Microevolutionary Parallels in the Population History of Japan and Aboriginal North America: The Evidence of Cranial Nonmetric Traits

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Population history is complex in regions which were peopled, not by a single migratory event, but rather by successive episodes in which indigenous inhabitants were intruded on by later arrivals with advanced technology and of a different genetic stock. This paper reviews findings based on normetric cranial traits which indicate demic diffusion in the population history of Japan and Northwestern North America; and, notwithstanding the vastly greater differences (genetic and cultural) between the indigenous and immigrant group in Japan than in North America, draws parallels between the two regions.

Materials and Methods

Twenty-five nonmetric traits of the skull provided the data for this research. Trivial features generally having neither clinical nor adaptive significance, their use in historical studies is based on the assumption that they are predominantly under genetic control. Presence/absence of each trait in each skull was scored by one observer for 55 cranial series (N3487). The samples included 4 from Japan, 7 from Siberia and 39 from northwestern North America. Non-Mongoloid comparisons were provided by 2 Black and 3 Eurasian samples. Using frequencies of the 25 traits in each cranial series, the Mean Measure of Divergence (MMD) statistic generated a triangular matrix of MMDs, estimates of biological distance between each population and every other one. A second dimension of biological distance was provided by Spearman's rank correlation coefficient, r_s, which measured the similarity between two population in terms of the rank order of their respective MMDs. Cluster analysis of MMDs was used to generate a series of dendrographs. Fully tabulated MMDs, 1980, 1980, 1990).

Summary data for the comparison in this essay between Japan and North America are presented in Table 1. The data are MMDs and r_s values for ten cranial series, five relevant to the population history of each region.

Cranial series	Jo	Ai	Ka	Ki	Tu	OBS	Esk	Ath	Al	LW
Jomon		.942	.737	.437	.319*					
Ainu	.0492		.765	.446	.321 *	14 a 14 a 14				
Kanto	.1323	.0727		.765	.668	1				
Kinki	.1683	.1033	.0361		.842					
Tungus	.2265	.1450	.0572	.0451			Sector Street			e di se
Old Bering Sea ²⁾	.2421	.1625	.1001	.0836	.1094		.956	.528	.465	.314 *
Yupik Eskimo	.2307	.1633	.1060	.0753	.0815	.0137		.607	.466	.318 *
Athapaskan	.2454	.1701	.1434	.1016	.1238	.0498	.0270		.928	.721
Aleut, Central and Eastern	.2290	.1717	.1412	.0994	.1244	.0802	.0522	.0141		.781
Late Woodland	.2726	.1740	.1915	.1392	.1901	.1415	.1083	.0413	.0383	1996

Table1. Mean Measures of Divergence (below diagonal) and values of Spearman's r_s (above diagonal)¹⁾ for ten cranial series from Japan, Siberia, and western North America.

The r_s value for any pair of cranial series quantifies the correlation between the ranks of their MMDs for all series. The total number of series used for r_s analysis was 20. In addition to the ten listed in the table were : Chukchi, recent Siberian Eskimo, Inupiaq Eskimo (north Alaska and Canada), Early Kodiak, Western Aleut, Tlingit, Haida, Namu, historic Plains tribes, Illinois Hopewell.

- 2) The Old Bering Sea series was an aggregate from the Ekven Cemetery (Chukotka) and Old Bering sea and Punuk phase remains from St. Lawrence Is.
- * Not significant at the 5% probability level.

Japan

MMDs in the total matrix for 55 cranial series ranged from 0.0023 indicating closest, to 0.4502 indicating most distant relationship. In that context, MMDs for the samples from Japan (Table 1) revealed, as expected, that contemporaneous Japanese from two Honshu districts were closely related (0.0361). But Ainu and Jomon also were closely related (0.0492) despite three or more millenia separating the populations. Thus, in agreement with craniometric (Howells, 1966; Yamaguchi, 1982; Hanihara, 1985) and dental evidence (Turner, 1976; Brace and Nagai, 1982; Mizoguch, 1986; Matsumura, 1989) nonmetric cranial traits supported the historical reconstruction whereby, of all Japan's present-day people, Ainu bear the strongest genetic heritage from her Neolithic aboriginals. Independently, other studies using nonmetric cranial traits have reached the same conclusion (Yamaguchi, 1985; Dodo, 1986; Mouri, 1988; Dodo and Ishida, 1990; Kozintsev, 1990).

Interestingly, the strong continuity between Jomon and Ainu was manifest not only in their MMD but also in their closely similar patterns of affinities with other Mongoloid cranial series (Spearman's $r_s 0.942$). Similarly, Kanto and Kinki MMDs showed high rank correlation ($r_s 0.765$). The positive linear relationship between MMD and r_s is displayed in Fig. 1.

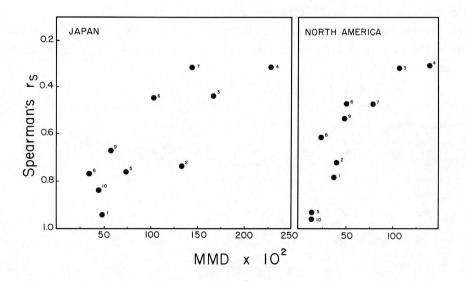


Fig.1. Parallel gradients of affinities in Japan and North America are illustrated in plots of Spearman's rank correlation coefficient r_s versus MMD. Data are from Table 1.

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Japa	n		North	America	
1	Jomon	- Ainu	1	Late Woodland	- Aleut
2		- Kanto	2		- Athapaskans
3		- Kinki	3		- Eskimo
4		- Tungus	4		- Old Bering Sea
5	Ainu	- Kanto	5	Aleut	- Athapaskans
6		- Kinki	6		- Eskimo
7	Kanto	- Tungus	7		- OBS
8		- Kinki	8	Athapaskans	- Eskimo
9		- Tungus	9		- OBS
10	Kinki	- Tungus	10	Eskimo	- OBS

Tungus, represented by an aggregate of 3 samples (Ulchi, Negidal, Evenki) were included in my study as members of the Classic Mongoloid stock of continental Northeast Asia. MMDs and r_s values for Tungus showed the following ranking with the 4 samples from Japan:

Tungus	MMD	rs
Kinki	.0451	.842
Kanto	.0572	.668
Ainu	.1450	.321
Jomon	.2265	.319

On the other hand, Jomon showed exactly the reverse order:

Jomon	MMD	rs
Ainu	.0492	.942
Kanto	.1323	.737
Kinki	.1683	.437
Tungus	.2265	.319

In all comparisons, both of MMD and of r_s , Ainu fell intermediate between Jomon and Kanto, while Kanto fell intermediate between Ainu and Kinki.

Of the four traits (os Japanicum trace, supraorbital foramen, pharyngeal fossa, trochlear spur) which ranked highest in terms of their power for discriminating Jomon from recent Japanese, and accounting for approximately 76% of the Jomon-Japanese MMD, the four cranial series consistently ranked: Jomon-Ainu-Kanto-Kinki. Using these four traits plus six others characterized by significant frequency differences in Japan (Ossenberg, 1986), I drew for each of the four cranial series a polygon in which the incidence of each trait was depicted as a length along the radius of a circle (Fig. 2). These shapes appear to metamorphose from one to the next along the same gradient. Of the 10 traits represented in the polygons, 7 showed a frequency difference (not necessarily significant) between Kanto and Kinki: for all 7 Ainu were closer to Kanto than to Kinki.

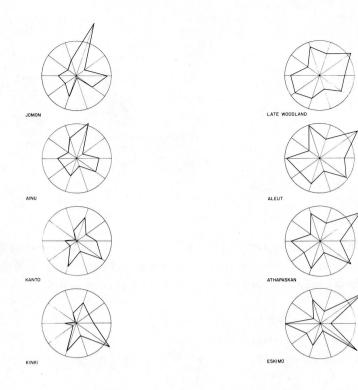


Fig.2. Ten-trait polygons for 4 cranial series from Japan and 4 from North America show gradients with respect to morphological pattern within each region. The percentage incidence of each trait was transformed to an angular value and plotted on the radius of a circle with 0% at its centre and radius representing 50%. Traits are listed in order from one o'clock :

To.		
Ja	pan	

- os Japonicum (trace)
- 2 marginal foramen, tympanic plate
- 3 pharyngeal fossa

1

- 4 supraorbital foramen
- 5 trochlear spur
- 6 postcondylar canal absent
- 7 mylohyoid bridge
- 8 pterygobasal bridge
- 9 odonto-occipital articulation
- 10 hypoglossal canal bridge

North America

- 1 supraorbrital foramen
- 2 mylohvoid bridge
- 3 wormian bones
- 4 pharyngeal fossa
- 5 frontal grooves
- 6 marginal formen tympanic plate
- 7 infraorbital suture
- 8 lateral pterygoid plate foramen
- 9 tympanic dehiscence
- 10 clinoid bridge

Thus, individual features as well as ranked MMDs followed a southwest to northeast gradient in the recent populations of Honshu and Hokkaido. Other researchers have demonstrated similar clines in the distribution of various morphological and genetic characters of Japan's recent population (Dodo, 1975; Yamaguchi, 1980, 1982; Hanihara, Kouchi and Koizumi, 1982; Omoto, 1990). And, although the pattern becomes more complex when secular as well as geographical differnces are analyzed (e. g. Kouchi, 1986; Mizoguchi, 1986), skeletal remains suggest that southwest-northeast clines have considerable time-depth. Cultural elements also show east-west differences (Hanihara, 1990). The clinal pattern manifest in the main part of the Archipelago does not, however, extend to its southernmost tip. Here, Ryukyuans have physical features relating them more closely to Ainu at the northern fringe than to Wajin Japanese in the intermediate regions.

While these patterns can be variously interpreted (reviewed by Hanihara, 1986; Mizoguchi, 1986), the reconstruction which many now favour is that they reflect ancient demic diffusion commencing with Yayoi era at about 300 B.C. when an immigrant population from continental Asia entered the Archipelago in north Kyushu and expanded eastward, assimilating the aboriginal inhabitants. In southwestern Japan, close to the point of entry, not only were the climate and terrain hospitable to the technology of rice agriculture introduced by the immigrants, but coincidentally, the indigenous population was lower than that in the northeast because of a less productive hunting-gathering economy (Aikens and Akazawa, 1986). Here, then, the genetic contribution of the newcomers to the resulting descendent population was greatest. It diminished to the northeast where Ainu preserved the major genetic heritage from Jomon.

With respect to relationships beyond Japan: Jomon, unadmixed Ainu and Okinawans have close affinities with Southeast Asians, Micronesians and Polynesians according to their shared dental pattern called "Sundadonty"; while recent Japanese appear to have ancestral roots in Northeast Asia according to their dental pattern. "Sinodonty" which they share with Chinese, Mongols, Native Siberians and all Native Americans (Turner, 1976, 1985, 1989). Other categories of physical anthropological data appear to cluster Mongoloid populations according to that dichotomy, though some ambiguities have been noted.

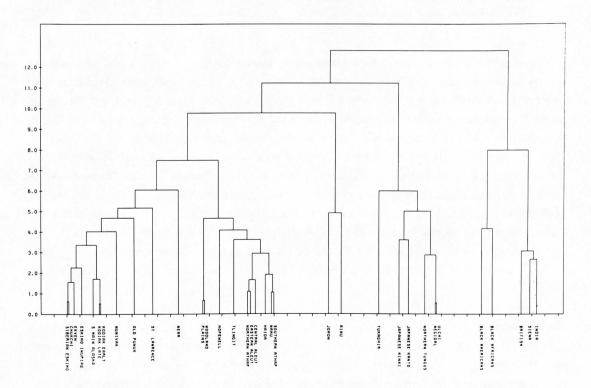


Fig.3. Dendrograph depicting relationships among cranial series from Eurasia, Japan, Siberia and North America based on MMDs for 25 cranial traits. Note that Ainu-Jomon join Americans and Arctic Siberians (Ekven, Chukchi and Eskimos) before Japanese-Tungus do.

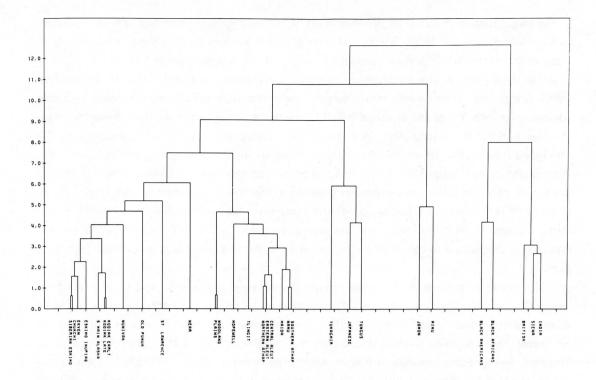


Fig.4. Dendrograph of relationships among the same series as in Fig.3. For this analysis three Tungus series were aggregated, as were Kanto and Kinki Japanese. With this change, the position of Tungus-Japanese and Ainu-Jomon in relation to Americans is reversed from that in Fig.3.

In my dendrographs, Ainu-Jomon consistently linked together; while Kinki and Kanto, closely linked, formed with Tungus and Yukaghir another distinct subcluster. However, the order with which those two subclusters joined Chukotkans and Native Americans was quite unstable depending on which samples were included and how they were aggregated. In Fig. 3 Ainu-Jomon join the large cluster containing Americans and Arctic Siberians first, before Japanese-Tungus do. However, in Fig. 4, which differs from the previous analysis only in that the two Japanese samples were aggregated as were the three Tungus samples, Japanese-Tungus join the Americans before Ainu-Jomon do. Whatever the vagaries of the Ainu-Jomon position among the Mongoloids according to these cluster analyses, it was nevertheless intuitively satisfying to find that in all cases Ainu-Jomon affiliated with the Northeast Asians and Americans rather than with the Blacks or Eurasians (upper clusters in Figs. 3, 4). This finding concurred with most current research concerning the major racial classification of Ainu.

North America

From the American side there was near, though not perfect, unanimity among the 39 samples with respect to their ranking of affinities with Northeast Asians. Mean MMDs of 8 American aggregates – Inupiaq Eskimo, Yupik Eskimo, Athapaskans, Eastern Aleut, Central Aleut, Na-Dene (Haida and Tlingit), Late Woodland and Plains – ranked Asian samples as follows:

Chukotkans	.0646
(Siberian Eskimo a	nd Chukchi)
Japanese	.1165
Tungus	.1348
Ainu	.1571
Jomn	.2294

These findings indicated that Americans, at least these particular groups, were derived from an Arctic Mongoloid rather than from the Classic Mongoloid stock ancestral to Tungus and Japanese. And, in keeping with the archaeological record (Chard, 1974) and dental morphology (Turner) the nonmetric cranial traits thus far indicated that Neolithic Japan exerted little or no influence on the New World.

In the fundamentally Sinodont New World, congruities in the distribution of genetic and cultural traits are interpreted to reflect three founding migrations from Northeast Asia in late Pleistocene times. The earliest (Paleo-Indian) gave rise to all South and Central Amerinds, and all North American except those in the third migration; the second brought Aleuts and Eskimos; the most recent was ancestral to Indians of the Alaskan interior (Athapaskans) and North Pacific Coast (people of Na-Dene and possibly other language families) (Turner, 1983, 1985; Greenberg, Turner and Zegura, 1986).

The 39 Amerind samples in my study represented descendents of the two most recent migrations postulated by Turner and colleagues. These samples did, indeed, distribute themselves consistently in two clusters in the dendrographs. But in disagreement with the prevailing view of their biological kinship, and totally at odds with their linguistic affiliation, Aleut joined Athapaskans, North Pacific Coast and Plains Indians rather than Eskimos (Figs. 3, 4). In fact, the Aleut-Athapaskan MMD (0.0141) suggested an even closer relationship than that between the two main Eskimo language groups (Yupik-Inupiaq 0.0373). For comparison with Japan, recall the Kanto-Kinki MMD (0. 0361). This finding was reinforced by MMDs based on a subset of traits most powerful for discriminating between Eskimos and Indians. Further, in *univariate* comparisons based on 10 of those traits, Aleut were closer to Athapaskan frequencies fell intermediate between Eskimo and Aleut, a pattern reminiscent of the Kinki-Kanto-Ainu trait frequency clines.

Because Arctic Siberians from Chukotka, among the Asian populations represented in my study, proved to be the people most closely related to Amerinds, the rank order of Chukotkan-Amerind MMDs was of particular interest. These followed a north-south gradient, with closest affinity to Eskimo, then decreasing in order: Athapaskans, Kodiak Island, Aleut, North Pacific Coast and Plains.

Interpreting these data with support from craniometrics, and archaeology (references in Ossenberg, 1989, 1990) I offered the following reconstruction. The two clusters represent two migrations, of which the earlier at about 12,000 B.C., which I have named "Paleoarctic Amerind", gave rise to Aleut and Indians of the greater Northwest. The most recent one, "Neoarctic Amerind", gave rise to Eskimo. The north-south gradient of affinities seen in the ranked MMDs was the product of demic diffusion beginning at about 1,000 B.C. during Nor-

ton times, but associated most strongly with the Thule expansion at about A.D. 1,000. The genetic impact of the Neoarctic expansion was strongest close to the Bering Strait entry point and eastward along the sparsely inhabited Arctic Coast (Inupiaq). As the newcomers moved south along the more densely populated Bering Sea Coast, Neoarctic-Paleoarctic hybridization would have occurred. The cultural parallel is the fusion in Norton of Neolithic ideas from Asia with elements from the North Pacific, where sea-mammal hunting had a long established tradition. Athapaskans of the subarctic interior also may have been influenced to some extent by Neoarctic gene flow. Aleut, however, enclaved in their island domain were isolated from Neoarctic gene flow and, up until Russian contact, represented a relict Paleoarctic population much as Ainu at the northeast margin of the Japan Archipelago represented a relict descendent of Jomon.

MMDs for Japan followed a gradient: Tungus-Kinki-Kanto-Ainu-Jomon. Data in Table 1 provide a parallel for western North America. Just as Tungus represented continental Asians of Classic Mongoloid stock possibly closely related to immigrants to Japan during Yayoi age, so ancient Siberians of Old Bering Sea phase were taken to represent Arctic Mongoloids possibly closely related to the population from which my hypothetical Neoarctic Amerind migration derived. In neither case, at this time, is the ancestral homeland of the immigrant group precisely known. There were no skeletal remains from Arctic-Subarctic North America sufficiently widespread and of an early enough time level (10,000-500 B.C.) to represent an indigenous population (my putative Paleoarctic Amerinds) analagous to Jomon. I chose instead the Late Woodland aggregate, 500B.C. - A.D.1,700, from the northeastern Plains' periphery, in mind both of its close relationship to Aleut according to nonmetric traits, as well as of older theories connecting Aleut and Plains Indians through a common ancestor.

MMDs and r_s values for Arctic Siberians showed the following ranking with the 4 American samples:

Old Bering Sea MM	$AD r_s$	
Eskimos	.0137	.956
Athapaskans	.0498	.528
Aleut	.0802	.465
Late Woodland	.1415	.314

On the other hand Late Woodland showed exactly the reverse order:

Late Woodland MM	MD r _s	
Aleut	.0383	.781
Athapaskans	.0413	.721
Eskimos	.1083	.318
Old Bering Sea	.1415	.314

Note that Aleut were consistently intermediate between Late Woodland and Athapaskans, similar to Ainu's position relative to Jomon and Kanto. Athapaskans were in all MMD and r_s comparisons intermediate between Aleut and Eskimo, reminiscent of Kanto's position relative

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to Ainu and Kinki. As in Japan, groups closely related to each other according to small MMD also tended to have strongly correlated rankings of MMDs versus other populations; for example, Aleut-Athapaskan MMD 0.0141, r_s 0.928. Parallel patterns between Japan and America in terms of positive linear relationship between MMD and r_s are shown in Fig. 1.

Fig. 2 has ten-trait polygons for four American cranial series which are seen, as those for Japan, to metamorphose from one shape to the next. There are two important characteristics however in which the Japanese polygons contrast with the American ones (aside from the two different 10-trait batteries used to create them). These characteristics reflect the population history unique to each region. First, the difference between Jomon and Kinki polygons is much more dramatic than the one between Late Woodland and Eskimo, because of the greater racial difference between the Proto-Mongoloid indigenous population and Classic Mongoloid immigrants to Japan than between the analagous founding groups in northwestern North America; both the latter were inferred to have been essentially of Arctic Mongoloid stock. Secondly, of the Japanese ploygons it is Jomon which stands out as most distinctive, whereas of the American ones it is Eskimo. This reflects the high immigrant/indigenous ratio in the genetic makeup of Japan's modern population, in contrast to the relatively small, because territorially restricted, impact of Neoarctic Amerind genes on the overall population of northwestern North America. These differences are apparent as well in Table 1 and Fig. 1.

Discussion and Conclusions

The population history of Japan, neatly circumscribed and increasingly well researched, is providing valuable models applicable to more general problems of Circum-Pacific dispersals. Demic diffusion in Japan provided the model for a parallel population structure hypothesized in northwestern North America. Because the range of MMDs providing the evidence of genetic mixture in America was relatively small, without Japan's well-defined precedent, the American evidence easily could have escaped notice.

Elsewhere I have reported significant rank correlation $(r_s = 0.69, 0.01 > p)$ between cranial MMDs and Turner's dental MMDs for eight samples common to both data sets (Ossenberg, 1990). Since each category of trait presumably samples a large, and to a major extent different, portion of the genome, this finding underscores the enormous potential of bones and teeth for historical research. Their value is enhanced significantly by the fact that certain questions can never be answered by genetic polymorphisms in the tissues of living populations, no matter how certain the mode of inheritance, numerous the data, nor sophisticated the techniques for collecting and analyzing them.

As are minor morphological features of the teeth, so those of the bony skull appear to be remarkably stable in the face of dramatic shifts in ecozone and subsistence economy. Relatively resistant to environmental pressures, either through plasticity or selection, the traits and biological distance measures derived from them may provide a reliable record of historical relationships.

Some maintain that Japanese were directly descended from Jomon with little or no immigrant genetic contribution, and that the morphological differences between the Neolithic and modern population developed gradually because of changes in diet and cluture. This might be plausible if no comparative data from outside Japan were available, However, data from continental Asia now show Japanese more like Tungus than like Ainu or Jomon. What parallel selective forces could have produced morphological convergence between modern Japanese and hunting-gathering peoples of the Siberian taiga? Similarly, in America, differences between Eskimos and Aleuts are attributed to thousands of years of isolate divergence in the unique and richly productive Aleutian biotic province. If so, why aren't Aleuts even *more* distinct from the Apache and Navajo of the desert Southwest than from Eskimo? These questions, incidentally, point to yet another historical parallel between Japanese and America. In both regions it appears that deference to outmoded dogma has impeded consideration of new and better evidence concerning ethnohistorical relationships.

In this study, gradients of MMDs in both regions were interpreted to result from gene flow between two distinct founding groups. In the case of maritime-adapted Arctic populations migration and gene flow always have been configured by the coasts in a linear fashion. It seems likely that in the islands of Japan also, because of their mountainous interior, people and ideas would have moved along the coasts. Highly relevant here is a paper by Cavalli-Sforza (1986) on population structure theory. He notes simulations demonstrating that linear gradients of gene frequency generated by demic expansion are remarkably stable and not easily dissolved by subsequent gene flow between neighbours.

In general, the nonmetric traits are thought to be controlled by multiple genes with additive effects, though in no case has the precise mode of inheritance been established. One could not predict that hybridization would necessarily result in frequencies of individual traits intermediate between those of the parent groups; for example, only a small proportion of traits placed Brazilian mulattos intermediate between Blacks and Whites of the same region (Wijsman and Neves, 1986). Explanations for the discordant effects could be dominance, threshold or environmental effects (Saunders, 1989). Surprisingly, in my study frequencies of the traits most powerful for Jomon-Japanese and Indian-Eskimo discrimination did, in fact, follow the same clines as the MMDs. In terms of the theory and methodology pertaining to nonmetric variation, this may be one of the most important findings of the study.

The parallel drawn here was a general one. It was based on incomplete data and portrays an oversimplified scenario for both regions. I have essayed it in the hope that it may highlight the unique potential of skeletal morphology for historical research.

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日本人および北アメリカ先住民における平行 小進化:頭骨の非計測的形質の研究

N. S. Ossenberg

集団の形成史は単純なヒトの移動というより、ある地域の在来の集団が、高度な文化と異な る遺伝的構成をもつ新移住者の中に巻き込まれてしまうという複雑な過程をたどることが多 い。この研究では頭骨に出現する非計測的形質に基づいて日本と北アメリカ北西部の集団を比 較した結果、在来集団と移住集団との関係が日本と北アメリカで相互に類似していることが明 らかにされた。

研究者の中には、食物や文化の変化によって縄文人が徐々に現代日本人に変わってきたので あって、移住者(渡来人)の影響はほとんど、または全くないと考えている人がいる。もし日 本以外のデータが得られないのなら、この考え方にも一理はある。しかし現在は多くのアジア 大陸のデータを使うことが可能で、それらは日本人がアイヌや縄文人よりもツングース系集団 に近いことを示している。また平均型差指数(MMD)によって比較すると、アイヌー関東日 本人-近畿日本人の順にみられる勾配はアリュートーアタパスカン・インディアンーエスキ モーのそれとほとんど一致しており、日本と北アメリカにおける在来集団と移住集団との関係 がよく似ていることが注目される。

(Summarized and translated by K. Hanihara)