FULL PAPER *Anatomy*

Insular Variation of the Craniodental Morphology in the Siberian Weasel *Mustela sibirica*

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ABSTRACT. We compared craniodental morphology among 5 populations of the Siberian weasel *Mustela sibirica* including 2 insular ones (Tsushima and Taiwan). Skulls of the insular individuals tended to be smaller than those of continental ones. Shape differences were also detected, but not so pronounced. Considering these results, the Taiwan population should be regarded as a distinct subspecies *M. s. taivana* from the mainland ones. The Tsushima population may also possibly be a distinct subspecies from the mainland ones, but more detailed studies using a larger number of specimens are needed for a conclusion. The introduced population in Honshu is also differentiated from the source population. This suggests a high morphological plasticity in *M. sibirica*.

KEY WORDS: craniodental morphology, geographic variation, island, *Mustela sibirica*, Siberian weasel.

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The Siberian weasel *Mustela sibirica* is one of the most widely distributed species among East Asian species of the Carnivora. Due to its wide distribution and habitat diversity, there should be considerable geographic variations. In fact, several authors have reported geographic variation in the skulls [2, 18]. In addition, the fact that many subspecies have been described should reflect their high morphological variability. However, the whole picture of geographic variations has not been clarified, and morphological differences among subspecies have not been well defined. Descriptions of subspecies in many cases have been based on comparisons of a small number of specimens, and statistical analyses have not been conducted. Therefore, re-examinations of subspecies considering variations within each population are needed.

The focus of this study is on insular variation, an important characteristic in *M. sibirica*. In many species of Carnivora, insular populations are often differentiated from mainland ones [9, 12–14], and have often been described as distinct subspecies. Two subspecies of *M. sibirica* from islands (*M. s. taivana* from Taiwan and *M. s. quelpartis* from Cheju Island, Korea) have been described [22, 23]. Furthermore, the Tsushima population is possibly an independent subspecies [1, 2]. However, comparative morphological studies using these insular and nearby mainland populations have not been done. In this study, the craniodental morphology in insular and mainland populations of *M. sibirica*, which belong to different (or possibly different) subspecies, was compared.

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MATERIALS AND METHODS

Study specimens: In this study, specimens of *M. sibirica* from 5 localities (Fig. 1) were compared. It is well known

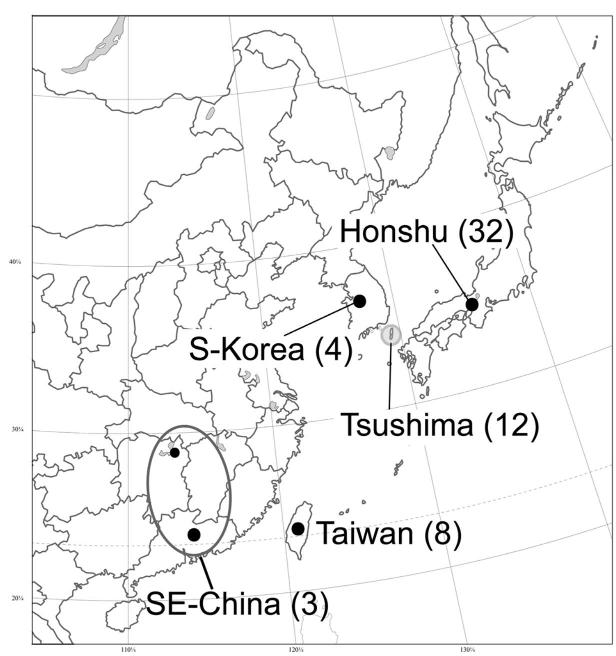

Fig. 1. Localities of specimens used in this study and number of samples.

that this species shows remarkable sexual dimorphism [1, 20] and sexes should not be mixed when comparative analyses are conducted. For some localities, there were few female specimens. For these reasons, only male specimens were used. All specimens are adult with completely erupted permanent teeth and completely closed bone sutures (e.g. nasal and palatal sutures). Although phylogenetic relationship between each local population is unclear, geological affinity suggests that the Taiwanese population and those from south-eastern China (SE-China) may be closely related, and those from Tsushima and southern part of the Korean peninsula (S-Korea) may also be closely related. Therefore, 2 pairs of comparisons were conducted. The former pair has often been regarded as the distinct subspecies, *M. s. taivana* in Taiwan and *M. s. davidiana* from SE-China. Some authors regarded them as the same subspecies, *M. s. davidiana* [4]. The latter pair has been regarded as the same subspecies *M. s. coreana*. However, some authors suggested the possibility that they are different subspecies [2]. In addition, specimens from Honshu, Japan were compared with those from the Korean peninsula and Tsushima. *Mustela sibirica* in Japan, except for Tsushima, was introduced from the Korean peninsula in the first half of the last century [15]. If there is a significant morphological differentiation after introduction to new places, this may suggest high adaptability to new environments and high morphological plasticity in the species. In such cases, substantial problem in taxonomy will be raised (i.e. are diagnostic characters stable?). Hereafter, the term Korea-Japan group for S-Korea, Tsushima and Honshu populations and China-Taiwan group for SE-China and Taiwan will be used.

All specimens are deposited in National Museum of Nature and Science, Tokyo (NSMT), National Museum of Natural Science, Taichung (NMNS), Endemic Species Research Institute, Jiji, Nantou (TESRI), South China Institute of Endangered Animals, Guangzhou (SCIEA), National Museum of Natural History, Washington, D.C. (USNM), a private collection of Mikiko Abe (MA) and College of Veterinary Medicine, Seoul National University (KJ) as follows: (1) Tsushima, NSMT-M14369, 14382, 14418, 14470, 14478, 14508, 14639, 14853, 14953, 14957–14958,15007; (2) S-Korea, KJ0203, 0478, 0717, 0754; (3) Honshu, MA1, 34–35, 45, 68, 104, 117, 130, 151, 212–213, 217, 225, 228–230, 280–281, 285, 288, 315–316, 325, 327, 354, 410, 448–450, 475, 591, 600; (4) Taiwan, NMNS-1074, 1193, 1944, TESRI-C0008, 0099, 0112–0113, NSMT-M31287; (5) SE-China, SCIEA-3014, 3032, USNM-239584.

Statistical Analyses: Univariate and multivariate analyses

Table 1. Skull measurements used in this study

No.	Acronym	Measurement
1	CBL	condylobasal length
2	NCL	neurocranial length
3	VCL	viscerocranial length
4	BBL	braincase basal length
5	PL	palatal length
6	ZL	zygomatic length
7	ABL	length of auditory bulla
8	CML	toothrow length from canine to molar
9	RL	rostrum length
10	ZB	zygomatic breadth
11	MB	mastoid breadth
12	BCB	braincase breadth
13	PB	palatal breadth
14	OCB	breadth of occipital condyle
15	PPB	breadth of postorbital process
16	PCB	breadth of postorbital constriction
17	RB	breadth of rostrum
18	IOB	interorbital breadth
19	ABB	breadth of the auditory bulla
20	NB	nasal breadth
21	LBB	least breadth between bullae
22	CH	cranial height
23	OTH	occipital triangle height
24	ML	maximum mandibular length
25	MTL	mandibular toothrow length
26	MH	mandibular height
27	MRB	breadth of mandibular ramus
28	MD	depth of mandible at the p3-p4 interdental gap
29	LP4	length of P4
30	BP4	breadth of P4
31	BM1	breadth of M1
32	Lm1	length of m1

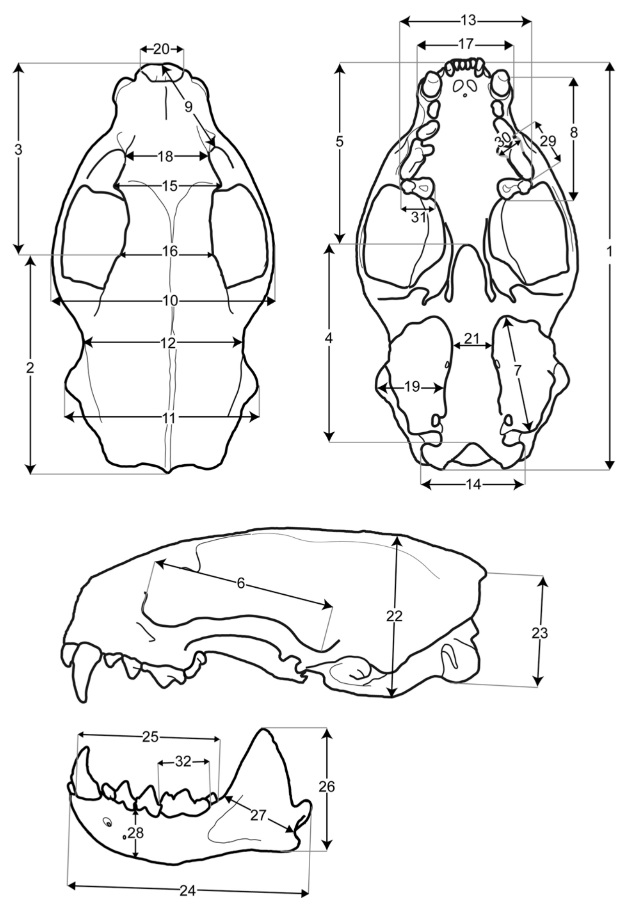

Fig. 2. Craniodental measurements used in this study.

were conducted to clarify craniodental characteristics in each local population. In these analyses, 32 measurements (Table 1, Fig. 2) were used. In univariate analyses, the mean value of localities was compared using Tukey's multiple comparison test and Welch's *t*-test for Korea-Japan group and China-Taiwan group, respectively. In the following multivariate analyses, log-transformed data of each measurement were used. First, the principal component analysis (PCA) was used. In the PCA for quantitative traits of skull, the first axis (PC1) represents skull size variation. The PCA was mainly used to extract size variation. Secondly, stepwise discriminant analysis (SDA) was conducted to extract variables which characterise each population. Using selected variables, canonical variate analysis (CVA) was conducted.

All statistical analyses were conducted with the software R.2.13.2 [16].

RESULTS

Univariate analyses: Within the Korea-Japan group, specimens from Honshu are larger than that from Tsushima for 27 measurements (Table 2). The S-Korea specimens showed intermediate tendency and no statistical difference from either the Honshu or Tsushima populations in most traits. In comparisons between the Honshu and S-Korea specimens, VCL, RB, OCB and MD were larger in the Honshu specimens, while BCB was larger in the S-Korea specimens. LP4, CH, BCB, Lm1, MH and MRB were larger in the S-Korea specimens compared to the Tsushima specimens. Among China-Taiwan group, 27 traits were larger in the SE-China specimens than the Taiwan specimens. There was no significant difference for rest of 5 measurements (PCB, PPB, OCB, LBB and BP4).

PCA: The first 4 axis explained more than 80% (81.87%) of total variation (Table 3). The first axis explained size variation, since all variables showed positive factor load-

Table 2. Mean values and standard deviations of measurements for each locality

Measurement	Tsushima (*n*=12)		S-Korea (*n*=4)		Honshu (*n*=32)		Taiwan (*n*=8)		SE-China (*n*=3)	
1 CBL	60.56 (1.208)	H	63.20 (2.559)		64.59 (2.042)	TS	61.01 (2.046)	C	67.51 (0.646)	TW
2 NCL	32.18 (1.102)	H	34.27 (0.975)		33.86 (1.684)	TS	30.74 (1.105)	C	35.46 (1.226)	TW
3 VCL	31.81 (1.131)	H	32.86 (1.979)	H	35.46 (1.548)	K, TS	32.91 (1.699)	C	37.17 (0.660)	TW
4 BBL	29.45 (0.604)	H	30.41 (1.451)		31.56 (0.948)	TS	29.50 (0.703)	C	32.01 (0.580)	TW
5 PL	26.77 (0.714)	H	28.06 (0.632)		28.31 (1.232)	TS	26.80 (1.153)	C	30.80 (0.469)	TW
6 ZL	26.39 (0.730)	H	27.48 (0.983)		28.36 (1.155)	TS	25.52 (1.044)	C	29.55 (0.236)	TW
7 ABL	18.17 (0.451)	H	18.82 (0.644)		18.97 (0.745)	TS	17.97 (0.569)	C	19.66 (0.520)	TW
8 CML	18.13 (0.362)	H	18.64 (0.401)		18.90 (0.724)	TS	18.00 (0.650)	C	19.72 (0.237)	TW
9 RL	14.58 (0.343)	H	15.09 (0.725)		15.73 (0.701)	TS	14.57 (0.741)	C	16.49 (0.431)	TW
10 ZB	32.46 (1.031)	H	33.46 (1.105)		34.81 (1.121)	TS	31.43 (1.314)	C	34.87 (1.059)	TW
11 MB	27.62 (0.723)	H	28.57 (1.293)		29.99 (1.165)	TS	26.69 (0.857)	C	30.47 (0.963)	TW
12 BCB	24.76 (0.492)	K	26.31 (0.918)	H, TS	24.93 (0.849)	K	24.94 (0.677)	C	26.14 (0.437)	TW
13 PB	18.86 (0.512)	H	19.58 (1.192)		20.36 (0.822)	TS	17.78 (0.529)	C	20.24 (0.284)	TW
14 OCB	15.60 (0.450)	H	15.68 (0.408)	H	16.42 (0.587)	K, TS	15.44 (0.336)		16.54 (0.527)	
15 PPB	16.23 (0.997)		16.02 (0.601)		15.61 (0.854)		14.73 (0.776)		16.35 (0.968)	
16 PCB	11.90 (0.781)	H	12.87 (0.303)		13.38 (0.854)	TS	13.56 (1.016)		12.70 (0.451)	
17 RB	13.17 (0.389)	H	13.59 (0.754)	H	14.88 (0.783)	K, TS	11.93 (0.706)	C	14.07 (0.297)	TW
18 IOB	12.28 (0.442)		12.71 (0.141)		12.57 (0.562)		11.63 (0.700)	C	12.87 (0.635)	TW
19 ABB	10.57 (0.280)	H	11.09 (0.546)		11.32 (0.534)	TS	10.04 (0.401)	C	11.70 (0.665)	TW
20 NB	6.55 (0.192)		6.63 (0.324)		6.73 (0.337)		6.04 (0.412)	C	6.86 (0.354)	TW
21 LBB	5.30 (0.315)	H	5.59 (0.676)		5.86 (0.419)	TS	5.45 (0.387)		5.77 (0.116)	
22 CH	22.18 (0.590)	H, K	23.95 (0.590)	TS	24.25 (0.826)	TS	21.86 (0.513)	C	25.31 (0.477)	TW
23 OTH	16.40 (0.425)	H	17.25 (0.782)		17.66 (0.715)	TS	16.33 (0.384)	C	18.36 (0.375)	TW
24 ML	35.10 (0.806)	H	36.49 (1.296)		37.65 (1.346)	TS	34.43 (1.290)	C	39.06 (0.376)	TW
25 MTL	20.52 (0.547)	H	21.43 (0.895)		21.86 (0.825)	TS	20.36 (0.795)	C	22.81 (0.306)	TW
26 MH	16.86 (0.743)	H, K	18.27 (1.059)	TS	18.88 (0.789)	TS	16.05 (0.917)	C	20.06 (0.552)	TW
27 MRB	10.21 (0.580)	H, K	11.42 (0.593)	TS	12.16 (0.768)	TS	10.27 (0.403)	C	12.78 (0.699)	TW
28 MD	6.21 (0.343)	H	6.66 (0.410)	H	7.31 (0.434)	K, TS	5.53 (0.316)	C	7.50 (0.182)	TW
29 LP4	6.36 (0.263)	H, K	6.75 (0.062)	TS	6.75 (0.226)	TS	6.43 (0.294)	C	6.99 (0.263)	TW
30 BP4	3.58 (0.167)		3.68 (0.232)		3.70 (0.235)		3.53 (0.102)		3.88 (0.375)	
31 BM1	5.04 (0.277)	H	5.21 (0.219)		5.24 (0.236)	TS	4.87 (0.286)	C	5.52 (0.165)	TW
32 Lm1	7.48 (0.282)	H, K	7.88 (0.309)	TS	8.02 (0.281)	TS	7.34 (0.257)	C	8.10 (0.207)	TW

Measurements are as shown in Table 1 and Fig. 1. Significant difference between localities in Tukey's multiple comparison test (Tsushima, S-Korea and Honshu) and Welch's *t*-test (Taiwan and SE-China) at the $P<0.05$ level are indicated by the following: TS=Tsushima, K=S-Korea, H=Honshu, TW=Taiwan, C=SE-China.

Table 3. The first 7 principal components which account for more than 90% of total variation from the PCA

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7
CBL	**0.922**	-0.102	0.159	0.207	-0.059	0.096	-0.097
NCL	**0.744**	0.083	0.116	0.185	0.026	0.145	0.479
VCL	**0.885**	-0.188	0.006	0.068	-0.039	0.032	-0.304
BBL	**0.891**	-0.123	0.064	-0.010	-0.111	-0.043	-0.039
PL	**0.822**	0.025	0.195	0.355	0.002	0.212	-0.130
ZL	**0.932**	-0.001	0.189	0.109	-0.030	-0.020	-0.068
ABL	**0.750**	0.132	-0.022	0.379	-0.064	0.128	-0.009
CML	**0.817**	0.048	0.077	0.090	0.278	0.142	-0.034
RL	**0.910**	-0.009	-0.011	0.108	0.082	0.155	-0.207
ZB	**0.914**	0.105	-0.033	-0.211	0.000	-0.041	-0.127
MB	**0.941**	-0.073	0.020	-0.089	-0.023	0.004	0.058
BCB	0.377	-0.267	0.314	0.334	0.331	0.356	0.289
PB	**0.916**	-0.020	-0.053	-0.095	0.105	-0.064	0.000
OCB	**0.774**	-0.091	-0.035	-0.122	0.134	0.185	0.032
PPB	0.237	**0.712**	0.030	-0.327	0.270	0.415	-0.102
PCB	0.175	**-0.777**	-0.474	-0.104	0.158	0.290	-0.040
RB	**0.884**	0.218	-0.207	-0.278	-0.070	-0.081	-0.017
IOB	**0.679**	0.391	0.135	-0.319	0.213	0.265	-0.193
ABB	**0.885**	0.034	0.031	0.076	0.076	0.012	0.130
NB	**0.778**	0.267	0.227	-0.023	0.077	0.076	0.081
LBB	**0.525**	**-0.503**	0.435	-0.474	-0.114	-0.017	0.093
CH	**0.861**	-0.074	-0.165	0.125	-0.131	0.181	0.256
OTH	**0.851**	-0.194	0.085	0.060	-0.056	0.194	0.130
ML	**0.963**	-0.030	0.123	0.122	-0.033	0.034	-0.067
MTL	**0.906**	-0.112	0.079	0.159	0.150	0.097	0.005
MH	**0.947**	-0.007	0.088	0.061	-0.130	0.038	0.060
MRB	**0.920**	-0.064	0.034	0.156	-0.225	-0.059	-0.176
MD	**0.919**	0.167	-0.270	-0.033	-0.077	-0.094	0.110
LP4	**0.686**	-0.271	0.059	-0.043	0.291	-0.266	-0.072
BP4	**0.521**	-0.062	-0.025	0.206	0.644	-0.237	0.003
BM1	**0.732**	-0.050	0.171	-0.013	0.418	-0.279	0.006
Lm1	**0.786**	-0.181	-0.038	-0.081	0.235	-0.393	0.009
Eigenvalue	0.083	0.010	0.005	0.005	0.004	0.003	0.003
Proportion (%)	66.283	7.713	4.048	3.823	3.477	2.734	2.082
Cumulative (%)	66.283	73.997	78.045	81.868	85.345	88.079	90.161

Bold: absolute value>0.5.

ings. Factor loadings were larger in PCB (−0.78), PPB (0.71) and LBB (−0.50) for PC2, PCB (−0.47) and LBB (0.44) for PC3 and LBB (−0.47) for PC4, respectively. Scores of PC1 tended to be larger in the Honshu and SE-China populations than in the 2 insular populations (Fig. 3A). The PC1 for S-Korea specimens was intermediate and significantly differed from Taiwan specimens and marginally differed from Tsushima specimens (P=0.060), respectively. Compared to PC1, there was less clear separation in PC2: the mean score for the Tsushima population was significantly larger than for the Honshu and Taiwan populations, while that for the Taiwan population was marginally smaller than for the Honshu population (P=0.056). PC3 and PC4 showed no separation between populations, except those scores of the SE-China population were larger than that of the Honshu population for PC4 (Fig. 3B).

SDA and CVA: In SDA, 9 variables were selected in the following order, MD, VCL, MH, PCB, BCB, PB, MRB, RL and RB, respectively. These traits represent mandible (MD, MH and MRB), skull breadth (PCB, BCB, PB and RB) and length of facial region (VCL and RL).

In CVA using these 9 variables, 4 axes explained 80.67, 14.09, 3.62 and 1.62% of total variation, respectively. By these axes, 5 populations were clearly separated (Fig. 4), and each specimen was correctly discriminated to its own population. CV1 explained most of the total variation (80.67%) (Table 4). Standardized canonical coefficients for the first axis (CV1) were largest in MH (1.84), VCL (−1.70) and RL (−1.62), respectively. Those for the rest of the axes were large in MRB (1.72), PB (−1.36) and VCL (1.27) for CV2, RB (1.34) and MD (−1.05) for CV3 and MRB (1.39), RB (1.30) and VCL (−1.21) for CV4, respectively. Mandibular traits and skull breadths except BCB contributed positively, and lengths of facial region (VCL and RL) contributed negatively to CV1 scores. CV2 also separated populations well.

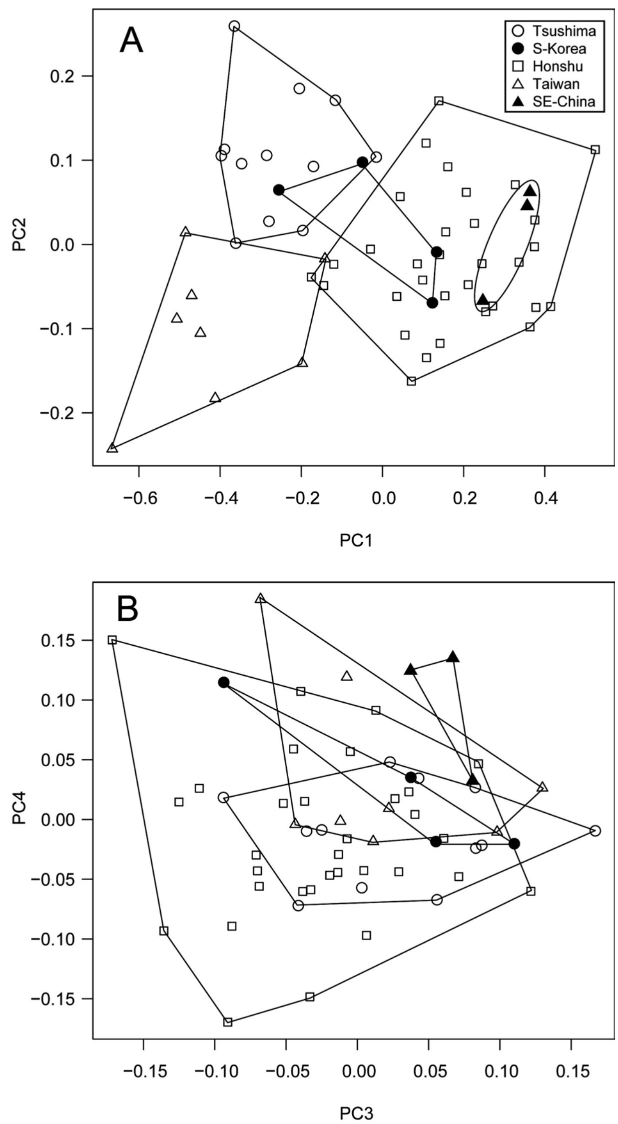

Fig. 3. Two dimensional plots of PC1 versus PC2 (A) and PC3 versus PC4 (B).

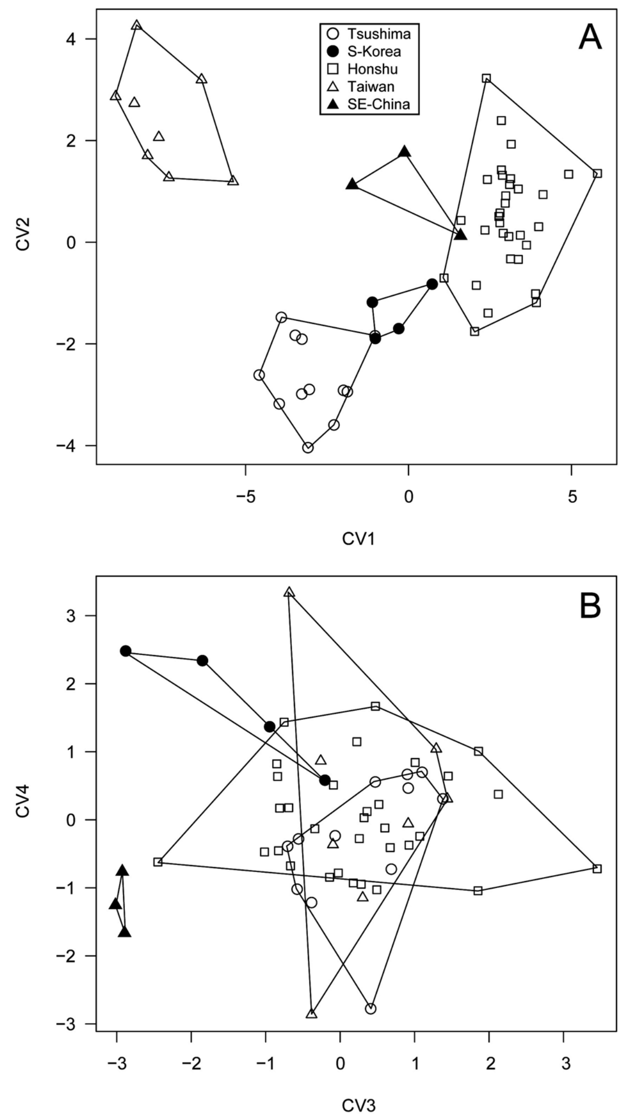

Fig. 4. Two dimensional plots of CV1 versus CV2 (A) and CV3 versus CV4 (B).

DISCUSSION

Previous descriptions of subspecies in *M. sibirica* have been based on small numbers of specimens and qualitative comparisons in many cases [22, 23]. Contrary to those, this study compared specimens from different localities with quantitative and statistical methods, revealing some important characteristics in each population and possibly contributing to the solution of taxonomical and evolutionary issues in *M. sibirica,* despite the limited number of specimens (especially for S-Korea and SE-China).

Variation in Korea-Japan group: Populations in South Korea and Tsushima are often regarded as the same subspecies *M. s. coreana* [7, 21]. However, some recent studies suggested that these should be regarded as separate subspecies [1, 2]. Several traits showed significant differences between them. According to PCA results, the skull from the Tsushima population is slightly smaller than that from the S-Korea population. CVA could clearly discriminate between them and suggested longer facial cranium and smaller mandible in the Tsushima population. There are also slight differences between the Honshu and S-Korea populations. Several traits were larger in the Honshu specimens, but BCB was larger in the S-Korea ones. There was no significant difference in each axis of PCA. However, the range of PC1 for the S-Korea population is not completely included in that from the Honshu one. CVA could clearly discriminate between them and suggests that the skull of the Honshu population has a relatively shorter facial cranium and larger mandible compared to that of the S-Korea population. These results suggest that the Honshu population has differentiated from the original populations from South Korea in short term after

Table 4. Standardized canonical coefficients, eigenvalues and proportion explained by each axis in Canonical variate analysis (CVA) using 9 variables selected by stepwise method

Variable	CV1	CV2	CV3	CV4
MD	1.490	-0.352	-1.045	-0.612
VCL	-1.697	1.266	0.379	-1.207
MH	1.841	-0.834	-0.905	-0.418
PCB	0.940	1.074	0.302	0.583
BCB	-1.017	-0.310	-0.663	0.791
PB	1.519	-1.355	0.724	-0.386
MRB	1.089	1.718	-0.050	1.392
RL	-1.617	0.261	-0.627	-0.676
RB	1.030	-0.381	1.341	1.298
Eigenvalues	16.050	2.802	0.720	0.323
Proportion (%)	80.674	14.086	3.617	1.622
Cumulative (%)	80.674	94.760	98.378	100.000

the introduction. *Mustela sibirica* was introduced to Honshu in the 1920's [15]. Therefore, craniodental differences are thought to have generated within 100 years. Morphological differentiation in short term after introduction from original range has been reported in some carnivoran species [19, 24]. This may reflect a high phenotypic plasticity and high adaptability to various environments in some carnivores. Therefore, the morphological difference revealed in this study does not necessarily reflect genetic differences between populations. To determine whether the Tsushima population is an independent subspecies or not, more specimens are needed to reconstruct morphological variation within each population in conjunction with population genetic studies. A molecular phylogenetic study showed considerable genetic difference between the S-Korea and Tsushima populations [11].

Variation in China-Taiwan group: Populations of SE-China and Taiwan are often regarded as distinct subspecies *M. s. davidiana* and *M. s. taivana*, respectively. However, Ellerman & Morrison-Scott [4] regarded them as the same subspecies *M. s. davidiana*. This study has shown a clear difference between them. In particular, the size difference is remarkable. Therefore, these 2 populations are substantially distinct and should be regarded as different subspecies. According to Hosoda *et al*. [6], divergence time of *M. sibirica* in Taiwan from the continent is estimated to be 0.63Ma (middle Pleistocene). Compared to this, divergence time between the S-Korea and Tsushima populations seems to be more recent [6, 11]. Therefore, divergence of craniodental morphology may reflect genetic difference to some extent.

Morphological differentiation in islands: Craniodental morphology of 2 insular populations studied here was different from continental ones. Both populations had smaller skulls than continental ones. Foster [5] suggested that body size of insular carnivores becomes smaller than that of continental ones which is an argument within the original "island rule". Later Lomolino [8] redefined the rule that body size of smaller mammals becomes larger and that of larger mammals becomes smaller in islands. Furthermore, Brown *et al*. [3] and Marquet and Taper [10] suggested that critical body mass in island mammals is about 100 g which can be an indication of small and large mammals (but see [14]). The body mass of *M. sibirica* is around 700 g in male and 360 g in female [17] which are heavier than the critical mass. Therefore, *M. sibirica* seems to have conformed to the island rule. In addition to skull size, skull shape is also differentiated in islands. However, shape differences detected are ambiguous compared to size differences. More specimens should be used in comparisons to clarify general differences in shape.

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