J.Anat. (2001) **199**, pp. 251–272, with 10 figures Printed in the United Kingdom

Frequency variations of discrete cranial traits in major human populations. III. Hyperostotic 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 2 February 2001*)

ABSTRACT

Seven discrete cranial traits usually categorised as hyperostotic characters, the medial palatine canal, hypoglossal canal bridging, precondylar tubercle, condylus tertius, jugular foramen bridging, auditory exostosis, and mylohyoid bridging were investigated in 81 major human population samples from around the world. Significant asymmetric occurrences of the bilateral traits were detected in the medial palatine canal and jugular foramen bridging in several samples. Significant intertrait associations were found between some pairs of the traits, but not consistently across the large geographical samples. The auditory exostosis showed a predominant occurrence in males. With the exception of the auditory exostosis and mylohyoid bridging in a few samples, significant sex differences were slight. The frequency distributions of the traits (except for the auditory exostosis) showed some interregional clinality and intraregional discontinuity, suggesting that genetic drift could have contributed to the observed pattern of variation.

Key words: Osteology; excessive ossification; nonmetric cranial traits; clinal variation; geographical variation.

INTRODUCTION

Our understanding of the significance of discrete cranial traits represent the cumulative efforts of many investigators: Le Double (1903, 1906), Sullivan (1922), Oetteking (1930), Wood-Jones (1931), Laughlin & Jörgensen (1956), Grünberg (1963), and Berry & Berry (1967). The early studies were mainly descriptive. After Torgersen's (1951) and Grünberg's (1963) genetic studies, discontinuous variants have been used for the investigation of population history (Berry & Berry, 1967; De Villiers, 1968; Hertzog, 1968; Ossenberg, 1969; Pietrusewsky, 1971, 1984; Dodo, 1974; Dodo & Ishida, 1990; Pardoe, 1991; and others). During the past few decades, biological consideration of discrete cranial traits such as their ontogeny, asymmetry, sex differences and intertrait association have been addressed to assess a possible genetic background (Ossenberg, 1970; Corruccini, 1974; Pucciarelli, 1974; Berry, 1975; Gottlieb, 1978; Cosseddu et al. 1979; Perizonius, 1979; Česnys, 1982; Bergman & Hauser, 1985; Dodo, 1980, 1986*a*), but adaptation to environment including postnatal stress factors as suggested by several investigators (Bennett, 1965; Mayhall et al. 1970; Ossenberg, 1970; Mayhall & Mayhall, 1971; Pucciarelli, 1974; Gottlieb, 1978; Trinkaus, 1978; Konigsberg et al. 1993) is hard to test precisely. Concerning the definition of 'epigenetic' variation (Berry & Searle, 1963) or 'quasi-continuous' variation (Grünberg, 1963), while evidence exists of environmental determination of several variants, other factors point to genetic influences.

In our previous studies concerning supernumerary ossicle and hypostotic variations, it was pointed out that the diversity of the frequencies of the variants on a world scale may not be fully explained within a functional, and biomechanical framework (Hanihara & Ishida, 2001*a*, *b*). In the present study, 7 hyperostotic cranial traits, the precondylar tubercle, condylus tertius, auditory exostosis, medial palatine canal, hypoglossal canal bridging, jugular foramen bridging, and mylohyoid bridging are examined in terms of side differences in bilateral traits, intertrait correlations,

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

sex differences, and the frequency variation of the 81 samples of modern human crania from around the world. Although environmental factors including nutritional and climatic influences, metabolic disorders and biomechanical stress are claimed to be loosely related to the expression of hyperostotic cranial traits in both fossil hominid and recent human populations (Smith, 1978; Trinkaus, 1978; Frayer, 1992; Manzi et al. 1996, 2000; Antón, 1997), it may be difficult to differentiate between idiosyncratic and taxonomically salient variation.

Interpretation of the morphological variation of modern human cranial features including discrete cranial traits and relationships between modern human groups depends on whether a long-standing local adaptation or genetic drift is assumed (Hanihara & Ishida, 2001*b*). If morphological differentiation is hypothesised to have occurred as a result of local adaptation across diverse populations, departures from the predominant frequency patterns such as represented by those of the Ainu, Negritos, Aleutian Islanders, some Polynesians and other marginal isolates remain unexplained or are not regarded as significant. If interpopulation variability is considered in the microevolutionary framework, on the other hand, the distinctiveness of such possible outliers may indicate the different genetic background and therefore give rise to variation in evolutionary histories (Hanihara & Ishida, 2001*a*, *b*).

With these in mind, the present study attempts a basic and controlled investigation of the 7 hyperostotic variations on a world scale.

MATERIALS AND METHODS

Morphological observations were made on discrete variables in 81 local and aggregated cranial series, involving more than 10000 individuals. Information on the samples used and the examined material were described in our previous study (Hanihara & Ishida, 2001*b*). In the present study, the following 7 hyperostotic traits were examined (Fig. 1).

1. *Medial palatine canal* (MPC): palatine bridging, canales palatini. An osseous connection or bridging covering the medial palatine groove near the intersection of the groove and the transverse palatine suture is recorded as positive (Dodo, 1974; Hauser & De Stefano, 1989).

2. *Hypoglossal canal bridging* (HGCB): hypoglossal canal, canalis hypoglossalis. Total division of the hypoglossal canal is recorded as positive (Dodo, 1974).

3. *Precondylar tubercle* (PCT): tuberculum precondylare. The inferior surface of the basioccipital bears bilaterally a small depression immediately anterior to the occipital condyle for attachment of the anterior rectus capitis muscle. On occasion, this is replaced by a small bony process (Soames, 1995). If such accessory tubercles are observed, it is recorded as positive.

4. *Condylus tertius* (CT): odonto-occipital articulation, third occipital condyle. The apical ligament is attached to the midline of the anterior margin of the foramen magnum. A facet type bony projection at this site is scored as positive (Dodo, 1974). Hauser & De Stefano (1989) regarded the precondylar tubercle and the condylus tertius as the same tubercle, but the explanation for the formation of these 2 tubercles differs. In the present study, therefore, the 2 traits are considered as separate characters.

5. *Jugular foramen bridging* (JFB): ponticuli foraminis jugularis. According to Dodo (1986*a*, *b*), bony bridging of the jugular foramen is established by contact of the intrajugular process of the temporal bone situated posterior to the triangular depression with the bony process of the occipital bone projecting either from just above the hypoglossal canal (type I, anterior type) or from a site posterior to the hypoglossal canal (type II, posterior type). Dodo (1986*b*) treated bridging of both types as a single trait because as the latter type is extremely rare. The 2 types are recorded separately for the samples examined here by T. H. In the present study, therefore, the frequencies of the 2 types are presented separately in the available samples.

6. *Auditory exostosis* (AEX): auditory torus, aural exostosis, torus auditivus, torus acusticus. Although several types of auditory exostosis such as superficial and deep meatal types have been reported (summarised by Hauser & De Stefano, 1989), it seems difficult to distinguish between them. In this study, we follow Dodo (1972).

7. *Mylohyoid bridging* (MHB): mylohyoid bridge, arcus mylohyoideus, ponticulus mylohyoideus, canalis mylohyoideus. This trait includes at least 2 types of bony bridging of the mylohyoid groove (Yamano & Yamaguchi, 1976). The distal type (type I) is defined as bridging formed by partial ossification of the periosteum overlying the centre of the mylohyoid groove, where the medial pterygoid muscle is attached. The proximal type (type II) is a bridging by posterior extension of the lingula resulting from ossification of the sphenomandibular ligament. In this study, types I and II are recorded separately where possible.

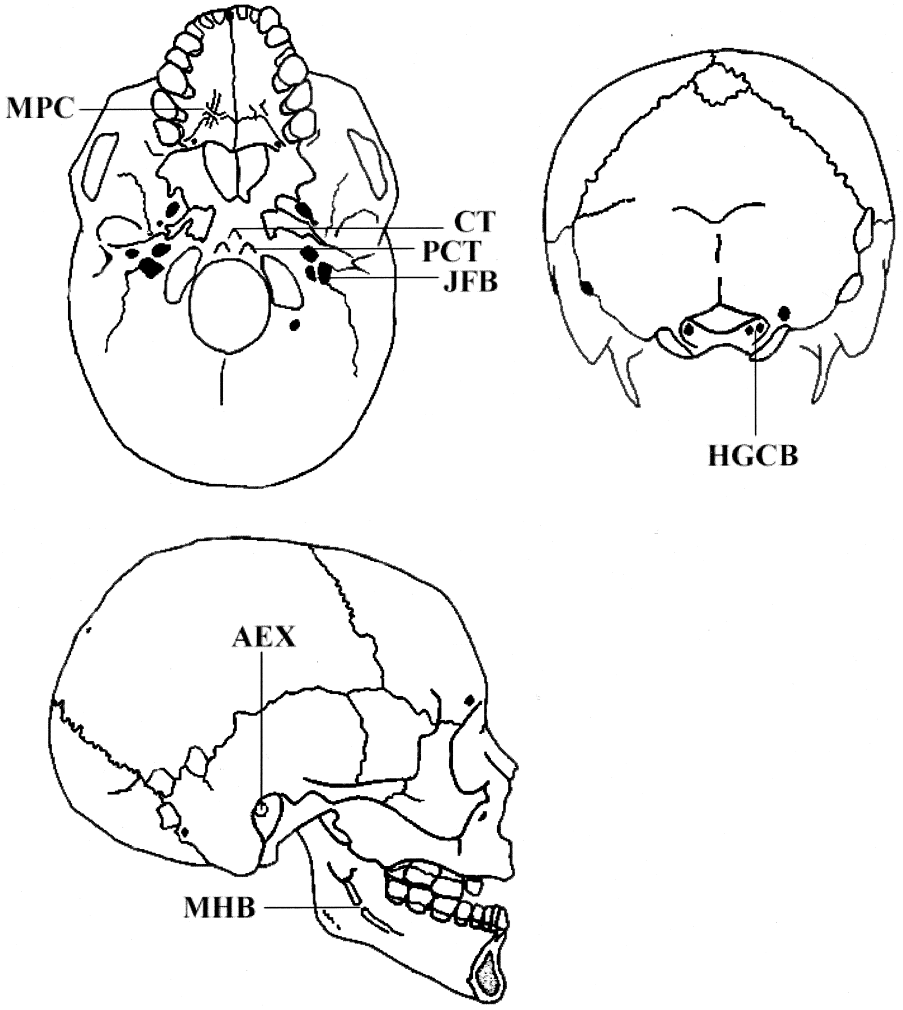

Fig. 1. Diagram of the skull with the 7 hyperostotic variations. MCP, medial palatine canal; PCT, precondylar tubercle; CT, condylus tertius; JFB, jugular foramen bridging; AEX, auditory exostosis; MHB, mylohyoid bridging; HGCP, hypoglossal canal bridging.

RESULTS

Within population variations

The results of phi coefficients, Yule's coefficients of association, and Fisher's exact probability test for side difference applied to the samples of large geographical groups are given in Appendix 1. Medial palatine canal and jugular foramen bridging occur asymmetrically in several samples, but no side preferences are detectable.

The pairs of traits showing significant intertrait association ascertained by Fisher's exact probability test and the phi coefficients based on the individual incidence are given in Appendix 2. Correlations between traits are also presented in Appendix 2. The occurrence of hypoglossal canal bridging is related to the precondylar tubercle, the condylus tertius, and to a lesser extent, the jugular foramen bridging and auditory exostosis. An association between precondylar tubercle and the jugular foramen bridging is found in 3 out of 20 samples. The associations between the hyperostotic traits presented in this study and the hypostotic traits including accessory ossicles reported in the previous study (Hanihara & Ishida, 2001*b*) are shown in Appendix 3. Significant associations occur in some pairs of the traits, but are not consistent across the samples.

As a whole, sex differences (Appendix 4) are rare, except for a higher frequency of auditory exostosis in males. The New World and the Polynesian samples with a significant sex difference show much higher frequencies of this trait than any other population samples. Mylohyoid bridging occurs predominantly in males in the Arctic, Melanesian, and Ainu samples, but in females in the Central Asian and UK samples.

Between population variations

Appendix 5 shows the combined sex incidences of the traits for the 81 samples, which are illustrated visually in Figures 2–8. The frequencies for the macrogeographical samples are given in Appendix 6, and

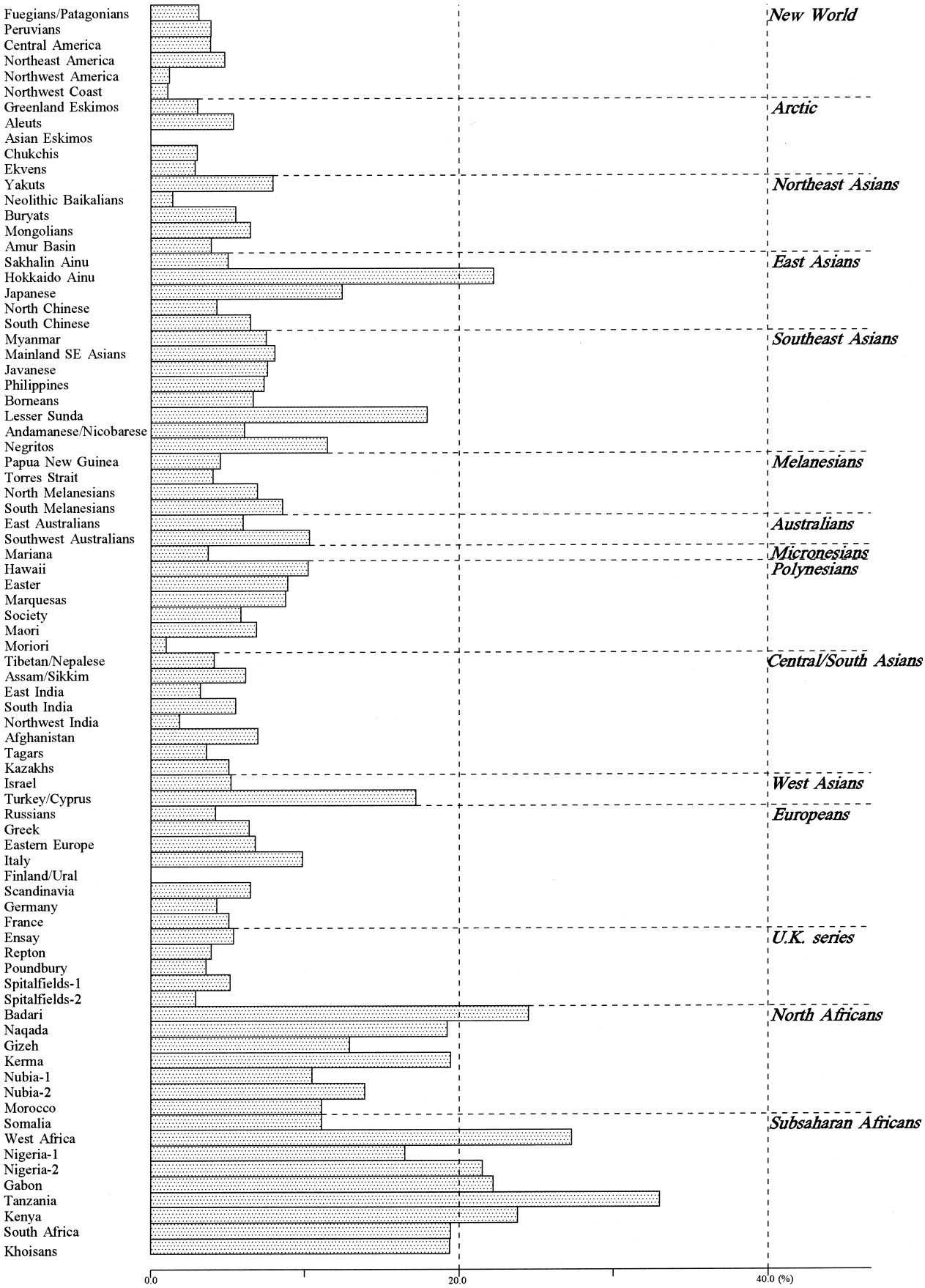

Fig. 2. Bar chart showing the frequency of a medial palatine canal among 81 human population samples.

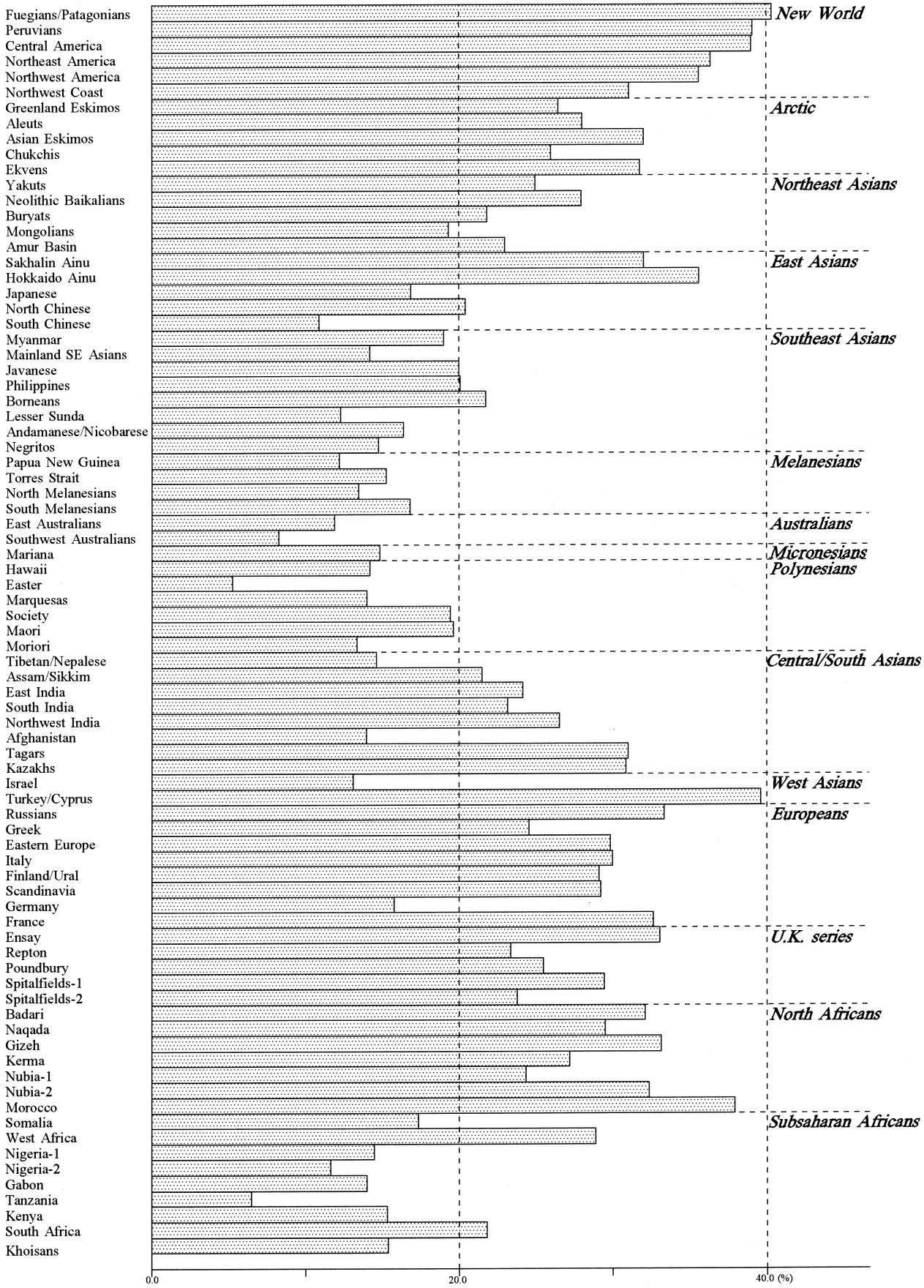

Fig. 3. Bar chart showing the frequency of hypoglossal canal bridging among 81 human population samples.

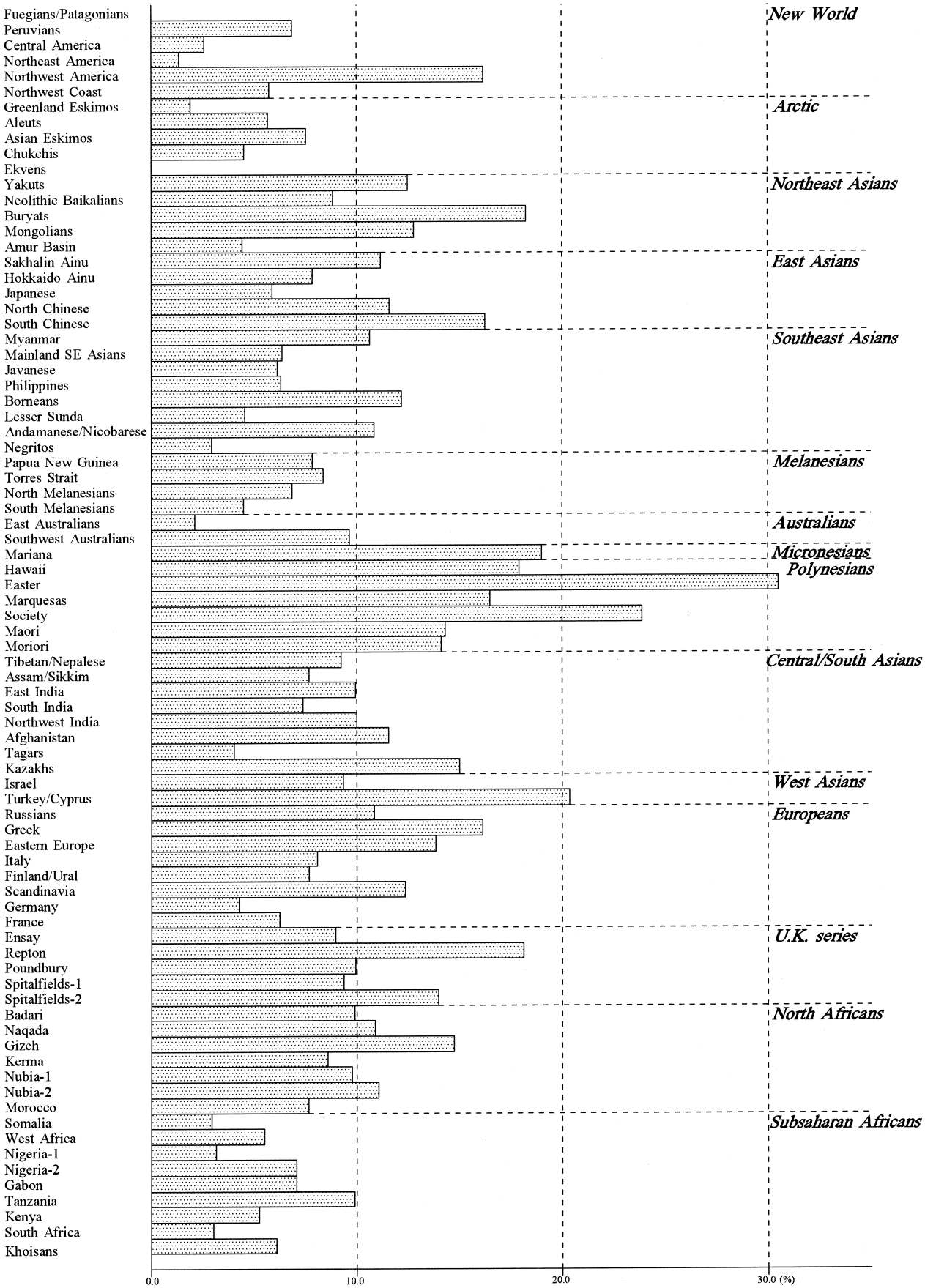

Fig. 4. Bar chart showing the frequency of a precondylar tubercle amomg 81 human population samples.

Fig. 5. Bar chart showing the frequency of condylus tertius among 81 human population samples.

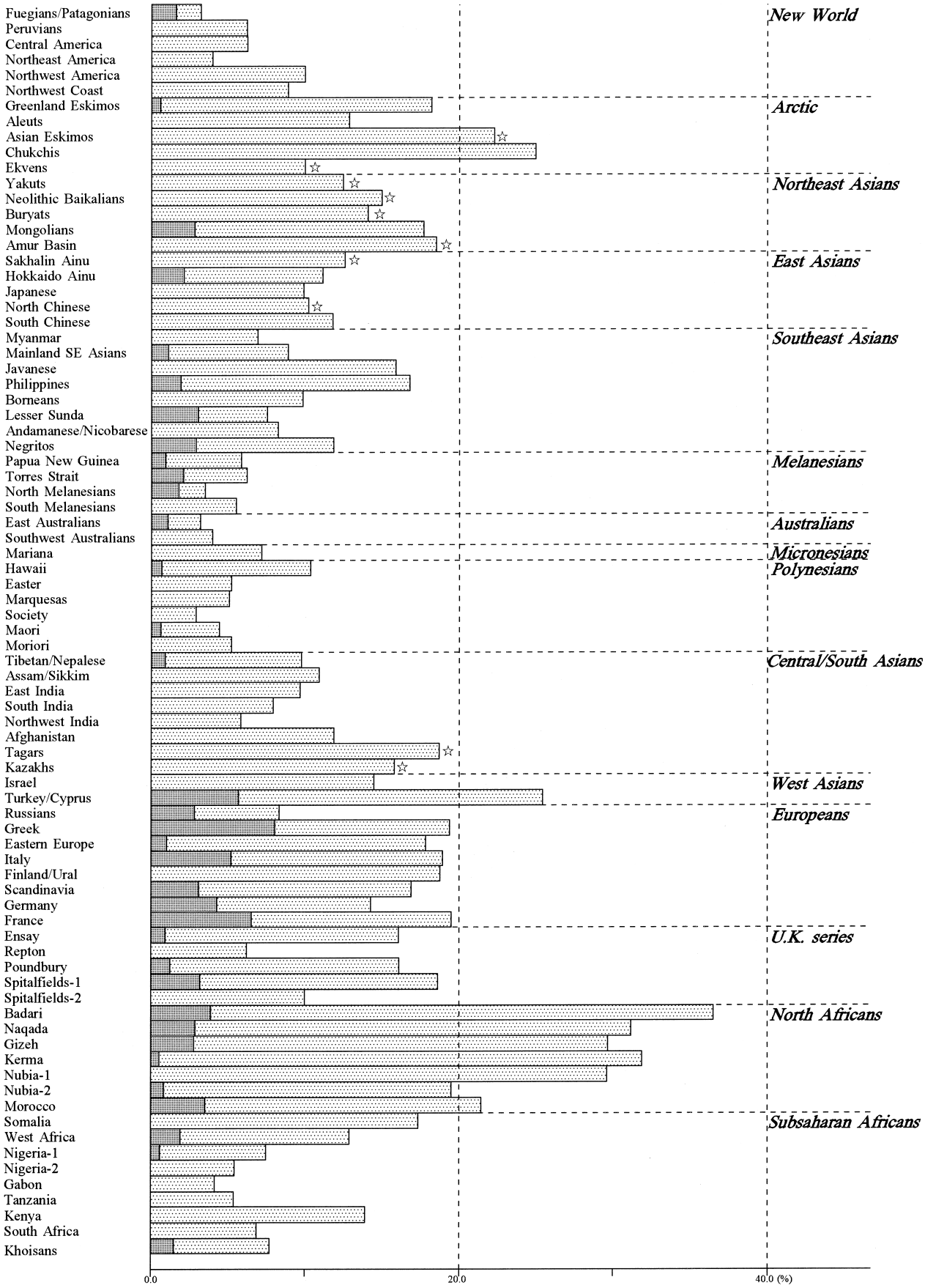

Fig. 6. Bar chart showing the frequency of jugular foramen bridging among 81 human population samples. Dense bars, type II; stippled bars, type I.

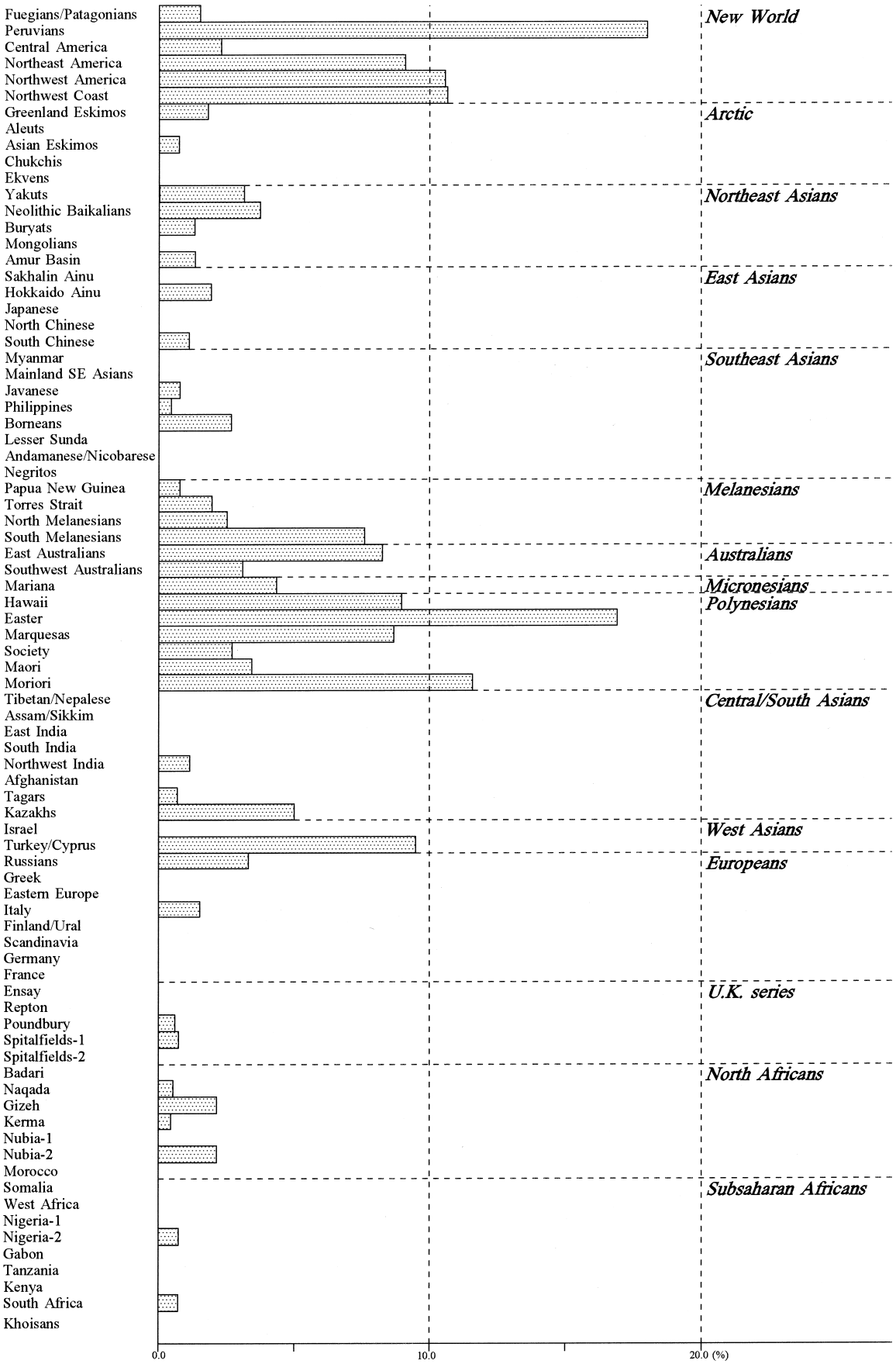

Fig. 7. Bar chart showing the frequency of auditory exostosis in 81 human population samples.

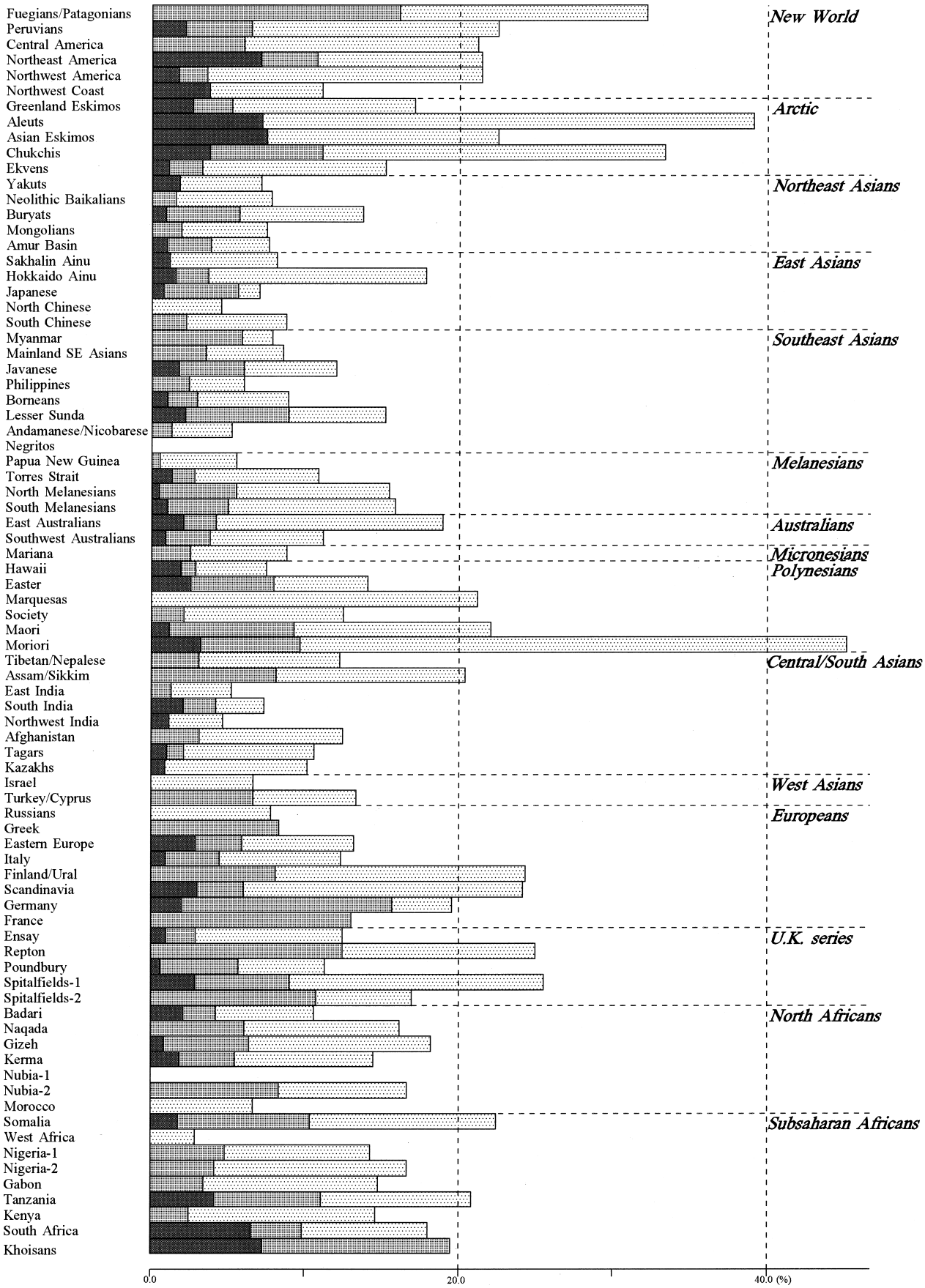

Fig. 8. Bar chart showing the frequency variation for mylohyoid bridging among 81 human population samples. Darkest portions, types I and II combined; intermediate density, type II; light stippling, type I.

expressed graphically on the world map in Figures 9 and 10.

The Subsaharan African samples, and to a lesser degree the North African samples, show on average the highest frequencies of a medial palatine canal (Figs 2, 10). The Hokkaido Ainu sample is the only other regional population showing a frequency of more than 20%. A clinal distribution from south to north is detectable in the western part of the Old World and to a lesser extent in the eastern part except for the Ainu sample. The frequency in the Neolithic Baikalian sample suggests a temporal shift in Northeast Asian region.

The East/Southeast Asian and the Pacific samples including the Australian ones show lower frequencies of hypoglossal canal bridging with the distinct exception of the Subsaharan African samples (Figs 3, 10). The Ainu sample is again the most obvious outlier in East Asian context with an incidence more than 30%. The frequencies of this trait become higher from Northeast Asia to the New World through Arctic region, indicating clinality. Among the Northeast Asian samples, the Neolithic Baikalian sample is somewhat similar to the Arctic and the New World samples. The South Asian samples are intermediate between the Southeast Asian/Tibetan and western Eurasian samples, favouring east-west clinality.

Figures 4 and 9 show the frequency distribution of the precondylar tubercle. This is basically a Micronesian and Polynesian trait. In the western part of the Old World, the variant is rare in Subsaharan African samples. In the eastern Asian and western Oceanian regions, northerly distributed population samples show slightly higher incidence than southern samples. This trait is relatively rare in Arctic and the New World.

A condylus tertius is relatively rare throughout the world (Figs 5, 9). In most cases, the frequencies are closer to 5%. This trait is more common in the Melanesian samples. The Neolithic Baikalian sample and to a lesser extent the Hokkaido Ainu sample are distinct from neighbouring population samples.

Figures 6 and 10 illustrate the frequencies of jugular foramen bridging. The length of the dense bars indicates the frequencies for type II jugular foramen bridging, and that of the stippled bars those of type I. In the samples marked with a star, the 2 types are not recorded separately. The North African samples show the highest frequencies for jugular foramen bridging. At the other extreme, the Pacific population samples including the Australian samples, along with the Subsaharan African, the South Asian, the Island Southeast Asian, and the New World samples, have frequencies less than 10%. The western Eurasian samples show relatively high frequencies for this trait. Type II jugular foramen bridging is rarely found outside Europe and North Africa. In the eastern Asian and Pacific regions, clinal variation from south to north is detectable. The New World samples break away from the Arctic and the Northeast Asian samples.

The auditory exostosis is found with a low and uniform incidence throughout the world, although there are a few important exceptions (Figs 7, 9). In contrast to many population groups, the New World and Pacific samples, especially the Polynesian, exhibit this trait at a relatively high frequency. The Turkey/Cyprus sample is the only group in the Eurasian region with an incidence near 10%.

Figures 8 and 10 show the frequency variations for mylohyoid bridging. In Figure 8, the darkest regions of the bars indicate the frequency for types I and II combined, intermediate density type II and light stippling type I. This trait is most common in the Arctic and New World samples, followed closely by those from western Eurasia. A westward shift in the occurrence of the trait is evident in the European region. The frequencies for the eastern Asian along with the South Asian samples are lower than the Pacific samples including those from Australia. The groups that are clear outliers are the Moriori, Hokkaido Ainu, and Assam/Sikkim samples. The geographical pattern for the proximal type variation is approximately similar to that total mylohyoid bridging.

DISCUSSION

According to Ossenberg (1970), hyperostotic cranial traits occur more frequently on the left side. In this study, asymmetric occurrences without any side preferences were detected for the medial palatine canal and jugular foramen bridging in several geographical populations, but with relatively low frequencies, as shown in Appendix 6. These lines of evidence are consistent with fluctuating asymmetry (O'Connell, 1975; Soule & Cuzin-Roudy, 1982; Livshits & Kobyliansky, 1991; Clarke, 1995; Livshits et al. 1998).

With regard to the intertrait association, hypoglossal canal bridging and other traits tend to correlate in their expression in a few population groups. The pairs of traits showing significant association are, however, not necessarily consistent over the different population groups, but instead are related to the absolute frequencies of the traits. This may allow us

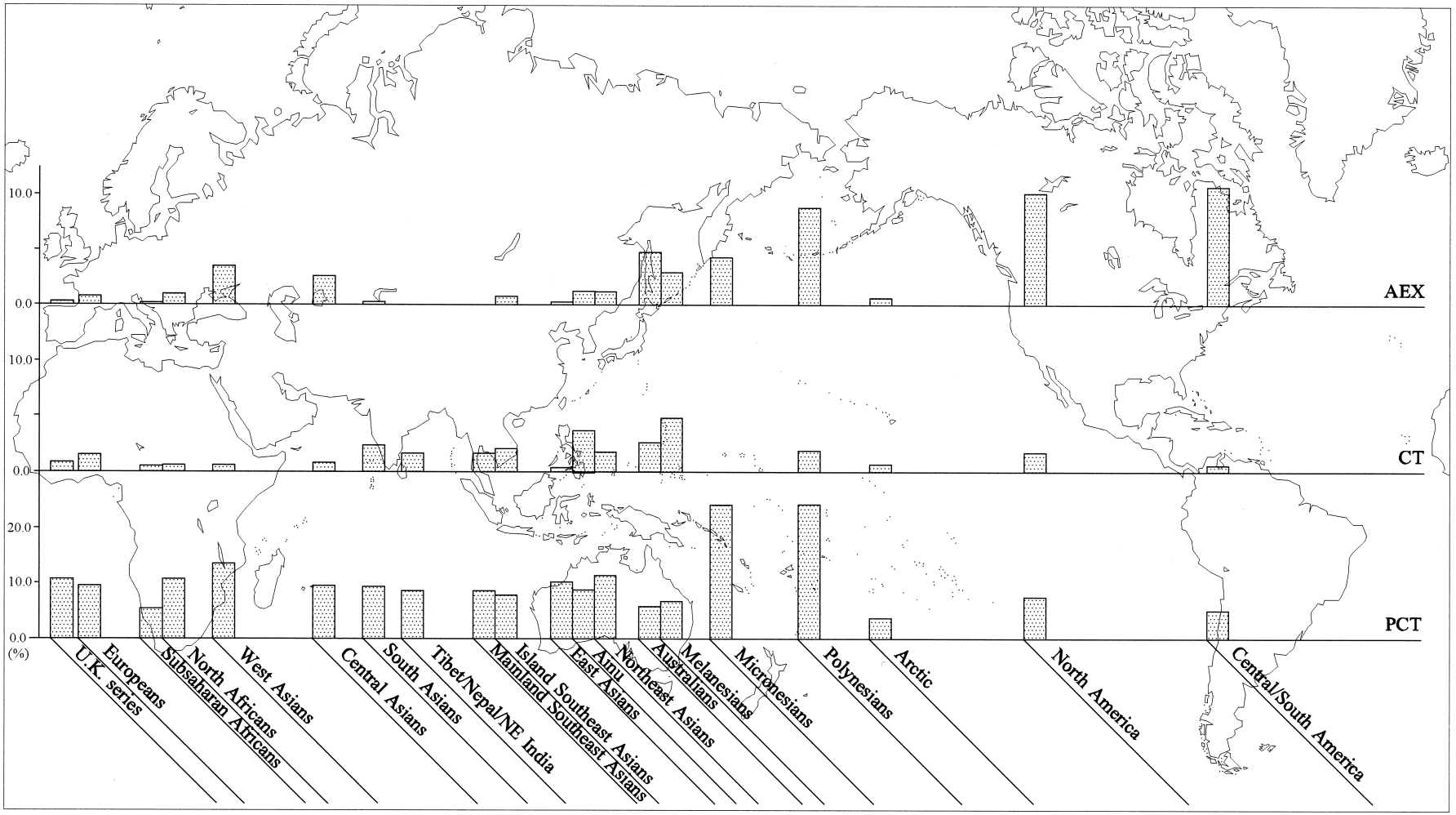

Fig. 9. Frequency variations of the precondylar tubercle (PCT), the condylus tertius (CT), and the auditory exostosis (AEX) based on the 2nd classification reproduced on the world map.

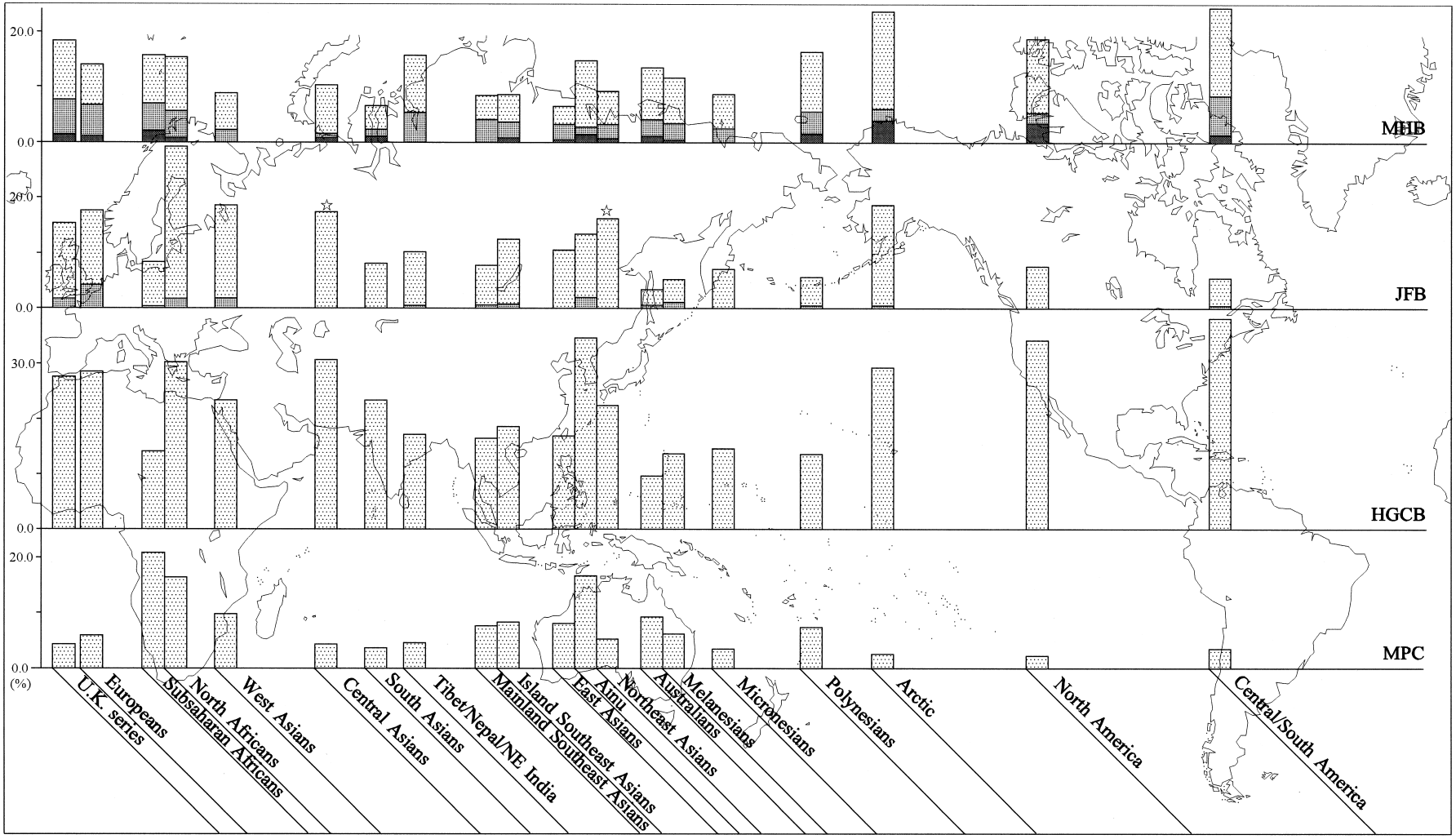

Fig. 10. Frequency of the 4 bridging type variations, the medial palatine canal (MPC), the hypoglossal canal bridging (HGCB), the jugular foramen bridging (JFB), and the mylohyoid bridging (MHB) based on the 2nd classification reproduced on the world map.

to suppose that, although not specifically tested, the associations occur at least partly by chance, as pointed out by Corruccini (1974) and Mouri (1976).

Auditory exostosis is the only character to show a tendency towards a higher incidence in males, and in some populations this reaches a significant level. A male predominant sex difference is also observed for mylohyoid bridging in Ainu and Arctic populations and in Melanesians. Central Asians and the UK, on the other hand, show a higher incidence of this trait in females. Ossenberg (1970) pointed out that hyperostotic traits occur more frequently in males and hypostotic ones more frequently in females. The worldwide analyses presented here and elsewhere (Hanihara & Ishida, 2001*a*, *b*) indicate that geography also influences sex differences.

Auditory exostosis has been linked to exposure to cold water (recently summarised by DiBartolomeo, 1979; Kennedy, 1986; Frayer, 1988; Standen et al. 1997). The results presented here indicate that the samples from coastal populations had the highest prevalence of the auditory exostosis, supporting the hypothesis that it is a subsistence-induced character.

With regard to the frequency distribution for the hyperostotic characters including the auditory exostosis, the New World populations occupy an extreme position on a world scale. They show the highest occurrences of hypoglossal canal and mylohyoid bridging, and the auditory exostosis. For most other discrete cranial traits, on the other hand, they fall at the low end of the world range. The high frequencies of hypoglossal canal and mylohyoid bridging link the New World populations and the Arctic people not to Northeast Asians but to Western Eurasians and, very significantly, to Ainu.

The Ainu sample is again the most obvious outlier in eastern Asian groups. Hokkaido Ainu with less admixture to the neighbouring Northeast Asians than Sakhalin Ainu (Ishida & Kida, 1991) occupies the high end of the world range for the medial palatine canal and hypoglossal canal bridging, and to a lesser extent, mylohyoid bridging and the condylus tertius as pointed out by Kodama (1970) and Dodo (1987). Concerning the medial palatine canal and the condylus tertius, the Ainu share this position with Subsaharan Africans and Melanesians, respectively.

In the eastern Asian and western Oceanian regions, clinal variation can be recognised in the incidences of the traits, especially in those of jugular foramen and hypoglossal canal bridging. The clinal variations in the frequencies of these 2 traits are also detectable from east to west in the Old World. In the western part of the Old World, on the other hand, such clinal variations are less clear. In this vast area, Subsaharan Africans break away from other geographical groups and align closer to the possible outliers of populations of Asian origin in the frequencies of the precondylar tubercle, medial palatine canal, hypoglossal canal bridging, and jugular foramen bridging.

Europeans exhibit relatively high incidences of 3 out of the 4 bridge type of hyperostotic characters, the hypoglossal canal, jugular foramen, and mylohyoid bridging. Dodo (1986*b*) pointed out that the posterior type (type II) of jugular foramen bridging was extremely rare. The overall range of the frequency variation for the posterior type is relatively low, less than 5%. In spite of this, there is a significant difference between western Eurasia and other regions in the world.

It is well known that the proximal type (type II) of mylohyoid bridging is often observed in the Neanderthals (Smith, 1978; Frayer, 1992; Stringer & Gamble, 1996; Jidoi et al. 2000). Thorne & Wolpoff (1992) regarded this trait as one of the characters that form the morphological basis of the multiregional model for the origin of anatomically modern humans in western Eurasia based on relatively high frequencies of this trait in upper Palaeolithic and recent Europeans. However, the proximal type is not restricted to Europeans, also occurring in the Arctic populations and Subsaharan Africans. This feature is a European regional character, but not uniquely so.

With the possible exception of the auditory exostosis, precise heritability or environmental influence for the occurrence of the traits presented in this study are far from obvious (as summarised by Hauser & De Stefano, 1989). However, the frequency distributions of the traits treated herein (except for the auditory exostosis) show some interregional clinality and intraregional discontinuity along with the temporal shift as seen in Northeast Asia, suggesting genetic drift as a possible cause for the variation. No traits precisely distinguish one geographical group from all others. This suggests that the diversity of discrete cranial traits in modern humans may, at least in part, have something to do with the differential retention or intensification from an ancestral pattern. As Lahr (1996) emphasised, spatial and temporal differences among modern human populations are the result of the process of population differentiation itself. If this is true, as seems likely, the present results together with our previous ones may shed light on the microevolutionary process of possible outliers in the world as represented by the Ainu, Arctic and New World populations, and peoples in the Pacific basin and rim.

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 Biologieque, Musée 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 of the 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, 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, Institute 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 a 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 the International Research Center for Japanese Studies (Nos 09208104 & 12012215), a Grant-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

ANTÓN SC (1997) Endocranial hyperostosis in Sangiran 2, Gibraltar 1, and Shanidar 5. *American Journal of Physical Anthropology* **102**, 111–122.

BENNETT KA (1965) The etiology and genetics of wormian bones. *American Journal of Physical Anthropology* **23**, 255–260.

BERGMAN P, HAUSER G (1985) Multi-dimensional complexes of skull traits. *Anthropologische Anzeiger* **43**, 165–171.

BERRY AC (1975) Factors affecting the incidence of nonmetrical skeletal variants. *Journal of Anatomy* **120**, 519–535.

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

BERRY RJ, SEARLE A (1963) Epigenetic polymorphism of the rodent skeleton. *Proceedings of Zoological Society in London* **140**, 577–615.

ČESNYS G (1982) Side difference of non-metrical cranial traits in the 1st–2nd millennia A.D. Lithuanian materials. *Homo* **33**, 201–209.

CLARKE GM (1995) The genetic basis of developmental stability 2. Asymmetry of extreme phenotypes revised. *American Naturalist* **146**, 708–725.

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.

COSSEDDU GG, FLORIS G, VONA G (1979) Sex and side differences in the minor non-metrical cranial variants. *Journal of Human Evolution* **8**, 685–692.

DIBARTOLOMEO JR (1979) Exostoses of the external auditory canal. *Annals of Otology, Rhinology and Laryngology* **88** (Suppl. **61**), 1–20.

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

DODO Y (1972) Aural exostosis in the human skeletal remains excavated in Hokkaido. *Journal of the Anthropological Society of Nippon* **80**, 11–22.

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 (1980) Appearance of bony bridging of the hypoglossal canal during the fetal period. *Journal of the Anthropological Society of Nippon* **88**, 229–238.

DODO Y (1986*a*) Observations on the bony bridging of the jugular foramen in man. *Journal of Anatomy* **144**, 153–165.

DODO Y (1986*b*) Population study of the jugular foramen bridging of the human cranium. *American Journal of Physical Anthropology* **69**, 15–19.

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.

DODO Y, ISHIDA H (1990) Population history of Japan as viewed from cranial nonmetric variation. *Journal of the Anthropological Society of Nippon* **98**, 269–287.

FRAYER DW (1988) Auditory exostosis and evidence for fishing at Vlasac. *Current Anthropology* **29**, 346–348.

FRAYER DW (1992) The persistence of Neanderthal features in post Neanderthal Europeans. In *Continuity or Replacement: Controversies in Homo sapiens evolution* (ed. Bräuer G, Smith FH), pp. 179–188. Rotterdam: A. A. Balkema.

GOTTLIEB K (1978) Artificial cranial deformation and the increased complexity of the lambdoid suture. *American Journal of Physical Anthropology* **48**, 213–214.

GRÜNBERG H (1963) *The Pathology of Development: A Study of Inherited Skeletal Disorders in Animals*. New York: Wiley-Liss.

HANIHARA T, ISHIDA H (2000) Os incae: frequency variation in major human population groups. *Journal of Anatomy* **198**, 137–158.

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

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

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

HERTZOG KP (1968) Associations between discontinuous cranial traits. *American Journal of Physical Anthropology* **29**, 397–404.

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.

JIDOI K, NARA T, DODO Y (2000) Bony bridging of the mylohyoid groove of the human mandible. *Anthropological Science* **108**, 345–370.

KENNEDY GE (1986) The relationship between auditory exostosis and cold water: a latitudinal analysis. *American Journal of Physical Anthropology* **71**, 401–415.

KODAMA S (1970) *Ainu: Historical and Anthropological Studies*. Sapporo: Hokkaido University School of Medicine.

KONIGSBERG LW, KOHN LAP, CHEVERUD JM (1993) Cranial deformation and nonmetric trait variation. *American Journal of Physical Anthropology* **90**, 35–48.

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

LAUGHLIN WS, JÖRGENSEN JB (1956) Isolate variation in Greenlandic Eskimo crania. *Acta Genetica* **6**, 3–12.

LE DOUBLE AF (1903) *Traité des Variations des Os du Cráne de l'Homme*. Paris: Vigot Frères.

LE DOUBLE AF (1906) *Traité des Variations des Os du la Face de l'Homme*. Paris: Vigot Frères.

LIVSHITS G, KOBYLIANSKY E (1991) Fluctuating asymmetry as a possible measure of developmental homeostasis in humans: a review. *Human Biology* **63**, 441–446.

LIVSHITS G, YAKOVENKO K, KLETSELMAN L, KARASIK D, KOBYLIANSKY E (1998) Fluctuating asymmetry and morphometric variation of hand bones. *American Journal of Physical Anthropology* **107**, 125–136.

MANZI G, VIENNA A, HAUSER G (1996) Developmental stress and cranial hypostosis by epigenetic trait occurrence and distribution: an exploratory study on the Italian Neandertals. *Journal of Human Evolution* **30**, 511–527.

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.

MAYHALL JT, DAHLBERG AA, OWEN DG (1970) Torus mandibularis in an Alaskan Eskimo population. *American Journal of Physical Anthropology* **33**, 57–60.

MAYHALL JT, MAYHALL MF (1971) Torus mandibularis in two Northwest Territories Villages. *American Journal of Physical Anthropology* **34**, 143–148.

MOURI T (1976) A study of non-metrical cranial variants of the modern Japanese in the Kinki district. *Journal of the Anthropological Society of Nippon* **84**, 191–203.

O'CONNELL BH (1975) Fluctuating asymmetry as a measure of developmental stability in Illinois Woodland populations. *American Journal of Physical Anthropology* **42**, 320–321.

OETTEKING B (1930) *The Jesup North Pacific Expedition XI, Craniology of the North Pacific Coast*. New York: G.E. Stechert.

OSSENBERG NS (1969) *Discontinuous morphological variation in the human cranium*. Ph.D. thesis, University of Toronto.

OSSENBERG NS (1970) The influence of artificial cranial deformation on discontinuous morphological traits. *American Journal of Physical Anthropology* **33**, 357–372.

PARDOE C (1991) Isolation and evolution in Tasmania. *Current Anthropology* **32**, 1–21.

PERIZONIUS WRK (1979) Non-metric cranial traits: sex difference and age dependence. *Journal of Human Evolution* **8**, 679–684.

PIETRUSEWSKY M (1971) Application of distance statistics to anthroposcopic data and a comparison of results with those obtained by using discrete traits of the skull. *Archaeology and Physical Anthropology in Oceania* **8**, 21–33.

PIETRUSEWSKY M (1984) Metric and nonmetric cranial variation in Australian Aboriginal populations compared with populations from the Pacific and Asia. *Occasional Papers in Human Biology* **3**, 1–113.

PUCCIARELLI HM (1974) The influence of experimental deformation on neurocranial wormian bones in rats. *American Journal of Physical Anthropology* **41**, 29–38.

SMITH FH (1978) Evolutionary significance of the mandibular foramen area in Neandertals. *American Journal of Physical Anthropology* **48**, 523–532.

SOAMES RW (1995) Skeletal system. In *Gray's Anatomy* (ed. Bannister LH, Berry MM, Collins P, Dyson M, Dussek JE, Ferguson MWJ), pp. 425–736. New York: Churchill Livingstone.

SOULE ME, CUZIN-ROUDY J (1982) Allometric variation. 2. Developmental instability of extreme phenotypes. *American Naturalist* **120**, 765–786.

STANDEN VG, ARRIAZA BT, SANTORO CM (1997) External auditory exostosis in prehistoric Chilean populations: a test of the cold water hypothesis. *American Journal of Physical Anthropology* **103**, 119–129.

STRINGER CB, GAMBLE C (1993) *In Search of the Neanderthals*. London: Thames & Hudson.

SULLIVAN LR (1922) The frequency and distribution of some anatomical variations in Amerind crania. *American Museum of Natural History, Anthropological Paper* **23**, 203–258.

THORNE AG, WOLPOFF MH (1992) The multiregional evolution of humans. *Scientific American* **266**, 76–83.

TORGERSEN JH (1951) Hereditary factors in the sutural pattern of the skull. *Acta Radiologica* **36**, 374–382.

TRINKAUS E (1978) Bilateral asymmetry of human skeletal nonmetric traits. *American Journal of Physical Anthropology* **49**, 315–318.

WOOD-JONES F (1931) The nonmetrical morphological characters of the skull as criteria for racial diagnosis. Part I. *Journal of Anatomy* **65**, 179–195.

YAMANO S, YAMAGUCHI B (1976) On the mylohyoid canal in the human mandible. *Bulletin of National Science Museum, Series D* **2**, 37–44.

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*

Sample name	MPC			HGCB			PCT			JFB			AEX		
	Phi	Yule	Fisher	Phi	Yule	Fisher	Phi	Yule	Fisher	Phi	Yule	Fisher	Phi	Yule	Fisher
East Asians	0.2213	0.8063	0.10	0.0687	0.3233	n.s.	0.4848	0.9368	0.00	0.2202	0.7911	0.07			
Ainu	0.3244	0.7946	0.00	0.2332	0.5436	0.00	0.6153	0.9807	0.00	0.3013	0.8377	0.00	0.5732	0.9942	0.03
Mainland Southeast Asians	0.2250	0.8300	0.24	0.1317	0.5207	2.04	0.6016	0.9717	0.00	0.0256	0.2500	n.s.			
Island Southeast Asians	0.2855	0.8579	0.00	0.1247	0.4617	0.23	0.6104	0.9744	0.00	0.2659	0.7801	0.00	0.7056	1.0000	0.00
Northeast Asians	0.3024	0.9103	0.00	0.1466	0.4705	0.06	0.4897	0.9341	0.00	0.2192	0.7114	0.00	0.2306	0.9683	2.84
Arctic	0.1231	0.8599	n.s.	0.2344	0.5724	0.00	0.6379	0.9892	0.00	0.2319	0.6883	0.00	0.6649	0.9982	0.01
North America	0.0108	−1.0000	n.s.	0.1328	0.3526	3.55	0.5600	0.9664	0.00	0.1689	0.7521	n.s.	0.8803	0.9982	0.00
Central/South America	0.1532	0.8541	n.s.	0.1486	0.3662	0.78	0.3353	0.9344	0.09	0.0874	0.6591	n.s.	0.7577	0.9874	0.00
Micronesians	0.0196	−1.0000	n.s.	0.1356	0.5423	n.s.	0.5606	0.9233	0.00	0.0315	−1.0000	n.s.	0.7120	0.9938	0.00
Polynesians	0.3130	0.8869	0.00	0.1269	0.5494	0.19	0.6096	0.9518	0.00	0.1434	0.7573	0.53	0.7084	0.9845	0.00
Melanesians	0.2296	0.8547	0.00	0.1083	0.5106	0.38	0.5400	0.9696	0.00	0.0681	0.6074	n.s.	0.5614	0.9888	0.00
Australians	0.2798	0.8360	0.00	0.1199	0.6033	3.34	0.5116	0.9841	0.00	0.0167	−1.0000	n.s.	0.6134	0.9860	0.00
Tibetans/Nepalese/ NE India	0.1827	0.8438	n.s.	0.0884	0.3874	n.s.	0.5830	0.9662	0.00	0.1564	0.6875	n.s.			
South Asians	0.2418	0.9099	0.14	0.2232	0.6069	0.00	0.6838	0.9830	0.00	0.2443	0.8638	0.01	0.7065	1.0000	0.37
Central Asians	0.4326	0.9673	0.03	0.1321	0.3846	3.79	0.6778	0.9862	0.00	0.3631	0.8294	0.00	0.6051	0.9921	0.00
West Asians	0.1886	0.7237	n.s.	0.2117	0.5510	4.10	0.4531	0.9047	0.00	0.2437	0.7094	1.17	0.7006	1.0000	0.00
Europeans	0.2853	0.8929	0.00	0.2539	0.6119	0.00	0.5076	0.9529	0.00	0.2537	0.7259	0.00	0.6531	1.0000	0.00
United Kingdom	0.2853	0.8929	0.00	0.2539	0.6119	0.00	0.5076	0.9529	0.00	0.2537	0.7259	0.00	0.6531	1.0000	0.00
North Africans	0.3019	0.7719	0.00	0.1505	0.4156	0.00	0.5348	0.9465	0.00	0.3408	0.7361	0.00	0.8809	1.0000	0.00
Subsaharan Africans	0.3591	0.7911	0.00	0.2770	0.7799	0.00	0.5795	0.9815	0.00	0.2958	0.8602	0.00	0.0010	−1.0000	n.s.

Sample name	MHB (type I)			MHB (type II)			MHB (type I+II)			MHB (total)		
	Phi	Yule	Fisher	Phi	Yule	Fisher	Phi	Yule	Fisher	Phi	Yule	Fisher
East Asians	0.5602	0.9832	0.00	0.6592	0.9925	0.00				0.6500	0.9829	0.00
Ainu	0.0473	0.2921	n.s.	0.4971	1.0000	1.52	0.8644	1.0000	0.00	0.2212	0.6885	0.26
Mainland Southeast Asians	0.2183	0.8942	n.s.	0.2046	0.8743	n.s.				0.1847	0.7538	n.s.
Island Southeast Asians	0.2024	0.8472	0.54	0.4833	0.9839	0.00	0.0039	−1.0000	0.68	0.3396	0.8839	0.00
Northeast Asians	0.3393	0.9158	0.00	0.4154	0.9786	0.01	0.4977	0.9955	0.90	0.4297	0.9238	0.00
Arctic	0.2396	0.6663	0.04	0.3664	0.9642	0.31	0.2676	0.9118	1.04	0.3772	0.7814	0.00
North America	0.2500	0.7468	3.55	0.0162	−1.0000	n.s.	0.0162	−1.0000	n.s.	0.4436	0.8780	0.01
Central/South America	0.4416	0.8832	0.00	0.6900	0.9860	0.00				0.5061	0.8820	0.00
Micronesians	0.3039	0.8857	2.08	0.3980	0.9714	4.19				0.5632	0.9637	0.00
Polynesians	0.3140	0.8249	0.00	0.6025	0.9864	0.00	0.6671	0.9965	0.00	0.5321	0.9214	0.00
Melanesians	0.1587	0.7197	0.42	0.2885	0.9411	0.05	0.8157	1.0000	0.00	0.2936	0.8224	0.00
Australians	0.2315	0.7978	0.16	0.4653	0.9858	0.01	0.8153	1.0000	0.01	0.4082	0.8842	0.00
Tibetans/Nepalese/ NE India	0.2219	0.7544	n.s.	0.0257	−1.0000	n.s.				0.2249	0.7015	4.80
South Asians	0.2179	0.8722	1.83	0.3268	0.9739	2.90	0.0046	−1.0000	n.s.	0.4394	0.9459	0.00
Central Asians	0.4004	0.9108	0.01				0.7053	1.0000	1.01	0.4872	0.9378	0.00
West Asians										0.0714	−1.0000	n.s.
Europeans	0.3862	0.9128	0.00	0.4535	0.9603	0.00	0.3497	0.9869	1.74	0.4953	0.9208	0.00
United Kingdom	0.3424	0.8442	0.00	0.4194	0.9354	0.00	0.3593	0.9797	0.08	0.5579	0.9245	0.00
North Africans	0.2678	0.7970	0.00	0.1350	0.7551	5.00	0.0042	−1.0000	n.s.	0.4313	0.8786	0.00
Subsaharan Africans	0.3685	0.8858	0.00	0.2807	0.8995	0.01	0.5278	0.9884	0.00	0.5505	0.9339	0.00

Appendix 2. *Intertrait association based on phi coefficients and Fisher's exact probability test in the samples of large geographical areas*

	HGCB	PCT	CT	JFB	AEX	MHB
MCP						
HGCB		0.1201 1.69[1]	0.1520 2.93[1]	0.1430 1.15[4]	0.1640 0.48[2]	
		0.1052 4.70[3]	0.1766 0.18[2]		0.1572 0.48[4]	
		0.1047 0.52[6]	0.1769 0.75[3]			
		0.1605 2.81[8]	0.1531 0.57[7]			
PCT			0.0992 2.15[10]	0.1866 2.90[9]	0.2263 2.20[5]	
				0.0963 1.42[11]		
				0.0778 2.36[12]		
CT						
JFB						
EX						

1, East Asians; 2, Ainu; 3, Mainland SE Asians; 4, Central/South Asians; 5, Micronesians; 6, Polynesians; 7, Melanesians; 8, Australians; 9, West Asians; 10, Europeans; 11, UK; 12, Subsaharan Africans

Appendix 3. *Phi coefficients and Fisher's exact probability test between the traits treated in this study and those of hypostotic variants in the large geographical samples*

	MCP	HGCB	PCT	CT	JFB	AEX	MHB
OL							0.1135 2.45[4]
PNB			0.1629 4.58[13]	0.1120 1.65[4]		0.1501 4.46[12]	
ASB						0.1582 2.07[2]	
						0.1338 3.05[6]	
						0.1085 0.24[9]	
OMB			0.1153 2.04[1]	0.1323 2.59[2]			
TD		0.1109 0.55[5]		0.1127 4.31[2]			
				0.1136 0.45[3]			
OSC		0.0941 2.26[5]			0.1200 2.96[1]		0.2211 1.66[12]
					0.1231 3.33[2]		
MET	0.1790 3.21[7]						
TZS		0.2823 1.73[8]	0.0920 4.23[14]			0.1843 3.86[10]	0.1211 1.934
BAS							0.1277 3.14[11]

1, East Asians; 2, Ainu; 3, Island SEA; 4, NE Asians; 5, Arctic; 6, North America; 7, Central/South America; 8, Micronesians; 9, Polynesians; 10, Australians; 11, South Asians; 12, Central Asians; 13, West Asians; 14, UK OL, ossicle at 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

Appendix 4. *Sex difference of the incidences of the hyperostotic traits based on Fisher's exact probability test*

	MPC	HGCB	PCT	CT	JFB (total)	AEX	MHB (total)
East Asians							
M	0.0769 (325)	0.1560 (327)	0.1054 (313)	0.0063 (317)	0.1125 (320)	0.0031 (320)	0.0766 (209)
F	0.0918 (98)	0.2178 (101)	0.0900 (100)	0.0000 (100)	0.0792 (101)	0.0000 (101)	0.0290 (69)
Ainu							
M	0.1514 (185)	0.3507 (211)	0.0936 (203)	0.0244 (205)	0.1373 (204)	0.0093 (216)	0.1796* (167)
F	0.1905 (126)	0.3379 (145)	0.0803 (137)	0.0571 (140)	0.0851 (141)	0.0204 (147)	0.1000 (110)
Mainland Southeast Asians							
M	0.0772 (272)	0.1782 (275)	0.0965 (259)	0.0193 (259)	0.0833 (264)	0.0000 (264)	0.0719 (153)
F	0.0899 (89)	0.1522 (92)	0.0652 (92)	0.0109 (92)	0.0549 (91)	0.0000 (91)	0.1515 (33)
Island Southeast Asians							
M	0.0784 (485)	0.1914 (491)	0.0687 (466)	0.0194 (465)	0.1364 (484)	0.0081 (492)	0.0882 (306)
F	0.1042 (192)	0.1979 (192)	0.0952 (189)	0.0265 (189)	0.1179 (195)	0.0100 (200)	0.0976 (123)
Northeast Asians							
M	0.0608 (378)	0.2148 (391)	0.1184 (380)	0.0181 (387)	0.1549 (381)	0.0151 (397)	0.0952 (273)
F	0.0362 (221)	0.2365 (241)	0.1102 (236)	0.0169 (236)	0.1775 (231)	0.0083 (242)	0.0884 (181)
Arctic							
M	0.0256 (312)	0.2911 (316)	0.0462 (303)	0.0128 (313)	0.2134 (314)	0.0062 (324)	0.3152*** (184)
F	0.0295 (237)	0.2944 (248)	0.0298 (235)	0.0000 (246)	0.1371 (248)	0.0078 (256)	0.1308 (107)
North America							
M	0.0255 (157)	0.3677 (155)	0.0867 (150)	0.0199 (151)	0.0654 (153)	0.1479*** (169)	0.1867 (75)
F	0.0167 (60)	0.2941 (68)	0.0455 (66)	0.0149 (67)	0.1045 (67)	0.0145 (69)	0.2800 (25)
Central/South America							
M	0.0324 (216)	0.4171* (211)	0.0485 (206)	0.0097 (206)	0.0810* (210)	0.1532*** (222)	0.2667 (105)
F	0.0588 (85)	0.3077 (91)	0.0449 (89)	0.0000 (89)	0.0110 (91)	0.0213 (94)	0.2308 (39)
Micronesians							
M	0.0374 (107)	0.1354 (96)	0.2088 (91)	0.0000 (93)	0.0957 (94)	0.0504 (119)	0.0732 (82)
F	0.0370 (81)	0.1688 (77)	0.1714 (70)	0.0000 (70)	0.0423 (71)	0.0349 (86)	0.1053 (76)
Polynesians							
M	0.0758 (488)	0.1399 (479)	0.2179* (436)	0.0253 (435)	0.0626 (447)	0.1359*** (471)	0.1885 (260)
F	0.0742 (256)	0.1341 (261)	0.1506 (239)	0.0126 (238)	0.0537 (242)	0.0161 (248)	0.1301 (123)
Melanesians							
M	0.0472 (551)	0.1371 (547)	0.0802 (237)	0.0508 (236)	0.0583 (240)	0.0397 (252)	0.1645***(310)
F	0.0790*(329)	0.1420 (324)	0.0544 (147)	0.0544 (147)	0.0467 (150)	0.0186 (161)	0.0664 (211)
Australians							
M	0.0796 (314)	0.0820 (305)	0.0606 (165)	0.0303 (165)	0.0427 (164)	0.0588 (170)	0.1385 (231)
F	0.1118 (152)	0.1258 (151)	0.0698 (86)	0.0233 (86)	0.0230 (87)	0.0333 (90)	0.1395 (129)
Tibetans/Nepalese/NE India							
M	0.0522 (134)	0.1866 (134)	0.0833 (132)	0.0152 (132)	0.0677 (133)	0.0000 (135)	0.1477 (88)
F	0.0455 (44)	0.1364 (44)	0.0682 (44)	0.0227 (44)	0.2045* (44)	0.0000 (44)	0.2000 (20)
South Asians							
M	0.0429 (396)	0.2312 (398)	0.0949 (390)	0.0230 (391)	0.0907 (397)	0.0050 (400)	0.0598 (234)
F	0.0345 (116)	0.2231 (121)	0.0917 (120)	0.0250 (120)	0.0667 (120)	0.0000 (120)	0.0896 (67)
Central Asians							
M	0.0420 (143)	0.3239 (142)	0.1079 (139)	0.0072 (139)	0.2000 (140)	0.0473* (148)	0.0672 (119)
F	0.0439 (114)	0.2897 (107)	0.0769 (104)	0.0096 (104)	0.1359 (103)	0.0000 (118)	0.1505* (93)
Europeans							
M	0.0623 (642)	0.2857 (644)	0.0944 (625)	0.0161 (622)	0.1707 (627)	0.0092 (650)	0.1405 (363)
F	0.0565 (177)	0.2816 (174)	0.1084 (166)	0.0120 (167)	0.1369 (168)	0.0057 (174)	0.1485 (101)
United Kingdom							
M	0.0413 (412)	0.2675 (415)	0.1073 (410)	0.0098 (407)	0.1565 (409)	0.0047 (426)	0.1645 (377)
F	0.0538 (223)	0.2903 (217)	0.1204 (216)	0.0093 (215)	0.1729 (214)	0.0044 (226)	0.2411* (224)
North Africans							
M	0.1504 (512)	0.2914 (525)	0.1348** (512)	0.0039 (512)	0.3027 (512)	0.0166* (541)	0.1700 (300)
F	0.1902 (326)	0.3077 (325)	0.0710 (324)	0.0093 (323)	0.2767 (318)	0.0000 (348)	0.1156 (147)
Subsaharan Africans							
M	0.2000 (600)	0.1552 (612)	0.0646* (604)	0.0033 (602)	0.0918 (610)	0.0031 (635)	0.1599 (369)
F	0.2255 (275)	0.1146 (288)	0.0346 (289)	0.0104 (288)	0.0756 (291)	0.0000 (302)	0.1560 (141)

* $P < 0.05$; $P < 0.01$; $P < 0.001$.

Appendix 5. *Frequency distribution for the 7 hyperostotic cranial traits in the 1st classification samples*

					JFB				MHB			
	MPC	HGCB	PCT	CT	type I	type II	total	AEX	type I	type II	type I II	total
East Asians												
Japanese	0.1243 (169)	0.1686 (172)	0.0585 (171)	0.0000 (172)	0.0988	0.0000	0.0988 (172)	0.0000 (171)	0.0140	0.0490	0.0070	0.0699 (143)
Hokkaido Ainu	0.2227 (211)	0.3557 (253)	0.0785 (242)	0.0449 (245)	0.1170	0.0213	0.1383 (94)	0.0193 (259)	0.1414	0.0209	0.0157	0.1780 (191)
Sakhalin Ainu	0.0500 (100)	0.3204 (103)	0.1122 (98)	0.0200 (100)			0.1116 (242) 0.1262 (103)	0.0000 (104)	0.0689	0.0000	0.0116	0.0814 (86)
North Chinese	0.0429 (163)	0.2048 (166)	0.1166 (163)	0.0060 (166)			0.1024 (166)	0.0000 (166)	0.0449	0.0000	0.0000	0.0449 (89)
South Chinese	0.0645 (93)	0.1087 (92)	0.1625 (80)	0.0125 (80)	0.1176	0.0000	0.1176 (85)	0.0116 (86)	0.0652	0.0217	0.0000	0.0870 (46)
Mainland Southeast Asians												
Myanmar	0.0749 (187)	0.1905 (189)	0.1064 (188)	0.0106 (188)	0.0691	0.0000	0.0691 (188)	0.0000 (188)	0.0196	0.0588	0.0000	0.0784 (51)
Mainland SE Asians	0.0802 (187)	0.1421 (190)	0.0636 (173)	0.0231 (173)	0.0782	0.0112	0.0894 (179)	0.0000 (180)	0.0500	0.0357	0.0000	0.0857 (140)
Island Southeast Asians												
Javanese	0.0758 (132)	0.2000 (135)	0.0615 (130)	0.0154 (130)	0.1591	0.0000	0.1591 (132)	0.0075 (134)	0.0603	0.0431	0.0172	0.1207 (116)
Philippine	0.0744 (215)	0.2009 (214)	0.0631 (206)	0.0294 (204)	0.1488	0.0186	0.1674 (215)	0.0046 (219)	0.0361	0.0241	0.0000	0.0602 (83)
Borneans	0.0667 (150)	0.2177 (147)	0.1221 (131)	0.0303 (132)	0.0979	0.0000	0.0979 (143)	0.0268 (149)	0.0594	0.0198	0.0099	0.0891 (101)
Lesser Sunda	0.1791 (67)	0.1231 (65)	0.0462 (65)	0.0000 (66)	0.0455	0.0303	0.0758 (66)	0.0000 (67)	0.0652	0.0652	0.0217	0.1522 (46)
Andamanese/ Nicobarese	0.0609 (115)	0.1639 (122)	0.1083 (120)	0.0083 (120)	0.0820	0.0000	0.0820 (122)	0.0000 (123)	0.0390	0.0130	0.0000	0.0519 (77)
Negritos	0.1143 (35)	0.1471 (34)	0.0294 (34)	0.0294 (34)	0.0882	0.0294	0.1176 (34)	0.0000 (36)	0.0000	0.0000	0.0000	0.0000 (26)
Northeast Asians												
Mongolians	0.0640 (172)	0.1934 (181)	0.1278 (180)	0.0111 (180)	0.2703	0.0270	0.2973 (74) 0.1768 (181)	0.0000 (183)	0.0561	0.0187	0.0000	0.0748 (107)
Buryats	0.0556 (144)	0.2185 (151)	0.1824 (148)	0.0000 (149)			0.1409 (149)	0.0133 (150)	0.0806	0.0484	0.0081	0.1371 (124)
Amur basin	0.0395 (152)	0.2303 (165)	0.0440 (159)	0.0188 (160)			0.1852 (162)	0.0061 (165)	0.0381	0.0286	0.0095	0.0762 (105)
Neolithic Baikalians	0.0139 (72)	0.2800 (75)	0.0882 (68)	0.0556 (72)			0.1500 (60)	0.0370 (81)	0.0625	0.0156	0.0000	0.0781 (64)
Yakuts	0.0794 (63)	0.2500 (64)	0.1250 (64)	0.0308 (65)			0.1250 (64)	0.0313 (64)	0.0536	0.0000	0.0179	0.0714 (56)
Arctic												
Ekvens	0.0288 (104)	0.3173 (104)	0.0000 (99)	0.0000 (102)			0.1000 (100)	0.0000 (110)	0.1196	0.0217	0.0109	0.1522 (92)
Chukchis	0.0299 (67)	0.2603 (73)	0.0455 (66)	0.0137 (73)	0.2800	0.0000	0.2800 (25)	0.0000 (73)	0.2222	0.0741	0.0370	0.3333 (27)
Aleuts	0.0536 (112)	0.2804 (107)	0.0571 (105)	0.0189 (106)	0.1633	0.0000	0.2500 (72) 0.1633 (49)	0.0000 (117)	0.3188	0.0000	0.0725	0.3913 (69)
Asian Eskimos	0.0000 (119)	0.3203 (128)	0.0756 (119)	0.0000 (127)			0.1284 (109) 0.2231 (130)	0.0076 (132)	0.1500	0.0000	0.0750	0.2250 (40)
Greenland Eskimos	0.0305 (164)	0.2651 (166)	0.0184 (163)	0.0061 (165)	0.1758	0.0061	0.1818 (165)	0.0181 (166)	0.1184	0.0263	0.0263	0.1711 (76)
New World												
Northwest Coast	0.0112 (89)	0.3111 (90)	0.0575 (87)	0.0000 (88)	0.0889	0.0000	0.0889 (90)	0.1064 (94)	0.0741	0.0000	0.0370	0.1111 (27)
Northwest America	0.0122 (82)	0.3562 (73)	0.1618 (68)	0.0299 (67)	0.1000	0.0000	0.1000 (70)	0.1059 (85)	0.1786	0.0179	0.0179	0.2143 (56)
Northeast America	0.0476 (63)	0.3636 (77)	0.0135 (74)	0.0263 (76)	0.0395	0.0000	0.0395 (76)	0.0909 (77)	0.1071	0.0357	0.0714	0.2143 (28)
Central America	0.0390 (77)	0.2840 (81)	0.0260 (77)	0.0128 (78)	0.0625	0.0000	0.0625 (80)	0.0233 (86)	0.1515	0.0606	0.0000	0.2121 (33)
Peruvians	0.0391 (179)	0.4181 (177)	0.0686 (175)	0.0057 (174)	0.0621	0.0000	0.0621 (177)	0.1803 (183)	0.1613	0.0430	0.0215	0.2258 (93)
Fuegians/ Patagonians	0.0313 (64)	0.4032 (62)	0.0000 (60)	0.0000 (60)	0.0161	0.0161	0.0323 (62)	0.0152 (66)	0.1613	0.1613	0.0000	0.3226 (31)
Micronesians												
Mariana	0.0368 (190)	0.1486 (175)	0.1902 (163)	0.0000 (165)	0.0600	0.0000	0.0600 (50) 0.0719 (167)	0.0435 (207)	0.0625	0.0250	0.0000	0.0875 (160)
Polynesians												
Hawaii	0.1026 (156)	0.1419 (155)	0.1788 (151)	0.0000 (151)	0.0968	0.0065	0.1032 (155)	0.0897 (156)	0.0467	0.0093	0.0187	0.0748 (107)
Easter	0.0890 (146)	0.0530 (151)	0.3053 (131)	0.0077 (130)	0.0526	0.0000	0.0526 (133)	0.1690 (142)	0.0641	0.0513	0.0256	0.1410 (78)
Marquesas	0.0874 (103)	0.1400 (100)	0.1649 (97)	0.0412 (97)	0.0505	0.0000	0.0505 (99)	0.0865 (104)	0.2121	0.0000	0.0000	0.2121 (33)
Society	0.0580 (69)	0.1940 (67)	0.2381 (63)	0.0159 (63)	0.0290	0.0000	0.0290 (69)	0.0270 (74)	0.1042	0.0208	0.0000	0.1250 (48)
Maori	0.0681 (191)	0.1966 (178)	0.1429 (154)	0.0261 (153)	0.0380	0.0063	0.0443 (158)	0.0341 (176)	0.1279	0.0814	0.0116	0.2209 (86)
Moriori	0.0097 (103)	0.1333 (105)	0.1413 (92)	0.0326 (92)	0.0526	0.0000	0.0526 (95)	0.1158 (95)	0.3548	0.0645	0.0323	0.4516 (31)

Appendix 5 (*cont.*)

					JFB				MHB			
	MPC	HGCB	PCT	CT	type I	type II	total	AEX	type I	type II	type I II	total
Melanesians												
Papua New Guinea	0.0456 (329)	0.1219 (320)	0.0783 (115)	0.0526 (114)	0.0504	0.0084	0.0588 (119)	0.0074 (135)	0.0497	0.0055	0.0000	0.0552 (181)
Torres Strait	0.0404 (99)	0.1531 (98)	0.0833 (96)	0.0521 (96)	0.0412	0.0206	0.0619 (97)	0.0194 (103)	0.0811	0.0135	0.0135	0.1081 (74)
North Melanesia	0.0693 (303)	0.1351 (296)	0.0684 (117)	0.0342 (117)	0.0171	0.0171	0.0342 (117)	0.0252 (119)	0.1000	0.0500	0.0050	0.1550 (200)
South Melanesia	0.0856 (187)	0.1684 (190)	0.0449 (89)	0.0562 (89)	0.0556	0.0000	0.0556 (90)	0.0761 (92)	0.1089	0.0396	0.0099	0.1584 (101)
Australians												
East Australians	0.0602 (133)	0.1194 (134)	0.0211 (95)	0.0105 (95)	0.0211	0.0105	0.0316 (95)	0.0825 (97)	0.1474	0.0211	0.0211	0.1895 (95)
Southwest Australians	0.1030 (301)	0.0828 (290)	0.0968 (124)	0.0323 (124)	0.0397	0.0000	0.0397 (126)	0.0310 (129)	0.0750	0.0292	0.0083	0.1125 (240)
Central/South Asians												
Tibetans/Nepalese	0.0410 (122)	0.1463 (123)	0.0924 (119)	0.0168 (119)	0.0894	0.0081	0.0976 (123)	0.0000 (125)	0.0923	0.0308	0.0000	0.1231 (65)
Assam/Sikkim	0.0615 (65)	0.2154 (65)	0.0769 (65)	0.0154 (65)	0.1094	0.0000	0.1094 (64)	0.0000 (64)	0.1224	0.0816	0.0000	0.2041 (49)
East India	0.0325 (123)	0.2419 (124)	0.0992 (121)	0.0165 (121)	0.0968	0.0000	0.0968 (124)	0.0000 (124)	0.0390	0.0130	0.0000	0.0519 (77)
South India	0.0549 (182)	0.2320 (181)	0.0739 (176)	0.0398 (176)	0.0791	0.0000	0.0791 (177)	0.0000 (180)	0.0316	0.0211	0.0211	0.0737 (95)
Northwest India	0.0181 (166)	0.2659 (173)	0.1000 (170)	0.0175 (171)	0.0575	0.0000	0.0575 (174)	0.0115 (174)	0.0345	0.0000	0.0115	0.0460 (87)
Afghanistan	0.0698 (43)	0.1395 (43)	0.1163 (43)	0.0000 (43)	0.1190	0.0000	0.1190 (42)	0.0000 (44)	0.0938	0.0313	0.0000	0.1250 (32)
Tagars	0.0362 (138)	0.3101 (129)	0.0407 (123)	0.0000 (123)			0.1870 (123)	0.0068 (146)	0.0851	0.0106	0.0106	0.1064 (94)
Kazakhs	0.0504 (119)	0.3083 (120)	0.1500 (120)	0.0167 (120)			0.1583 (120)	0.0500 (120)	0.0932	0.0000	0.0085	0.1017 (118)
West Asians												
Israel	0.0526 (95)	0.1310 (84)	0.0935 (107)	0.0000 (106)	0.1456	0.0000	0.1456 (103)	0.0000 (109)	0.0667	0.0000	0.0000	0.0667 (30)
Turkey/Cyprus	0.1724 (58)	0.3962 (53)	0.2037 (54)	0.0179 (56)	0.2075	0.0566	0.2641 (53)	0.0952 (63)	0.0667	0.0667	0.0000	0.1333 (15)
Europeans												
Russians	0.0417 (120)	0.3333 (120)	0.1083 (120)	0.0083 (120)	0.1389	0.0278	0.1667 (36) 0.0833 (120)	0.0331 (121)	0.0777	0.0000	0.0000	0.0777 (103)
Greece	0.0635 (63)	0.2459 (61)	0.1613 (62)	0.0323 (62)	0.1129	0.0806	0.1935 (62)	0.0000 (64)	0.0000	0.0833	0.0000	0.0833 (24)
Eastern Europe	0.0672 (119)	0.2984 (124)	0.1386 (101)	0.0099 (101)	0.1683	0.0099	0.1782 (101)	0.0000 (101)	0.0735	0.0294	0.0294	0.1324 (68)
Italy	0.0979 (194)	0.3000 (190)	0.0811 (185)	0.0164 (183)	0.1368	0.0526	0.1895 (190)	0.0149 (202)	0.0796	0.0354	0.0088	0.1239 (113)
Finland/Ural	0.0000 (80)	0.2911 (79)	0.0769 (78)	0.0128 (78)	0.1875	0.0000	0.1875 (80)	0.0000 (81)	0.1622	0.0811	0.0000	0.2432 (37)
Scandinavia	0.0645 (62)	0.2923 (65)	0.1231 (65)	0.0000 (65)	0.1385	0.0308	0.1692 (65)	0.0000 (65)	0.1818	0.0303	0.0303	0.2424 (33)
German	0.0429 (70)	0.1571 (70)	0.0429 (70)	0.0143 (70)	0.1000	0.0429	0.1429 (70)	0.0000 (70)	0.0392	0.1373	0.0196	0.1961 (51)
France	0.0505 (99)	0.3263 (95)	0.0625 (96)	0.0313 (96)	0.1304	0.0652	0.1957 (92)	0.0000 (108)	0.0000	0.1304	0.0000	0.1304 (23)
UK series												
Ensay	0.0536 (112)	0.3304 (112)	0.0901 (111)	0.0000 (111)	0.1518	0.0089	0.1607 (112)	0.0000 (114)	0.0962	0.0192	0.0096	0.1250 (104)
Repton	0.0392 (51)	0.2340 (47)	0.1818 (44)	0.0000 (44)	0.0625	0.0000	0.0625 (48)	0.0000 (57)	0.1250	0.1250	0.0000	0.2500 (24)
Poundbury	0.0361 (166)	0.2547 (161)	0.0994 (161)	0.0126 (159)	0.1484	0.0129	0.1613 (155)	0.0060 (168)	0.0566	0.0503	0.0063	0.1132 (159)
Spitalfields-1	0.0514 (253)	0.2946 (258)	0.0941 (255)	0.0119 (253)	0.1548	0.0317	0.1865 (252)	0.0077 (261)	0.1646	0.0617	0.0288	0.2551 (243)
Spitalfields-2	0.0294 (102)	0.2376 (101)	0.1400 (100)	0.0100 (100)	0.1000	0.0000	0.1000 (100)	0.0000 (101)	0.0625	0.1071	0.0000	0.1696 (112)
North Africans												
Badari	0.2453 (53)	0.3208 (53)	0.0980 (51)	0.0000 (48)	0.3269	0.0385	0.3654 (52)	0.0000 (57)	0.0638	0.0213	0.0213	0.1064 (47)
Naqada	0.1923 (182)	0.2951 (183)	0.1093 (183)	0.0055 (183)	0.2841	0.0284	0.3125 (176)	0.0054 (186)	0.1010	0.0606	0.0000	0.1616 (99)
Gizeh	0.1292 (178)	0.3315 (184)	0.1475 (183)	0.0000 (184)	0.2692	0.0275	0.2967 (182)	0.0217 (184)	0.1190	0.0556	0.0079	0.1825 (126)
Kerma	0.1942 (206)	0.2718 (206)	0.0859 (198)	0.0101 (198)	0.3131	0.0051	0.3182 (198)	0.0044 (226)	0.0909	0.0364	0.0182	0.1455 (110)
Nubia-1	0.1047 (86)	0.2439 (82)	0.0976 (82)	0.0000 (82)	0.2963	0.0000	0.2963 (81)	0.0000 (88)	0.0000	0.0000	0.0000	0.0000 (9)
Nubia-2	0.1385 (130)	0.3235 (136)	0.1111 (135)	0.0148 (135)	0.1880	0.0075	0.1955 (133)	0.0214 (140)	0.0833	0.0833	0.0000	0.1667 (48)
Morocco	0.1111 (27)	0.3793 (29)	0.0769 (26)	0.0000 (27)	0.1786	0.0357	0.2143 (28)	0.0000 (32)	0.0667	0.0000	0.0000	0.0667 (15)
Subsaharan Africans												
Somalia	0.1111 (72)	0.1739 (69)	0.0294 (68)	0.0000 (68)	0.1739	0.0000	0.1739 (69)	0.0000 (73)	0.1207	0.0862	0.0172	0.2241 (58)
West Africa	0.2727 (55)	0.2885 (52)	0.0556 (54)	0.0000 (53)	0.1111	0.0185	0.1296 (54)	0.0000 (56)	0.0286	0.0000	0.0000	0.0286 (35)
Nigeria-1	0.1645 (152)	0.1456 (158)	0.0318 (157)	0.0000 (157)	0.0692	0.0063	0.0755 (159)	0.0000 (164)	0.0952	0.0476	0.0000	0.1429 (126)
Nigeria-2	0.2149 (121)	0.1163 (129)	0.0709 (127)	0.0157 (127)	0.0543	0.0000	0.0543 (129)	0.0075 (133)	0.1250	0.0417	0.0000	0.1667 (24)
Gabon	0.2222 (144)	0.1399 (143)	0.0709 (141)	0.0071 (141)	0.0420	0.0000	0.0420 (143)	0.0000 (149)	0.1136	0.0341	0.0000	0.1477 (88)
Tanzania	0.3297 (91)	0.0645 (93)	0.0989 (91)	0.0000 (91)	0.0538	0.0000	0.0538 (93)	0.0000 (100)	0.0972	0.0694	0.0417	0.2083 (72)
Kenya	0.2044 (137)	0.1533 (137)	0.0526 (133)	0.0076 (132)	0.1397	0.0000	0.1397 (136)	0.0000 (146)	0.1220	0.0244	0.0000	0.1463 (41)
South Africa	0.1938 (129)	0.2180 (133)	0.0303 (132)	0.0000 (132)	0.0687	0.0000	0.0687 (131)	0.0075 (134)	0.0820	0.0328	0.0656	0.1803 (61)
Khoisan	0.1935 (62)	0.1538 (65)	0.0615 (65)	0.0000 (65)	0.0615	0.0154	0.0769 (65)	0.0000 (66)	0.0000	0.1220	0.0732	0.1951 (41)

Appendix 6. Frequency distribution for the 7 hyperostotic cranial traits in the 2nd classification samples

					JFB				MHB			
	MPC	HGCB	PCT	CT	type I	type II	total	AEX	type I	type II	type I II	total
Eastern Asia												
East Asians	0.0800 (425)	0.1698 (430)	0.1014 (414)	0.0048 (418)	0.1051	0.0000	0.1051 (257) 0.1040 (423)	0.0024 (423)	0.0324	0.0288	0.0036	0.0647 (278)
Ainu	0.1672 (311)	0.3455 (356)	0.0882 (340)	0.0377 (345)	0.1176	0.0196	0.1373 (102) 0.1159 (345)	0.0138 (363)	0.1191	0.0144	0.0144	0.1480 (277)
Mainland Southeast Asians	0.0775 (374)	0.1662 (379)	0.0859 (361)	0.0166 (361)	0.0736	0.0054	0.0790 (367)	0.0000 (368)	0.0419	0.0419	0.0000	0.0838 (191)
Island Southeast Asians	0.0826 (714)	0.1883 (717)	0.0787 (686)	0.0204 (686)	0.1166	0.0098	0.1264 (712)	0.0082 (728)	0.0490	0.0290	0.0089	0.0869 (449)
Northeast Asians	0.0514 (603)	0.2248 (636)	0.1147 (619)	0.0176 (626)	0.2475	0.0198	0.2673 (101) 0.1623 (616)	0.0124 (643)	0.0592	0.0263	0.0066	0.0921 (456)
Arctic/New World												
Arctic	0.0270 (555)	0.2928 (567)	0.0388 (541)	0.0071 (562)	0.1842	0.0044	0.1886 (228) 0.1752 (565)	0.0068 (587)	0.1773	0.0201	0.0401	0.2375 (299)
North America	0.0214 (234)	0.3417 (240)	0.0742 (229)	0.0173 (231)	0.0763	0.0000	0.0763 (236)	0.1016 (256)	0.1351	0.0180	0.0360	0.1892 (111)
Central/South America	0.0375 (320)	0.3813 (320)	0.0449 (312)	0.0064 (312)	0.0533	0.0031	0.0564 (319)	0.1075 (335)	0.1592	0.0701	0.0127	0.2420 (157)
Pacific/Oceania												
Micronesians	0.0368 (190)	0.1486 (175)	0.1902 (163)	0.0000 (165)	0.0600	0.0000	0.0600 (50) 0.0719 (167)	0.0435 (207)	0.0625	0.0250	0.0000	0.0875 (160)
Polynesians	0.0728 (797)	0.1387 (786)	0.1905 (714)	0.0197 (712)	0.0543	0.0041	0.0584 (736)	0.0879 (774)	0.1117	0.0397	0.0149	0.1638 (403)
Melanesians	0.0610 (918)	0.1394 (904)	0.0695 (417)	0.0481 (416)	0.0402	0.0118	0.0520 (423)	0.0290 (449)	0.0827	0.0288	0.0054	0.1169 (556)
Australians	0.0913 (482)	0.0975 (472)	0.0599 (267)	0.0262 (267)	0.0262	0.0075	0.0337 (267)	0.0469 (277)	0.0968	0.0296	0.0108	0.1344 (372)
Central/South/ West Asia												
Tibetans/Nepalese/ NE India	0.0481 (187)	0.1702 (188)	0.0870 (184)	0.0163 (184)	0.0963	0.0053	0.1016 (187)	0.0000 (189)	0.1053	0.0526	0.0000	0.1579 (114)
South Asians	0.0389 (540)	0.2330 (545)	0.0938 (533)	0.0243 (534)	0.0810	0.0000	0.0810 (543)	0.0036 (548)	0.0417	0.0128	0.0096	0.0641 (312)
Central Asians	0.0428 (257)	0.3092 (249)	0.0947 (243)	0.0082 (243)	0.1728	0.0000	0.1728 (243)	0.0263 (266)	0.0896	0.0047	0.0094	0.1038 (212)
West Asians	0.0980 (153)	0.2336 (137)	0.1304 (161)	0.0062 (162)	0.1731	0.0192	0.1859 (156)	0.0349 (172)	0.0667	0.0222	0.0000	0.0889 (45)
Europe												
Europeans	0.0600 (834)	0.2852 (831)	0.0958 (804)	0.0150 (802)	0.1368	0.0408	0.1776 (687) 0.1636 (807)	0.0083 (839)	0.0784	0.0508	0.0106	0.1398 (472)
UK	0.0439 (684)	0.2784 (679)	0.1073 (671)	0.0090 (667)	0.1394	0.0165	0.1544 (667)	0.0043 (701)	0.1075	0.0623	0.0140	0.1838 (642)
Africa												
North Africans	0.1636 (862)	0.3013 (873)	0.1096 (858)	0.0058 (857)	0.2776	0.0176	0.2906 (850)	0.0099 (913)	0.0947	0.0485	0.0088	0.1520 (454)
Subsaharan Africans	0.2085 (940)	0.1445 (962)	0.0535 (953)	0.0053 (950)	0.0811	0.0031	0.0842 (962)	0.0020 (1002)	0.0884	0.0497	0.0203	0.1584 (543)