
- Sherry ST, Rogers AR, Harpending H, Soodyall H, Jenkins T, Stoneking M (1994) Mismatch distributions of mtDNA reveal recent human population expansions. *Hum Biol* 66:761-775
- Shriver MD, Jin L, Boerwinkle E, Chakraborty R (1995) A novel measure of genetic distance for highly polymorphic tandem repeat loci. *Mol Biol Evol* 12 (in press)
- Shriver MD, Jin L, Chakraborty R, Boerwinkle E (1993) VNTR allele frequency distributions under the stepwise mutation model: a computer simulation approach. *Genetics* 134:983-993
- Smouse PE, Long JC, Sokal RR (1986) Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Syst Zool* 35:627-632
- Spuhler JN (1993) Population genetics and evolution in the genus *Homo* in the last two million years. In: Sing CF, Hanis CL (eds) *Genetics of cellular, individual, family, and population variability*. Oxford University Press, New York, pp 262-297
- Spurdle AB, Jenkins T (1992) The Y chromosome as a tool for studying human evolution. *Curr Opin Genet Dev* 2:487-491
- Stoneking M (1993) DNA and recent human evolution. *Evol Anthropol* 2:60-73
- Stoneking M, Jorde LB, Bhatia K, Wilson AC (1990) Geographic variation of human mitochondrial DNA from Papua New Guinea. *Genetics* 124:717-733
- Sykes BC (1983) DNA in heritable disease. *Lancet* 2:787-788
- Tajima F (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* 123:585-595
- Takahata N, Palumbi SR (1985) Extranuclear differentiation and gene flow in the finite island model. *Genetics* 109:441-457
- Templeton AR (1993) The "Eve" hypothesis: a genetic critique and reanalysis. *Am Anthropol* 95:51-72
- Vigilant L, Pennington R, Harpending H, Kocher TD, Wilson AC (1989) Mitochondrial DNA sequences in single hairs from a southern African population. *Proc Natl Acad Sci USA* 86:9350-9354
- Vigilant L, Stoneking M, Harpending H, Hawkes K, Wilson AC (1991) African populations and the evolution of human mitochondrial DNA. *Science* 253:1503-1507
- Watkins WS, Bamshad MJ, Jorde LB. Population genetics of trinucleotide repeat polymorphisms. *Hum Mol Genet* (in press)
- Weber JL, Wong C (1993) Mutation of human short tandem repeats. *Hum Mol Genet* 2:1123-1128
- Wright S (1965) The interpretation of population structure by F-statistics with special regard to systems of mating. *Evolution* 19:395-420