

Geographic Variation in Body Form of Prehistoric Jomon Males in the Japanese Archipelago: Its Ecogeographic Implications

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ABSTRACT Diversity of human body size and shape is often biogeographically interpreted in association with climatic conditions. According to Bergmann's and Allen's rules, populations in regions with a cold climate are expected to display an overall larger body and smaller/shorter extremities than those in warm/hot environments. In the present study, the skeletal limb size and proportions of prehistoric Jomon hunter-gatherers, who extensively inhabited subarctic to subtropical areas in the ancient Japanese archipelago, were examined to evaluate whether or not the inter-regional differences follow such ecogeographic patterns. Results showed that the Jomon intralimb proportions including relative distal limb lengths did not differ significantly among five regions from northern Hokkaido to the southern Okinawa Islands. This suggests a limited co-variability of the intralimb proportions with climate, particularly within genealogically close popula-

tions. In contrast, femoral head breadth (associated with body mass) and skeletal limb lengths were found to be significantly and positively correlated with latitude, suggesting a north-south geographical cline in the body size. This gradient therefore comprehensively conforms to Bergmann's rule, and may stem from multiple potential factors such as phylogenetic constraints, microevolutionary adaptation to climatic/geographic conditions during the Jomon period, and nutritional and physiological response during ontogeny. Specifically, the remarkably small-bodied Jomon in the Okinawa Islands can also be explained as an adjustment to subtropical and insular environments. Thus, the findings obtained in this study indicate that Jomon people, while maintaining fundamental intralimb proportions, displayed body size variation in concert with ambient surroundings. *Am J Phys Anthropol* 149:125–135, 2012. ©2012 Wiley Periodicals, Inc.

Body size and shape exhibit considerable variation among modern human populations globally, which is frequently interpreted in association with the ecogeographic rules of Bergmann (1847) and Allen (1877). According to Bergmann's rule, human groups living in cold climates can be expected to possess a larger/heavier body than those in warm environments, to decrease the ratio of surface area to body mass. Likewise, according to Allen's rule, humans in cold areas are expected to have smaller/shorter appendages relative to the body trunk size. Furthermore, effects of insular environments on animal body size are also proposed, commonly known as the island rule or Foster's (1964) rule, which can lead to insular dwarfism and gigantism of large and small animals, respectively (MacArthur and Wilson, 1967). Given this rule, humans living on moderately small and isolated islands may tend to have a smaller body size than those on the mainland. A number of anthropological studies have yielded results in general congruence with these ecogeographic rules (e.g., Schreider, 1950, 1957, 1964, 1975; Newman, 1953; Roberts, 1953; Newman and Munro, 1955; Roberts and Bainbridge, 1963; Crognier, 1981; Trinkaus, 1981; Jacobs, 1985; Cavalli-Sforza, 1986; Ruff, 1991, 1994, 2002; Katzmarzyk and Leonard, 1998; Baba, 2000; Stock and Migliano, 2009;

Wells, 2012). Even amongst regional groups of modern Japanese, Kouchi (1983) demonstrated a significant negative correlation between annual mean temperature and body mass, although no significant correlation between temperature and body height.

In addition, from the perspective of Allen's rule, relative lengths of distal to proximal limb segments (i.e., brachial and crural indices for upper and lower limbs, respectively) have also been examined as indicators of phenotypic adaptation to climatic conditions (e.g., Trin-

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kaus, 1981; Ruff, 1994, 2002; Holliday and Falsetti, 1995; Holliday, 1997a,b, 1999; Katzmarzyk and Leonard, 1998; Temple et al., 2008; Holliday and Hilton, 2010), where relatively short distal extremities reflect evolutionary adjustment to cold climate.

However, results of earlier comparative studies on skeletal body form, specifically on the limb segment proportions, did not always coincide with ecogeographic predictions (e.g., Bindon and Baker, 1997; Katzmarzyk and Leonard, 1998; Kurki et al., 2008; Holliday and Hilton, 2010). Kurki (2008) found that some small-bodied human groups did not necessarily possess expected body/limb proportions for the regions in question. Furthermore, comparing body proportions among two circumpolar Inuit groups from “precontact” periods and other global modern human groups, Holliday and Hilton (2010) showed most body-shape measurements to be indistinguishable both between two Inuit groups from different latitudes and between the Inuit samples and Europeans. Such ambiguous results may stem partly from analyzing temporally and geographically distant populations together (Ruff, 1994, 2002; Katzmarzyk and Leonard, 1998).

In this context, for further corroboration of the ecogeographic significance of human phenotypic diversity, it should be reasonable to investigate the body form of prehistoric foragers who inhabited continuous latitudinal areas in an equivalent chronological period. Jomon people were hunter-gatherer-fishers distributed throughout the Japanese archipelago for ~10,000 years of “Jomon period” (ca., 13000–2350 yBP). Jomon culture is associated with pottery characterized by its cord/rope impressions and flame-like patterns. Active debate still remains regarding the origin and biological diversity of Jomon people (e.g., Hanihara and Ishida, 2009; Nakashima et al., 2010; Adachi et al., 2011; Mizoguchi, 2011), but both metrical and nonmetrical craniodental studies indicate Jomon people as having population continuity from northern Hokkaido to southern Okinawa, particularly during the latter half of the Jomon period (e.g., Dodo, 1982; Yamaguchi, 1982; Kondo, 1994; Matsumura et al., 2001; Matsumura, 2007; Hanihara and Ishida, 2009; Ishida et al., 2009; Fukase et al., 2012). Despite the fact that the Okinawa Islands are located close to Taiwan, archeological evidence indicates a considerable cultural gap between the two areas during the Japanese Jomon period (Okinawa Prefectural Culture Promotion Foundation, 2003). Matsukusa et al. (2010) recently showed little genetic connection between modern inhabitants of Okinawa, including the most southwestern Sakishima islanders, and Taiwan aborigines. This finding partly supports the distinct population histories of the two regions.

The arc-shaped Japanese archipelago consists of four major islands (Hokkaido, Honshu, Shikoku, and Kyushu) and numerous ancillary islands including the southern Okinawa Islands (see Fig. 1). The ~3,000 km of this northeastern to southwestern range extends from the subarctic to subtropical zones, although the middle part of the archipelago largely lies in the temperate zone. Previous ecogeographic studies have revealed a tendency of some extant mammals in Japan (e.g., deer, wild boar, and Japanese macaques, all of which consist of some subspecies) to become larger/heavier in northern/colder regions, conforming to Bergmann’s rule (Hamada, 1986; Ohtaishi, 1986; Hamada et al., 1996a,b; Endo et al., 2002; Ozaki et al., 2007; Anezaki et al., 2008). In particular, several extant/extinct large mammals on the

Okinawa Islands display excessively smaller body size than mainland and/or ancestral counterparts, which is therefore also interpreted as an adaptation to the subtropical insular environment (Matsumoto and Otsuka, 2000; Albarella et al., 2009; van der Geer et al., 2010).

Concerning geographic variation in Jomon body size, Ogata (1973, 1981) found that skeletal limb dimensions tended to be greater overall in northeastern than in southwestern Honshu. Recently, comparing femoral head breadth and estimated relative body mass between individuals from Hokkaido and central Honshu, Temple and Matsumura (2011) also demonstrated greater body mass of the northern Jomon. Conversely, the Jomon on the southern Okinawa Islands are shown to have significantly shorter long bones than those on Honshu (Matsumura and Ohta, 1993; Doi et al., 2000; Doi, 2003).

In terms of intralimb proportions, Jomon people are known to exhibit relatively elongated distal limbs compared with both Yayoi-period immigrants, thought to have come from the Asian continent to the Japanese Islands subsequent to the Jomon period (i.e., during the Yayoi period of 2350–1650 yBP), and modern Japanese (Okamoto and Seki, 1930; Yamaguchi, 1982, 1989, 1994; Doi et al., 2000; Wada and Motomura, 2000; Takigawa, 2005, 2006; Temple et al., 2008, 2011; Temple, 2011). However, the number of earlier studies that argued geographic differences in Jomon intralimb proportions is limited. Yamaguchi (1989) indicated a slight northeast-southwest gradient in brachial and crural indices within Honshu, implying an association with Allen’s rule. However, Takigawa (2006) and Temple and Matsumura (2011) subsequently showed that the indices are higher in Hokkaido compared to Honshu Jomon people, which does not conform to expectations based on Allen’s rule (Temple and Matsumura, 2011).

Thus, previous studies have collectively suggested some ecogeographic significance in Jomon body size and proportions, but only a few regions of the Japanese archipelago were examined in each study. Therefore, the present study compared the skeletal limb size and proportions among five regions of Japan: Okinawa, Kyushu, Kanto-Tokai, Tohoku, and Hokkaido (Fig. 1), with particular attention paid to the body form of the Okinawa Jomon experiencing subtropical and insular environments. The main working hypothesis tested in this study was whether or not overall Jomon body size and intralimb proportions covary with latitude.

MATERIALS AND METHODS

The skeletal materials used in the present study are listed in Table 1. Adult male specimens without apparent skeletal deformation and pathological traits were selected. Sex of the Jomon sample was evaluated mostly from pelvic morphology (Buikstra and Ubelaker, 1994). For several specimens that lacked sufficiently preserved associated pelvic remains, sex estimation was made from appendicular morphology including general size and muscle attachment development, particularly considering well-developed femoral pilasters as a key indicator of Jomon males (Mizushima et al., 2004). The size of the skeletal sample from the “Incipient” to “Initial” Jomon period of about 13,000 to 6,000 yBP is currently very limited (Kohara et al., 2011). In addition, individuals from the Initial Jomon period have been reported as more gracile, or less robust, than those from the subsequent Jomon period (Ogata, 1981; Nakahashi and Oka-

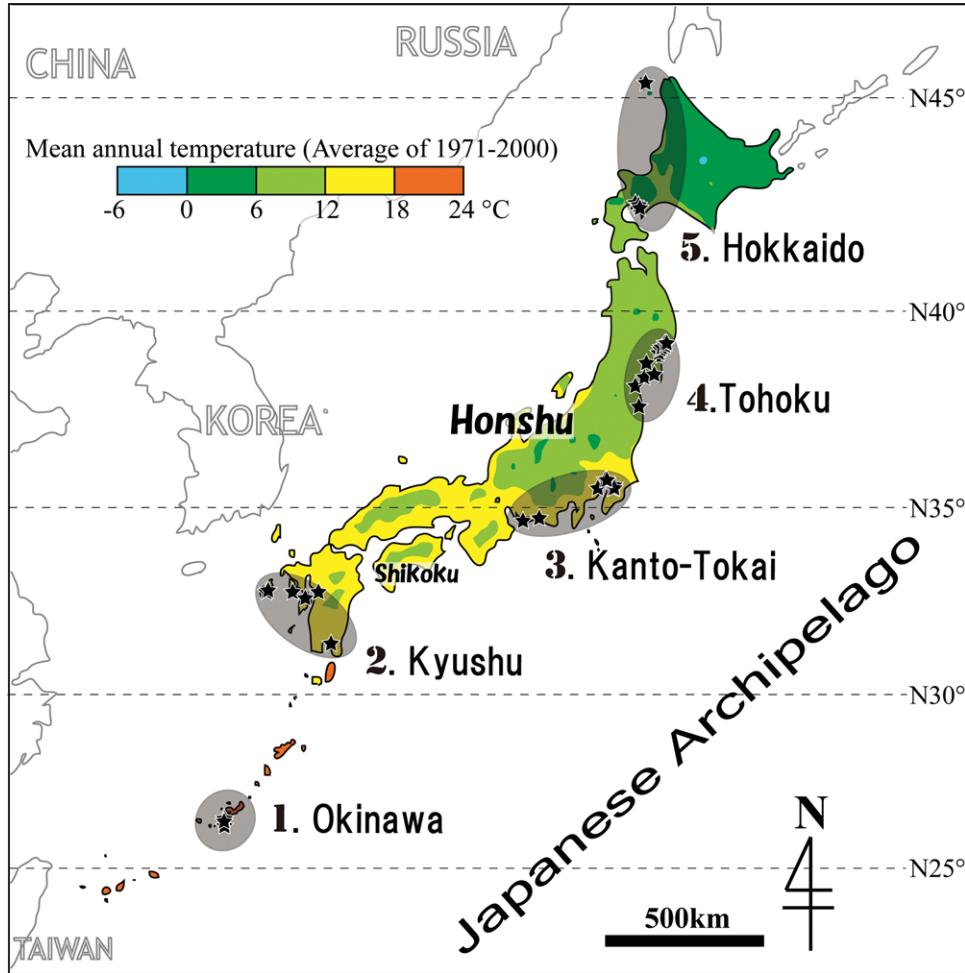


Fig. 1. Mean annual temperature distribution map [redrawn from a meteorological map made by Japan Meteorological Agency (2012)]. Stars on the map represent the Jomon site locations used in this study. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

zaki, 2009; Kohara et al., 2011). This study therefore used the available specimens spanning from the “Early” to “Final” Jomon periods (ca., 6000 to 2350 yBP) for analysis. However, part of the sample from Okinawa is dated from the Final Jomon to Early Yayoi period (ca., 3000 to 2250 yBP), during which the hunting-fishing-gathering subsistence strategy continued in Okinawa, unlike in Honshu (Imamura, 1996a; Okinawa Prefectural Culture Promotion Foundation, 2003). Furthermore, Ikeda (1985) found that coastal Jomon populations had more robust limb bones than inland/mountain groups. Isotope analyses of human remains have demonstrated significantly different dietary habits between coastal and inland/mountain Jomon groups (Minagawa, 1995, 2001; Akazawa, 1999). For this reason, the Jomon sites used in this study were confined to coastal sites. The “modern Japanese” sample was additionally used merely as a referential out-group that has long been compared to the Jomon. The modern Japanese specimens come from anatomy department collections made by the University of Tokyo from ~1890 to 1910 AD.

Region numbers, one to five, were assigned to the geographic areas of the Jomon sites, as seen in Figure 1, from southern Okinawa to northern Hokkaido. 1) Okinawa is the southernmost part of the Japanese archipel-

ago, ~600 km remote from the southern end of Kyushu, and is characterized by a subtropical insular environment. According to the Japan Meteorological Agency (2012), mean temperatures of 1950–2000 AD were 22.6°C (yearly average), 16.5 °C (February), and 28.1°C (August) in Naha, the capital city of Okinawa Prefecture. 2) Kyushu is one of the four major Japanese Islands, located southwest of Honshu. A large part of Kyushu is in the temperate zone with vegetation consisting of evergreen broadleaf trees. The above mean temperatures were 16.7, 7.3, and 27.6°C, respectively, in Nagasaki, Nagasaki Prefecture. 3) Kanto-Tokai denotes a region located at the center of Honshu, experiencing temperatures of 15.6, 5.7, and 26.9°C, respectively, in Tokyo. 4) Tohoku, literally meaning “northeast,” is a northeastern region in Honshu, and largely lies in the temperate zone with vegetation of deciduous broadleaf trees. The temperatures were 12.0, 1.5, and 24.0°C, respectively, in Sendai, Miyagi Prefecture. 5) Hokkaido is the northernmost part of the archipelago, largely being in the subarctic zone characterized by its coniferous woodland vegetation. The temperatures in Sapporo were 8.3, -3.8, and 21.8°C, respectively. It must be noted that the climate in this archipelago has certainly varied since the Early Jomon period, but the variation range of the an-

TABLE 1. *Materials*

Group		<i>N</i>	Sex	Site name and latitude ^a	Dates	Institution
Jomon	1. Okinawa	18	Male	Bugeido (26.14), Mashiki-Azamabaru (26.28), Kumaya (26.33)	3000-2250 BP	NU, OPMAM
	2. Kyushu	21	Male	Kunugibaru (31.46), Okinohara (32.55), Wakimisaki (32.58), Miyashita (32.62), Shirahama (32.66), Todoroki (32.68)	6000-2350 BP	KPAC, NU, UMUT
	3. Kanto-Tokai	33	Male	Hobi (34.63), Shijimizuka (34.71), Saihiro (35.49), Ichihara (35.52), Kikuma-tenaga (35.54), Rokutsu (35.55), Chidorikubo (35.57), Kasori (35.62), Kosaku (35.72), Ubayama (35.74), Horinouchi (35.75), Yoyama (35.75)	5000-2350 BP	SMU, STMU, UMUT
	4. Tohoku	34	Male	Sanganji (37.83), Kawakami (38.19), Satohama (38.34), Numazu (38.43), Aoshima (38.67), Tagara (38.90), Nakazawahama (38.95), Monzen (38.98), Usozawa (38.98), Hosoura (39.00), Miyano (39.05), Oohora (39.07)	5000-2350 BP	HMJO, THM, TUM, UMUT
	5. Hokkaido	23	Male	Motowanishi (42.35), Kitakogane (42.40), Takasago (42.53), Funadomari (45.43)	6000-2350 BP	SMU, UMUT
Modern Japanese		31	Male	(collection made at the Kanto district of Japan in ca.1890-1910 AD)		UMUT

N, Sample size.

HMJO, The Historical Museum of Jomon Village Okumatsushima; KPAC, Kagoshima Prefectural Archaeological Center; NU, Nagasaki University; OPMAM, Okinawa Prefectural Museum & Art Museum; SMU, Sapporo Medical University; STMU, St. Marianna University School of Medicine; THM, Tohoku History Museum; TUM, The Tohoku University Museum; UMUT, The University Museum, The University of Tokyo.

^aLatitudinal unit is degree of north latitude.

nual mean temperature is estimated to fall approximately within 2°C (Yasuda, 1994; Koizumi, 2008).

Metric attributes of postcranial morphology were collected with a digital caliper and an osteometric board, following Martin's definitions and methods (Martin and Saller, 1957; Knussmann, 1988). The measurements used in this study were antero-posterior femoral head breadth (abbreviation, FHB; Martin's No., M-19), bicondylar femoral length (FemL, M-2), maximum tibial length (TibL, M-1a), maximum humeral length (HumL, M-1), and maximum radial length (RadL, M-1). Specifically, FHB was used as an indicator of body mass, following many earlier studies (e.g., Ruff et al., 1991, 2012; McHenry, 1992; Ruff, 1994; Grine et al., 1995; Auerbach and Ruff, 2004; Weinstein, 2005; Kurki et al., 2008, 2012; Auerbach, 2011b; Temple and Matsumura, 2011). Body mass was then estimated from FHB using a recently proposed equation by Ruff et al. (2012): BM (males) = 2.80 × FHB – 66.7. However, although this equation was developed from a large number of European Holocene skeletons, the direct application to Jomon samples may be problematic. Furthermore, accuracy limitations must be considered for body mass estimation only from FHB (see Auerbach and Ruff, 2004; Ruff et al., 2012). For these reasons, the estimates were merely presented as referential values, and not employed for further analysis in this study.

The ratios of FHB to FemL and FHB to lower limb length (defined by FemL+TibL) were then derived for rough estimation of body mass/height proportions. Biliac breadth and skeletal trunk height (the summed height of vertebral column) should additionally be required to obtain closer estimates of body trunk proportions (e.g., Ruff, 1994; Kurki et al., 2008; Holliday and Hilton, 2010). However, unfortunately, these data were not collected in this study, chiefly because many of the individuals lacked well-preserved associated pelvic and vertebral remains. For comparisons of intralimb proportions, brachial and crural indices were calculated as RadL/HumL × 100 and TibL/FemL × 100, respectively.

To test the presence of a south-north geographic gradient in the limb dimensions and proportions within the Jomon groups, Spearman's rank correlation coefficients between the measurements and the latitudes of the sample sites (Table 1) were evaluated. Two-tailed Scheffe's multiple comparison tests were then conducted for the interregional comparisons both within the Jomon groups and among the Jomon and modern Japanese groups. Furthermore, to summarize the measured dataset and present an overview of individual positions in the total variation, principal component analysis (PCA) was performed using the five linear measurements. Individuals with more than two missing values were excluded from the PCA. However, missing values were, when present

for the specimens employed, complemented with values estimated by within-group stepwise multiple regression using available variables. This approach, despite many inherent limitations in missing value estimation (see Auerbach, 2011a), should not drastically affect eventual consequence. The PCA was conducted with a correlation matrix derived from standardized (*Z*-score) values. All statistical analyses were carried out using the software IBM SPSS Statistics (Version 20, IBM). Statistical significance of $P < 0.05$ is referred to in describing the results.

RESULTS

Results of the measurements and statistical analyses are listed in Table 2 and shown as box plots in Figure 2. Among the Jomon groups, the femoral head breadth and all limb lengths were significantly and positively correlated with latitude. Multiple comparison tests also demonstrate that, in most cases, the Jomon in Okinawa had significantly smaller/shorter values than those in Tohoku and/or Hokkaido. In contrast, all the indices showed no correlational relationships, nor did they differ statistically among the five regions. These observations indicate that the overall body size/mass of Jomon people tended to be larger in northeastern regions than in southwestern regions of the Japanese archipelago, but the intralimb proportions did not differ geographically.

Compared to the modern Japanese, the Jomon possessed relatively longer distal limbs, and indeed exhibited significantly greater values in both brachial and crural indices, as observed by many earlier studies (e.g., Okamoto and Seki, 1930; Yamaguchi, 1982, 1989, 1994; Doi et al., 2000; Takigawa, 2005, 2006; Temple et al., 2008). Both ratios of FHB to FemL and FHB to lower limb length tended to be lower in the Jomon groups than in the modern Japanese, which is however not statistically significant.

Results of the PCA are displayed in Figure 3. The first two principal components in total reached ~90% contribution to the overall variation. The first principal component (eigenvalue, 4.0; contribution ratio, 80.3%) is associated with general limb size (Fig. 3A), clearly showing a positive correlation with the region number (Fig. 3B). The second principal component (eigenvalue, 0.5; contribution ratio, 9.4%) mainly involves femoral head breadth and distal limb lengths. When compared to the modern Japanese, the Jomon samples had relatively longer distal limb lengths, resulting in their lesser PC2 scores. However, the eigenvalue fell far below 1.0, which would limit the interpretation that could be derived from PC2.

DISCUSSION

Regarding intralimb proportions, all the ratio measurements examined in the present study did not indicate a north-south geographic cline, nor did they differ significantly among the five regional Jomon groups. This finding totally coincides with results of previous studies (Kato and Ogata, 1989; Yamaguchi, 1989; Takigawa, 2006; Temple and Matsumura, 2011), and suggests that, despite variation in ambient climate, Jomon people from subarctic Hokkaido to subtropical insular Okinawa shared similar body proportions. Such limited regional variation is also observed in Jomon craniofacial attributes (Dodo, 1982; Yamaguchi, 1982; Kondo, 1994; Matsumura et al., 2001; Matsumura, 2007; Hanihara and Ish-

ida, 2009; Ishida et al., 2009; Fukase et al., 2012). Furthermore, the intralimb proportions were clearly and consistently distinctive from modern Japanese. These facts suggest that brachial and crural indices may not always exhibit a high correlation with climatic conditions within genealogically close human groups, implying genetic and developmental constraints on expression of population-specific intralimb proportions. For instance, differences and similarities in intralimb proportions are found among the Jomon and comparative samples at very early stages of postnatal ontogeny (Temple et al., 2011; Cowgill et al., 2012), mirrored by other studies of intralimb index development (Johnston, 1968; Y'Edynak, 1976; Ruff and Walker, 1993; Ruff et al., 2002). Studies of fetal skeletons demonstrate that these differences are present prior to birth (Schultz, 1923; Warren et al., 2002).

However, the limb segment proportions are also potentially influenced by nonclimatic elements such as allometry, since distal limb length scales with positive allometry relative to proximal limb length, specifically for lower limbs (Meadows and Jantz, 1995; Holliday, 1999; Jantz and Jantz, 1999; Holliday and Ruff, 2001; Sylvester et al., 2008; Auerbach and Sylvester, 2011). This might be partially responsible for the comparatively high crural index value in the large-bodied Hokkaido Jomon. Nevertheless, the results failed to show a geographic gradient in the intralimb proportionality of the Jomon, and accordingly could not support the ecogeographic covariation of the Jomon relative distal limb length to climate.

In contrast to the ratio measurements, all the linear measurements (i.e., femoral head breadth and maximum limb lengths) exhibited a clear north-south geographic cline, which is collectively consistent with results of previous studies (Ogata, 1981; Ishida et al., 1988; Matsushita and Ohta, 1993; Takigawa, 2006; Temple and Matsumura, 2011). This indicates a gradual increase in Jomon body size with latitude, coinciding with Bergmann's rule. The findings also suggest that, although body height is not necessarily correlated strongly with climate among world-wide human populations (e.g., Ruff, 1994), the regional difference in Jomon body size is observable in both body mass and height.

It must be noted, however, that the present study merely clarified the presence of a northeast-southwest gradient in body size, and hence it remains an open question when and how the cline became manifest. Considering contexts relevant to the Jomon people, this issue involves at least three aspects: 1) phylogenetic constraint or retention of ancestral physique, 2) micro-evolutionary adaptation to climate during the Jomon period, and 3) nutritional and physiological response to growing conditions. These models have also been discussed in explaining the contrasting intralimb proportions between the Jomon and the subsequent Yayoi immigrants (Nakahashi et al., 1989; Yamaguchi, 1994; Temple et al., 2008).

First, the phylogenetic constraint model concerns the origin and migration history of the Jomon. Several human migration routes to the Japanese Islands during the Late Pleistocene are proposed: a southwestern route via the Ryukyu Islands including the Okinawa Islands, a western route via the Korean Peninsula, and a northern route via Sakhalin Island (e.g., Ikeda, 1998; Adachi et al., 2009, 2011; Hanihara and Ishida, 2009; Nakashima et al., 2010; Mizoguchi, 2011). In this light, a significant body-size difference can be simultaneously assumed among the ancestral populations, perhaps

TABLE 2. Statistics of measurements

	Jomon					MJ	Correlation ^a		Scheffe's multiple comparison test ^b	
	1. Okinawa	2. Kyushu	3. Kanto-Tokai	4. Tohoku	5. Hokkaido		Jomon	Jomon + MJ	Jomon	Jomon + MJ
Antero-posterior femoral head breadth (FHB, in mm)	N	14	29	25	16	30	0.315 ^{**}	1 < 5	1 < 5	
	Mean	42.4	43.9	44.0	45.1	45.7				
	SD	3.0	3.1	2.0	1.7	2.1				
Estimated body mass from FHB (in kg) ^c	Mean	52.0	56.2	56.5	59.5	61.3				
Bicondylar femoral length (FemL, in mm)	N	11	11	24	18	16	0.298 ^{**}	1 < 4, 5	1 < 4	
	Mean	392.6	406.2	413.8	420.3	418.5				
	SD	28.2	24.9	16.6	20.4	15.5				
Maximum tibial length (TibL, in mm)	N	6	10	16	15	14	0.433 ^{**}	1 < 5	1, MJ < 5	
	Mean	325.0	336.2	342.0	349.9	355.1				
	SD	12.9	27.7	17.9	19.3	14.9				
Maximum humeral length (HumL, in mm)	N	6	12	20	19	12	0.385 ^{**}	1 < 4, 5	1 < 4, 5, MJ	
	Mean	269.7	287.7	290.0	294.9	300.2				
	SD	25.4	7.8	12.8	19.8	12.3				
Maximum radial length (RadL, in mm)	N	5	11	18	18	11	0.497 ^{**}	1 < 4, 5	1, 2 < 5	
	Mean	219.4	225.9	230.2	238.0	242.3		2 < 5	MJ < 4, 5	
	SD	19.3	10.4	8.7	12.9	9.4				
The ratio of FHB to FemL (FHB / FemL x 100)	N	7	9	23	17	15	0.075	-	-	
	Mean	10.9	10.9	10.8	10.7	10.9				
	SD	0.36	0.32	0.37	0.39	0.52				
The ratio of FHB to lower limb length [FHB / (FemL+TibL) x 100]	N	3	9	14	12	11	-0.201	-	-	
	Mean	5.88	5.97	5.89	5.85	5.81				
	SD	0.24	0.17	0.20	0.23	0.30				
Crural index (TibL / FemL x 100)	N	3	9	14	12	11	0.113	-	MJ < 5	
	Mean	84.0	83.3	82.7	83.4	84.8				
	SD	1.7	2.1	1.7	1.5	1.9				
Brachial index (RadL / HumL x 100)	N	3	10	14	15	9	0.074	-	MJ < 1, 2, 3, 4, 5	
	Mean	81.7	79.4	80.6	80.3	80.3				
	SD	2.2	1.9	2.0	4.2	1.7				

N, sample size. MJ, modern Japanese.

^a Spearman's rank correlation coefficient between measurement and latitude. Significance level: * $P < 0.05$; ** $P < 0.01$.

^b Significance level: $P < 0.05$. No significant difference is denoted by "-".

^c Body mass was estimated from a FHB equation proposed by Ruff et al. (2012).

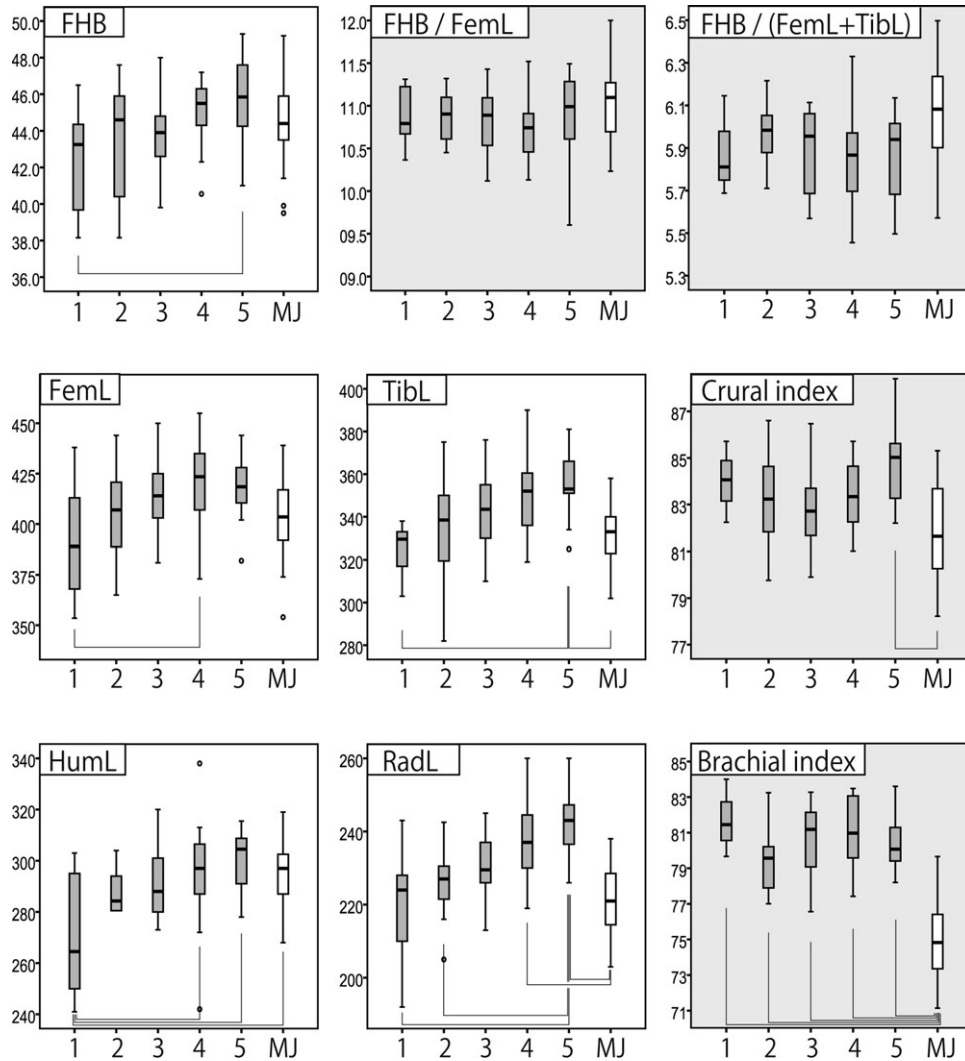


Fig. 2. Results of the measurements. Upper and lower margins of boxplots represent the 75th and 25th percentiles, respectively. The median is the line bisecting the box. Boxes of the Jomon samples and the chart backgrounds of ratio measurements are darkly colored. Numbers on the horizontal axis correspond to region numbers in Figure 1 (1, Okinawa; 2, Kyushu; 3, Kanto-Tokai; 4, Tohoku; 5, Hokkaido). MJ, modern Japanese. Significantly different groups in Scheffe’s multiple comparison test (the rightmost column in Table 2) are connected by lines in each box-plot.

resulting in the basis of the geographic cline observed in this study. In fact, similar to the Okinawa Jomon, Minatogawa fossil humans from Okinawa (ca., 18,000 yBP) are characterized by remarkably short stature (Baba and Endo, 1982; Baba and Narasaki, 1991; Baba, 2000). It is, however, an unresolved issue whether the Minatogawa humans had a direct genealogical relationship with the subsequent Jomon population (e.g., Suzuki and Hanihara, 1982; Baba, 2003; Kaifu et al., 2011; Kubo et al., 2011; Mizoguchi, 2011; Saso et al., 2011; Suwa et al., 2011). Ultimately, validation of this model requires additional discovery of Paleolithic human fossils in the Japanese Islands, particularly of presumed northern immigrants who introduced the Siberia-derived microblade technology into Hokkaido and Honshu between 20,000 and 14,000 yBP (Imamura, 1996b; Kimura, 1997; Hanihara and Ishida, 2009).

Second, the micro-evolutionary adaptation model premises selective pressure on individual and/or population body size in general accordance with ecogeographic

patterning of Bergmann’s rule, hypothesizing that the geographic cline was achieved mostly during the Jomon period. Additionally, considering the small body size of the Okinawa Jomon, the apparent north-south gradient may also include the effect of the subtropical insular environment. The “pygmy” phenotype is frequently seen among modern human populations living in warm-humid insular conditions, and has been therefore interpreted as an evolutionary adaptation for energy efficiency associated with food limitation, mobility in rainforests, and life-history strategy (see reviews in Perry and Domingy, 2009; Stock and Migliano, 2009; van der Geer et al., 2010). In this regard, even though they had had little phylogenetic continuity with the Late Pleistocene inhabitants of the Okinawa Islands (Kaifu et al., 2011), the Okinawa Jomon might also have been driven to reduce their body size in harmony with natural ambience.

Finally, the nutritional and physiological model expects that the regional difference in Jomon body size should be to some extent acquired in a single generation

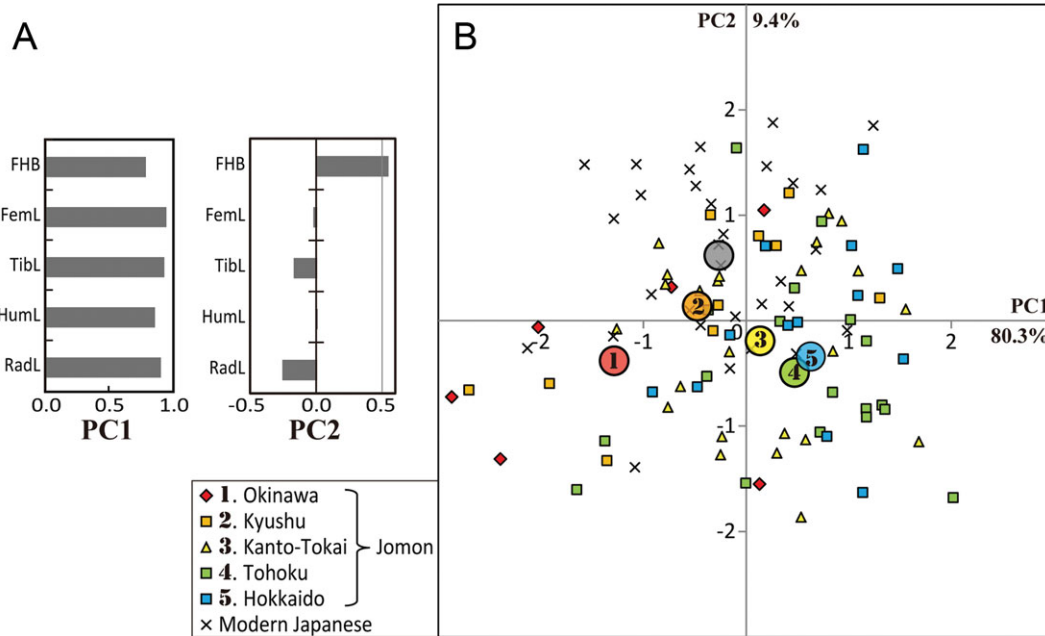


Fig. 3. Results of PCA. (A) Factor loadings of the measurements. (B) Principal components graph. Large circles with and without region numbers represent centroids for the Jomon groups and the modern Japanese, respectively. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

owing to growth conditions. Isotopic analyses of Jomon skeletal remains have clarified region-specific dietary habitats among coastal sites in Japan (e.g., Takamiya et al., 1970; Minagawa, 1995, 2001; Yoneda et al., 2002; Takamiya and Chisholm, 2004), and showed that Jomon people in Hokkaido and Okinawa particularly consumed larger marine mammals and reef fishes/shells, respectively, compared with those in Honshu (Yoneda et al., 2011). This could cause regional differences in the calorie and protein intake during growth, contributing to the adult body size differences observed. In addition, body/limb proportions are associated with nutrition, partially accompanied by general body size change (Shapiro, 1939; Tanner et al., 1982; Bogin et al., 2002; Bogin and Varela-Silva, 2010). Future studies that assess Jomon nutritional status regionally may help explain the apparently more truncated limbs in Okinawa compared to main-island Honshu. Furthermore, numerous physiological experiments have demonstrated that, conforming to Bergmann's and Allen's rules, a laboratory animal reared under a satisfactory food supply in cool/cold ambient temperature tends to gain more weight and exhibit a stockier body trunk with shorter extremities than that in hot/hot-humid environments (e.g., Sumner, 1909; Sundstroem, 1922; Ogle, 1933; Ashoub, 1958; Harrison et al., 1959; Harrison, 1963; Lee et al., 1969; Weaver and Ingram, 1969; Riesenfeld, 1973; Al-Hilli and Wright, 1983). However, a variety of rearing conditions have also provided inconsistent results in particular on body weight, partly because extreme cold stress early during the postnatal stage encompasses considerable growth retardation (Emery et al., 1940; Barnett et al., 1959; Barnett and Scott, 1963; Chevillard et al., 1963; Riesenfeld, 1973; Serrat et al., 2008).

Thus, the mechanisms underlying the geographic cline in Jomon body size largely remain to be investigated. The aforementioned models therefore need to be tested by future research including ontogenetic studies that elucidate when population differences were expressed during

development (e.g., Fukase and Suwa, 2008, 2010; Mizushima et al., 2010; Holmes and Ruff, 2011; Temple et al., 2011). Nevertheless, the findings obtained in the present study indicate that Bergmann's ecogeographic rule should be comprehensively valid for the prehistoric human population, as well as for other larger mammals inhabiting the same archipelago.

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