Comparative studies of the Ainu, their ancestors, and neighbors: assessment based on metric and nonmetric dental data

Masanori KABURAGI^{1,3}, Hajime ISHIDA², Masaaki GOTO³, Tsunehiko HANIHARA^{4*}

¹*Department of Anatomy and Biological Anthropology, Saga Medical School, Saga 849-8501, Japan*

²*Department of Anatomy, Faculty of Medicine, University of the Ryukyus, Nishihara 903-0215, Japan*

³*Department of Oral and Maxillofacial Surgery, Saga Medical School, Saga 849-8501, Japan*

⁴*Department of Anatomy, Kitasato University School of Medicine, Sagami-hara 252-0374, Japan*

Received 3 June 2009; accepted 16 September 2009

Abstract Using Mahalanobis' generalized distance for odontometric data and Smith's mean measure of divergence for nonmetric dental data, interpopulation similarities between four local Ainu groups from Sakhalin Island and Hokkaido, as well as their supposedly ancestral and neighboring populations, were analyzed. In this study, multidimensional scaling and multidimensional plots by Andrews were applied to the distance matrices to visualize the intergroup relationships. The results obtained reconfirm the dental association between the prehistoric Jomon and the recent Ainu. However, the diversity of the recent Ainu in Hokkaido is not necessarily accommodated in a single regional populational lineage, the Jomon. The present findings also suggest that admixture between the immigrants from Northeast Asia as represented by the Okhotsk culture people and the indigenous inhabitants in Hokkaido during the 5th–12th centuries AD may in part have contributed to the formation of the physical characteristic of the recent Ainu. In particular, the female Okhotsk culture sample shows closer affinity to the northeastern Hokkaido and the Sakhalin Ainu in some of the analyses presented in this study. Such findings are compatible with those obtained by craniometric analyses, supporting the hypothesis of higher migration rates among females than among males due to patrilocality or the shorter matrilineal generation interval.

Key words: Okhotsk culture people, Northeast Asia, admixture, Jomon, population history

Introduction

It is generally accepted that Japan has two related but ethnically and physically distinguishable major population groups, the Ainu, the indigenous inhabitants of Hokkaido, and the non-Ainu Japanese. This consensus emerged in the 1960s (Yamaguchi, 1967, 1973; Hanihara, 1968, 1970; Omoto, 1972), and was re-evaluated in the 'dual structure model' of the origins and affinities of Japanese proposed by Hanihara (1991).

Patterns of genetic variation and morphological traces can be interpreted as showing that the Ainu and non-Ainu Japanese have deep roots in the Neolithic Jomon population (Yamaguchi, 1982; Turner, 1987, 1990; Brace and Hunt, 1990; Dodo and Ishida, 1990; Kozintsev, 1990, 1992; Horai et al., 1991; Omoto and Saitou, 1997; Ossenberget al., 2006). The incoming populations bringing rice agriculture and metalworking technologies from the continental East/Northeast Asia to southwestern part of Japan, the main ancestors of current non-Ainu Japanese, began to disperse

across the entire Japanese archipelago in the period from the end of the Jomon age to the early historic age, from 2300 years BP to 1300 years BP (Yamaguchi, 1982; Turner, 1987; Hanihara, 1991; Habu, 2004). However, such waves of expansion and the subsequent admixture between the immigrants and the indigenous people did not reach geographically isolated Hokkaido (Turner, 1987; Hanihara, 1991; Fitzhugh and Dubreuil, 1999). The historic time periods of Hokkaido after the Jomon period are, therefore, different from those of main-island Japan and divided as follows: Epi-Jomon (2300–1300 years BP), Satsumon (1300–700 years BP), and Ainu culture periods.

During the 5th–12th centuries AD, migration of people with a distinct culture, known as the Okhotsk culture, from Northeast Asia into Hokkaido has been identified (Amano, 2003). This culture, characterized by considerable maritime structure, spread along the coastal region of the Sea of Okhotsk to the easternmost part of Hokkaido (Ishida, 1988; Amano, 2003; Sato et al., 2007). In spite of such migration and a possible gene flow from this external source, the present Ainu retain a good number of genetic and phenotypic characteristics shared by the prehistoric Hokkaido inhabitants represented by the Jomon (Howells, 1986; Turner, 1987, 1990; Hanihara, 1991; Horai et al., 1991; Dodo and Ishida, 1990; Brace et al., 2001; Dodo and Kawakubo, 2002; Ossenberget al., 2006).

Many dental anthropologists see the Ainu (and the

* Correspondence to: Tsunehiko Hanihara, Department of Anatomy, Kitasato University School of Medicine, 1-15-1 Kitasato, Minamiku, Sagami-hara 252-0374, Japan.
E-mail: hanihara@med.kitasato-u.ac.jp

Published online 1 December 2009
in J-STAGE (www.jstage.jst.go.jp) DOI: 10.1537/ase090603

Jomon) as Southeast Asian sundadonts (Turner, 1987, 1990, 1992a, b; Hanihara, 1991; Matsumura, 1995, 2007; Matsumura and Hudson, 2005; Manabe et al., 2008; Matsumura et al., 2009). It is often pointed out, moreover, that extensive dental size reduction occurs exclusively in Ainu and their Jomon predecessors, together with the Philippine Negritos in eastern Asia (Brace et al., 1989, 1991; Brace and Hunt, 1990; Hanihara and Ishida, 2005; Matsumura and Hudson, 2005).

Contrary to several lines of dental anthropological evidence, many genetic investigations suggest that the Ainu (and Jomon) are members of populations originating in Northeastern Asian (Nei, 1995; Omoto, 1995; Omoto and Saitou, 1997; Tajima et al., 2004; Adachi et al., 2009). This perceived affinity of the Ainu with Northeast Asians at the genetic level has often been contrasted with what are seen as substantial and obvious differences at the craniofacial morphological level (Yamaguchi, 1982; Hanihara, 1991; Dodo and Ishida, 1990; Ossenbeger et al., 2006).

Although many investigations have shown that the Ainu and Jomon differ in their morphological characteristics from the neighboring population groups, recent studies based on nonmetric cranial traits and quantitative genetic analyses developed by Relethford and Blangero (1990) and Relethford (1994) suggest a possible genetic influence from Northeast Asians on the formation of physical characteristic of the recent Ainu (Shigematsu et al., 2004; Komesu et al., 2008; Hanihara et al., 2008; Hanihara and Ishida, 2009; Hanihara, 2010a, b). However, similar assessments have not been elucidated from a classic dental anthropological approach (Manabe et al., 2008; Matsumura et al., 2009).

Given this background, we test for the presence of northern elements brought mainly by the Okhotsk culture people in dental features of the Ainu by analyzing the affinities between four local Ainu groups and four comparative series

covering temporal and spatial scales in order to understand the possible process of population differentiation.

Materials and Methods

The materials of the Ainu are derived from four geographic regions: Sakhalin Island, southwestern Hokkaido, southeastern Hokkaido, and northeastern Hokkaido. Groupings of the three Hokkaido series are based on the administrative divisions of subprefectures, which correspond almost exactly to watersheds (Kondo, 1995; Hanihara et al., 2008; Hanihara, 2010a, b). The four comparative samples were selected in order to estimate patterns of morphological resemblance and dissimilarities between Ainu and their spatial and temporal neighbors: the Neolithic Jomon from Hokkaido and Tohoku region, Epi-Jomon/Satsumon, Okhotsk culture people, and modern non-Ainu Japanese.

Brief information on the nature of the eight samples is given in Table 1. Figure 1 presents the location of the population groups investigated. The northeastern region of Hokkaido overlaps the area containing the sites of the Okhotsk culture people that have been discovered thus far (Shigematsu et al., 2004; Hanihara et al., 2008; Hanihara, 2010a, b).

In the present study, morphological variation and differentiation was evaluated using metric and nonmetric dental data. The metric data consist of mesiodistal and buccolingual crown diameters of all right teeth, a total of 32 variables. When a right tooth was missing or badly damaged, the corresponding left tooth was measured. Nonmetric trait observations were made on 11 crown variables in the permanent dentition. Table 2 shows the criteria used to score the nonmetric crown traits (Hanihara, 2008, 2010a). All the data were recorded by one of the present authors (T.H.) to avoid possible interobserver errors. The nonmetric traits used in

Table 1. Material used and brief information

Sample name	Brief information
<i>Recent Ainu</i>	
Hokkaido	
Southwest	Sapporo and the neighboring cities (Ishikari subprefecture) (University of Tokyo, Sapporo Medical University) Otaru, Yoichi, and Iwanai (Shiribeshi subprefecture) (University of Tokyo)
Southeast	Hiroo and Ohtsu (Tokachi subprefecture) (University of Tokyo) Urakawa, Atsubetsu, Horoizumi, Mitsuishi, Saru, Shizunai, and Urakawa (Hidaka subprefecture) (University of Tokyo, Sapporo Medical University)
Northeast	Esashi, Wakkanai, and Rebun (Soya subprefecture) (University of Tokyo, Sapporo Medical University) Abashiri, Monbetsu, Shari, and Tokoro (Abashiri subprefecture) (University of Tokyo, Sapporo Medical University) Nemuro (Nemuro subprefecture) (University of Tokyo, Sapporo Medical University)
Sakhalin Island	Sakaehama and Honto villages (Kyoto University)
<i>Comparative samples</i>	
Jomon/Hokkaido and Tohoku	Usu-Moshiri, Kitakogane, Takasago, Irie, Motowa-Nishi (Iburi), Yakumo-Kotan (Oshima), Tenneru (Kushiro), Shimamaki (Shiribeshi), and other sites in Hokkaido Ebishima, Nakazawahama, Ohora, Hosoura (Iwate Prefecture), Sanganji (Fukushima Prefecture), Sakai-Numazu, Hashimotogakoi, Satohama (Miyagi Prefecture), Kashidokoro (Akita Prefecture), and other sites in Tohoku region of Eastern Japan (University of Tokyo, National Museum of Nature and Science, Sapporo Medical University)
Epi-Jomon/Satsumon	Epi-Jomon samples: Ohkawa, Ikeda 3 (Shiribeshi), and Usu sites (Iburi) Satsumon samples: Oyakotsu (Iburi) and Ohkawa sites (Shiribeshi)
Okhotsk culture people	5–12 century AD Hamanaka (Rebun Island), Ohmisaki (Soya), Moyoro (Abashiri), and Susuya sites (Sakhalin Island) (Hokkaido University, Sapporo Medical University, Kyoto University)
Modern Japanese	Mainly from Tokyo (University of Tokyo)

Figure 1. Geographical location of the dental samples used (capital letters) in the present study.

Table 2. Standards for the 11 nonmetric dental traits

Trait observed	Criteria
1. Shoveling (UI1)	The depth of Lingual fossa deeper than 0.5 mm is scored as present (Hanihara et al., 1970).
2. Shoveling (UI2)	The teeth classified as the ASU system's grade 3–7 are scored as present (Turner et al., 1991; Scott and Turner, 1997).
3. Carabelli's cusp (UM1)	Dahlberg's (1963) d-g grade is scored as present.
4. Hypocone (UM2)	Presence corresponds to 4– and 4+ of Plaque P9, Dahlberg (1949).
5. Sixth cusp (LM1)	Cusp is scored as present regardless of the size (ASU system).
6. Seventh cusp (LM1)	Cusp is scored as present regardless of the size (ASU system).
7. Deflecting wrinkle (LM1)	Following Weidenreich (1937), if the medial ridge of metaconid deflected distally, the trait is scored as present. Presence corresponds to grade 2–3 of the ASU system.
8. Protostylid (LM1)	The ASU system's 2–7 were scored as present.
9. Distal trigonid crest (LM1)	Follows the original description by Weidenreich (1937).
10. Hypoconulid (LM2)	Follows the ASU system.
11. Sixth cusp (LM2)	Follows the ASU system.

this study include crown characters defined as Mongoloid dental complex (Hanihara, 1968), four out of six key crown traits distinguishing sundadonty from sinodonty (Turner, 1990), Caucasoid dental complex (Mayhall et al., 1982), Australian proto-sundadont dental pattern (Hanihara, 1992), and sub-Saharan African dental complex (Irish, 1997, 1998). For nonmetric dental data, sexes were combined since the difference in frequency distributions by sex was not significant in most of the samples (Hanihara, 2008, 2010b). While nonmetric observations were made on both the right and left antimeres for each trait, the individual count method was

used: if a trait was present on either or both sides, it was scored as present (Turner et al., 1991; Hanihara et al., 2003; Hanihara, 2008).

The analytical approaches applied in this study are classic multivariate procedures such as Mahalanobis' generalized distance and Smith's mean measure of divergence (MMD) distance (Mahalanobis, 1936; Berry and Berry, 1967; Constandse-Westermann, 1972). For metric data, the raw measurements were converted into C-scores according to the procedure described by Howells (1989) and Brace and Hunt (1990). Although some researchers have criticized the

application of *C*-score data to multivariate analyses (e.g. Jungers et al., 1995), the transformation to *C*-scores has little effect on the reliability of the pattern of interpopulation relationships (Pietrusewsky, 1997; Kawakubo et al., 2009). After transforming raw data to *C*-scores by the double centering method, the effects of dental size factors can be removed from the data. In the present study, the validity of the normal distribution of the *C*-scores for each variable was examined in the Japanese sample (with relatively large sample size) using P-P and Q-Q plots.

To visualize the patterning of intergroup relationships, the multidimensional scaling (MDS) method developed by Torgerson (1952) was applied to the distance matrices obtained. In addition to the two (or three) dimensional display, the multidimensional plot by Andrews (1972) was used to illustrate information obtained by MDS. In this method, multidimensional scores for each sample with p variables ($x_1, x_2, \dots, x_p$) are entered in a Fourier trigonometric function:

$$f(t) (x_1, x_2, \dots, x_p) = x_1\sqrt{2} + x_2\sin t + x_3\cos t + x_4\sin 2t + x_5\cos 2t + \dots + x_p\sin(pt/2),$$

where p is an even number, and

$$f(t) (x_1, x_2, \dots, x_p) = x_1\sqrt{2} + x_2\sin t + x_3\cos t + x_4\sin 2t + x_5\cos 2t + \dots + x_p\cos((p-1)t/2),$$

where p is an odd number. The values of t (and thus of f) are periodic over the range of $-\pi$ to $+\pi$. The value of f is plotted for values of t along this scale to form the curve for each group.

Results

Table 3 gives the results of basic statistics of dental measurements for male and female samples separately. Descriptive statistics for nonmetric traits are presented in Table 4.

In the metric data analyses, *C*-score-based Mahalanobis' generalized distances between every pair of samples were calculated for sex-combined samples (Table 5). Before the male and female samples were pooled, the *Z*-score standardization was performed within each sex separately (Relethford, 1994, 2009; Hanihara et al., 2008). Prior to applying multivariate analyses, possible sampling errors due to the small sample size of the upper and lower first incisors of the northeastern Hokkaido Ainu sample (less than 10 individuals in the sex-combined case) was examined. The correlation between Mahalanobis generalized distance matrices based on 32 measurements and 28 measurements (excluding mesiodistal and buccolingual crown diameters of the upper and lower first incisors) evaluated by mantel test was 0.984 ($P < 0.001$). Such findings may allow us to use all the items measured for multivariate analyses.

In the present study, though preliminary, Mahalanobis' generalized distances for each sex were calculated (Table 6) to investigate sex-related difference of intergroup relationships observed in craniometric analyses (Hanihara et al., 2008).

Multidimensional scaling was applied to the distance matrices. Table 7 gives the information obtained from this dimension-reduced procedure. Figure 2 is a plot of the groups on the first two dimensions for sex-pooled samples as well as separately for the male and female samples. Relative to the Ainu populations, the most peripherally posi-

tioned group is modern Japanese, followed by the Jomon and Epi-Jomon/Satsumon series. The Jomon and the subsequent Epi-Jomon/Satsumon samples show closer affinities to either or both the southwestern and southeastern Hokkaido Ainu series than to the northeastern Hokkaido and Sakhalin Ainu series, although this pattern is not clear in females. The three Ainu samples from Hokkaido tend to form a cluster. Among four recent Ainu series, the Sakhalin Ainu sample shows a relatively dispersed arrangement in both scattergrams and the distance values themselves. The Okhotsk culture series shows inconsistent arrangement in the three scattergrams (Figure 2a, b, c). The Okhotsk culture sample is plotted between the Sakhalin Ainu and Hokkaido Ainu samples in the sex-pooled analysis. In the male samples, the Okhotsk series shares similar dental features with those of the Japanese sample on the first axis, which expresses approximately 60% of the total variance. They show close affinities to northeastern Hokkaido Ainu on the second axis, expressing approximately 17% of the total variance. On the other hand, the Okhotsk sample falls within the Hokkaido Ainu cluster in the female case. The biological distances between the Okhotsk culture series and recent Ainu samples shown in Table 5 and Table 6 suggest the inheritance of northern element in the odontometric characteristics of the Sakhalin and northeastern Hokkaido Ainu series.

Next, multivariate procedures are applied to the nonmetric dataset recorded in the same samples used in the metric analyses. The information for the results of MDS applied to the Smith's MMD given in Table 8 is presented in Table 9. Figure 3 shows the two-dimensional expression of the intergroup relationship that results from MDS. The modern Japanese and Epi-Jomon/Satsumon dental series form differentiated constellations. The dental series of the Ainu are scattered within a grouping that includes the Jomon. The Okhotsk culture series are slightly removed from this clustering. The northeastern Hokkaido Ainu sample, when seen on the first axis representing approximately 70% of the total variance, shows close affinity to the Okhotsk culture sample. The close affinity between the northeastern Hokkaido Ainu and the Okhotsk culture series is also suggested in the MMD distance matrix shown in Table 8.

Figure 4 and Figure 5 are drawn using the multidimensional plots of Andrews (1972) to display information obtained by MDS based on Mahalanobis' generalized distance and Smith's MMD distance, respectively. In these figures, the dimensions extracted by MDS modulate a plotted curve for each group, which allows a visual impression of the degree of conformity among them. This method can remove certain limitations of clustering or of having to plot the relative positions of groups on only two or three axes at a time (Howells, 1986; Hanihara, 1997). In this analysis, we focus on possible affinities between the four Ainu dental series and the Okhotsk culture series which are suggested in the previous presentations (Figure 2, Figure 3). In Figure 4, the curve of the Sakhalin Ainu and to a lesser extent the northeastern Hokkaido Ainu series show a different pattern from that of the southwestern and southeastern Hokkaido Ainu samples. In the female samples, the curve of the northeastern Hokkaido Ainu sample deviates in the direction of

Table 3. Mesiodistal and buccolingual crown diameters of the eight samples used in the present study

Tooth	Male																							
	Southwest Hokkaido Ainu			Southeast Hokkaido Ainu			Northeast Hokkaido Ainu			Sakhalin Ainu			Jomon//Hokkaido/Tohoku			Epi-Jomon/Satsumon			Okhotsk culture			Modern Japanese		
	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD
U11-MD	12	8.11	0.49	21	7.93	0.51	5	8.44	0.04	10	8.14	0.32	13	8.53	0.35	9	8.02	0.45	6	8.51	0.82	86	8.65	0.44
U12-MD	9	6.82	0.63	26	6.76	0.48	7	6.72	0.56	13	7.05	0.38	15	6.83	0.60	8	6.81	0.87	10	7.15	0.51	87	7.31	0.58
UC-MD	16	7.66	0.42	32	7.46	0.40	6	7.47	0.44	19	7.74	0.40	17	7.38	0.32	8	7.72	0.37	10	7.91	0.42	87	8.13	0.43
U11-MD	16	6.93	0.39	38	6.88	0.35	11	6.68	0.38	20	7.07	0.30	31	6.73	0.33	13	6.67	0.32	7	7.44	0.41	87	7.58	0.42
UP2-MD	17	6.65	0.43	43	6.28	0.37	12	6.40	0.42	13	6.61	0.31	24	6.29	0.46	11	6.40	0.49	5	6.89	0.34	87	7.14	0.43
UM1-MD	25	10.24	0.58	44	10.22	0.49	14	10.25	0.44	18	10.46	0.45	29	10.08	0.55	14	10.14	0.67	11	10.87	0.60	84	10.63	0.50
UM2-MD	20	9.62	0.51	45	9.48	0.55	13	9.53	0.66	18	9.74	0.26	35	9.17	0.57	13	9.35	0.71	10	9.68	0.38	72	10.29	0.59
UM3-MD	7	8.86	0.79	23	8.70	0.71	6	9.31	0.65	8	8.92	0.52	14	8.14	0.59	12	8.74	0.88	4	8.80	0.70	6	8.42	0.62
L11-MD	9	5.22	0.40	16	5.20	0.38	2	4.92	0.03	11	5.23	0.16	8	5.18	0.21	9	5.27	0.23	12	5.56	0.41	86	5.57	0.33
L11-MD	12	5.75	0.29	27	5.68	0.34	7	5.50	0.28	13	5.79	0.25	12	5.75	0.31	8	6.01	0.37	14	6.01	0.26	88	6.15	0.34
LC-MD	12	6.65	0.34	36	6.60	0.28	10	6.52	0.39	13	6.76	0.41	20	6.54	0.25	9	6.58	0.51	10	6.94	0.44	88	7.09	0.43
LP1-MD	14	6.79	0.42	39	6.82	0.35	10	6.71	0.36	17	6.99	0.24	24	6.89	0.37	10	6.78	0.30	9	7.20	0.40	87	7.44	0.41
LP2-MD	16	6.82	0.50	43	6.66	0.32	12	6.75	0.43	14	6.79	0.32	23	6.86	0.44	10	6.77	0.33	7	7.05	0.20	84	7.46	0.47
LM1-MD	20	11.22	0.62	45	11.23	0.46	11	11.22	0.58	14	11.50	0.43	29	11.45	0.52	14	11.11	0.44	20	11.79	0.38	86	11.58	0.52
LM2-MD	18	10.56	0.81	41	10.47	0.53	11	10.36	0.71	15	10.62	0.46	32	10.55	0.69	12	10.36	0.50	9	10.36	0.23	67	11.09	0.62
LM3-MD	8	9.87	1.08	27	10.33	0.73	9	9.72	0.75	8	10.99	0.61	20	10.12	0.90	9	9.81	0.80	7	10.34	0.72	8	10.58	0.65
U11-BL	12	6.94	0.41	24	6.99	0.44	4	6.83	0.38	12	7.17	0.50	26	7.21	0.42	7	6.80	0.28	9	7.03	0.45	77	7.16	0.59
U12-BL	9	6.25	0.53	25	6.49	0.37	7	6.29	0.48	12	6.69	0.48	20	6.53	0.43	6	6.20	0.49	13	6.43	0.25	76	6.51	0.50
UC-BL	16	7.97	0.56	33	7.74	0.50	7	7.60	0.55	18	7.95	0.57	17	7.59	0.49	8	7.74	0.37	13	7.91	0.45	81	8.13	0.49
U11-BL	16	9.09	0.46	36	9.08	0.50	11	8.87	0.38	20	9.16	0.46	32	9.05	0.54	11	9.13	0.50	10	9.58	0.40	87	9.82	0.48
UP2-BL	19	9.05	0.66	44	8.72	0.56	11	8.70	0.49	13	8.81	0.59	28	8.90	0.55	9	9.11	0.33	7	9.23	0.26	87	9.61	0.57
UM1-BL	24	11.31	0.57	46	11.43	0.54	12	11.12	0.49	19	11.23	0.37	34	11.37	0.53	17	11.05	0.50	12	11.65	0.55	85	11.49	0.46
UM2-BL	21	11.24	0.78	44	11.20	0.60	12	10.89	0.79	18	11.04	0.52	37	11.16	0.68	12	10.78	0.41	11	10.81	0.56	74	11.59	0.60
UM3-BL	7	10.89	0.93	22	10.67	0.56	5	10.66	0.49	9	10.37	0.33	15	10.41	0.93	10	10.43	0.70	5	10.42	0.29	7	10.52	1.05
L11-BL	11	5.44	0.37	24	5.66	0.42	4	5.42	0.41	13	5.51	0.41	13	5.62	0.34	8	5.51	0.19	14	5.61	0.38	85	5.95	0.39
L12-BL	13	6.00	0.38	30	5.92	0.30	8	5.51	0.30	16	5.90	0.39	15	6.02	0.35	7	5.92	0.21	14	6.07	0.35	88	6.27	0.45
LC-BL	13	7.46	0.53	37	7.30	0.43	10	7.11	0.64	15	7.13	0.56	23	7.18	0.46	7	7.11	0.42	11	7.45	0.33	85	7.55	0.50
LP1-BL	13	7.44	0.47	39	7.56	0.49	10	7.42	0.51	17	7.53	0.53	25	7.61	0.57	10	7.63	0.44	11	7.87	0.27	87	8.12	0.43
LP2-BL	16	7.76	0.55	42	7.99	0.46	10	7.57	0.37	14	7.84	0.49	25	8.16	0.43	8	7.94	0.48	9	8.21	0.57	84	8.58	0.53
LM1-BL	20	10.67	0.47	45	10.81	0.56	10	10.77	0.55	14	10.80	0.43	33	11.09	0.43	14	10.53	0.55	21	10.92	0.42	86	10.89	0.53
LM2-BL	17	10.16	0.59	41	10.30	0.55	9	10.00	0.59	16	9.96	0.43	32	10.24	0.57	11	9.91	0.74	10	9.80	0.30	72	10.59	0.56
LM3-BL	8	9.60	0.63	27	9.81	0.71	8	9.48	0.57	8	10.08	0.32	20	9.95	0.69	9	9.51	0.58	8	9.80	0.71	8	10.24	0.56

Table 3. (continued)

Tooth	Female																															
	Southwest Hokkaido Ainu				Southeast Hokkaido Ainu				Northeast Hokkaido Ainu				Sakhalin Ainu				Jomon/Hokkaido/Tohoku				Epi-Jomon/Satsumon				Okhotsk culture				Modern Japanese			
	<i>n</i>	Mean	SD		<i>n</i>	Mean	SD		<i>n</i>	Mean	SD		<i>n</i>	Mean	SD		<i>n</i>	Mean	SD		<i>n</i>	Mean	SD		<i>n</i>	Mean	SD		<i>n</i>	Mean	SD	
UI1-MD	4	7.69	0.46		12	8.09	0.57		3	7.94	0.32		6	8.16	0.50		11	7.94	0.54		5	8.16	0.71		8	7.90	0.57		36	8.64	0.45	
UI2-MD	5	6.71	0.68		12	6.93	0.43		4	6.89	0.30		6	6.83	0.45		10	6.64	0.43		3	6.37	0.02		6	6.88	0.44		39	7.23	0.50	
UC-MD	10	7.37	0.44		19	7.53	0.45		5	7.38	0.45		10	7.55	0.38		8	7.14	0.65		4	7.24	0.06		8	7.74	0.35		44	7.88	0.41	
UPI-MD	13	6.75	0.52		21	6.82	0.47		8	6.74	0.54		9	6.77	0.33		12	6.54	0.39		5	6.33	0.61		9	6.90	0.40		41	7.51	0.53	
UP2-MD	12	6.28	0.46		20	6.53	0.41		10	6.49	0.62		8	6.44	0.34		16	6.14	0.51		3	5.87	0.45		5	6.49	0.24		48	7.00	0.53	
UM1-MD	14	10.19	0.51		23	10.37	0.49		12	10.06	0.46		8	10.27	0.36		16	9.77	0.55		3	10.27	0.75		8	10.06	0.74		53	10.48	0.51	
UM2-MD	11	9.33	0.52		20	9.57	0.43		10	9.30	0.44		10	9.49	0.16		18	8.83	0.70		4	9.24	0.72		10	9.38	0.19		43	9.97	0.59	
UM3-MD	6	8.34	0.60		13	8.87	0.52		8	8.56	0.54		8	8.52	0.48		6	8.03	0.96		4	8.02	0.02		6	8.41	0.68		10	8.92	0.72	
LI1-MD	5	4.92	0.26		12	5.23	0.27		2	4.99	0.22		5	5.22	0.46		10	5.14	0.35		4	4.87	0.31		5	5.25	0.45		32	5.49	0.33	
LI2-MD	7	5.68	0.42		13	5.76	0.41		3	5.77	0.10		5	5.78	0.24		8	5.57	0.25		4	5.54	0.07		3	5.45	0.50		33	6.02	0.33	
LC-MD	10	6.44	0.34		20	6.46	0.40		5	6.45	0.24		8	6.66	0.28		9	6.52	0.57		4	6.36	0.31		8	6.79	0.37		41	6.60	0.38	
LP1-MD	11	6.68	0.35		24	6.75	0.44		5	6.74	0.39		9	6.51	0.32		9	6.60	0.39		4	6.48	0.12		6	6.61	0.46		44	7.21	0.53	
LP2-MD	13	6.62	0.37		24	6.53	0.48		8	6.66	0.49		7	6.37	0.42		10	6.61	0.47		6	6.53	0.43		6	6.64	0.32		42	7.33	0.53	
LM1-MD	12	11.01	0.62		25	11.23	0.64		8	10.96	0.62		8	11.16	0.59		17	10.96	0.66		4	10.69	0.20		5	10.82	0.69		48	11.27	0.55	
LM2-MD	13	9.99	0.82		24	10.51	0.50		8	10.07	0.46		10	10.11	0.44		18	10.02	0.54		7	10.08	0.37		4	10.08	0.22		31	10.38	0.65	
LM3-MD	8	9.53	1.09		17	10.50	0.88		8	9.90	0.74		4	10.04	0.59		9	9.59	0.63		6	9.96	0.81		8	10.39	0.60		11	10.25	0.73	
UI1-BL	4	6.63	0.31		12	6.98	0.50		3	6.84	0.09		12	6.93	0.38		11	7.06	0.41		3	6.62	0.27		12	7.10	0.48		35	7.15	0.52	
UI2-BL	5	6.33	0.38		13	6.37	0.47		4	6.05	0.23		10	6.33	0.34		9	6.24	0.43		2	6.43	0.64		10	6.45	0.29		34	6.46	0.47	
UC-BL	10	7.31	0.57		19	7.62	0.46		5	7.85	0.45		12	7.54	0.38		9	7.63	0.61		2	7.82	0.02		10	7.95	0.61		41	7.99	0.55	
UPI-BL	13	8.87	0.52		20	9.07	0.41		8	9.12	0.41		9	8.62	0.52		14	8.56	0.74		6	8.88	0.49		10	9.31	0.65		41	9.64	0.59	
UP2-BL	12	8.53	0.55		21	8.89	0.50		9	8.64	0.51		10	8.37	0.40		16	8.27	0.73		4	8.70	0.32		9	8.66	0.45		48	9.45	0.60	
UM1-BL	14	10.94	0.60		24	11.30	0.60		12	10.88	0.54		12	11.12	0.39		17	10.90	0.43		3	11.14	0.40		12	11.17	0.81		53	11.31	0.50	
UM2-BL	11	10.58	0.78		20	11.11	0.59		11	10.65	0.46		10	10.46	0.36		17	10.60	0.93		4	10.88	0.52		10	10.79	0.54		45	11.14	0.65	
UM3-BL	6	9.69	0.79		12	10.76	0.44		8	10.12	0.56		8	9.84	0.61		7	10.04	0.83		3	10.50	0.20		7	9.98	1.12		10	10.70	0.69	
LI1-BL	6	5.40	0.37		11	5.51	0.54		2	5.37	0.03		8	5.21	0.25		10	5.52	0.42		5	5.73	0.43		6	5.37	0.23		31	5.81	0.38	
LI2-BL	8	5.78	0.54		13	5.81	0.40		3	5.69	0.49		9	5.81	0.30		8	5.78	0.18		5	5.82	0.20		3	5.69	0.12		33	6.15	0.37	
LC-BL	10	6.91	0.48		20	7.12	0.57		6	6.88	0.68		9	6.90	0.27		9	7.13	0.44		5	7.39	0.40		10	7.25	0.55		40	7.14	0.59	
LP1-BL	11	7.27	0.36		24	7.40	0.42		5	7.40	0.25		9	7.15	0.40		10	6.90	0.53		4	7.48	0.22		7	7.67	0.62		44	7.96	0.56	
LP2-BL	13	7.73	0.52		24	7.92	0.45		8	7.99	0.42		7	7.54	0.48		11	7.72	0.71		4	7.82	0.18		5	8.15	0.75		42	8.45	0.62	
LM1-BL	13	10.46	0.58		25	10.70	0.51		8	10.40	0.55		11	10.62	0.32		18	10.54	0.61		4	10.35	0.14		9	10.60	1.01		48	10.62	0.55	
LM2-BL	13	9.87	0.72		24	10.07	0.66		8	9.78	0.39		10	9.77	0.46		17	9.65	0.59		5	9.69	0.14		7	10.02	0.69		37	10.27	0.73	
UM3-BL	7	9.27	1.06		17	9.91	0.50		8	9.46	0.38		4	9.30	0.24		9	9.07	0.48		6	9.39	0.39		8	9.93	0.85		11	9.81	0.59	

Table 4. Frequencies of nonmetric crown traits for eight samples

Traits (tooth)	Southwest Ainu		Southeast Ainu		Northeast Ainu		Sakhalin Ainu	
	<i>n</i>	Freq.	<i>n</i>	Freq.	<i>n</i>	Freq.	<i>n</i>	Freq.
Shovel (UI1)	14	0.7143	29	0.7586	5	0.6000	25	0.8000
Shovel (UI2)	14	0.8571	32	0.7500	13	0.7692	25	0.9200
Carabelli's cusp (UM1)	36	0.0556	63	0.0317	19	0.0000	28	0.1071
Hypocone (UM2)	35	0.8286	65	0.7538	22	0.6818	33	0.8485
6th cusp (LM1)	30	0.2333	66	0.1970	13	0.0769	27	0.1111
7th cusp (LM1)	32	0.0625	66	0.0455	15	0.0000	30	0.0667
Deflecting wrinkle (LM1)	22	0.1818	48	0.1875	7	0.5714	23	0.3043
Distal trigonid crest (LM1)	27	0.2222	59	0.1525	10	0.3000	24	0.1250
Protostylid (LM1)	27	0.0000	59	0.0508	15	0.0667	21	0.0476
Hypoconulid (LM2)	32	0.4062	59	0.5085	17	0.5882	30	0.6000
6th cusp (LM2)	29	0.1379	58	0.0862	16	0.0625	29	0.1379

Traits (tooth)	Jomon		Epi-Jomon/Satsumon		Okhotsk Culture		Modern Japanese	
	<i>n</i>	Freq.	<i>n</i>	Freq.	<i>n</i>	Freq.	<i>n</i>	Freq.
Shovel (UI1)	21	0.6667	7	0.7143	14	0.8571	69	0.9855
Shovel (UI2)	28	0.8214	6	0.6667	17	0.9412	69	0.8696
Carabelli's cusp (UM1)	29	0.1379	14	0.0000	14	0.0000	70	0.1000
Hypocone (UM2)	44	0.7500	15	0.9333	12	0.9167	64	0.9375
6th cusp (LM1)	38	0.3684	14	0.2857	26	0.1923	59	0.4237
7th cusp (LM1)	44	0.0682	13	0.0000	25	0.0400	51	0.0588
Deflecting wrinkle (LM1)	29	0.2759	10	0.0000	21	0.6190	30	0.2000
Distal trigonid crest (LM1)	32	0.0313	12	0.0000	24	0.2917	28	0.0000
Protostylid (LM1)	29	0.1034	12	0.0000	25	0.0400	59	0.0339
Hypoconulid (LM2)	47	0.6170	17	0.5294	13	0.6154	50	0.7200
6th cusp (LM2)	39	0.1538	16	0.1250	13	0.0000	43	0.0930

Table 5. Mahalanobis' generalized distance based on C-scores for sex-combined sample

	1	2	3	4	5	6	7	8
1. Southwest Hokkaido Ainu	—							
2. Southeast Hokkaido Ainu	35.2643	—						
3. Northeast Hokkaido Ainu	27.7479	43.5357	—					
4. Sakhalin Ainu	37.2484	48.7207	45.1142	—				
5. Jomon	62.9433	31.6490	71.9023	80.9072	—			
6. Epi-Jomon/Satsumon	34.4193	48.8817	42.8842	72.5704	64.1336	—		
7. Okhotsk culture	57.8424	76.2251	69.1894	51.5562	95.8866	55.3584	—	
8. Japanese	81.0241	97.7207	84.6173	104.9581	121.7003	76.4812	71.5183	—

Table 6. Mahalanobis' generalized distance based on C-scores for male (upper half) and female (lower half) samples

	1	2	3	4	5	6	7	8
1. Southwest Hokkaido Ainu	—	38.4727	38.7443	43.3752	59.8205	42.7582	77.3502	80.7673
2. Southeast Hokkaido Ainu	39.6322	—	43.2083	45.6003	23.5454	59.0356	91.4448	90.9620
3. Northeast Hokkaido Ainu	32.0409	36.0576	—	51.0443	62.7989	50.4958	76.4458	89.1416
4. Sakhalin Ainu	39.4992	43.2099	63.9988	—	73.8479	63.4164	66.2583	80.0959
5. Jomon	70.0876	33.0832	64.8219	66.8513	—	73.8654	106.4459	106.6863
6. Epi-Jomon/Satsumon	86.9337	77.6011	83.3138	109.3591	70.0906	—	44.7720	53.1390
7. Okhotsk culture	54.0404	47.3496	43.2912	50.3297	58.9391	75.9828	—	58.4618
8. Japanese	52.8261	67.0835	41.5611	99.8864	99.4177	111.4767	73.2348	—

the Okhotsk culture series. In Figure 5, the Sakhalin Ainu sample, and to a lesser extent the northeastern Hokkaido Ainu sample, shift to the Okhotsk culture series.

The affinities between the samples presented in Figure 2 and Figure 4 are more or less different from each other. This may be at least in part attributed to additional information not included in the two-dimensional expression by MDS in

Figure 2 but included in Figure 4. The intergroup similarities shown in Figure 5 are parallel to those presented in Figure 3, because almost all variance was expressed in both Figure 3 and Figure 5.

Table 7. Coordinate scores and contribution rates of multidimensional scaling based on Mahalanobis' generalized distances

Sample names	Males + Females				Males					Females			
					Dimension								
	1	2	3	4	1	2	3	4	5	1	2	3	4
Southwest H Ainu	4.879	4.611	10.301	-4.281	14.311	7.174	-2.876	-19.550	15.493	-20.517	4.159	-10.839	21.361
Southeast H Ainu	29.012	-8.089	3.319	13.132	35.534	-6.219	8.508	2.370	-1.829	1.400	9.917	17.265	3.919
Northeast H Ainu	4.745	4.613	27.405	-10.060	16.839	17.183	-17.804	-9.623	-17.619	-18.245	-12.318	1.538	-2.966
Sakhalin Ainu	12.412	43.355	3.862	7.597	4.280	26.997	26.119	2.589	0.701	-8.876	51.155	-11.394	4.385
Jomon	51.147	-26.005	-15.425	7.334	49.595	-23.042	-1.190	15.994	0.685	33.452	14.407	27.478	-4.972
Epi-Jomon/Satsumon	-3.875	-18.987	-6.932	-24.526	-18.545	-9.802	-19.669	-1.917	6.856	59.289	-34.853	-13.479	8.512
Okhotsk culture	-29.894	24.475	-28.634	-3.570	-49.890	15.111	-8.386	20.651	2.983	3.013	5.285	-18.332	-26.996
Modern Japanese	-68.426	-23.972	6.111	14.374	-52.122	-27.403	15.297	-10.514	-7.270	-49.516	-37.751	7.764	-3.243
Proportion (%)	55.390	25.142	12.135	7.333	60.292	16.774	10.928	7.914	4.091	46.904	34.068	11.125	7.903
Cumulative prop. (%)	55.390	80.532	92.667	100.000	60.292	77.066	87.994	95.908	100.000	46.904	80.972	92.097	100.000

Table 8. Smith' MMD based on 11 nonmetric dental data

	1	2	3	4	5	6	7	8
1. Southwest Hokkaido Ainu	—							
2. Southeast Hokkaido Ainu	0.0034	—						
3. Northeast Hokkaido Ainu	0.0871	0.0459	—					
4. Sakhalin Ainu	0.0097	0.0192	0.0648	—				
5. Jomon	0.0676	0.0422	0.1416	0.0296	—			
6. Epi-Jomon/Satsumon	0.1302	0.1259	0.3472	0.2199	0.1862	—		
7. Okhotsk culture	0.1352	0.1319	0.0189	0.0856	0.2192	0.4366	—	
8. Japanese	0.2016	0.1802	0.3963	0.1280	0.1207	0.1792	0.2664	—

Table 9. Coordinate scores and contribution rates of multidimensional scaling based on MMDs

Sample names	Dimension	
	1	2
Southwest Hokkaido Ainu	0.004	0.064
Southeast Hokkaido Ainu	0.005	0.059
Northeast Hokkaido Ainu	0.224	0.113
Sakhalin Ainu	0.036	-0.040
Jomon	-0.041	-0.008
Epi-Jomon/Satsumon	-0.270	0.131
Okhotsk culture	0.233	-0.119
Modern Japanese	-0.191	-0.200
Proportion (%)	69.903	30.097
Cumulative prop. (%)	69.903	100.000

Discussion

In spite of temporal and spatial differences, it is often emphasized that the present Ainu retain a number of phenotypic features that can be traced back to those of the Neolithic inhabitants of the Japanese archipelago, the Jomon lineage (Hanihara, 1991; Dodo and Kawakubo, 2002). However, recent genetic and morphological studies suggest inter-regional difference between local groups of the Jomon skeletal series, including the Hokkaido Jomon sample on the one hand (Adachi et al., 2009; Hanihara and Ishida, 2009), and a possible genetic influence from an external source on the early inhabitants of Hokkaido during the post-Jomon period on the other (Ishida, 1996; Shigematsu et al., 2004; Tajima et al., 2004; Sato et al., 2007, 2009; Hanihara et al., 2008; Hanihara, 2010a, b).

The present findings re-evaluate the relationships between the Jomon and recent Ainu based on metric and non-metric dental traits. At the same time, however, as shown in Figure 2 and Figure 3, overall post-Neolithic spatial and temporal population continuity, from the Jomon to Ainu through the Epi-Jomon/Satsumon series, is not necessarily indicated in the case of female metric and sex-combined nonmetric analyses. Such discrepancies between sexes and types of data may confuse the interpretation of population affinities and history. In the present results, however, the discordance may be attributed at least in part to the sampling errors due to the relatively small sample sizes. This is particularly of concern regarding the female Epi-Jomon/Satsumon metric and combined-sex nonmetric datasets. At the same time, it remains possible that sex-related population history and subsistence pattern, as well as differential retention/speciation of phenotypic characteristics between metric and nonmetric dental features, have something to do with such discordance (Hanihara and Ishida, 2005; Hanihara et al., 2008; Hanihara, 2010a; Matsumura et al., 2009).

Using the *R*-matrix approach, one of the present authors (T.H.) indicated that among several local groups of the Ainu, the differentiation of cranial and dental features is distinct in the groups from the coastal region along the Sea of Okhotsk and the easternmost region of Hokkaido. Moreover, the northeastern Hokkaido Ainu group is more northern-like than the other Ainu series (Hanihara et al., 2008; Hanihara, 2010a, b). Such patterns of differentiation were not necessarily detected in the results obtained in the present paper.

As presented in Figure 2, however, the Okhotsk culture sample clusters with the Hokkaido Ainu groups in females. Moreover, the female Okhotsk culture series shows closer

Figure 2. Two-dimensional scattergrams drawn by MDS based on Mahalanobis' generalized distance calculated by using odontometric data for sex-pooled (a), male (b), and female (c).

affinities to the northeastern Hokkaido Ainu than the male series in Figure 4 and Table 6. Similar results have been presented in previous craniometric studies (Hanihara et al., 2008). Furthermore, it has been pointed out that the affinities of the Ainu with Northeast Asians measured by mtDNA se-

Figure 3. Two-dimensional expression drawn by using the MDS scores based on MMDs calculated from nonmetric dental data.

quence types (maternal lineage) are greater than those by Y-haplotypes (paternal lineage) (Tajima et al., 2004). Based on such findings, Tajima et al. (2004) suggested maternal contacts between the Ainu and Northeast Asians, or at least unidirectional migration from Northeast Asia to Hokkaido over time. Several researchers have suggested a higher female than male migration rate due to the widespread practice of patrilocality or a shorter matrilineal generation interval, at least on a global scale (Seielstad et al., 1998; Stoneking, 1998; Oota et al., 2001; Helgason et al., 2003; Wilder et al., 2004; Shriver, 2005). The different pattern of interpopulation relationships depending on sex presented herein reflect patrilocal residence or different generation time between males and females, although larger skeletal samples are needed to confirm this hypothesis.

The Sakhalin Ainu series show again more or less close affinities to the Okhotsk culture series as suggested in the previous studies (Ishida and Kida, 1991; Ishida, 1996; Hanihara et al., 2008; Matsumura et al., 2009). However, archeological evidence suggests that the Ainu expanded from Hokkaido to the Sakhalin Island during the 14th and 15th centuries AD (Ohya, 1985; Ishida and Kida, 1991; Hanihara, 1998; Fitzhugh and Dubreuil, 1999), long after the Okhotsk culture had disappeared from both Hokkaido and Sakhalin. The northern part of the Sakhalin island group has been inhabited by other ethnic groups: Nivkh, Uilta, and Orochs (Ishida and Kida, 1991; Matsumura et al., 2009). Taking these into account, the northern-like characteristics of the Sakhalin Ainu may be explained by a genetic contribution of more recent indigenous groups of Sakhalin Island.

Classic analysis of biological distances between populations such as Mahalanobis' generalized distance for metric data and Smith's MMD distance for nonmetric data has been a central method in studies of the reconstruction of population history (Relethford and Blangero, 1990; Relethford, 1994). However, a potential danger in these studies is that such methods will only be useful when factors such as gene flow, genetic drift, climatic and subsistence adaptation, etc., which have had an impact on morphological variation that

Figure 4. A multidimensional plots (Andrews, 1972) for the four local Ainu samples and the Okhotsk culture series based on the MDS scores calculated from odontometric data: (a) sex-combined samples; (b) male samples; (c) female samples.

reflect affinities between populations, have an effect large enough to be detected. If the effects of such factors are small, comparative morphological analysis may not detect them. The present findings do imply a substantial interpopulation relationship between the Okhotsk culture people and Ainu-Jomon lineages at least in northeastern Hokkaido, along the coastal region of the Sea of the Okhotsk, as pointed out in previous studies (Shigematsu et al., 2004; Hanihara et al., 2008; Hanihara, 2010a, b). This suggests that gene flow to northeastern Hokkaido from an external source after the Jomon periods cannot be disregarded.

Figure 5. A multidimensional plot (Andrews, 1972) for the four local Ainu samples and the Okhotsk culture series based on the MDS scores calculated from nonmetric dental data.

Acknowledgments

We thank Gen Suwa, the associate editor, for his constructive suggestions for improving the manuscript. We wish to express our sincere thanks to T. Amano of Hokkaido University Museum, Sapporo; M. Matsumura of the Department of Anatomy, Sapporo Medical University, Sapporo; Y. Dodo of the Department of Anatomy, Tohoku University School of Medicine, Sendai; G. Suwa of the Department of Anthropology, University Museum, The University of Tokyo, Tokyo; H. Baba of the Department of Anthropology, National Museum of Nature and Science, Tokyo; K. Katayama of the Department of Zoology, Kyoto University, Kyoto; for their kind permission to study the materials under their care. This study was supported in part by Grants-in-Aid for Scientific Research (Nos. 18570220 and 21405027 to T.H.) from the Ministry of Education, Culture, Sports, Science and Technology of Japan; a Japan Fellowship for Research in United Kingdom (T.H.) from the Japan Society for the Promotion of Science; and the Smithsonian Institution Fellowship Program, Smithsonian Opportunities for Research and Study (Senior Fellowship in 2001–2002 to T.H.).

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