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Morphometric Geographic Variation in the Asian Lesser White-Toothed Shrew *Crocidura shantungensis* (Mammalia, Insectivora) in East Asia

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ABSTRACT—This study investigated geographic variation in the Asian lesser white-toothed shrew, *Crocidura shantungensis* Miller, 1901, among a number of localities in East Asia, including the Korean Peninsula, Tsushima Island, Cheju Island, and Taiwan, using univariate and multivariate analyses of cranial morphometric characters. Sexual differences were found in Taiwanese shrews, but were not evident in those from Korea or Tsushima. The samples from Taiwan had a larger overall cranial size than those from Korea and Tsushima, and were well separated from the latter two samples in the discriminant analyses. The overall size of the Cheju shrews was also greater, but lay within the variation of those from Taiwan. *Crocidura dsinezumi quelpartis* Kuroda, 1934, described from Cheju Island, is actually a junior synonym of *C. shantungensis*, and is not related to *C. dsinezumi*.

Key words: systematics, *Crocidura shantungensis*, *C. s. hosletti*, *C. s. quelpartis*, sexual dimorphism

INTRODUCTION

White-toothed shrews of the genus *Crocidura* form the largest genus of mammals, and include at least 164 species distributed in the Palaearctic, Oriental, and Afrotropical regions (Wolsan and Hutterer, 1998). The Asian lesser white-toothed shrew, *Crocidura shantungensis* Miller, 1901, is a small species distributed in eastern China, the Korean Peninsula, Ullung Island of Korea, Cheju Island, Tsushima Island, and Taiwan (Fig. 1; Fang *et al.*, 1997; Motokawa, 1999; Jiang and Hoffmann, 2001; Iwasa *et al.*, 2001). This species has been considered a junior synonym of the European *C. suaveolens* since Ellerman and Morrison-Scott (1951) lumped *C. shantungensis* with *C. suaveolens*; *C. suaveolens* has long been regarded as a widely distributed species in the Eurasian continent, found from Europe to East Asia (Hutterer, 1993; Hoffmann, 1996).

Recently, Hoffmann (1996) revised *C. suaveolens* *sensu lato*, and separated it into three different species based on color pattern, distribution range, and overall size using three external and seven cranial measurements. According to Hoffmann (1996), the central Asian populations were referred to *C. gmelini*, which was originally described by Pallas (1811) as *Sorex gmelini*, possibly from Bujnurd (=Khorassan, Iran). The East Asian populations are referred to *C. shantungensis*, originally described by Miller (1901), from Shandong in eastern China. According to Hoffmann (1996), *C. shantungensis* is distributed in Shandong, Sichuan, Shanxi, and Zhejiang as subspecies *C. s. shantungensis*, including *C. ilensis phaeopus* Allen, 1923 as a junior synonym, and in the Korean Peninsula as subspecies *C. s. coreae* Thomas, 1907 (Hoffmann, 1996).

Jiang and Hoffmann (2001) made an additional analysis of these three species (*C. shantungensis*, *C. gmelini*, and *C. suaveolens*) based on multivariate analyses of cranial morphometric characters. Several specimens referred to as *C. gmelini* by Hoffmann (1996) were assigned to *C. shantungensis* by Jiang and Hoffmann (2001) based on the multi-

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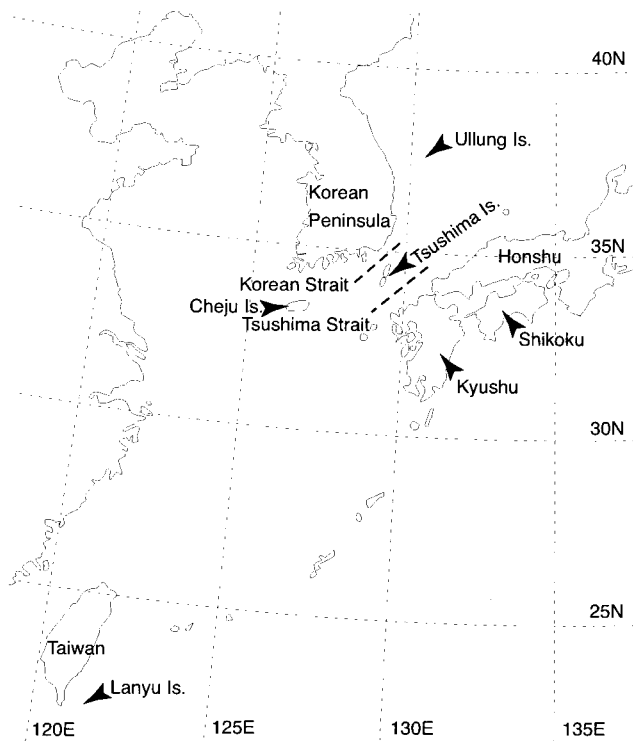


Fig. 1. Map showing East Asia and the sampling localities of *Crocidura shantungensis* used in this study (Korean Peninsula, Cheju Island, Tsushima Island, and Taiwan).

variate analyses. The distribution of *C. shantungensis* in the continent includes the Korean Peninsula, southeastern Siberia, and eastern China, extending west to Shaanxi, Qinghai, and northern Sichuan, and south to Jiangxi and Zhejiang. They recognized *C. s. phaeopus* from Sichuan as a subspecies by the difference in foot color, and the other populations as a nominotypical subspecies, *C. s. shantungensis*. The morphometric variation among *C. shantungensis* populations on the continent, including the Korean Peninsula, is thought to be small, because Jiang and Hoffmann (2001) did not comment on the geographic variation among them. Jiang and Hoffmann (2001) did not examine the specimens from the East Asian islands.

Fang *et al.* (1997) recognized the Taiwan population as a subspecies of *C. shantungensis* (as *C. suaveolens hosletti*), but they did not compare it with the other populations. The Cheju population has been recently discovered by the karyological and nuclear rDNA RFLP evidences (Iwasa *et al.*, 2001). Motokawa *et al.* (2000) revealed the close genetic relationships between populations in Tsushima Island and Taiwan from analysis of the mitochondrial cytochrome *b* gene. The morphological geographic variation, however, has not been studied among the East Asian insular populations of *C. shantungensis*. Because the erroneous identification had been seen in these areas between *C. shantungensis* and other congeneric species, an accurate identification is required.

In this study, we examined the morphometric geo-

graphic variation in *C. shantungensis* collected from the Korean Peninsula, Cheju Island, Tsushima Island, and Taiwan. We then discuss the biogeography and systematics of *C. shantungensis* based on our results and previously published data.

MATERIALS AND METHODS

This study examined a total of 71 specimens of *C. shantungensis* from the Korean Peninsula (=Korea), Cheju Island (=Cheju), Tsushima Island (=Tsushima), and Taiwan (Fig. 1; Appendix). Species identification was carefully made, based on external and cranial characters. In the Korean Peninsula, *C. lasiura* is sympatric with *C. shantungensis*, but *C. shantungensis* is easily distinguished from the former by its smaller size, as discussed by Jones and Johnson (1960). In Tsushima, only *C. shantungensis* is known to occur (Abe, 1967; Motokawa, 1999). In Cheju, *C. shantungensis* (as *C. suaveolens*) was reported recently (Iwasa *et al.*, 2001), and *C. dsinezumi* has also been reported previously (Jones and Johnson, 1961), with possible confusion with *C. shantungensis* as shown by Iwasa *et al.* (2001). In Taiwan, Fang *et al.* (1997) recognized three *Crocidura* species: *C. attenuata*, *C. shantungensis* (as *C. suaveolens hosletti*), and *C. kurodai*. Of these, *C. attenuata* is easily distinguished from the remaining two by its larger size, but the other two have similar overlapping cranial measurements (Fang *et al.*, 1997). For the identification purpose, we also examined 16 specimens of *C. dsinezumi* from Japan and 14 specimens of *C. kurodai* from Taiwan (Appendix).

Four external measurements were taken in the field from fresh material, or obtained from the label attached to museum specimens whenever possible. These measurements were: head and body length (HB), tail length (T), hind foot length without claw (HF), and ear length (E). These variables were not compared statistically because they may well include inter-observer variation. Sixteen cranial measurements were taken following Heaney and Timm (1983), Heaney and Ruedi (1994), and Ruedi (1995) for the cranium, and Motokawa *et al.* (1996) for the mandible. These include: condylo-incisive length (CIL), rostral length (RL), postpalatal length (PPL), condyle to glenoid length (CG), rostral breadth (RB), interorbital breadth (IOB), breadth of braincase (BB), postpalatal depth (PPD), upper toothrow length (UIM), length of upper molariform teeth (UPM), greatest width at the second molars (MM), palatal width at the third molars (PW), mandibular length (ML), mandibular height (MH), lower toothrow length (LIM), and lower molar row length (LM). In addition, the greatest maxillary breadth (MW) was measured for comparison with the published data, because several authors used MW instead of MM. These measurements were taken with digital calipers to the nearest 0.01 mm by one of us (MM).

Of these characters, we selected seven for univariate comparison: CIL, BB, UIM, MM, MW, ML, and LIM. These characters were often used in *Crocidura* systematics (*e.g.*, Jenkins, 1976, 1982). Sexual differences were determined in geographic samples from Korea, Tsushima, and Taiwan tested with Student's *t*-test (when $p > 0.05$ in the two-tailed variance ratio test) or Aspin-Welch's *t*-test if the variances differed between sexes (when $p \leq 0.05$ in the two-tailed variance ratio test) at the 0.05 significance level. Geographic differences among Korea, Tsushima, and Taiwan were tested using analysis of variance (ANOVA) and Tukey's multiple comparison test (when $p > 0.05$ in Bartlett's test) or Dunn's multiple comparison test if the variances differed among samples (when $p \leq 0.05$ in Bartlett's test; see Zar [1999] for ANOVA and multiple comparison test). The Cheju specimens were excluded from the statistical comparison due to the small sample size. The latter comparisons were conducted separately for both sexes.

To investigate the geographic variation in *C. shantungensis*, a

Table 1. External and cranial measurements (mm) in *Crocidura shantungensis*. Values are given as the mean \pm SD, followed by sample sizes in parentheses in the upper column and the ranges in the lower column. For Cheju sample, the latter measurements are from the holotype of *C. dsinezumi quelpartis*. See the text for the character abbreviations.

Character	Korea		Cheju	Tsushima		Taiwan	
	Male	Female	Male	Male	Female	Male	Female
HB	59.91 \pm 6.93 (11)	61.81 \pm 5.08 (16)	61.00, 70.00 (2)	63.88 \pm 4.21 (4)	55.38 \pm 2.29 (4)	70.46 \pm 5.48 (12)	63.95 \pm 7.60 (11)
	50.00–77.00	55.00–73.00		59.00–69.00	53.00–58.00	59.50–79.00	53.00–74.00
T	36.91 \pm 2.21 (11)	36.63 \pm 3.12 (16)	41.00, 45.00 (2)	44.00 \pm 2.48 (4)	37.70 \pm 2.73 (5)	45.83 \pm 3.91 (12)	41.59 \pm 3.89 (11)
	33.00–40.00	31.00–43.00		42.00–47.50	34.00–40.50	41.50–53.00	36.00–46.00
E	7.86 \pm 0.81 (11)	7.44 \pm 0.93 (16)	8.30, 8.50 (2)	8.38 \pm 0.55 (4)	7.88 \pm 1.23 (5)	8.12 \pm 0.97 (12)	7.80 \pm 0.87 (11)
	6.00–9.00	6.00–9.50		7.60–8.90	5.80–9.00	6.20–9.60	6.70–9.70
HF	11.91 \pm 0.58 (11)	11.59 \pm 0.46 (16)	11.10, 12.50 (2)	11.83 \pm 0.64 (4)	11.50 \pm 0.35 (5)	11.44 \pm 0.34 (12)	10.72 \pm 0.49 (11)
	11.00–13.00	11.00–12.00		10.90–12.40	11.00–12.00	10.90–12.00	10.00–11.70
CIL	16.71 \pm 0.38 (10)	17.06 \pm 0.39 (14)	18.22, – (1)	17.59 \pm 0.57 (5)	17.24 \pm 0.57 (5)	18.22 \pm 0.51 (13)	17.15 \pm 0.46 (11)
	16.14–17.31	16.31–17.76		16.60–18.02	16.58–18.00	17.53–19.35	16.48–17.99
RL	6.51 \pm 0.28 (11)	6.53 \pm 0.27 (12)	7.07, – (1)	6.51 \pm 0.24 (7)	6.42 \pm 0.12 (6)	6.97 \pm 0.23 (13)	6.63 \pm 0.15 (11)
	5.95–6.86	6.16–7.15		6.10–6.76	6.30–6.62	6.45–7.30	6.34–6.89
PPL	7.52 \pm 0.19 (10)	7.74 \pm 0.17 (11)	8.00, – (1)	8.02 \pm 0.32 (5)	7.79 \pm 0.37 (5)	8.03 \pm 0.30 (13)	7.55 \pm 0.26 (11)
	7.23–7.76	7.53–7.99		7.50–8.30	7.43–8.40	7.64–8.74	7.21–8.19
CG	7.06 \pm 0.19 (10)	7.24 \pm 0.13 (11)	7.48, – (1)	7.48 \pm 0.29 (5)	7.34 \pm 0.27 (5)	7.51 \pm 0.23 (13)	7.08 \pm 0.19 (11)
	6.75–7.28	7.05–7.55		7.00–7.70	7.04–7.70	7.22–8.02	6.80–7.47
RB	2.00 \pm 0.09 (11)	1.98 \pm 0.13 (16)	2.00, 2.00 (2)	2.09 \pm 0.14 (7)	1.97 \pm 0.17 (7)	2.25 \pm 0.13 (13)	2.11 \pm 0.10 (11)
	1.87–2.14	1.80–2.19		1.80–2.20	1.75–2.19	1.99–2.44	1.96–2.26
IOB	3.75 \pm 0.11 (11)	3.76 \pm 0.15 (12)	3.97, – (1)	3.76 \pm 0.10 (5)	3.72 \pm 0.13 (6)	3.96 \pm 0.11 (13)	3.81 \pm 0.11 (11)
	3.59–3.92	3.53–4.03		3.60–3.87	3.51–3.88	3.83–4.23	3.59–3.95
BB	7.80 \pm 0.19 (11)	7.83 \pm 0.23 (14)	8.00, – (1)	8.06 \pm 0.25 (5)	7.82 \pm 0.05 (5)	8.13 \pm 0.23 (13)	7.93 \pm 0.19 (10)
	7.60–8.13	7.57–8.30		7.70–8.38	7.77–7.90	7.77–8.52	7.60–8.17
PPD	3.21 \pm 0.11 (11)	3.23 \pm 0.11 (12)	3.48, – (1)	3.28 \pm 0.12 (5)	3.14 \pm 0.15 (5)	3.64 \pm 0.13 (13)	3.55 \pm 0.07 (11)
	3.01–3.40	3.06–3.43		3.10–3.40	3.00–3.34	3.44–3.83	3.46–3.66
UIM	7.38 \pm 0.22 (11)	7.35 \pm 0.26 (16)	7.96, 8.40 (2)	7.41 \pm 0.24 (8)	7.26 \pm 0.26 (7)	7.96 \pm 0.27 (13)	7.59 \pm 0.25 (11)
	7.01–7.74	6.89–7.86		7.00–7.79	6.90–7.50	7.52–8.36	7.14–7.87
UPM	4.32 \pm 0.15 (11)	4.28 \pm 0.17 (12)	4.71, – (1)	4.42 \pm 0.13 (7)	4.31 \pm 0.16 (6)	4.66 \pm 0.11 (13)	4.42 \pm 0.14 (11)
	4.06–4.58	3.90–4.59		4.30–4.67	4.03–4.50	4.47–4.79	4.24–4.60
MM	5.02 \pm 0.16 (11)	4.95 \pm 0.11 (12)	5.37, – (1)	4.91 \pm 0.14 (6)	4.90 \pm 0.22 (6)	5.39 \pm 0.16 (13)	5.19 \pm 0.18 (11)
	4.78–5.32	4.77–5.18		4.70–5.07	4.70–5.20	5.07–5.65	4.95–5.57
MW	5.22 \pm 0.12 (11)	5.18 \pm 0.16 (16)	5.58, 5.80 (2)	5.13 \pm 0.19 (6)	4.99 \pm 0.28 (7)	5.73 \pm 0.17 (13)	5.52 \pm 0.19 (11)
	5.01–5.42	5.00–5.56		4.80–5.32	4.60–5.33	5.43–6.01	5.22–5.77
PW	2.00 \pm 0.08 (11)	2.04 \pm 0.09 (12)	2.15, – (1)	1.99 \pm 0.14 (6)	2.01 \pm 0.12 (6)	2.13 \pm 0.12 (13)	2.03 \pm 0.12 (11)
	1.84–2.11	1.90–2.17		1.85–2.20	1.80–2.10	2.00–2.42	1.87–2.25
ML	10.22 \pm 0.26 (11)	10.27 \pm 0.32 (15)	11.04, 11.60 (2)	10.37 \pm 0.50 (8)	10.14 \pm 0.47 (6)	11.02 \pm 0.40 (13)	10.48 \pm 0.26 (11)
	9.94–10.82	9.71–10.90		9.60–11.05	9.40–10.70	10.07–11.73	10.08–10.95
MH	3.99 \pm 0.19 (11)	3.99 \pm 0.19 (15)	4.16, 4.50 (2)	3.85 \pm 0.11 (8)	3.74 \pm 0.20 (8)	4.40 \pm 0.15 (13)	4.13 \pm 0.15 (11)
	3.67–4.35	3.75–4.40		3.71–4.00	3.40–4.00	4.14–4.64	3.93–4.34
LIM	6.76 \pm 0.19 (11)	6.71 \pm 0.19 (15)	7.23, 7.60 (2)	6.69 \pm 0.27 (8)	6.60 \pm 0.32 (8)	7.21 \pm 0.38 (13)	6.93 \pm 0.25 (11)
	6.45–7.08	6.35–7.11		6.20–7.02	5.90–6.87	6.15–7.66	6.41–7.23
LM	3.62 \pm 0.17 (11)	3.65 \pm 0.19 (12)	3.80, – (1)	3.68 \pm 0.06 (4)	3.51 \pm 0.18 (3)	3.83 \pm 0.13 (13)	3.64 \pm 0.22 (11)
	3.24–3.87	3.44–4.04		3.61–3.74	3.30–3.62	3.66–4.07	3.28–3.96

principal component analysis (PCA) was carried out with the PRINCOMP procedure of SAS version 6 (SAS Institute Inc. 1990) using the correlation matrix of cranial measurements of all specimens of *C. shantungensis*. A canonical discriminant analysis (CDA) was also made using the CANDISC procedure of SAS to discriminate among samples. Sixteen measurements (MW was excluded) were used in the PCA and CDA. MW was excluded from the analyses, because it was only measured for comparisons with published data. All measurements were log-transformed before the PCA and CDA. In the CDA, specimens from Korea, Tsushima, and Taiwan were analyzed by grouping them into 6 locality-sex samples. Specimens with missing values were excluded from the PCA and CDA.

RESULTS

Seventy-one specimens were identified with *C. shantungensis* and distinguished from *C. kurodai* and *C. dsinezumi* by several morphological characters. Long bristles are distributed over more than two thirds of the proximal region of the tail in *C. shantungensis*, whereas they are sparsely observed over less than half the proximal region of the tail in *C. kurodai*; moderately distributed on less than the proximal two thirds of the tail in *C. dsinezumi*. In the cranial characters, *C. shantungensis* has a wider maxilla; the parastyle of the fourth premolar nearly equals the second premolar anteroposteriorly in the lateral aspect; broad anterior cusp of the first upper incisor; and broader ascending ramus with a reduced narrow condyle. By contrast, *C. kurodai* has a narrower maxilla; the parastyle of the fourth premolar nearly equals half of the second; slender anterior cusp of the first upper incisor; and anteroposteriorly shortened ascending ramus with a long broad condyle. *Crociodura dsinezumi* has a wider maxilla; the parastyle of the fourth premolar less than half of the second premolar; and broad anterior cusp of the first upper incisor; and broad ascending ramus with a long broad condyle. The holotype of *C. dsinezumi quelpartis* was identified with *C. shantungensis*.

The external and cranial measurements of *C. shantungensis* are given in Table 1. The results of the univariate comparison are in Table 2. In Taiwan, the male sample was significantly larger than the female sample in all the characters compared. In Korea and Tsushima, no sexual differences were found, except for CIL in the samples from Korea, in which the female is larger than the male. Geographic differences were found in many characters. In males, the sample from Taiwan was larger than the samples from Korea and Tsushima in most characters. Furthermore, in females, the means of several characters in the sample from Taiwan was larger than those of the samples from Korea and Tsushima. The only significant difference between the samples from Korea and Tsushima was in CIL in males. Two male specimens from Cheju were large. The values for most of the characters from the Cheju specimens were greater than the maximum value of male specimens from Korea and Tsushima, but were within the range of the male specimens from Taiwan.

The results of the PCA and CDA are in Table 3 and Fig. 2. The first and second principal component axes explained

Table 2. Univariate comparison of the selected cranial measurements in *Crociodura shantungensis*. Sexual differences in each locality were tested with Student's *t*-test or Aspin-Welch's *t*-test (*), and geographic differences among localities were tested with Tukey's multiple comparison test or Dunn's multiple comparison test (*). M, male; F, female; K, Korea; J, Tsushima; T, Taiwan; ns, non significant. See the text for the character abbreviations.

Character	Sexes			Localities	
	Korea	Tsushima	Taiwan	Male	Female
CIL	F>M	ns	M>F	T>K, J>K	ns
BB	ns	ns*	M>F	T>K	ns*
UIM	ns	ns	M>F	T>K, T>J	T>J
MM	ns	ns	M>F	T>K, T>J	T>K, T>J
MW	ns	ns	M>F	T>K, T>J	T>K, T>J
ML	ns	ns	M>F	T>K, T>J	ns
IM	ns	ns	M>F	T>K, T>J	T>J

Table 3. Eigenvectors of the first two principal component axes and first two canonical axes based on cranial characters of *Crociodura shantungensis*. See the text for the character abbreviations.

Character	PC1	PC2	CAN1	CAN2
CIL	0.287	0.223	1.348	-0.644
RL	0.268	-0.106	0.015	-0.511
PPL	0.230	0.519	-1.560	-0.141
CG	0.230	0.555	-0.209	0.018
RB	0.214	-0.208	-0.215	-0.160
IOB	0.255	0.002	-0.919	-0.311
BB	0.232	0.218	0.102	0.181
PPD	0.231	-0.226	2.814	0.668
UIM	0.288	-0.130	-0.999	-0.172
UPM	0.263	-0.103	-0.507	-1.145
MM	0.257	-0.256	1.178	0.419
PW	0.204	-0.246	0.263	0.642
ML	0.280	0.057	-0.314	-3.013
MH	0.257	-0.184	0.565	0.887
LIM	0.258	-0.157	0.686	2.193
LM	0.226	0.061	0.197	0.554
Eigenvalue	9.594	0.250	9.751	3.236
Proportion	0.674	0.074	0.667	0.221

67.4 and 7.4% of the total variation, respectively. In the first axis, all the variables showed similar positive loading. In the second axis, CG (positive) and PPL (positive) showed relatively large loading. In the PC1 axis, the male sample from Taiwan had larger values than the remaining samples. In the second axis, the values are large in the samples from Tsushima, intermediate in the samples from Korea, and small in the samples from Taiwan, with large overlapping among samples.

In the CDA, the first and second canonical axes explained 66.7 and 22.1% of the total variation, respectively.

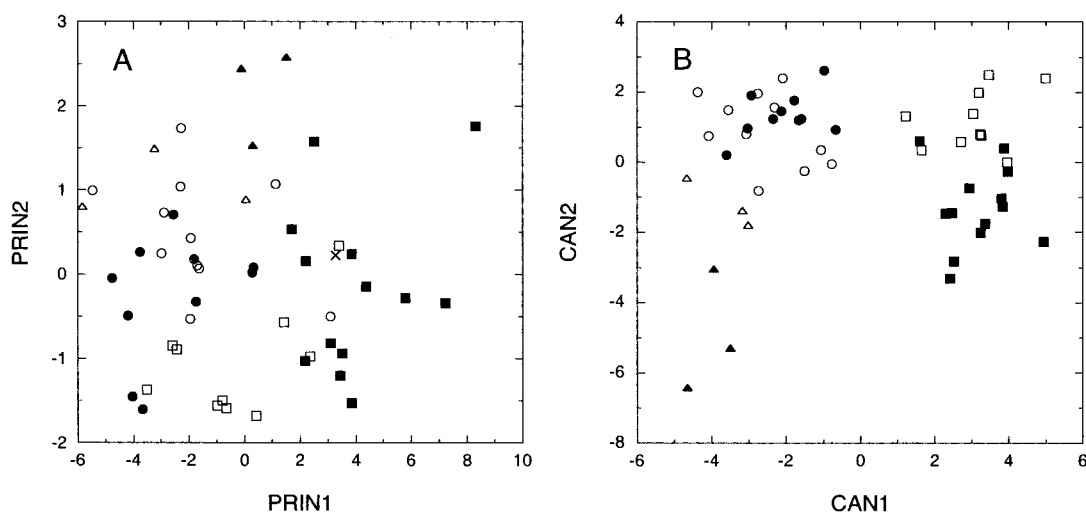


Fig. 2. Scatter plots of the scores on the first and second principal component axes (A) and first and second canonical axes (B) based on the cranial characters of *Crocidura shantungensis*. Circles, Korea; triangles, Tsushima; squares, Taiwan (open symbols indicate males and closed symbols females); crosses, Cheju (male only).

In the first axis, PPD (positive) and PPL (negative) showed relatively large loading. In the second axis, ML (negative) and LIM (positive) showed relatively large loading. In the first axis, the samples from Taiwan had positive scores and were separated from the samples from Korea and Tsushima, which had negative values (Fig. 2). In the second axis, the samples from Korea were separated from the samples from Tsushima, as they had larger values.

DISCUSSION

Geographic variation and biogeography

In general, no sexual dimorphism exists in small- or medium-size *Crocidura* shrews (Ruedi, 1995; Motokawa *et al.*, 1996; Sara and Vogel, 1996), with the exception of *C. maxi* reported by Kitchener *et al.* (1994). Our results, however, indicate the occurrence of sexual dimorphism in *C. shantungensis*. It is interesting that this sexual difference is evident in Taiwan, but is small or not detected in Korea and Tsushima. In Taiwan, males are larger than females and the sexual difference is thought to be an overall size difference. In Korea, sexual difference was found only in CIL, and females are larger than males. The sexual difference in Korea appears small judging from the overlapping plots in the PCA and CDA scores between sexes. The different pattern in sexual differences among localities may be related to the different life history between subtropical and temperate regions (Rychlik, 1998), but the data for the life history are insufficient in *C. shantungensis*.

The geographic variation seems to be clear between the Taiwan population and those in Korea and Tsushima. This geographic variation is likely attributed mostly to overall size difference. The Taiwan population, especially in males, may be characterized by larger overall size compared with those in Korea and Tsushima, as shown in the larger

univariate measurements (Tables 1 and 2) and larger PRIN1 scores which can be interpreted as the overall size from similar loading among variables (Fig. 2, Table 3). The Cheju population shows larger size than those in Korea and Tsushima (Table 1), and shows greater PC1 score similar to the Taiwan population (Fig. 2). The Taiwan population is separated from those in Korea and Tsushima in CDA (Fig. 2). This suggests that the Taiwan population is morphologically diverged from those in Korea and Tsushima.

Cheju Island and Taiwan are part of the eastern continental shelf and are thought to have been connected with the continent during sea level lowering in the last (=Würm) glacial period in the late Pleistocene, about 20,000–15,000 years ago, and subsequently separated from the continent (Ohshima, 1990; Ota, 1998). *Crocidura shantungensis* could have migrated to Cheju and Taiwan via the land connection from the continent and subsequently obtained larger overall sizes independently as a consequence of isolation on these islands.

By contrast, Tsushima Island is thought to have been separated from the Korean Peninsula by the Korean Strait in the late Pleistocene, about 100,000 years ago (Ohshima, 1990), and from Kyushu by the Tsushima Strait in the same period (Ohshima, 1990) or after the last glacial period (Ota, 1998). Therefore, the non-volant terrestrial mammal fauna of Tsushima is characterized by close affinities with those of both the Korean Peninsula and Japanese Hondo (=Kyushu, Shikoku, and Honshu complex; 8 species), or only with that of the Japanese Hondo (3 species) reflecting the paleogeographical scenario (Abe, 1999). While, three species in Tsushima, *C. shantungensis*, the Siberian weasel, *Mustela sibirica*, and the Bengal cat, *Prionailurus bengalensis*, are not distributed in the Japanese Hondo, but have conspecific populations on the Korean Peninsula and continent (Abe, 1999). These three species are regarded as the "Korean

element" and their origins were discussed from a biogeographic point of view (Imaizumi, 1970; Abe, 1999). Of these three species, *C. shantungensis* is much smaller and is thought to have been more severely affected by land bridge formation; thus, its origin is often discussed.

Thomas (1908) thought that the Tsushima population of *C. shantungensis* had its origin in human introduction, because it resembles Korean populations morphologically. By contrast, Imaizumi (1970) argued that *C. shantungensis* reached Tsushima in the last glacial period from the Korean Peninsula via a land bridge. However, no land bridge connection in the last glacial period has been suggested from the paleogeographical scenario. Abe (1999) suggested that *C. shantungensis* crossed a reduced narrow strait between Tsushima and the Korean Peninsula during the last glacial period.

Our results confirm the morphological similarity between populations from the Korean Peninsula and Tsushima, as already suggested by Thomas (1908), Imaizumi (1970), and Abe (1999). Since the Korean Strait, which separate the Korean Peninsula and Tsushima, may have been narrower in the last glacial period than it is at present (Ohshima, 1990), *C. shantungensis* could have crossed the strait via over-water dispersal, as suggested by Abe (1999). The two carnivores, *Mustela sibirica* and *Prionailurus bengalensis*, are much larger and could cross such a strait more easily than *C. shantungensis*.

Taxonomic implications

Jameson and Jones (1977) studied the small species of *Crociodura* from Taiwan for the first time, and described *C. russula hosletti* and *C. horsfieldii kurodai* as new subspecies. These subspecies are currently considered as *C. shantungensis* and *C. kurodai*, respectively, at species level (Fang *et al.*, 1997; see Introduction). The male holotype (USNM 358640) and one paratype (USNM 358670) of *C. r. hosletti* have tail bristle conditions "most abundant near base", same to *C. shantungensis* (Jameson and Jones, 1977; our direct examination for USNM 358670), while another paratype (USNM 358671) has bristles "on [the] basal 21% of [the] tail" (Jameson and Jones, 1977) and actually identified with *C. kurodai* (our direct examination). This demonstrates that the paratypes of *C. r. hosletti* is a mixture of *C. shantungensis* and *C. kurodai*. Because the Taiwan population of *C. shantungensis* is distinguishable morphologically from those in Korea and Tsushima, *C. s. hosletti* probably represents a valid subspecies following the subspecies criterion of mammals (Corbet, 1997).

Kuroda (1934) described *C. dsinezumi quelpartis* based on a male specimen collected from Seikiho, Quelpart Island (=Sogui'p'o, Cheju Island). The holotype is deposited in the Yamashina Institute for Ornithology in Abiko (YIO-135) as a skin and a broken skull with a preserved rostrum and mandible; it is identified with *C. shantungensis*, but different from *C. dsinezumi*, as shown above. For the bristle hairs, Kuroda (1934) noted, "tail well haired, with bristles numerous as in

coreae", and he thought that *C. coreae* (= *C. shantungensis*) in Korea and *C. dsinezumi* in Japan were closely related species, and that *C. d. quelpartis* was an intermediate between them. Here, we consider that Kuroda's (1934) *C. dsinezumi quelpartis* is *C. shantungensis* at species level, although it was regarded as a subspecies or junior synonym of *C. dsinezumi* previously (Jones and Johnson, 1961; Hutterer, 1993). The Cheju population may have larger overall size than those in Korea and Tsushima. Validity of the subspecific status of *hosletti* and *quelpartis* should be determined in future by the revisional study of *C. shantungensis* on the basis of more specimens.

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APPENDIX

All of specimens used in this study are deposited in the Natural History Museum, London (BMNH); the National Museum of Natural History, Washington, D. C. (USNM); the National Science Museum, Tokyo (NSMT); the Yamashina Institute for Ornithology, Abiko (YIO); the Taiwan Endemic Species Research Institute, Chichi (TESRI); the National Pingtung Science and Technology University, Pingtung (NPSTU); the Osaka City University Graduate School of Medicine, Osaka (OCUMS); Department of Biology, Tunghai University, Taichung (TU); and the Zoological Collection of Kyoto University Museum, Kyoto (KUZ).

C. shantungensis. Korea: 10 miles N of Taegu, BMNH 6.12.6.26; Mun-gy'ong, 110 miles SE of Seoul, BMNH 6.12.6.27, holotype of *C. coreae*, -28 through -36; Mok'po, Cholla-Namdo, BMNH 6.12.6.37, YIO 138, 139; Penchan, 50 miles NE of Seoul, BMNH 7.6.3.9; K'umhwa, 65 miles NE of Seoul, BMNH 7.6.3.10; Chong-ju, Ch'ungch'ong-Bukto, BMNH 7.6.3.11, -12; Pochon Gun, Kyonggi-Do, BMNH 75.701 through -706; Paju Gun, Kyonggi-Do, BMNH 75.707, -708; Bampo (probably near Unggi; Jones and Johnson [1960]), YIO 136, 137. Tsushima: Izuhara, Izuhara T., BMNH 8.2.26.18, NSMT-M 13778, 13780, 14233, 14234; Kechi, Izuhara T., NSMT-M13779, 13781 through 13783; Waniura, Kamitsushima T., NSMT-M14232; Kisaka, Mine T., KUZ-M 591; Sasuna, Kamiagata T., BMNH 8.2.26.16, -17; Shitaru, Kamiagata T., KUZ-M 335; Toyo, Kamiagata T., KUZ-M 1432, 1438, 1582. Cheju: Seikiho (=Soguip'o), YIO 135, holotype of *C. dsinezumi quelpartis*; Hallim, KUZ-M 2202. Taiwan: Tamsui, Taipei Hsien, USNM 358670; campus of Tunghai University, Taichung City, KUZ-M 966, 976, 979 through 986, 1127 through 1131; the vicinity of Ta-mai Tsun, Kueijen Hsien, Tainan Hsien, KUZ-M 756, 757, 885, 886, 888 through 891; Kuanyin, Taoyuan Hsien, OCUMS 3204.

C. kurodai. Lung Yuen Bridge, Nantou Hsien, USNM 332813, skull inside skin; 30 km of 210 Road, Tahsueh Shan, Taichung Hsien, OCUMS 7256; Ha-pen River, Wulai, Taipei Hsien KUZ-M 1655; Tengchih, Kaohsiung Hsien, KUZ-M 3319; Changhu, Kukeng Shin, Yunlin Hsien, 1 TESRI, uncatalogued; Wutai, Pingtung Hsien, 4 NPSTU, uncatalogued; Nan-zen Mt., National Ken-ting Park, Pingtung Hsien, 3 TU, uncatalogued; not specific in Taiwan, USNM 311473, 358671.

C. dsinezumi. Takamori, Kumamoto Pref., BMNH 6.1.4.39 through -41; Kawachi, Miyazaki Pref., BMNH 6.1.4.42; Hikosan Mt., Fukuoka Pref., NSMT-M 11281, 11322; Sasakuri T., Fukuoka Pref., NSMT-M 28681, 28682; Homan River, Fukuoka Pref., KUZ-M 865, 870, 1154; Chikugo River, Fukuoka Pref., KUZ-M 1155; Yamakei T., Oita Pref., KUZ-M 867; Kuju T., Oita Pref., KUZ-M 868, 869, 1153.