Genetic Origins of the Japanese: A Partial Support for the Dual Structure Hypothesis

KEIICHI OMOTO[1]* AND NARUYA SAITOU[2]
[1]*International Research Center for Japanese Studies, Kyoto, 610-11 Japan;*
[2]*National Institute of Genetics, Mishima, 411 Japan*

ABSTRACT   Based on the morphological characteristics of the skull and teeth, Hanihara ([1991] Japan Review *2*:1–33) proposed the "dual structure model" for the formation of modern Japanese populations. We examine this model by dividing it into two independent hypotheses: 1) the Upper Paleolithic population of Japan that gave rise to the Neolithic Jomon people was of southeast Asian origin, and 2) modern Ainu and Ryukyuan (Okinawa) populations are direct descendants of the Jomon people, while Hondo (Main Island)-Japanese are mainly derived from the migrants from the northeast Asian continent after the Aeneolithic Yayoi period. Our aim is to examine the extent to which the model is supported by genetic evidence from modern populations, particularly from Japan and other Asian areas. Based on genetic distance analyses using data from up to 25 "classic" genetic markers, we find first that the three Japanese populations including Ainu and Ryukyuan clearly belong to a northeast Asian cluster group. This negates the first hypothesis of the model. Then, we find that Ainu and Ryukyuans share a group contrasting with Hondo-Japanese and Korean, supporting the second hypothesis of the model. Based on these results, we propose a modified version of the dual structure model which may explain the genetic, morphological, and archaeological evidence concerning the formation of modern Japanese populations. Am J Phys Anthropol 102:437–446, 1997.   © 1997 Wiley-Liss, Inc.

Questions about the origins of modern Japanese have a long history of debate (for references see Hanihara, 1991). In short, the controversies were between "continuity" and "admixture" models. The advocates of the former model believed that the inhabitants of the Japanese Islands were genetically unchanged from prehistoric to historic times, while their morphology showed secular changes (e.g., Suzuki, 1969). The advocates of the latter model emphasized the drastic changes in morphology and culture which took place synchronically about 2,300 years ago, mainly in the western part of Japan, and considered these as evidence for admixture (e.g., Kanaseki et al., 1960).

In 1991, Hanihara proposed a hypothesis for the formation of Japanese populations, which he called the "dual structure model."

It is clearly on the side of the admixture school and is the most comprehensive current hypothesis on the formation of modern Japanese populations.

To test this hypothesis, we divide it into two parts that are briefly summarized as follows: 1) the Upper Paleolithic populations of Japan came from somewhere in southeast Asia and gave rise to Jomonese, or the people of the Neolithic Jomon period (12,000–2,300 years BP), and 2) modern Japanese populations were formed by the mixture of mainly two population groups with different

*Correspondence to: K. Omoto, International Research Center for Japanese Studies, 3-2 Oeyama-cho, Goryo, Nishikyo-ku, Kyoto, 610-11 Japan. Email: ko8516@nichibun.ac.jp

TABLE 1. Nei's standard genetic distances (lower diagonal matrix) and modified Cavalli-Sforza distances (above diagonal matrix) for the four populations

	Hondo-Japanese	Korean	Ainu	Ryukyuan
Hondo-Japanese	—	0.00354	0.00747	0.00217
Korean	0.00404	—	0.01155	0.00707
Ainu	0.00808	0.01043	—	0.00642
Ryukyuan	0.00336	0.00899	0.00696	—

ancestries: Ainu and Ryukyuan are relatively pure descendants of Jomonese, while Hondo (Main Island)-Japanese have received strong genetic infusions from migrant populations who came to western Japan during the Aeneolithic Yayoi period (300 BC–300 AD) and the Proto-historic Kofun period (300–700 AD). These migrants came from northeast Asia via the Korean peninsula and from there spread to eastern and southern Japan.

We believe that questions on the origins of human populations are better addressed by genetic approaches than by other approaches, be they morphological or, definitely, cultural (e.g., archaeological and linguistic) ones. In this paper, we present the results of two genetic distance analyses that use "classic" genetic marker gene frequency data. The first analysis tests whether Japanese populations have roots in southeast Asia. The second one seeks to determine whether there is a dual structure among Japanese populations. On the basis of our findings, we propose that the first question cannot but the second question can be supported. We discuss the anthropological significance of these results and present a modified version of the dual structure model.

MATERIALS AND METHODS

In the first genetic distance analysis, 26 populations of the world, including three Japanese (Ainu, Ryukyuan and Hondo-Japanese), were compared. The populations examined other than Japanese were: three African, four Indo-European, three native American, nine east Asian, one native Australian, one New Guinean (Papuan), and two Pacific populations. Gene frequency data on a total of 20 polymorphic loci were available for these populations: eight blood group systems (ABO, MNSs, P, Fy, Rh, Jk, Di, K), seven red cell enzyme systems (ACP, PGD, PGM1, PGM2, ADA, GPT, ESD), and five serum protein systems (Hp, Tf, Gc, Gm,

Inv). Most data on Japanese populations were taken from the compilation by JIBP Synthesis, Volume 2 (Watanabe et al., 1975). The sources of some additional data were as follows: GPT (Ueda et al., 1979) and ESD (Omoto et al., 1975). The data on blood genetic markers of Koreans were taken from Yuan et al. (1984) and Goedde et al. (1984). The data on other populations were obtained from Roychoudhury and Nei (1988) and Masatoshi Nei (personal communication), with the exception of our unpublished data on two Negrito populations of the Philippines.

In the second genetic distance analysis, the three Japanese populations mentioned above and Koreans were compared using gene frequency data from 25 polymorphic loci. In addition to those mentioned above, we were able to use data from five polymorphic loci: pseudocholinesterase-1, cerumen, PTC taste sensitivity, color blindness, and INH inactivator types (Watanabe et al., 1975).

For calculation of genetic distances, Nei's standard distance (D_{st}) (Nei, 1972) and the modified Cavalli-Sforza distance (D_A) (Nei et al., 1983) were used (Table 1). To cluster each set of genetic distances, we employed the neighbor-joining (NJ) method (Saitou and Nei, 1987). This approach to tree construction has been shown to be superior to other methods such as the UPGMA method (Sokal and Sneath, 1963) in recovering the true branching pattern of the genetic relationship of populations (Saitou and Nei, 1987; Nei and Takezaki, 1994). To evaluate the branching pattern statistically, we used the bootstrap test (Efron, 1982). This test determines the probability of reproducing the particular branching pattern in the phylogenetic tree by using randomly recombined gene frequency data for the given populations.

RESULTS

In the first set of our calculations, a total of 26 populations of the world were com-

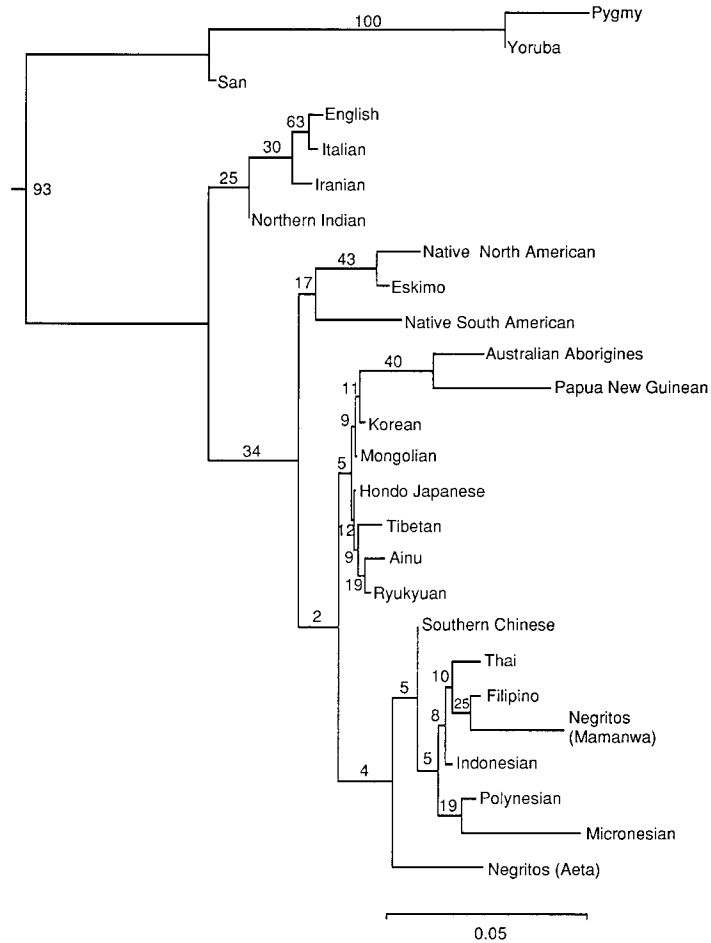Fig. 1. A neighbor-joining (NJ) genetic tree for 26 populations of the world based on standard genetic distance (D_{st}). Allele frequency data of 20 polymorphic loci are used. Numbers along the branches are bootstrap probability values (%).

pared (Figs. 1, and 2). In both genetic trees, using the genetic distances D_{st} and D_A, the African populations are very different from non-African populations. The bootstrap value for this separation is very high (93–96%). Among non-Africans, the Indo-European population group is first separated from the rest, though the bootstrap probability values are not as high as those showing separation of the African groups. Further, Native American populations including Eskimos are separated from Asian/Pacific populations. However, with regard to clustering of Native Australian and New Guinean populations, the two trees show a noteworthy difference from each other. In the tree based on D_{st} (Fig. 1), they are clustered with the northeast Asian group, which is unexpected, given the anthropological view that the roots of

Australian and New Guinean populations are in southeast Asia. In the tree based on D_A, however, Australians and New Guineans are clearly separated from other Asian-Pacific populations (Fig. 2).

Among the rest of the Asian-Pacific populations, two cluster groups may be recognized, although the bootstrap values for their separation are low: northeast Asian and southeast Asian/Pacific groups. Three Japanese populations—Korean, Tibetan, and Mongolian—form the northeast Asian cluster group, while southern Chinese, Thai, Filipino, Indonesian, Micronesian, Polynesian, and two Negrito populations belong to the southeast Asian/Pacific cluster group.

In the second set of phylogenetic analyses, three ethnic groups of Japan (Ainu, Ryukyuan, and Hondo-Japanese) are com-
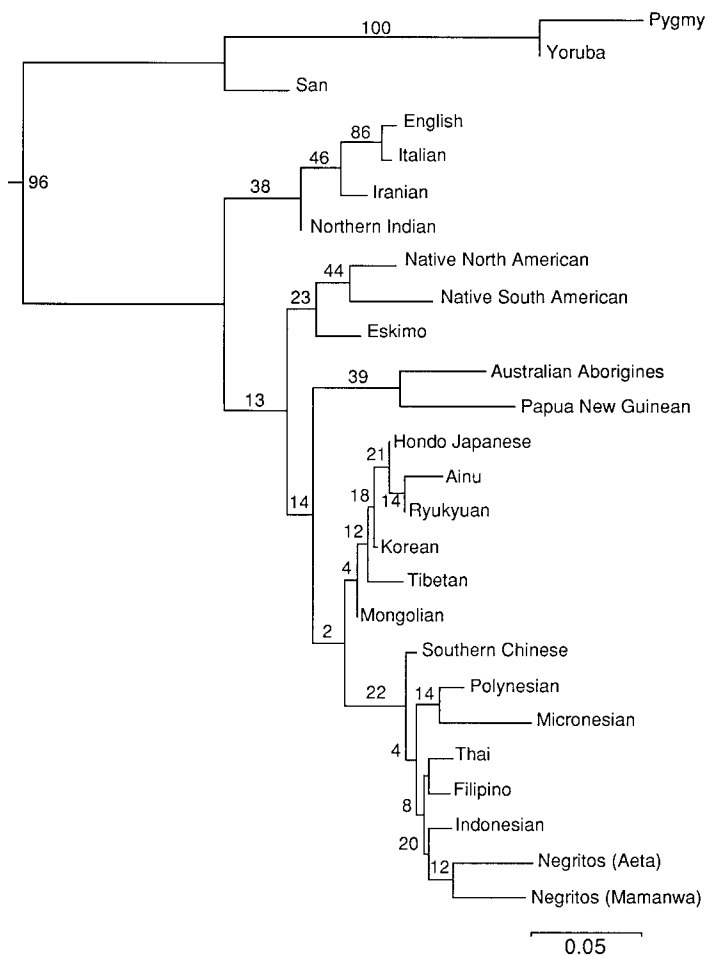
Fig. 2. A neighbor-joining (NJ) genetic tree for 26 populations of the world based on modified Cavalli-Sforza distance (D_A). The gene frequency data used is the same as in Fig. 1. Numbers along the branches are bootstrap probability values (%).

pared with the Korean sample as the control. We had to restrict our analyses to these samples because we wanted to maximize the genetic data used in the analyses. Only 20 genetic loci are available for the other populations, but 25 loci have been examined in these three Japanese and the Korean population samples. The NJ networks show that Ainu and Ryukyuan samples are clustered together in contrast to Hondo-Japanese and Korean. The two genetic distance measures used (D_{st} and D_A) gave essentially the same topology, although the bootstrap values for the separation of the Ainu/Ryukyuan branch were slightly different: 74% for the one based on D_{st} and 85% for D_A (Fig. 3).

DISCUSSION

Background of the dual structure model

Hanihara's model is primarily based on findings arising from studies on cranial and dental features (Hanihara, 1991, 1992). The basic observation supporting this model is the morphological similarity of Ainus, and to some extent of Ryukyuans, to the Neolithic populations of the Jomon period, who are usually regarded as descendants of the Upper Paleolithic population of Japan represented by Minatogawa Man (Howells, 1966; Suzuki, 1982; Hanihara, 1984). Furthermore, the difference in cranial morphology between the Jomon and the Aeneolithic Yayoi

(A)

Bootstrap probability = 85%
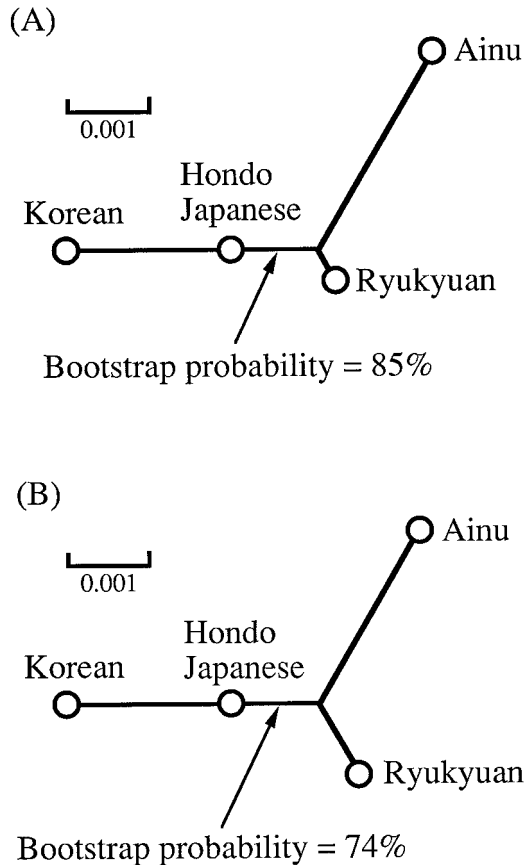
(B)

Bootstrap probability = 74%

Fig. 3. The NJ genetic tree comparing three Japanese populations (Ainu, Ryukyuan, and Hondo-Japanese) with Korean as a control, based on allele frequency data of 25 polymorphic loci. Genetic distance measures used are D_A (**A**) and D_{st} (**B**). Note that the bootstrap probability values (85% for A and 74% for B) are much higher than those under the random expectation (33%).

populations in the western part of Japan is so remarkable and occurred so suddenly at about 2,300 years BP that a continuity model provides insufficient explanation. Hanihara (1987) also used computer simulation to estimate the number of migrant people who came to the western part of Japan. He proposed that over the 1,000 years elapsed since the beginning of the Yayoi period (300 BC) and the end of the Kofun period (700 AD) an unexpectedly large number of migrant people may have entered Japan: 1.5 million, assuming the annual growth rate of the migrant Yayoi rice farmers was 0.2 percent (Hanihara, 1987).

Although the validity of this figure can be examined through more detailed simulation studies, we think that Hanihara's dual structure model is superior to many other models on the origins of the Japanese that have been proposed because most of these are rather nonquantitative and speculative.

The strong advocate for the dual origin and admixture model for the formation of the Japanese populations, as well as the idea that the ancestors of the Jomon people came from southeast Asia is Christy Turner (Turner, 1976, 1987, 1992). He demonstrated that east Asian populations can be divided into two distinct groups on the basis of dental patterns: the northeast Asian group exhibit "Sinodonty" and the southeast Asian group shows "Sundadonty." According to him, the Ainu and Jomon populations are sundadonts, whereas the Hondo-Japanese are sinodonts (Turner, 1976).

Mitochondrial DNA (mtDNA) extracted from ancient bones also seemed to suggest a common origin for the Jomon and Ainu populations (Horai et al., 1989, 1991). In these studies, mtDNA was extracted from the bones of five Jomonese, carbon 14–dated at about 6,000 years BP, and six early-modern Ainu (seventeenth to eighteenth century AD). A 190 base-pair (bp) segment of the D-loop region of mtDNA was sequenced, and the sequences were compared with those of modern individuals from various regions of the world. An identical sequence was observed among four Jomonese, two Ainu, and three southeast Asian as well as 15 non-Ainu Japanese mtDNAs. Although Horai and his colleagues are cautious about their conclusions on the origins of Jomonese and Ainu (Horai et al., 1989), this result has been cited as positive evidence for the southeast Asian origin of the first population of Japan (Hanihara, 1991). However, it is worth noting that there is a big difference between the phylogeny of molecules and the phylogeny of populations. It is well known that molecular splits may far antedate population splits (Nei, 1987). In the molecular genetic tree of Horai et al. (1991), mtDNAs of non-Ainu Japanese are scattered around the whole tree, among mtDNAs of Europeans and Africans, and do not cluster.

The question of northern or southern origins

Contrary to the assumptions of the dual structure model, classic genetic marker data show that Japanese populations, including Ainu, have definite northern affinities. Matsumoto (1984, 1988) found that serum gammaglobulin (Gm) types showed a clear-cut north/south dichotomy of east Asian populations and that Japanese belonged to the northern group. He also showed that Japanese populations are relatively homogeneous in the distribution of Gm allele frequencies, which contradicts Hanihara's dual structure model. Matsumoto's conclusion, that the homeland of all Japanese populations may have been in the Lake Baikal area in Siberia, however, met with strong objection from Japanese anthropologists, including Kazuro Hanihara. We also believe that conclusions about the origins of human populations should be based on information from many genetic loci rather than a single genetic locus.

Nei and Roychoudhury (1993) analyzed 26 populations from around the world using gene frequency data from 29 polymorphic loci of classic genetic markers and examined the resulting dendrograms by bootstrap tests. Among east Asians, they compared Japanese (Hondo-Japanese), Koreans, Mongolians, Tibetans, southern Chinese, Thais, Filipinos, and Indonesians. They did not recognize northern and southern cluster groups and used the traditional term *Mongoloid* to denote all east Asian and Pacific populations.

Recently, Nei published phylogenetic trees that show the relationships of Japanese populations (Nei, 1995). This time, he compared Ainu, "Japanese of Okinawa," (Ryukyuan) and "Japanese of Tokyo" (Hondo-Japanese) with neighboring populations using data from 18 polymorphic loci. He showed that the three Japanese populations are close to Korean, while southern Chinese, Native Taiwanese, Thai, and Filipino samples cluster as a separate group. On the basis of this result, he challenged Hanihara's hypothesis as a whole with respect to the origins and the dual structure of Japanese populations.

Omoto (1995) examined the problem of the origins of Ainu in detail. He compared Native Australian, New Guinean, Micronesian, and Polynesian populations plus 11 east Asian populations on the basis of NJ trees with D_A distances, using classic genetic markers from 23 polymorphic loci. Ainu clearly fell in to the northeast Asian group, with Korean, Mongolian, and Tibetan samples, while southern Chinese, Thai, Filipino, Indonesian, and two Negrito populations were linked with the southeast Asian group.

The overall Hondo-Japanese admixture rate in the original sample of about 500 Ainu from the District of Hidaka on Hokkaido, which is the northernmost island of Japan, was estimated to be approximately 30–40% (Omoto, 1972). Omoto (1995), however, determined the impact of admixture on the position of the Ainu population in the tree by correcting gene frequencies for admixture. No change occurred even when an admixture estimate of 40% was employed and Ainu remained in the northeast Asian cluster group. However, the branch length to the Ainu elongated considerably. When a hypothetical admixture rate of 60% was used to correct gene frequencies, the Ainu remained in the northeast Asian cluster group, but the Native Australian/New Guinean cluster moved near the root of the long branch leading to the Ainu. The genetic relationships of other populations were essentially unchanged. Although it is not possible to draw a conclusion from such a simulation, it lends support the view that Ainu and Native Australians/New Guineans both are derived directly from the Upper Paleolithic populations of east Asia (Omoto, 1995). The possibility that Ainu origins lie in ancestral population groups in northeast Asia has also been shown recently by a DNA-based study of HLA Class II genes (Bannai et al., 1996).

Our study confirms that three Japanese populations, including Ainu and Ryukyuan, belong to the northeast Asian group, along with Koreans, Mongolians, and Tibetans. This group appears separated from the southeast Asian group comprising southern Chinese, Thai, Filipino, Indonesian, Micronesian, Polynesian, and two Negrito populations, although the bootstrap probability for

this separation is rather low and is statistically not significant (22% in Fig. 2).

With regard to the origins of the Mongoloid populations, the currently popular view assumes that southeast Asia was the center of dispersals (e.g., Turner, 1995). This view, which is based primarily on morphological traits, was examined by Omoto (1995). He considered genetic evidence and favored a model which assumes independent origins of northeast Asian, southeast Asian, and Native American population groups. Nei (1995) seems to be skeptical about the dichotomy of northern and southern Mongoloid groups because the branching yields relatively low bootstrap values. However, in view of the genetic, archaeological, and linguistic evidence for large-scale dispersals of northern groups into southeast Asia and the Pacific during the last 10,000 years (e.g., Bellwood, 1979, 1996), we assume as a working hypothesis that the dichotomy in our genetic tree (Fig. 2) has historical validity.

Hanihara's view that the Upper Paleolithic population of Japan originated somewhere in southeast Asia may have been based partly on the observation of Suzuki (1982) on Minatogawa Man (Hanihara, 1991). Suzuki considered that the skull of Minatogawa No. 1 dated at approximately 18,000 years BP is morphologically similar to Jomonese. He further assumed that Minatogawa Man is more closely related to Liujang Man of southern China than to the specimen No. 101 of Upper Cave of Zhoukoudian, northern China. However, we doubt that observations on a single skull can provide all that needs to be known about origins. After examining our genetic data, we propose a counterhypothesis that the Upper Paleolithic populations of Japan are derived from those of northeast Asia and did not necessarily originate in southeast Asia. A critical examination of the three specimens from Upper Cave are particularly important in this regard.

We believe that our hypothesis is more in agreement with prehistoric evidence than is Hanihara's. According to most archaeologists in Japan, stone-tool cultures of the Upper Paleolithic and the successive Jomon period show definite northern affinities (Chosuke Serizawa, personal communication).

The microblade tradition accompanying the Araya type burin was widely distributed from eastern Siberia to the Japanese archipelago from the postglacial period until the beginning of the Jomon period (approximately 20,000–12,000 years BP). No stone-tool culture of southeast Asian affinities has been discovered in Japan for this period (Kimura, 1993; Tanaka et al., 1995).

Dual structure of the Japanese populations

Omoto (1972, 1992) and Omoto and Misawa (1976) have shown that Ainu and Ryukyuan peoples are genetically rather similar to each other but are different from Hondo-Japanese. This finding seemed to fit well with the admixture model for the formation of the Japanese populations. In these previous reports, however, the dichotomy of Ainu/Ryukyuan and Hondo-Japanese was emphasized, without the relationship being tested statistically. In the present study, three Japanese populations are compared to each other, with Korean as the control on the basis of the largest data set ever used: 25 polymorphic loci. Also, the separation between the Ainu/Ryukyuan cluster and the Hondo-Japanese/Korean group in the NJ network was statistically evaluated by bootstrap probabilities (Fig. 3). While two genetic distance measures, D_{st} and D_A, gave essentially the same topology, the bootstrap value is slightly higher (85%) in the tree using D_A than that using D_{st} (74%). Although this difference in bootstrap values is statistically not significant, we have noted that D_A is superior to D_{st} in producing reliable genetic relationships of populations (Figs. 1, 2). Since the expected value of the bootstrap probability for four populations under no genetic relationship ("star phylogeny") is 33%, the observed values are much higher than this random expectation. Recently, theoretical studies on the bootstrap test have been extensively conducted (e.g., Sitnikova et al., 1995; Zharkikh and Li, 1995; Efron et al., 1996). However, it is still not clear how bootstrap probabilities for genetic trees should be treated with the usual statistical tests. Therefore, we do not consider reliance on bootstrap probabilities as critical. In any case, we believe that our

results give support for the separation between Ainu/Ryukyuan and Hondo-Japanese/ Korean clusters. If this clustering is real, it in turn gives a partial support for Hanihara's dual structure model, in terms of the duality of the Japanese populations.

It is worth noting that our conclusions are different from those of Nei (1995). He published a phylogenetic tree based on 18 polymorphic loci that shows the relationships of Ainu, Hondo-Japanese, and Okinawan (Ryukyuan) with neighboring populations. He expressed his doubt about Hanihara's dual structure model as a whole (Nei, 1995). However, when the hypothesis is broken into two components, the evidence, we suggest, shows that there may in fact be a duality in Japanese populations. This difference in interpretation will be cleared by future studies with much more and better data. At this moment, we think that the details of a population's origin are unlikely to be revealed by using a worldwide data set such as used by Nei (1995). To understand local biological history, one has to examine the genetic profiles of the populations that have been hypothesized to be ancestral to it and to do this with as large a number of genetic loci as possible. Of course, we do not consider our findings to be final, particularly because of our relatively low bootstrap values. Probably, our study represents a microscopic rather than a macroscopic approach in reconstructing the population history of Japan.

Recently, a detailed genetic comparison of Asian populations, including Ainu and Ryukyuan, which used mtDNA sequence data was published (Horai et al., 1996). The results from this study are in agreement with ours in that Hondo-Japanese and Koreans are genetically very close to each other and the admixture model of the formation of the modern Japanese is favored. However, with regard to the relationship between the Ainu and the Ryukyuan, no evidence for a common ancestry is found. Future studies are needed to clear up the position of Rykyuans.

Finally, when origins are considered, questions about linguistic evidence commonly arise. Our view can be summarized as follows. If a large number of migrants to Japan actually came from northeast Asia, perhaps via the Korean peninsula starting around 2,300 years BP, as Hanihara's dual structure model maintains, why is the language of Hondo-Japanese (i.e., Japanese) so different from Korean or other Altaic languages? In our view, language changes during population mixture are complex social phenomena that cannot be simply defined or measured chronologically, as can biological phenomena. Given the almost complete absence of quantitative and statistical comparisons between Japanese (including Ainu and Ryukyuan) and other languages in Asia, except for the work of Biten Yasumoto, which has no general support among Japanese linguists, we have at present no clear answer, either pro or con, to our question. It is interesting to note that, on the basis of statistical comparisons of basic words among east Asian languages including the Ainu, he reached the conclusion that Ainu and Korean languages may have common ancient ancestry in what he calls the Paleo-Far-Eastern language group (Yasumoto and Honda, 1978; Yasumoto, personal communication). For this reason, we do not put emphasis on language now and have focussed our attention on genetic, morphological and archaeological evidence.

CONCLUSIONS

We propose a modified version of the dual structure model of the origins of Japanese populations. Two fundamental population groups are ancestral to modern Japanese populations (Ainu, Ryukyuan, and Hondo-Japanese). One group, represented by the Jomonese who gave rise to the modern Ainu and probably also the Ryukyuan populations, has its origin in the Upper Paleolithic populations of northeast Asia, which were not necessarily derived from southeast Asia. The other group is the later migrants of the Yayoi and Kofun periods who also came from northeast Asia but were different genetically and morphologically from the first group. Intermixtures occurred between these two groups, but the genetic influence of the second group is predominant in the majority of modern Japanese (Hondo-Japanese). Clearly, further studies are necessary which include more information, particularly on

ancient and modern DNAs of Ainu, Ryukyuan, and other populations of Japan and east Asia, to clarify the origins of the Japanese people.

ACKNOWLEDGMENTS

LITERATURE CITED

Bannai M, Tokunaga K, Imanishi T, Harihara S, Fujisawa K, Juji T, and Omoto K (1996) HLA class II alleles in Ainu living in Hidaka district, Hokkaido, northern Japan. Am. J. Phys. Anthropol. *101:*1–9.

Bellwood P (1979) Man's Conquest of the Pacific. New York: Oxford University Press.

Bellwood P (1996) Early agriculture and the dispersal of the southern Mongoloids. In T Akazawa and E Szathmary (eds.): Prehistoric Mongoloid Dispersals. New York: Oxford University Press, pp. 287–302.

Efron B (1982) The Jackknife, the Bootstrap and Other Resampling Plans. Philadelphia: Society for Industrial and Applied Mathematics.

Efron B, Halloran E, and Holmes S (1996) Bootstrap confidence levels for phylogenetic trees. Proc. Natl. Acad. Sci. U. S. A. *93:*7085–7090.

Goedde HW, Benkmann H-G, Kriese L, Bogdanski P, Du R, Chen L, Cui M, Yuan Y, Xu J, Li S, and Wang Y (1984) Population genetic studies in three Chinese minorities. Am. J. Phys. Anthropol. *64:*277–284.

Hanihara, K (1984) Origins and affinities of Japanese as viewed from cranial measurements. Acta Anthropogenet. *8:*149–158.

Hanihara, K (1987) Estimation of the number of early migrants to Japan: A simulative study. J. Anthrop. Soc. Nippon *95:*391–403.

Hanihara, K (1991) Dual structure model for the population history of the Japanese. Japan Review *2:*1–33.

Hanihara K (1992) Dual structure model for the formation of the Japanese population. In K Hanihara (ed.): Japanese as a Member of the Asian and Pacific Populations. International Symposium Vol. 4, Kyoto: Intern. Res. Cent. Japan. Stud., pp. 244–251.

Horai S, Hayasaka K, Murayama K, Wate N, Koike H, and Nakai N (1989) DNA amplification from ancient human skeletal remains and their sequence analysis. Proc. Jpn. Acad. *65(Ser. B):*229–233.

Horai S, Kondo R, Murayama K, Hayashi S, Koike H, and Nakai N (1991) Phylogenetic affiliation of ancient and contemporary humans inferred from mitochondrial DNA. Philos. Trans. R. Soc. Lond. [Biol.] *333:*409–417.

Horai S, Murayama K, Hayasaka K, Matsubayashi S, Hattori Y, Fucharoen G, Harihara S, Park K-S, Omoto K, and Pan I-H (1996) mtDNA polymorphism in east Asian populations, with special reference to the peopling of Japan. Am. J. Hum. Genet. *59:*579–590.

Howells, WW (1966) The Jomon population of Japan: A study by discriminant analysis of Japanese and Ainu

crania. Pap. Peabody Mus. Archeol. Ethnol., Harvard Univ., *57:*1–4.

Kanaseki T, Nagai M, and Sano H (1960) Craniological studies of the Yayoi-period ancients, excavated at the Doigahama site, Yamaguchi Prefecture. Jinruigaku Kenkyu, *7(Suppl.):*1–36. (in Japanese with English summary)

Kimura H (ed.) (1993) The Origin and Dispersal of Microblade Industry in Northern Eurasia. Proc. International Conference, Sapporo Univ. Archeol. Mus, Sapporo.

Matsumoto H (1984) On the origin of the Japanese race. Studies of genetic markers of the immunoglobulins. Proc. Jpn. Acad. *60:*211–216.

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

Nei M (1972) Genetic distances between populations. Am. Nat. *106:*283–292.

Nei M (1987) Molecular Evolutionary Genetics. New York: Columbia University Press.

Nei M (1995) The origins of human populations: Genetic, linguistic, and archeological data. In S Brenner and K Hanihara (eds.): The Origin and Past of Modern Humans as Viewed from DNA. Singapore: World Scientific, pp. 71–91.

Nei M, and Roychoudhury AK (1993) Evolutionary relationships of human populations on a global scale. Mol. Biol. Evol. *10:*927–943.

Nei M, and Takezaki N (1994) Estimation of genetic distances and phylogenetic trees from DNA analysis. In: Proceedings of the 5th World Congress on Genetics Applied to Livestock Production, Vol. 21. pp. 405–412.

Nei M, Tajima F, and Tateno Y (1983) Accuracy of estimated phylogenetic trees from molecular data. II. Gene frequency data. J. Mol. Evol. *19:*153–170.

Omoto, K (1972) Polymorphisms and genetic affinities of the Ainu of Hokkaido. Hum. Biol. Oceania *1:*278–288.

Omoto, K (1992) Some aspects of the genetic composition of the Japanese. In K Hanihara (ed.): Japanese as a Member of Asian and Pacific Populations. International Symposium Vol. 4, Kyoto: Intern. Res. Cent. Japan. Stud., pp. 138–145.

Omoto K (1995) Genetic diversity and the origins of the "Mongoloids." In S Brenner and K Hanihara (eds.): The Origin and Past of Modern Humans as Viewed from DNA. Singapore: World Scientific, pp. 92–109.

Omoto K, and Misawa S (1976) The genetic relations of the Ainu. In RL Kirk and AG Thorne (eds.): The Origin of the Australians. Canberra: The Australian Inst. Aboriginal Stud., pp. 365–376.

Omoto K, Aoki K, and Harada S (1975) Polymorphism of esterase D in some population groups in Japan. Hum. Hered. *25:*378–381.

Roychoudhury AK, and Nei M (1988) Human Polymorphic Genes: A World Distribution. Oxford: Oxford University Press.

Saitou N, and Nei M (1987) The neighbor-joining method: A new method for constructing phylogenetic trees. Mol. Biol. Evol. *4:*406–425.

Sitnikova TL, Rzhetsky A, and Nei M (1995) Interior-branch and the bootstrap tests of phylogenetic trees. Mol. Biol. Evol. *12:*319–333.

Sokal R, and Sneath PAP (1963) Principles of Numerical Taxonomy. San Francisco: WH Freeman.

Suzuki H (1969) Microevolutionary changes in the Japanese population from the prehistoric age to the present-day. J. Fac. Sci. Univ. Tokyo, Sec. V3, 279–308.

Suzuki H (1982) Skulls of the Minatogawa Man. In H Suzuki and K Hanihara (eds.): The Minatogawa Man: The Upper Pleistocene Man from the Island of Okinawa. Bull. Univ. Mus., Univ. Tokyo, 19, pp. 7–49.

Tanaka M, Sasaki K, and Sagawa M (1995) Japanese archaeology. In: An Introductory Bibliography for Japanese Studies, Vol. 9, Part 2: Humanities 1991–92. Tokyo: Japan Foundation, pp. 1–30.

Turner CG II (1976) Dental evidence on the origins of the Ainu and Japanese. Science *193:*911–913.

Turner CG II (1987) Late Pleistocene and Holocene population history of East Asia. Am. J. Phys. Anthropol. *73:*305–321.

Turner CG II (1992) Sundadonty and Sinodonty in Japan: The dental basis for a dual origin hypothesis for the peopling of the Japanese Islands. In K Hanihara (ed.): Japanese as a Member of the Asian and Pacific Populations. International Symposium Vol. 4. Kyoto: Intern. Res. Cent. Japan. Stud., pp. 96–112.

Turner CG II (1995) Shifting continuity: Modern human origin. In S Brenner and K Hanihara (eds.): The Origin and Past of Modern Humans as Viewed from DNA. Singapore: World Scientific, pp. 216–243.

Ueda S, Omoto K, Park KS, and Kudo T (1979) Polymorphism of red cell glutamic-pyruvic transaminase in Japanese: Gene frequencies in samples from northern Japan. Hum. Hered. *29:*208–212.

Watanabe S, Kondo S, and Matsunaga E (eds.) (1975) Anthropological and Genetic Studies on the Japanese, JIBP Synthesis 2. Tokyo: University of Tokyo Press.

Yasumoto B, and Honda M (1978) Nihongo no Tanjo [The Birth of the Japanese Languages]. Tokyo: Daishukan (in Japanese).

Yuan Y, Du R, Chen L, Xu J, Cui M, Wang Y, Li S, Goedde HW, Benkmann H-G, Kriese L, and Bogdanski P (1984) Distribution of eight blood group systems and ABH secretion in Mongolian, Korean, and Zhuang nationalities in China. Ann. Hum. Biol. *11:*377–388.

Zharkikh A, and Li W-H (1995) Estimation of confidence in phylogeny: Complete-and-partial bootstrap technique. Mol. Phyl. Evol. *4:*44–63.