Regional variations in the Jomon population revisited on craniofacial morphology

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Abstract Considering the geographical setting of the Japanese archipelago at the periphery of the Asian continent, regional variation in Jomon phenotypes can be interpreted as an outcome of population history. In this paper, we focused on regional variation in the Jomon craniofacial morphology and assumed that the observed regional differences were a reflection of the formation process of the Jomon population, which is a mixture of intrinsic expansion of an initial population with extrinsic influence of hypothetical gene flow. Compiled craniometric data from archeological site reports indicate that Jomon skulls, especially in the neurocranium, exhibit a discernible level of northeast-to-southwest geographical cline across the Japanese archipelago, placing the Hokkaido and Okinawa samples at both extreme ends. A quantitative genetic approach using an R-matrix method indicates that the cranial parts of the neurocranium and mandible exhibit a proportionately larger regional variation, the former of which confirms a trend of geographical cline and reveals the respective region presumably having different population histories with their respective local backgrounds. The following scenarios can be hypothesized with caution: (a) the formation of Jomon population seemed to proceed in eastern or central Japan, not western Japan (Okinawa or Kyushu regions); (b) the Kyushu Jomon could have a small-sized and isolated population history; and (c) the population history of Hokkaido Jomon could have been deeply rooted and/or affected by long-term extrinsic gene flows.

Key words: Population history of Jomon, R-matrix method, quantitative genetics

Introduction

The Jomon people are prehistoric natives of the Japanese islands, who existed from about 16000 to 2500 BP (Habu, 2004). Thus, they constitute an essential element of Japanese population history, which is now widely accepted as being described by a ‘dual structure model’ (Hanihara, 1991), previously referred to as a ‘hybridization hypothesis’ (see Yamaguchi, 1990 for a review). The origin or formation process of the Jomon people, however, has yet to be clarified. In terms of the human fossil remains, Pleistocene human skeletons are still few and fragmentary in Japan (Matsu’ura, 1999), and Pleistocene specimens from Asia and Australia do not consistently show any close relationship to Jomon (Mizoguchi, 2011). During the formation of the Jomon population, we can easily assume the significant effects of immigrants or gene flows from the Asian continent, as in the case

for the later population history of the Japanese. Based on accumulating Upper Paleolithic research in Japan, it seems that people might have been able to move over the land bridge or via island steps during the drop in sea level after c. 38000 calBP (see Izuho and Kaifu, 2015), and could have become founders of the Jomon population. Considering the geographical setting of the Japanese archipelago at the periphery of East Asia, we can hypothesize plausible routes connecting the rest of the Asian continent to Japan, which include the north (Siberia–Sakhalin to Hokkaido), west (Korean Peninsula to west Japan), and southwest routes (Taiwan to Ryukyu Islands). However, we cannot identify who these origin migrants were or how they have affected the initial Jomon population.

In this situation, it seems worth considering the geographical variation in the Jomon population. Assuming that the northward and southward immigrants were genetically and phenotypically different from each other, the population that formed would become heterogeneous in the geographically long Japanese archipelago. If the initial population had been homogeneous, the geographical variation would increase with time and distance from the hypothetical center of human expansion. If we know the regional variation in the Jomon population at a specific time as well as its time course,

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we can identify the formation process of this population. This can be done without identifying the plausible ancestors among the fossil specimens in the surrounding continents.

We used this approach on craniometric data for the Jomon population. Using the R-matrix method (Relethford and Blangero, 1990; Relethford and Harpending, 1994), we applied the model of within- and between-population variances in the population genetics to regional variation in Jomon craniofacial morphology. The R-matrix method extends genetic theory to phenotypic traits by using heritability, assuming the phenotypic variation to be in principle parallel to the genetic variation. It calculates *F*_{st} values, which is the proportion of the regional variance to the total variance, and assesses the magnitude of variance within a subpopulation in terms of fixation (bottleneck effect) or extrinsic gene flows. Although a similar approach had already been used in a previous study (Hanihara and Ishida, 2009), we revisit it with additional regional samples from the Kyushu and Okinawa regions and in a revised and detailed craniometric comparison using neurocranium, face, and mandible.

Regional variation in Jomon skeletal remains

The regional variation in Jomon crania has been documented in a pioneering study of Yamaguchi (1981), and suggests geographical cline from Kanto via Chubu (Yoshiko shell-mound) to Chugoku (Tsukumo shell-mound) regions based on the seven cranial measurements. From Kanto toward the west, the cranium becomes anteroposteriorly shorter and the face becomes flatter, although the regional difference is not significant, falling within a 1SD range from the means of Tsukumo Jomon samples (Yamaguchi, 1981). The mandible of the Hokkaido Jomon is noted to have a wider ramus than those in the other regions (Kaifu, 1995; Maeda, 2002). Considering the higher dietary dependency on marine mammals (Minagawa, 1995) and the lower caries frequency in the Hokkaido Jomon (Ohshima, 1996), Maeda speculated that the wider mandibular ramus of the Hokkaido Jomon was an adaptation to the different subsistence or diet compared with those in Honshu or Kyushu (Maeda, 2002).

Postcranial remains of Jomon skeletons have also provided interesting results regarding geographical variation (Fukase et al., 2012). These authors measured the lengths of the humerus, radius, femur, and tibia from the Early to the Final Jomon period and compared them among five regional divisions: Hokkaido, Tohoku, Kanto and Tokai, Kyushu, and Okinawa. Although the intermembral indices of radius-to-humerus and tibia-to-femur do not differ among the five regions, the respective lengths of the long bones showed a north-to-south cline from Hokkaido to Okinawa. In addition, the size of the femoral head showed the same tendency of geographical cline. The lengths of the postcranial long bones and the size of the femoral head can be interpreted as a proxy of the body size (stature and body weight). Fukase et al. attributed the observed cline of the body size to 'Bergmann's rule'; however, they did not exclude other factors, such as phylogenetic dissimilarity or ad hoc growth differences among the Jomon population (Fukase et al., 2012).

In addition, the magnitude of the regional differences has also been studied with respect to the maximum lengths and the midshaft diameters of Jomon limb bones (Takigawa,

2006). Mahalanobis distances calculated from 18 metrics among Hokkaido, Tohoku, Kanto, Tokai, Sanyo, and Kyushu regions showed an average of 8.64 in Jomon males, which was about 2.5 times as large as the average distance of 3.25 in modern Japanese males. The average distance was 14.73 in Jomon females, about 3 times as large as that in modern Japanese females (average = 4.70). These indicate that the morphological differences in limb bones among Hokkaido, Honshu, and Kyushu regions were larger in the Jomon population samples than those in the modern Japanese population.

In contrast to the results from the limb bones, the regional differences in craniofacial morphology have been regarded as relatively homogeneous. Yamaguchi calculated Penrose shape distances on 22 cranial measurements from Jomon males, and stated that the distances among the three regions of Kanto, Chubu (Yoshiko shell-mound), and Chugoku (Tsukumo shell-mound) were almost equivalent to those in modern Japanese males from Tohoku, Hokuriku, and Kinai regions (Yamaguchi, 1982). Thereafter, studies on regional differences in Jomon crania were repeated with the addition of Tohoku Jomon (Dodo, 1982) and those in southern Hokkaido (Dodo, 1986); the magnitude of the regional differences has been considered to be consistently the same as or even smaller than that found in the modern Japanese population. Kondo (1994) investigated the inter-site variation, calculating Mahalanobis distances on the cranium from Jomon sites in Kanto and Tokai areas and reported that the inter-site distances within the local Tokyo Bay or Mikawa Bay areas were often larger than the inter-regional distances.

Distance analyses based on non-metric cranial traits indicated a distinct position of the Tsukumo Jomon people in Chugoku region compared to those of the other regions (Yoshiko, Inariyama, Hobi and Ohta) (Mouri, 1988). A recent comparison among broader regional samples from Hokkaido, eastern Honshu (Tohoku and Kanto), and western Japan (Chugoku and Kyushu) has found no statistical significance between the regional samples, indicating the Jomon population to be relatively homogeneous (Dodo et al., 2012).

Based on dental morphology, Matsumura (1989) noted that the absolute and proportionate crown sizes of the Hokkaido Jomon are slightly different from those of others. In contrast, analysis of 21 dental non-metric traits revealed that the regional differences are quite limited, with the five regional Jomon subsamples of Hokkaido, Tohoku, Kanto, Tokai, and Sanyo showing a tight cluster (Matsumura, 2007).

Excluding a few cranial metrics, a consensus has emerged on the Jomon regional variation: this population was relatively homogeneous based on cranial and dental morphologies. In this paper, we investigated additional details on the regional variation in the cranial, facial, and mandibular morphologies of the Jomon population, who resided in the geographically extended Japanese archipelago. Reconsideration of the Jomon regional variation will provide us with further information about the formation process of the Jomon population in Japan, which can be interpreted as a genetic population structure using the R-matrix method.

Materials and Methods

A group of individual craniometric data was compiled from previously published excavation reports of Jomon sites or osteological studies of Jomon skeletal remains. The database is downloadable from the internet (<http://www.bs.s.u-tokyo.ac.jp/~keitai/JCdata.html>), although most of the individual reports were written in Japanese. During the compilation of data, we focused on chronological ages or associated layers with each Jomon skeleton and the definition of the craniometric measurements. Concerning the time periods, we focused on Early, Middle, Late, and Latest Jomon periods, omitting those from the Earliest (and Incipient) Jomon; we did not use specimens from the initial formation stage of the Jomon culture; however, we investigated those after the establishment of the Jomon culture that sustained a substantial population and flourished with sedentary hunting, gathering, and fishery subsistence patterns. Most of the site locations were shell-mounds, including several sites in caves or on coastal sand dunes. The regional divisions were, from north to south across the Japanese archipelago, Hokkaido, Tohoku, Kanto, Chubu, Kinki, Chugoku, Kyushu, and Okinawa. The data in the Hokkaido region include those of the Jomon and Epi-Jomon periods, the latter of which has been considered a direct descendant of Hokkaido Jomon in the succeeding time period of Yayoi in mainland Honshu. However, because the Hokkaido Epi-Jomon people were peculiar to and distinguished from other Jomon specimens in univariate and bivariate comparisons, we excluded the epi-Jomon samples from the multivariate R-matrix analysis of Jomon regional variation.

Sample sizes for each region (nine groups, including the two Hokkaido subgroups) are summarized in Table 1. In each region, sample distribution varied depending on the scale of each Jomon site; in some cases, a few major sites dominated the region. In the Kinki region, the total sample size was small, whereas the Kou site from Osaka prefecture occupied much of the sample. Based on the burial pit distribution, associated pottery type, and tooth ablation pattern, the human remains from the Kou site were considered a mixture of Early and Latest Jomon specimens with a few intrusions from the Yayoi period. We excluded those belonging to this period. A recent reanalysis of the chronology has suggested inclusion of the Middle Jomon specimen in the Kou site (Kusaka et al., 2015). In Okinawa, only two sites were available: Mabuni-hantabaru site and Iwadata site from

Gushikawa Island. These major sites, which had numerous individuals, have the potential to affect the regional variation analyses. Especially in the later multivariate R-matrix analyses where well-preserved specimens were used selectively, the effect of a few major sites may be very significant. Thus, we checked the sample distribution for each region, which should be non-biased and include as many individuals from many sites as possible.

Table 2 shows the cranial measurements and indices used in the present analyses. The linear measurements were selected to represent the craniofacial variation effectively in length, breadth, and height of the neurocranium and the face. In total, 17 measurements and 6 indices were compared using the analysis of variance (ANOVA) among the 9 subgroups; thereafter, Tukey's post-hoc multiple comparisons were conducted on each pair of interest. In addition, the size and shape of the neurocranium and the face were compared in the cranial modulus ($C_{mod} = (GOL + XCB + BBH)/3$), cranial length–breadth index ($XCB/GOL \times 100$), cranial breadth–height index ($BBH/XCB \times 100$), upper facial modulus ($UF_{mod} = (BPL + NPH + ZYB)/3$), upper facial index ($UF_{ind} = NPH/ZYB \times 100$), and ramus breadth–height index ($ramB/ramH \times 100$), respectively. Among-group comparisons are depicted in the boxplot. Significance level was set to 1% in the one-way ANOVA and multiple comparison methods.

Multivariate comparisons were designed to express the neurocranial, facial, and mandibular variations, each of which was composed of four, seven, and six measurements, respectively (Table 2). This was because the skull is considered a composite structure of several functional and developmental units, which may express different degrees of genetic stability or environmental plasticity. Under this assumption, the three units may exhibit different degrees of regional differentiation. After assessing the magnitude and the pattern of the regional variation along the Japanese archipelago, we could hypothesize a reasonable history for the Jomon population.

In order to avoid reduction in the number of available specimens by complete selection of the multiple measurements, we included a few missing values after linear interpolation: two missing values in the neurocranium, four in the face, and two in the mandible. In order to gain higher correlations between the variables in the linear interpolation, we added the measurements of porion–bregma height (pbH) in the neurocranium, and ectoconchion breadth (EKB) and zygomaxillary breadth (ZMB) in the face. Furthermore, in order to incorporate more individuals into each selected region, we combined the data for males and females after standardizing the individual data with the means and standard deviations for males and females, respectively.

The R-matrix method developed by Relethford and Blangero (1990) was applied to assess the craniofacial variation among and within the selected regions. As described by the original authors (Relethford and Blangero, 1990; Relethford and Harpending, 1994) and others (Roseman, 2004; Hanihara and Ishida, 2009), the R-matrix method has certain useful properties in studying the genetic relationships among populations based on the phenotypic traits. For example, (i) the average diagonal of an R-matrix provides an

Table 1. Sample sizes of the Jomon cranial series

Region	Abb.	Female	Male	F + M
Hokkaido Jomon	HokJ	23	15	38
Hokkaido Epi-Jomon	HokZ	6	21	27
Tohoku	Toh	41	58	99
Kanto	Kan	76	112	188
Chubu	Cbu	75	120	195
Kinki	Kin	13	15	28
Chugoku	Cgk	38	38	86
Kyushu	Kyu	24	33	57
Okinawa	OkI	9	15	24

Table 2. Craniofacial measurements used in the present study

	Abb.	Neurocranium	Face	Mandible
M1 max. cranial length	GOL	○		
M5 cranial base length	BNL	○		
M8 max. cranial breadth	XCB	○		
M17 basion–bregma height	BBH	○		
M20 porion–bregma height	pbH	△		
M40 facial length	BPL		○	
M44 bi-orbital breadth	EKB		△	
M45 bi-zygomatic breadth	ZYB		○	
M46 mid-facial breadth	ZMB		△	
M48 upper facial height	NPH		○	
M51 orbital breadth	Obmf		○	
M52 orbital height	OBH		○	
M54 nasal breadth	NLB		○	
M55 nasal height	NLH		○	
M65 bi-condylar breadth	kdLB			○
M66 bi-gonial breadth	goB			○
M68 mandibular length	pgL			○
M69 symphysial height	id-gnH			○
M70 ramus height	ramH			○
M71 ramus breadth	ramB			○
cranial modulus	Cmod			
cranial length–breadth index	XCB/GOL			
cranial breadth–height index	BBH/XCB			
upper facial modulus	UFmod			
upper facial index	UFind			
ramus breadth–height index	ram.ind			

Circle (○): used in the respective R-matrix analyses. Triangle (△): used only for missing value estimation.

estimate of the interpopulation variation represented by F_{st} ; (ii) the elements of an R-matrix are transformable to genetic distances, which can be visually represented (in the principal coordinate analysis in the present study); (iii) the diagonal elements of the R-matrix are the genetic distances of each population to the ‘centroid,’ defined in terms of the average genetic (phenotypic) measures over all populations; and (iv) under equilibrium conditions between gene flow and genetic drift, the expected variation in the population (i) and the distance from the centroid (r_{ii}) is expected to be linearly related (Relethford and Harpending, 1994). Relethford and Blangero (1990) have shown that deviations from this model of local population structure can be attributed to the differences in the rate of long-term gene flow. A population with greater long-range gene flows will show greater within-group variations than expected, and that with genetic isolation and/or drift will show less within-group variations than expected. In actual practice, deviation from equilibrium was depicted in the plot of the distance from the centroid and the observed within-group variance in the population. The residuals from the linear equilibrium were tested through the computation of its standard error, which was estimated using the jackknife method (Relethford and Harpending, 1994; Hanihara and Ishida, 2009). Regarding the requirement for the R-matrix procedure, an estimate of the heritability for cranial measurements was set to 0.55 following the previous studies (Relethford and Harpending, 1994; Roseman, 2004; Hanihara and Ishida, 2009), and estimates of the relative ef-

fective population size among the regional units were all set to ‘1’ because of the lack of available estimates for the Hokkaido and Okinawa Jomon population sizes. For the fixed heritability ($h^2 = 0.55$), we checked the difference in the case for $h^2 = 1$, which resulted in minimum F_{st} values; however, substantial effects on the relative genetic relationships (or distances) between the regions were not found. Although we do not have any reasonable rationale to use the fixed heritability estimate among the variables, the negative effect may be reduced by analyzing the three anatomical units of the skull separately. Concerning the relative effective population size, we checked the R-matrix results from the selected regions with the population size estimates of Koyama (1978) (i.e. excluding Hokkaido and Okinawa samples), and confirmed almost no difference in the degree and the pattern of population apportionment.

All computations and comparisons were conducted using R version 2.8.1, and the R-matrix method was performed using Rmet version 5.0.

Results

Figure 1 shows the regional variation in six parameters representing the size and shape of the neurocranium, face, and mandible. In general, the distinctive positions of Hokkaido Epi-Jomon and Okinawa Jomon are notable; one of the reasons could be in the chronological difference for Hokkaido Epi-Jomon and in the small number of available sites

Figure 1. Boxplots of the Jomon regional variation. The data represent the size and shape of the neurocranium, face, and mandible. Region and measurement abbreviations are presented in Table 1 and Table 2. Asterisks (**) indicate a significant (<1%) difference in Tukey's multiple comparisons.

(only two) for Okinawa Jomon, respectively. In the neurocranium, a trend of north-to-south cline was detectable, where the one-way ANOVA detected a significant be-

tween-group difference in three cases: length–breadth index in males (XCB/GOL); breadth–height index in males and females (BBH/XCB) (see Appendix 1 and Appendix 2). Al-

Figure 1. (continued)

though the geographical cline did not persist over the entire range of the Japanese archipelago, at least several succeeding regions exhibited the north-to-south cline even when

Hokkaido Epi-Jomon samples were excluded; this means that the northern Jomon people have a relatively larger, narrower, and higher neurocranium than the southern Jomon

people. In contrast, no trend of geographical cline was observed in the size and shape of the face and the mandible. The ramus length–breadth index exhibited significant population differences in both males and females (ANOVA), where the Hokkaido Jomon (in males and females) and Epi-Jomon (in males) were distinguished from the others in the post hoc multiple comparisons. The Hokkaido Jomon (and Epi-Jomon males) samples have a significantly wider mandibular ramus, which has been previously recognized and reported (Kaifu, 1995; Maeda, 2002).

In order to observe the different patterns of geographical variation in the cranial parts, the R-matrix method was separately applied to the neurocranium, face, and mandible. The Jomon population had a maximum of eight regional divisions in the analyses of the neurocranium and face and seven in the analysis of the mandible because of the lack of Okinawa data. Additional analyses were performed for the neurocranium, excluding the Okinawa Jomon samples with peculiarity in the boxplots (number of division = 7) and for those with estimates of regional population sizes (Koyama, 1978) (number after excluding Okinawa and Hokkaido = 6).

Table 3 shows the F_{st} values, which are a measure of the genetic diversity among the regions, calculated from the R-matrix method. The F_{st} value in the analysis of the neurocranium ($F_{st} = 0.111$) was larger than that of the face ($F_{st} = 0.0641$). Considering the same regional subdivision applied in these analyses, this means that the neurocranial measurements exhibit greater regional diversity than those of the face. In the comparisons of the neurocranium and the mandible where we excluded the Okinawa samples, the F_{st} value for the mandible (0.0941) was larger than that for the neurocranium (0.0413). This may be simply a reflection of the wide mandibular ramus in the Hokkaido Jomon, which was speculated to be an adaptive response to the different subsistence or diet (Maeda, 2002). In the three analyses for the neurocranium, the F_{st} value gradually decreased with the successive exclusion of the Okinawa and Hokkaido sam-

Table 3. F_{st} values among the Jomon subpopulations for the respective cranial parts

Cranial parts	No. of populations	No. of variables	F_{st}	SE ^a
Neurocranium	8	4	0.1110	0.0211
Neurocranium excluding Okinawa	7	4	0.0413	0.0102
Neurocranium with sample size collection	6	4	0.0084	0.0040
Face	8	7	0.0641	0.0107
Mandible	7	6	0.0941	0.0119

^a SE, standard error.

ples. This means that, conversely, the Okinawa and Hokkaido Jomon samples possess relatively different neurocranial morphology from the Jomon samples of other regions.

The genetic distances among the eight regional divisions calculated in the neurocranium were visualized in principal coordinates I and II (Figure 2a), which collectively accounted for 97.1% of the total variation. Among the Jomon regional divisions, Okinawa Jomon was the most distant from the others. The dispersion from the hypothetical equilibrium between the observed within-group variance, $V(\text{obs})$, and the genetic distance from the centroid were calculated (Table 4) and visualized (Figure 2b). Okinawa Jomon was again distant from the centroid, although the residual from the equilibrium was not significant (Table 4).

Exclusion of Okinawa Jomon, though reducing the proportion of the regional variation as seen in F_{st} , helps to understand the variation among Hokkaido, mainland Honshu, and Kyushu Jomon populations (Table 5, Figure 3). Among them, Chugoku Jomon was the most distinct, and the estimated genetic relationships exhibited a trend of geographical cline along the principal coordinate I, except for Kyushu (Figure 3a). As for the residuals from the equilibrium, the regions of Hokkaido and Kinki had positive deviations and

Figure 2. Eight regional divisions of the Jomon neurocranium. Region abbreviations are presented in Table 1. Principal coordinate plot (I and II accounting for 97.1% of the variation) of the genetic distances (a), and the plot of the distances from the centroid (r_{ii}) versus the observed variance (b).

Table 4. Eight regional divisions of the Jomon neurocranium: genetic distances to the centroid (r_{ii}) and observed, expected, and residual variances

Popula- tion ^a	r_{ii}	Within-group phenotypic variance			SE ^b	T (df = 3)
		Observed	Expected	Residual		
HokJ	0.077	1.150	0.993	0.156	0.248	0.630
Toh	0.033	0.963	1.040	-0.077	0.164	-0.469
Kan	0.009	1.040	1.067	-0.027	0.143	-0.189
Cbu	0.000	0.912	1.076	-0.164	0.086	-1.910
Kin	0.020	1.181	1.054	0.127	0.200	0.634
Cgk	0.190	0.869	0.871	-0.002	0.183	-0.011
Kyu	0.044	0.887	1.029	-0.141	0.108	-1.309
Oki	0.515	0.650	0.522	0.128	0.517	0.248

^a See population abbreviations in Table 1.

^b SE, standard error calculated by the jackknife method (Relethford and Harpending, 1994; Hanihara and Ishida, 2009).

those of Chubu and Kyushu had negative deviations (Figure 3b), suggesting additive gene flows from the outside in the former case and long isolation with genetic drift in the latter case. However, the degree of deviation was not statistically significant (Table 5).

The among-region relationships calculated on the face and mandible are shown in Figure 4. The peculiarity of the Hokkaido and Okinawa (absent in the mandible) Jomon samples was confirmed in the two principal coordinate plots. No trends of geographical cline were observed. Based on the R-matrix result on the face (Table 6), the observed within-group variance for the Kanto Jomon was significantly greater than expected (<1%). The result on the mandible (Table 7) exhibited the significantly smaller variance for the Tohoku Jomon (<5%). These results are difficult to interpret in the context of population genetics such as gene flow or genetic drift for the specific regional Jomon samples. Considering the geographical positions among the Japanese archipelago,

Table 5. Seven regional divisions of the Jomon neurocranium (excluding Okinawa): genetic distances to the centroid (r_{ii}) and observed, expected, and residual variances

Popula- tion ^a	r_{ii}	Within-group phenotypic variance			SE ^b	T (df = 3)
		Observed	Expected	Residual		
HokJ	0.059	1.148	0.981	0.167	0.234	0.714
Toh	0.047	0.962	0.993	-0.031	0.032	-0.977
Kan	0.004	1.039	1.039	0.000	0.100	0.000
Cbu	0.000	0.915	1.043	-0.128	0.142	-0.903
Kin	0.032	1.179	1.009	0.170	0.181	0.938
Cgk	0.134	0.868	0.903	-0.035	0.144	-0.243
Kyu	0.012	0.887	1.030	-0.143	0.087	-1.645

^a See population abbreviations in Table 1.

^b SE, standard error calculated by the jackknife method (Relethford and Harpending, 1994; Hanihara and Ishida, 2009).

these may be due to simple sample biases or indicative of a level of adaptation to the local environment.

Discussion

The peculiarity of the Hokkaido Epi-Jomon and Okinawa Jomon samples can be seen by comparing their cranial metrics. Hokkaido Epi-Jomon crania exhibited an anteroposteriorly longer neurocranium with the mesocephalic cranial length-breadth index. The face was high compared to its breadth. On the other hand, Okinawa Jomon crania were characterized as a small-sized neurocranium (especially anteroposteriorly short) with the brachycephalic cranial index. The face was also small (especially superoinferiorly low).

A weak but clear geographical cline was discernible in a few neurocranial metrics even after excluding the Hokkaido Epi-Jomon or Okinawa Jomon samples. In the previous study by Yamaguchi (1981), the geographical cline was already reported among three regions: Kanto, Chubu (Yoshiko

Figure 3. Seven regional divisions of the Jomon neurocranium. Region abbreviations are presented in Table 1. Principal coordinate plot (I and II accounting for 91.6% of the variation) of the genetic distances (a), and the plot of the distances from the centroid (r_{ii}) versus the observed variance (b).

Figure 4. Principal coordinate plot in the eight regional divisions of the Jomon face (a) explaining 83.1% of the variation and that in the seven regional divisions of the Jomon mandible (b) explaining 92.6% of the variation. Region abbreviations are presented in Table 1.

Table 6. Eight regional divisions based on the face: genetic distances to the centroid (r_{ii}) and observed, expected, and residual variances

Population ^a	r_{ii}	Within-group phenotypic variance			SE ^b	T (df = 6)
		Observed	Expected	Residual		
HokJ	0.157	0.899	0.813	0.086	0.088	0.979
Toh	0.040	0.869	0.926	-0.057	0.086	-0.660
Kan	0.039	1.141	0.927	0.214	0.047	4.585**
Cbu	0.017	0.949	0.948	0.001	0.096	0.010
Kin	0.000	1.004	0.965	0.040	0.231	0.173
Cgk	0.039	0.768	0.927	-0.159	0.092	-1.734
Kyu	0.053	0.915	0.914	0.001	0.120	0.008
Oki	0.168	0.677	0.803	-0.126	0.148	-0.852

^a See population abbreviations in Table 1.

^b SE, standard error calculated by the jackknife method (Relethford and Harpending, 1994; Hanihara and Ishida, 2009).

** Significant <1%.

Table 7. Seven regional divisions based on the mandible (excluding Okinawa): genetic distances to the centroid (r_{ii}) and observed, expected, and residual variances

Population ^a	r_{ii}	Within-group phenotypic variance			SE ^b	T (df = 5)
		Observed	Expected	Residual		
HokJ	0.348	0.856	0.700	0.155	0.175	0.886
Toh	0.035	0.883	1.036	-0.152	0.046	-3.302*
Kan	0.054	0.956	1.016	-0.060	0.105	-0.570
Cbu	0.042	0.929	1.028	-0.099	0.108	-0.921
Kin	0.100	0.997	0.966	0.031	0.215	0.144
Cgk	0.073	0.992	0.995	-0.003	0.087	-0.035
Kyu	0.007	1.194	1.066	0.128	0.184	0.696

^a See population abbreviations in Table 1.

^b SE, standard error calculated by the jackknife method (Relethford and Harpending, 1994; Hanihara and Ishida, 2009).

* Significant <5%.

site), and Chugoku (Tsukumo site). The present study expanded the comparative regions to the entire Japanese archipelago and confirmed it with the size and shape of the neurocranium. Cmod and XCB/GOL exhibited the cline, although the statistical tests were not significant (Figure 1).

Among the discernible geographical clines, the cranial index (XCB/GOL) is worth mentioning, where the smaller (mesocephalic) to greater (brachycephalic) indices were found in the northern and southern-end regions (even with the extreme positions for Hokkaido Epi-Jomon and Okinawa samples). Interestingly, the cline is in reverse direction versus the empirical correlations between cranial shape and climate, indicating that the brachycephalic people live in higher latitudes or colder regions (e.g. Beals, 1972). While the inconsistency may be due to the local population history of the Jomon in Japan, it may relate to brachycephalization. Recent studies have indicated that the dolico/brachycephalic classification does not reflect the genetic architecture (Martínez-Abadías et al., 2009), and that the cephalic variation associated with cranial length can be partly caused by diachronic changes in environment (Mizoguchi, 2007). Among the present Jomon regional variation, the cline of cranial index may be mainly due to changes in the cranial length (GOL), not in the breadth (XCB) (see Appendix 2). The regional variation in the cranial length should be thus considered as an outcome of genetic (or phylogenetic) effects and environmental adaptation.

Multivariate approaches using R-matrix analysis exhibited different degrees and patterns of regional variation among the three craniofacial morphologies. Based on the magnitude (F_{st} values) and interpretability within the context of Jomon population history among the Japanese archipelago, we focus in the following discussion mainly on results from the neurocranial measurements.

The R-matrix analysis of the neurocranial measurements also confirmed a trend of geographical cline from north-to-south in the Japanese archipelago (Figure 2, Figure 3). Ac-

cepting the Okinawa Jomon sample as an outlier, the other Jomon groups, except Kyushu, could be arranged to fit the north-to-south cline in axis II (Figure 2a) and I (Figure 3a).

Fukase et al. (2012) pointed out the geographical cline of Jomon postcranial metrics, which was recognized as a reflection of Bergmann's law, i.e. a body size difference from north to south in Japan. In addition, Fukase et al. postulated the body size cline was generated in the process of adaptation during the formation of the Jomon period and suggested a possible scenario of mixing phylogenetically different populations who had different body sizes. In terms of cranial metrics, a previous study applying the R-matrix method to Jomon regional variation indicated a degree of geographical cline from northeast-to-southwest along the Japanese islands (Hanihara and Ishida, 2009). Although their results cannot be directly compared with ours because of inconsistency of samples, regional divisions, and sex handling, where the within-region variation in Hokkaido Jomon in males was largest, while that in females was fourth among the five comparative regions, they proposed a simple hypothesis of the Jomon formation process, namely the Jomon ancestors in Hokkaido expanded southward to Honshu island (Hanihara and Ishida, 2009).

Based on the plots of the genetic distances from the centroid and the observed variance within the region (Figure 2b, Figure 3b), we can infer a couple of interesting points about the population history. On the one hand, the Chugoku Jomon, which was the most distant from the centroid, excluding Okinawa, fitted well with the line of equilibrium, suggesting a magnitude of within-region variance equivalent to the observed genetic distance. On the other hand, that for the Kyushu Jomon was smaller than expected based on the genetic distance from the centroid. The unexpectedly smaller genetic variation in the Kyushu Jomon indicates that it had experienced a relatively long isolation period and/or a level of genetic drift with a small bottlenecked population. By contrast, the Hokkaido Jomon, which possessed much greater variance than expected, could have been affected by gene flow from outside or could have accumulated the variance internally over a relatively longer period of time. Among the actual observed variances, the largest one was in Kinki Jomon, followed by Hokkaido Jomon (Table 4, Table 5).

In addition to the previous data presented by Hanihara and Ishida (2009), the present study provides additional information on the smaller genetic variance within the Kyushu Jomon. As already noted, the Kyushu Jomon, whose within-group variance was smaller than expected in terms of the estimated genetic distance to the centroid, might have experienced a relatively long isolation period with small population size during its formation process. In the case of Hokkaido Jomon, the magnitude of the within-region variance was the second largest following the Kinki region; there were no significant differences among those for the Hokkaido, Tohoku, Kanto, and Kinki regions. Thus, although we cannot identify a hypothetical center for the expansion or formation of the Jomon population, it would have been much less likely for the Kyushu region to occupy such an imaginary center of the Jomon population. The greater within-group variance in Hokkaido Jomon would indicate a long-term influence from the northern route (Siberia–Sakhalin to Hokkaido).

We should note the observed peculiarity of the Okinawa Jomon samples. The peculiarity of Okinawa Jomon was also confirmed in the R-matrix analyses, where *Fst* calculation from the neurocranial measurements was conducted three times to change the number of comparative regions from eight to six (Table 3). The eight regional divisions included all the regional samples of Jomon: Hokkaido, Tohoku, Kanto, Chubu, Kinki, Chugoku, Kyushu, and Okinawa. The next seven divisions excluded the Okinawa sample. The last six divisions excluded the Hokkaido sample in order to use the population size estimates by Koyama (1978). The calculated *Fst* values decreased gradually with the exclusion of the Okinawa and Hokkaido samples. Considering the definition of *Fst* as the proportion of the regional variance to the total variance, the gradual decrease of *Fst* would mean an increase in homogeneity with the exclusion of Okinawa and Hokkaido, suggesting the higher peculiarity of the Okinawa and Hokkaido Jomon samples in reverse.

Although the available Okinawa samples consist of 24 individuals from only two sites, Mabuni-Hantabaru (Matsushita et al., 2011) and Gushikawa Island (Matsushita and Ohta, 1993), the distinctive features of the Okinawa Jomon have triggered discussion on the origin of the Jomon population, especially the relationship with the Pleistocene human remains in the Ryukyu Islands, such as the Minatogawa people. While earlier studies generally supported morphological similarities and ancestor–descendant relationships between the Minatogawa and later Jomon (Suzuki, 1982; Yamaguchi, 1992; Baba et al., 1998), recent studies have questioned such direct relationships (Kaifu et al., 2011; Saso et al., 2011; Suwa et al., 2011). Thus, we now know there is considerable regional variation in the Jomon craniofacial morphology with a peripheral position of the Okinawa Jomon samples in the present study. It is time to re-evaluate the ancestor–descendant relationships in a more limited regional context. Interestingly, the characteristics of Okinawa Jomon, such as small-sized brachycephalic cranium and lower face, seem to be strengthened in later Yayoi people on the Amami and Ryukyu Islands, such as the Hirota on Tanegashima Island (Nakahashi, 2003). Although we should be cautious due to the custom of artificial skull deformation among these specimens (Nakahashi, 2003), the peculiarity of Okinawa Jomon should be reconsidered both in terms of human migration (or phylogenetic) history and from local environmental perspectives.

Previous analyses on cranial and dental morphologies suggested that the ancestral population of the Jomon people originated from Southeast Asia (Turner, 1987; Hanihara, 1991; Matsumura, 2007), whereas other morphological analyses (Hanihara and Ishida, 2009; Nakashima et al., 2010) and mtDNA sequence data (Adachi et al., 2009) suggested that their ancestors were of Northeast Asian origin. A new nuclear genomic sequence of a Sanganji Jomon (Tohoku region) specimen indicated that the Jomon people were derived from an ancestral East Eurasian population prior to the currently recognizable population diversification (Kanzawa-Kiriyama et al., 2016), as previously mentioned from an osteological point of view (Yamaguchi, 1992). Determining the geographic origins of the candidate Jomon ancestral populations is still difficult; thus, we should expand

the plausible target to more ancient Pleistocene fossils as previously suggested (Yamaguchi, 1992; Mizoguchi, 2011) and attempt to recover more genetic data on relevant ancient populations.

Conclusions

Several Jomon cranial measurements exhibited a cline from Hokkaido to Okinawa across the Japanese archipelago. This can be interpreted as an effect of global or local adaptation to environments or as a result of population history, such as gene flow with population movement or genetic drift with isolation. From the latter standpoint, R-matrix analyses of among- and within-region variances revealed a relatively wider within-region variance of Hokkaido, indicating a possible long-term gene flow from the north and a relatively smaller variance in the Kyushu region, indicating an effect of possible genetic drift with isolation. In addition, the uniqueness of the Okinawa Jomon was conspicuous. The present result seems to minimize an effect of human movement from the south, although the present Okinawa Jomon sample was small, from only two sites. We need more data from this region and we need to analyze samples from a longer time span, including Pleistocene fossils and prehistoric/historic inhabitants of the Amani and Ryukyu Islands.

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Appendix 1. (continued)

Female							
Region	Abb.	Cmod	XCB/GOL	BBH/XCB	UFmod	UFind	ram.ind
Hokkaido Jomon	HokJ	151.8	79.4	96.7	98.6	45.7	64.5
Hokkaido Epi-Jomon	HokZ	152.7	77.4	99.1	101.6	51.0	58.9
Tohoku	Toh	148.8	79.1	98.2	96.8	47.2	58.4
Kanto	Kan	150.6	79.4	96.1	98.3	47.4	60.6
Chubu	Cbu	150.4	79.7	95.2	96.7	48.1	58.6
Kinki	Kin	149.5	82.0	92.1	98.9	46.4	59.5
Chugoku	Cgk	148.8	80.5	91.2	97.8	47.9	57.6
Kyushu	Kyu	149.6	79.2	95.5	96.8	50.8	59.1
Okinawa	OkI	145.7	83.7	96.9	94.3	46.1	NA
ANOVA (prob)		0.070	0.012	0.000**	0.559	0.002***	0.006**
Tukey's multiple comparisons		NS	NS	Toh-Cgk	NS	HokJ-Kyu	HokJ-Cbu HokJ-Cgk
Male							
Region	Abb.	Cmod	XCB/GOL	BBH/XCB	UFmod	UFind	ram.ind
Hokkaido Jomon	HokJ	156.6	78.2	98.2	104.2	47.3	64.0
Hokkaido Epi-Jomon	HokZ	158.6	75.7	100.8	107.0	49.6	71.9
Tohoku	Toh	155.5	78.4	98.4	103.3	46.6	56.2
Kanto	Kan	155.8	78.4	97.2	104.0	48.6	59.0
Chubu	Cbu	153.6	79.4	95.9	102.7	46.7	55.5
Kinki	Kin	154.6	80.2	94.9	104.7	46.1	58.0
Chugoku	Cgk	154.9	78.7	93.6	103.7	49.7	53.5
Kyushu	Kyu	153.2	78.3	95.4	105.0	48.0	57.7
Okinawa	OkI	153.9	81.1	96.7	103.2	45.7	NA
ANOVA (prob)		0.018	0.002***	0.002**	0.203	0.058	0.000***
Tukey's multiple comparisons		HokZ-Cbu	HokZ-Cbu HokZ-OkI	HokZ-Cgk	NS	NS	HokJ-Toh HokJ-Cbu HokJ-Cgk HokZ-Toh, Kan, Cbu, Kin, Cgk, Kyu Kan-Cgk

Measurement abbreviations are presented in Table 2. Asterisks (**) indicate a significant (<1%) difference in ANOVA.

Appendix 2. Boxplots of the Jomon regional variation. Region and measurement abbreviations are presented in Table 1 and Table 2. Asterisks (**) indicate a significant (<1%) difference in Tukey's multiple comparisons.

Appendix 2. (continued)