Variation in Limb Proportions Between Prehistoric Jomon Foragers and Yayoi Agriculturalists from Prehistoric Japan

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ABSTRACT Variation in limb proportions between prehistoric Jomon and Yayoi people of Japan are explored by this study. Jomon people were the descendents of Pleistocene nomads who migrated to the Japanese Islands around 30,000 yBP. Phenotypic and genotypic evidence indicates that Yayoi people were recent migrants to Japan from continental Northeast Asia who likely interbred with Jomon foragers. Limb proportions of Jomon and Yayoi people were compared using RMA regression and “Quick-Test” calculations to investigate relative variability between these two groups. Cluster and principal components analyses were performed on size-standardized limb lengths and used to compare Jomon and Yayoi people with other groups from various climatic zones. Elongated distal relative to proximal limb lengths were observed among Jomon compared to Yayoi people. Jomon limb proportions were similar to human groups from temperate/tropical climates at lower latitudes, while Yayoi limb proportions more closely resemble groups from colder climates at higher latitudes. Limb proportional similarities with groups from warmer environments among Jomon foragers likely reflect morphological changes following Pleistocene colonization of the Japanese Islands. Cold-derived limb proportions among the Yayoi people likely indicate retention of these traits following comparatively recent migrations to the Japanese Islands. Changes in limb proportions experienced by Jomon foragers and retention of cold-derived limb proportions among Yayoi people conform to previous findings that report changes in these proportions following long-standing evolution in a specific environment. Am J Phys Anthropol 137:164–174, 2008. DOI 10.1002/ajpa.20853

This study documents and interprets variation in limb proportions between prehistoric Jomon foragers and Yayoi agriculturalists from Japan. Variation in body proportions such as surface area to body mass ratios and brachial (radial relative to humeral length) and crural (tibial relative to femoral length) indices may in part reflect how humans biologically respond to climate and altitude (Bergmann, 1847; Allen, 1877; Trinkaus, 1981; Ruff, 1994; Holliday, 1997a; Katzmarzyk and Leonard, 1998; Weinstein, 2005; Auerbach, 2007; Temple, 2007a) as well as the impact of stress on the human phenotype (Meadows-Jantz and Jantz, 1999; Bogen et al., 2002; Temple, 2007a).

Geographic distributions of limb length proportions generally follow Allen's rule (Ruff, 1994, 2002; Katzmarzyk and Leonard, 1998; and others). Allen's rule states that polytypic homeothermic organisms that evolve in colder environments have shorter appendages; organisms of the same species from warmer climates have elongated appendages (Allen, 1877). Reduction of appendage size decreases surface area for heat loss in colder environments, while greater appendage size increases surface area for improved evaporative cooling in warm environments (Futuyma, 1998). The relationship between body proportions and climate is assumed to evidence ecogeographic adaptation in concert with natural selection because these trends cross numerous geographically diverse species and are not likely due to chance (Mayr, 1963; Futuyma, 1998).

The earliest, widely-accepted colonization of the Japanese Islands dates to around 30,000 BP, although dates are currently under evaluation (Imamura, 1996a). These groups were part of a Paleolithic foraging tradition that persisted until approximately 13,000 BP, when these cultures were subsumed under the Jomon spectrum (Imamura, 1996a). Jomon period foragers occupied modern-day Japan for approximately 10,000 years (13,000 to 2,500 yBP) (Imamura, 1996a). Cranio-dental morphology suggests that Jomon people were the descendents of Pleistocene nomads who migrated to Japan from either Southeast or North/Central Asia around 30,000 yBP (Hanihara, 1991; Turner, 1976, 1990, 1992; Imamura, 1996a; Omoto and Saitou, 1997; Pietrusewsky, 1999; Hanihara and Ishida, 2005; Matsumura and Hudson, 2005; Hammer et al., 2006; Seguchi et al., 2007). Genetic variation among current Ainu populations, the
living descendents of Jomon people, supports a North-eastern or Central Asian origin for the ancestors of Jomon foragers (Omoto and Saitou, 1997; Hammer et al., 2006).

Similar sources of data indicate that Yayoi period (2,500–1,700 yBP) agriculturalists were the descendents of people from modern-day Korea or northern China who migrated to Japan and interbred to varying degrees with indigenous Jomon foragers (Brace and Nagai, 1982; Hanihara, 1991; Nakahashi, 1985; Omoto and Saitou, 1997; Pietrusewsky, 1999; Hammer et al., 2006). Migrations from continental Asia during the Yayoi period introduced wet rice agriculture to the Japanese Islands (Imamura, 1996a,b; Hudson, 1999; Tsude, 2001). This pattern of subsistence differed from the plant gathering/ domestication and fishing/hunting based economies of the Jomon period (Imamura, 1996a,b; Tsude, 2001; Matsui and Kanehara, 2006).

Tool kit distributions indicate that Jomon foragers from eastern Japan had a more sophisticated system of maritime food procurement compared to those from western and inland regions (Akazawa, 1987, 1999). Such differences are supported by studies of enamel hypoplasia that indicate a greater level of stress for Jomon people from western compared to eastern Japan in concert with less sophisticated maritime food procurement systems (Temple, 2007b). Variation in stress levels related to diet among Jomon period foragers was not drastic, however, as stature between these regions did not differ (Temple, 2008). In addition, dental caries prevalence suggests that Jomon people consumed significant amounts of starchy carbohydrates, especially following climate changes recorded around 4,300 yBP (Temple, 2007b). This shift in diet did not precipitate an agricultural economy per se, as evidence for significant energy expenditure on the care of plants is not recorded among Jomon period foragers (Imamura, 1996a,b; Tsude, 2001; Matsui and Kanehara, 2006).

Significant energy expended on the care of domesticated plants is recorded during the Yayoi period in the form of large-scale agricultural ecosystems based around wet rice farming (Imamura, 1996b; Hudson, 1999; Tsude, 2001). Precipitous increases in carious tooth frequencies with less sophisticated maritime food procurement systems (Temple and Larsen, 2007; and others).

Cranial and dental size and shape varied between Jomon and Yayoi people in association with environment and gene flow (Suzuki, 1969; Brace and Nagai, 1982; Mizoguchi, 1986; Hanihara, 1991; Turner, 1992; Matsumura, 1995; Nakahashi, 1995; Pietrusewsky, 1999; Okazaki, 2004). This variability is further illustrated through differences in limb proportions between the two groups (Kato and Ogata, 1989; Yamaguchi, 1989). Previous studies report that Jomon foragers had higher brachial and crural indices than Yayoi people and were similar in limb proportions to low latitude, tropical groups such as the African San (Yamaguchi, 1989). In this (i.e., Yamaguchi, 1989) and other studies (i.e., Wada and Motomura, 2000), differences in limb proportions between Jomon and Yayoi people were analyzed via bivariate methods that did not explain relative limb variability. Statistical comparisons of the limb proportions between Jomon and Yayoi people and groups from different ecogeographic regions were also not performed.

This study extends previous research (i.e., Yamaguchi, 1989; Kato and Ogata, 1989; Wada and Motomura, 2000) by employing statistical analyses that help explain how relative limb length differed between Jomon and Yayoi people. Size-standardized limb lengths are then incorporated into multivariate statistical procedures that are used to reveal underlying similarities between Jomon and Yayoi people with samples from different ecogeographic regions. These patterns of variation are then discussed and interpreted within the context of Jomon and Yayoi environment and migration.

The above-mentioned goals for this study are realized by testing three specific hypotheses. First, the basic hypothesis that Jomon and Yayoi people express significant differences in tibial relative to femoral length and radial relative to humeral length is tested. Second, the hypothesis that this pattern of variation will be associated with comparatively reduced distal relative to proximal limb length among Yayoi people and comparatively increased distal relative to proximal limb length among Jomon people is tested. Third, the hypothesis that Jomon limb proportions are similar to those of people from temperate/tropical climates at lower latitudes, while Yayoi limb proportions are similar to those of people from higher latitude, colder environments is tested.

MATERIALS

This study focuses on Jomon foragers who occupied the coastal regions of eastern and western Honshu as well as Yayoi people from western Honshu and northern Kyushu (see Fig. 1). Data were collected from human skeletal remains excavated from four archaeological sites dated to the Late through Final Jomon period (4,000–2,300 yBP). Data were also collected from human skeletal material recovered from three archaeological sites dating to the Yayoi period (2,500–1,700 yBP). Curators, dates, locations, and names of all sites from which data were collected are listed and shown in Table 1 and Figure 1.

Regions associated with the Jomon and Yayoi skeletal material included in this study are all located within the temperate zones of Japan. Temperate climates average temperatures greater than 10°C during the warmest months and −3°C to 18°C during the coldest months (McKnight and Hess, 2004). Eastern and western Japan, including the regions of Tokai through northern Kyushu, experience annual temperatures that range between 0°C and 37°C with a mean annual temperature between 15 and 16°C (Fukui, 1977). This land mass encompasses a northern latitudinal range of approximately 33.6° through 35.0°.

Comparative samples include 16 geographically diverse groups (n = 436) (Table 2). Approximate latitudes combined with the Köppen climatic classification of each group (McKnight and Hess, 2004) are also included in Table 2. The Köppen climatic system is based on similarities in native vegetation combined with annual temperatures and precipitation rates (McKnight and Hess, 2004). All comparative samples have a minimum number of 10 individuals.

One exception to this requirement is the Minatogawa I postcranial remains (derived from Baba and Endo, 1982). Minatogawa I represents the most complete currently known human skeleton associated with the Paleolithic cultures of Japan (Suzuki, 1982; Baba and Endo, 1982). Skeletal remains of the Minatogawa I individual were excavated from the Minatogawa fissure on Oki-nawa Island. Minatogawa has been dated to approximately 18,000 yBP based on radiocarbon analysis of charcoal fragments (Matsu’ura, 1982). Cranio metric
studies suggest that the skeletal remains of Minatogawa I do not represent a direct ancestor of Jomon people, but that the individual was possibly derived from the same migratory group (Suzuki, 1982; Baba et al., 1999). Measurements for Minatogawa I are included here to understand how the body form associated with early inhabitants of the Japanese Islands, specifically Okinawa Island, compare with later prehistoric people.

Craniometric and dental morphological data indicate that long-standing in situ evolutionary processes are associated with the morphological features exhibited by the comparative samples drawn from North- and Southeast Asia (Pietrusewsky, 2005, 2006). It should, however, be noted that interpretations of dental morphology suggest that Northeast Asian people may have migrated to and bred with the indigenous people of Southeast Asia, particularly Thailand (Matsumura and Hudson, 2005; Matsumura, 2006). These biological interpretations are, however, largely based on dental material excavated from archaeological sites that are not included in this study. This suggests that the present comparative samples drawn from North- and Southeast Asia should exhibit limb proportions that were likely not influenced by significant gene flow from surrounding environments.

**Table 1. Sites, dates, and curatorial centers for the Jomon and Yayoi skeletal material**

<table>
<thead>
<tr>
<th>Site</th>
<th>Period</th>
<th>Dates</th>
<th>Institution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hobi</td>
<td>Late/Final Jomon</td>
<td>4000–2500 BP</td>
<td>University Museum, Tokyo</td>
</tr>
<tr>
<td>Inariyama</td>
<td>Late/Final Jomon</td>
<td>4000–2500 BP</td>
<td>Kyoto University</td>
</tr>
<tr>
<td>Tsukumo</td>
<td>Late/Final Jomon</td>
<td>4000–2500 BP</td>
<td>Kyoto University</td>
</tr>
<tr>
<td>Yoshigo</td>
<td>Late/Final Jomon</td>
<td>4000–2500 BP</td>
<td>Kyoto University</td>
</tr>
<tr>
<td>Doigahama</td>
<td>Yayoi</td>
<td>2500–1400 BP</td>
<td>Kyushu University</td>
</tr>
<tr>
<td>Kanenokuma</td>
<td>Yayoi</td>
<td>2500–1400 BP</td>
<td>Kyushu University</td>
</tr>
<tr>
<td>Koura</td>
<td>Yayoi</td>
<td>2500–1400 BP</td>
<td>Kyushu University</td>
</tr>
</tbody>
</table>

**Fig. 1.** Map indicating archaeological sites yielding the Jomon and Yayoi skeletal remains utilized by this study. Jomon: A) Tsukumo; B) Inariyama; C) Yoshigo; D) Hobi. Yayoi: 1) Kanenokuma; 2) Doigahama; 3) Koura.
TABLE 2. Comparative samples

<table>
<thead>
<tr>
<th>Group</th>
<th>N</th>
<th>Latitude</th>
<th>Climate</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inupiat, Kodiak Island</td>
<td>18</td>
<td>58.0</td>
<td>N</td>
<td>Polar</td>
</tr>
<tr>
<td>Sadlermiut, Southampton Island</td>
<td>54</td>
<td>64.1</td>
<td>N</td>
<td>Polar</td>
</tr>
<tr>
<td>19th/20th CE Ainu, Hokkaido</td>
<td>11</td>
<td>43.0</td>
<td>N</td>
<td>Continental</td>
</tr>
<tr>
<td>Late Iron Age Poundbury, UK</td>
<td>50</td>
<td>50.0</td>
<td>N</td>
<td>Temperate</td>
</tr>
<tr>
<td>Early Archaic, Windowover Pond, FL</td>
<td>40</td>
<td>28.6</td>
<td>N</td>
<td>Temperate</td>
</tr>
<tr>
<td>Early Medieval, Straßkirchen, Germany</td>
<td>39</td>
<td>48.9</td>
<td>N</td>
<td>Temperate</td>
</tr>
<tr>
<td>Edo Period, Japan</td>
<td>21</td>
<td>40.0</td>
<td>N</td>
<td>Temperate</td>
</tr>
<tr>
<td>Pueblo IV, Cliff Dwellings, Puye, NM</td>
<td>37</td>
<td>35.9</td>
<td>N</td>
<td>Temperate</td>
</tr>
<tr>
<td>Shi San Hang, Taiwan</td>
<td>11</td>
<td>25.0</td>
<td>N</td>
<td>Temperate</td>
</tr>
<tr>
<td>Late Pleistocene, Okinawa Island,</td>
<td>1</td>
<td>26.0</td>
<td>N</td>
<td>Temperate</td>
</tr>
<tr>
<td>Minatowgawa I</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late 19th CE Aboriginal Australians</td>
<td>26</td>
<td>27.0</td>
<td>S</td>
<td>Tropical</td>
</tr>
<tr>
<td>”Negrito” Philippines</td>
<td>27</td>
<td>13.0</td>
<td>N</td>
<td>Tropical</td>
</tr>
<tr>
<td>African Pygmy</td>
<td>10</td>
<td>2.0</td>
<td>N</td>
<td>Tropical</td>
</tr>
<tr>
<td>19th CE South African San</td>
<td>19</td>
<td>25.0</td>
<td>N</td>
<td>Tropical</td>
</tr>
<tr>
<td>Ban Chiang, Non Nok Tha, Thailand1, 2</td>
<td>15</td>
<td>16.5</td>
<td>N</td>
<td>Tropical</td>
</tr>
<tr>
<td>Uganda</td>
<td>46</td>
<td>0.0</td>
<td>N</td>
<td>Tropical</td>
</tr>
</tbody>
</table>

1 Ban Chiang postcranial measurements are available via the World Wide Web: http://seasia.museum.upenn.edu/skeletal/nonnoktha_data.htm
2 Non Nok Tha postcranial measurements are available via the World Wide Web: http://seasia.museum.upenn.edu/skeletal/nonnoktha_data.htm

TABLE 3. Sex specific samples

<table>
<thead>
<tr>
<th>Group</th>
<th>N RL vs. HL</th>
<th>N TL vs. BFL</th>
<th>N Multivariate Sample</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jomon Female</td>
<td>32</td>
<td>28</td>
<td>14</td>
</tr>
<tr>
<td>Jomon Male</td>
<td>39</td>
<td>40</td>
<td>29</td>
</tr>
<tr>
<td>Total Jomon</td>
<td>71</td>
<td>68</td>
<td>43</td>
</tr>
<tr>
<td>Yayoi Female</td>
<td>29</td>
<td>27</td>
<td>21</td>
</tr>
<tr>
<td>Yayoi Male</td>
<td>33</td>
<td>28</td>
<td>20</td>
</tr>
<tr>
<td>Total Yayoi</td>
<td>62</td>
<td>55</td>
<td>41</td>
</tr>
<tr>
<td>Total Combined</td>
<td>133</td>
<td>123</td>
<td>84</td>
</tr>
</tbody>
</table>

A number of samples used by this study to model ecogeographic variation originate from outside Asia (Table 2). Limb proportions should, however, remain consistent between groups from similar climates, regardless of ancestry, assuming these groups occupied their respective environments for sufficient time (Holliday and Ruff, 1997). All samples that originate from regions outside of Asia have limb proportions that conform to ecogeographic expectations (Ruff and Walker, 1993; Holliday, 1995, 1997a; Auerbach, 2007).

**METHODS**

**Sex determination and osteometric measurements**

Jomon and Yayoi samples were divided into male and female groups. Biological sex was determined using morphological features of the pelvis such as ventral arc presence, thickness of the ischiopubic ramus, subpubic cleft, and greater sciatic notch shape (Phenice, 1969; Walker et al., 2005). Morphological features of the skull were not used to determine sex as these methods have proven unreliable in the absence of population-specific discriminant functions applied to cranial measurements (Meindl et al., 1985). Table 3 lists the sex-specific sample sizes used in the bivariate and multivariate methods described below. Numbers of individuals that constitute the bivariate samples differ from those used for the multivariate samples.
tivariate methods because bivariate comparisons relied only on preservation of the tibia and femur or humerus and radius rather than all four elements.

All long bone measurements were collected with a standard osteometric board and recorded to the nearest millimeter. Each bone for the Jomon and Yayoi samples was measured three times by DHT with the maximum or modal measurement recorded as correct. Under circumstances where the modal measurement fell below the maximum, the modal measurement was used. Bicondylar femoral length (BFL), tibial length (TL) (measured from the most superior point of the lateral condyle to the most inferior point of the medial malleolus), maximum humeral length (HL), and maximum radial length (RL) were measured to examine variation in limb proportions according to standard protocols (Buikstra and Ubelaker, 1994). BFL measurements were not available for the Yayoi sample. Maximum femoral length (MFL) measurements were converted to BFL for the Yayoi sample by multiplying MFL by 0.991. This factor represents the average ratio of BFL to MFL for modern Japanese and Jomon foragers (Yamaguchi, 1989). It was necessary to convert MFL to BFL for the Yayoi sample because the majority of comparative studies interested in relative limb length and ecogeographic expectations compare these measurements to TL relative to BFL (e.g., Trinkaus, 1981; Holliday, 1995, 1997a,b; Weinstein, 2005).

Comparison of Jomon and Yayoi limb proportions

Log-transformed limb lengths were used to evaluate differences and similarities in RL relative to HL and TL relative to BFL. Relative variation in Jomon and Yayoi long bone lengths were compared according to sex-specific groups because these indices are often different for males and females (Trinkaus, 1981; Yamaguchi, 1989). Log-transformed measurements of TL relative to BFL as well as RL relative to HL were compared using reduced major axis (RMA) regression combined with the “Quick-Test” method described by Tsutakawa and Hewett (1977). RMA regression is used because these data were measured with error and do not include dependent and independent variables (Sokal and Rohlf, 1995). The “Quick-Test” calculation tests the null-hypothesis that the joint distribution of measurements (X, Y) above and below the RMA regression line for any two samples does not significantly differ (Tsutakawa and Hewett, 1977). These methods help test the hypotheses of the study by graphically illustrating the relationship between Jomon and Yayoi limb proportions and helping to explain how these samples differ in terms of relative limb length.

Limb proportions and ecogeography

Prior to use of the multivariate statistical methods outlined below, Jomon and Yayoi limb lengths were size-standardized. This standardization follows procedures described by Darroch and Mosimann (1985), where size-standardized data are calculated as the ratio of each variable to the geometric mean for all variables of a given individual. Geometric means were derived by multiplying together every long bone measurement (BFL, TL, HL, RL) for each individual and calculating the nth root of this product (Darroch and Mosimann, 1985). The nth root is determined by the overall number of measurements for the individual. Thus, geometric means derived from the samples under consideration take the fourth root of this product.

Similarities in limb shape were calculated using hierarchical cluster analysis with group average linkage methods (HL, RL, BFL, TL) and UPGMA output for all samples listed in Tables 1 and 2 to help depict similarities in limb proportions between the Jomon, Yayoi, and groups from similar environments. Cluster analysis of size-standardized limb lengths were utilized by previous research to portray similarities in limb proportions between Neandertals and modern human groups drawn from various climates (Holliday, 1997a). It is important to note that close clustering of groups based on limb shape does not necessarily reflect close biological ancestry. Rather, the purpose for using cluster analysis was to examine similarities and differences in morphology related to ecogeographic variation. Thus, similarities in limb shape between distantly related groups are possible. Principal components analysis of size-standardized limb lengths was then used to explain how these variables contributed to variation in limb proportions between these groups.

Multivariate procedures used a pooled sex sample. Previous multivariate analyses of limb proportions performed calculations on males and females separately to offset biases stemming from size-dimorphism (Weinstein, 2005). This study differs from Weinstein, 2005) by using size-standardized limb lengths in the multivariate analyses. Past studies (i.e., Holliday, 1997a) also pooled males and females together after skeletal measurements were standardized for size. It is noted that size is sometimes correlated with shape in inter-sex or species comparisons even after measurements are standardized by individual geometric means (Mosimann, 1987; Jungers et al., 1995) and this may create unrealistic similarities between groups of different sizes (Corruccini, 1987). Errors such as these are, however, mostly reported among distantly related species or between males and females within species that have considerable levels of sexual dimorphism (Corruccini, 1987; Jungers et al., 1995).

RESULTS

RMA regression plots of RL relative to HL and TL relative to BFL are reported in Figures 2 through 5. Table 4 lists the results of the “Quick-Test” analysis performed on these data. Jomon males and females were statistically significantly more frequently observed above the RMA regression line for RL relative to HL and TL relative to BFL, while Yayoi males and females were more frequently observed below the RMA regression line for RL relative to HL and TL relative to BFL. This relationship appears to be driven by longer radii and tibiae relative to humeri and femora among Jomon compared to Yayoi people, or alternatively, shortened tibiae and radii relative to femora and humeri among Yayoi compared to Jomon people. This finding supports the first hypothesis of the study by illustrating significant differences in relative limb length between Jomon and Yayoi people. In addition, the second hypothesis that predicts greater distal relative to proximal limb lengths among Jomon compared to Yayoi people and reduced distal relative to proximal limb length among Yayoi compared to Jomon people is also supported.

Two important similarities are revealed by the cluster analysis of size-standardized limb lengths. First, Jomon limb shape is similar to groups from tropical environ-
ments at lower latitudes (see Fig. 6). These groups include samples from Africa, Australia, Florida, the Philippines, and Thailand. Second, similarities between the Yayoi and individuals from higher latitudes and colder environments are observed. These groups originate from Alaska (Inupiat), Germany, England, and Kyoto. This finding supports the third hypothesis of the study that predicts greater similarity in limb shape between Jomon people and groups from warm, low latitude environments and Yayoi people with groups from colder, high latitude locations. In addition, it is important to note similarity in limb proportions between Minatogawa I and groups from colder, high latitude environments. Similarities in limb proportions between the modern Japanese sample from Kyoto with the Yayoi and other groups from colder, high latitude environments are also observed.

Principal components analysis bears out both the similarities and differences of limb shape between these groups (Table 5; Fig. 7). Eigenvectors of the first principal component contribute to approximately 50.9% of the variation observed between these groups. Eigenvectors of the first principal component contrast femoral and humeral length with tibial and radial length. This indicates that the first principal component is related to shape that illustrates variation in distal and proximal limb elements. Here, Jomon limb proportions are similar to groups from warmer, low latitude environments. These groups have elongated distal relative to proximal limb lengths. Yayoi agriculturalists appear to exhibit similarities in limb proportions with groups from colder, high latitude environments in association with reduced distal relative to proximal limb lengths.

TABLE 4. Results of Quick-Test analysis on limb indices

<table>
<thead>
<tr>
<th>Index</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>TL vs. BFL</td>
<td>Jomon &gt; Yayoi (P &lt; .004)</td>
<td>Jomon &gt; Yayoi (P &lt; .002)</td>
</tr>
<tr>
<td>RL vs. HL</td>
<td>Jomon &gt; Yayoi (P &lt; .004)</td>
<td>Jomon &gt; Yayoi (P &lt; .05)</td>
</tr>
</tbody>
</table>
exception to the Philippines sample. It is possible that this result is associated with greater climatic susceptibility for the lower compared to upper limb, where differences between RL relative to HL are less pronounced than those observed in TL relative to BFL. Limb proportion variation related to climate is often more pronounced in the lower limb (Trinkaus, 1981; Yamaguchi, 1989; this study), while secular studies of relative limb length indicate a relatively faster rate-of-change in the lower limb following migration and environmental diversification of indigenous groups from the New World (Auerbach, 2007).

**DISCUSSION**

**Jomon limb proportions**

Relatively increased distal limb length among Jomon compared to Yayoi people is observed. Jomon foragers have similar limb proportions to groups from temperate and/or tropical environments from lower latitudes. This pattern of variation could be the outcome of two possible evolutionary scenarios. First, the Paleolithic ancestors of Jomon people may have arrived in Japan from a temperate/tropical environment and retained limb proportions associated with such climates. In contrast, the second scenario proposes that limb proportions of the earliest Paleolithic foragers from Japan were initially similar to high latitude groups from colder environments, but changed after experiencing the warmer environment of Japan over considerable amounts of time.

Either of these scenarios is possible given the fact that Pleistocene Japan was climatically mild: Pleistocene ancestors of the Jomon people arrived in Japan around 30,000 yBP (Imamura, 1996a). The last glacial maximum in Japan (25,000–10,000 yBP) is characterized by glacial spread only on the mountain peaks of Honshu and Hokkaido and coniferous trees adapted to warm, moist environments in Honshu and Northern Kyushu (Tsukada, 1986). Postglacial warming is recorded from 10,000 through 4,300 yBP. Mean annual temperatures during this time were 3°C warmer than modern climates across the Japanese Islands. Cooling trends began around 4,300 yBP and are associated with a rise in *Fagus*, *Tsuga soeboldii*, *Abies firma*, and general coniferous forests (Tsukada, 1986).

The Sundaland is a biogeographical region that includes the Sunda Platform and Shelf. The Sunda Platform supports the Malay Peninsula and Archipelago as well as the Philippine Islands, Java, Palawan, Sumatra, and Borneo, while the Sundan Shelf is a southerly extension of the Southeast Asian continent. These regions (i.e., the Sunda Shelf and Platform) were exposed during the Pleistocene, making the Sundaland a contiguous landmass. Pollen spectra indicate that the environmental characteristics of Pleistocene Sundaland included tropical lowland forests and mangrove trees set along the edges of rivers, while mountain environments were primarily associated with rainforest (Sun et al., 2000). Tropical environments for the Sundaland are further supported by Late Pleistocene faunal assemblages recovered from Borneo including pigs (*Sus barbatus*), leaf eating monkeys and macaques, and monitor lizards (Barker et al., 2007). Global variation in human tooth size and

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**TABLE 5.** Principal components analysis of size-standardized limb lengths for Jomon, Yayoi, and comparative samples.

<table>
<thead>
<tr>
<th>Principle Components</th>
<th>BFL</th>
<th>TL</th>
<th>HL</th>
<th>RL</th>
<th>% VAR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvectors of PC1</td>
<td>0.673</td>
<td>-0.407</td>
<td>0.442</td>
<td>-0.431</td>
<td>50.9</td>
</tr>
<tr>
<td>Eigenvectors of PC2</td>
<td>0.497</td>
<td>0.640</td>
<td>-0.487</td>
<td>-0.327</td>
<td>34.6</td>
</tr>
</tbody>
</table>

*Fig. 6.* UPGMA output of hierarchic cluster analysis performed on size-standardized limb lengths of Jomon, Yayoi, and comparative samples: Inupiat, Kodiak Island (Inupiat); Sadlermiut, Southampton Island (Sadlermiut); 19th/20th CE Ainu, Hokkaido (Ainu); Late Iron Age Poundsbury, UK (England); Early Archaic, Windover Pond, FL (Florida); Early Medieval, Straßkirchen Germany (Germany); Edo Period, Japan (Kyoto); Pueblo IV, Cliff Dwellings, Puye, NM (New Mexico); Shi San Hang, Taiwan (Taiwan); Late Pleistocene, Okinawa Island, Minatogawa I (Minatogawa); Late 19th CE Aboriginal Australians (Aborigine); ”Negrito” Philippines (Philippines); African Pygmy (Pygmy); 19th CE South African San (San); Ban Chiang, Non Nok Tha, Thailand (Thailand); Uganda (Uganda).

*Fig. 7.* Principal components graph of size-standardized limb lengths for Jomon, Yayoi, and comparative samples. Comparative sample titles follow those listed in Figure 6.
shape supports the clustering of Jomon foragers with indigenous groups from Australia, Melanesia, and Southeast Asia (Hanihara and Ishida, 2005; Matsumura and Hudson, 2006). More specifically, however, Jomon people possess a battery of dental traits associated with spondadonty (Turner, 1992). These dental traits date to the Late Pleistocene and were characteristic of people who initially colonized Sundaland (Turner, 1990). Inhabitants of Sundaland are hypothesized to have migrated to Japan, Northeast Asia, and Southeast Asia via this now submerged land bridge around 30,000 yBP (Turner, 1990; Turner et al., 2000).

If Jomon people were descendants of the prehistoric inhabitants of Sundaland, then it is likely that the ancestors of the Jomon arrived in Japan with temperate/tropical limb proportions. Thus, increased distal relative to proximal limb lengths observed among Jomon people would indicate retention of an ancestral trait and not biological adjustment to the late Pleistocene/early Holocene climate of the Japanese Islands. It is, however, important to note that people with dental traits associated with spondadonty migrated from Southeast Asia to northern China and Siberia before 30,000 yBP (Turner et al., 2000). These findings suggest that the spondadonty dental pattern observed in Jomon people may reflect migrations to Japan via Northeast Asia, rather than directly from Sundaland. It is also important to point out that the some of the dental traits associated with spondadonty carry a reasonable degree of environmental influence and low heritability (Nichol, 1988). Thus, the possibility that Jomon people experienced a change in limb proportions following the arrival of Pleistocene nomads to the Japanese Islands from Northeast or North/Central Asia is also quite likely.

Currently, North/Central Asia experiences annual temperatures ranging from −4 to 11 °C with a considerably cooler climate recorded during the last glacial maximum (Zhuo et al., 1998). Levels of permafrost observed in the Altai Mountains were, for example, approximately 1000 m lower than current levels (Zhuo et al., 1998). This environment significantly differs from the mild conditions reported for Late Pleistocene Honshu and Kyushu.

Biodistance analysis of morphometric and genetic data indicates that the ancestors of Jomon people migrated to Japan from colder environments. Similarities in craniometric features are noted between Jomon people and those from modern Japan, mainland China, and Taiwan (Pietrusewsky, 1999). Cranio- and odontometric data show closer relationships between Jomon people and those of the archaic New World rather than those from Neolithic China, Korea, or Southeast Asia; relationships between Jomon people and those of the archaic New World argue for a common North/Central Asian ancestry for these populations (Seguchi et al., 2007). Genetic analysis of haplogroups (Y-chromosome) and polymorphic loci on nuclear DNA, both collected from living Ainu, further highlight similarities between Jomon and Northeastern or North/Central Asian people (Omoto and Saitou, 1997; Hammer et al., 2006). In addition, estimated body breadth (via femoral head breadth) among Jomon foragers is similar to groups from colder environments (Temple, 2007a), and in fact, comparable to the Minatogawa I specimen (Baba and Endo, 1982). This finding is particularly important to the results and interpretations of this study because body breadth is a highly conserved trait that reflects ancestral climatic adaptation (Ruff, 1994, 2002; Auerbach, 2007). Wide body breadths for Jomon foragers and Minatogawa I are indicative of migrations to Japan from a colder environment such as that reported for North/Central Asia.

Inclusion of postcranial measurements from the Minatogawa I skeleton (derived from Baba and Endo, 1982) in the cluster analysis suggests that the early inhabitants of the Japanese Islands had limb shapes associated with groups from higher latitudes and colder climates (Figs. 6, 7). Minatogawa I only represents the remains of a single individual. If, however, Minatogawa I shares a common ancestor with Jomon people (see Suzuki, 1982; Baba et al., 1999) and represents the limb shape of the earliest inhabitants of the Japanese Islands, then Jomon limb proportions represent morphological change experienced after colonization of the Japanese Islands. Such changes would have occurred over a period of approximately 20,000 years. This depth-of-time is similar to that reported by past studies addressing secular change in limb proportions (Hollliday, 1997b; Auerbach, 2007).

Experimental studies of relationships between environment and limb proportions suggest greater plasticity in the distal elements. Mammals exposed to cold temperatures experience vasoconstriction of the distal appendages, particularly the tibia, and shortening of these limbs (Weaver and Ingram, 1969; Lee et al., 1969; Riesenfeld, 1973), possibly in response to the inhibition of epigenetic signals involved in growth (Serrat et al., 2007). Greater variation of distal compared to proximal limb segments is also observed in comparisons of relative limb segment variability between broad cross-sections of global populations (Hollliday and Ruff, 2001). This indicates that variation in limb proportions is driven by plasticity of distal elements.

Similar proximal limb lengths between Jomon people and the Minatogawa I specimen combined with evidence for significant variation in distal limb lengths between the two groups are observed (Baba and Endo, 1982). In this sense, Jomon limb proportions may represent a transitional variant between colder and temperate climates. Distal elements possibly responded to the environment of Late Pleistocene and Holocene Japan through elongation, while proximal elements remained similar to ancestral groups.

**Yayoi limb proportions**

Yayoi people are characterized by short distal relative to proximal limb segments and cluster with groups from colder environments at higher latitudes, most notably, modern Japanese (see Fig. 6). This result is not surprising given the consistency of findings that indicate Yayoi people were the descendants of Northeast Asian migrants to the Japanese Islands and, to a lesser extent, Jomon foragers (Brace and Nagai, 1982; Mizoguchi, 1986; Hanihara, 1991; Turner, 1992; Nakahashi, 1995; Matsumura, 1995; Omoto and Saitou, 1997; Pietrusewsky, 1999; Hammer et al., 2006). That is, once Yayoi period migrants arrived in the Japanese Islands from Northeast Asia, the majority of Jomon people, particularly those in western Japan, were genetically subsumed by these groups.

Environments in Northeast Asia differed from the temperate climate of Holocene Japan. Modern Northeast China and Korea are continental microthermal climates with lower mean annual temperatures than Honshu and Kyushu (Fukui, 1977; McKnight and Hess, 2004). Indeed, palynological studies of Holocene Northeastern
of migrations to this region from Northeast Asia (Harihara, 1991; Turner, 1992; Nakahashi, 1995; Omoto and Saitou, 1997; Pietrusewsky, 1999; Hammer et al., 2006), maintained cold-derived limb proportions. Both of these observations conform to previous studies (i.e., Trinkaus, 1981; Holliday, 1997a; Auerbach, 2007) that suggest considerable depths of time before limb proportions change in response to climatic variation.

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