Ethnogenesis and craniofacial change in Japan from the perspective of nonmetric traits

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Abstract
To examine population affinities in light of the ‘dual structure model’, frequencies of 21 nonmetric cranial traits were analyzed in 17 prehistoric to recent samples from Japan and five from continental northeast Asia. Eight bivariate plots, each representing a different bone or region of the skull, as well as cluster analysis of 21-trait mean measures of divergence using multidimensional scaling and additive tree techniques, revealed good discrimination between the Jomon-Ainu indigenous lineage and that of the immigrants who arrived from continental Asia after 300 BC. In Hokkaido, in agreement with historical records, Ainu villages of Hidaka province were least, and those close to the Japan Sea coast were most, hybridized with Wajin. In the central islands, clines were identified among Wajin skeletal samples whereby those from Kyushu most resembled continental northeast Asians, while those from the northernmost prefectures of Tohoku apparently retained the strongest indigenous heritage. In the more southerly prefectures of Tohoku, stronger traces of Jomon ancestry prevailed in the cohort born during the latest Edo period than in the one born after 1870. Thus, it seems that increased inter-regional mobility and gene flow following the Meiji Restoration initiated the most recent episode in the long process of demic diffusion that has helped to shape craniofacial change in Japan.

Key words: ethnogenesis in Japan, Tohoku, Ainu, cranial nonmetric traits

Introduction
The hybridization model of Japanese population history now widely accepted was proposed almost eight decades ago by Kiyono (1926, cited by Yamaguchi, 1982) and subsequently revitalized by the research of Yamaguchi (1982) and his students. With additional supporting data and a detailed outline, it is now known as the ‘dual structure model’ (Hanihara, 1991). According to this model, Japan’s people today embody two ancestral lineages. First came the Jomon: the Neolithic foraging, hunting, and fishing groups who inhabited the archipelago from about 10,000 BC. The second lineage is that of the Yayoi, who arrived from continental northeast Asia around 300 BC, bringing rice agriculture and metal-working technologies, along with a different language and culture. Derived from widely divergent branches of the great Mongoloid racial tree, these two ancestral populations have contributed profoundly and indelibly to the unique cultural and genetic characteristics of the Japanese.

The Yayoi people established the first immigrant communities close to their ports of entry in the region of northern Kyushu and westernmost Honshu. Here, not only were the climate and terrain hospitable to rice paddy agriculture but also, coincidentally, the indigenous population was sparser than in the northeast where the ecosystem was more productive for hunting and foraging. The precise nature of prehistoric contact with the native people has yet to be determined. In any case, contact between the two groups was inevitable as the successive generations descended from continental immigrants expanded northeastward along the archipelago.

During the subsequent Kofun period, 300–700 AD, the population in western and central Japan grew. Reinforced by new immigrants and influences from the Asian continent, these communities became increasingly integrated by a social and political system centered on the imperial court in the Kinki district. By the early 8th century under a policy enacted by the imperial court, Wajin influence had spread northeast to the Kanto and neighboring regions. However, during the proto-historic Kofun and early historic periods, Hokkaido and the Tohoku region of Honshu were still the territory of the so-called Ezo, Emishi or ‘barbarians’ (Hanihara, 1990); i.e. the non-Wajin descendents of the Jomon who were still following a lifestyle based on hunting, fishing, and foraging. Eventually, by stages, these territories too were subjugated and colonized.

Studies of skeletal remains have documented large differences between the two founding groups in stature, limb bone proportions, and morphological features of the skull and teeth. Regional variations, in a somewhat mosaic pattern
with respect to degree of similarity to one or the other founding group, were manifest during the Yayoi period. Subsequently, the population of Japan seems to have become increasingly homogeneous over time. In particular, nonmetric cranial studies (Dodo and Ishida, 1990; Dodo et al., 1992) emphasize the contrast between the regional and temporal homogeneity over the past 2000 years among populations of the central islands of Japan, and the highly significant differences between the latter and the Jomon. Nevertheless, regional variations among populations of the central islands are recognizable throughout all post-Jomon periods, and persist even to the present day with respect to genetic polymorphisms in the blood and other characteristics.

Significantly, these traits appear to vary regionally in a clinal pattern similar to those shown in other parts of the world to have been generated by differential gene flow due to demic diffusion (Weiss, 1988), occurring when an immigrant people expands into an already occupied territory. In the case of Japan, a gradient of affinities would have resulted from differential gene flow as descendants of the immigrant population, the Wajin Japanese, expanded from western Japan northeastward along the archipelago, assimilating or, perhaps in some cases being assimilated by, the aboriginal inhabitants. The genetic contribution from continental Asian ancestors is strongest in people of northern Kyushu and western Honshu and diminishes to the northeast, so that among the present-day people of Japan it is the Ainu of Hokkaido who preserve the strongest genetic heritage from the Jomon.

Clines generated by ancient demic expansion are demonstrated to be remarkably stable (Cavalli-Sforza, 1986). The dual structure model also assumes that the dual ancestry of the Japanese people is evident even today, and that intermixing is still going on.

In view of the history of events related to the expansion of Wajin influence, we expected that the most northerly regions of Japan would reveal particularly strong evidence in support of the dual structure model. Therefore, this investigation focused on Tohoku and Hokkaido with the primary objective of determining whether or not the pattern of temporal and regional population affinities within northern Japan revealed by nonmetric cranial traits fits the model. Secondly, we aimed to examine the data for evidence of a southwest to northeast gradient of affinities as predicted by the model. Thirdly, within a broader comparative framework, we hoped to corroborate the findings of other studies concerning relationships of Japan’s two ancestral lineages to other northeast Asians.

**Materials**

**Japan**

Jomon samples were derived from many sites throughout the central islands of the archipelago as well as Hokkaido. These are middle to final Jomon period sites with dates ranging from about 3500 BC to 300 BC. Epi-Jomon sites in Hokkaido are later, roughly contemporaneous with Yayoi and Kofun periods, 300 BC to 700 AD. For this study the sites were aggregated regionally. Those located in the western portion of the main islands (present-day Kyushu, Shikoku, Chugoku and Kinki districts) provided the West Jomon skeletal sample \( n = 102 \) individuals. The Central Jomon sample \( n = 69 \) is from sites in present-day Tokai and Kanto districts, while North Jomon \( n = 60 \) sample derives from Tohoku district. The other two samples are Hokkaido Jomon \( n = 34 \) and Epi-Jomon \( n = 25 \). Jomon remains are curated at several institutions. Those reported here were studied in the Department of Anatomy, Sapporo Medical University; Department of Anatomy and Anthropology, Tohoku University School of Medicine; The University Museum, The University of Tokyo; National Science Museum, Tokyo; and the Laboratory of Physical Anthropology, Faculty of Science, Kyoto University.

Ainu skeletons examined for this study were those excavated by Koganei (1893, 1894) from Edo period cemeteries associated with abandoned villages throughout Hokkaido. The series was studied at The University Museum, The University of Tokyo. Most investigators have used this series as a single sample to represent relatively pure Ainu, i.e. minimally affected by Wajin admixture. Here, however, because of our focus on northern Japan and in light of historical documents (Kodama, 1970) we partitioned the Koganei series three ways: Southeast Ainu (Hidaka and Tokachi provinces: \( n = 36 \)), Northeast Ainu (Kushiro, Nemuro, Abashiri and Soya provinces as well as Kunashiri Island: \( n = 50 \)), and West Ainu (Rumoi, Ishikari, and Shirebeshi provinces: \( n = 31 \)).

Wajin Japanese samples used in this study were defined both regionally and temporally. The boundaries of West, Central, and North regions are identical to those as defined above for the Jomon. However, because of our focus on northern Japan we wanted a more fine-grained analysis of Tohoku than that attempted in previous investigations. Accordingly, Tohoku was partitioned into South (Fukushima, Yamagata, and Miyagi prefectures) and North (Akita, Iwate, and Aomori).

From about 1880 and until about 1960 universities in Japan assembled (as did those in Europe and North America) collections of skeletons from the dissecting-room subjects used to teach medical students. When carefully prepared and curated along with records giving for each individual the place and date of birth as well as date and cause of death, these collections are a priceless resource for many kinds of clinical and basic osteological research. In general, anthropological research uses such dissecting-room series to represent simply ‘modern’ or ‘recent’ Japanese. However, considering that with the increased mobility of the population following the Meiji Restoration in 1868 microevolutionary change is ongoing in Japan even today, and that during all periods Tohoku was impacted by Wajin gene flow later than were other regions of the central islands, we deemed it worthwhile to separate the Tohoku University dissecting-room series into two cohorts according to birth date. Accordingly, the South Tohoku Edo sample \( n = 79 \) represented individuals with birth dates between 1820 and 1870, i.e. towards the very end of the Edo period. The South Tohoku Recent sample \( n = 73 \) comprised those born 1871 or after, i.e. at least three years after the beginning of the Meiji Restoration. Most of these persons were born in Miy-
agii prefecture.

The North Tohoku Edo sample (n = 42), curated in the Department of Anatomy and Anthropology at the Tohoku University School of Medicine, was comprised of skeletons excavated from Edo period graves at various sites in the three northern prefectures. Birth dates of these individuals are unrecorded, but would perhaps fall in the range 1700–1800 AD, i.e. several generations earlier than the very-late-Edo dissecting-room subjects.

Central Wajin: The Medieval period sample (n = 70) was from two 14th-century sites in the present-day city of Kamakura believed to represent the mass burials of warriors killed in battle. The Kamakura sample is predominantly young adults, 44 men and 26 women, and is curated at The University Museum, The University of Tokyo. The Central Edo sample (n = 117) is comprised mainly of crania from the Joshinji Cemetery dating from approximately 1650 to 1850 AD (Mizoguchi, 1997), and is curated at the National Science Museum. The dissecting-room series of skeletons at Chiba University was partitioned according to recorded date of birth in the same way as for Tohoku, and data for the very-late-Edo cohort of 29 individuals were combined with those for the Joshinji Cemetery. The Central Recent sample (n = 88) was comprised of dissecting-room subjects born after 1870.

West Wajin: These three samples were studied at the museum of the Faculty of Medicine, Kyushu University. The Yayoi sample (n = 31), dating from about 100 AD, was derived mainly from the Doi-gahama site in westernmost Honshu, but with a few crania also from the northern Kyushu Kanenokuma site. The West Edo sample (n = 45) was retrieved from the 18th-century Tenpukuji cemetery. The West Recent sample (n = 58) of dissecting-room skeletons was not partitioned by birth cohort and so encompasses a slightly greater temporal depth than do the other two recent period samples.

Continental northeast Asia

Included in our study were five samples representing continental northeast Asians. Mongols (n = 40) from Urga (Ulaanbaatar) were studied at the United States National Museum. Chinese (n = 72) from northeastern China (formerly Manchuria) are curated at The University Museum, The University of Tokyo. The Tungus, a sample comprised of individuals from the Ulchi, Negidal, and Evenki tribes (n = 83) and the Chukchi (n = 44) were studied at the Institute of Ethnography of St Petersburg. These four series are from the 17th century or later. An Okhotsk sample (n = 36), representing a prehistoric sea-mammal hunting people whose origins lay perhaps in the Amur region but who lived for a time on the north coast of Hokkaido (Ishida, 1996), were studied at the Department of Anatomy, Sapporo Medical College.

Methods

Cranial nonmetric traits


The present investigation was based on a battery of traits developed by the senior author over 40 years of research focused mainly on the peopling of northwestern North America. This trait-list differs from those used by Japanese workers; for example, of 23 features routinely scored by Ishida and Dodo (1992, Table 1) only nine are common to both trait-lists. Note that Ossenberg does not collect data for four of the 10 traits shown by Dodo and Ishida (1990) to be most highly discriminatory between the Jomon-Ainu and Wajin lineages: ossicle at lambda, biasterionic suture trace, foramen of Vesalius, and medial palatine canal. On the other hand, her battery includes a number of informative features not routinely scored by other osteologists. Therefore, it was hoped that the findings reported here would complement the many previous studies of ethnogenesis in Japan based on this category of morphological evidence. With exceptions noted in footnotes to Table 1, all observations were made by N.S.O. during the period September 2001–March 2002.

Table 1 lists the 21 features according to eight regions of the skull, and gives their frequencies in 22 cranial samples as well as in Jomon, Ainu, and Wajin aggregated samples. Data for adults of both sexes were pooled and for certain features juvenile data also were included. Descriptions of the features and criteria for selecting and scoring them have been documented in earlier reports (Ossenberg, 1970, 1976, 1994, 2004); however, brief explanatory notes concerning certain features may be useful here.

Occipito-mastoid bone ratio is the number of sides (left plus right) with a supernumerary ossicle in the occipito-mastoid suture divided by the total of: the number of sides with an occipito-mastoid bone, plus the number of sides with an asterionic bone, plus the number of sides with a parietal notch bone.

Of the three variants involving facial sutures, transversozygomatic suture trace is the most familiar, long recognized as one of the most powerful traits for circum-Pacific population studies. Note that frequencies in Table 1 are higher and show greater dispersion than those of Dodo and Ishida because N.S.O. counts as ‘trait present’ any discernible trace, whereas her colleagues count only cases 5 mm or more in length. Infraorbital suture variant (Figure 2) and orbital suture variant are described by Kozintsev (1992b) as two of the five traits he has found most valuable for ethnogenetic research on a world-wide scale. In the dissecting-room series the number of observations of the former variant were limited by age-regressive obliteration of the infraorbital
Analytic methods

For each of eight skull regions a bivariate plot was constructed in order to examine the consistency among the different traits and skull regions with respect to pattern of population relationships. The value plotted for each trait was not the raw frequency but rather the arcsine value, \( \theta \), an angular transformation which serves to stabilize the variance of the frequencies. As defined in the modified formula for Smith's mean measure of divergence (MMD) statistic (Sjøvold, 1977), \( \theta \) theoretically (i.e. in very large samples) varies from 1.5 (zero frequency) to −1.5 (100%), but in practice falls short of these extremes owing to a factor correcting for sample size.

Multivariate biological distances between samples were assessed by the MMD statistic, which is essentially a mean sum of squares, over all traits, of the \( \theta \) differences between two samples. An MMD is regarded as larger than zero at the \( \theta \) scale for each trait was tailored to its own range. However, in contrast to Mahalanobis' \( D \) employed as a distance statistic in craniometric analysis, which equalizes the range of a large feature such as maximum cranial breadth and a small feature such as nasal breadth in terms of its contribution to \( D \), MMD does not equalize the effective range from one trait to another. This might be seen as a weakness or a strength of MMD according to one's theoretical position as to how features should be weighted taxonomically. Another difference between D and MMD is that the latter incorporates no correction factor for sample size.

Table 1. Side incidence of nonmetric traits in 22 cranial series from Japan and continental northeast Asia

<table>
<thead>
<tr>
<th>Jomon</th>
<th>Ainu</th>
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<tbody>
<tr>
<td></td>
<td>West</td>
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<tr>
<td></td>
<td>n</td>
</tr>
<tr>
<td>Sutural bones</td>
<td></td>
</tr>
<tr>
<td>Occipito-mastoid bone</td>
<td>125</td>
</tr>
<tr>
<td>Occipito-mastoid bone ratio</td>
<td>117</td>
</tr>
<tr>
<td>Facial sutures</td>
<td></td>
</tr>
<tr>
<td>Transverso-zygomatic suture trace</td>
<td>141</td>
</tr>
<tr>
<td>Infraorbital suture variant</td>
<td>27</td>
</tr>
<tr>
<td>Orbital suture variant</td>
<td>5</td>
</tr>
<tr>
<td>Frontal bone</td>
<td></td>
</tr>
<tr>
<td>Supraorbital foramen</td>
<td>165</td>
</tr>
<tr>
<td>Frontal grooves</td>
<td>155</td>
</tr>
<tr>
<td>Troclear spur</td>
<td>126</td>
</tr>
<tr>
<td>Occipital bone</td>
<td></td>
</tr>
<tr>
<td>Postcondylar canal absent</td>
<td>102</td>
</tr>
<tr>
<td>Lateral condylar canal</td>
<td>60</td>
</tr>
<tr>
<td>Hypoglossal canal bridged</td>
<td>142</td>
</tr>
<tr>
<td>Pharyngeal fossa</td>
<td>68</td>
</tr>
<tr>
<td>Temporal bone</td>
<td></td>
</tr>
<tr>
<td>Marginal foramen of tympanic plate</td>
<td>139</td>
</tr>
<tr>
<td>Tympanic dehiscence</td>
<td>178</td>
</tr>
<tr>
<td>Sphenoid bone</td>
<td></td>
</tr>
<tr>
<td>Pterygobasal spur or bridge</td>
<td>142</td>
</tr>
<tr>
<td>Claidoid bridge</td>
<td>69</td>
</tr>
<tr>
<td>Accessory optic canal</td>
<td>62</td>
</tr>
<tr>
<td>Mandible</td>
<td></td>
</tr>
<tr>
<td>Accessory mental foramen</td>
<td>177</td>
</tr>
<tr>
<td>Mylohyoid bridge</td>
<td>164</td>
</tr>
<tr>
<td>Teeth</td>
<td></td>
</tr>
<tr>
<td>Upper third molar suppressed</td>
<td>112</td>
</tr>
<tr>
<td>Three-rooted lower first molar</td>
<td>153</td>
</tr>
</tbody>
</table>

All observations were recorded by the senior author in 2001 and 2002 except as indicated in the following footnotes:

* Data recorded for the Tsukumo site in 1981 were combined with those from the 2001/2 survey.

suture; while in archaeologically retrieved remains, especially Jomon, few observations of the orbital suture variant were possible owing to post-mortem damage to the fragile orbital walls.

Figures for supraorbital foramen in Table 1 are frequencies weighted by counting twice a left or right side with two or more foramina, and hence tend to be higher and show greater dispersion than those reported by other workers.

Although not customary in cranial nonmetric studies, the list includes two relatively easy-to-score dental variants: upper third molar suppressed and three-rooted lower first molar. These are among the key features of the Sinodont dental complex (Turner, 1990).
intertrait correlation. However, with the exception of supernumerary ossicle traits (wormian bones in various vault sutures), intertrait correlation among nonmetric traits is generally shown to be either absent or so low as to have little effect on the MMDs (Saunders, 1989).

The triangular matrix containing MMDs for all pairwise population comparisons was analyzed by two different clustering techniques in order to produce two-dimensional arrays of the samples. The clustering programs cannot handle negative numbers, so to prepare the data for entry into the multidimensional scaling program ALSCAL (SPSS for Windows, version 7.0), negative MMD values were eliminated by raising all the MMDs by the amount of the largest negative value in the matrix. For analysis with the program ADDITIVE TREE (SYSTAT for Windows, version 7.0, SPSS), all negative MMDs were simply converted to zero.

Results

Bivariate plots

The bivariate plots are shown in Figure 1 and Figure 2. Table 2 is the triangular matrix of MMDs, and Figure 5, Figure 6, Figure 7 and Figure 8 are the cluster diagrams based on those MMDs.

The sutural bones plot (Figure 1a) show fairly good separation of Jomon from Wajin owing to the lower frequencies of occipito-mastoid bone in the latter. Ainu tend to be intermediate. Regional variation among Jomon seems to be as great as among historic period Japanese. In the central region of the plot there is considerable overlap involving Epi-Jomon, West Ainu and Central Edo, with North Tohoku Edo also close to this region. Yayoi seems misplaced, sitting conspicuously in the middle of the Jomon cluster.

The facial sutures (Figure 1b, Figure 3) give excellent separation of Jomon from Wajin, with Ainu clearly intermediate. Among the Ainu the Southeast group is closest to Jomon, while West Ainu is closest to the Wajin cluster. Again, as with the sutural bones the Wajin samples closest to the Jomon-Ainu lineage are those from the Tohoku region, especially North Tohoku Edo. A striking feature in this diagram is the small cluster of the three Recent Wajin samples within the larger one containing all Wajin.

The temporal bone plots (Figure 1c, Figure 4) provide excellent separation between Jomon and Wajin, with Ainu clearly intermediate and not overlapping. The dispersion of samples within each cluster is considerable. In these respects the plots in Figure 1a, Figure 1b and Figure 1c are consistent. However, closer inspection shows that each pair of traits produces a somewhat different arrangement of samples within the clusters; for example, the facial sutures place Southeast Ainu...
seems to provide, at least in this analysis, no coherent picture of population affinities in Japan.

The occipital bone diagram (Figure 2a) overlays for Jomon and Ainu, but separates the Jomon-Ainu lineage fairly well from the Wajin. The three Recent Wajin samples form a cluster within the larger one encompassing Wajin of all time periods. In Japan, postcondylar canal absent appears to be a better discriminator than pharyngeal fossa.

The configuration of samples produced by the sphenoid bone (Figure 2b) looks peculiar. This is mainly because accessory optic canal with frequency ranging from 0 to 8% is such a rare trait. In seven of the 17 samples (Table 1) not one individual exhibited this anomaly. If these samples (Yayoi, Kamakura, Southeast Ainu, and four Jomon) had been very large, yet still produced no case of this trait, then all seven would have been located at $\theta=1.5$ (0%) at the origin of the $\gamma$-axis. The actual dispersion of these samples along the $\gamma$-axis simply reflects the correction for sample size in the calculation of $\theta$ (Sjøvold, 1977). Another peculiarity is the placement of Southeast Ainu in the lower right corner of the diagram, apart from all the other samples, because of its zero frequency of the former trait together with its large range, 3–53%.

Table 1. (continued)

<table>
<thead>
<tr>
<th></th>
<th>Japan: aggregated samples</th>
<th>Northeast Asia</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Jomon</td>
<td>Ainu</td>
</tr>
<tr>
<td>Sutural bones</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Occipito-mastoid bone</td>
<td>284 24.3</td>
<td>226 18.1</td>
</tr>
<tr>
<td>Occipito-mastoid bone ratio</td>
<td>298 29.9</td>
<td>117 35.0</td>
</tr>
<tr>
<td>Facial sutures</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Transverso-zygomatic suture trace</td>
<td>322 82.9</td>
<td>192 64.6</td>
</tr>
<tr>
<td>Orbital suture variant</td>
<td>125 3.2</td>
<td>151 19.2</td>
</tr>
<tr>
<td>Frontal bone</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Supraorbital foramen</td>
<td>408 12.5</td>
<td>228 21.5</td>
</tr>
<tr>
<td>Frontal grooves</td>
<td>360 26.4</td>
<td>217 17.1</td>
</tr>
<tr>
<td>Trocleolar spur</td>
<td>329 1.8</td>
<td>228 6.1</td>
</tr>
<tr>
<td>Occipital bone</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Postcondylar canal absent</td>
<td>239 15.5</td>
<td>229 14.4</td>
</tr>
<tr>
<td>Lateral condylar canal</td>
<td>154 18.8</td>
<td>205 30.2</td>
</tr>
<tr>
<td>Hypoglossal canal bridged</td>
<td>342 14.3</td>
<td>232 23.3</td>
</tr>
<tr>
<td>Pharyngeal fossa</td>
<td>170 18.8</td>
<td>116 17.2</td>
</tr>
<tr>
<td>Temporal bone</td>
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<td>Marginal foramen of tympanic plate</td>
<td>371 3.2</td>
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<td>Tympanic dehiscence</td>
<td>442 27.2</td>
<td>227 17.6</td>
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<tr>
<td>Pterygobasal spur or bridge</td>
<td>356 11.2</td>
<td>231 23.8</td>
</tr>
<tr>
<td>Clinoïd bridge</td>
<td>147 7.5</td>
<td>215 10.2</td>
</tr>
<tr>
<td>Accessory optic canal</td>
<td>102 1.0</td>
<td>210 1.9</td>
</tr>
<tr>
<td>Mandible</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Accessory mental foramen</td>
<td>441 17.5</td>
<td>178 15.8</td>
</tr>
<tr>
<td>Mylohyoid bridge</td>
<td>404 14.9</td>
<td>166 9.6</td>
</tr>
<tr>
<td>Teeth</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper third molar suppressed</td>
<td>260 12.7</td>
<td>163 29.5</td>
</tr>
<tr>
<td>Three-rooted lower first molar</td>
<td>386 3.4</td>
<td>143 4.9</td>
</tr>
</tbody>
</table>

All observations were recorded by the senior author in 2001 and 2002 except as indicated in the following footnotes:

- a The Koganei Ainu series was recorded in 1981 (Ossenberg, 1986), and again in 2001/2 for analysis of intra-observer replicability in scoring. The latter data were used. The MMD between the two scoring sessions was 0.0005 (standard deviation 0.003), statistically insignificant.
- c Recorded at the Institute of Ethnography, Leningrad in 1981.
- d These data were recorded by A. Kozintsev and kindly sent by him (pers. comm. 1992) to Ossenberg.
erally having higher frequencies of accessory optic canal and lower frequencies of clinoid bridge than does the indigenous lineage.

The traits of the mandible (Figure 2c) produced yet another configuration which distinguishes Jomon-Ainu from Wajin. Again note the smaller Recent Wajin cluster within the main one. Among the Jomon samples with their generally higher frequencies of both accessory mental foramen and mylohyoid bridge, Hokkaido stands out with its very high frequency of the latter, 34%. This peculiarity has already been noted by Yamano and Yamaguchi (1976).

Both dental traits included in this study are key Sinodont features and thus show, as expected, higher frequencies in Wajin Japanese than in Ainu or Jomon (Figure 2d). Certain patterns seen in previous plots are reiterated here; among the Ainu the Southeast is closest to Jomon, the West closest to Wajin. Among Wajin the Tohoku samples as well as Kamakura are the ones closest to Jomon-Ainu; while the three Recent samples representing west, central and north regions of the main islands of Japan, tend to form a subcluster within the larger Wajin cluster.

Each of the bivariate plots gave its own unique version of population affinities. At the same time, some common themes emerged:
1. All eight skull regions provide good discrimination between the Jomon and Wajin lineages.
2. In four of the diagrams Ainu is clearly intermediate; in four, Ainu overlaps with Jomon.
3. Among Ainu the Southeast group tends to lie closest to Jomon; the West is closest to Wajin.
4. Yayoi tends to be an outlier.
5. Among Wajin the Tohoku samples tend to be closest to Jomon-Ainu; this tendency is strongest in North Tohoku Edo.
6. Among Wajin there is a tendency to increasing regional homogeneity over time, i.e. the three Recent samples form a subcluster within the bigger one containing Wajin from all periods.

Cluster analysis of 21-trait MMDs: Japan

Multidimensional scaling of MMDs for the 17 samples from Japan (Table 2) produced the configuration shown in Figure 5. Each of the six themes hinted at in the bivariate plots is consolidated here. Ainu lie in the center of the plot, clearly separated from Jomon on the left and Wajin on the right, with Southeast Ainu closest to Jomon and West Ainu closest to Wajin. Within the large cluster containing nine samples representing Wajin Japanese from all periods lies the tight subcluster containing Recent West, Central, and Tohoku regional populations. From left to right along the x-axis there is the hint of a regional gradient of affinities among Wajin; the three Tohoku samples are generally the ones closest to the Jomon-Ainu lineage, followed by the Central samples, except that Kamakura seems slightly displaced towards Jomon-Ainu. Furthest to the right are West Edo (Tenpukuji) and Yayoi. Among Wajin, Yayoi seems somewhat aberrant.

The advantage of the additive tree clustering technique is that in joining populations in stepwise fashion it can reveal the intermediate position of a population with respect to others. Therefore it is well suited to examine the data for gradients and for evidence of hybridization. For this additive tree
| 86.6 | 162.5 | 22.5* | 262.1 | 13.6* | 3.5* | 45.4 | 22.4* | -4.4* | -4.4* | -4.4* | 42.0 | 25.8 | 19.0 | 60.1 | 20.6 | 13.6* | 83.1 | 12.7 | 84.1 | 3.2* | 75.6 | 91.2 | 71.3 |
| 22.5* | 162.5 | 72.6 | 262.1 | 9.2* | 3.5* | 57.8 | 41.5 | 24.3 | 3.5 | 4.4 | 13.9 | 15.4 | 16.8 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 78.7 | 262.1 | 69.2 | 262.1 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 70.7 | 297.1 | 51.8 | 297.1 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 87.7 | 276.7 | 114.7 | 276.7 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 111.8 | 377.4 | 114.7 | 377.4 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 101.7 | 214.5 | 182.5 | 214.5 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 179.5 | 214.5 | 182.5 | 214.5 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 181.5 | 214.5 | 182.5 | 214.5 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 188.6 | 214.5 | 182.5 | 214.5 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 206.7 | 214.5 | 182.5 | 214.5 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 182.3 | 214.5 | 182.5 | 214.5 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 266.9 | 214.5 | 182.5 | 214.5 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 275.7 | 214.5 | 182.5 | 214.5 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 180.1 | 214.5 | 182.5 | 214.5 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 83.2 | 214.5 | 182.5 | 214.5 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 185.9 | 214.5 | 182.5 | 214.5 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 257.5 | 334.4 | 282.1 | 334.4 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |
| 257.5 | 334.4 | 282.1 | 334.4 | 24.5 | 15.4* | 69.5 | 41.5 | 24.3 | 3.5 | 4.4 | 15.4 | 15.4 | 22.0 | 24.3 | 1.6 | 16.8 | 45.1 | 3.2* | 13.9 | 91.2 | 75.6 | 71.3 |

* Each MMD is multiplied by 103.
* An asterisk indicates a non-significant value; i.e. less than twice its standard deviation.
analysis (Figure 6) four Jomon samples were aggregated, as were the three Recent Wajin. The Jomon-Ainu lineage forms a cluster distinct from that containing the Wajin Japanese. Within the former there is a clear four-step gradient towards Wajin consistent with the pattern noted in previous diagrams: Jomon, Epi-Jomon, Southeast Ainu, Northeast Ainu, West Ainu. Within the Wajin cluster there is a three-stage gradient of affinities away from Jomon-Ainu: North Tohoku Edo, Kamakura; and five other populations in a subcluster with no readily interpretable pattern of relationships.

Cluster analysis of 21-trait MMDs: Japan and continental northeast Asia

Figure 7 is a multidimensional scaling analysis of relationships of Japan’s two lineages within a broader geographical context. Perhaps the most striking feature of this plot is that, with the addition of five continental northeast Asian samples, those from Japan maintain the same relationships to each other as when analyzed by themselves. Thus, from left to right along the x-axis in increasing distance from Jomon are: Southeast, Northeast and West Ainu; premodern Wajin series from North Tohoku, South Tohoku, Central region, and West. Moreover, the Recent Wajin aggregate maintains the same more or less central position relative to Edo and earlier samples as did the Recent North, Central, and West subcluster in Figure 5.

Wajin Japanese as a whole are more closely related to continental northeast Asians than to Jomon, being affiliated particularly with Mongols and north Chinese, a finding wholly in agreement with that of other investigations. The Chukchi sample, which in the present study is the only representative of the ‘Arctic Mongolid’ (Alexseev, 1979) is an outlier in this plot. Although Chukchi and Okhotsk (also an outlier) are closer to each other than either is to any other sample, nevertheless the position of Okhotsk is slightly
shifted towards the other northeast Asians, including Wajin Japanese and Ainu. Ishida (1996) finds the affinities of Okhotsk complicated, owing perhaps to admixture with Ainu and other neighbors.

The additive tree shown in Figure 8 summarizes and highlights relationships of Japan’s two lineages to other northeast Asians (excluding Chukchi). For this analysis regional samples of Wajin across all time periods were aggregated, i.e. Wajin West is an aggregate of Yayoi, Edo, and Recent samples. Again, away from continental northeast Asians and towards Jomon-Ainu, the biological distances of Wajin Japanese samples form a geographical gradient: West, Central, South Tohoku, and North Tohoku. The overall relationships within and between the two ancestral lineages remain the same.

### Discussion

#### Jomon

Our data concerning the strong differentiation between Japan’s two founding groups and the relationships of these to other northeast Asians were in agreement with virtually all previous studies based on a variety of evidence (Dodo, 1975; Yamaguchi, 1982, 1992; Hanihara, 1985; Howells, 1986; Mizoguchi, 1986, 1988a; Turner, 1990; Ishida and Dodo, 1992; Omoto, 1992; Ishida, 1993, 1995; Matsumura, 1995; Jin et al., 1996; Liu, 1996; Pietrusewsky, 1996; Horai and Omoto, 1998, and others). Notably, patterns of relationships involving Jomon apparently did not reflect varying degrees of affiliation between Jomon and any particular people of continental northeast Asia. Jomon was closer to all Japanese than to any other group of northeast Asians (Table 2, Figure 7, Figure 8) or native North Americans (Ossenberg, 1994). Jomon’s closest affiliations, at least in the limited context of this study, appeared to be entirely within the Japanese archipelago; and, as emphasized by other researchers (Yamaguchi, 1982, 1992; Hanihara, 1992; Ishida and Dodo, 1992; Pietrusewsky, 1996), included not just the Ainu but, indeed, through successive episodes of population movement and admixture since Yayoi times, all present-day Japanese.

Other skeletal and dental researchers have described local differences among the Jomonese. Although the patterns of inter-regional relationships vary somewhat from one study to another (Yamaguchi, 1980, 1982, 1992; Howells, 1966, 1986; Dodo, 1982; Mizoguchi, 1988b; Mouri, 1988; Matsumura, 1989, 1995; Maeda, 2002; and others) a common pattern seems to be a west to northeast gradient of affinities, possibly consistent with the isolation by distance model or with adaptation to different environments. However, in spite of marked differences with respect to ecozone, subsistence strategies, and population density from western Honshu to Hokkaido (Akazawa, 1996) and regardless of the great temporal depth of the Jomon, the range of physical variation is generally found to be narrower than that among modern Japanese (Dodo, 1982; Yamaguchi, 1982; Hanihara, 1991).

In Figure 5 the five Jomon samples spread out along the y-axis appear to display a degree of regional differentiation comparable to that among Wajin. However, Table 2 contradicts this: in contrast to 64% (of 36) within-Wajin MMDs, only 40% (of 10) within-Jomon MMDs were larger than zero at a statistically significant level. The size of the Jomon cluster reflected mainly the large MMDs involving the West and Central samples. In fact, the largest of 49 within-group distances in Japan (36 Wajin, 10 Jomon, 3 Ainu) was the MMD, 0.087, for Central versus West Jomon. In contrast, none of the four within-Jomon MMDs for the North sample were statistically significant and, with one exception, a geographical gradient of affinities was not observed. The exception was Epi-Jomon for which MMDs were ranked: Hokkaido, 0.002; North, 0.015; Central, 0.069; West, 0.079.

#### Ainu

Cranio metric and nonmetric analyses by several workers (reviewed by Dodo and Kawakubo, 2002) suggest that the
Epi-Jomon inhabitants of Hokkaido, with little or no genetic influence from their Yayoi or Kofun contemporaries (ca. 300 BC to 700 AD) in central Japan, were transitional in microevolutionary change from Jomon to Ainu. Cranial MMDs from the present study agreed with those of Dodo and Kawakubo (2002) in providing evidence for this reconstruction, i.e. in both studies MMDs for comparisons within the Jomon-Ainu lineage are much smaller than those between the Jomon-Ainu and Wajin lineages (Table 3).

But the question remains: which Jomon population was ancestral to Epi-Jomon and hence to Ainu? Comparisons in the Dodo and Kawakubo study do not include separate regional samples. One by Matsumura (1995) based on 21 dental crown and root traits, though it does not include Epi-Jomon, does include regional Jomon samples for which ranked MMDs versus Ainu (Hokkaido, 0.019; Central, 0.035; North, 0.068; and West Jomon, 0.120) suggest that the Jomon to Ainu microevolutionary change could have occurred within Hokkaido with little genetic influence from Honshu. On the other hand, according to Yamaguchi (1982), Epi-Jomon and Ainu do show a close affinity to Jomon remains from Honshu, including the Tohoku region. Findings in the present study agreed with those of Yamaguchi. From Table 2 the pertinent MMDs for Jomon and Southeast Ainu (representing the least Wajin-mixed sample) were ranked as follows:

- Epi-Jomon to Hokkaido Jomon, 0.002;
- Epi-Jomon to North Jomon, 0.015;
- Ainu SE to North Jomon, 0.019;
- Hokkaido Jomon to North Jomon, 0.020;
- Epi-Jomon to Ainu, 0.037;
- Ainu SE to Central Jomon, 0.052;
- Ainu SE to Hokkaido Jomon, 0.058;
- Ainu SE to West Jomon, 0.071.

Although in the above summary the Ainu values were those of the Southeast sample, in fact MMDs for each of the three Ainu regional samples versus North Jomon were smaller than those versus either Epi-Jomon or Hokkaido Jomon (Table 2).

Skeletal radioisotope data provide dietary evidence that prehistoric hunter-fisher-foragers in Hokkaido throughout the last 6000 years shared with the Ainu a primary dependence on marine resources, in contrast to the more mixed woodland/marine resource base in northeastern Honshu (Akazawa, 1996). Therefore, the closer affinity of Hokkaido Ainu to North Jomon than to Hokkaido Jomon could hardly be attributed to some hypothetical shift in Ainu subsistence strategies from the Hokkaido marine-based to the northeastern Honshu mixed pattern. Even if such a shift were to have occurred, it probably would not have distorted the cranial nonmetric trait evidence for Ainu ancestry; other studies (cited in Ossenberg, 1994) have underscored the remarkable conservatism of these features in the face of major environmental changes. A more plausible explanation for the observed pattern of affinities (assuming that the MMDs truly reflect genetic relationships and not error due to unrepresentative and undersized samples) is that the microevolutionary transition in Hokkaido from Jomon to Ainu was impacted strongly by aboriginal gene flow from northeastern Honshu.

To account for the Ainu’s apparent divergence away from Hokkaido Jomon and convergence towards North Jomon we offer the following reconstruction. It is based on the crucial premise that in the most northeastern region of Honshu some communities preserved a predominantly Jomon genetic heritage well into the medieval age. These would have been the so-called Emishi, first described in 7th-century Kofun period historical accounts. It is recorded that people belonging to the same tribe as the one in Hokkaido, Watarishima Emishi, inhabited the northernmost peninsulas of Honshu from the 7th to 12th centuries (Kodama, 1970; Hanihara, 1990). Migration/interaction may have occurred in both directions across the Tsugaru Strait during Jomon times, i.e. we noted that the Hokkaido-North Jomon MMD of 0.020 was not significantly greater than zero. However, based on the pattern of MMDs, we hypothesized that there was a significant interval from Epi-Jomon through Satsumon periods, roughly 100 BC to 1100 AD, during which aboriginal gene flow was predominantly from Honshu to Hokkaido. This interval would have coincided with the ancient through early medieval ages in central Japan when warfare, colonizing initiatives, and social dislocations would have caused population pressure generally tending in a northeasterly direction. Kazuro Hanihara (1990), citing the works of historians, notes that the influence of the imperial court reached Miyagi prefecture in south Tohoku by the 7th century and expanded north to Iwate prefecture by the 10th century. Soldiers sent to these posts were accompanied by their families. At the same time local Wajin chieftains began to collect a great amount of gold and to build large Buddhist temples. Hence, Tohoku became a mixed-residence quarter of Emishi and settlers who had moved from west Japan. By the 12th century the powerful northern Fujiwara family had established a polity over the Tohoku region which was to some extent independent of the imperial court, and may have developed significant trade contacts instrumental in the change from Satsumon to Formative Ainu culture in Hokkaido (Hudson, 1990).
With respect to the timing and strength of gene flow such that gene pool of the remnant west Ainu communities would have become even more vulnerable to dilution through Wajin admixture. There is also a possibility that, in addition to gene flow from the Japanese, the western Ainu were influenced directly via invasion by a continental tribe, the Ashihase, originally from north China, who had inhabited the region near the mouth of the Ishikari River prior to their rout in 660 AD by an expedition sent by the Japanese emperor (Kodama, 1970, pp. 6–11).

In contrast, communities in the southcentral/southeastern provinces of Hidaka and Tokachi retained the strongest Jomon heritage. Hidaka was the most densely populated province and, because the villages were dispersed along the upper reaches of the salmon-fishing rivers and were not conveniently accessible to Japanese, up to 1945 the south central and southeastern Ainu retained their traditional customs and habits and were the least racially mixed (Kodama, 1970, pp. 40–46).

**Wajin**

Compared to other populations sampled from the central islands of Japan, the Edo period population of North Tohoku retained the strongest genetic heritage from the Jomon-Ainu lineage as the following MMDs from Table 2 show.

<table>
<thead>
<tr>
<th>Ainu aggregate to:</th>
<th>0.038</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>eight other Wajin samples, 0.063–0.150.</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Jomon aggregate to:</th>
<th>0.107</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>eight other Wajin samples, 0.156–0.262.</td>
</tr>
</tbody>
</table>

This finding is consistent with our reconstruction in the preceding section where we hypothesized that migration from Jomon and its descendent Emishi populations on the northern tip of Honshu, possibly well into medieval times, played a key role in the ethnogenesis of Hokkaido Ainu. To some extent microevolutionary transition in northern Tohoku may have paralleled that in Hokkaido. In the 15th century, Ainu-speakers lived in what are now Aomori, Iwate, and Akita prefectures (Inoue, 1999). Moreover, historical records indicate that after the 16th century some Hokkaido Ainu migrated to north Tohoku (Hanihara, 1990). According to archaeological and skeletal findings it appears that Ainu lived here even up to recent times (Kodama, 1970; Hanihara, 1990). To the present day the communities here retain cultural and linguistic (Inoue, 1999; Wang and Ogura, 1996), somatometric (Kouchi, 1983), and molecular genetic traits (Misawa and Hayashida, 1968; Omoto, 1992; Takeshita et al., 2001), as well as varieties of the house mouse and domestic dog (Tanabe, 1992) which attest to the unique history of Tohoku as the most recent part of central Japan to come under Wajin influence.

West to northeast clines quantified in many independent studies on stature, craniofacial characteristics, and genetic factors in the blood in regional Japanese populations of the central islands constitute one of the cornerstones of support for the dual structure model (Hanihara, 1991). MMDs in the present study also tended to follow a west to northeast gradient (Table 2, Figure 5, Figure 6, Figure 7, Figure 8). This pattern is most striking in the ranking of MMDs for the Jomon aggregate sample versus Edo period Japanese and...
north Chinese, the latter sample representing a group possibly closely related to the continental ancestor: North Tohoku Edo, 0.107; South Tohoku Edo, 0.156; Central Edo, 0.201; West Edo 0.262; North Chinese, 0.268.

Clinal patterns were less apparent in rankings of Wajin versus Wajin MMDs, perhaps because of the confounding effects of temporal differences and small samples, e.g. Yayoi. And, as already noted, 36% of these values were statistically insignificant. In any case, we should probably not look too narrowly for geographical gradients. Archaeological and historical records provide invaluable information about early travel routes, settlement patterns, and specific episodes and events, according to which affinities in certain cases might better fit a mosaic than a cline model.

In the case of Kamakura, a relatively closer affinity of Japan’s aboriginal lineage to this medieval sample than to other post-Jomon samples from the central islands was noted in the present study. Similar findings in previous studies based on other categories of data (Howells, 1966; Yamaguchi, 1982; Brace et al., 1989; Pietrusewsky, 1996) have provoked controversy. Brace and colleagues, apparently assuming that warriors killed at a medieval massacre site must have been samurai, concluded from craniometric evidence of Kamakura’s affinity to Ainu that samurai must therefore have been Ainu. However, others (Hanihara, 1991; Pietrusewsky, 1996) have pointed out that the warriors massacred at this site were more likely to have been retainers or servants of the Kamakura Shogunate. These lower-class warriors may very well have been drawn from communities whose ancestry was preponderantly aboriginal. Samurai, on the other hand, belonged to a noble warrior caste more likely descended from continental immigrants. Thus, persistence in Japan of caste, class, or occupational identity differentiated along racial lines would, according to the dual structure model, be expected to present a mosaic pattern of affinities among cemeteries.

Perhaps the most important finding in the present study was the evidence of increased inter-regional population homogeneity throughout the central islands since the end of the Edo period. Recent Tohoku, Central, and West samples form a tight subcluster within the larger configuration containing Wajin samples from all periods (Figure 5). In Miyagi and the other southern Tohoku prefectures people born at the very end of the Edo period retained a slightly stronger trace of Jomon ancestry than those born after 1870, as suggested by analysis of two subsamples of the Tohoku University dissecting-room cranial series. The MMDs were:

- Ainu aggregate to:
  - South Tohoku Edo, 0.063;
  - South Tohoku Recent, 0.085.
- Jomon aggregate to:
  - South Tohoku Edo, 0.156;
  - South Tohoku Recent, 0.173.

The Edo period, 1603–1867, is known to have been a time of stability and social control when people tended to spend their lives in or close to their birth communities. With the Meiji Restoration in 1867, however, the mobility of the Japanese people increased. Even though on average only two generations separated the pre- from post-Meiji birth cohorts represented in the dissecting-room series, MMDs suggest that there may have been sufficient migration from central and west Japan over that interval to dilute the aboriginal representation in the Tohoku gene pool.

Similarly, regional analysis of somatometric data shows that the characteristics of western Honshu diffuse gradually to the northeast, and diachronic analysis of these data shows that the secular change in local populations is quite evident even between birth cohorts separated, on average, by as little as 30 years (Kouchi, 1983). This would reflect increased mobility of the post-Edo population and is wholly consistent with the dual structure model.

**Summary and Conclusions**

1. The findings of this study corroborated those of other investigations in support of the dual structure model of ethnogenesis in Japan.
2. The unique battery of somatometric traits used in this study powerfully differentiated between Japan’s indigenous Jomon-Ainus and immigrant northeast Asian ancestral lineages.
3. The continental roots of the Wajin Japanese were closer to those of Mongols and north Chinese than to those of the Tungus, Okhotsk, or Chukchi. The Jomon had no relatives in northeast Asia other than its descendants in Japan.
4. Gene flow between immigrant and aboriginal descendant communities initiated during the Yayoi period resulted in west to northeast gradients of morphological characteristics and affinities which seemed to have become stabilized during the Edo period.
5. Following the Meiji Restoration of 1867, increased mobility of the population resulted in renewed gene flow whereby the population of Japan became more homogeneous.
6. Affinities of Edo and recent period populations of Tohoku and Hokkaido are consistent with historical records and with other cultural and biological evidence indicating, that these regions were the latest to come under the influence of Wajin Japanese. Among regional populations of the Ainu, those from western Hokkaido were most, while those from the southeast (Hidaka and Tokachi districts) were least mixed.
7. In Hokkaido the microevolutionary transition from Jomon through Epi-Jomon to Ainu may have occurred in close parallel to population changes in the most northeastern region of Honshu, and may have been influenced during the Kofun and medieval periods by immigration of Jomon descendants, the Emishi, across the Tsugaru Strait. More archaeological and skeletal remains representing the poorly documented interval from Final Jomon to Edo are needed to piece together the ethnohistorical picture for northeastern Honshu.
8. Craniofacial changes in Japan effected through microevolutionary adaptation or through plastic response to factors such as diet would have been superimposed on a genetic substrate which was continually being reshaped by gene flow between descendants of the two founding lineages.
Acknowledgments

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