J.Anat. (2001) **199**, pp. 273–287, with 6 figures Printed in the United Kingdom

Frequency variations of discrete cranial traits in major human populations. IV. Vessel and nerve related variations

TSUNEHIKO HANIHARA[1] AND HAJIME ISHIDA[2]

[1] *Department of Anatomy, Saga Medical School, Saga, and* [2] *Department of Anatomy, School of Medicine, University of the Ryukyus, Okinawa, Japan*

(*Accepted 6 February 2001*)

ABSTRACT

This concludes a series of descriptive statistical reports on discrete cranial traits in 81 human populations from around the world. Four variants classified as vessel and nerve related characters were investigated: patent condylar canal; supraorbital foramen; accessory infraorbital foramen; and accessory mental foramen. A significant asymmetric occurrence without any side preference was detected for the accessory mental foramen. Significant intertrait associations were found between the accessory infraorbital and supraorbital foramina in the panPacific region and Subsaharan African samples. The intertrait associations between the accessory infraorbital foramen and some traits classified as hypostotic were found mainly in the samples from the western part of the Old World, and those as hyperostotic traits in the samples from eastern Asian and the related population samples. With a few exceptions, the occurrence of a patent condylar canal and a supraorbital foramen was predominant in females, but the accessory infraorbital and accessory mental foramina were predominant in males. The frequency distributions of the traits showed interregional clinality and intraregional discontinuity. A temporal trend was found in the Northeast Asian region in the frequencies of the accessory infraorbital and accessory mental foramina. The diversity of modern human discrete cranial traits may at least in part be attributable to differential retention or intensification from an ancestral pattern.

Key words: Osteology; geographic variation; nonmetric cranial traits.

INTRODUCTION

In our previous studies, 3 categories of discrete cranial traits, supernumerary ossicle variants, and hypostotic and hyperostotic variants were examined in terms of right and left correlations, intertrait associations, sex differences, and between group variations (Hanihara & Ishida, 2001 *a*, *b*, *c*). According to Ossenberg (1970), most discrete cranial traits can be classified either as hyperostotic or hypostotic, but emissary foramina were classified as a third category (Ossenberg, 1970). In the present study, vessel and nerve related traits including emissary foramina, patent condylar canal and supraorbital, accessory infraorbital and accessory mandibular foramina were examined.

The intensely studied variations within and between populations suggest that the occurrence of discrete cranial traits may result from a process of adaptation to various environmental and subsistence patterns as well as random drift by population size, network, isolation and edge factors, resulting in the development of regional frequency patterns (reviewed and discussed by Hanihara & Ishida, 2001 *a*, *b*, *c*). However, no matter how the phenotype is regulated, we are faced with the need to explain the development of the different regional morphologies in relation to the question of the origin and diversification of modern human populations (Lahr, 1994, 1995, 1996). The presentation of regional morphologies on a world scale in our previous studies (Hanihara & Ishida, 2001 *a*, *b*, *c*) suggests that recent populations differ not only in their morphological characterisation but also in the pattern of such characterisation and their level of distinctiveness as Lahr pointed out (1996). Lahr (1996) and Lahr & Wright (1996) emphasised that in order to investigate the evolution of modern human

Correspondence to Dr Tsunehiko Hanihara, Department of Anatomy, Saga Medical School, 5-1-1 Nabeshima, Saga 849-8501, Japan. Tel: +81-952-34-2220; fax: +81-952-34-2038; e-mail: hanihara@post.saga-med.ac.jp

diversity, attention should be focused on the pattern in the temporal and spatial distribution of morphologies, and the evolutionary process by which this pattern could have been developed.

With these considerations in mind, the purpose of the present study along with the previous ones is to elucidate modern human variations that shed light on the geographical distribution of discrete cranial traits relating to the process of modern human diversity.

MATERIALS AND METHODS

The materials used and the descriptive and analytical procedures presented in this study are the same as those given in our previous studies (Hanihara & Ishida, 2001*a*, *b*). As stated in the Introduction, the following 4 traits relating to the vessels and nerves were investigated (Fig. 1).

1. *Patent condylar canal* (CCP): condylar canal, canalis condylaris emissarium condyloideum. If the canal from behind the occipital condyle to the medial edge of the jugular foramen is present and does not end blindly (tested with a fine wire), it is scored as positive (Dodo, 1974; Hauser & De Stefano, 1989).

2. *Supraorbital foramen* (SOF): canalis supraorbitalis. Any foramen in the supraorbital margin opening into the orbital cavity is recorded as a supraorbital foramen (Dodo, 1974, 1987; Korey, 1980). The frontal and supratrochlear foramina are therefore included in this trait, which is often classified as a hyperostotic character (Ossenberg, 1970; Dodo, 1987; Manzi et al. 2000). Dodo (1987) pointed out that this trait occurs in fetuses, although less frequently than in adults. Ossenberg (1970) stated that the supraorbital foramen together with the supratrochlear foramen and frontal groove might be classed as hyperostotic, but only in a relative sense. In the present study, this trait is tentatively classified as a vessel and nerve related character.

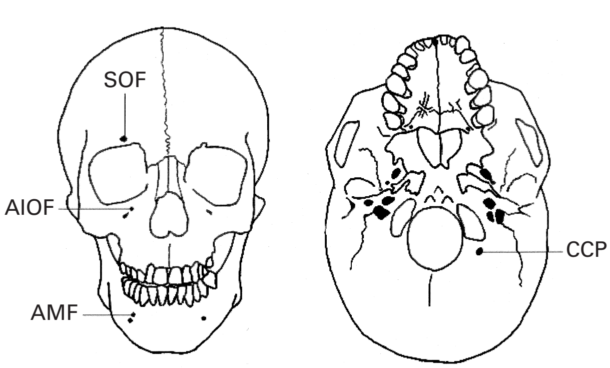

Fig. 1. Location of the 4 traits treated in this study. CCP, patent condylar canal; SOF, supraorbital foramen; AIOF, accessory infraorbital foramen; AMF, accessory mental foramen.

3. *Accessory infraorbital foramen* (AIOF): accessory infraorbital foramen patent, foramen infraorbitale accessorium. Following Berry & Berry (1967), a second foramen lying adjacent to the infraorbital foramen is recorded as positive without any detailed scoring procedure such as shape, size, or number.

4. *Accessory mental foramen* (AME): any accessory foramina well separated by a tongue of bone and situated anterosuperior, posterosuperior, posterior or inferior to the main foramen are scored as positive (Murphy, 1957; De Villiers, 1968; Gershenson et al. 1986).

RESULTS

Within population variations

As shown in Appendix 1, side differences for the expression of bilateral traits are absent except for the occurrence of the accessory mental foramen in the Arctic, New World, Australian, Central Asian and West Asian samples. Asymmetric occurrence in the West Asian samples is not reliable because of the very small sample size. No side preferences are found in the 4 population samples, although this is not shown in Appendix 1.

Appendix 2 gives the pairs of traits showing significant intertrait association ascertained by Fisher's exact probability test and the phi coefficients. The correlation levels presented by phi coefficients are, however, not high. The supraorbital and infraorbital foramina are 2 traits that show significant associations with each other in 6 out of the 20 population samples. In 2 samples, a significant intertrait association was detected between the supraorbital foramen and the accessory mental foramen. The samples with significant association between the 2 traits are all from the eastern Asian and Pacific regions except for the Subsaharan African sample. The associations between the traits presented in this study and hyper and hypostotic traits including accessory ossicles reported in our previous studies (Hanihara & Ishida, 2001*a*, *b*, *c*) are given in Appendix 3. It may be of interest that the associations between the accessory infraorbital foramen and the hypostotic traits tend to be detected in the western part of the Old World samples, and those between the former and the hyperostotic traits in the eastern Asian and the Pacific samples.

A patent condylar canal and the supraorbital foramen appear to be more frequent in females and

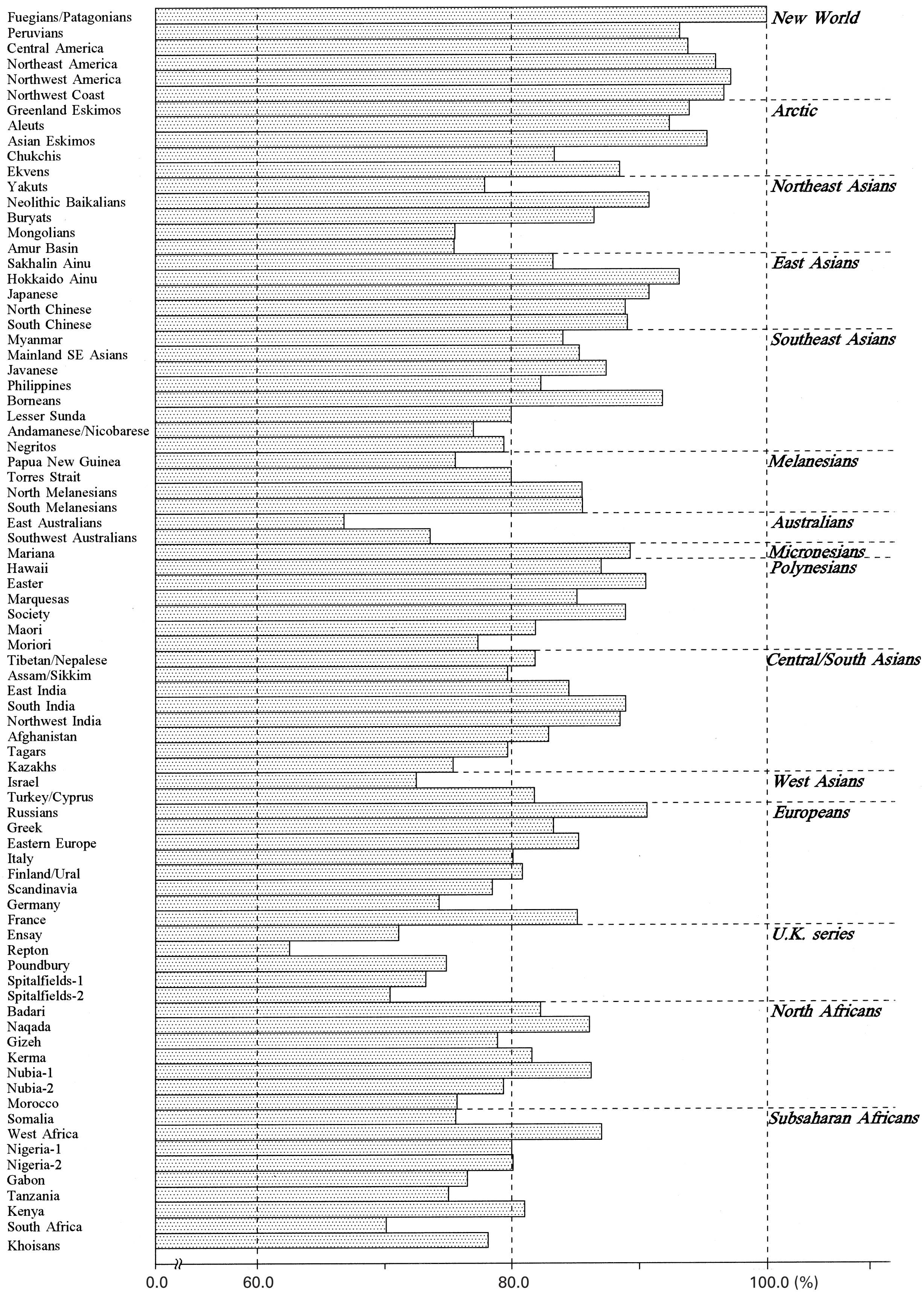

Fig. 2. Bar chart showing the frequency variation of a patent condylar canal among 81 human population groups.

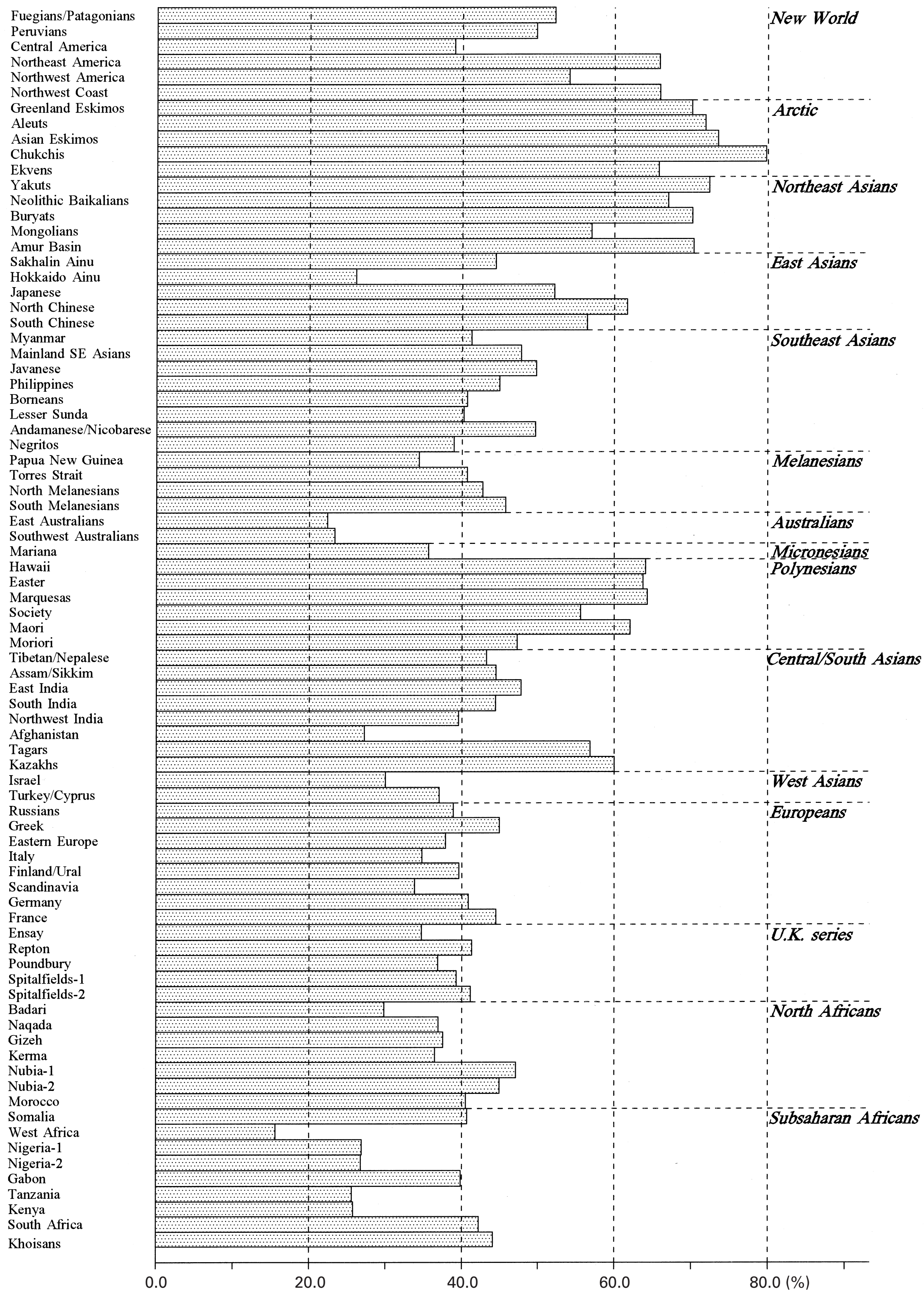

Fig. 3. Bar chart showing the frequency variation of a supraorbital foramen among 81 human population samples.

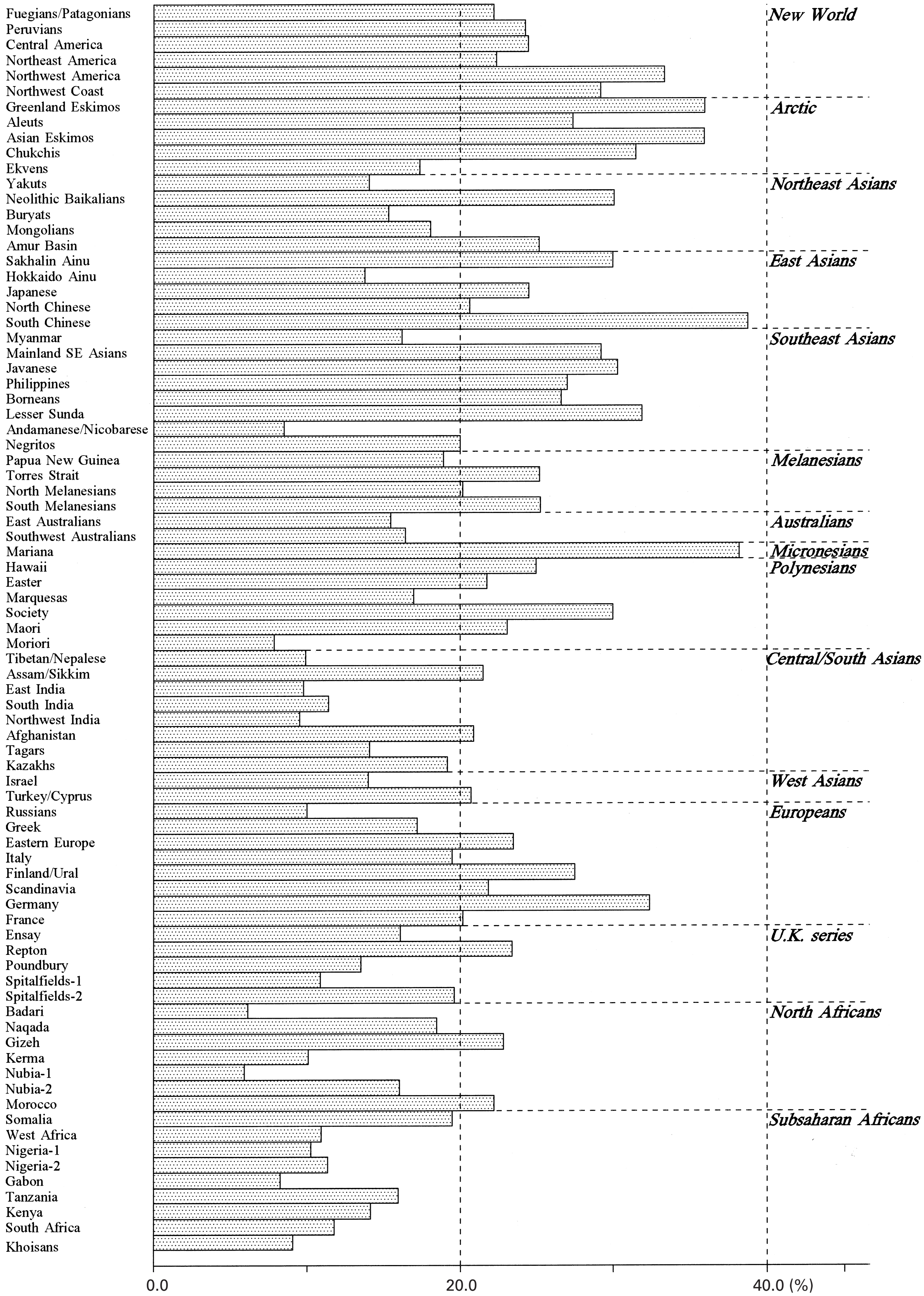

Fig. 4. Bar chart showing the frequency variation of an accessory infraorbital foramen among 81 human population samples.

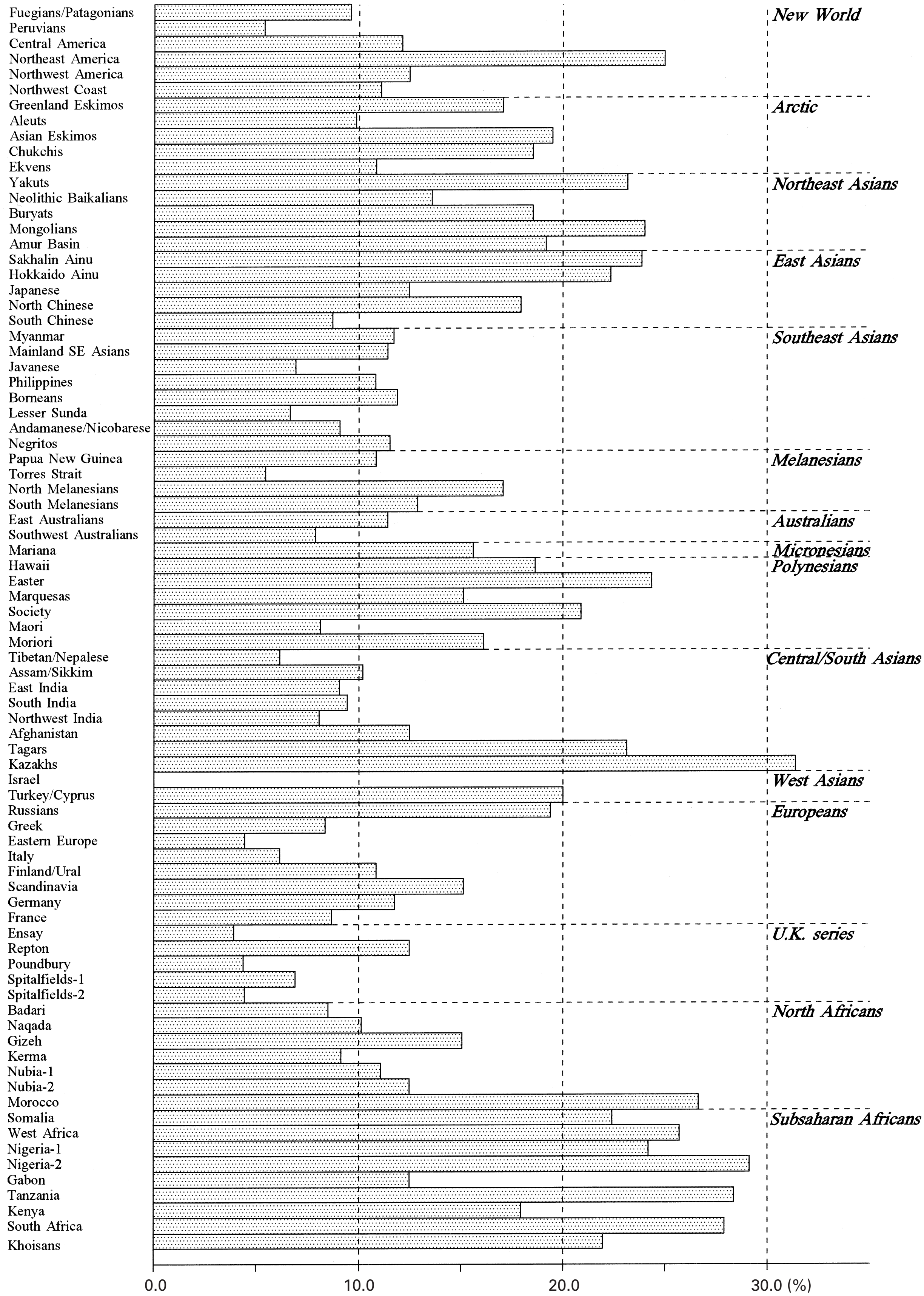

Fig. 5. Bar chart showing the frequency variation of the accessory mental foramen among 81 human population samples.

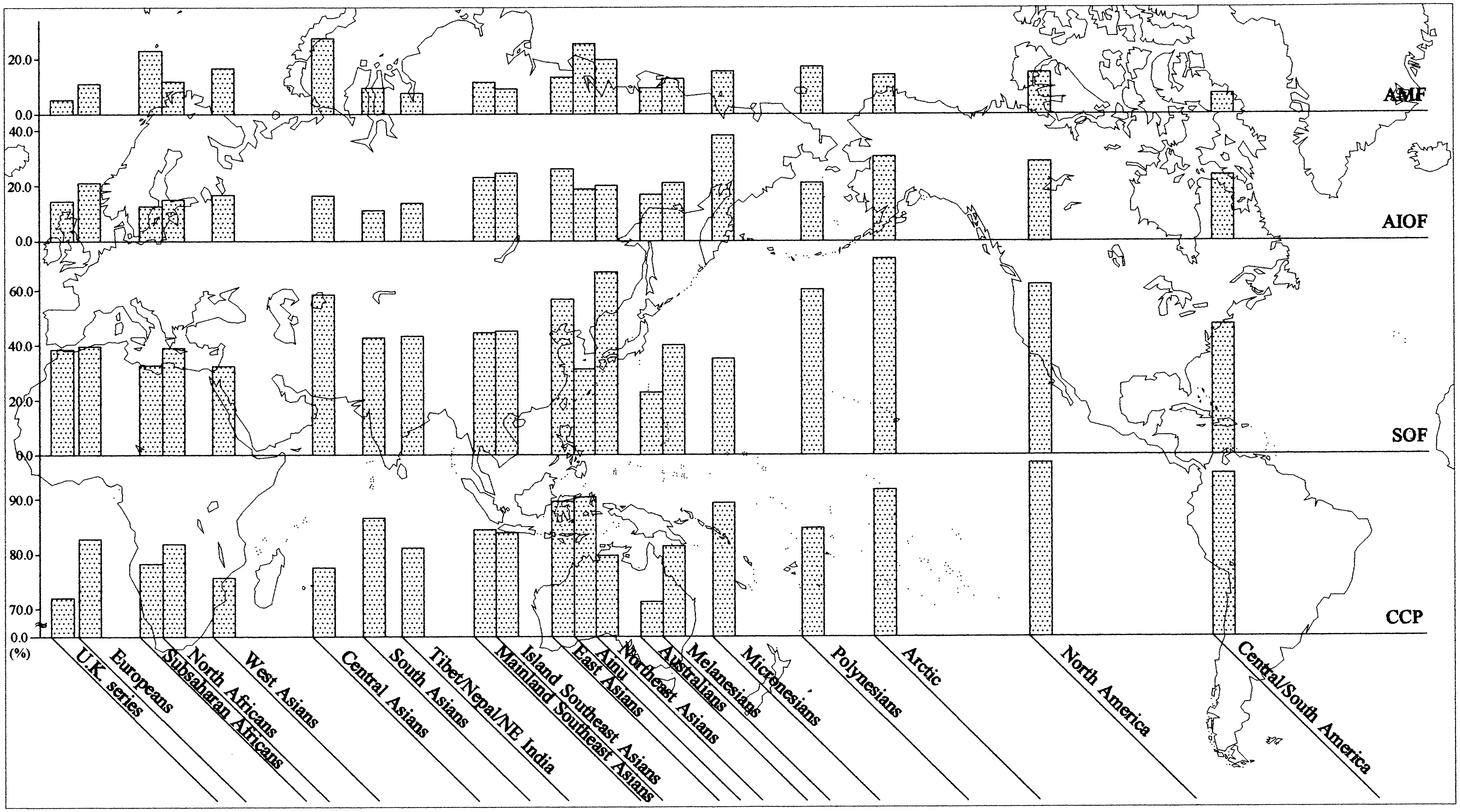

Fig. 6. Frequency variations of the patent condylar canal (CCP), supraorbital foramen (SOF), accessory infraorbital foramen (AIOF), and accessory mental foramen (AMF) among major regional pooled samples.

the accessory infraorbital foramen in males, that in some samples reaches a significant level (Appendix 4).

Between population variations

The sex combined incidences of the 4 traits for the 81 geographical samples are presented in Appendix 5, and expressed visually in Figures 2–5. Appendix 6 gives the frequencies for the pooled samples, which are superimposed on the world map in Figure 6.

As shown in Figures 2 and 6, the Australian and the UK samples show on average the lowest frequencies for a patent condylar canal, the highest frequencies being shown by the New World samples, followed closely by the Arctic, East Asian, and Ainu samples. Temporal and regional shifts in the Northeast Asian region are evident. The frequency in the Neolithic Baikalian sample is comparable to that in the New World samples. The incidence for the samples from the western part of the Old world is somewhat lower than in the eastern Asian samples, suggesting clinal variation from east to west.

With a few exceptions, the supraorbital foramen divides the world into 3 major clusters (Figs 3, 6). The samples from Northeast Asia to North America through the Arctic region together with the Polynesian samples show higher frequencies than any other population samples. The frequencies gradually decrease from north to south in eastern Asia and the Pacific basin. Except for the Central Asian samples, those from the western hemisphere of the Old World have intermediate frequencies. Several Subsaharan African samples, however, show the world's lowest frequencies, comparable to the Australian samples. The Ainu sample is the most obvious outlier in an eastern Asian context with an incidence less than 30%.

An accessory infraorbital foramen is most common in the South Chinese and the Micronesian samples, followed closely by the Arctic, the Northwest American and the Southeast Asian samples (Figs 4, 6). The frequencies for the Northeast Asian samples are slightly lower except for the Neolithic Baikalian sample showing a higher frequency comparable with the New World samples. The groups that are clear outliers in the eastern Asian and Pacific regions are the Ainu, Andamanese/Nicobarese, and Moriori samples which show this trait at frequencies of less than 15%, indicating intraregional discontinuity. In the western part of the Old World, the European samples show, on average, the highest frequencies. The frequencies gradually decrease from Europe to South Asia through West and Central Asia on the one hand, and to Subsaharan Africa through North Africa on the other, favouring west-east and north-south clinality.

The worldwide frequencies of the accessory mental foramen are illustrated in Figures 5 and 6. The Central Asian and the Subsaharan African samples show, on average, the highest frequencies for this trait. At the other extreme, the 3 samples from the UK have the frequencies of less than 5%. The Northeast Asian, Ainu, and Polynesian samples and to a lesser extent the Arctic samples show relatively high frequencies. On the other hand, this trait is less common in the European, South Asian, East and Southeast Asian (except for the Ainu), western Oceanian, and South American samples. As a whole, spatial and temporal shifts within each circumscribed geographic area are evident, suggesting intraregional discontinuity.

DISCUSSION

It has often been suspected that non-metrical traits in the same category, such as hyperostotic traits, hypostotic traits, or vessel and nerve related variants, have a potential for expressing similar side preference in the unilateral occurrence of bilateral traits, coincidental expression between the traits, and/or a tendency for predominance in sex differences (Ossenberg, 1970; Corruccini, 1974; Hauser & De Stefano, 1989). The results presented in this study along with the previous ones (Hanihara & Ishida, 2001*a*, *b*, *c*) demonstrate, however, that the patterns of side difference, intertrait associations, and sex differences are not consistent among population groups.

The precise cause for the predominant asymmetric occurrence for the accessory mental foramen is far from obvious. However, this trait may be somewhat different from other traits in terms of developmental stability (Livshits & Kobyliansky, 1991). The change in the position of the mental foramen with age, loss of teeth and alveolar bone resorption is well known (Warwick, 1950; Gershenson et al. 1986).

The intertrait association between the accessory infraorbital foramen and other traits is detected in several samples.

The pattern of sex difference is not consistent across traits. The supraorbital foramen is often regarded as a hyperostotic trait (Ossenberg, 1970; Dodo, 1987). According to Ossenberg (1970), the traits in the hyperostotic category tend to occur more frequently in males than in females. However, a good number of the population samples show a tendency for predominance in females, that in some populations reaches significance.

In the present study together with the previous ones, we have illustrated how various discrete cranial traits show patterned geographic variation between major regions. In general, morphological differentiation occurs between populations at a regional level. However, some small population groups, or possible outliers, often exist within a circumscribed region and may exhibit different forms of population structure (Scott & Turner, 1997).

The Hokkaido Ainu once again constitute the most obvious outlier in the eastern Asian region. On the other hand, Sakhalin Ainu are more northern like, suggesting an admixture from neighbouring Northeast Asians such as Nivkhs, Ulchs, Orochs, and other populations as indicated by Turner (1990) and Ishida & Kida (1991). Among the 4 traits presented here, the frequency of the supraorbital foramen for Hokkaido Ainu is comparable with that for Australians and Subsaharan Africans. Andamanese/Nicobarese, Maori, and Moriori are also possible outliers or marginal isolates in the eastern Asian and Pacific regions for the incidences of some traits. Such regional shifts without any identifiable local adaptation value are recognised to a greater or lesser extent in each region.

A temporal shift is indicated for the Neolithic Baikalians and more recent Northeast Asians in the incidence of the accessory infraorbital and accessory mental foramina. The Neolithic Baikalians break away from neighbouring Northeast Asians and align more closely with the Arctic and New World populations on the one hand and Southeast Asians on the other.

These lines of evidence indicate that modern human differentiation occurred at different rates and to different extents in different groups as described by Lahr (1995, 1996). This may allow us to hypothesise that founder effects, genetic drift and population structure are at least in part the underlying cause for interregional variations in the discrete cranial traits presented here.

Weidenreich (1936) reported that multiple mental foramina are present in all specimens of Zhoukoudian *Homo erectus* (*Sinanthropus pekinensis*). It is well known, moreover, that multiple mental foramina are one of the diagnostic morphological features in Neanderthals (Weidenreich, 1936; Akazawa et al. 1995; Tillier, 1996). On the other hand, this trait is most common in Central Asians and Subsaharan Africans among recent human populations.

The results obtained in our present and previous studies (Hanihara & Ishida, 2001 *a*, *b*, *c*) suggest that the diversity of modern human discrete cranial traits may at least in part be attributed to differential retention or intensification from an ancestral pattern caused possibly by genetic, ecological, adaptational, and demographic background.

ACKNOWLEDGEMENTS

We express our sincere gratitude to Drs T. Molleson, R. Kruszynski, L. T. Humphrey and C. Stringer, Natural History Museum (London); Drs R. Foley and M. Bellatti, Department of Biological Anthropology, University of Cambridge; Professor A. Langaney and Dr Miya Awazu Pereira da Silva, Laboratoire d'Anthropologie Biologique, Muśee de l'Homme, Paris; Drs J. Spechit, P. Gordon, L. Bonshek and N. Goodsell, Department of Anthropology, Australian Museum, Sydney; Professor J. Stone and Dr D. Donlon, Department of Anatomy and Histology, University of Sydney; Mr D. Henley, New South Wales Aboriginal Land Council, Sydney; Dr M. Chow, a dentist in Sydney; Professor M. Hanihara, School of Languages, Macquarie University, Sydney; Drs C. Pardoe and G. L. Pretty, Department of Anthropology, South Australian Museum, Adelaide; Drs I. Tattersall, K. Mowbray and G. Sawyer, Department of Anthropology, American Museum of Natural History, New York; Dr Y. H. Sinoto of the Department of Anthropology, B. P. Bishop Museum, Honolulu; Dr D. H. Ubelaker, National Museum of Natural History, Smithsonian Institution; the late Dr V. P. Alekseev, Institution of Archaeology, Moscow; Dr T. I. Alekseeva, Moscow State University; Drs I. I. Gokhman and A. G. Kozintsev, Museum of Anthropology and Ethnography, St Petersburg; Drs A. P. Derevyanko and T. A. Chikisheva, Institution of Ethnography and Archaeology, Novosibirsk; Dr G. I. Medbedev, Irkutsk State University; Emeritus Professor T. Akazawa, Department of Prehistory, University Museum, University of Tokyo; Professor Y. Dodo, Department of Anatomy, Tohoku University School of Medicine; and Professor G. Murakami of the Department of Anatomy, Sapporo Medical University, for their kind permission to study the materials under their care.

This study was supported in part by Grant-in-Aid for Scientific Research on Priority Areas 'Interdisciplinary Study on the Origins of Japanese Peoples and Cultures' headed by Professor K. Omoto of International Research Center for Japanese Studies (Nos 09208104 & 12012215), Grants-in-Aid for Scientific Research (No. 09839003) from the Ministry of Education, Science and Culture in Japan, and a Japan Fellowship for Research in the former Soviet Union (H.I.) and UK (T.H.) from the Japan Society for the Promotion of Science.

REFERENCES

AKAZAWA T, MUHESEN S, DODO Y, KONDO O, MIZOGUCHI Y, ABE Y et al. (1995) Neanderthal infant burial from the Dederiyeh cave in Syria. *Paléorientals* **21**, 77–86.

BERRY AC, BERRY RJ (1967) Epigenetic variation in the human cranium. *Journal of Anatomy* **101**, 361–379.

CORRUCCINI RS (1974) An examination of the meaning of cranial discrete traits for human skeletal biological studies. *American Journal of Physical Anthropology* **40**, 425–446.

DE VILLIERS H (1968) *The Skull of the South African Negro*. Johannesburg: Witwatersrand University Press.

DODO Y (1974) Non-metrical cranial traits in the Hokkaido Ainu and the northern Japanese of recent times. *Journal of the Anthropological Society of Nippon* **82**, 31–51.

DODO Y (1987) Supraorbital foramen and hypoglossal canal bridging: the two most suggestive nonmetric cranial traits in discriminating major racial groupings of man. *Journal of the Anthropological Society of Nippon* **95**, 19–35.

GERSHENSON A, NATHAN H, LUCHANSKY E (1986) Mental foramen and mental nerve: changes with age. *Acta Anatomica* **126**, 21–28.

HANIHARA T, ISHIDA H (2001*a*) Frequency variations of discrete cranial traits in major human populations: I. Supernumerary ossicle variations. *Journal of Anatomy* **198**, 689–706.

HANIHARA T, ISHIDA H (2001*b*) Frequency variations of discrete cranial traits in major human population: II. Hypostotic variations. *Journal of Anatomy* **198**, 707–725.

HANIHARA T, ISHIDA H (2001*c*) Frequency variations of discrete cranial traits in major human populations: III. Hyperostotic variations. *Journal of Anatomy* **199**, 251–272.

HAUSER G, DE STEFANO GF (1989) *Epigenetic Variants of the Human Skull*. Stuttgart: Schweizerbart.

ISHIDA H, KIDA M (1991) An anthropological investigation of the Sakhalin Ainu with special reference to nonmetric cranial traits. *Journal of the Anthropological Society of Nippon* **99**, 23–32.

KOREY KA (1980) The incidence of bilateral nonmetric skeletal traits: a reanalysis of sampling procedures. *American Journal of Physical Anthropology* **53**, 19–23.

LAHR MM (1994) Multiregional model of modern human origins: a reassessment of its morphological basis. *Journal of Human Evolution* **26**, 23–56.

LAHR MM (1995) Patterns of modern human diversification: implications for Amerindian origins. *Yearbook of Physical Anthropology* **38**, 163–198.

LAHR MM (1996) *The Evolution of Modern Human Diversity*. Cambridge: Cambridge University Press.

LAHR MM, WRIGHT RVS (1996) The question of robusticity and the relationship between cranial size and shape in *Homo sapiens*. *Journal of Human Evolution* **31**, 157–191.

LIVSHITS G, KOBYLIANSKY (1991) Fluctuating asymmetry as a possible measure of developmental homeostasis in humans: a review. *Human Biology* **63**, 441–466.

MANZI G, GRACIA A, ARSUAGA J-L (2000) Cranial discrete traits in the middle Pleistocene humans from Sima de los Huesos (Sierra de Atapuerca, Spain). Does hypostosis represent any increase in 'ontogenetic stress' along the Neanderthal lineage? *Journal of Human Evolution* **38**, 425–446.

MURPHY T (1957) The chin region of the Australian Aboriginal mandible. *American Journal of Physical Anthropology* **15**, 517–535.

OSSENBERG NS (1970) The influence of artificial cranial deformation on discontinuous morphological traits. *American Journal of Physical Anthropology* **33**, 375–372.

SCOTT GR, TURNER CG II (1997) *The Anthropology of Modern Human Teeth*. Cambridge: Cambridge University Press.

TILLIER AM (1996) The Pech de l'Aze and Roc de Marsal children (middle Paleolithic, France): skeletal evidence for variation in Neanderthal ontogeny. *Human Evolution* **11**, 113–119.

TURNER CG II (1990) Major features of sundadonty and sinodonty, including suggestions about East Asian microevolution, population history, and late Pleistocene relationships with Australian Aboriginals. *American Journal of Physical Anthropology* **82**, 295–317.

WARWICK R (1950) The relation of the direction of the mental foramen to the growth of the human mandible. *Journal of Anatomy* **84**, 116–120.

WEIDENREICH F (1936) *The Mandibles of Sinanthropus pekinensis: A Comparative Study*. Beijing: Palaeontologia Sinica.

Appendix 1. Phi coefficients, Yule's coefficient associations, and Fisher's exact probability tests (%) between right and left sides for the occurrence of the traits

	CCP			SOF			AIOF			AMF		
Sample name	Phi	Yule	Fisher	Phi	Yule	Fisher	Phi	Yule	Fisher	Phi	Yule	Fisher
East Asians	0.1504	0.3486	0.18	0.3962	0.6916	0.00	0.3706	0.7657	0.00	0.2600	0.7656	0.06
Ainu	0.2763	0.6252	0.00	0.4126	0.7785	0.00	0.4377	0.8536	0.00	0.1423	0.4545	2.70
Mainland Southeast Asians	0.2742	0.5512	0.00	0.4943	0.8129	0.00	0.4343	0.8377	0.00	0.2765	0.8207	0.45
Island Southeast Asians	0.3569	0.6804	0.00	0.4424	0.7637	0.00	0.4917	0.8728	0.00	0.2376	0.7950	0.02
Northeast Asians	0.3367	0.6290	0.00	0.5211	0.8211	0.00	0.4306	0.8517	0.00	0.1748	0.5584	0.08
Arctic	0.3007	0.6834	0.00	0.4288	0.7288	0.00	0.4296	0.7949	0.00	0.1043	0.4752	n.s.
North America	0.2545	0.7078	0.12	0.5499	0.8451	0.00	0.4089	0.7963	0.00	0.0303	0.1742	n.s.
Central/South America	0.2765	0.7002	0.00	0.4433	0.7588	0.00	0.3461	0.7702	0.00	0.3796	0.9205	0.24
Micronesians	0.4048	0.7835	0.00	0.3812	0.7321	0.00	0.3309	0.6577	0.00	0.2891	0.7781	0.43
Polynesians	0.2703	0.5497	0.00	0.3765	0.6667	0.00	0.3541	0.7911	0.00	0.1252	0.4888	1.98
Melanesians	0.3953	0.7154	0.00	0.4257	0.7606	0.00	0.4495	0.8554	0.00	0.2413	0.7543	0.00
Australians	0.3542	0.6429	0.00	0.2891	0.7014	0.00	0.2997	0.7552	0.00	0.0727	0.4744	n.s.
Tibetans/Nepalese/NE India	0.3615	0.6641	0.00	0.5257	0.8420	0.00	0.3685	0.8512	0.01	0.3837	0.9439	1.28
South Asians	0.2329	0.4931	0.00	0.3921	0.7168	0.00	0.3345	0.8551	0.00	0.1916	0.7399	0.93
Central Asians	0.3565	0.6499	0.00	0.4539	0.7560	0.00	0.3553	0.8485	0.00	0.0082	0.0316	n.s.
West Asians	0.5239	0.8436	0.00	0.5640	0.8927	0.00	0.1967	0.6232	4.35	0.0976	−1.0000	n.s.
Europeans	0.3141	0.6082	0.00	0.4086	0.7477	0.00	0.3474	0.7761	0.00	0.2081	0.7542	0.05
United Kingdom	0.3608	0.6429	0.00	0.4045	0.7437	0.00	0.3040	0.7916	0.00	0.2611	0.8800	0.00
North Africans	0.2710	0.5335	0.00	0.3468	0.6769	0.00	0.3820	0.8508	0.00	0.1955	0.7111	0.12
Subsaharan Africans	0.3914	0.6990	0.00	0.3848	0.7502	0.00	0.3256	0.8572	0.00	0.1306	0.4312	0.41

Appendix 2. Intertrait association based on phi coefficients and Fisher's exact probability test in the samples of 2nd classification

	SOF	AIOF		AMF	
CCP					
SOF		0.1121	4.17[1]	0.1047	3.52[4]
		0.1090	2.40[2]	0.1363	1.19[5]
		0.1284	0.08[3]		
		0.0843	0.99[4]		
		0.0844	4.46[5]		
		0.0746	1.15[6]		
AIOF					
AMF					

1, Ainu; 2, Mainland SE Asians; 3, Northeast Asians; 4, Polynesians; 5, Australians; 6, Subsaharan Africans.

Appendix 3. Phi coefficients and Fisher's exact probability test between the traits treated in this study and those of hyper and hypostotic variants in the major regional pooled samples

	CCP	SOF		AIOF		AMF	
OL		0.1079	3.49[6]			0.1686	1.58[11]
PNB				0.0727	2.49[14]		
ASB				0.1418	0.36[1]		
				0.1802	2.41[12]		
				0.0759	2.18[13]		
OMB						0.1802	2.87[7]
TD							
OSC							
MET				0.1046	0.28[9]		
TZS				0.1049	0.40[15]		
BAS		0.1055	0.31[3]	0.1194	4.00[2]		
MPC				0.1007	3.44[1]		
				0.0903	3.07[4]		
				0.1033	0.45[8]		
HGCB		0.1066	0.68[5]			0.2732	1.43[10]
PCT		0.1005	0.64[3]	0.0943	0.99[3]		
CT							
JFB				0.0863	2.77[4]	0.1305	2.72[8]
				0.1330	2.75[6]		
AEX				0.1220	2.71[6]		
MHB						0.1118	1.78[13]
						0.0905	4.74[14]

1, East Asians; 2, Ainu; 3, Island SEA; 4, NE Asians; 5, Arctic; 6, C/S America; 7, Micronesians; 8, Polynesians; 9, Melanesians; 10, Tibetan/Nelanese/NE India; 11, Central Asians; 12, West Asians; 13, Europeans; 14, North Africans; 15, Subsaharan Africans. OL, ossicle at the lambda; PNB parietal notch bone; ASB, asterionic bone; OMB, occipitomastoid bone; TD, tympanic dehiscence; OSC, ovale-spinosum confluence; MET, metopism; TZS, transverse zygomatic suture; BAS, biasterionic suture; MPC, medial palatine canal; HGCB, hypoglossal canal bridging; PCT precondylar tubercle; CT, condylus tertius; JFB, jugular foramen bridging; AEX auditory exostosis; MHB, mylohyoid bridging.

Appendix 4. Sexual difference of frequency distributions in the major regional pooled samples based on Fisher's exact probability test

	CCP	SOF	AIOF	AMF
East Asians				
M	0.8862 (325)	0.5749 (327)	0.2691 (327)	0.1571 (210)
F	0.9300 (100)	0.5400 (100)	0.2200 (100)	0.0725 (69)
Ainu				
M	0.8942 (208)	0.3175 (211)	0.1957 (184)	0.2424 (165)
F	0.9155 (142)	0.3169 (142)	0.1727 (110)	0.2056 (107)
Mainland Southeast Asians				
M	0.8577 (274)	0.4638 (276)	0.2251 (271)	0.1111 (153)
F	0.8152 (92)	0.4130 (92)	0.2360 (89)	0.1212 (33)
Island Southeast Asians				
M	0.8282 (489)	0.4440 (500)	0.2753*(494)	0.1078 (306)
F	0.8756 (193)	0.4975 (201)	0.1927 (192)	0.0661 (121)
Northeast Asians				
M	0.7668 (373)	0.6414 (396)	0.2048 (376)	0.2255 (275)
F	0.8535 (232)**	0.6926 (244)	0.1965 (229)	0.1602 (181)
Arctic				
M	0.9061 (309)	0.6890 (328)	0.3355*(313)	0.1459 (185)
F	0.9306 (245)	0.7520 (254)	0.2627 (236)	0.1284 (109)
North America				
M	0.9551 (156)	0.6059 (170)	0.3333 (159)	0.1600 (75)
F	1.0000 (69)	0.7000 (70)	0.2295 (61)	0.1200 (25)
Central/ South Americans				
M	0.9524 (210)	0.4622 (225)	0.2765*(217)	0.0762 (105)
F	0.9341 (91)	0.4946 (93)	0.1778 (90)	0.0769 (39)
Micronesians				
M	0.8454 (97)	0.3250 (120)	0.4811**(106)	0.1205 (83)
F	0.9481 (77)*	0.4022 (92)	0.2564 (78)	0.2000 (75)
Polynesians				
M	0.8344 (477)	0.5748 (508)	0.2206 (494)	0.1769 (260)
F	0.8880 (259)*	0.6741**(270)	0.2091 (263)	0.1707 (123)
Melanesians				
M	0.8315 (546)	0.4028 (566)	0.2327*(550)	0.1433 (307)
F	0.8025 (319)	0.4048 (336)	0.1777 (332)	0.1208 (207)
Australians				
M	0.7291 (299)	0.2059 (374)	0.1692 (325)	0.0948 (232)
F	0.6939 (147)	0.2746*(193)	0.1538 (156)	0.0916 (131)
Tibetans/Nepalese/Northeast India				
M	0.8106 (132)	0.4444 (135)	0.1353 (133)	0.0795 (88)
F	0.7907 (43)	0.3778 (45)	0.1333 (45)	0.0000 (20)
South Asians				
M	0.8712 (396)	0.4169 (403)	0.1134 (397)	0.0940 (234)
F	0.8595 (121)	0.4836 (122)	0.0932 (118)	0.1045 (67)
Central Asians				
M	0.7681 (138)	0.5369 (149)	0.1849 (146)	0.3140 (121)
F	0.7870 (108)	0.6387 (119)	0.1379 (116)	0.2283 (92)
Europeans				
M	0.8135 (638)	0.3735 (672)	0.2190 (653)	0.1016 (364)
F	0.8743 (175)*	0.4536* (183)	0.1761 (176)	0.1485 (101)
United Kingdom				
M	0.6825 (400)	0.3868 (424)	0.1429 (399)	0.0630 (381)
F	0.7752 (218)**	0.4115 (226)	0.1528 (216)	0.0531 (226)
North Africans				
M	0.7946 (516)	0.3775 (543)	0.1624 (511)	0.1167 (300)
F	0.8576 (323)*	0.4052 (348)	0.1337 (329)	0.1301 (146)
Subsaharan Africans				
M	0.7767 (609)	0.3286 (636)	0.1322 (605)	0.2453* (371)
F	0.7958 (284)	0.3267 (300)	0.1277 (274)	0.1690 (142)

Appendix 5. Frequency distributions of the traits in the 81 human population samples, and in the major regional pooled samples

Sample name	CCP	SOF	AIOF	AMF
East Asia				
Japanese	0.9070 (172)	0.5205 (171)	0.2456 (171)	0.1250 (144)
Hokkaido Ainu	0.9315 (248)	0.2610 (249)	0.1373 (204)	0.2234 (188)
Sakhalin Ainu	0.8333 (102)	0.4519 (104)	0.3000 (90)	0.2381 (84)
Northern Chinese	0.8896 (163)	0.6145 (166)	0.2061 (165)	0.1798 (89)
Southern Chinese	0.8913 (92)	0.5652 (92)	0.3871 (93)	0.0870 (46)
Southeast Asia				
Myanmar	0.8404 (188)	0.4127 (189)	0.1622 (185)	0.1176 (51)
Mainland SE Asians	0.8526 (190)	0.4792 (192)	0.2926 (188)	0.1143 (140)
Javanese	0.8741 (135)	0.4964 (137)	0.3030 (132)	0.0696 (115)
Philippines	0.8224 (214)	0.4495 (218)	0.2706 (218)	0.1084 (83)
Borneans	0.9178 (146)	0.4076 (157)	0.2662 (154)	0.1188 (101)
Lesser Sunda	0.8000 (65)	0.4030 (67)	0.3182 (66)	0.0667 (45)
Andamanese/Nicobarese	0.7705 (122)	0.4959 (123)	0.0847 (118)	0.0909 (77)
Negritos	0.7941 (34)	0.3889 (36)	0.2000 (35)	0.1154 (26)
Northeast Asia				
Mongolians	0.7556 (180)	0.5683 (183)	0.1808 (177)	0.2407 (108)
Buryats	0.8658 (149)	0.7020 (151)	0.1533 (150)	0.1855 (124)
Amur basin	0.7546 (163)	0.7048 (166)	0.2516 (155)	0.1923 (104)
Neolithic Baikalians	0.9074 (54)	0.6709 (79)	0.3016 (63)	0.1364 (66)
Yakuts	0.7778 (63)	0.7231 (65)	0.1406 (64)	0.2321 (56)
Arctic				
Ekvens	0.8854 (96)	0.6577 (111)	0.1735 (98)	0.1087 (92)
Chukchis	0.8333 (72)	0.7973 (74)	0.3143 (70)	0.1852 (27)
Aleuts	0.9238 (105)	0.7179 (117)	0.2736 (106)	0.0986 (71)
Asian Eskimos	0.9531 (128)	0.7348 (132)	0.3594 (128)	0.1951 (41)
Greenland Eskimos	0.9398 (166)	0.7006 (167)	0.3598 (164)	0.1711 (76)
New World				
Northwest Coast	0.9670 (91)	0.6596 (94)	0.2921 (89)	0.1111 (27)
Northwest America	0.9733 (75)	0.5412 (85)	0.3333 (81)	0.1250 (56)
Northeast America	0.9600 (75)	0.6582 (79)	0.2239 (67)	0.2500 (28)
Central America	0.9375 (80)	0.3908 (87)	0.2439 (82)	0.1212 (33)
Peruvians	0.9318 (176)	0.4973 (183)	0.2431 (181)	0.0538 (93)
Fuegians/Patagonians	1.0000 (63)	0.5224 (67)	0.2222 (63)	0.0968 (31)
Micronesia				
Micronesians	0.8920 (176)	0.3651 (214)	0.3817 (186)	0.1563 (160)
Polynesia				
Hawaii	0.8701 (154)	0.6410 (158)	0.2500 (156)	0.1869 (107)
Easter	0.9060 (149)	0.6375 (160)	0.2171 (152)	0.2436 (78)
Marquesas	0.8515 (101)	0.6415 (106)	0.1698 (106)	0.1515 (33)
Society	0.8971 (68)	0.5541 (74)	0.3000 (70)	0.2083 (48)
Maori	0.8192 (177)	0.6212 (198)	0.2308 (195)	0.0814 (86)
Moriori	0.7714 (105)	0.4722 (108)	0.0777 (103)	0.1613 (31)
Melanesia				
Papua New Guinea	0.7556 (315)	0.3453 (333)	0.1890 (328)	0.1086 (175)
Torres Strait	0.8000 (95)	0.4078 (103)	0.2525 (99)	0.0548 (73)
North Melanesia	0.8552 (297)	0.4207 (309)	0.2020 (307)	0.1709 (199)
South Melanesia	0.8586 (191)	0.4564 (195)	0.2527 (186)	0.1287 (101)
Australian				
East Australians	0.6667 (135)	0.2254 (142)	0.1544 (136)	0.1146 (96)
Southwest Australians	0.7357 (280)	0.2333 (390)	0.1635 (312)	0.0785 (242)
Central/South Asia				
Tibetans/Nepalese	0.8182 (121)	0.4320 (125)	0.0984 (122)	0.0615 (65)
Assam/ Sikkim	0.7969 (64)	0.4462 (65)	0.2154 (65)	0.1020 (49)
East India	0.8455 (123)	0.4677 (124)	0.0976 (123)	0.0909 (77)
South India	0.8895 (181)	0.4457 (184)	0.1141 (184)	0.0947 (95)
Northwest India	0.8851 (174)	0.3943 (175)	0.0958 (167)	0.0805 (87)
Afghanistans	0.8293 (41)	0.2727 (44)	0.2093 (43)	0.1250 (32)
Tagars	0.7969 (128)	0.5676 (148)	0.1408 (142)	0.2316 (95)
Kazakhs	0.7542 (118)	0.6000 (120)	0.1917 (120)	0.3136 (118)

Appendix 5 (*cont.*)

Sample name	CCP	SOF	AIOF	AMF
West Asia				
Israel	0.7245 (98)	0.3000 (110)	0.1400 (100)	0.0000 (15)
Turkey/Cyprus	0.8182 (55)	0.3710 (62)	0.2069 (58)	0.2000 (15)
Europe				
Russians	0.9068 (118)	0.3884 (121)	0.1000 (120)	0.1942 (103)
Greece	0.8333 (60)	0.4493 (69)	0.1719 (64)	0.0833 (24)
East Europe	0.8525 (122)	0.3790 (124)	0.2353 (119)	0.0441 (68)
Italy	0.8010 (191)	0.3480 (204)	0.1949 (195)	0.0614 (114)
Finland/Ural	0.8077 (78)	0.3951 (81)	0.2750 (80)	0.1081 (37)
Scandinavia	0.7846 (65)	0.3385 (65)	0.2188 (64)	0.1515 (33)
German	0.7429 (70)	0.4085 (71)	0.3239 (71)	0.1176 (51)
France	0.8526 (95)	0.4444 (108)	0.2019 (104)	0.0870 (23)
UK series				
Ensay	0.7117 (111)	0.3478 (115)	0.1636 (110)	0.0385 (104)
Repton	0.6250 (48)	0.4138 (58)	0.2340 (47)	0.1250 (24)
Poundbury	0.7483 (151)	0.3690 (168)	0.1358 (162)	0.0438 (160)
Spitalfields-1	0.7323 (254)	0.3930 (257)	0.1083 (240)	0.0688 (247)
Spitalfields-2	0.7030 (101)	0.4118 (102)	0.1961 (102)	0.0446 (112)
North Africa				
Badari	0.8235 (51)	0.2982 (57)	0.0612 (49)	0.0851 (47)
Naqada	0.8611 (180)	0.3690 (187)	0.1848 (184)	0.1010 (99)
Gizeh	0.7880 (184)	0.3750 (184)	0.2278 (180)	0.1508 (126)
Kerma	0.8159 (201)	0.3656 (227)	0.1010 (208)	0.0917 (109)
Nubia-1	0.8625 (80)	0.4719 (89)	0.0588 (85)	0.1111 (9)
Nubia-2	0.7941 (136)	0.4500 (140)	0.1603 (131)	0.1250 (48)
Morocco	0.7586 (29)	0.4063 (32)	0.2222 (27)	0.2667 (15)
Subsaharan Africa				
Somalia	0.7571 (70)	0.4079 (76)	0.1944 (72)	0.2241 (58)
West Africa	0.8704 (54)	0.1455 (55)	0.1091 (55)	0.2571 (35)
Nigeria-1	0.8000 (155)	0.2683 (164)	0.1020 (147)	0.2422 (128)
Niberia-2	0.8016 (126)	0.2672 (131)	0.1138 (123)	0.2917 (24)
Gabon	0.7692 (143)	0.3986 (148)	0.0828 (145)	0.1250 (88)
Tanzania	0.7500 (92)	0.2551 (98)	0.1596 (94)	0.2838 (74)
Kenya	0.8102 (137)	0.2568 (148)	0.1418 (134)	0.1795 (39)
South Africa	0.7023 (131)	0.4222 (135)	0.1172 (128)	0.2787 (61)
Khoisans	0.7813 (64)	0.4412 (68)	0.0909 (66)	0.2195 (41)

Appendix 6. Frequency distributions of the 4 traits based on the regional pooled of the samples shown in Appendix 1

Sample name	CCP	SOF	AIOF	AMF
Eastern Asia				
East Asians	0.8970 (427)	0.5664 (429)	0.2611 (429)	0.1362 (279)
Ainu	0.9029 (350)	0.3173 (353)	0.1871 (294)	0.2279 (272)
Mainland Southeast Asians	0.8466 (378)	0.4462 (381)	0.2279 (373)	0.1152 (191)
Island Southeast Asians	0.8394 (716)	0.4499 (738)	0.2462 (723)	0.0940 (447)
Northeast Asians	0.7980 (609)	0.6630 (644)	0.2003 (609)	0.1987 (458)
Arctic/New World				
Arctic	0.9191 (556)	0.7136 (590)	0.3045 (555)	0.1424 (302)
North America	0.9668 (241)	0.6202 (258)	0.2869 (237)	0.1532 (111)
Central/South America	0.9467 (319)	0.4748 (337)	0.2393 (326)	0.0764 (157)
Pacific/Oceania				
Micronesians	0.8920 (176)	0.3551 (214)	0.3817 (186)	0.1563 (160)
Polynesians	0.8493 (783)	0.6014 (833)	0.2123 (810)	0.1737 (403)
Melanesians	0.8151 (898)	0.4000 (940)	0.2130 (920)	0.1277 (548)
Australians	0.7143 (462)	0.2277 (584)	0.1670 (497)	0.0960 (375)
Central/South/West Asia				
Tibetans/Nepalese/NE India	0.8108 (185)	0.4368 (190)	0.1390 (187)	0.0789 (114)
South Asians	0.8674 (543)	0.4268 (553)	0.1105 (543)	0.0962 (312)
Central Asians	0.7764 (246)	0.5821 (268)	0.1641 (262)	0.2770 (213)
West Asians	0.7582 (153)	0.3256 (172)	0.1646 (158)	0.1667 (28)
Europe				
Europeans	0.8293 (826)	0.3874 (870)	0.2088 (843)	0.1099 (473)
United Kingdom	0.7203 (665)	0.3843 (700)	0.1467 (661)	0.0556 (647)
Africa				
North Africans	0.8188 (861)	0.3886 (916)	0.1516 (864)	0.1192 (453)
Subsaharan Africans	0.7832 (955)	0.3180 (1003)	0.1239 (944)	0.2271 (546)