

# Characterization of Biological Diversity Through Analysis of Discrete Cranial Traits

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**KEY WORDS** nonmetric cranial traits; geographical variation; interpopulation relationships; modern human origins

**ABSTRACT** In the present study, the frequency distributions of 20 discrete cranial traits in 70 major human populations from around the world were analyzed. The principal-coordinate and neighbor-joining analyses of Smith's mean measure of divergence (MMD), based on trait frequencies, indicate that 1) the clustering pattern is similar to those based on classic genetic markers, DNA polymorphisms, and craniometrics; 2) significant interregional separation and intraregional diversity are present in Subsaharan Africans; 3) clinal relationships exist among regional groups; 4) intraregional discontinuity exists in some populations inhabiting peripheral or isolated

areas. For example, the Ainu are the most distinct outliers of the East Asian populations. These patterns suggest that founder effects, genetic drift, isolation, and population structure are the primary causes of regional variation in discrete cranial traits. Our results are compatible with a single origin for modern humans as well as the multiregional model, similar to the results of Relethford and Harpending ([1994] *Am. J. Phys. Anthropol.* 95:249–270). The results presented here provide additional measures of the morphological variation and diversification of modern human populations. *Am J Phys Anthropol* 121: 241–251, 2003. © 2003 Wiley-Liss, Inc.

For many years, both the single-origin and multiregional hypotheses were used to explain modern human variation (Cann et al., 1987; Cavalli-Sforza et al., 1988; Stringer and Andrews, 1988; Howells, 1989; Wolpoff, 1989). Lahr (1996) wrote that if genetic, chronological, morphological, and archaeological evidence are taken into consideration, a single common origin for *Homo sapiens* in Africa explains regional differences in modern human populations. Others (Thorne and Wolpoff, 1981; Wolpoff, 1989, 1992; Wolpoff et al., 1984) have consistently maintained that the multiregional hypothesis explains morphological (and genetic) variation in fossil and modern humans. However, Relethford (1994, 1999) and Relethford and Harpending (1994, 1995) demonstrated that both African replacement and multiregional models explain patterns of the genetic and morphological variation if a larger long-term African population size and gene flow are allowed. More recently, Templeton (2002) demonstrated the inadequacies of both the out-of-Africa replacement model and the simple trellis model of Wolpoff (1989, 1992), based on the genetic data. Subsaharan Africans have been found to be genetically though not morphologically distant from other populations (Cann et al., 1987; Cavalli-Sforza et al., 1988; Nei and Roychoudhury, 1993). Several studies of dental and cranial morphological variation have shown that Subsaharan Africans and Australasians are distinct

(Howells, 1973a, 1989, 1995; Turner, 1992; Lahr, 1995; Relethford and Harpending, 1995; Scott and Turner, 1997; Powell and Neves, 1999). Morphological differentiation in response to environmental factors is often suggested for these differences (Beals, 1972; Guglielmino-Matessi et al., 1979; Scott and Turner, 1997). Although the relationship between craniofacial form and environmental factors was examined by Beals (1972) and Guglielmino-Matessi et al. (1979), adaptive responses to different selective forces over a period of time cannot be directly tested. How can the morphological diversity of modern humans be explained in the framework of modern hu-

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TABLE 1. Range of *N* in samples (since each of traits observed has a different *N*) and numbers of mandibles in parentheses for males and females, and brief information<sup>1</sup>

Sample name	N		Brief information and location of collections
	Males	Females	
East Asians			
1. Japanese	98–108 (94)	62–64 (59)	Tokyo and Tohoku (Northern Japan) regions (UT, TU)
2. Hokkaido Ainu	122–151 (113)	84–108 (76)	Recent Ainu people (SMU, UT)
3. Sakhalin in Ainu	62–65 (54)	28–29 (32)	Southern Sakhalin (MAE, MSU, KU, MH)
4. North Chinese	132–139 (75)	26–27 (14)	Mainly from Liaoning Prefecture (UT, KU)
Southeast Asians			
5. Myanmar	132–135 (48)	47–49 (3)	Recent Burmese (NHM, UC)
6. Mainland SE Asians	125–141 (105)	41–43 (30)	Thai, Vietnam, Laos, Cambodia, and Malay (NHM, UC, MH)
7. Javanese	94–97 (83)	32–26 (32)	Greater Sunda islands (NHM, UC, MH, AMNH)
8. Philippines	135–144 (49)	62–66 (31)	Non-Negrito Filipinos (NHM, UC, MH)
9. Borneans	78–109 (74)	37–40 (21)	Mainly land Dayaks (NHM, UC, MH)
10. Lesser Sunda	52–54 (39)	11–12 (6)	Timor, Bali, Sumbawa, Flores, and Celebes Islands (NHM, UC, MH, AMNH)
11. Andamanese/Nicobarese	65–71 (43)	40–43 (30)	Andaman Negritos and Nicobar Islands (NHM, UC, MH)
Northeast Asians			
12. Mongolians	116–121 (69)	53–59 (38)	Ulan Bator (Urga) and other regions (MH, NMNH, AMNH)
13. Buryats	76–81 (65)	64–69 (58)	From Northeast Siberia (MAE, MH, NMNH)
14. Amur Basin	85–92 (57)	67–74 (48)	Ulchs, Nanaians, Negidals, Nivkhs, and Orochs (MAE, MSU, MH)
15. Neolithic Baikilians	40–59 (45)	14–22 (19)	From around Lake Baikal (MAE, MSU, ISU)
16. Yakuts	43–45 (38)	19–20 (18)	From Northeast Siberia (MAE, MSU, MH)
Arctic			
17. Ekvens	45–55 (48)	49–56 (44)	Iron-Age people from Ekven site, Chukot Peninsula (MSU)
18. Chukchis	43–48 (17)	22–26 (10)	From Arctic region of Northeast Siberia (MAE, MSU, MH, NMNH, AMNH)
19. Aleuts	63–67 (48)	30–43 (17)	Mainly from Unalaska Island (NMNH, AMNH)
20. Asian Eskimos	66–73 (48)	53–59 (16)	From Arctic region of Northeast Siberia (MAE, MSU)
21. Greenland Eskimos	82–85 (47)	70–76 (25)	West Coast of Greenland (NHM, UC, MH, AMNH, NMNH)
New World			
22. Northwest Coast	53–59 (15)	29–35 (12)	Northwest Coast of Canada (NHM, UC)
23. Northwest America	48–61 (40)	19–24 (16)	Plateau, Great Basin, California, and Southwest Cultural areas (NHM, UC, MH)
24. Northeast America	42–50 (20)	21–29 (8)	Great Plains, Northeast, and Southeast Cultural areas (NHM, UC)
25. Central America	45–58 (21)	24–30 (12)	Mexico, Colombia, Ecuador, Carib, Venezuela, and Guyana (NHM, UC)
26. Peruvians	115–123 (60)	55–60 (33)	Cerro del Oro, Huacho, Pisagua, etc. (NHM)
27. Fuegians/Patagonians	39–44 (24)	20–23 (7)	Terra del Fuego and Patagonia region (NHM, UC, MH)
Micronesians			
28. Mariana	91–120 (82)	70–93 (75)	Guam, Saipan, and Tinian (BM, MH)
Polynesians			
29. Hawaii	82 (58)	63–64 (42)	Mainly from Oahu Island (NHM, UC)
30. Easter	63–79 (41)	59–71 (31)	Easter Islanders (NHM, UC, MH, AM, US, SAM)
31. Marquesas	55–61 (24)	39–42 (9)	Mainly from Uahuka Island (NHM, MH)
32. Maori	109–140 (58)	37–49 (23)	New Zealand (NHM, UC, AM, US, SAM)
33. Moriori	66–78 (24)	18–20 (6)	Chatham Islands (NHM, UC, AM, US)
Melanesians			
34. Papua New Guinea	54–175 (84)	51–154 (83)	Purari River delta, Fly River delta, Sepik River Delta, etc. (NHM, AM, US, SAM)
35. Torres Strait	59–65 (37)	35–38 (37)	Island of Torres Strait (NHM, UC, MH)
36. North Melanesians	64–196 (119)	41–103 (72)	New Ireland, New Britain, Solomon, and Santa Cruz (NHM, UC, AM, US, SAM)
37. South Melanesians	58–137 (67)	27–57 (33)	Loyalty, New Caledonia, Vanuatu, and Fiji (NHM, UC, AM, US, SAM)
Australians			
38. East Australians	53–88 (55)	33–46 (36)	New South Wales, Queensland, and Victoria (AM, NHM, UC, MH, AMNH)
39. South/West Australians	86–260 (159)	34–128 (77)	South Australia and Western Australia (SAM, NHM, UC, MH, AMNH)
Tibet/Nepal/Northeast India			
40. Tibetans/Nepalese	91–94 (58)	23–25 (4)	Tibetan Soldiers (19th Century), lowland of Nepal (NHM, UC)
41. Assam/Sikkim	40–41 (30)	23–24 (19)	Darjeeling, Assam, and Sikkim districts (NHM)
South Asians			
42. Northeast India	90–93 (61)	23–24 (14)	Bengal and Bihar districts (NHM)
43. South India	123–127 (65)	45–46 (30)	Madras, Tamil Nadu, Malabar Coast, and Karnataka (NHM)
44. Northwest India	125–131 (71)	32–35 (16)	Punjab and Kashmir districts (NHM)
Central Asians			
45. Tagars	62–72 (44)	60–76 (50)	Iron-Age Tagar culture (MAE, MSU)
46. Kazakhs	75–77 (75)	42–43 (42)	From Central Asia, Kazakh (MAE)

(continued)

TABLE 1. (Continued)

Sample name	N		Brief information and location of collections
	Males	Females	
Europeans			
47. Russians	72–74 (74)	45–47 (41)	Recent Russians (NHM, UC, MAE, MSU)
48. Greece	46–54 (20)	12–16 (4)	Ancient and recent Greece (NHM)
49. Eastern Europeans	80–98 (52)	18–24 (16)	Slav group: Poland, Czecho, Hergegovina, Bulgaria, and Yugoslavia (NHM)
50. Italy	131–146 (82)	42–47 (31)	Recent Italians (NHM)
51. Finland/Ural	72–75 (35)	5–6 (2)	Including a few samples of Ural-language people (NHM, MH)
52. Scandinavia	57–60 (30)	5 (3)	Norwegians and Swedish (NHM, UC)
53. Germany	58–61 (44)	9–10 (7)	Recent German (NHM, UC)
54. France	74–86 (23)	18–21 (0)	Recent French (NHM, UC, MH)
UK series			
55. Ensay	64–68 (58)	29–30 (30)	Late Medieval to post-Medieval periods, Scotland (NHM)
56. Poundbury	97–109 (106)	46–52 (47)	Late Roman period, Southwest England (NHM)
57. Spitalfields-1	122–135 (121)	104–113 (106)	Mid-Victorian, London (NHM)
58. Spitalfields-2	73–74 (75)	17–19 (35)	Pre-17th century, London (UC)
North Africans			
59. Naqada	82–87 (57)	89–93 (39)	Predynastic Egypt, ca. 5,000–4,000 BP (UC)
60. Gizeh	122–125 (91)	46–51 (32)	26th–30th Dynasty, Egypt, 664–343 BC (UC)
61. Kerma	114–132 (58)	79–92 (51)	12th–13th Dynasty of Nubia (UC)
62. Nubia	86–92 (39)	42–47 (9)	Early Christian or Christian date Nubia (UC)
Subsaharan Africans			
63. Somalia	58–64 (53)	10–12 (5)	Erigavo District, Ogaden Somali (US)
64. Nigeria-1	74–83 (72)	65–76 (53)	Ibo tribe (NHM, UC)
65. Nigeria-2	73–80 (17)	46–53 (7)	Ashanti tribe (NHM, UC)
66. Gabon	82–86 (47)	55–57 (36)	Fernand Vaz River (NHM, NMNH)
67. Tanzania	69–75 (54)	20–25 (17)	Haya tribe, Musira Island, Lake Victoria (UC, NHM)
68. Kenya	71–82 (31)	55–63 (10)	Bantu-speaking people from Kenya (UC, NHM)
69. South Africa	100–109 (53)	21–25 (8)	Zulu and once called Kaffir tribes (UC, NHM, AMNH)
70. Khoisans	43–36 (28)	17–22 (13)	Bushmans and Hottentots (NHM, UC, AMNH)

<sup>1</sup> NHM, Natural History Museum, London, UK; UC, University of Cambridge, Duckworth Laboratory, Cambridge, UK; MH, Musée de l'Homme, Paris, France; MAE, Museum of Anthropology and Ethnography, St. Petersburg, Russia; MSU, Moscow State University, Institute of Anthropology, Moscow, Russia; AM, Australian Museum, Sydney, Australia; US, University of Sydney, Sydney, Australia; SAM, South Australian Museum, Adelaide, Australia; AMNH, American Museum of Natural History, New York; NMNH, National Museum of Natural History, Smithsonian Institution, Washington, DC; BM, Bishop Museum, Honolulu; UT, University of Tokyo, University Museum, Tokyo, Japan; TU, Tohoku University, Department of Anatomy and Anthropology, Sendai, Japan; KU, Kyoto University, Kyoto, Japan; SMU, Sapporo Medical University, Sapporo, Japan.

man evolution? Several pioneering examinations of craniofacial and dental variation may provide an answer.

Howells (1989) found that modern regional craniofacial differences are small relative to the differences between modern populations and Neanderthals. Relethford (1994) and Relethford and Harpending (1994) also found that the amount of morphological variation among major geographic groups is relatively low, and is compatible with those based on the genetic data. Further, Relethford and Harpending (1994) showed that Subsaharan African populations were the most divergent once regional differences in population size were taken into account in computing biological distances between regions. Lahr (1994, 1995, 1996) and Lahr and Wright (1996) concluded that the morphological characters often cited as evidence of the multiregional model are actually due to the differential retention of traits from a single ancestor.

Scott and Turner (1997) summarized dental morphology data from thousands of individuals and hundreds of groups. The numerical scale and worldwide synthesis of global variation rival quantitatively and qualitatively the craniometric data gathered by Howells (1973a, 1989, 1995). Cladistic

analyses of dental morphological traits generally support the single-origin hypothesis for anatomically modern humans (Irish, 1997, 1998; Stringer et al., 1997; Tyrrell and Chamberlain, 1998).

Except for a few studies (Berry and Berry, 1967; Hertzog, 1968; Hauser and De Stefano, 1989; Manzi et al., 1996, 2000), large-scale analyses of discrete cranial traits to assess interpopulation relationships have not been performed. In morphological studies, we are faced with a need to explain the evolutionary processes by which the morphological variation likely developed (Relethford and Harpending, 1994; Lahr, 1995, 1996; Lahr and Wright, 1996). Our previous studies (Hanihara et al., 1998a,b; Hanihara and Ishida, 2001a–e) suggest that many discrete cranial traits show distinctive geographical variation, interregional clines, intraregional discontinuity, and changes over time. We concluded that founder effect, genetic drift, and population structure are the underlying causes for the observed regional variation. The purpose of this paper is to analyze and interpret interregional relationships of worldwide human populations, using discrete cranial traits. We address how the analysis of these traits contributes to our understanding of modern human origins.

TABLE 2. Discrete cranial traits used in this study and references

Traits	References
Supernumerary ossicles	Hanihara and Ishida (2001b)
Ossicle at lambda	Dodo (1974)
Parietal notch bone	Dodo (1974)
Asterionic bone	Ossenber (1969, 1970)
Occipitomastoid bone	Dodo (1974), Ossenber (1970)
Hypostotic traits	Hanihara and Ishida (2001c)
Tympanic dehiscence	Dodo (1974)
Ovale-spinosum confluence	Dodo (1974)
Metopism	Hauser and De Stefano (1989)
Biasterionic suture	Dodo (1974), Ossenber (1969), Hanihara and Ishida (2001a)
Transverse zygomatic suture	Dodo (1974), Hanihara et al. (1998a)
Hyperostotic traits	Hanihara and Ishida (2001d)
Medial palatine canal	Dodo (1974), Hauser and De Stefano (1989)
Hypoglossal canal bridging	Dodo (1974)
Jugular foramen bridging	Dodo (1986a,b)
Mylohyoid bridging	Dodo (1974), Jidoi et al. (2000)
Precondylar tubercle	Hanihara and Ishida (2001d)
Condylus tertius	Dodo (1974)
Auditory exostosis	Dodo (1972), Kennedy (1986), Standen et al. (1997)
Vessel/nerve-related traits	Hanihara and Ishida (2001e)
Condylar canal patent	Dodo (1974), Hauser and De Stefano (1989)
Supraorbital foramen	Dodo (1974, 1987)
Accessory infraorbital foramen	Berry and Berry (1967)
Accessory mental foramen	Murphy (1957), De Villiers (1968), Gershenson et al. (1986)

## MATERIALS AND METHODS

Seventy samples with a relatively large sample size were used in the multivariate statistical analysis. Table 1 provides the sample names, sample sizes, and brief information on each sample. All samples were made up of adult specimens without cranial deformations. The principal criteria used to determine adult status were complete fusion of the sphenoccipital synchondrosis and fully erupted third molars, if available.

Twenty discrete cranial traits (Table 2) were analyzed with respect to sex and side differences, intertrait association, and frequency distributions in a series of 70 late prehistoric, historic, and recent samples, totaling more than 8,000 individuals from around the world. The details of samples and their archaeological, geographical, and ethnological contexts are provided elsewhere (Hanihara and Ishida, 2001b–e). The scoring procedures for each trait are further described in Hanihara and Ishida (2001b–e). The scoring of graded traits (transverse zygomatic suture vestige, biasterionic suture vestige, jugular foramen bridging, and mylohyoid bridging) was converted to present or absent, following Dodo (1974). While observations were made for each side in bilateral traits, the individual count method was used; if a trait was present on either or both sides, it was scored as present (Dodo, 1974; Hauser and De Stefano, 1989; Turner et al., 1991). For all groups, Fisher's exact probability test showed that the expres-

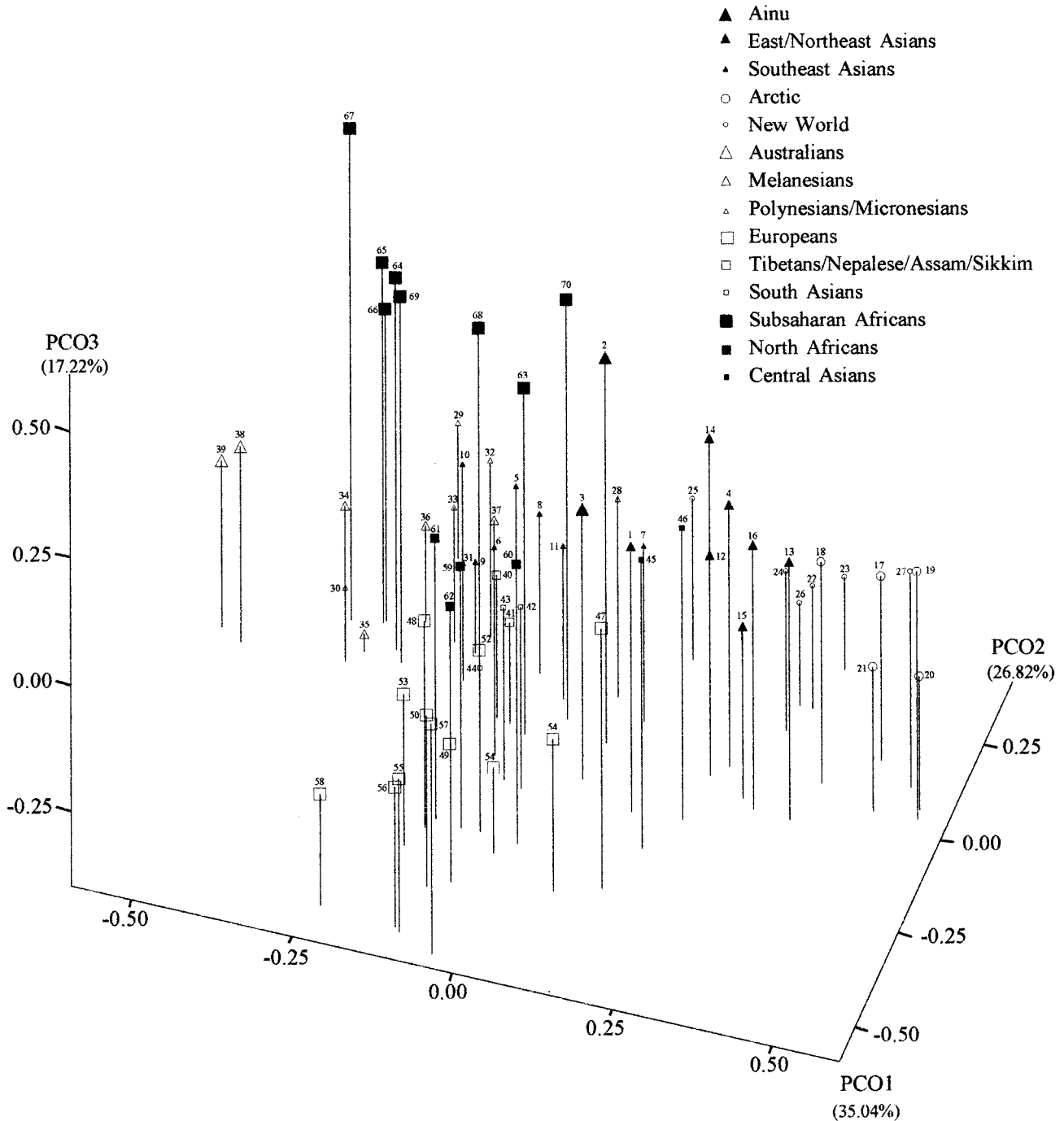
sion of most traits does not differ significantly between the right and left sides and does not show any side preference in unilateral expression (Hanihara and Ishida, 2001b–e).

Sex differences were found in a few traits, such as presence of asterionic bone, biasterionic suture vestige, and tympanic dehiscence. However, the sexes were pooled in this study because of a roughly consistent male/female ratio (2:1–3:1) in the majority of samples, except for the European samples, which are overwhelmingly male.

Although several statisticians and geneticists (e.g., Balakrishnan and Sanghvi, 1968; Edwards and Cavalli-Sforza, 1972; Konigsberg, 1990) have developed a wide array of techniques for estimating biological distance using genetic or phenotypic trait frequencies in samples, the modified Smith's mean measure of divergence (MMD) (Sjøvold, 1973) was applied for estimating biological divergence between each pair of samples in this study. Although the development and use of different distance statistics have proceeded with some controversy, and some authors have pointed out the advantages of one particular method and the weaknesses of alternative approaches, the usefulness for MMD was recently addressed (Scott and Turner, 1997; Dodo et al., 1998). Since many workers specializing in discrete cranial and dental traits often employ MMD (e.g., Berry and Berry, 1967; Turner, 1987, 1992; Ossenber, 1986; Dodo et al., 1992, 1998; Irish, 1997, 1998; Scott and Turner, 1997), the results obtained by MMD statistics in this study can be directly compared with such previous works without methodological controversy. According to Cavalli-Sforza et al. (1994), moreover, the distances calculated by different formulae are always highly correlated.

The MMD is not based on population genetic models. As such, it is a model-free, rather than model-bound measure (Howells, 1973b; Relethford and Lees, 1982). The MMD is based on an assumption of trait independence. In our previous studies, the average intertrait correlation in each sample was low, with Phi coefficients ranging from 0.00–0.28, with a mean correlation of 0.08. Higher correlations among morphogenetically similar (hyperostotic or hypostotic) traits have been found (Berry and Berry, 1967; Hertzog, 1968; Ossenber, 1969; Corruccini, 1974; Hauser and De Stefano, 1989). However, the patterns of geographical variation tend to be different from trait to trait, even in the same category, suggesting the more or less independent expression of these traits (Hanihara and Ishida, 2001b–e). Based on these results, we assume that the MMD will not be seriously biased.

Principal coordinate analysis and the neighbor-joining method (Saitou and Nei, 1987) were applied to the MMD distance matrix to visualize the intergroup relationships with a minimum loss of information present in the original distances.



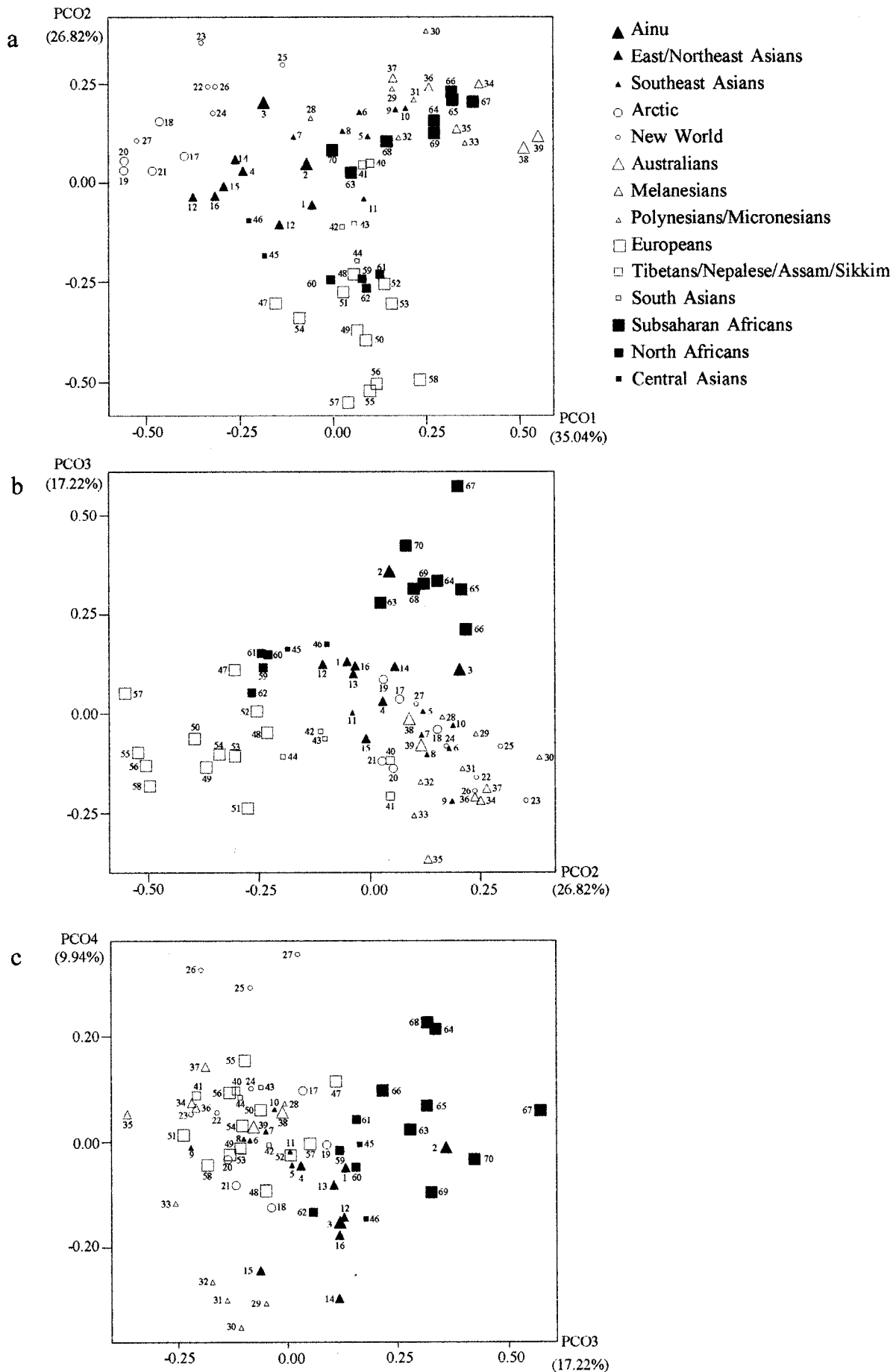
**Fig. 1.** Three-dimensional display of sample affinities by principal coordinate analysis based on MMD distance matrix. Numbers correspond to sample numbers in Table 1.

**RESULTS**

The principal coordinate analysis of the MMD matrix (not shown because of its unwieldy size) was performed first. With a few exceptions (some pairs in Southeast Asian samples), the MMD between each pair of samples was significant at the 5% level or less. A plot of the 70 samples on the first three principal coordinates is presented in Figure 1. The first three coordinates represent approximately 80%

of the information in the distance matrix. To aid in interpretation, two-dimensional scatter plots were drawn, using the first through fourth principal coordinates, all of which have eigenvalues greater than 1.0 (Fig. 2).

Roughly three major constellations are evident. The Subsaharan African, Southeast Asian, and Oceanian samples form a cluster in one quadrant of Figure 2a. However, the Subsaharan African sam-



**Fig. 2.** Two-dimensional scattergrams drawn by using first-second (a), second-third (b), and third-fourth (c) principal coordinates. Numbers correspond to sample numbers in Table 1.

ples form a distinct grouping, well removed from the Southeast Asian and Oceanian samples on the third and fourth principal coordinates. In Figures 1 and 2, the Subsaharan African samples show significant separation from other regions, as well as diversity among themselves. The East/Northeast Asian and European samples form two additional discernable clusters. The New World and Arctic samples are peripheral subgroups in the large East/Northeast Asian cluster, and the two Ainu samples are outliers to other East Asians. The Central Asian samples are located between the Eastern Asian and European clusters. In the bottom half of Figure 2a, the South Asian samples are nearest to the center of all groups, the North African samples are a bit further removed, and the European samples are more separated, having the lowest scores on principal axis 2.

Applying the neighbor-joining method to the MMD distances results in the dendrogram illustrated in Figure 3. The initial split, suggesting the greatest dissimilarity, is between Subsaharan Africans and the rest of the world. The Europeans, North Africans, and South Asians are then separated from the remaining groups. Oceania and the Southeast Asian groups form a separate branch that is separated from a large grouping of Central and East/Northeast Asian, Arctic, and New World series clusters. The Arctic cluster, which includes groups from northeasternmost Siberia, is deep in a branch containing all New World groups. The Ainu samples are more similar to mainland groups from the Amur River basin and Lake Baikal than to the Japanese.

## DISCUSSION

In the present study, we analyzed discrete cranial data from several thousand individuals and many populations from around the world. The results of our multivariate analyses provide support for the geographical distinctiveness of the populations. In fact, the patterns of divergence shown in Figures 1–3 are roughly consistent with the genetic and craniometric trees (Howells, 1989; Cavalli-Sforza et al., 1994). The clustering pattern presented here suggests, at the same time, that the variation in discrete cranial traits is, at least in part, due to intergroup genetic differences rather than mainly environmental factors. We acknowledge, however, that discrete cranial traits have an underlying threshold mode of inheritance, and thus the use of frequencies in MMD may not directly reflect underlying allele frequencies.

This study revealed the clinal nature of discrete cranial trait variation across regions and the morphological discontinuity in isolated populations such as the Ainu, Andamanese/Nicobarese, and Pacific peoples. These results suggest that limited gene flow and local adaptation allowed such peripheral groups to maintain their distinctiveness. These results are consistent with the interpretation of Lahr (1996) that the diversity of modern human cranial features may be attributed to the differential retention, spe-

cialization, loss, and intensification of certain morphological traits from ancestral patterns. If this is true, as seems likely, then we suggest that it is still too soon to accept any particular model of modern human diversity and interpopulation relationships such as those proposed by Omoto (1995), Brace et al. (2001), and others. Genetic and craniometric data provide only part of the evidence needed to answer questions of modern human origins and the evolution of modern human diversity. Additionally, data should illuminate the population histories and affinities of peripheral groups such as the Ainu.

Another notable result is the significant regional differences between Subsaharan Africans and the other regional populations in the world. According to many geneticists (e.g., Cann et al., 1987; Vigilant et al., 1991; Stoneking, 1993) and morphological anthropologists (Stringer and Andrews, 1988), the single-origin hypothesis for the emergence of anatomically modern humans entails that the greatest difference of physical characteristics will be found between Subsaharan Africans and other geographical populations. However, the present findings are also consistent with the multiregional hypothesis (Thorne and Wolpoff, 1981; Wolpoff, 1989, 1992; Wolpoff et al., 1984). Certainly, regional morphological diversity will reflect the combination of several factors, such as adaptation to different environments, different subsistence patterns, random drift, gene flow, and isolation (Howells, 1989; Turner, 1990; Relethford, 1994; Lahr, 1995).

Although the clustering pattern shown in Figure 3 is roughly compatible with those constructed by genetic data (Cavalli-Sforza et al., 1988; Nei and Roychoudhury, 1993; Ruiz-Linares et al., 1995; Omoto and Saitou, 1997) and cladistic trees using dental data (Stringer et al., 1997; Irish, 1998; Tyrrell and Chamberlain, 1998), it is also compatible with a model of regional differences in population size and rates of gene flow. As shown in Relethford and Harpending (1994, 1995), Relethford (1999), and Relethford and Jorde (1999), differences in population size and gene flow can easily mimic a recent Subsaharan African origin. A model with Subsaharan Africa having the largest long-term population size and greater gene flow out of Africa than into Africa replicates the observed patterns of higher within-region variation in Africa and greater separation of Africans from non-African populations (Relethford and Harpending, 1995; Relethford, 1999; Relethford and Jorde, 1999). Such results inform us about patterns of gene flow and population size, and do not necessarily support one model of modern human origins over another.

As described previously, the purpose of the present study was not to test the multiregional vs. single-origin hypotheses. Our main purpose was to stress that discrete cranial traits provide biological distances similar to those found in genetic and other morphological analyses. Regardless of which modern-human-origins model is correct (if either is ab-

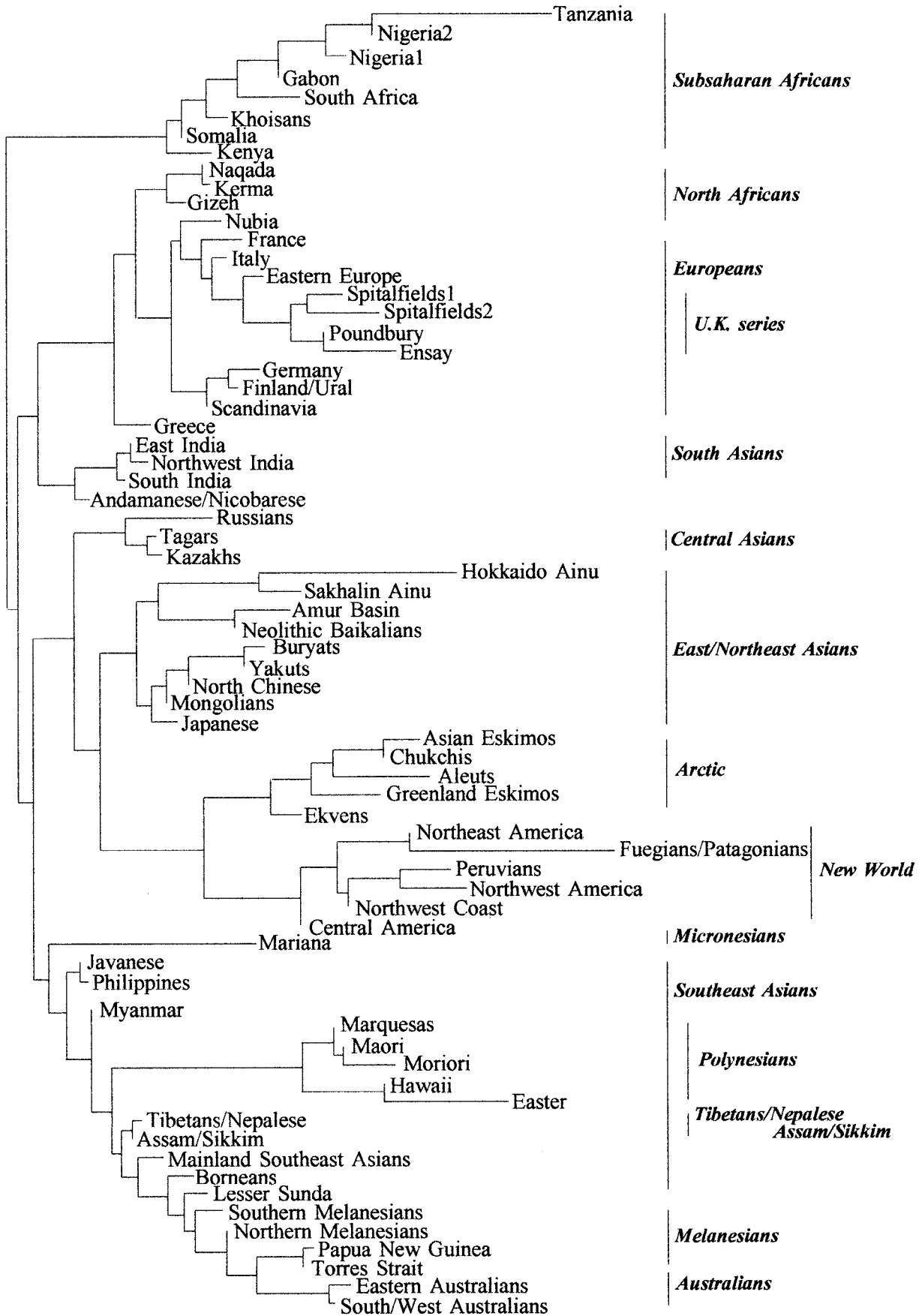


Fig. 3. Result of clustering by neighbor-joining method applied to MMD distance matrix.



solutely), or whether such analyses can decisively test the models, it is clear that different types of data reflect similar patterns, whether or not we can know for certain the causes of such patterns.

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