Evolutionary Relationships of Human Populations on a Global Scale[1]

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Using gene frequency data for 29 polymorphic loci (121 alleles), we conducted a phylogenetic analysis of 26 representative populations from around the world by using the neighbor-joining (NJ) method. We also conducted a separate analysis of 15 populations by using data for 33 polymorphic loci. These analyses have shown that the first major split of the phylogenetic tree separates Africans from non-Africans and that this split occurs with a 100% bootstrap probability. The second split separates Caucasian populations from all other non-African populations, and this split is also supported by bootstrap tests. The third major split occurs between Native American populations and the Greater Asians that include East Asians (mongoloids), Pacific Islanders, and Australopapuans (native Australians and Papua New Guineans), but Australopapuans are genetically quite different from the rest of the Greater Asians. The second and third levels of population splitting are quite different from those of the phylogenetic tree obtained by Cavalli-Sforza et al. (1988), where Caucasians, Northeast Asians, and Amerindians form the Northeurasian supercluster and the rest of non-Africans form the Southeast Asian supercluster. One of the major factors that caused the difference between the two trees is that Cavalli-Sforza et al. used unweighted pair-group method with arithmetic mean (UPGMA) in phylogenetic inference, whereas we used the NJ method in which evolutionary rate is allowed to vary among different populations. Bootstrap tests have shown that the UPGMA tree receives poor statistical support whereas the NJ tree is well supported. Implications that the phylogenetic tree obtained has on the current controversy over the out-of-Africa and the multiregional theories of human origins are discussed.

Introduction

The evolutionary relationships of human populations can be revealed only when a large number of loci are examined (Nei and Roychoudhury 1974, 1982; Astolfi et al. 1981). Using gene frequency data for 120 alleles, Cavalli-Sforza et al. (1988) concluded that the major split of human populations separates Africans from non-Africans and that the second split separates the Northeurasian supercluster (Caucasians, Northeast Asians, and Amerindians) from the Southeast Asian supercluster (Southeast Asians, Australians, Papua New Guineans, and Pacific Islanders). This conclusion is based on an unweighted pair-group method with arithmetic mean (UPGMA) cluster

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analysis (Sneath and Sokal 1973, p. 230), in which the evolutionary rate is assumed to be constant.

However, Livshits and Nei (1990) have shown that the bottleneck effect, or the effect of an extended period of reduced population size, often increases the genetic distance between populations drastically, and thus the assumption of constant rate of evolution does not hold for human populations. Natural selection identified at some loci (e.g., HLA loci; Hughes and Nei 1988) may also violate this assumption. For these reasons, phylogenetic trees obtained by UPGMA are usually less reliable than those obtained by statistical methods allowing varying rates of evolution for different human populations. Indeed, using the neighbor-joining (NJ) method that allows rate heterogeneity (Saitou and Nei 1987), Nei and Ota (1991) have constructed a phylogenetic tree of human populations, which is quite different from Cavalli-Sforza et al.'s (1988). However, this study was based on a relatively small number of genetic loci and populations, and no statistical test has been done on the reliability of the tree obtained. We have therefore conducted a more extensive study on this problem. The results obtained are presented in this paper.

Material and Methods

On the basis of anthropological interest and the availability of gene frequency data for polymorphic loci shared by all populations, we chose 26 representative populations from around the world. Of these populations, 4 were chosen from Africa [Babinga Pygmies of central Africa, Nigerians (Yoruba), Bantus in southern Africa, and Sans (Bushmen) in Botswana], 5 from Europe (Lapps living in northern Scandinavia, Finns, Germans, English, and Italians), 10 from Asia (Iranians, northern Indians mainly from Punjab, Japanese, Koreans, Tibetans, Mongolians, Thais, Filipinos, Indonesians, and southern Chinese mainly from Fujian province, Taiwan, and Hong Kong), 4 from Australia and Oceania (Native Australians, Papuans from the Highlands of Papua New Guinea, Micronesians from the Caroline and Kiribati Islands, and Polynesians from the Samoa Islands), and 3 from America (Amerindians in Alaska and Canada representing North Amerindians, Amerindians in northern and central South America representing South Amerindians, and Eskimos in Alaska and Canada).

The populations of Papuans, Native Australians, North Amerindians, South Amerindians, and Eskimos consist of many tribal populations, and some of them have a considerable amount of gene admixture from other populations, such as Europeans. In this study, we used only those populations whose admixture rate is lower than a few percent. Furthermore, to minimize the effect of inbreeding, we used the average gene frequencies for three to seven tribal populations for each of the five ethnic groups. For example, the Papuan gene frequencies used were averages of the gene frequencies for the north-central, western, eastern, and central district Highlanders, and the Australian data were averages of those for the Elcho Island, northern, central, and western Australians. Similarly, the average gene frequencies of Athapaskan Indians in Alaska and Dogrib and Ojibwa Indians in Canada were used for North Amerindians. [Although the Athapaskan and the Dogrib belong to the Na-Dene language family and the Ojibawa to the Amerind family (Ruhlen 1987, pp. 195–251), we pooled them because they are geographically proximate.] In the case of South Amerindians, the average gene frequencies for three populations of Brazil (Baniwa, Cayapo, and Macushi), two populations of Venezuela (Makiritare and Yanomama), and one popu-

lation each from Suriname (Trio) and Colombia (Noanama) were used. Eskimo data were averages of those for three Eskimo populations of Alaska (northern and southwestern Alaska and St. Lawrence Island) and Igloolik Eskimos in Canada.

In addition to the study using average gene frequencies for several tribal populations, we also conducted a phylogenetic analysis using one population from each of the above ethnic groups. The results obtained were essentially the same as those for the above data set. Therefore, we shall not present the results of the latter analysis.

Our primary purpose in this paper is to infer the major pattern of population splitting in early human evolution. Therefore, we have excluded populations that are clearly products of recent gene admixture as documented by history (e.g., northern Africans and Middle Easterns), except those in Europe. Most European populations (e.g., Finns, Germans, English, and Italians) have exchanged genes during the past few thousand years, but they are included here as a group, for study of their evolutionary relationships with other populations. In the early stage of evolution, human populations probably evolved by a continuous splitting process as they expanded their territories, since this is the general evolutionary pattern for most organisms (Cavalli-Sforza et al. 1988). Of course, some extent of gene admixture must have occurred between neighboring populations, but the admixture rate should have diminished as the populations moved away from each other and occupied different territories or acquired different languages.

Obviously, this view of human evolution is too simplistic, and occasionally gene admixture should have occurred even between quite divergent populations. For example, Iranians and northern Indians probably have had gene admixture with East Asians, though they are now primarily Caucasians. Since there is no way to know the extent of gene admixture in early human evolution, our phylogenetic analysis presented here is an attempt to obtain a rough picture of the history of the evolution of various human populations. All the phylogenetic analyses of human populations in the past have been done with this understanding.

The number of polymorphic loci now known in humans is very large (Roychoudhury and Nei 1988). However, the populations in which the gene frequency data are available are largely confined to western Europe, North America, and eastern Asia. For this reason, the number of shared loci rapidly declines as the number of populations increases. Therefore, if one wants to use a large number of loci, the number of populations that can be used becomes very small. Cavalli-Sforza et al. (1988) avoided this problem by including many unshared loci; in their analysis the number of shared loci for all 42 populations was only five (21 alleles), and the allele × population matrix contained 24% missing elements (gaps) (L. L. Cavalli-Sforza, personal communication, 1990). In our experience, these gaps often introduce unreasonable branching patterns into phylogenetic trees. We therefore collected gene frequency data for as many shared loci as possible. The present study with the 26 populations mentioned above is based on data for 29 polymorphic loci with 121 alleles. The loci used are ABO, DI, FY, JK, K, MNS, P, RH, SE, ACP1, ADA, AK1, ESD, GLO1, G6PD, GPT, PGD, PGM1, PGM2, GC, HP, PI, TF, HBB, GM, KM, HLA-A, HLA-B, and PTC [for gene symbols, see Roychoudhury and Nei (1988, pp. 21–31) or McKusick (1986)]. In addition to these, four more polymorphic loci (CA1, CA2, CHE1, and LU) were used when only 15 populations were studied (see below). Most of the gene frequency data for these loci were taken from the compilation of Roychoudhury and Nei (1988). However, whenever new data were available for any locus or any population that had not been previously studied, they were included. For example, gene frequency data for Tibetans were taken mainly from Ai et al. (1987) and Papiha et al. (1989), and those for

Koreans were from Goedde et al. (1987) and Ohkura et al. (1989). The data for southern Chinese and for Micronesians and Polynesians were obtained from Saha (1989) and Kirk (1979, 1985, 1989), respectively. Gene frequency data for the HLA-A and HLA-B loci for the Oceanian populations were taken from Serjeantson et al. (1982, 1983). HLA data for Iranians and GM and KM data for Polynesians were taken from Aizawa (1986) and Dehay et al. (1987), respectively. All the gene frequency data used in this study are available on request.

Previously, we used Nei's (1972) standard distance (D) for measuring genetic distances between populations. However, Nei et al. (1983) have shown that their new distance D_A (modified Cavalli-Sforza distance) has a more discriminatory power for closely related populations, such as those in man, though it is not linearly related to evolutionary time when it is large. (Incidentally, D_A is a metric satisfying the triangle inequality.) In this study, we therefore used this distance measure and reconstructed a phylogenetic tree, using the NJ method. The NJ method is based on the principle of minimum evolution (Rzhetsky and Nei 1992*a*), but it is quite different from Cavalli-Sforza and Edwards' (1967) minimum-evolution (minimum-string) method, which is intended to construct a Steiner tree (see Bowcock et al. 1991). The NJ method is known to be more efficient than most other distance methods of phylogenetic reconstruction in obtaining the correct tree (Saitou and Imanishi 1989; Rzhetsky and Nei 1992*b*). The reliability of the tree obtained was examined by a bootstrap test with 500 replicate resamplings of loci. The null hypothesis of this test was "no cluster of populations," i.e., a star tree with all interior branches of the tree being equal to 0. [This null hypothesis does not apply to Felsenstein's (1985) bootstrap consensus trees.] If there is population clustering, the reliability of each cluster or of an interior branch that produces the cluster is measured by a bootstrap probability.

Results

Major Subdivision of Human Populations

The average heterozygosities and genetic distances for all populations are given in figure 1, whereas the phylogenetic (unrooted) tree obtained is represented in figure 2. There are four major clusters of human populations: (A) Africans, (B) Caucasians, (C) the Greater Asians including Australians, New Guineans, and Pacific Islanders, and (D) Amerindians including Eskimos. This is similar to the traditional grouping of human populations (Howells 1967; Brues 1977), except that (*a*) Australians and New Guineans are included in the Greater Asian cluster and (*b*) Amerindians form a cluster separate from East Asians. The phylogenetic tree in figure 2 is unrooted. To find the root of a tree, it is customary to use an outgroup species. However, there are no gene frequency data for the genetic loci used here for any outgroup species (chimpanzee or gorilla). We therefore followed Farris (1972) and put the root to the midpoint of the longest branch between a pair of populations. This method gives the root to the branch between Africans and non-Africans, indicating that the first split of human populations occurred between these two groups. This is consistent with the previous results obtained by different methods (Nei and Roychoudhury 1974, 1982; Cavalli-Sforza et al. 1988; Bowcock et al. 1991). This split was reproduced in all of the 500 bootstrap replicate trees when Whittam's (1992) computer program was used. This confirms Nei and Livshits' (1989) results indicating that the genetic distance between Caucasians and Orientals is significantly smaller than either that between Caucasians and Africans or that between Orientals and Africans.

Vigilant et al. (1991) used the chimpanzee sequence to root their mitochondrial

Population	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)	(20)	(21)	(22)	(23)	(24)	(25)	(26)
(1) Pygmy	27.8																									
(2) Nigerian	3.1	31.2																								
(3) Bantu	3.8	2.7	29.9																							
(4) San	7.9	7.5	3.7	33.0																						
(5) Lapp	14.7	14.5	12.3	11.0	33.1																					
(6) Finn	13.1	13.3	10.7	9.8	1.8	34.4																				
(7) German	13.0	13.1	10.6	9.8	2.4	.5	34.4																			
(8) English	13.3	13.3	10.8	9.7	2.5	.5	.2	34.9																		
(9) Italian	13.5	13.0	10.6	9.8	2.5	.8	.6	.7	34.6																	
(10) Iranian	13.2	13.6	10.4	10.1	3.6	2.0	1.8	2.2	1.6	36.1																
(11) N. Indian	12.7	13.5	10.8	9.9	3.0	1.5	1.6	2.0	1.5	1.6	35.9															
(12) Japanese	14.5	14.9	11.7	10.8	6.1	5.4	5.7	6.1	5.5	5.0	4.0	32.1														
(13) Korean	14.3	14.3	11.5	10.5	6.4	5.4	5.7	6.1	5.5	5.2	4.0	.6	32.0													
(14) Tibetan	14.8	15.3	12.1	11.5	6.3	6.1	6.6	7.0	6.0	5.0	4.5	1.1	1.2	32.4												
(15) Mongolian	13.6	14.1	11.2	10.4	5.9	4.8	5.2	5.5	5.1	4.6	3.3	1.2	.7	1.5	33.3											
(16) S. Chinese	15.0	15.5	12.5	11.7	7.8	6.8	6.8	7.3	6.5	6.0	5.0	2.3	2.1	2.4	1.6	31.0										
(17) Thai	15.3	16.1	13.4	12.6	8.3	7.3	7.3	8.1	7.0	6.1	4.7	3.0	2.7	3.1	2.3	1.3	30.6									
(18) Filipino	14.4	15.0	12.3	11.8	7.0	6.6	6.8	7.4	6.4	5.9	4.7	2.6	2.9	3.1	2.4	1.8	1.8	28.9								
(19) Indonesian	15.3	15.1	12.7	11.9	7.1	6.4	6.4	7.0	6.1	5.6	4.2	3.1	3.0	3.2	2.7	2.1	1.8	1.6	30.2							
(20) Polynesian	16.3	16.6	14.6	14.5	10.0	8.7	8.9	9.6	8.9	8.2	7.1	3.5	3.4	4.0	2.9	2.1	2.7	3.2	3.5	31.1						
(21) Micronesian	16.7	16.9	14.8	14.8	9.6	9.2	9.0	9.7	8.9	8.8	7.2	3.8	4.2	4.8	4.2	3.5	3.8	2.3	2.8	2.9	25.2					
(22) Australian	17.0	17.6	15.7	14.4	10.4	10.8	12.1	12.2	11.7	12.2	10.4	6.2	5.5	6.8	5.9	7.6	8.1	8.2	8.5	6.0	7.9	21.0				
(23) Papuan	17.7	17.4	15.7	15.0	9.7	10.2	10.8	11.3	10.6	10.8	9.1	5.7	5.9	6.1	6.2	6.8	7.4	6.5	5.8	5.6	5.3	4.4	24.3			
(24) N. Amerindian	15.4	15.8	12.7	11.2	7.1	6.6	7.4	7.6	6.9	7.3	6.6	4.2	4.1	4.5	4.4	6.3	7.5	6.2	7.9	7.8	9.3	8.0	10.0	26.8		
(25) S. Amerindian	15.9	15.8	13.3	12.6	8.0	7.3	8.0	7.9	7.5	9.3	7.2	5.5	5.5	6.0	6.2	7.2	8.9	7.0	8.5	8.4	8.9	8.9	10.8	3.6	28.7	
(26) Eskimo	15.8	15.8	13.2	11.2	5.9	6.2	7.1	7.3	6.7	6.9	5.9	4.1	4.2	4.4	4.5	5.9	7.2	6.0	6.9	6.7	8.3	6.8	7.2	2.3	5.6	28.4

FIG. 1.—Estimates of average heterozygosities (H) and D_A distances for 26 representative populations from around the world. Both H (on diagonal) and D_A (below diagonal) values are multiplied by 100. These values are based on gene frequency data for 29 polymorphic loci. The D_A values in the boxes are highlighted to make it easier to compare them between different groups of populations.

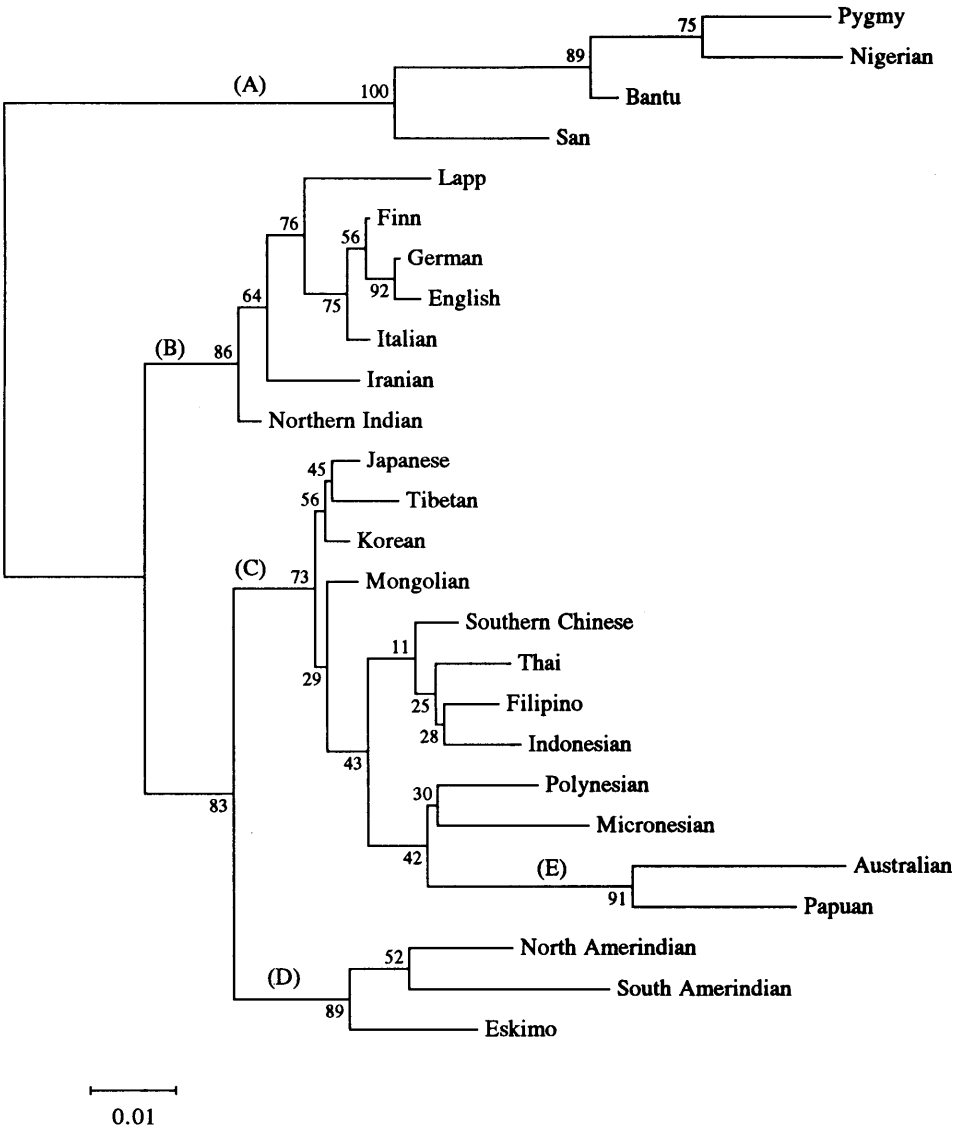

FIG. 2.—Phylogenetic tree for 26 representative human populations. This tree was produced by the NJ method from data in D_A values in fig. 1, and the bootstrap probability for each interior branch was obtained by Whittam's (1992) computer program. The scale of branch lengths is in units of $D_A/2$. Major groups of human populations are Africans (A), Caucasians (B), Greater Asians (C), Amerindians (D), and Australopapuans (E).

DNA (mtDNA) tree from various human populations. The root obtained was not very reliable, because, in terms of the information contributing to the phylogenetic inference, mtDNA is equivalent to a single locus (Nei 1985), and the parsimony analysis used did not give any resolution to the problem of rooting (Hedges et al. 1992; Templeton 1992). Yet, Hedges et al.'s (1992) and Tamura and Nei's (1993) reanalysis of Vigilant et al.'s data by using the NJ method suggested that the first split of human populations occurred between Africans and non-Africans.

Figure 2 shows that the second split of human populations occurred between

Caucasians and all other non-Africans. This pattern of divergence is different from that of the phylogenetic trees constructed by UPGMA for other data sets (Nei and Roychoudhury 1982; Cavalli-Sforza et al. 1988; Nei and Ota 1991), but the bootstrap test has shown that this split is quite stable and that all Caucasian populations form one cluster in 86% of the bootstrap trees; the other cluster shows an 83% bootstrap value. Of course, if we use the 95% bootstrap value as the statistically significant level, the Caucasian cluster is not significant. This apparently has occurred because we have included Iranians and northern Indians, whose gene pool probably has had some admixture with that of East Asian populations. As will be seen later, if we exclude these two populations and use more loci, the cluster of European Caucasians has a 100% bootstrap value.

The third major split separates the Native Americans from the Greater Asians. All the three populations of America—namely, North Amerindians, South Amerindians, and Eskimos—clustered together in 89% of the bootstraps, while North Amerindians stayed together with South Amerindians in 52% of the bootstraps. The Greater Asian cluster was also quite stable and was reproduced in 73% of the bootstraps. At any rate, this clustering pattern is also different from that of the previous UPGMA analyses (Nei and Roychoudhury 1982; Cavalli-Sforza et al. 1988).

Although Native Australians and Papuans belong to the Greater Asians, they are together in 91% of the bootstraps and are considerably different from other members of the Greater Asians. Figure 1 shows that the genetic distances between Japanese, Koreans, Tibetans, Mongolians, southern Chinese, Thais, Filipinos, Indonesians, Polynesians, and Micronesians are all <0.050, whereas the distances between these populations, on one hand, and Australians and Papuans, on the other hand, are all >0.050. These large distances associated with Australians and Papuans are apparently caused by the inbreeding effect in these populations, as will be discussed later. At any rate, if we consider the extent of genetic differentiation, Australians and Papuans may be regarded as the fifth major ethnic group.

Figure 2 also shows that Sans are separated from other Africans with an 89% bootstrap value. This is reasonable because Sans are considered a remnant group of old Africans who previously occupied a large portion of sub-Saharan Africa (Howells 1967, pp. 321–325) and contain several alleles (e.g., *Pep* D^3, $Gm^{1,13,17}$, and *HLA-Aw43*) that are unique or of high frequency compared with those in other populations (Nurse et al. 1985, pp. 117–121). European populations (Finns, Germans, English, Italians, and Lapps) also make a rather tight cluster (76% bootstrap value). These populations show short branch lengths and high heterozygosities, clearly reflecting recent gene admixture among them.

In figure 2, Tibetans show a close genetic relationship with Japanese, Koreans, and Mongolians rather than with southern Chinese. This is apparently due to the fact that both Tibetans and Mongolians originated from nomadic, pastoral tribes inhabiting the great steppe in northern China (McNally 1982, pp. 136–137). It also suggests that Japanese, Koreans, Mongolians, and Tibetans shared a common ancestral population.

Conflict between UPGMA and NJ Trees

One of the major differences between Cavalli-Sforza et al.'s (1988) results and ours is that in Cavalli-Sforza et al.'s UPGMA tree, the second split of human populations occurs between the Northeurasian supercluster and the Southeast Asian supercluster, whereas in our tree it occurs between Caucasians and non-Caucasians. The splitting pattern of the former tree was poorly supported by bootstrap tests (see Cavalli-

Sforza et al. 1988), whereas ours has much better statistical support, as mentioned earlier. Nevertheless, the bootstrap value for our splitting pattern did not reach the 95% level. We therefore reexamined this problem by eliminating several intermediate populations such as Iranians, northern Indians, and Eskimos and by increasing the number of polymorphic loci (33 loci with 131 alleles). The D_A values for these data are presented in figure 3, and the NJ tree is given in figure 4.

Figure 4 shows that Caucasian populations in Europe now form a firm cluster, the bootstrap value being 100%. The Greater Asian + Amerindian cluster also shows a 98% bootstrap value. In this phylogenetic analysis, the northeastern Asians (Japanese and Koreans) never joined the European cluster in 500 replicate bootstraps, though they sometimes joined the groups of Chinese, Australians, and New Guineans. These genetic relationships can also be confirmed by examining the D_A values in figure 3. That is, the genetic distances between Northeast Asians and southern Chinese (Southeast Asians) are less than half the distances between Europeans and Northeast Asians. The genetic distances between Northeast Asians and Australopapuans are also about half the distances between Europeans and Australopapuans.

Actually, figure 1 also shows essentially the same genetic relationships as the above, even if we include Iranians, northern Indians, and Lapps into the Caucasian cluster; Mongolians and Tibetans into the northeastern Asians; and Thais, Filipinos, Indonesians, Polynesians, and Micronesians into the Southeast Asians. This strongly suggests that our phylogenetic tree is more reliable than Cavalli-Sforza et al.'s. Incidentally, figure 1 shows that Micronesians and Polynesians are closer to Southeast Asians or Northeast Asians than to Australopapuans. This result is consistent with the view that Micronesians and Polynesians are primarily descendants of Southeast Asians, though they have had some gene admixture with Australopapuans (Bellwood 1989).

One reason for this difference is that the allele × population matrix in Cavalli-Sforza et al.'s analysis had many missing elements, whereas ours had none. However, the major reason is that Cavalli-Sforza et al. (1988) used UPGMA in phylogenetic analysis, whereas we used the NJ method. Actually, if we apply UPGMA to our data set in figure 1, we obtain a tree that is quite different from that in figure 2 (see figure 5). In this tree the second split of human populations occurs between Australopapuans and the rest of the non-African populations. This pattern is the same as that of Nei and Roychoudhury (1982) and Nei and Ota (1991), for smaller data sets, but it

Population	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)
(1) Pygmy	24.92														
(2) Nigerian	2.80	28.27													
(3) Bantu	3.42	2.44	27.23												
(4) San	7.10	6.86	3.55	28.96											
(5) Finn	11.72	11.89	9.62	8.63	30.43										
(6) German	11.64	11.68	9.57	8.70	0.41	30.45									
(7) English	11.88	11.93	9.72	8.59	0.45	0.22	31.04								
(8) Italian	12.03	11.70	9.53	8.70	0.70	0.50	0.67	30.72							
(9) Japanese	12.89	13.34	10.52	9.45	4.80	5.01	5.47	4.92	28.25						
(10) Korean	12.67	12.84	10.33	9.22	4.79	5.09	5.43	4.93	0.53	28.15					
(11) S. Chinese	13.35	13.88	11.28	10.25	5.98	6.01	6.48	5.81	2.03	1.88	27.22				
(12) Australian	15.23	15.79	14.14	12.74	9.61	10.75	10.91	10.45	5.59	4.97	6.76	18.83			
(13) Papuan	15.69	15.51	14.02	13.15	8.99	9.55	10.06	9.40	5.00	5.17	5.95	3.96	21.34		
(14) N. Amerindian	13.71	14.16	11.44	9.87	5.87	6.59	6.74	6.16	3.73	3.62	5.53	7.12	8.75	23.57	
(15) S. Amerindian	14.08	14.06	11.93	11.03	6.45	7.07	7.04	6.63	4.88	4.84	6.35	7.93	9.50	3.13	25.27

FIG. 3.—Estimates of H (on diagonal) and D_A (below diagonal) for 15 representative populations based on data for 33 polymorphic loci. H and D_A values are multiplied by 100.

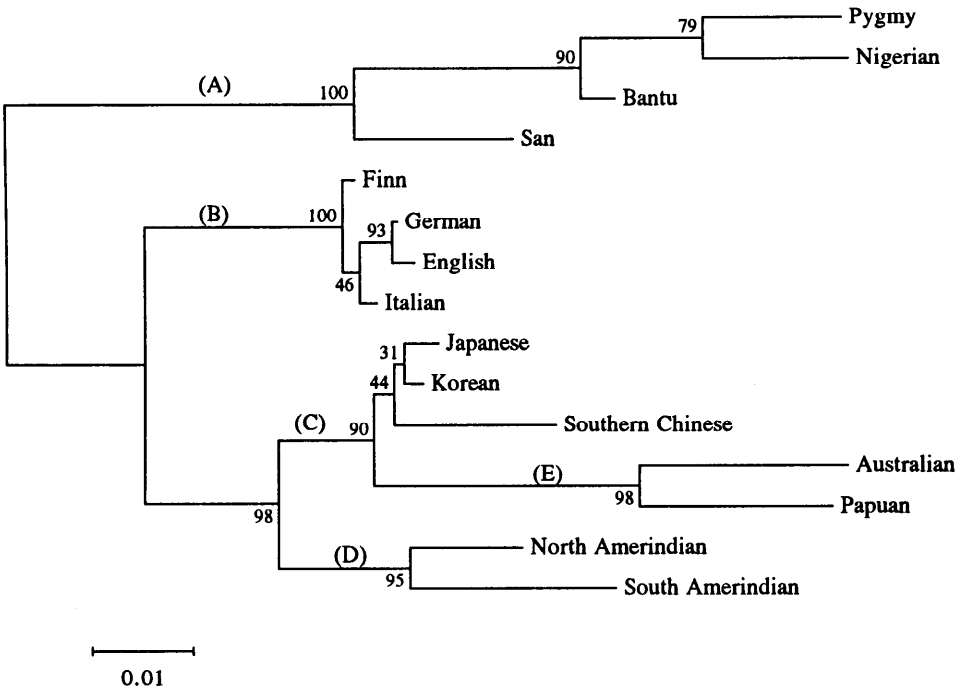

FIG. 4.—NJ tree for 15 representative populations. This tree is based on D_A values in fig. 3. Other aspects are the same as those in fig. 2.

receives very weak support by bootstrap tests. The third level of splitting is between the Caucasian cluster and the remainder, whereas the fourth level is between the American cluster (Amerindians and Eskimos) and the cluster of Asians and Oceanians. However, these splitting patterns again do not receive good support from bootstrap tests, though the Caucasian cluster has a high bootstrap value. Essentially the same conclusions were obtained from the UPGMA tree (not shown) constructed from D_A values in figure 3.

The relatively long branches for Australians, Papuans, and South Amerindians, in figures 2 and 4, are apparently caused by the inbreeding effect, as is evidenced by their low average heterozygosities (gene diversities) (figs. 1 and 3; also see Kirk 1989; Livshits and Nei 1990). This is so despite our effort to minimize this effect by using average gene frequencies of different tribal populations (see Material and Methods). The genetic distances between these populations and the African populations are generally higher than those between the Northeast Asian and the African populations, though the time of separation from the African populations is probably the same for the Northeast Asian, American, Australian, and Papuan populations. These large genetic distance values are also probably caused by inbreeding effects. For these reasons, UPGMA trees are unlikely to be correct.

To defend their UPGMA tree, Cavalli-Sforza et al. (1988) tested the hypothesis of constant-rate evolution for several populations, computing the ratio (R) of genetic distance to the time of population divergence as estimated from archeological data. The R value varied from 0.12 to 0.81, depending on the population pair considered, even if the standard errors of R were neglected. This result is clearly inconsistent with the hypothesis of rate constancy, though Cavalli-Sforza et al. concluded otherwise.

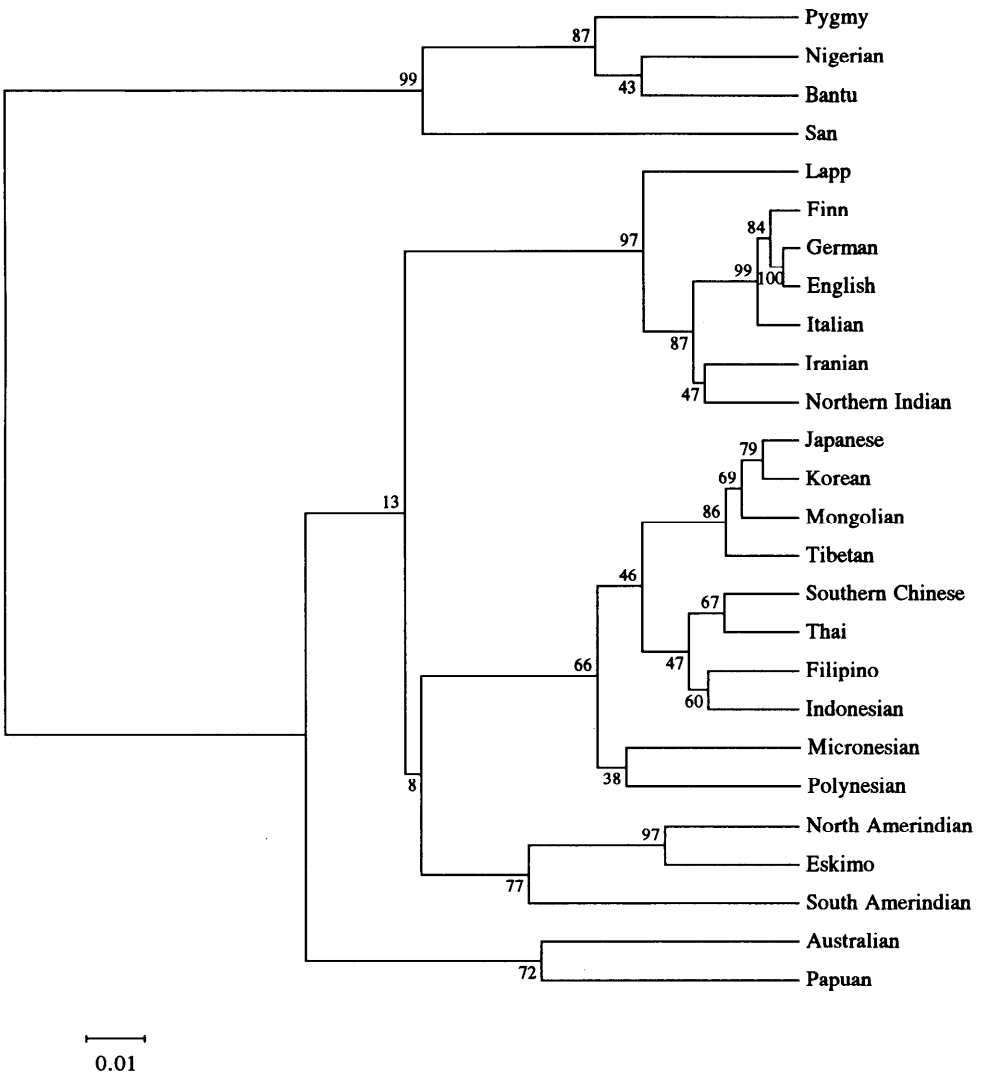

FIG. 5.—UPGMA tree for 26 representative populations. This tree is based on D_A values in fig. 1.

Furthermore, the archaeological data used are so uncertain that Cavalli-Sforza et al. themselves admitted that this type of test does not produce reliable results. At any rate, the NJ method is known to be superior to UPGMA in obtaining a correct phylogeny, regardless of whether evolutionary rate is constant (Saitou and Nei 1987; Rzhetsky and Nei 1992*a*). Therefore, there is no reason to prefer the tree in figure 5 to that in figure 2.

Discussion

In this paper, we have attempted to identify the major groups of human populations and to infer their evolutionary relationships. The major groups identified here are more similar to those recognized by classical anthropologists than to those by Cavalli-Sforza et al. (1988). That is, human populations can be subdivided into five major groups: (A) negroid (Africans), (B) caucasoid (Europeans and their related

populations), (C) mongoloid (East Asians and Pacific Islanders), (D) Amerindian (including Eskimos), and (E) australoid (Australians and Papuans). (There are intermediate populations, which are apparently products of gene admixture of these major groups, but they are ignored here.) However, the evolutionary relationships of these major groups are hierarchical rather than parallel, and some groups apparently originated from a population belonging to some other groups (e.g., australoid).

The phylogenetic tree (fig. 2) presented here is more consistent with data on morphological differences, archaeological records, and geographic distributions of populations than are previous trees, excluding some exceptions that will be discussed later. For example, Amerindians apparently migrated into North America 12,000–40,000 years ago (Dillehay and Collins 1988; Morrell 1990), and their morphological characters are quite similar to those of Northeast Asians and Southeast Asians. By contrast, Caucasians, particularly Northwest Europeans, are morphologically distinct from Northeast Asians or Amerindians and seem to have lived in Europe for $\geq$30,000 years (Stringer 1990). In Cavalli-Sforza et al.'s tree, Northeast Asians are closer to Europeans than to Southeast Asians (Southern Chinese, Filipinos, Thais, Indonesians, etc.), whereas in our tree the converse is true. Morphological characters of these populations are obviously consistent with our tree.

Analyzing the gene frequency data for the GM and KM loci in East Asian populations, Matsumoto (1988) and Zhao and Lee (1989) noticed substantial differences in gene frequencies between Northeast Asians and Southeast Asians. However, when they included African and European populations in their analysis, Northeast Asian and Southeast Asian populations were much closer to each other than to Europeans or Africans (Zhao and Lee 1989).

The origin of Australians and Papuans has been controversial for many decades. In terms of genetic distance, they are most closely related to East Asians, if we exclude Pacific Islanders. This suggests that the ancestors of these populations migrated from eastern Asia probably during the last glaciation, when the sea level was much lower than it is now. Indeed, archaeological data suggest that human colonization in Australia and New Guinea started 30,000–50,000 years ago (Bellwood 1989; Roberts et al. 1990). [Coastal New Guineans and Pacific Islanders are genetically close to Southeast Asians (Hertzberg et al. 1989*a*, 1989*b*; Chen et al. 1992), and they are apparently recent migrants (<3,500 years ago) from Southeast Asia (Bellwood 1989).]

One problem with this hypothesis is that Australians and Papuans have several characteristics (e.g., dark skin, frizzled hair, etc.) that are similar to those of black Africans. This problem can be explained either by the hypothesis of convergent evolution or by the hypothesis (Nei and Ota 1991) that there are two routes of migration of people to Australia and New Guinea from Africa, where *Homo sapiens* probably originated ~200,000 years ago (Stringer 1990). According to the latter hypothesis, one group of people moved to Northeast Asia through the Middle East before or during the early stage of the Würm-Wisconsin glaciation and later formed the Asian (mongoloid) group. They then moved southward to occupy Southeast Asia. A second group migrated to the Indian Subcontinent and then to Southeast Asia, where they had gene admixture with the mongoloid group (fig. 6). The resultant population absorbed most of its gene pool from the mongoloid group but retained the genes for dark skin, frizzled hair, etc., from Africans, because of natural selection in tropical conditions. This population then moved to New Guinea and Australia ~40,000 years ago. The Indian Subcontinent and Southeast Asia were later invaded by caucasoids and mongoloids, respectively, and further gene admixture occurred. This hypothesis

is supported by the fact that in these areas there are isolated populations (e.g., Philippine Negritos, Andamanese, Dravidians) with African traits.

By contrast, the hypothesis of independent (convergent) evolution of African traits in the mongoloid stock of New Guinea and Australia seems to have two problems. First, the time of divergence between Northeast Asians and Australopapuans seems to be too short for the conspicuous difference in pigmentation and hair texture to evolve, because Nei's (1985) mathematical computation suggests that it would take at least ~100,000 years to develop such a difference, though the computation depends on a number of assumptions. Second, if there was no migration of African stocks into the Indian Subcontinent, then we must invoke another independent evolution of African traits in this area. Therefore, Nei and Ota's (1991) explanation is more parsimonious than this hypothesis.

At the present time, there is a heated controversy over the origin of *H. sapiens*. Andrews (1986) and Stringer and Andrews (1988) have proposed that *H. sapiens* originated ~200,000 years ago in Africa and later spread through the world by migration (the out-of-Africa theory). By contrast, Wolpoff et al. (1984) have suggested that *H. sapiens* evolved from *H. erectus* simultaneously in several different areas of the world during the past 1 Myr (the multiregional theory). To resolve this controversy, Cann et al. (1987), Vigilant et al. (1991), and others constructed a phylogenetic tree of mtDNA and estimated the time of the common ancestor of all human mtDNAs. However, partly because this estimate is not very reliable (Nei 1992) and partly because the population structure of *H. erectus* and *H. sapiens* during the past 1 Myr is unknown (Takahata 1993), we cannot resolve the controversy by using mtDNA data.

However, the phylogenetic tree of human populations that is presented in figure 2 is consistent with the out-of-Africa theory rather than with the multiregional theory. Although the tree is unrooted, African populations are genetically quite different from the other populations. Therefore, it is likely that the first evolutionary splitting of humans occurred between the African and non-African populations. Furthermore, using electrophoretic data, Nei and Roychoudhury (1974) estimated that Negroids diverged from the caucasoid and mongoloid group ~115,000 years ago, whereas the latter two major ethnic groups diverged ~55,000 years ago. These estimates are certainly very rough, but the estimated time of the first divergence is consistent with fossil records suggesting that anatomically archaic *H. sapiens* apparently originated ~200,000 years ago in Africa (Andrews 1986; Stringer and Andrews 1988) and that modern *H. sapiens* already existed ~100,000 years ago in the Middle East (Israel), as well as in east-central and southern Africa (Stringer and Andrews 1988; Valladas et al. 1988). [However, for a different view, see Klein (1992).] It is therefore possible that the people who were living at that time in the Middle East later produced the caucasoid and mongoloid group (fig. 6).

There seem to be no fossil records that suggest the time of divergence between caucasoids and mongoloids. Nei and Ota (1991) speculated that the divergence of these two groups occurred during the Würm-Wisconsin ice age, through the barriers caused by the mountains that lie south (Himalaya Mountains) and west (Hindu Kush and other mountains) of Tibet. If this was the case, then one group of modern *H. sapiens* in the Middle East seems to have moved to China, either before this ice age (70,000 years ago) or during an intermittent period (50,000 years ago) of the ice age which was relatively warm; they then became a group of mongoloids. By contrast, the population that later became caucasoid apparently moved northwest to occupy Europe; Cro-Magnon, who lived ~10,000–30,000 years ago in Europe, are apparently ancestors

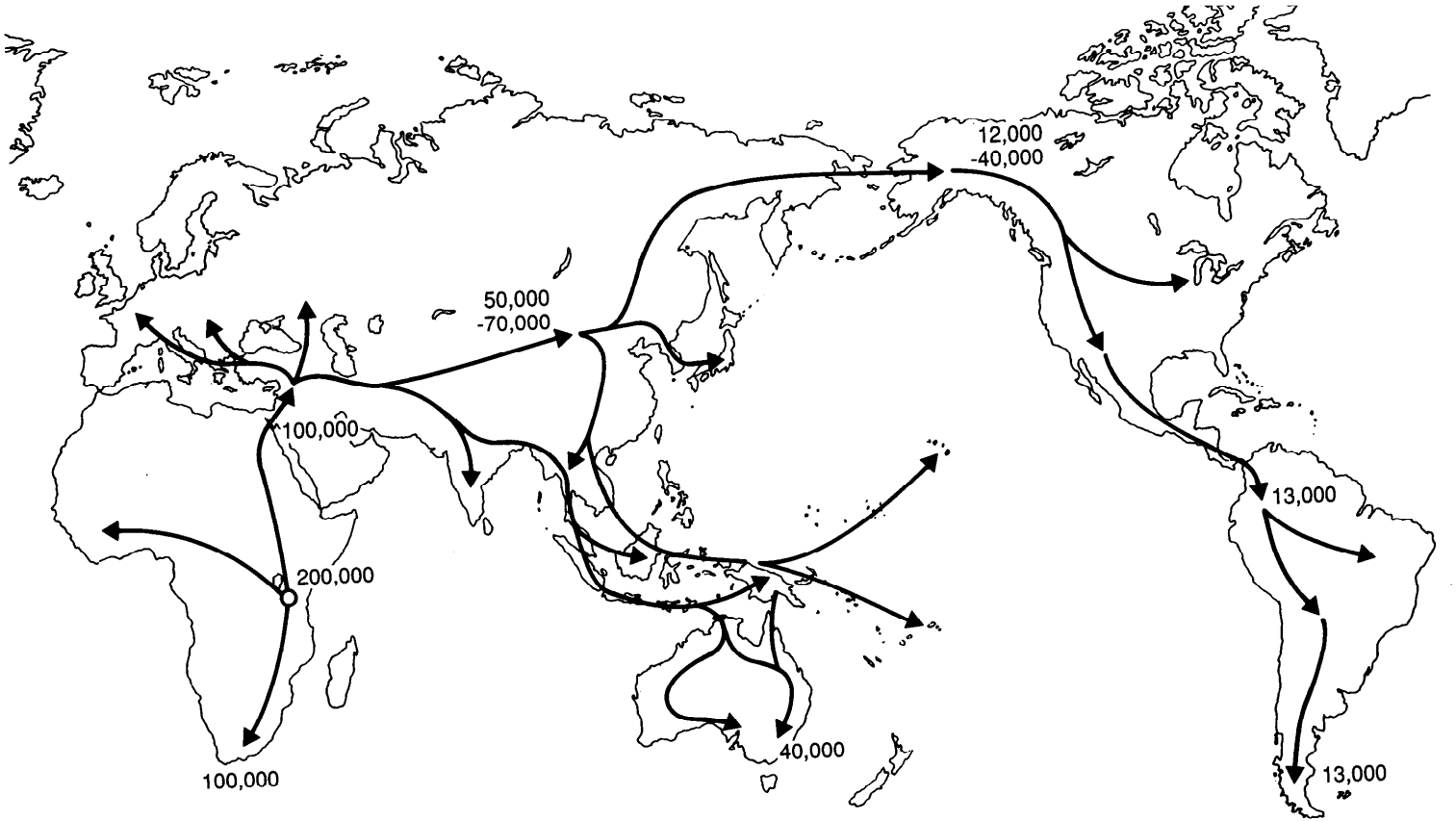

FIG. 6.—Scenario of the origins of major groups of human populations. This scenario is largely a speculation based on paleontological, archaeological, and genetic data available now. It is presented as a hypothesis to be tested in the future. Many anthropologists in the United States seem to believe that Amerindians entered into North America no earlier than 12,000 years ago. However, since there are archaeological data that are claimed to be 13,000–50,000 years old (Bahn 1993), it is possible that the colonization of America by mongoloids occurred much earlier. Furthermore, the phylogenetic trees in figs. 2 and 4 suggest that Amerindians and the current Northeast Asians had been separated before Amerindians migrated into North America. For details, see the text. This scenario is modified from that of Nei and Ota (1991).

of the present Europeans (fig. 6). Archaeological data also suggest that modern humans lived in Europe ~40,000 years ago (Klein 1992). Of course, this view is not without controversy (Thorne and Wolpoff 1992), but it is consistent with the phylogenetic tree in figure 2 or figure 4.

According to the multiregional theory, *H. sapiens* evolved simultaneously from *H. erectus* in at least four different regions of the world—i.e., Europe, East Asia, Australia, and Africa—but in each of these regions local characters, such as shovel-shaped incisors in Northeast Asians and prominent browridge in Australians, have been maintained for the past 500,000 years. Although some extent of gene flow is assumed to have occurred among these regions, it seems difficult to explain the two opposite trends of evolution, i.e., parallel evolution of the same modern anatomical humans in all regions and yet the maintenance of regional characters for such a long evolutionary time. (Is there any migration rate that makes both types of evolution possible?) In our view, this is one of the most serious problems in the multiregional theory. In most animal species, evolution occurs mainly by splitting of populations, as mentioned earlier. Note that the number of traits that show similarity between the present and fossil crania in some regions is small, that the traits are not always well defined, and that they are often observed in other populations (Groves 1990).

Thorne and Wolpoff (1992) have criticized the out-of-Africa theory by stating that there is little paleontological and archeological evidence that *H. erectus,* which is believed to have lived worldwide, was replaced by *H. sapiens* during the past 100,000 years without interbreeding with *H. erectus.* However, there is no reason to believe that the population size of *H. erectus* was very large when modern *H. sapiens* started to move out of Africa. It is possible that the population size of *H. erectus* was never very large or that this species was on the brink of extinction ~100,000 years ago. If this was the case, then Thorne and Wolpoff's criticism is no longer forceful.

Comparing their phylogenetic tree with the linguistic tree (Ruhlen 1987, pp. 284–378), Cavalli-Sforza et al. (1988) concluded that there is a rough correspondence between the two trees, though there are several exceptions. This conclusion is controversial (e.g., see Bateman et al. 1990), and we are not interested in engaging in the controversy. However, if our phylogenetic tree is correct, then the agreement between the genetic and linguistic trees becomes poor. This is because the Eurasiatic or Nostratic linguistic superphylum, consisting of languages spoken by Caucasians and Northeast Asians, no longer corresponds to the genetic clustering.

Earlier we emphasized the importance of using a large number of loci in the study of human evolution. This is because (*a*) the interpopulational genetic variation is very small compared with intrapopulational variation and (*b*) the evolution of a single gene (or mtDNA) is subject to large stochastic errors (Nei and Livshits 1989; Livshits and Nei 1990). In this study, using gene frequency data for 29 genetic loci, we could reconstruct an evolutionary history of human populations that seems likely to be less controversial and more enduring than some current alternatives.

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LITERATURE CITED

AI, Q., Y. YUAN, H. ZHAO, S. LI, and R. DU. 1987. Distribution of red cell blood group systems in Yi, Tibetan and Manchu ethnic groups in China. Gene Geogr. **1**:169–176.

AIZAWA, M. 1986. HLA in Asia-Oceania 1986. Hokkaido University Press, Sapporo, Japan.

ANDREWS, P. 1986. Fossil evidence on human origins and dispersal. Cold Spring Harb. Symp. Quant. Biol. **51**:419–428.

ASTOLFI, P., K. K. KIDD, and L. L. CAVALLI-SFORZA. 1981. A comparison of methods for reconstructing evolutionary trees. Syst. Zool. **30**:156–169.

BAHN, P. G. 1993. 50,000-year-old Americans of Pedra Furada. Nature **362**:114–115.

BATEMAN, R., I. GODDARD, R. O'GRADY, V. A. FUNK, R. MOOI, W. J. KRESS, and P. CANNELL. 1990. Speaking of forked tongues. Curr. Anthropol. **31**:1–24.

BELLWOOD, P. S. 1989. The colonization of the Pacific: some current hypotheses. Pp. 1–59 *in* A. V. S. HILL and S. W. SERJEANTSON, eds. The colonization of the Pacific: a genetic trail. Clarendon, Oxford.

BOWCOCK, A. M., J. R. KIDD, J. L. MOUNTAIN, J. M. HEBERT, L. CAROTENUTO, K. K. KIDD, and L. L. CAVALLI-SFORZA. 1991. Drift, admixture, and selection in human evolution: a study with DNA polymorphisms. Proc. Natl. Acad. Sci. USA **88**:839–843.

BRUES, A. M. 1977. People and races. Macmillan, New York.

CANN, R. L., M. STONEKING, and A. C. WILSON. 1987. Mitochondrial DNA and human evolution. Nature **325**:31–36.

CAVALLI-SFORZA, L. L., and A. W. F. EDWARDS. 1967. Phylogenetic analysis: models and estimation procedures. Am. J. Hum. Genet. **19**:233–257.

CAVALLI-SFORZA, L. L., A. PIAZZA, P. MENOZZI, and J. MOUNTAIN. 1988. Reconstruction of human evolution: bringing together genetic, archaeological, and linguistic data. Proc. Natl. Acad. Sci. USA **85**:6002–6006.

CHEN, L. Z., S. EASTEAL, P. G. BOARD, and R. L. KIRK. 1992. Genetic affinities of Oceanic populations based on RFLP and haplotype analysis of genetic loci on three chromosomes. Hum. Biol. **64**:1–15.

DEHAY, C., B. GENTILE, M. JEANNET, E. THORSBY, A. MARCELLI-BARGE, and J. DAUSSET. 1987. HLA and non-HLA phenotyping and genotyping in Austral and Gambier Polynesian Archipelagos. Tissue Antigens **30**:49–62.

DILLEHAY, T. D., and M. B. COLLINS. 1988. Early cultural evidence from Monte Verde in Chile. Nature **332**:150–152.

FARRIS, J. S. 1972. Estimating phylogenetic trees from distance matrices. Am. Nat. **106**:645–668.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution **29**:783–791.

GOEDDE, H. W., Y. K. PAIK, C. C. LEE, H. G. BENKMANN, L. KRIESE, P. BOGDANSKI, and M. WINKLER. 1987. Red cell and serum protein polymorphisms in three population groups of south Korea. Gene Geogr. **1**:177–188.

GROVES, C. P. 1990. Out of Africa—here we go again. Proc. Aust. Soc. Hum. Biol. **3**:13–25.

HEDGES, S. B., S. KUMAR, K. TAMURA, and M. STONEKING. 1992. Human origins and analysis of mitochondrial DNA sequences. Science **255**:737–739.

HERTZBERG, M., K. JAHROMI, V. FERGUSON, H. H. M. DAHL, J. MERCER, K. N. P. MICKLESON, and R. J. TRENT. 1989*a*. Phenylalanine hydroxylase gene haplotypes in Polynesians: evolutionary origins and absence of alleles associated with severe phenylketonuria. Am. J. Hum. Genet. **44**:382–387.

HERTZBERG, M., K. N. P. MICKLESON, S. W. SERJEANTSON, J. F. PRIOR, and R. J. TRENT. 1989*b*. An Asian-specific 9-bp deletion of mitochondrial DNA is frequently found in Polynesians. Am. J. Hum. Genet. **44**:504–510.

HOWELLS, W. 1967. Mankind in the making, rev. ed. Doubleday, Garden City, N.Y.

HUGHES, A. L., and M. NEI. 1988. Pattern of nucleotide substitution at major histocompatibility complex loci reveals overdominant selection. Nature **335**:167–170.

KIRK, R. L. 1979. Genetic differentiation in Australia and its bearing on the origin of the first Americans. Pp. 211–237 *in* W. S. LAUGHLIN and A. B. HARPER, eds. The first Americans: origins, affinities, and adaptations. Gustav Fischer, New York.

———. 1985. Pacific peoples: origins and genetic relationships. Pp. 62–79 *in* Y. R. AHUJA and J. V. NEEL, eds. Genetic microdifferentiation in human and other animal populations. Indian Anthropological Association, Delhi.

———. 1989. Population genetic studies in the Pacific: red cell antigen, serum protein, and enzyme systems. Pp. 60–119 *in* A. V. S. HILL and S. W. SERJEANTSON, eds. The colonization of the Pacific: a genetic trail. Clarendon, Oxford.

KLEIN, R. G. 1992. The archeology of modern human origins. Evol. Anthropol. **1**:5–14.

LIVSHITS, G., and M. NEI. 1990. Relationships between intrapopulational and interpopulational genetic diversity in man. Ann. Hum. Biol. **17**:501–513.

MCKUSICK, V. A. 1986. Mendelian inheritance in man, 7th ed. Johns Hopkins University Press, Baltimore.

MCNALLY, R. 1982. The atlas of mankind. Rand McNally, New York.

MATSUMOTO, H. 1988. Characteristics of Mongoloid and neighboring populations based on the genetic markers of human immunoglobulins. Hum. Genet. **80**:207–218.

MORRELL, V. 1990. Confusion in earliest America. Science **248**:439–441.

NEI, M. 1972. Genetic distance between populations. Am. Nat. **106**:283–292.

———. 1985. Human evolution at the molecular level. Pp. 41–64 *in* T. OHTA and K. AOKI, eds. Population genetics and molecular evolution. Springer, Berlin.

———. 1992. Age of the common ancestor of human mitochondrial DNA. Mol. Biol. Evol. **9**:1176–1178.

NEI, M., and G. LIVSHITS. 1989. Genetic relationships of Europeans, Asians and Africans and the origin of modern *Homo sapiens*. Hum. Hered. **39**:276–281.

NEI, M., and T. OTA. 1991. Evolutionary relationships of human populations at the molecular level. Pp. 415–428 *in* S. OSAWA and T. HONJO, eds. Evolution of life. Springer, Tokyo.

NEI, M., and A. K. ROYCHOUDHURY. 1974. Genic variation within and between the three major races of man, caucasoids, negroids, and mongoloids. Am. J. Hum. Genet. **26**:421–443.

———. 1982. Genetic relationship and evolution of human races. Evol. Biol. **14**:1–59.

NEI, M., F. TAJIMA, and Y. TATENO. 1983. Accuracy of estimated phylogenetic trees from molecular data. J. Mol. Evol. **19**:153–170.

NURSE, G. T., J. S. WEINER, and T. JENKINS. 1985. The peoples of southern Africa and their affinities. Clarendon, Oxford.

OHKURA, K., T. MIYASHITA, H. HASEKURA, H. NAKAJIMA, H. MATSUMOTO, Y. S. KANG, and C. C. LEE. 1989. Distribution of blood groups in Korea. Hum. Hered. **39**:223–229.

PAPIHA, S. S., S. S. MASTANA, and A. STEPHENSON. 1989. Serogenetic investigations of Tibetans and Himachalis from Himachal Pradesh, India: genetic relationship between Tibetans and certain selected Mongoloid populations. Jpn. J. Hum. Genet. **34**:143–157.

ROBERTS, R. G., R. JONES, and M. A. SMITH. 1990. Thermoluminescence dating of a 50,000-year-old human occupation site in northern Australia. Nature **345**:153–156.

ROYCHOUDHURY, A. K., and M. NEI. 1988. Human polymorphic genes: world distribution. Oxford University Press, New York.

RUHLEN, M. 1987. A guide to the world's languages. Vol. **1**. Classification. Stanford University Press, Stanford.

RZHETSKY, A., and M. NEI. 1992*a*. A simple method for estimating and testing minimum-evolution trees. Mol. Biol. Evol. **9**:945–967.

———. 1992*b*. Statistical properties of the ordinary least-squares, generalized least-square, and minimum-evolution methods of phylogenetic inference. J. Mol. Evol. **35**:367–375.

SAHA, N. 1989. Blood genetic markers in the Chinese of two eastern provinces. Am. J. Phys. Anthropol. **80**:295–303.

SAITOU, N., and T. IMANISHI. 1989. Relative efficiencies of the Fitch-Margoliash, maximum-parsimony, maximum-likelihood, minimum-evolution, and neighbor-joining methods of phylogenetic tree construction in obtaining the correct tree. Mol. Biol. Evol. **6**:514–525.

SAITOU, N., and M. NEI. 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. Mol. Biol. Evol. **4**:406–425.

SERJEANTSON, S. W., R. L. KIRK, P. RANFORD, and M. BEAUCHAMP. 1983. HLA antigens and non-HLA chromosome 6 markers in Micronesians from Nauru. Tissue Antigens **22**:49–58.

SERJEANTSON, S. W., D. P. RYAN, and A. R. THOMPSON. 1982. The colonization of the Pacific: the story according to human leukocyte antigens. Am. J. Hum. Genet. **34**:904–918.

SNEATH, P. H. A., and R. R. SOKAL. 1973. Numerical taxonomy. W. H. Freeman, San Francisco.

STRINGER, C. B. 1990. The emergence of modern humans. Sci. Am. (December), pp. 98–104.

STRINGER, C. B., and P. ANDREWS. 1988. Genetic and fossil evidence for the origin of modern humans. Science **239**:1263–1268.

TAKAHATA, N. 1993. Allelic genealogy and human evolution. Mol. Biol. Evol. **10**:2–22.

TAMURA, K., and M. NEI. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Mol. Biol. Evol. **10**: 512–526.

TEMPLETON, A. L. 1992. Human origins and analysis of mitochondrial DNA sequences. Science **255**:737.

THORNE, A. G., and M. H. WOLPOFF. 1992. The multiregional evolution of humans. Sci. Am. (April), pp. 76–83.

VALLADAS, H., J. L. REYSS, J. L. JORON, G. VALLADAS, O. BAR-YOSEF, and B. VANDERMEERSCH. 1988. Thermoluminescence dating of Mousterian 'Proto-Cro-Magnon' remains from Israel and the origin of modern man. Nature **331**:614–616.

VIGILANT, L., M. STONEKING, H. HARPENDING, K. HAWKES, and A. C. WILSON. 1991. African populations and the evolution of human mitochondrial DNA. Science **253**:1503–1507.

WHITTAM, T. S. 1992. NJBOOT: neighbor-joining bootstrap analysis, version 1.1. Institute of Molecular and Evolutionary Genetics, Pennsylvania State University, University Park.

WOLPOFF, M. H., X. Z. WU, and A. G. THRONE. 1984. Modern *Homo sapiens* origins: a general theory of hominid evolution involving the fossil evidence from East Asia. Pp. 411–483 *in* F. H. SMITH and F. SPENCER, eds. The origins of modern humans: a world survey of the fossil evidence. Alan R. Liss, New York.

ZHAO, T., and T. D. LEE. 1989. Gm and Km allotypes in 74 Chinese populations: a hypothesis of the origin of the Chinese nation. Hum. Genet. **83**:101–110.

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