Three-dimensional craniofacial variation and occlusal wear severity among inhabitants of Hokkaido: comparisons of Okhotsk culture people and the Ainu

Ikuya FUKUMOTO¹, Osamu KONDO^{1*}

¹*Department of Biological Sciences, Division of Anthropology, Graduate School of Science, The University of Tokyo, Tokyo 113-0033, Japan*

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Abstract Hokkaido is an intriguing region for studies of population history in Japan because of its geographical position both at the periphery in the Japanese archipelago and at the gateway to the north-eastern Eurasian continent. This paper focuses on the biological relationship between two populations, Okhotsk culture people and Ainu, and investigates craniofacial variation and dental wear severity between and within the populations. Fifty-six anatomical landmarks were digitized in order to capture craniofacial shape and size components, and occlusal wear scores on the maxillary dentition were recorded as a proxy for the degree of masticatory stress. Population differences are clear in the craniofacial form: the Okhotsk skull is characterized by a high and broad face but a relatively smaller palate, high and anteriorly protruding zygoma as well as mediosuperiorly positioned temporal muscle origins, large infratemporal and mandibular fossae. However, this morphological shift is not proportional to that of the east–west regional difference within the Ainu males, each of which is detected along distinct and mutually independent principal components. Dental wear is stronger in Okhotsk than in Ainu although without any regional difference in the respective sample. Moderate association is found between the dental wear scores and the craniofacial shape components only in the Okhotsk males, suggesting that they might have suffered from a substantial amount of functional demands. These results do not reject, but suggest modifications of, a previous simple model of genetic contribution from Okhotsk culture people to the formation of the Ainu regional variation. The formation process of the Ainu remains to be studied further in both biological and cultural contexts.

Key words: Geometric morphometrics, population history, Japan

Introduction

During the 5th–12th centuries AD, an eastern region of Hokkaido was immigrated by an exotic human population, Okhotsk culture people, whose physical characteristics, subsistence, and culture have been assumed to be quite distinct from those of indigenous Jomon or the subsequent Ainu inhabitants of Hokkaido. The subsistence of the Okhotsk culture people seems to have depended deeply on marine resources. The archeological sites of the Okhotsk culture, including dwellings and temporary camps, are distributed within 1 km of the Okhotsk Sea coast, and their faunal remains consist of a high percentage of marine fishes and mammals (Amano, 2003). Carbon and nitrogen stable isotope analyses of the human bone collagen have supported this view, indicating higher dependence on marine resources

in their diet (Yoneda, 2002). Analyses of cranial metric and nonmetric data have confirmed a biological affinity closer to east Siberians from the lower Amur River such as the Nivkh and Ulch, compared to Jomon or Epi-Jomon and Ainu in the Hokkaido region (Yamaguchi, 1974; Ishida, 1994, 1995, 1996; Shigematsu et al., 2004; Komesu et al., 2008). By contrast, studies of mitochondrial DNA (mtDNA) sequence data have argued that the Okhotsk culture people are as close to the Ainu as to the Nivkh and Ulch (Sato et al., 2007, 2009a).

Formation of Ainu culture is considered to have been a gradual process that united a number of different preceding cultures, including Satsumon culture, which is contemporaneous with Okhotsk culture in Hokkaido. The cultural and biological origins of the Satsumon is believed to lie in Jomon and Epi-Jomon predecessors with a variable degree of incorporation from outside, both north and south. In terms of biology, previous anthropological studies have clarified that the Ainu is one of the circumpacific, East Asian populations, and that it is osteologically closer to Neolithic Jomon than to the other East Asians (Yamaguchi, 1982; Howells, 1986; Dodo and Ishida, 1990; Kozintsev, 1990; Ossenberg et al., 2006). Meanwhile, regional variation of Hokkaido Ainu was thought to be indicative of a degree of interaction with Okhotsk culture people (Ito, 1967; Yamaguchi, 1981;

* Correspondence to: Osamu Kondo, Department of Biological Sciences, Division of Anthropology, Graduate School of Science, The University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo 113-0033, Japan.
E-mail: kondo-o@biol.s.u-tokyo.ac.jp

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Kondo, 1995). Recent analyses involving the application of quantitative genetics to craniometric variation (Relethford and Blangero, 1990) have evoked the idea of genetic contribution of Okhotsk culture people to the formation of the Ainu (Kondo, 2005; Hanihara et al., 2008; Ishida et al., 2009), although the degree and pattern of phenotypic contribution seems unclear (Yamaguchi, 1974; Ishida, 1994, 1995, 1996; Shigematsu et al., 2004; Komesu et al., 2008).

In this context, more detailed comparisons of the craniofacial variation and further considerations of genotype and phenotype interaction will improve the present state of knowledge. The former should include scrutinizing the population difference and its relation to the regional difference within a population. Considering the above-mentioned background to the population history of Hokkaido, we can hypothesize that the regional variation of Ainu ought to be due to a limited invasion of the Okhotsk culture people in both temporal and regional dimensions, and thus the morphological shift could be matched to the interpopulation difference between the Okhotsk and the Ainu.

As a way to estimate the environmental effect on craniofacial variation, we use an indirect approach to evaluate morphological interactions between different parts, each of which could be subjected to different levels of functional demands. To this end, assuming dental wear severity as a proximate trait strongly affected by environment, we investigate the degree and pattern of association between dental wear and craniofacial variation among local inhabitants of Hokkaido, Okhotsk culture people, and the Ainu. The two groups are linked with each other both temporally and regionally in the population history of Hokkaido, and thus both genetic and cultural interaction would be plausible in variable degrees.

Studies of dental wear patterns are, by themselves, of importance in providing testable approaches for past people's activity and subsistence because they relate closely with the

diet and also with the feeding/masticatory process of the diet. Many orthodontists have conducted a variety of quantitative studies on dental wear patterns and their relationship to cranial morphology, and it has been pointed that the degree of dental wear relates to the cranial morphology, especially to the face (Krogstad and Dahl, 1985; Richards, 1985; Kiliaridis et al., 1995; Zengingul et al., 2007). In bioarcheological perspectives, on the other hand, the degree of dental wear has often been described in terms of subsistence or culture, where the heavy dental wear can be ascribed to intentional use of dentition as a tool, inclusion of hard dietary foodstuffs, or commingling of tough ingredients such as sand during the cooking process (Molnar, 1971; Powell, 1985).

Concerning the dental wear of the two populations, an initial descriptive work (Kodama, 1948) indicated that the Okhotsk culture people had relatively strong dental wear. Hudson (2004) measured the degree of dental wear on the Okhotsk culture people and reported no regional difference between the northern and the eastern subpopulations, although he did not expand the comparison to the other populations. As for the Ainu, except for descriptions in each archeological site report, there have been no comprehensive studies on the degree of dental wear. It is plausible that the poor basic comparative data has limited variable interpretations as masticatory apparatus, or as cultural properties in their subsistence patterns.

Materials and Methods

Cranial samples studied consist of 74 Okhotsk culture people (44 males and 30 females) and 84 Ainu (51 males and 33 females) of adult age (Figure 1) stored at The University Museum, The University of Tokyo, Hokkaido University Museum, and Sapporo Medical University. Adult age assessment depends on complete ossification of basi-occipital

Figure 1. Frontal view of a male cranium of Okhotsk culture people (left) unearthed from Moyoro shell mound (former ID Moyoro 15, new ID no. 1006 in Hokkaido University Museum), and a male cranium of the Ainu (right) unearthed from Usu-4 site in Date City, Iburi sub-prefecture of Hokkaido (Usu4 GP020).

synchronosis and eruption of third molars. Sexing was according mainly to individual records cataloged in the respective museums and institutions and partly to gross observations of sexing criteria in the skull. Table 1 shows the age distribution of the two samples. Individual age at death was estimated based on cranial suture closure patterns (Meindl and Lovejoy, 1985). The two samples do not show any significant difference in their age distributions in both males ($\chi^2 = 1.81$, $df = 2$) and females ($\chi^2 = 1.12$, $df = 2$).

Figure 2 shows the locality of the site used in this study. We set two regional divisions, North and East subsamples, for the Okhotsk culture site. This division implies a site distribution pattern and prospects a North-to-East expansion of the Okhotsk culture (Ushiro, 1995; Amano, 2003). As for the Ainu, we originally used four regional divisions, i.e. Southwest (SW), Southeast (SE), Northeast (NE) and Central (C), which were expected to exhibit a high degree of

intergroup heterogeneity (Kondo, 1995, 2005). In preliminary comparisons, however, we could only detect significant differences between SW and the others, and thus combined the latter three into one division (East). The East region is presumably overlapped with the Okhotsk culture distribution, although it does not match perfectly. The details of the local divisions, sample sizes for each site/prefectural local region are shown in Table 2.

Craniofacial morphology was quantified in terms of geometric morphometrics using 56 anatomical landmarks, which were digitized with a 3D digitizer (MicroScribe G2, Immersion Co.). In order to investigate relationships between dental wear and craniofacial morphology, additional landmarks were established from functional perspectives that could be related to mastication. Most of them are in Martin's textbook (Martin and Knussmann, 1988) and some others were originally defined by the authors with reference to González-José et al. (2008) (Table 3, Figure 3). After capturing the 3D data for the landmarks, we undertook generalized Procrustes analysis (GPA) and principal component analysis (PCA) using a morphometrics program, Morphologika2 (O'Higgins and Jones, 1998). During the GPA process, the size factor for each individual was calculated and removed as the 'Centroid Size,' and the landmark data were rotated to fit synonymous landmarks together as much as possible. The residuals from the average 'consensus' position for each landmark were then used for calculating the principal components to describe the individual shape variation. Interpopulation or regional variations were

Table 1. Age distribution of the Okhotsk culture people and the Ainu

	Number of individuals (%)			
	Young	Middle	Old	Total
Male				
Okhotsk	19 (45.2)	15 (35.7)	8 (19.0)	42
Ainu	22 (44.0)	13 (26.0)	15 (30.0)	50
Total	41	28	24	92
$\chi^2 = 1.81$, $df = 2$, NS				
Female				
Okhotsk	14 (60.9)	5 (21.7)	4 (17.4)	23
Ainu	20 (60.6)	10 (30.3)	3 (9.1)	33
Total	34	15	7	56
$\chi^2 = 1.12$, $df = 2$, NS				

Three age categories, Young (20–34 years), Middle (35–49 years), and Old (50+ years) are defined through evaluation of cranial suture closure (Meindl and Lovejoy, 1985).

Figure 2. Geographical divisions for the samples used in this study.

Table 2. Number of individuals for the two local divisions of Okhotsk culture people and the Ainu

Okhotsk	Site	Male	Female
North	Rebun Island	12	9
	Susuya	7	
	Ohmisaki	10	5
	North Okhotsk total	27	21
East	Moyoro	17	6
	Utoro-Jinjayama	0	3
	East Okhotsk total	17	9
Ainu	Prefectural region	Male	Female
South West (SW)	Ishikari	6	1
	Shiribeshi	12	11
	Iburi	3	3
	Oshima	2	0
	Hidaka	11	8
	SW Ainu total	34	23
East ^a	Tokachi (C)	11	2
	Kushiro (SE)	1	1
	Nemuro (SE)	1	2
Northeast	Teshio (NE)	1	1
	Kitami (NE)	3	4
	East Ainu total	17	10

^a East region of the Ainu is composed of three regional units: Central (C), Southeast (SE), and Northeast (NE).

Table 3. Definition of landmarks

Landmark	Definition
1 Prosthion	The most anterior point in the midline on the alveolar process of the maxilla.
2, 3 Ectomolare (r/l)	The most lateral point on the alveolar borders on the maxilla.
4 Subspinale	The deepest point in the concavity between the anterior nasal spine and prosthion.
5, 6 Alare (r/l)	The most lateral point on the margin of the nasal aperture.
7 Nasion	Intersection of the nasofrontal suture with the midsagittal plane.
8, 9 Maxillofrontale (r/l)	The point where the anterior lacrimal crest of the maxilla meets the frontomaxillary suture.
10, 11 Frontomolare orbitale (r/l)	The point where the frontozygomatic suture crosses the inner orbital rim.
12 Glabella	The most anterior midline point on the frontal bone.
13 IPS	Intersection of the median palatine suture with the transverse palatine suture.
14, 15 Alveolar point (r/l)	Posterior limit of the maxillary alveolar arch at the pterygoalveolar suture.
16, 17 Zygoorbitale (r/l)	The point where the zygomaticomaxillary suture crosses the outer orbital rim.
18, 19 Zygomaxillare (r/l)	The most inferior point of the zygomaticomaxillary suture.
20, 21 Midpoint zo-zm (r/l)	The midpoint of the zygoorbitale–zygomaxillare segment.
22, 23 Jugale (r/l)	The point in the depth of the notch between the temporal and frontal processes of the zygomatic.
24, 25 Stephanion (r/l)	The point where the coronal suture crosses the temporal line.
26, 27 Temp sup (r/l)	Upper temporal line at the coronal intersection.
28 Inner prosthion	The midline point at the most posterior point on the alveolar process of the maxilla.
29, 30 Inner C-P3 (r/l)	Point on the inner surface of the alveolar margins of the maxilla between C and P3.
31, 32 Inner P4-M1 (r/l)	Point on the inner surface of the alveolar margins of the maxilla between P4 and M1.
33, 34 Inner M2-M3 (r/l)	Point on the inner alveolar margin between M2 and M3.
35, 36 Outer C-P3 (r/l)	Point on the outer alveolar margin between C and P3.
37, 38 Outer P4-M1 (r/l)	Point on the outer alveolar margin between P4 and M1.
39, 40 Outer M2-M3 (r/l)	Point on the outer alveolar margin between M2 and M3.
41, 42 Ant. preglenoid plane (r/l)	The most anterior point on the pre-glenoid plane.
43, 44 Post. glenoid fossa (r/l)	Posterior border of the glenoid cavity.
45, 46 Lateral glenoid fossa (r/l)	The most lateral point on the border of the glenoid cavity.
47, 48 Innermost SFS (r/l)	The most medial point on the sphenofrontal suture.
49, 50 Post. infratemporal fossa (r/l)	The most posterior point in the infratemporal fossa.
51 Hormion	The most posterior midpoint on the vomer.
52 Opisthion	Midpoint at the posterior margin of the foramen magnum.
53 Inion	An ectocranial midpoint at the base of the external occipital protuberance.
54, 55 Zygion (r/l)	The most lateral point on the zygomatic arch.
56 Basion	The midpoint at the anterior margin of the foramen magnum.

Figure 3. Landmarks and wireframe networks (shown only for one side) used in this study. See Table 3 for definitions of the landmarks.

assessed based on the given principal components scores.

Dental wear pattern was assessed on the occlusal surface of maxillary dentition except for the third molar, because a substantial number of the cranial samples lacked a mandible. We used Molnar’s quantification criteria for dental wear (Molnar, 1971) which categorizes the degree of dental wear into eight successive scores. We chose this as a simple and

convenient way to describe the degree of dental wear, rather than other detailed methods such as a principal axis method by Scott (1979). Most of the specimens showed horizontal occlusal wear, but we excluded specimens with heavily slanted wear which would be indicative of intentional use as tools. We calculated average scores for individuals with all preserved maxillary dentitions, and those with anterior

(incisor and canine) and posterior (premolar and molar) dentitions. The aim of this analysis mainly focuses on the degree and pattern of association between the dental wear severity and the craniofacial morphology. In addition, we performed simple comparisons of dental wear severity scores, after we confirmed negligible age-dependent effects because of the similar age distribution patterns among populations.

Statistical calculations were conducted using the software package S-plus (S-PLUS Co.). Mann–Whitney *U*-test was used for comparison of means of the dental wear scores, and Spearman rank-order correlation coefficient was calculated between the mean dental wear scores and the principal components of the craniofacial variation. Regional craniofacial variation within each population and interpopulation craniofacial variation were assessed, and tested by Welch's *t*-test or the Kruskal–Wallis test. A 5% level of significance was used for all the statistical tests.

Results

Craniofacial variation

Craniofacial shape difference was significant between the Okhotsk culture people and the Ainu. After conducting PCA on the male data, a significant difference between the two populations was detected along PC1 and PC4, where the proportions to total variance explained were 29.59% and 6.47%, respectively. The two-dimensional plot clearly separates the two populations (Figure 4, mean PC1: Okhotsk = -0.035 , Ainu = 0.020 , $P < 0.01$; mean PC4: Okhotsk = 0.007 , Ainu = -0.003 , $P < 0.05$). Shape changes along PC1 and PC4 can be visualized through the thin-plate spline function (Figure 5). After we set the 'reference shape' as with the maximum PC1 (0.06) and the minimum PC4 (-0.07) values and also set the 'target shape' with the minimum PC1 (-0.10) and the maximum PC4 (0.04) values, we could visualize the

deviation from the reference to target shape in the degree and pattern of the deformed grid. Compared to the Ainu male (high PC1 and low PC4), the Okhotsk male (low PC1 and high PC4) possesses a more upper medial position of the temporal muscle origin, a large infratemporal space, and a large mandibular fossa. In addition, the Okhotsk male has a high and anterolaterally protruding zygoma, and a relatively posteroinferior position of the incisive alveolus. The latter forms a high, broad, and flat face and a relatively smaller palate in the Okhotsk male. The centroid size, which negatively correlates with the PC1 in a moderate degree ($r = -0.49$, $P < 0.01$), is significantly larger in the Okhotsk male than that of the Ainu male (mean centroid size: Okhotsk = 47.81 , Ainu = 45.22 , $P < 0.01$).

Interpopulation difference among female samples shows almost the same pattern as in males. Only along PC1 (26.21% of total variance explained) was significant difference detected between the Okhotsk female (mean PC1 = -0.048) and the Ainu female (mean PC1 = 0.015 , $P < 0.01$). Shape changes along PC1 are generally identical to those found between the male samples, but the degree of shape difference is smaller than in males. The centroid size, which correlates negatively with PC1 ($r = -0.65$, $P < 0.01$), also shows significant difference (Okhotsk female = 45.33 , Ainu female = 43.05 , $P < 0.01$).

Regional shape variation within the respective population was investigated using principal components scores of the size-adjusted landmark data. Based on the 18 Okhotsk males, no significant difference was detected between North and East regions along all the PCs (the plot along PC1 and PC2 is shown in Figure 6). As for the size, the centroid size correlates negatively with the PC2 ($r = -0.66$, $P < 0.01$), although it does not exhibit North–East regional difference. Wire-frame warp along PC2 indicates that the specimen with smaller values (possessing larger centroid size) tends to

Figure 4. Plot of PC1 and PC4 scores based on male samples of Okhotsk culture people and the Ainu. PC1 represents 29.59% of total variance (x-axis), and PC4 represents 6.47% of total variance (y-axis), respectively. Two regional groups in the Okhotsk and Ainu samples are shown.

Figure 5. Deformation grids showing warps from Ainu (middle rows) to Okhotsk (bottom rows) males along PC1 and PC4. The reference shape (Ainu male) represented by the maximum PC1 (0.06) and the minimum PC4 (−0.07) scores, and the target shape (Okhotsk male) represented by the minimum PC1 (−0.10) and the maximum PC4 (0.04) scores. The deformation grid is aligned passing through the zygomatic bone and the origin of temporalis muscle (a), the grid passing through the infratemporal fossa and the mandibular fossa (b), and the grid passing through the palate (c).

have a medial upper location of the temporal muscle origin, a large infratemporal fossa, and a high and large face. Based on the female Okhotsk samples ($n = 7$), no regional difference was detected in PCs nor in centroid sizes. No significant correlation between the centroid size and the PCs was found.

Regional difference within the Ainu population was detected only in males. Based on 31 Ainu males, only PC2 shows a significant difference between SW and East regions (mean: SW = −0.005, East = 0.011, $P < 0.01$) (Figure 7). Shape changes along PC2 are visualized in Figure 8. East Ainu, which possesses a larger value along PC2, tends to have a relatively large infratemporal fossa, mediosuperior position of the temporal muscle origin, a large gap between superior and inferior temporal lines, a large palate, and mediolaterally thick alveoli. In addition, it shows a laterally flared zygomatic and anteriorly protruding hard palate. The centroid size does not show significant correlation with any PCs or regional differences. Based on the 22 Ainu females, no regional differences were detected.

Dental wear severity

Table 4 summarizes the mean dental wear scores of all teeth, anterior and posterior dentitions for Okhotsk culture people and the Ainu, respectively. In all comparisons between the two populations, significant differences were observed in both males and females, where Okhotsk culture people always suffer from stronger dental wear than the Ainu. Among the Okhotsk local samples, no significant differences were observed between sites and between North and East regions (Table 5). Among the Ainu, no regional differences were found between SW and East regions in both males and females (Table 6).

Correlation between the dental wear severity and the craniofacial variation

We calculated Spearman's rank correlation coefficients between the dental wear scores and the centroid size, as well as the detected principal components based on the craniofacial shape variation (Table 7). No significant correlation was detected for the centroid size in respective Okhotsk and

Figure 6. Plot of PC1 and PC2 scores showing craniofacial variation within Okhotsk male samples. No significant difference was detected between Northern and Eastern regions. PC1 represents 26.34%, and PC2 represents 16.18%, of total variance.

Figure 7. Plot of PC1 and PC2 scores showing craniofacial variation within Ainu male samples. Original three regional groups (open circles, Central; open squares, Northeast; open triangles, Southeast) are combined into one (East). Significant difference was detected between SW and East regions along PC2. PC1 represents 19.13%, and PC2 represents 11.82%, of total variance.

Figure 8. Deformation grids showing warps from SW Ainu (middle rows) to East Ainu (bottom rows) males along PC2. The reference shape (SW Ainu) represented by the minimum PC2 (-0.06), and the target shape (East Ainu) represented by the maximum PC2 (0.04) scores. The deformation grid is aligned passing through the zygomatic bone and the origin of temporalis muscle (a), the grid passing through the infratemporal fossa and the mandibular fossa (b), the parasagittal grid passing through the zygoma and the temporal muscle (c).

Table 4. Summary of dental wear severity scores in Okhotsk culture people and Ainu

	All teeth		Anterior teeth (I1, I2, C)		Posterior teeth (P1, P2, M1, M2)	
	Mean (<i>n</i>)	SD	Mean (<i>n</i>)	SD	Mean (<i>n</i>)	SD
Male						
Okhotsk	4.9 (43)	1.43	4.8 (37)	1.34	5.0 (43)	1.55
Ainu	3.1 (50)	1.29	3.2 (31)	1.42	3.0 (50)	1.29
Mann-Whitney <i>U</i> -test	$P < 0.001$		$P < 0.001$		$P < 0.001$	
Female						
Okhotsk	4.8 (24)	1.52	4.8 (18)	1.28	4.9 (31)	1.62
Ainu	2.6 (32)	0.97	2.7 (18)	0.85	2.5 (31)	1.00
Mann-Whitney <i>U</i> -test	$P < 0.001$		$P < 0.001$		$P < 0.001$	

Ainu samples in both sexes. A significant correlation with the shape components was detected only in Okhotsk males, where a moderate degree of negative correlation was found between PC2 and the dental wear scores (Table 7). As already noted, PC2 of the Okhotsk males shows a negative correlation with centroid size. This indicates a plausible positive association between centroid size and dental wear se-

verity in this sample. Wire-grid warps along PC2 imply that those who have a bigger face with stronger dental wear exhibit a more medial upper position of the temporal muscle origin, a large infratemporal space, a high upper face, and a laterally flared zygomatic bone. No significant correlation was found in the other comparisons of Okhotsk females, Ainu males and females (Table 7).

Table 5. Regional comparisons of dental wear scores among North and East Okhotsk samples

	All teeth		Anterior teeth (I1, I2, C)		Posterior teeth (P1, P2, M1, M2)	
	Mean (<i>n</i>)	SD	Mean (<i>n</i>)	SD	Mean (<i>n</i>)	SD
Male						
Ohmisaki	5.3 (10)	1.55	5.2 (10)	1.46	5.3 (10)	1.72
Rebun Island	4.1 (12)	1.25	4.2 (11)	1.15	4.3 (12)	1.36
Susuya	5.3 (5)	1.05	6.3 (2)	1.06	5.0 (5)	1.04
Moyoro	5.1 (16)	1.47	5.1 (14)	1.47	5.3 (16)	1.66
North vs. East Mann–Whitney <i>U</i> -test	<i>P</i> = 0.45, NS		<i>P</i> = 0.90, NS		<i>P</i> = 0.64, NS	
Female						
Ohmisaki	4.8 (5)	1.80	4.3 (2)	0.42	4.8 (5)	1.93
Rebun Island	5.3 (8)	1.41	5.3 (6)	1.24	5.4 (8)	1.53
Susuya	4.5 (2)	2.12	6 (1)	—	4.5 (2)	2.12
Moyoro	3.9 (6)	1.43	3.9 (6)	1.38	3.9 (6)	1.51
Utoro-Jinjayama	5.7 (3)	0.87	5.3 (3)	0.67	5.8 (3)	0.89
North vs. East Mann–Whitney <i>U</i> -test	<i>P</i> = 0.23, NS		<i>P</i> = 0.20, NS		<i>P</i> = 0.34, NS	

Table 6. Regional comparisons of dental wear scores among Southwest (SW) and East Ainu samples

	All teeth		Anterior teeth (I1, I2, C)		Posterior teeth (P1, P2, M1, M2)	
	Mean (<i>n</i>)	SD	Mean (<i>n</i>)	SD	Mean (<i>n</i>)	SD
Male						
SW Ainu	3.1 (34)	1.23	3.2 (23)	1.19	3.0 (34)	1.25
East Ainu	3.2 (16)	1.46	3.2 (8)	2.06	3.2 (16)	1.43
Mann–Whitney <i>U</i> -test	<i>P</i> = 0.80, NS		<i>P</i> = 0.15, NS		<i>P</i> = 0.91, NS	
Female						
SW Ainu	2.4 (23)	0.80	2.6 (15)	0.68	2.4 (23)	0.98
East Ainu	3.2 (9)	1.14	3.2 (2)	1.61	3 (8)	0.98
Mann–Whitney <i>U</i> -test	<i>P</i> = 0.08, NS		<i>P</i> = 0.90, NS		<i>P</i> = 0.17, NS	

Table 7. Spearman's rank correlation coefficients between dental wear scores and both centroid size and principal components based on craniofacial shape variation

	Centroid size		Okhotsk			Ainu		
	Okhotsk	Ainu	PC1	PC2	PC3	PC1	PC2	PC3
Male								
All teeth	0.27	−0.18	−0.02	−0.55*	0.02	0.14	0.10	−0.23
Anterior teeth (I1, I2, C)	0.23	−0.27	−0.03	−0.55*	−0.19	−0.14	−0.06	−0.39
Posterior teeth (P1, P2, M1, M2)	0.31	−0.16	−0.01	−0.53*	−0.05	0.22	0.09	0.23
Female								
All teeth	−0.26	0.30	−0.49	−0.71	−0.14	−0.21	−0.32	−0.42
Anterior teeth (I1, I2, C)	−0.26	0.23	−0.49	−0.71	−0.14	0.12	−0.14	−0.27
Posterior teeth (P1, P2, M1, M2)	−0.26	0.25	−0.49	−0.71	−0.14	−0.14	−0.22	−0.42

Significant level: * $P < 5\%$.

Discussion

Craniofacial variation between or within Okhotsk culture people and Ainu

Since the early discovery of the Okhotsk culture people from Susuya shell mounds in Sakhalin, their skeletal mor-

phology has been shown to differ from that of the other inhabitants of Hokkaido (Kiyono, 1925). In particular, the differences are conspicuous in the face, where the following characteristics are repeatedly recognized: high upper face, broad, anteriorly protruding zygomatic bone, relatively flat face (Kiyono, 1925; Kodama, 1948; Ito, 1949, 1965;

Yamaguchi, 1974, 1981; Ishida, 1996). Three-dimensional geometric morphometrics in this study confirmed the previous results, i.e. the Okhotsk cultural people have a longitudinally high, anteriorly protruding zygomatic bone and a high and broad face. In addition, it revealed the other characteristics of a relatively medial upper position of the temporal muscle origin, a broad infratemporal fossa, and a large mandibular fossa, which had not been recognized by previous studies of linear dimensional comparisons. As for the centroid size, significant difference was detected between the two populations, metrically describing a larger cranium of the Okhotsk people than the Ainu at least in terms of the facial size.

No regional difference could be detected in craniofacial morphology between North and East Okhotsk people. Based on archeological data, the Okhotsk culture itself is considered to differ between North and East during the course of its cultural expansion (Ushiro, 1995; Amano, 2003). The earlier expansion to the North and the later expansion to the East differ in terms of the archeological records of faunal proportions in the respective regions (Nishimoto, 1978, 1984). An analysis of non-metric cranial traits indicates a less conspicuous difference between the North and East Okhotsk people (Komesu et al., 2008). As viewed from morphological perspectives, the Okhotsk cultural people can be regarded as a less variable and homogeneous population.

As for the Ainu, significant regional difference was detected between SW and East regions along PC2 in males. The East Ainu male exhibits following morphological characteristics compared to the SW Ainu: large infratemporal fossa, medial upper position of the temporal muscle origin, anterolaterally flared zygomatic bone, and anteriorly protruding/laterally thickening alveolus. Of these features, the position of the temporal muscle origin and the flared zygomatic bone are common with those of Okhotsk male compared to the whole Ainu male sample. However, a high upper face of Okhotsk male characteristics is absent in the East

Ainu male, and, in addition, the relatively small and posteriorly positioned palate of the Okhotsk male contrasts with the large, anteriorly protruding palate of the East Ainu male.

We now scrutinize both the interpopulation and regional variations in the plot of combined samples of Okhotsk and Ainu males (Figure 4). As already noted, we can detect interpopulation differences along PC1 and PC4. However, the regional difference of SW and East Ainu males is not significant along both PCs (mean PC1: SW-Ainu = 0.021, East-Ainu = 0.018, $P = 0.67$; mean PC4: SW-Ainu = 0.007, East-Ainu = -0.008, $P = 0.65$). Among the other PCs, significant regional difference was only detected along PC2 (mean PC2: SW-Ainu = 0.007, East-Ainu = -0.008, $P < 0.01$), where the whole Ainu male and the Okhotsk male do not separate from each other in this direction (Figure 9). These results indicate that the regional difference among SW and East Ainu males does not directly correspond to the interpopulation morphological variation between the Ainu and the Okhotsk males. Rather, it clarifies different patterns of the morphological shift (i.e. PC2 vs. PC1/PC4) in the respective variations.

Although the formation process of the Ainu people remains to be resolved, recent studies have accumulated both genetic and morphological evidence to suggest a significant contribution of North-Eastern Asians, including the Okhotsk culture people, to the formation of the Ainu. Analyses of mtDNA and Y chromosomal haplotypes of Ainu and the other East Asian populations have indicated a possible gene flow from North-Eastern Asian to the Ainu (Tajima et al., 2004). Further genetic studies of mtDNA (Sato et al., 2007, 2009a) and of an autosomal locus for earwax genes (Sato et al., 2009b) have suggested that the assumed gene flow was mediated by the Okhotsk culture people. Several cranial studies have also supported this view: greater phenotypic diversity within the Ainu (Kondo, 2005; Hanihara et al., 2008) or among the Japanese Islanders (Ishida et al., 2009) might be due to a degree of genetic contribution from the Okhotsk

Figure 9. Plot of PC1 and PC2 scores from the analysis of combined Okhotsk and Ainu males. PC2 depicts the two regional divisions for Ainu, but nothing between Okhotsk and Ainu.

culture people. The present results suggest that this idea should be revised or developed. The formation of the Ainu population in biological terms may not fit a simple genetic contribution model.

Association of occlusal wear severity and craniofacial variation

If we can accept the hypothetical use of dental wear severity as a proxy for the degree of functional demands of mastication, the result of comparisons of the dental wear scores, and its relationship to the craniofacial variation will bring several lines for additional discussion.

Comparisons of the dental wear severity clarified a significantly higher degree of wear in the Okhotsk culture people compared to the Ainu (Table 4). In general, strong dental wear can be ascribed to heavy use of dentition as a tool or hard/tough ingredients in diet. Based on our observation, the occlusal surface of the Okhotsk dentition rarely exhibits chipping and rounding of the enamel or artificial linear grooves, which are typically associated with the use of dentition as a tool (Lukacs and Pastor, 1988; Molnar, 2008). In terms of dietary practices, irrespective of the high dependence of the Okhotsk culture people on marine resources for their diet (Yoneda, 2002; Amano, 2003), its relevance to strong dental wear is still open to further investigation.

Experimental studies of masticatory mechanics on living humans and animals have indicated that the strong dental wear is linked with a relatively higher pressure of bite force (Helkimo and Ingervall, 1978; Johansson, 1992; Kiliaridis et al., 1995). This is clearly reminiscent of a level of correspondence with a morphological shift in the masticatory apparatus. In fact, previous studies have investigated the relationship of bite force to facial form and suggested that it is positive, as such strong bite force should be produced with a higher and broader facial form (Raadsheer et al., 1999; Castelo et al., 2008). The present study confirmed the similar characteristics of a higher and broader upper face in the Okhotsk sample as indicated previously (Ishida, 1996), and clarified the possession of additional traits of a mediosuperior position of the temporal muscle origin, a large infratemporal fossa, and a large mandibular fossa. Inclusion of the latter traits, which are attributable to masticatory adaptive signals, implies that the craniofacial morphology in the Okhotsk people might have been exposed to this kind of functional demand.

In terms of association between dental wear severity and craniofacial form, we found a significant, but moderate, degree of correlation only in the Okhotsk male samples along one axis of PC2 ($\rho = -0.53$ to -0.55 , Table 7). However, the Ainu samples did not exhibit any associations. This means that only Okhotsk males could manifest a significant number of masticatory adaptive signals, but this could not be seen in the variation of Ainu craniofacial form. In this line, the regional variation detected in the Ainu craniofacial form may not be ascribed to functional adaptation such as higher stress in the masticatory system. This view is supported by archaeological investigations which have also postulated no regional difference in subsistence patterns among SW and East Ainu populations.

Conclusion

Craniofacial variation and dental wear severity in prehistoric inhabitants of Hokkaido, Okhotsk culture people and Ainu, indicate several conclusions:

1. The craniofacial form of Okhotsk people, when compared to the Ainu, is characterized by high and anteriorly protruding zygoma, high and broad face, mediosuperiorly positioned temporal muscle origins, large infratemporal, and mandibular fossae.
2. As far as regional differences are concerned, none was detected in the Okhotsk culture people, while East and SW regional difference was detected in the Ainu males. Craniofacial modifications along this regional difference were not fully compatible with those differentiating the Ainu from the Okhotsk males. This means that the formation process of the regional differentiation of the Ainu craniofacial form may not be explained by a simple gene flow model due to migration of the Okhotsk culture people.
3. Okhotsk culture people exhibit stronger occlusal dental wear compared to the Ainu. No regional difference was found in the Okhotsk nor the Ainu samples, respectively.
4. Only moderate association was found between dental wear severity and craniofacial form in the Okhotsk males, indicating a positive relation of masticatory function to craniofacial size and shape. However, the regional difference in the Ainu craniofacial form could not be ascribed to such an adaptive modification.

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