Variation in Limb Proportions Between 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.   © 2008 Wiley-Liss, Inc.

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; Bogin 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 earlier 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, 1995; 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 follow this economic shift and bear further testament to the importance of carbohydrate-heavy crops during the Yayoi cultural horizon (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° 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° 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 measurements (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 Okinawa Island. Minatogawa has been dated to approximately 18,000 yBP based on radiocarbon analysis of charcoal fragments (Matsu'ura, 1982). Craniometric

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

Site	Period	Dates	Institution
Hobi	Late/Final Jomon	4000–2500 BP	University Museum, Tokyo
Inariyama	Late/Final Jomon	4000–2500 BP	Kyoto University
Tsukumo	Late/Final Jomon	4000–2500 BP	Kyoto University
Yoshigo	Late/Final Jomon	4000–2500 BP	Kyoto University
Doigahama	Yayoi	2500–1400 BP	Kyushu University
Kanenokuma	Yayoi	2500–1400 BP	Kyushu University
Koura	Yayoi	2500–1400 BP	Kyushu University

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 South-east 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 2. *Comparative samples*

Group	N	♂:♀	Institution[3]	Latitude	Climate	Reference
Inupiat, Kodiak Island	18	10:8	NMNH	58.0° N	Polar	Holliday, 1995, 1997a
Sadlermiut, Southampton Island	54	26:28	CMC	64.1° N	Polar	Auerbach, 2007
19th/20th CE Ainu, Hokkaido	11	7:4	Sapp. Med. Univ.	43.0° N	Continental Microthermal	This Study
Late Iron Age Poundbury, UK	50	26:24	NHM	50° N	Temperate	Auerbach and Ruff, 2004
Early Archaic, Windover Pond, FL	40	17:23	FSU	28.6° N	Temperate	Auerbach, 2007
Early Medieval, Straßkirchen, Germany	39	13:26	SfAP	48.9° N	Temperate	Auerbach and Ruff, 2004
Edo Period, Japan	21	12:9	Kyoto Univ.	40.0° N	Temperate	Auerbach and Ruff, 2004
Pueblo IV, Cliff Dwellings, Puye, NM	37	20:17	NMNH	35.9° N	Temperate	Auerbach, 2007
Shi San Hang, Taiwan	11	4:7	Acad. Sinica; SMA	25° N	Temperate	Pietrusewsky, 2001; Pietrusewsky and Tsang, 2003
Late Pleistocene, Okinawa Island, Minatowgawa I	1	1:0	UTOK	26.0° N	Temperate	Baba and Endo, 1982
Late 19th CE Aboriginal Australians	26	8:18	AMNH; NMNH; DC; MdH; MNdAE; NM; NHM	27.0° S	Tropical	Auerbach and Ruff, 2004
"Negrito" Philippines	27	6:21	MdH	13.0° N	Tropical	Auerbach and Ruff, 2004
African Pygmy	10	3:7	IRSN; Univ. Gen	2.0° N	Tropical	Holliday, 1995, 1997a
19th CE South African San	19	8:11	SAM	25.0° N	Tropical	Slome, 1929
Ban Chiang, Non Nok Tha, Thailand[1,2]	15	14:1	Univ. Hawai'i; UNLV; MUMS	16.5° N	Tropical	Pietrusewsky and Douglas, 2002; Douglas, 1996
Uganda	46	19:27	MU; KNM	0.0° N	Tropical	Ruff and Walker, 1993

[1] Ban Chiang postcranial measurements are available via the World Wide Web: http://seasia.museum.upenn.edu/skeletal/banchiang_data.htm

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

[3] **Acad. Sinica**: Academia Sinica, Taipei, Taiwan; **AMNH**: American Museum of Natural History, New York, NY; **DC**: Duckworth Osteological Collection, Cambridge, UK; **IRSN**: Institut Royale des Sciences Naturelles, Brussels, Belgium; **KNM:** Kenya National Museum, Nairobi, Kenya; **Kyoto Univ**: Kyoto University, Kyoto, Japan; **MdH**: Musée de l'Homme, Paris, France; **MNdAE**: Muzeo Nationale di Antropologia e Etnologia, Florence, Italy; **MU**: Makerere University, Kampala, Uganda; **MUMS**: Maidol University Medical School, Siriraj Hospital, Bangkok, Thailand; **NM**: Naturhistorishes Museum, Vienna, Austria; **NHM**: Natural History Museum, London, UK; **NMNH**: National Museum of Natural History, Washington, DC; **Sapp. Med. Univ**: Sapporo Medical University, Sapporo, Japan; **SAM**: South African Museum, Capetown, South Africa; **SfAP**: Staatssammlung für Anthropologie und Palaeoanatomie, Munich, Germany **SMA**: Shihsanhang Museum of Anthropology, Tapei, Taiwan; **Univ. Gen**: University of Geneva, Geneva Switzerland; **Univ. Hawai'i**: University of Hawai'i, Manoa, HI; **UNLV**: University of Nevada at Las Vegas, Las Vegas, NV; **UTOK**: University of Tokyo, Tokyo, Japan.

A number of samples used by this study to model eco-geographic 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 con-

TABLE 3. *Sex specific samples*

Group	N RL vs. HL	N TL vs. BFL	N Multivariate Sample
Jomon Female	32	28	14
Jomon Male	39	40	29
Total Jomon	71	68	43
Yayoi Female	29	27	21
Yayoi Male	33	28	20
Total Yayoi	62	55	41
Total Combined	133	123	84

cavity, 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 mul-

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 as 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 hierarchic 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-
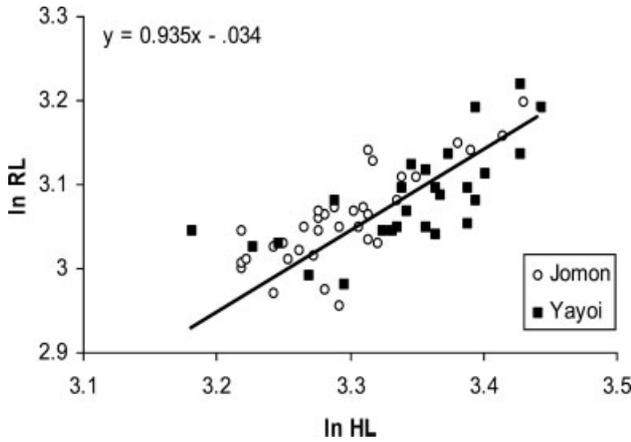
Fig. 2. Bivariate plot with RMA regression line of log-transformed RL relative to HL for females. Jomon are represented by open circles; Yayoi are represented by shaded squares.
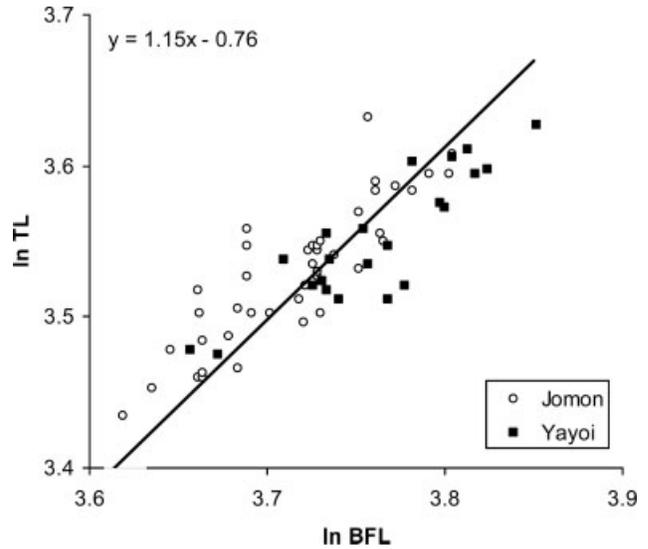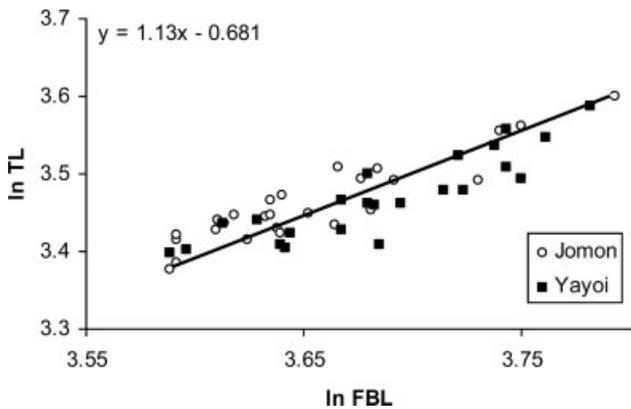

Fig. 3. Bivariate plot with RMA regression line of log-transformed TL relative to BFL for females. Jomon are represented by open circles; Yayoi are represented by shaded squares.
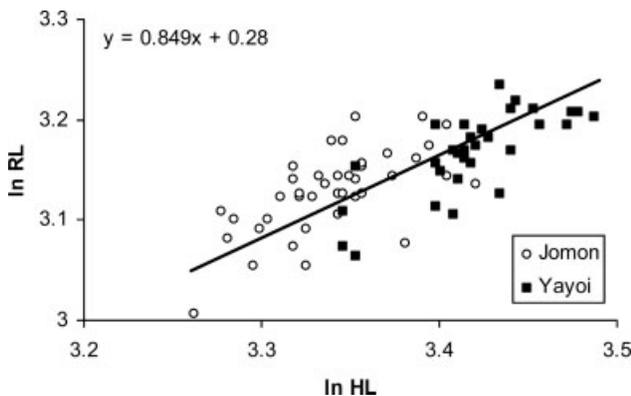

Fig. 4. Bivariate plot with RMA regression line of log-transformed RL relative to HL for males. Jomon are represented by open circles; Yayoi are represented by shaded squares.

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
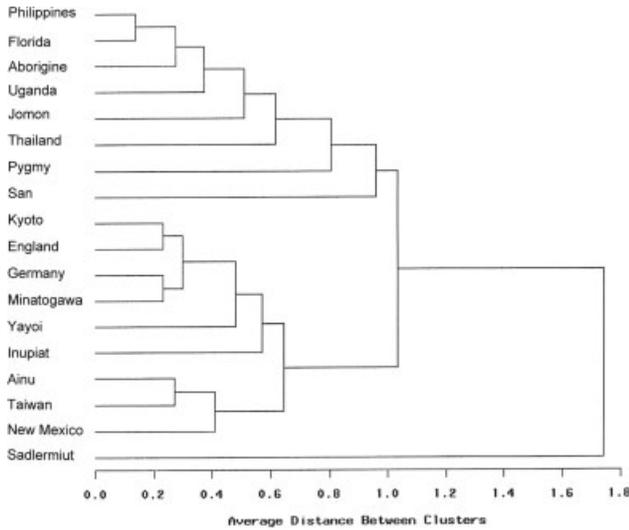

Fig. 5. Bivariate plot with RMA regression line of log-transformed TL relative to BFL for males. Jomon are represented by open circles; Yayoi are represented by shaded squares.

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

Index	Males	Females
TL vs. BFL	Jomon > Yayoi ($P \leq .004$)	Jomon > Yayoi ($P \leq .002$)
RL vs. HL	Jomon > Yayoi ($P \leq .004$)	Jomon > Yayoi ($P \leq .05$)

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.

Eigenvectors of the second principal component account for 34.6% of the variation between these groups and contrast femur and tibia with humerus and radius. This indicates that the second principal component is related to shape that illustrates variation associated with upper versus lower limb segments with notable

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 Poundbury, UK (England); Early Archaic, Windover Pond, FL (Florida); Early Medieval, Straβkirchen Germany (Germany); Edo Period, Japan (Kyoto); Pueblo IV, Cliff Dwellings, Puye, NM (New Mexico); Shi San Hang, Taiwan (Taiwan); Late Pleistocene, Okinawa Island, Minatowgawa 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).
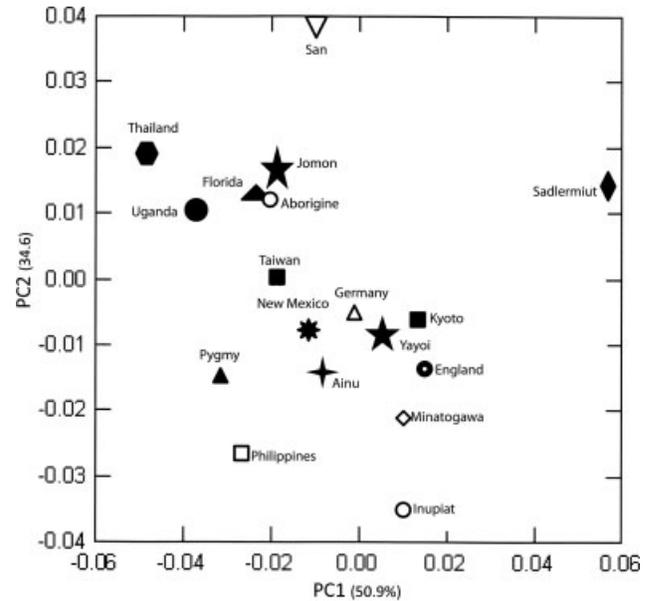
TABLE 5. Principal components analysis of size-standardized limb lengths for Jomon, Yayoi, and comparative samples

Principle Components	BFL	TL	HL	RL	% VAR
Eigenvectors of PC1	0.673	−0.407	0.442	−0.431	50.9
Eigenvectors of PC2	0.497	0.640	−0.487	−0.327	34.6

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

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.

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 Sunda 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

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 sundadonty (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 descendents 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 sundadonty migrated from Southeast Asia to northern China and Siberia before 30,000 yBP (Turner et al., 2000). These findings suggest that the sundadonty 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 sundadonty 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 cold 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 (Holliday, 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; Riesenfield, 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 (Holliday 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 descendents 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

China indicate vegetation zones consisting of deciduous broad leafed and mixed coniferous forests similar to those found in colder, high latitude environments (Shi et al., 1993). Comparatively wide body breadths also support the contention that the Yayoi people evolved in a colder environment (Temple, 2007a). These findings suggest that the Yayoi people had limb proportions that indicate retention of cold-adapted morphology.

Depth-of-time is an important consideration regarding the retention of cold-derived limb proportions among the Yayoi people. Intralimb indices among Early Upper Paleolithic people from Europe are similar to groups from warm, low latitude climates in association with migrations into this region, most likely from Africa (Trinkaus, 1981; Holliday, 1997b). Evidence for brachial and crural index variation among Early Upper Paleolithic humans in response to the periglacial conditions of Europe are, however, absent indicating that these changes occur over significant periods of time (Trinkaus, 1981; Holliday, 1997b). This idea is also supported by tighter correlations between the intralimb indices of immigrants with the mean annual temperature found in their homeland, rather than living location (Trinkaus, 1981). More recently, secular studies of indigenous North Americans have reported a significant depth-of-time between the initial colonization of specific regions in the Americas and changes in intralimb indices that correspond to specific climates (Auerbach, 2007). All Yayoi sites in this study are dated to points very near the first arrival of these migrant groups to Honshu and Northern Kyushu (2,500 through 1,700 yBP). It is, therefore, likely that the Yayoi people experienced little change in limb shape in association with a relatively brief colonization of the Japanese Islands. Similarity in limb proportions between the Yayoi and modern Japanese samples (Figs. 6, 7), which were separated by a temporal period of approximately 2,500 years, further supports this hypothesis.

CONCLUSIONS

This study documented relative limb length variability and relationships between limb shape and climatic adjustment between Jomon and Yayoi people. Jomon foragers had comparatively longer distal relative to proximal appendages when compared to Yayoi people. Multivariate analysis suggests Jomon people had limb proportions that were similar to other groups from tropical/temperate environments at lower latitudes, while Yayoi people express limb proportions that were more similar to groups who occupied colder environments at higher latitudes.

Biodistance analyses indicate that the ancestors of Jomon people migrated to Japan from North/Central or Southeast Asia around 30,000 yBP (Turner, 1976; Turner, 1990; Hanihara, 1991; Turner, 1992; Imamura, 1996a; Pietrusewsky, 1999; Matsumura and Hudson, 2005; Seguchi et al., 2007). Hypotheses suggesting a North/Central or Northeast Asian ancestry for the ancestors of Jomon people are, however, supported by genetic studies drawn from living Ainu (Omoto and Saitou, 1997; Hammer et al., 2007). Based on evidence that suggests the ancestors of Jomon foragers migrated to Japan from a colder environment, it is likely that Jomon limb proportions changed following long-standing colonization of the climatically mild Japanese Islands. In contrast, Yayoi people, who represent a more contemporary series

of migrations to this region from Northeast Asia (Hanihara, 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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