Developmental variation in facial forms in Japan

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Abstract Significant differences in facial form between the Jomon and the post-Jomon series of the Yayoi, Medieval, and Early Modern period have been interpreted in terms of the gene flow from the Asian continent or the reduction of masticatory stress through the Jomon to the Early Modern period. However, the developmental process that produced these differences in facial form between the two groups has remains unknown. In this study we examined the factors contributing to differences in facial form by studying the developmental patterns of facial form using data from 311 subadult individuals from the middle-late Jomon (c. 5000–2500 BP) to the Early Modern period (1900–1950 AD). We found statistically significant differences in facial form among the temporally defined groups at early stages of development. Differences in upper facial height between the Jomon and the post-Jomon series were significant during both childhood (3–6 years, $P < 0.05$) and adolescence (12–20 years, $P < 0.01$). Differences in simotic index and bigonial breadth between the Jomon and the post-Jomon series were significant, beginning in childhood ($P < 0.05$), and differences in symphyseal height between the series were significant during both infancy (0–3 years, $P < 0.05$) and adolescence ($P < 0.01$). Based on previous ethnographical data, studies on the wear of the deciduous dentition in the Jomon and post-Jomon populations, and stable isotope analyses for reconstructing weaning diets in Jomon and Medieval children, it seems to be the first-stage juvenile stage (6–9 years) when the differences in masticatory load among the chronological groups become conspicuous enough to act on the functional adaptation of facial bones. Therefore, the patterns of group differences which begin in infancy or childhood and become remarkable in adolescence do not contradict the former explanation that the gene flow from the Asian continent largely contributed to the change of facial form during the transition between the Jomon and Yayoi periods.

Key words: Jomon, Yayoi, growth patterns, dual structure model, masticatory stress

Introduction

The goal of this study was to investigate the variation in facial growth that contributed to differences in facial form among temporally defined Japanese groups. Variation in facial size and shape has been well demonstrated among modern human populations, and these differences have been interpreted from various viewpoints, including microevolutionary history (e.g. Howells, 1973; Hanihara, 1993a, b, 2006; Relethford and Harpending, 1994; Kozintsev et al., 1999; Pietrusewsky, 2000; Hanihara and Ishida, 2009), a combination of climate selection and gene flow (e.g. Wolpoff, 1968; Shea, 1977; Carey and Steegmann, 1981; Franciscus and Long, 1991; Hernandez et al., 1997; Sardi et al., 2005), allometric growth with body size (e.g. Serikov et al., 1997; Hall, 2005), and developmental responses to changing masticatory stress (Carlson and Van Gerven, 1977;

Larsen, 1995; Gonzáles-José et al., 2005).

One of the most serious problems encountered when interpreting such differences is that bone morphology is influenced by environmental factors such as mechanical stress or nutritional factors during the ontogenetic growth period (Pearson and Lieberman, 2004). Therefore, clarifying the differences in developmental processes is essential for understanding the factors that contribute to such group differences. However, few studies have reconstructed the ontogenetic processes that produce these divergent forms (y'Edynak and İşcan, 1993; O'Higgins and Strand-Viðarsdóttir, 1999; Ponce de Leon and Zollikofer, 2001; Strand-Viðarsdóttir et al., 2002; Nara and Suzuki, 2003; Okazaki, 2004; Kondo et al., 2005; Fukase and Suwa, 2008, 2010). Kondo et al. (2005) showed that the ontogenetic trajectory of mandibular dimensions was more accelerated in Neanderthals compared to modern humans, while there were no notable significant differences in the trajectories of either the neurocranial or upper facial dimensions between the two groups. Kondo et al. stressed the necessity of researching the extent of variation in growth patterns among modern human populations, including prehistoric/historic groups, in order to determine whether the accelerated growth trajectory of the Neanderthal's mandible was derived from species-specific

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genetic factors or functional demands, such as the difference in subsistence patterns (Kondo et al., 2005).

In Japan, dramatic changes in adult skeletal morphology at the transition between the Jomon and the Yayoi (c. 500/400 BC–250/300 AD) or the Kofun (c. 300–600 AD) periods have been broadly demonstrated (Suzuki, 1969; Mizoguchi, 1988; Nakahashi and Nagai, 1989; Nakahashi, 1993; Kaifu, 1997). Upper facial height, in particular, increases abruptly between the Jomon and the Yayoi period, and decreases gradually from the Yayoi period to the Medieval period in western Japan, after which upper facial height increases again, while bimaxillary breadth decreases to produce the relatively high-narrow face seen in the Early Modern period (Nakahashi, 1993). One other distinct change in face form observed at the transition from the Jomon to Yayoi periods is the simotic and interorbital form. Individuals in the Jomon period are characterized by a wide and marked horizontally curved nasal bone, while those of the Yayoi period have a flat nasal bone. The prominence index of the nasal root, for example, increases dramatically at the transition between the Jomon and the Yayoi or the Kofun periods, and gradually becomes smaller in the later periods (Nakahashi, 1993).

The dramatic changes during the transition between the Jomon and Yayoi or Kofun periods include varieties of cranial and dental non-metric traits, limb proportions, estimated statures, dental sizes and shapes, in addition to facial forms (Brace and Nagai, 1982; Dodo, 1987; Dodo and Ishida, 1990; Matsumura, 1994; Kaifu, 1997; Kitagawa et al., 2002; Temple et al., 2008). These changes in physical characteristics can be explained by the gene flow from the Asian continent, because the suite of biological traits shared between the Yayoi people and later groups is broadly similar to those of the Korean Peninsula and China (Kim et al., 1993; Yamaguchi and Huang, 1995; Doigahama Site Anthropological Museum and The Cultural Relics and Archaeology of Shangdong Province, 2000; Nakahashi and Li, 2002). A genetic study of modern Asian people by Omoto and Saitou (1997) provisionally supports this so-called “dual structure model” (Hanihara, 1991), which was developed as an academically synthetic model from an earlier “hybridization theory” (Kanaseki et al., 1960), even though these studies do not agree regarding the origins of the Jomon people and the Yayoi people (Nakahashi and Li, 2002; Hanihara, 2006; Hanihara and Ishida, 2009).

Accordingly, the dramatic changes in facial form during the transition between the Jomon and Yayoi periods could be one of the proofs of gene flow from the Asian continent. However, considering the fact that changes in facial form occurred during historical periods (especially during the Medieval period or Meiji era) without significant gene flow (Suzuki et al., 1956; Nakahashi and Nagai, 1985), and considering the drastic change of lifestyle that occurred during the Yayoi period, a more detailed examination is needed to determine whether the change in facial form during the transition between the Jomon and Yayoi periods could be ascribed, for example, to environmental factors during an ontogenetic growth period, when diminished chewing stress coincided with the intensification of wet-rice agriculture and the development of an array of new food-processing tech-

niques. In this paper, we intend to discuss the factors contributing to the change in facial form among temporally defined Japanese groups by clarifying the pattern of ontogenetic acquisition of group differences. To our knowledge, this is the first work to use ontogenetic acquisition for the examination of facial form in ancient Japanese.

Materials and Methods

Samples

The skeletal samples considered in this study and the geographic locations from where they originated are shown in Table 1 and Figure 1, respectively. The Jomon skeletal remains, dating to the Middle–Final Jomon period (c. 5000–2500 BP), were excavated in Honshu, Hokkaido, Shikoku, and Kyushu. Despite several studies showing a geographical cline in Jomon cranial morphology, Jomon adult skeletal remains are relatively homogeneous, at least in comparison with those of more recent populations (Yamaguchi, 1982; Dodo, 1982; Takigawa, 2006; Hanihara and Ishida, 2009).

The Yayoi skeletal remains (c. 500/400 BC–250/300 AD) were excavated in northern Kyushu and western Honshu (i.e. the Yamaguchi region). According to studies by Kanaseki et al. (1960), Hanihara (1991), Dodo (1987), and Nakahashi (1993), these collections are largely composed of immigrants from the Asian continent and their immediate descendants. A number of previous studies using adult cranial series from the same regions have demonstrated an appreciable similarity among these regional groups as compared with those of other time periods (Nakahashi and Nagai, 1989; Dodo, 1995).

The Medieval (c. 1300–1600 AD) skeletal remains were excavated in western Honshu, the Kanto, and Tohoku regions. Medieval skulls display distinct morphological features, i.e. elongated crania, pronounced alveolar prognathism, horizontally flat nasal bones, and low facial height. These features are characteristic of Medieval individuals from several other areas of the Japanese archipelago, but are not characteristic of Japanese from other periods (Suzuki et al., 1956; Nakahashi and Nagai, 1985).

The Early Modern skeletal sample consists of the remains of individuals who died between 1900 and 1950 AD and were dissected at medical schools. According to available records, these individuals originated from the Tohoku, Kanto, and Kinki regions, as well as western Japan. For the purposes of this study, all Early Modern crania were pooled into a single, temporally defined series.

The mean dimensions of adult crania from each of the time periods under consideration were obtained from earlier craniometric studies: Kiyono and Miyamoto (1926) and Kintaka (1928) for Jomon; Nakahashi and Nagai (1989) for Yayoi; Suzuki et al. (1956) and Nakahashi and Nagai (1985) for Medieval; and Miyamoto (1924), Morita (1950), Harada (1954) and Nakahashi (unpublished) for Early Modern.

Age estimation

Age at death was estimated using the protocol of Smith (1991), adjusted to reflect Japanese data as in Kaneda (1957), and smoothed using the moving-average method (Lovejoy et al., 1990). The accuracy of these estimates was

Table 1. Materials used in this study

Samples	Dates ⁴	Location	Age categories (years)	No. of individuals	Collection ⁵
Jomon ¹	c. 5000–2500 BP	Hokkaido, Honshu, Shikoku, Kyushu	Infancy (0.3–3)	20	SMU, TUM, NUMD UMT, NMNS, PAKU KUM
			Childhood (3–6)	26	
			Juvenile 1 (6–9)	22	
			Juvenile 2 (9–12)	17	
			Adolescence (12–20)	26	
			Total	111	
Yayoi ²	c. 500/400 BC–250/300 AD	northern Kyushu Yamaguchi	Infancy (0.3–3)	23	KUM, ECC
			Childhood (3–6)	11	
			Juvenile 1 (6–9)	10	
			Juvenile 2 (9–12)	5	
			Adolescence (12–20)	6	
			Total	55	
Medieval ³	c. 1300–1600 AD	Kanto and Yamaguchi	Infancy (0.3–3)	21	UMT, NMNS, KUM
			Childhood (3–6)	12	
			Juvenile 1 (6–9)	5	
			Juvenile 2 (9–12)	16	
			Adolescence (12–20)	15	
			Total	69	
Early Modern	1900–1950 AD	Tohoku, Kanto, Kinki western Japan	Infancy (0.3–3)	14	TUM, UMT, PAKU KUM
			Childhood (3–6)	11	
			Juvenile 1 (6–9)	13	
			Juvenile 2 (9–12)	12	
			Adolescence (12–20)	26	
			Total	76	

¹ Recovered from the Yoshigo, Tsukumo, Yosekura, Takasago, Hobi, Ubayama, Ebishima, and Kamikuroiwa sites.

² Recovered from the Kuma-Nishioda, Kanenokuma, Doigahama, and Koura sites.

³ Recovered from the Yoshimohama, Zaimokuza, Gokurakuji, and Satohama sites.

⁴ Dates are based on Mizoguchi (2006) for Jomon and Yayoi; Suzuki et al. (1956), as well as Nakahashi and Nagai (1985) for Medieval. The majority of Jomon specimens analyzed stem from middle-final Jomon (5000–2500 years uncalibrated BP). Yayoi dates are based on comparison of associated finds with artifacts of known date from mainland East Asia. All other series in the study were dated using associated historical records.

⁵ SMU = Sapporo Medical University; TUM = Tohoku University School of Medicine; NUMD = Niigata University Graduate School of Medical and Dental Science; UMT = The University Museum, The University of Tokyo; NMNS = National Museum of Nature and Science; PAKU = Laboratory of Physical Anthropology, Kyoto University; KUM = Kyushu University Museum; ECC = Educational Committee of Chikushino City.

evaluated by comparing age estimates to age records for the Early Modern sample (Okazaki, 2009). Errors in estimated age were generally under 0.5 years until the age of 6–7 years, but increased to 2 or 3 years after the age of 13 years. This increased error is likely due to variation in the timing of third molar development and emergence. For individuals thought to be older than 13 years, priority was given to skeletal epiphysis closure (Scheuler and Black, 2000). Five age categories were defined for the total subadult sample: infancy (0.5–3 years); childhood (3–6 years); juvenile 1 (6–9 years); juvenile 2 (9–12 years); and adolescence (12–20 years) (see Table 1). Because the sexing of juvenile skeletal remains is problematic (Sutter, 2003), no attempt was made to divide the sample groups according to sex.

Measurements

Measurements of immature crania were taken mainly in accord with the methods of Martin and Saller (1957), as defined for adult crania. This method allows for comparison between the subadults in this study and prior adult data. To detect the ontogenetic acquisition of group differences observed in adults, the following measurements and resulting indices were assessed because there were significant differences between the Jomon and the post-Jomon adult skeletal

assemblages (Suzuki, 1969; Mizoguchi, 1988; Nakahashi and Nagai, 1989; Nakahashi, 1993; Kaifu, 1997): upper facial breadth (M43), bimaxillary breadth (M46), upper facial height (M48), anterior interorbital breadth (M50), anterior interorbital arc (F), orbital breadth (M51), orbital height (M52), nasal breadth (M54), nasal height (M55), minimum nasal breadth or simotic chord (M57 or SC), simotic subtense (SS), angle of frontal process in maxilla (AFPM), bigonial breadth (M66), mandibular length (M68), symphyseal height (M69), upper facial index (M48/46), orbital index (M52/51), nasal index (M54/55), mandibular index (M68/66), anterior interorbital index (M50/F), and simotic flatness (SC/SS). F and AFPM were measured according to the method of Suzuki (1969), and SS was measured according to the method of Yamaguchi (1973).

An alveolar margin around the prosthion is morphologically reduced with the eruption of permanent anterior teeth, so individuals with reduced alveolar margins (aged 6–7 years) were excluded from the upper facial height measurement (M48) to avoid this influence. For individuals under 1 year of age, bigonial breadth and mandibular length were not measured when the right and left halves of the specimen were separated at the symphysis. Crania deformed by post-mortem environmental conditions were excluded from the study.

Figure 1. Geographic location of archaeological sites and regions of Japan discussed in the paper. The main Jomon period sites are listed with numbers: (1) Yoshigo; (2) Tsukumo; (3) Yosekura; (4) Takasago; (5) Hobu; (6) Ubayama; (7) Ebishima; (8) Kamikuroiwa. The main Yayoi period sites are listed with capital letters: (A) Kuma-Nishioda; (B) Kanenokuma; (C) Doigahama; (D) Koura. The main Medieval sites are listed with lowercase letters: (a) Yoshimohama; (b) Zaimokuza; (c) Gokurakuji; (d) Satohama.

Statistical treatment

While all individuals studied were grouped into age categories (Table 1), we were concerned that a slightly uneven age distribution within each cohort—i.e. differing proportions of individuals close to the upper or lower age-cohort margins—might result in biased comparisons among the groups. To avoid this effect of sample bias by age distribution, we coordinated the means within each age group by the covariate adjustment method. The resulting values are referenced as age-adjusted means.

Linear, quadratic, or cubic functions that showed the highest coefficient of determination (R) with significant reliability were chosen to describe the trajectory of change in facial form relative to age. Given the relatively small sample sizes involved, the use of more complex functions to draw the growth curves would not have produced a more accurate result. The differences of age-adjusted means within each age category were evaluated statistically using analysis of covariance (ANCOVA), with the Jomon, Yayoi, Medieval, and Early Modern series as grouping factors and age as a covariate. When the interaction between group and age was statistically significant within each age cohort, a Mann-Whitney U -test was performed to test for group differences, instead of ANCOVA. In order to test for differences in the trajectories of total growth changes, the interaction of ANCOVA between the ages of 0.3 and 20 years was additionally examined. Although it is unknown that the indices used in this study exhibit a normal distribution, ANCOVA

was applied for them in order to determine the approximate changes with advancing age and the intergroup differences. Thus, it was carefully checked whether the results of ANCOVA were contradicted between the indices and the both dimensions that were used for calculating the corresponding indices.

These analyses were performed using the computer program package STATISTICA (StatSoft Inc., 1996).

Results

Table 2 summarizes differences in the age-adjusted means of facial dimensions across the entire range of age groups and time periods considered. Group differences of the age-adjusted means per age category were statistically examined using ANCOVA. Some of the more remarkable results are presented below.

Upper facial dimensions and the upper facial index

In terms of bimaxillary breadth, the Yayoi sample consistently displayed the greatest values among the temporally defined groups, beginning in childhood (Table 2). Significant differences of bimaxillary breadth were consistently found between the Yayoi sample and the Early Modern sample in the childhood to adolescent cohorts ($P < 0.05$). The bimaxillary breadth of the Jomon sample was significantly larger than that of the Early Modern sample for the adolescent cohort ($P = 0.017$), but there was little difference

in bimaxillary breadth between the two samples until the second juvenile stage.

The pattern of differences in upper facial height and nasal height was mostly fixed from childhood to adolescence: Yayoi > Medieval or Early Modern > Jomon (Table 2). Significant differences in both dimensions among the temporally defined groups were found during both childhood and adolescence ($P < 0.05$), while the differences in both juvenile cohorts were relatively obscured, so that the difference in upper facial height did not become statistically significant in either juvenile cohort, and the difference in nasal height did not become statistically significant in the first-stage juvenile cohort.

The ranking of upper facial index was hardly consistent, and significant differences were limited to the adolescent cohort ($P < 0.05$). The upper facial index (UFI) for Yayoi adolescents (UFI = 71.3) was significantly greater than those for Jomon adolescents (UFI = 64.4) and Medieval adolescents (UFI = 66.2) ($P = 0.007$ and 0.032 , respectively). The UFI for Early Modern adolescents (UFI = 72.3) was the greatest among the temporally defined groups (Table 2).

Figure 2A–C illustrates how facial dimensions and proportions change with advancing age. Table 3 indicates the regression coefficients and the adult means plotted at the age of 22.5 years as a reference. In the Early Modern series, the UFI increased with age (changed to a vertically higher and horizontally narrower face), which was best approximated by a cubic function ($R = 0.53$, $P < 0.001$) (Figure 2A). The UFI for the Yayoi series also increased with age, which was best approximated by a quadratic function ($R = 0.25$, $P = 0.515$), although the Yayoi sample had a lower UFI compared to the Early Modern sample, beginning at the age of 5–7 years. In contrast, in the Jomon and the Medieval series, the UFI decreased with age. The UFI for the Jomon sample best fit a quadratic function ($R = 0.45$, $P = 0.156$), decreasing from the age of 9–11 years. The UFI for the Medieval sample, also best approximated by a quadratic function ($R = 0.50$, $P = 0.139$), decreased from at least the age of 2–4 years to the age of 13–15 years and remained constant thereafter. Differences in the trajectory of change in the UFI were tested using the interaction of ANCOVA. Significant differences in the trajectory of change were found between the Jomon and the Early Modern series, and between the Medieval and the Early Modern series ($P < 0.001$).

The growth curves of the upper facial height and bimaxillary breadth were examined separately (Figure 2B, C). Upper facial heights for the Early Modern series ($R = 0.92$, $P < 0.001$) and the Yayoi series ($R = 0.92$, $P < 0.001$), best approximated by a cubic function, continued to increase up to late adolescence (Figure 2B). In contrast, upper facial heights for the Jomon series ($R = 0.90$, $P < 0.001$) and the Medieval series ($R = 0.86$, $P < 0.001$), also best fitted by a cubic function, finished increasing at the age of 12–14 years. Significant differences in the trajectory of change in upper facial height were observed between the Jomon series and the Early Modern series ($P = 0.001$), between the Yayoi series and the Medieval series ($P = 0.031$), and between the Medieval series and the Early Modern series ($P < 0.001$).

Bimaxillary breadth for the Early Modern series, best approximated by a cubic function ($R = 0.90$, $P < 0.001$),

continued to increase up to late adolescence (Figure 2C). This trajectory of change in bimaxillary breadth was similar to those of the other samples. However, bimaxillary breadth for the Yayoi sample, best fitted by a cubic function ($R = 0.93$, $P < 0.001$), sharply increased until the age of 7–9 years, but showed a decreasing growth rate thereafter, while that of the Jomon sample, best fitted by a quadratic function ($R = 0.94$, $P < 0.001$), maintained a constant growth rate for a longer period compared to the other samples. Accordingly, bimaxillary breadth for the Jomon sample was much smaller than that of the Yayoi sample and comparable to that of the Early Modern sample until the second-stage juvenile period. Thereafter, the bimaxillary breadth of Jomon adolescents mostly caught up with that of Yayoi adolescents (Table 2).

Interorbital dimensions and the associated indices

The pattern of differences in anterior interorbital breadth was consistent, beginning in the second-stage juvenile cohort: Jomon > Yayoi > Medieval > Early Modern (Table 2). Significant differences were observed in anterior interorbital breadths of second-stage juvenile and adolescent individuals between the Jomon series and both the Medieval and Early Modern series ($P < 0.05$). A significant difference was also found between the Yayoi and Early Modern second-stage juveniles ($P = 0.022$).

The pattern of differences in the anterior interorbital index was also consistent, beginning in at least the childhood cohort: Medieval or Early Modern > Yayoi > Jomon; however, significant differences were limited to second-stage juveniles and adolescents because of the small sample size for this index (Table 2). Significant differences were found for Jomon second-stage juveniles in comparison with the other three groups ($P < 0.05$), and between Jomon and Medieval adolescents ($P = 0.047$).

Minimum nasal breadth (simotic chord) consistently showed the following pattern of differences, beginning in at least the childhood cohort: Jomon > Yayoi > Medieval or Early Modern (Table 2). Significant differences in minimum nasal breadth were found between the prehistoric series (Jomon and Yayoi) and both the Medieval and the Early Modern series ($P < 0.05$), while no significant difference was observed between the Jomon and the Yayoi series.

The Jomon sample had the highest or the second-highest simotic index among the temporally defined groups, beginning in the childhood cohort. Significant differences in the simotic index were found between the Jomon and both the Medieval and Early Modern samples during both childhood and the second-stage juvenile period ($P < 0.05$).

The angle of frontal process in maxilla (AFPM) for the Jomon series was the smallest among the temporally defined groups, beginning in the second-stage juvenile category. Significant differences in the AFPM were found between the Jomon and both the Medieval and Early Modern samples for the second-stage juvenile category ($P < 0.05$).

Figure 3A–D shows the comparisons of the interorbital dimensions and resulting index among the temporally defined groups. For this analysis, the five age cohorts were assembled into two age divisions since the sample size and changes with advancing age were relatively small in the interorbital measurements: the first-half (from infancy to the

Table 2. Age-adjusted means of facial dimensions and resulting indices among time periods¹

Age stages (years)	Groups	M43 biorbital breadth			M46 bimaxillary breadth			M48 upper facial height			M50 anterior interorbital breadth			F anterior interorbital arc			M51 orbital breadth				
		n	Mean	P/I	P/2	n	Mean	P/I	P/2	n	Mean	P/I	P/2	n	Mean	P/I	P/2	n	Mean	P/I	P/2
Infancy (0.3–3)	Jomon	2	75.2			1	67.5			1	45.7			0				1	31.9		
	Yayoi	15	80.4	0.853		8	69.2	—		7	47.4	—		6	13.0	—		5	14.1	—	
	Medieval	12	75.4	0.055	0.000	1	64.0	—		2	45.6	—	0.897	2	13.5	—	0.803	2	15.1	—	0.335
	Modern	11	77.5	0.245	0.012	9	69.7	—	0.275	10	45.6	—	0.001	6	13.8	—	0.607	3	12.9	—	0.003
Childhood (3–6)	Jomon	6	87.2			1	74.4			4	47.4			2	15.8			1	20.4		
	Yayoi	5	86.4	0.516		7	82.4	—		3	55.7	0.002		4	14.8	0.608		1	13.9	—	0.094
	Medieval	5	86.7	0.811	0.693	3	77.8	—	0.078	5	53.0	0.005	0.356	4	15.1	0.681	0.900	4	16.0	—	0.688
	Modern	11	82.9	0.016	0.101	11	74.0	—	0.000	11	51.1	0.025	0.047	11	12.9	0.097	0.143	6	13.8	—	0.111
Juvenile 1 (6–9)	Jomon	6	91.8			4	78.8			6	55.2			3	15.8			3	18.3		
	Yayoi	6	91.5	0.836		5	84.1	0.003		6	57.3	0.265		6	14.5	0.446		5	15.9	0.126	
	Medieval	4	90.1	0.425	0.327	3	81.3	0.186	0.104	3	55.4	0.943	0.398	3	17.3	0.366	0.080	2	18.5	0.945	0.156
	Modern	13	88.4	0.134	0.085	12	78.3	0.546	0.002	9	56.4	0.484	0.594	12	14.0	0.176	0.484	11	15.9	0.090	0.994
Juvenile 2 (9–12)	Jomon	8	98.3			5	87.4			4	59.5			5	18.3			5	22.0		
	Yayoi	2	98.4	0.962		2	93.5	0.130		1	59.8	—		3	16.5	0.147		3	18.6	0.046	
	Medieval	11	94.8	0.025	0.149	8	87.7	0.924	0.097	10	60.0	0.712	0.425	6	16.1	0.036	0.721	5	17.6	0.005	0.535
	Modern	12	91.6	0.000	0.011	12	85.3	0.456	0.035	12	58.9	0.993	0.311	12	13.9	0.000	0.022	11	15.4	0.000	0.032
Adolescence (12–20)	Jomon	14	101.5			8	94.5			10	61.3			4	18.6			4	21.9		
	Yayoi	3	100.7	0.996		3	96.6	0.304		4	69.5	0.000		4	16.8	0.222		1	19.5	—	
	Medieval	11	97.2	0.017	0.134	8	94.2	0.759	0.421	9	62.5	0.299	0.003	8	15.3	0.012	0.232	8	17.0	0.000	0.248
	Modern	25	96.5	0.000	0.010	25	91.0	0.017	0.008	25	65.7	0.009	0.013	25	15.3	0.002	0.083	24	17.0	0.000	0.211

Table 2. (continued)

Age stages (years)	Groups	M52 orbital height			M54 nasal breadth			M55 nasal height			M57 minimum nasal breadth			Simotic subtense			AFPM				
		n	Mean	P1	P2	n	Mean	P1	P2	n	Mean	P1	P2	n	Mean	P1	P2	n	Mean	P1	P2
Infancy (0.3–3)	Jomon	1	27.3			5	19.3			1	31.9			0				0			
	Yayoi	11	29.5	—		11	18.7	0.235		7	33.5	—		7	8.0	—		5	1.3	—	
	Medieval	2	27.4	—	0.556	7	18.7	0.461	0.657	2	33.2	—	0.403	4	7.6	—	0.531	4	1.2	—	0.044
	Modern	9	29.7	—	0.097	10	18.0	0.005	0.027	9	34.4	—	0.010	8	6.4	—	0.092	4	0.9	—	0.025
Childhood (3–6)	Jomon	4	31.0			6	20.0			3	34.1			3	9.5			2	2.7		
	Yayoi	5	31.8	0.128		8	20.8	0.253		3	39.3	0.003		4	8.0	0.173		1	2.0	—	
	Medieval	5	31.9	0.057	0.650	6	20.7	0.317	0.938	4	38.5	0.003	0.820	4	6.0	0.004	0.058	3	0.9	0.002	—
	Modern	11	31.3	0.269	0.467	11	19.5	0.655	0.075	11	36.7	0.029	0.069	11	6.1	0.001	0.028	6	0.4	0.000	—
Juvenile 1 (6–9)	Jomon	5	31.7			7	20.5			5	38.8			4	9.4			4	2.6		
	Yayoi	7	32.5	0.436		6	23.1	0.002		6	42.1	0.126		6	7.9	0.224		5	1.1	0.049	
	Medieval	3	31.3	0.750	0.321	4	21.8	0.277	0.068	3	40.7	0.250	0.548	2	5.7	0.010	0.057	1	1.3	—	—
	Modern	13	31.1	0.510	0.095	12	21.1	0.307	0.008	12	39.2	0.442	0.067	12	6.2	0.002	0.025	10	1.4	0.060	0.680
Juvenile 2 (9–12)	Jomon	6	31.3			5	22.6			5	41.5			5	9.3			5	2.8		
	Yayoi	3	32.7	0.237		2	23.2	0.514		2	47.1	0.007		3	9.1	0.899		2	2.3	0.443	
	Medieval	10	31.6	0.641	0.360	11	23.1	0.455	0.852	11	43.2	0.182	0.036	12	8.1	0.228	0.354	5	1.3	0.015	0.225
	Modern	12	32.0	0.349	0.562	12	22.2	0.724	0.339	12	42.1	0.383	0.016	12	6.4	0.002	0.012	9	1.1	0.003	0.117
Adolescence (12–20)	Jomon	11	32.5			11	24.0			9	45.2			5	10.3			5	3.4		
	Yayoi	4	34.5	0.072		5	24.3	0.551		4	50.4	0.005		2	9.1	0.464		1	3.5	—	—
	Medieval	8	33.2	0.404	0.268	11	23.9	0.954	0.582	8	46.5	0.295	0.047	8	6.6	0.001	0.090	5	1.9	0.011	—
	Modern	25	33.1	0.463	0.139	25	23.6	0.348	0.180	24	47.7	0.086	0.052	25	6.7	0.000	0.080	23	1.8	0.001	—
																		25	98.3	0.095	—

Table 2. (continued)

Age stages (years)	Groups	M66 bigonial breadth			M68 mandibular length			M69 symphyseal height			M48/46 upper facial index			M50/F anterior interorbital index			M52/51 orbital index				
		n	Mean	P/I	P/2	n	Mean	P/I	P/2	n	Mean	P/I	P/2	n	Mean	P/I	P/2	n	Mean	P/I	P/2
Infancy (0.3–3)	Jomon	11	62.7			10	40.9			20	19.8			1	67.8			0	1	85.8	
	Yayoi	10	68.0	0.061		9	42.5	0.870		14	19.5	0.128		7	68.0	—		5	92.7	—	—
	Medieval	11	65.7	0.624	0.154	10	41.7	0.940	0.928	12	19.3	0.019	0.377	1	72.1	—	—	2	90.6	—	0.523
	Modern	7	65.1	0.117	0.002	3	42.0	0.496	0.434	5	18.4	0.002	0.041	8	65.9	—	0.099	3	91.4	—	0.720
Childhood (3–6)	Jomon	12	72.2			8	50.0			23	23.2			1	61.2			1	85.6		—
	Yayoi	6	80.8	0.001		6	51.4	0.453		5	23.6	0.377		3	70.1	—		1	86.1	—	—
	Medieval	7	76.4	0.141	0.065	6	51.8	0.523	0.914	8	23.7	0.239	0.930	3	70.4	—	0.915	4	94.0	—	—
	Modern	7	73.6	0.469	0.015	7	47.9	0.432	0.151	7	22.4	0.596	0.259	11	68.7	—	0.539	6	90.1	—	—
Juvenile 1 (6–9)	Jomon	11	79.9			9	56.5			17	24.2			3	67.8			3	86.0		—
	Yayoi	2	90.6	0.003		2	60.1	0.283		5	24.6	0.730		4	69.0	0.835		5	88.6	0.216	—
	Medieval	2	85.4	0.127	0.185	3	57.0	0.879	0.303	2	23.2	0.482	0.403	2	67.4	0.645	0.762	2	90.8	0.140	0.576
	Modern	8	79.3	0.804	0.003	8	54.6	0.396	0.121	7	23.8	0.589	0.476	9	72.8	0.298	0.165	11	88.7	0.182	0.955
Juvenile 2 (9–12)	Jomon	9	88.8			8	62.6			11	25.2			3	69.0			5	83.1		—
	Yayoi	3	95.3	0.033		4	61.8	0.675		3	26.6	0.187		1	67.1	—		3	89.4	0.046	—
	Medieval	8	88.1	0.695	0.019	6	62.2	0.887	0.780	5	25.3	0.994	0.235	7	67.0	0.582	—	5	91.8	0.003	0.411
	Modern	9	85.6	0.173	0.003	9	61.2	0.531	0.936	9	27.1	0.062	0.994	12	68.6	0.861	—	11	90.4	0.005	0.792
Adolescence (12–20)	Jomon	19	91.7			16	68.3			20	27.3			7	64.4			4	85.1		—
	Yayoi	2	107.3	0.000		3	68.7	0.848		4	30.9	0.002		3	71.3	0.007		1	88.5	—	—
	Medieval	12	95.0	0.121	0.003	11	70.3	0.116	0.441	10	28.6	0.172	0.041	8	66.2	0.368	0.032	8	90.3	0.047	—
	Modern	23	91.7	0.629	0.000	23	62.7	0.000	0.004	22	29.6	0.009	0.092	25	72.3	0.000	0.408	24	89.6	0.095	—

Table 2. (continued)

Age stages (years)	Groups	M54/55 nasal index			M68/66 mandibular index			SS/M57 simotic index		
		<i>n</i>	Mean	<i>P1</i>	<i>P2</i>	<i>n</i>	Mean	<i>P1</i>	<i>P2</i>	<i>P2</i>
Infancy (0.3–3)	Jomon	1	57.7			10	65.1			0
	Yayoi	7	55.6	—		8	62.8	0.281		5 15.4 —
	Medieval	2	55.9	—	0.749	10	63.5	0.416	0.751	4 15.2 — 0.860
	Modern	9	53.3	—	0.612	3	63.4	0.569	0.834	4 14.1 — 0.683
Childhood (3–6)	Jomon	2	53.3			8	68.1			2 26.6
	Yayoi	3	52.3	0.749		6	63.7	0.171		1 24.1 —
	Medieval	4	54.2	0.987	0.716	6	66.8	0.681	0.361	3 12.3 0.046 —
	Modern	11	53.4	0.942	0.717	7	65.6	0.413	0.557	6 6.6 0.007 —
Juvenile 1 (6–9)	Jomon	5	52.2			9	71.4			4 27.9
	Yayoi	6	55.6	0.249		2	66.3	0.336		5 14.2 0.164
	Medieval	3	53.6	0.791	0.468	2	65.8	0.257	0.887	1 15.6 — —
	Modern	12	54.2	0.477	0.512	8	69.1	0.532	0.564	10 20.5 0.384 0.422
Juvenile 2 (9–12)	Jomon	3	53.7			8	71.3			5 30.6
	Yayoi	2	49.5	0.136		3	66.7	0.097		2 24.7 0.499
	Medieval	11	53.7	0.874	0.103	6	72.2	0.613	0.053	5 13.8 0.019 0.217
	Modern	12	52.9	0.547	0.196	9	71.8	0.816	0.067	9 15.1 0.015 0.245
Adolescence (12–20)	Jomon	9	52.8			15	74.2			5 32.9
	Yayoi	4	47.7	0.108		2	66.2	0.036		1 33.7 —
	Medieval	8	51.1	0.572	0.252	11	73.9	0.996	0.040	5 24.9 0.250 —
	Modern	24	50.0	0.088	0.576	23	68.8	0.005	0.380	23 26.2 0.238 —

¹ Means were adjusted for the age within each age category by ANCOVA. Significant differences from the Jomon people (*P1*) and the Yayoi people (*P2*) were tested by multiple comparisons (LSD test) of ANCOVA. At the nasal height M55 of the first-stage juvenile cohort, the means without age adjustment were calculated, and a Mann–Whitney *U*-test was conducted, instead of ANCOVA, because the interaction between the grouping and age factors was significant ($P = 0.038$). Significance is set at $P < 0.05$; significant probabilities are in bold face.

Figure 2. Changes in facial proportions and dimensions with advancing age. Because juvenile skeletons were unsexed, for comparative purposes adult means are shown as a midpoint between male and female dimensions. Mean dimensions of adult crania from each of the time periods under consideration were plotted at the age of 22.5 years. (A) Change in upper facial index M48/M46 with age. (B) Change in upper facial height M48 with age. (C) Change in bimaxillary breadth M46 with age.

Table 3. Regression coefficients and adult means plotted at the age of 22.5 years for demonstrating changes in facial dimensions and resulting index with advancing age¹

M48/46 upper facial index							
	<i>n</i>	<i>R</i> ²	M0	M1	M2	M3	Adult mean ³
Jomon	15	0.45	74.20	-1.07	0.03		63.1
Yayoi	18	0.25	67.51	0.34	-0.01		70.3
Medieval	21	0.50	64.67	0.62	-0.04		65.7
Early Modern	65	0.53	63.21	1.49	-0.09	0.00	72.1

M48 upper facial height							
	<i>n</i>	<i>R</i>	M0	M1	M2	M3	Adult mean
Jomon	25	0.90	36.11	3.66	-0.17	0.00	63.7
Yayoi	21	0.92	42.25	2.80	-0.09	0.00	71.9
Medieval	29	0.86	42.68	2.57	-0.10	0.00	64.1
Early Modern	67	0.92	37.26	3.68	-0.18	0.00	69.5

M46 bimaxillary breadth							
	<i>n</i>	<i>R</i>	M0	M1	M2	M3	Adult mean
Jomon	19	0.94	62.90	2.80	-0.05		101.5
Yayoi	25	0.93	57.68	6.74	-0.42	0.01	102.3
Medieval	23	0.88	62.44	3.32	-0.08		99.2
Early Modern	69	0.90	61.69	3.31	-0.14	0.00	96.5

¹ The regression equation is: (growth curve) = M0 + M1 × (age) + M2 × (age)² + M3 × (age)³.

² The correlation coefficients were listed as the index of fitness of the regression equations.

³ The midpoint between male and female as adults was calculated using the previous studies.

first-stage juvenile period) and the second-half (from the second-stage juvenile period to adolescence) of development. The pattern of group differences was consistent between the first half and the second half of growth in the anterior interorbital index (Figure 3A), minimum nasal breadth (Figure 3B), and simotic index (Figure 3C). Conversely, the pattern of group differences of AFPM was different between the two age divisions (Figure 3D). The AFPM of the Yayoi sample was larger than that of the Jomon sample in the second half of development, in parallel with the finding in adults (Suzuki, 1969). However, in the first half of development, the value of the Yayoi sample (AFPM = 80.0) was smaller than that of the Jomon sample (AFPM = 84.7) (Figure 3D).

Mandibular dimensions and the associated index

The bigonial breadth of the Yayoi sample was the largest among the temporally defined groups for all the age categories (Table 2). Significant differences in bigonial breadth were repeatedly found between the Yayoi sample and the other groups. In particular, significant differences in bigonial breadth were consistently found between the Yayoi sample and the Jomon or Early Modern samples, beginning in the childhood cohort ($P < 0.05$, $P < 0.003$, respectively). In contrast, significant differences in mandibular length were limited to the adolescent cohort. The mandibular length of the Early Modern adolescents was significantly smaller compared to those of both the Jomon and Yayoi adolescents

Figure 3. Comparisons in interorbital flatness and dimension among the temporally defined groups at the two age divisions. Cruciform plots indicate the individuals during the first half of growth (0.3–9 years), while circle plots show individuals during the second half of growth (9–20 years). The plots are slightly transversely scattered within each group when the plots overlap each other. Transverse bars indicate each average value. (A) Comparison in anterior interorbital index M50/F. (B) Comparison in minimum nasal breadth M57 (SC). (C) Comparison in simotic flatness SC/SS. (D) Comparison in angle of frontal process in maxilla (AFPM).

($P < 0.001$, $P = 0.004$, respectively). Accordingly, the pattern of differences in the mandibular index was consistent in the infancy, childhood and adolescent cohorts: Jomon > Medieval > Early Modern > Yayoi. Again, statistically significant differences were limited to the adolescent cohort.

Symphysal height of the Jomon sample was significantly higher in infancy, but lower in adolescence as compared with that of the Early Modern sample ($P < 0.01$). This catch-up increase in symphyseal height of the Early Modern individuals was also observed in relation to both the Yayoi and Medieval samples, although those differences did not reach a statistically significant level. Consequently, the comparison of symphyseal height did not show consistent ranking among the groups and age categories.

In summary, differences in facial size and shape between the Jomon and the post-Jomon series were generally observable at the early stages of development (infancy or child-

hood). The other notable result of this study is that the mode of change in group differences with growth varied among vertical measurements (e.g. upper facial height, nasal height), horizontal measurements (e.g. bimaxillary breadth, bigonial breadth), and facial flatness (e.g. anterior interorbital index, simotic index).

Discussion

Facial height

Ontogenetic growth processes producing differences in facial form between the Jomon and the post-Jomon series

Strand-Viðarsdóttir et al. (2002) demonstrated developmental patterns in facial forms using juvenile crania from 10 geographically distinct populations and suggested that differences in adult facial form bring together three types of growth factors and their interaction: differences in early developmental patterning (fundamental differences), growth

patterning (ontogenetic trajectory), and growth timing and rate (ontogenetic scaling). They found few constant patterns in the combinations among fundamental differences, ontogenetic trajectory, and scaling (Strand-Viðarsdóttir et al., 2002). Strand-Viðarsdóttir et al.'s results led us to speculate that the pattern of ontogenetic processes to develop group differences in facial forms varies among populations studied, because each group difference may be caused by different factors (e.g. bone functional adaptation to different environments during growth or genetic factors, or synergistic effects among them).

The present study focused on vertical facial height, since this dimension is one of the most effective values for discriminating between the Jomon and the Yayoi skeletal samples (Nakahashi, 1993). For upper facial height (UFH), statistically significant differences were found between the Jomon and the post-Jomon groups for the childhood cohort, while the differences in the infancy cohort were unknown due to the small sample size of Jomon individuals (Table 2). Interestingly, however, differences in UFH between the Jomon series and the post-Jomon series were provisionally reduced during both juvenile periods and thereafter were increased again for the adolescent cohort. Significant differences in UFH between the Jomon and the post-Jomon adolescents are apparent based on the differences in the growth trajectory between the two groups (Figure 2B). This pattern of ontogenetic acquisition of group differences was consistent with that of nasal height, although symphyseal height showed a unique change with advancing age cohorts of relative ranking of population means (Table 2), which could be related to the difference in the spatial size for anterior teeth formation between the Jomon and Early Modern groups (Fukase and Suwa, 2010). In contrast, no significant differences in growth trajectory were found for maxillary breadth or bigonial breadth among the chronologically defined groups (Figure 2C).

In summary, differences in growth patterns contributed to adult differences in facial height more than did adult differences in facial breadth. This primacy of the contribution made by growth patterns was responsible for the significant difference in UFI between adolescents of the Jomon and the post-Jomon series.

Two possible factors contributing to the differences in facial form between the Jomon and the post-Jomon series—gene flow from the continent and diminished chewing stress—coincided with the intensification of wet-rice agriculture

A set of changes in human ecology associated with the introduction of wet-rice agriculture was observed during the transition between the Jomon and the Yayoi periods. While some authors have suggested that rice agriculture was already practiced to a limited extent in Japan during the Jomon period, direct evidence in the form of rice remains (*Oryza sativa japonica*) and constructed paddies found at well-dated archaeological sites indicates that people of the Yayoi period were the pioneers of full-scale wet-rice production in the Japanese archipelago (Imamura, 1996; Miyamoto, 2000; Tasaki, 2002; Yamasaki, 2005; Crawford, 2006).

Notwithstanding the overwhelming evidence of large-scale wet-rice agriculture during the Yayoi period, stable

isotope analyses of human bone suggest that the diets of the Yayoi people varied considerably in different parts of the archipelago (Chisholm and Koike, 1999; Yoneda, 2005). Paleobotanical data also suggests that a diversification of the diet established by the Jomon people (e.g. acorns) was still firmly maintained in the Yayoi period in western Japan (Terasawa and Terasawa, 1981; Komoto, 1986, 1991; Fujio, 1993). The development of new food-processing techniques and increasing emphasis on rice production resulted in a shift to a softer textured, less coarse diet after the Yayoi period (Saito, 1987). The results of *in vivo* experiments that recorded the chewing time and the number of mastications of subjects fed model diets reconstructed for the different historical periods indicate that a significant decline in mastication demands occurred between the Jomon and Edo periods (Saito, 1987). The same conclusion was supported by an analysis of dental wear in cranial collections, which showed that the reduction of occlusal dental wear became significant in the Medieval period (Kaifu, 1999).

The developmental responses of facial bones to changing masticatory environments have been studied in variety of populations (Carlson and Van Gerven, 1977; Larsen, 1995; González-José et al., 2005). Reduced masticatory stress might be responsible for the inhibition of transverse growth at the median palatine suture, and thereby for the excessive downward growth of the face and ultimately the higher face in modern humans (y'Edynak and İçcan, 1993). Therefore, it is not unreasonable to suppose that declining masticatory stress may have contributed to the increases in UFH between the cranial series of the Jomon and Yayoi periods and/or those of the Medieval and Early Modern periods.

It is not easy to determine the probable age at which the differences of masticatory stress begin to be conspicuous enough to act mechanically on the functional adaptation of facial bones. Suzuki (2008) shows that wear of the deciduous dentition in Jomon was not significantly heavier than in post-Jomon populations, whereas the permanent dentition in Jomon is thought to have suffered from severe attrition. The results of Suzuki appear to parallel those of ethnographical studies indicating that infants are generally fed with breast milk and weaning foods, which tend to be much softer than the diet of adults (Sellen and Smay, 2001; Fouts et al., 2005). Furthermore, the results of stable isotope analysis conducted by Shimomi et al. (2007) on Jomon infants from the Yoshigo site and Medieval Japanese infants from Yuigahama-minami suggest that Jomon and Medieval Japanese peoples had similar schedules for weaning and the introduction of solid foods. Based on the analysis of nitrogen isotope ratios ($\delta^{15}\text{N}$), Shimomi et al. (2007) proposed that both Jomon and Medieval children were first weaned onto cereal-based gruels and only later exposed to tougher comestibles (e.g. seafood). Consequently, while intergroup variation in chewing loads might have contributed to facial differences among adolescents and adults, there is little reason to believe that toughness of diet would have played any significant role in facial variation among infants.

Given these observations, the masticatory stress explanation leads to the expectation that the group differences of facial dimensions are gradually developed during the juvenile periods (6–12 years), with increased exposure to solid foods

of varying textures (Sellen and Smay, 2001; Fouts et al., 2005). Contradicting this, the significant differences in UFH between the Jomon and the post-Jomon groups were already observable in childhood and disappeared in both juvenile cohorts. The differences at the early developmental stages observed in this study, as well as the decrease of the differences between childhood and both juvenile stages, suggest that the change in facial height may not be related principally to the diminished chewing stress coincident with the intensification of wet-rice agriculture and the development of an array of new food-processing techniques beginning with the Yayoi period and continuing into the Edo period. However, this explanation cannot rule out the possibility that the morphological traits of the Jomon crania were largely formed by early, genetically based developmental patterning that arose through natural selection for hard chewing over hundreds or thousands of generations (Kaifu, 1997; Fukase and Suwa, 2008).

One of the interesting results of this study is that, as mentioned above, the differences in facial height become conspicuous during adolescence. Regarding the adolescent cohort, a series of studies comparing growth patterns among modern populations in different living environments suggested that the amount of growth during an adolescent spurt may be mostly decided by genetic factors, while the amount of growth before an adolescent spurt is significantly influenced by differences in nutrition factors and morbidity (Bogin, 1999; Stinson, 2000). Thus, the differences in UFH between adolescents of the Jomon and post-Jomon series might be due to a genetic factor that became significant during an adolescent spurt.

The growth patterns of facial height observed in this study are characterized by early stages of growth and adolescent spurts that produced significant differences between the Jomon and the post-Jomon series. Considering the expectation that the growth pattern during these two age stages is significantly influenced by genetic factors, as mentioned above, the results of this study do not contradict the former studies indicating the introduction of new alleles to the Japanese archipelago (e.g. Kanaseki et al., 1960; Hanihara, 1991).

Facial flatness

The degree of facial flatness, especially in the interorbital region, is also one of the most valuable tools for discriminating between the Jomon and the Yayoi cranial series (Suzuki, 1969; Nakahashi, 1993). Although the facial flatness of post-Jomon Japanese is significantly greater than that of the Jomon group, the facial flatness values of the post-Jomon Japanese are not particularly different from those of populations in Northeastern Asia (northern China, Korea, Mongol, eastern Siberia) (Ishida, 1992; Ishida and Dodo, 1997; Hanihara, 2000). Applying Allen's (1877) rule, Coon (1955) explained that natural selection in response to cold and dry air in eastern Siberia resulted in significant facial flatness of populations that originated in the region. The cold engineering model set up by Coon (1955) is still a possible explanation of the factors contributing to the flat faces of post-Jomon Japanese (Omoto, 1995; Yamaguchi, 1999; Nakahashi, 2005). Numerous investigators have reached this conclusion

despite the fact that experimental studies do not support the relationship between relatively flat faces and the risk of cold stress (Stegmann, 1965, 1967, 1970, 1972).

The masticatory stress hypothesis (Carlson and Van Gerven, 1977) is another possible explanation for changes in facial flatness among populations. For instance, populations from colder environments generally adapt to tough diets such as animal meat or use incisors as a tool for tanning. For the Inuit people, the position of the temporalis and masseter was shifted anteriorly to increase biomechanical efficiency during hard chewing (Hylander, 1975, 1977; Spencer and Demes, 1993). Although the biomechanical relation between the flatness of the interorbital region of the face and masticatory stress is not fully understood at present, probably because of the intricate construction of the interorbital region, Endo (1984) explains that the widened and three-dimensional interorbital region of the Jomon sample is mechanically more suitable for harder masticatory stress compared to the narrow and flat region of the Early Modern sample.

The results of the present study show that differences between the Jomon and the post-Jomon groups in simotic breadth, simotic subtense, and the associated index are significant after childhood: the differences during infancy are unknown due to the lack of Jomon infants (Table 2, Figure 3B, C). These results parallel the findings of the study by Nara and Suzuki (2003), which compared the interorbital forms between Jomon and Yayoi infants and children (0.5–6 years). The interesting point of that study was that it demonstrated that the frequency of the types of supraorbital marginal shape was significantly different between the Jomon and the Yayoi infants and children as well as between the Jomon and Yayoi adults: the supraorbital margins were straighter in the Jomon series than in the Yayoi series. In the present study, the group differences of the interorbital dimensions except for the simotic part were relatively obscure. Although the anterior interorbital breadth and arc were larger in children of the Jomon group than in children of the post-Jomon groups, the anterior interorbital breadth and arc, their index, and AFPM were not significantly different between the Jomon and the post-Jomon groups until the first-stage juvenile period, probably because the grouping by relatively small year spans reduced the sample size within each age group (Table 2, Figure 3A, D).

If the difference in masticatory stress is the main factor contributing to the group differences of interorbital forms, the group differences should begin increasing after children become accustomed to tougher adult foods (at least after the age of 6: Sellen and Smay, 2001; Fouts et al., 2005). Therefore, the differences of simotic dimensions between the Jomon and the post-Jomon crania in the childhood cohort (3–6 years) still seem to be better understood in terms of an explanation linking gene flow to Japan from the mainland. However, the interorbital dimensions, except for those of the simotic portion, do not show distinct differences between the Jomon and the post-Jomon series until the first-stage juvenile cohort, so it cannot be excluded that differences in masticatory stress have an influence on the functional adaptation of the interorbital forms during growth except those of the simotic portion.

The results of this study which are difficult to explain are the differences between the Yayoi and the Early Modern infants observed in several dimensions related to vertical facial height and transverse facial breadth. In particular, the significant difference in bigonial breadth between the Yayoi and the Early Modern series was consistent from infancy to the adolescent age cohort. One possible explanation for this contradiction is that it may have been due to the different sampling localities between the Yayoi and the Early Modern groups. The Early Modern crania of this study were gathered from various regions of Japan, including the Kanto and Tohoku areas, while the Yayoi crania were gathered only from the north Kyushu and western Honshu: the infants of the Early Modern period consisted of eight infants from the TUM and UMT collections and six infants from the KUM collection (Table 1). The studies on geographical variation of cranial forms have repeatedly indicated that the degree of the admixture with Jomon natives becomes greater toward the east or north in Japan (e.g. Mizoguchi, 1988; Hanihara, 1991; Nakahashi, 1993; Kaifu, 1997; Takigawa, 2006; Kawakubo et al., 2009). Kaifu (1997) explained the difference of the Jomon and Yayoi mandibles, as observed in bigonial breadth, in terms of genetic selection relative to the subsistence of their ancestors: the ancestors of the Yayoi group are presumed to have engaged in hunter-gathering, probably in Northeast Asia, whereas the Jomon group ancestors are presumed to have engaged in culinary practices associated with a pottery-making tradition. Accordingly, including the Early Modern sample with infants from the Tohoku and Kanto areas might have resulted in the difference of facial forms between the Early Modern and Yayoi infants, even though significant population flow in Japan ended after Yayoi, or, at the latest, after the Kofun period (Mizoguchi, 1988; Matsumura, 1994; Nakahashi, 1993; Kaifu, 1997).

Finally, the present findings may shed light on the controversial issue of the changes at the transition between the Jomon and Yayoi period. Differences in morphological features between the Jomon and the post-Jomon groups have been demonstrated and interpreted as evidence for the dual-structure model (e.g. Mizoguchi, 1988; Dodo and Ishida, 1990; Hanihara, 1991; Nakahashi, 1993; Matsumura, 1994; Kaifu, 1997). However, few studies have shown the relationship between these morphological changes and functional adaptation during growth. Researchers have continued to consider the possibility that changes in living environments, specifically the transition to wet-rice agriculture, contributed to the morphological differences between the Jomon and the post-Jomon groups (e.g. Suzuki, 1969). With respect to the vertical facial height, which has been considered the most significant difference between the Jomon and Yayoi crania (Nakahashi, 1993), the growth patterns of this study showed that the differences between the Jomon and the post-Jomon groups were most observable at the early stages of development and then again in the adolescent stage, following a reduction of this difference during the two juvenile stages. As discussed above, this pattern of ontogenetic acquisition of group differences is not considered to be well explained only by changes in living environments. Although the differences of masticatory load among infants of chronologically de-

fined groups are expected to be further clarified (Suzuki, 2008), at present the most likely explanation is that gene flow from the Asian continent produced the change in facial form between the Jomon and the post-Jomon series.

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References

- Allen J.A. (1877) The influence of physical conditions on the genesis of species. *Radical Review*, 1: 108–140.
- Bogin B. (1999) *Patterns of Human Growth*, 2nd edn. Cambridge University Press, Cambridge.
- Brace C.L. and Nagai M. (1982) Japanese tooth size: past and present. *American Journal of Physical Anthropology*, 59: 399–411.
- Carey J.W. and Steegmann A.T. (1981) Human nasal protrusion, latitude, and climate. *American Journal of Physical Anthropology*, 56: 313–319.
- Carlson D.S. and Van Gerven D.P. (1977) Masticatory function and post-pleistocene evolution in Nubia. *American Journal of Physical Anthropology*, 46: 495–506.
- Chisholm B. and Koike H. (1999) Reconstructing prehistoric Japanese diet using stable isotopic analysis. In: Omoto K. (ed.), *Inter-disciplinary Perspectives on the Origins of the Japanese*. International Research Center for Japanese Studies, Kyoto, pp. 69–73.
- Coon C.S. (1955) Some problems of human variability and natural selection in climate and culture. *The American Naturalist*, 89: 257–279.
- Crawford G.W. (2006) East Asian plant domestication. In: Stark M.T. (ed.), *Archaeology of Asia*. Blackwell, Oxford, pp. 77–95.
- Dodo Y. (1982) A metrical analysis of Jomon crania from the Tohoku district. *The Journal of the Anthropological Society of Nippon*, 90 (supplement): 119–128 (in Japanese with English summary).
- Dodo Y. (1987) Supraorbital foramen and hypoglossal canal bridging: the two most suggestive nonmetric cranial traits in discriminating major racial groupings of man. *The Journal of the Anthropological Society of Nippon*, 95: 19–35.
- Dodo Y. (1995) Origins of Japanese. In: Dodo Y. (ed.), *Lands for Mongoloids 3: Formation of Japanese*. The University of

- Tokyo Press, Tokyo, pp. 129–191 (in Japanese).
- Dodo Y. and Ishida H. (1990) Population history of Japan as viewed from cranial nonmetric variation. *The Journal of the Anthropological Society of Nippon*, 98: 269–287.
- Doigahama Site Anthropological Museum and The Cultural Relics and Archaeology of Shangdong Province (2000) Searching in the continent for the root of immigrant Yayoi people. Report of the Joint Research between Japan and China 1, Yamaguchi and Shangdong (in Japanese and Chinese).
- Endo B. (1984) Biomechanics and anthropology: morphology and structure of vertebra and cranium. In: *The Anthropological Society of Nippon* (ed.), *Anthropology: Its Diverse Development*. Nikkei Science Inc., Tokyo, pp. 110–123 (in Japanese).
- Fouts H.N., Hewlett B.S., and Lamb M.E. (2005) Parent–offspring weaning conflicts among the Bofi farmers and foragers of central Africa. *Current Anthropology*, 46: 29–50.
- Franciscus R.G. and Long J.C. (1991) Variation in human nasal height and breadth. *American Journal of Physical Anthropology*, 85: 419–427.
- Fujio S. (1993) Jomon to Yayoi as seen through subsistence. *Bulletin of the National Museum of Japanese History*, 48: 1–64 (in Japanese).
- Fukase H. and Suwa G. (2008) Growth-related changes in prehistoric Jomon and modern Japanese mandibles with emphasis on cortical bone distribution. *American Journal of Physical Anthropology*, 136: 441–454.
- Fukase H. and Suwa G. (2010) Influence of size and placement of developing teeth in determining anterior corpus height in prehistoric Jomon and modern Japanese mandibles. *Anthropological Science*, 118: 75–86.
- González-José R., Ramírez-Rozzi F., Sardi M., Martínez-Abadías N., Hernández M., and Pucciarelli H.M. (2005) Functional-cranial approach to the influence of economic strategy on skull morphology. *American Journal of Physical Anthropology*, 128: 757–771.
- Hall R.L. (2005) Energetics of nose and mouth breathing, body size, body composition, and nose volume in young adult males and females. *American Journal of Human Biology*, 17: 321–330.
- Hanihara K. (1991) Dual structure model for the population history of the Japanese. *Japan Review*, 2: 1–33.
- Hanihara T. (1993a) Craniofacial features of Southeast Asians and Jomonese: a reconsideration of their microevolution since the Late Pleistocene. *Anthropological Science*, 101: 25–46.
- Hanihara T. (1993b) Population prehistory of East Asia and the Pacific as viewed from craniofacial morphology: the basic populations in East Asia, VII. *American Journal of Physical Anthropology*, 91: 173–187.
- Hanihara T. (2000) Frontal and facial flatness of major human populations. *American Journal of Physical Anthropology*, 111: 105–134.
- Hanihara T. (2006) Interpretation of craniofacial variation and diversification of East and Southeast Asians. In: Oxenham M. and Tayles N. (eds.), *Bioarchaeology of Southeast Asia*. Cambridge University Press, Cambridge, pp. 91–111.
- Hanihara T. and Ishida H. (2009) Regional differences in craniofacial diversity and the population history of Jomon Japan. *American Journal of Physical Anthropology*, 139: 311–322.
- Harada T. (1954) Craniometrical studies on the south-western Japanese populations. *The Quarterly Journal of Anthropology*, 1: 1–51 (in Japanese with English summary).
- Hernandez M., Fox C.L., and Garcia-Moro C. (1997) Fuegian cranial morphology: the adaptation to a cold, harsh environment. *American Journal of Physical Anthropology*, 103: 103–117.
- Howells W.W. (1973) Cranial variation in man: a study by multivariate analysis of patterns of difference among recent human populations. *Papers of the Peabody Museum of American Archaeology and Ethnology*, 67. Harvard University, Cambridge, MA.
- Hylander W.L. (1975) The human mandible: lever or link? *American Journal of Physical Anthropology*, 43: 227–242.
- Hylander W.L. (1977) The adaptive significance of Eskimo craniofacial morphology. In: Dahlberg A.A. and Graber T.M. (eds.), *Orofacial growth and development*. Mouton Publishers, the Hague and Paris, pp. 129–169.
- Imamura K. (1996) Jomon and Yayoi: the transition to agriculture in Japanese prehistory. In: Harris D.R. (ed.), *The Origins of Agriculture and Pastoralism in Eurasia*. Smithsonian Institution Press, Washington, DC, pp. 442–464.
- Ishida H. (1992) Flatness of facial skeletons in Siberian and other circum-Pacific populations. *Zeitschrift für Morphologie und Anthropologie*, 79: 53–67.
- Ishida H. and Dodo Y. (1997) Cranial variation in prehistoric human skeletal remains from the Marianas. *American Journal of Physical Anthropology*, 104: 399–410.
- Kaifu Y. (1997) Changes in mandibular morphology from the Jomon to Modern periods in eastern Japan. *American Journal of Physical Anthropology*, 104: 227–243.
- Kaifu Y. (1999) Changes in the pattern of tooth wear from the prehistoric to recent periods in Japan. *American Journal of Physical Anthropology*, 109: 485–499.
- Kanaseki T., Nagai M., and Sano H. (1960) Craniological studies of the Yayoi-period ancients, excavated at the Doigahama site, Yamaguchi prefecture. *The Quarterly Journal of Anthropology*, 7 (Supplement): 1–36 (in Japanese with English summary).
- Kaneda Y. (1957) A study on chorological age of permanent tooth formation in Japan. *Shika Geppo*, 30: 167–172 (in Japanese).
- Kawakubo Y., Sawada J., and Dodo Y. (2009) In search for Ainu's signs in the Tohoku region, Japan: cranial metric and nonmetric analyses of unearthened human skeletal remains. *Anthropological Science (Japanese Series)*, 117: 65–87 (in Japanese with English summary).
- Kim J.J., Ogata T., Mine K., Takenaka M., Sakuma M., and Seo Y.N. (1993) Human skeletal remains from Yeanri site, Kimhae, Korea. *Archaeological Research Report of the University Museum, Pusan National University*, 15: 281–334 (in Korean).
- Kintaka K. (1928) *Anthropologische Untersuchungen über das Skelett der Yoshiko-Steinzeitmenschen*. *The Journal of the Anthropological Society of Nippon*, 43 (Supplement): 497–736 (in Japanese with German title).
- Kitagawa Y., Manabe Y., Oyamada J., and Rokutanda A. (2002) Japanese deciduous tooth size: past and present. *Anthropological Science*, 110: 335–347.
- Kiyono K. and Miyamoto H. (1926) *Anthropologische Untersuchungen über das Skelett der Tsukumo-Steinzeitmenschen*. *The Journal of the Anthropological Society of Nippon*, 41: 95–140, 151–208 (in Japanese with German title).
- Komoto M. (1986) Foods of Yayoi people. *Archaeology Quarterly*, 14: 29–33 (in Japanese).
- Komoto M. (1991) Spread of the agriculture at the Yayoi period. *Archaeology Quarterly*, 37: 29–33 (in Japanese).
- Kondo O., Ishida H., Hanihara T., Wakebe T., Dodo Y., and Akazawa T. (2005) Cranial ontogeny in Neandertal children: evidence from neurocranium, face and mandible. In: Zadninska E. (ed.), *Current trends in dental morphology research*. University of Lodz Press, Lodz, pp. 243–255.
- Kozintsev A.G., Gromov A.V., and Moiseyev M.G. (1999) Collateral relatives of American Indians among the Bronze Age populations of Siberia? *American Journal of Physical Anthropology*, 108: 193–204.
- Larsen C.S. (1995) Biological changes in human populations with agriculture. *Annual Review of Anthropology*, 24: 185–213.
- Lovejoy C.O., Russell K.F., and Harrison M.L. (1990) Long bone growth velocity in the Libben population. *American Journal of Human Biology*, 2: 533–541.
- Martin R. and Saller K. (1957) *Lehrbuch der Anthropologie*. Bd. T. Gustav Fisher Verlag, Stuttgart.

- Matsumura H. (1994) A microevolutionary history of the Japanese people from a dental characteristics perspective. *Anthropological Science*, 102: 93–118.
- Miyamoto H. (1924) *Anthropologische Untersuchungen über das Skelett der rezenten Japaner*. The Journal of the Anthropological Society of Nippon, 39: 307–451, 1–48 (Appendix) (in Japanese with German title).
- Miyamoto K. (2000) Jomon agriculture and Jomon society. In: Sahara M. and Tsude H. (eds.), *Points at Issue of Ancient History*, Vol. 1. Syogakukan, Tokyo, pp. 115–138 (in Japanese).
- Mizoguchi K. (2006) Self-identification in the Modern and post-Modern world and archaeological research: a case study from Japan. In: Stark M.T. (ed.), *Archaeology of Asia*. Blackwell, Oxford, pp. 55–73.
- Mizoguchi Y. (1988) Affinities of the protohistoric Kofun people of Japan with pre- and proto-historic Asian populations. The Journal of the Anthropological Society of Nippon, 96: 71–109.
- Morita S. (1950) Anthropological study of the skulls of the Japanese from Kanto. Report of Department Anatomy, Jikei University School of Medicine, 3: 1–59 (in Japanese).
- Nakahashi T. (1993) Temporal craniometric changes from the Jomon to the Modern period in western Japan. *American Journal of Physical Anthropology*, 90: 409–425.
- Nakahashi T. (2005) *The Origins of Japanese*. Kodansha, Tokyo (in Japanese).
- Nakahashi T. and Li M. (2002) Ancient People in the Jiangnan Region, China: Anthropological Study on the Origin of the Yayoi People in Northern Kyushu. Kyushu University Press, Fukuoka.
- Nakahashi T. and Nagai M. (1985) Human skeletal remains from Yoshimohama site, Yamaguchi. In: Educational Committee of Shimonoseki City (ed.), *Yoshimohama site*. Shimonoseki, pp. 154–225 (in Japanese).
- Nakahashi T. and Nagai M. (1989) The physical features of the Yayoi people. In: Nagai M., Nasu T., Kanaseki H., and Sahara M. (eds.), *A Study of the Yayoi Culture I*. Yuzankaku Press, Tokyo, pp. 76–95 (in Japanese).
- Nara T. and Suzuki T. (2003) An infant skeletal remain of Yayoi period excavated at the Abakuchi cave site, Ohasama, Iwate Prefecture. In: Dodo Y. and Sawada J. (eds.), *In Search of Pleistocene Human fossils in Kitakami Mountain Areas: Excavation of the Abakuchi and Kaza'ana Cave Sites*, Ohasama, Iwate Prefecture. Tohoku University Press, Sendai, pp. 54–89 (in Japanese).
- O'Higgins P. and Strand-Viðarsdóttir U. (1999) New approaches to the quantitative analysis of craniofacial growth and variation. In: Hoppa R.D. and FitzGerald C.M. (eds.), *Human Growth in the Past*. Cambridge University Press, Cambridge, pp. 128–160.
- Okazaki K. (2004) A morphological study on the growth patterns of ancient people in the northern Kyushu-Yamaguchi region, Japan. *Anthropological Science*, 112: 219–234.
- Okazaki K. (2009) Human growth patterns of the Jomon, Yayoi, Medieval, and early Modern people: a comparison of morphological traits and reconstruction of life using the data from juvenile skeletal remains. *Kashoin*, Fukuoka (in Japanese).
- Omoto K. (1995) The distribution of Mongoloid. In: Dodo Y. (ed.), *Lands for Mongoloids 3: Formation of Japanese*. The University of Tokyo Press, Tokyo, pp. 1–31 (in Japanese).
- Omoto K. and Saitou N. (1997) Genetic origins of the Japanese: A partial support for the dual structure hypothesis. *American Journal of Physical Anthropology*, 102: 437–446.
- Pearson O.M. and Lieberman D.E. (2004) The aging of Wolff's law: ontogeny and responses to mechanical loading in cortical bone. *American Journal of Physical Anthropology*, 47: 63–99.
- Pietrusewsky M. (2000) Metric analysis of skeletal remains: methods and applications. In: Katzenberg M.A. and Saunders S.R. (eds.), *Biological Anthropology of the Human Skeleton*. Wiley-Liss, New York, pp. 375–415.
- Ponce de Leon M.S. and Zollikofer C.P.E. (2001) Neanderthal cranial ontogeny and its implications for late hominid diversity. *Nature*, 412: 534–538.
- Relethford J.H. and Harpending H.C. (1994) Craniometric variation, genetic theory, and modern human origins. *American Journal of Physical Anthropology*, 95: 249–270.
- Saito S. (1987) Mastication and mechanocytology. In: Kubota K. (ed.), *Introduction to the Masticatory System*. Fujin-sha, Tokyo, pp. 115–129 (in Japanese).
- Sardi M.L., Rozzi F.R., González-José R., and Pucciarelli H.M. (2005) South Amerindian craniofacial morphology: diversity and implications for Amerindian evolution. *American Journal of Physical Anthropology*, 128: 747–756.
- Scheuler L. and Black S. (2000) *Developmental Juvenile Osteology*. Academic Press, San Diego.
- Sellen D.W. and Smay D.B. (2001) Relationship between subsistence and age at weaning in "preindustrial" societies. *Human Nature*, 12: 47–87.
- Serikov V.B., Jerome E.H., Fleming N.W., Moore P.G., Stawitche F.A., and Staub N.C. (1997) Airway thermal volume in humans and its relation to body size. *Journal of Applied Physiology*, 83: 668–676.
- Shea B.T. (1977) Eskimo craniofacial morphology, cold stress and the maxillary sinus. *American Journal of Physical Anthropology*, 47: 289–300.
- Shimomi A., Hirata K., Nagaoka T., and Yoneda M. (2007) Reconstruction of the breastfeeding pattern based on isotopic analysis of the Kamakura population from the Yuigahama-minami site. *Anthropological Science*, 115: 248.
- Smith B.H. (1991) Standards of human tooth formation and dental age assessment. In: Kelley M.A. and Larsen C.S. (eds.), *Advances in Dental Anthropology*. Wiley-Liss, New York, pp. 143–168.
- Spencer M.A. and Demes B. (1993) Biomechanical analysis of masticatory system configuration in Neandertals and Inuits. *American Journal of physical Anthropology*, 91: 1–20.
- StatSoft Inc. (1996) *User's manual for STATISTICA*. StatSoft Japan, Tokyo (in Japanese).
- Stegmann A.T. (1965) A study of relationships between facial cold response and some variables of facial morphology. *American Journal of Physical Anthropology*, 23: 355–362.
- Stegmann A.T. (1967) Frostbite of the human face as a selective force. *Human Biology*, 39: 131–144.
- Stegmann A.T. (1970) Cold adaptation and the human face. *American Journal of Physical Anthropology*, 32: 243–250.
- Stegmann A.T. (1972) Cold response, body form, and craniofacial shape in two racial groups of Hawaii. *American Journal of Physical Anthropology*, 37: 193–222.
- Stinson S. (2000) Growth variation: biological and cultural factors. In: Stinson S., Bogin B., Huss-Ashmore R., and O'Rourke D. (eds.), *Human Biology: An Evolutionary and Biocultural Perspective*. Wiley-Liss, New York, pp. 425–463.
- Strand-Viðarsdóttir U., O'Higgins P., and Stringer C. (2002) A geometric morphometric study of regional differences in the ontogeny of the modern human facial skeleton. *Journal of Anatomy*, 201: 211–229.
- Sutter R.C. (2003) Nonmetric subadult skeletal sexing traits: I. A blind test of the accuracy of eight previously proposed methods using prehistoric known-sex mummies from Northern Chile. *Journal of Forensic Sciences*, 48: 927–935.
- Suzuki H. (1969) Microevolutional changes in the Japanese population from the prehistoric age to the present-day. *Journal of the Faculty of Science, University of Tokyo, Section 5: Anthropology*, 3: 279–309.
- Suzuki H., Hayashi T., Tanabe Y., and Sakura H. (1956) The characters of skulls. In: *Anthropological Society of Nippon* (ed.), *Medieval Japanese Skeletons from the Burial Site at Zaimokuza, Kamakura City*. Iwanami-shoten, Tokyo, pp. 75–148 (in Japanese with English summary).

- Suzuki T. (2008) Temporal changes of tooth wear on the deciduous dentition of the Japanese. *Anthropological Science*, 116: 273.
- Takigawa W. (2006) Inter-regional variation of metric traits of limb bones in Jomon and modern Japanese. *Anthropological Science (Japanese Series)*, 114: 101–129 (in Japanese with English summary).
- Tasaki H. (2002) The wet-rice cultivation in Japanese Archipelago: the examination on the remains of paddy during the 1st millennium BC. In: Gotou T. and Mogi M. (eds.), *Archaeology of East Asia and Japan: No. 4 Subsistence*. Douseisha, Tokyo, pp. 73–117 (in Japanese).
- Temple D.H., Auerbach B.M., Nakatsukasa M., Sciulli P.W., and Larsen C.S. (2008) Variation in limb proportions between Jomon foragers and Yayoi agriculturalists from prehistoric Japan. *American Journal of Physical Anthropology*, 137: 164–174.
- Terasawa K. and Terasawa T. (1981) The basic study about vegetable foods at the Yayoi period: the beginning of cultivation. *Koukougaku-Ronko*, 5: 1–129 (in Japanese).
- Wolpoff M.H. (1968) Climatic influence on the skeletal nasal aperture. *American Journal of Physical Anthropology*, 29: 405–424.
- Yamaguchi B. (1973) Facial flatness measurements of the Ainu and Japanese crania. *Bulletin of the National Science Museum*, 16: 161–171.
- Yamaguchi B. (1982) A review of the osteological characteristics of the Jomon population in prehistoric Japan. *The Journal of the Anthropological Society of Nippon*, 90: 77–90.
- Yamaguchi B. (1999) The background of Japanese from the view of physical anthropology. Misuzu, Tokyo (in Japanese).
- Yamaguchi B. and Huang X. (1995) Studies on the human skeletal remains from Jiangnan, China. *National Science Museum Monographs*, No. 10, Tokyo.
- Yamasaki S. (2005) West Japan Jomon agriculture hypothesis. In: Keinan Bunkazai Kenkyu-in (ed.), *Neolithic Agriculture in Korea and Japan*. Korean Neolithic Research Association, Busan, pp. 33–55 (in Japanese).
- y'Edynak G.J. and İşcan M.Y. (1993) Craniofacial evolution and growth. In: İşcan M.Y. and Helmer R.P. (eds.), *Forensic Analysis of the Skull: Craniofacial Analysis, Reconstruction, and identification*. Wiley-Liss, New York, pp. 11–27.
- Yoneda M. (2005) Element analysis of bone for determining the foodstuffs. In: The National Science Museum, Tokyo, National Museum of Japanese History and Yomiuri Newspaper Office (eds.), *Special exhibition "Jomon vs. Yayoi."* Yomiuri Newspaper Office, Tokyo, pp. 100–101 (in Japanese).