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Morphological Comparison of Ryukyu Mouse *Mus caroli* (Rodentia: Muridae) Populations from Okinawajima and Taiwan

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Masaharu Motokawa, Liang-Kong Lin and Junko Motokawa (2003) Morphological comparison of Ryukyu mouse *Mus caroli* (Rodentia: Muridae) populations from Okinawajima and Taiwan. *Zoological Studies* **42**(2): 258-267. We performed univariate, bivariate, and multivariate analyses of 4 external and 17 cranial morphometric characters in the Ryukyu mouse, *Mus caroli* Bonhote, 1902 (Mammalia: Rodentia: Muridae), using 177 specimens collected from Okinawajima in the central Ryukyus and from Taiwan. There were clear morphological differences between populations from Okinawajima and Taiwan. The univariate and bivariate analyses indicated that the Okinawajima population differs from the Taiwan population by a shorter tail, smaller ear and auditory bulla, less robust incisors, larger molar row, narrower cranium in the orbital region, and longer postpalatal region. Principal component and canonical discriminant analyses based on cranial variables also suggested morphological divergence between the 2 populations. http://www.sinica.edu.tw/zool/zoolstud/42.2/258.pdf

Key words: *Mus caroli*, *M. formosanus*, Taxonomy, Morphometric analyses, Allometry.

The Ryukyu mouse, *Mus caroli*, is distributed in the Ryukyu Archipelago (Japan), Taiwan, Hainan, and southern China to the Malay Peninsula, and on Sumatra, Java, and Flores (Corbet and Hill 1992). Bonhote (1902) originally described this species as *M. caroli* based on specimens obtained from Okinawajima, in the central Ryukyus of Japan.

Subsequently, Kuroda (1925) described a new species, *M. formosanus*, based on 1 male specimen collected from Taihoku (= Taipei) in Taiwan. The type material of *M. formosanus* was destroyed during World War II (Marshall 1977a). Tokuda (1941) first considered *M. formosanus* a junior synonym of *M. caroli*, mainly based on the proodont upper incisors. In a revision of the Asian species of *Mus*, Marshall (1977a) regarded *M. formosanus* as a junior synonym of *M. caroli caroli*, and many authors have followed this view, including Corbet and Hill (1992) and Musser and Carleton (1993), although some authors still recognize it as a valid species (e.g., Lin and Lin 1983).

Another name included in *M. caroli* is *M. ouwensi*, described from Java by Kloss (1921). Marshall (1977a b) considered *M. ouwensi* to be a subspecies of *M. caroli*, and this view was followed by Corbet and Hill (1992) and Musser and Carleton (1993).

Kuroda (1930) described *M. caroli boninensis* from the Bonin (= Ogasawara) Islands of Japan. However, Tokuda (1941) considered this name is a junior synonym of *M. musculus*. Recent genetic and morphological studies have revealed that mice from the Ogasawara Islands belong to the *M. musculus*–*M. domesticus* lineage, and not to the *M. caroli* lineage (Bonhomme et al. 1989, Takada et al. 1994).

Two species of the genus *Mus* are distributed in the Ryukyu Archipelago: *M. caroli* and *M. musculus* (Kaneko 1994). Motokawa (1995) discussed the identification and distribution of these 2 mouse

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species in the Ryukyus. *Mus musculus* is distributed throughout most of the Ryukyus, whereas *M. caroli* is restricted to Okinawajima, in the central Ryukyus, where it is sympatric with *M. musculus* (Motokawa 1995). On Okinawajima, *M. caroli* is distributed in lowland areas altered by humans, such as grasslands and sugar cane fields (Motokawa 1995). Although similar environments are very common throughout the Ryukyus, where we have conducted intensive trapping of small mammals, *M. caroli* has not been recorded from any other island in the Ryukyus (Motokawa 1995, unpubl. data).

The central Ryukyus, including Okinawajima, are thought to have been isolated from the continental mainland, Taiwan, and the rest of the Ryukyus until the Pliocene, and the mammalian fauna of the central Ryukyus is characterized by a high level of endemism (Ota 1998, Motokawa 2000). Most terrestrial non-volant mammalian species in the central Ryukyus are endemic species that are well differentiated from related taxa and are considered endemic elements of the Miocene, except for some introduced species: the house mouse, *M. musculus*; black rat, *Rattus tanezumi*; house rat, *R. norvegicus*; musk shrew, *Suncus murinus*; and wild boar, *Sus scrofa* (Motokawa 2000).

Motokawa (2000) suspected that the Okinawajima population of *M. caroli* is also an introduced population, since its distribution in the central Ryukyus is disjunct from the remaining range of this species (see Corbet and Hill 1992), and because it is restricted to Okinawajima (Motokawa 2000). Moreover, *M. caroli* is suggested to have the potential to expand its range with human activities, because populations of *M. caroli* in the Malay Peninsula south to the Isthmus of Kra and on Southeast Asian islands are thought to have been introduced inadvertently (Musser and Newcomb 1983, Musser and Carleton 1993).

Marshall (1977a) recognized 5 geographic groups of *M. caroli* based on differences in color pattern. 1) The Okinawajima and Taiwan populations and a Fukien (Fujian Province, China) specimen were classified into the same group, which has a different color pattern from the other 4 groups: the populations of 2) Hainan Island and Yunnan Province of China, and Vietnam; 3) northern and northeastern Thailand; 4) central and southeastern Thailand; and 5) Java. Of the 5 geographic groups, Marshall (1977a) assigned the populations of Okinawajima, Taiwan, and Fujian to the subspecies, *M. caroli caroli*, those of Java to *M. caroli ouwensi*, but did not comment on the subspecific status of the remaining 3 geographic groups. These groupings suggest that the Okinawajima population is closely related to the populations in Taiwan and Fujian, and has its origin in these populations.

In this study, we compared external and cranial morphometric characters between populations from Okinawajima and Taiwan. Since mice show overall size variation related to age (Corbet and Hill 1992), ontogenetic variation must be considered. We used analysis of covariance (ANCOVA) in order to circumvent ontogenetic variation and to analyze allometric growth. In addition, principal component and canonical discriminant analyses were carried out to assess the overall differentiation between populations.

MATERIALS AND METHODS

In total, 177 specimens of *Mus caroli* collected from Okinawajima and Taiwan were examined (Table 1; Fig. 1). Specimens from Taiwan were collected from widely scattered localities (counties and/or cities of Taipei, Taichung, Changhua, Tainan, Pingtung, Taitung, and Hualien) to represent the island-wide population. They are deposited in the Zoological Collections of the Kyoto University Museum, Kyoto, Japan (KUZ) and the National Museum of Natural Science, Taichung, Taiwan (NMNS) as follows: Okinawajima KUZ-M 1, 4-6, 9, 11, 12, 18-20, 24, 34, 36, 38, 39, 342-346, 356, 358, 359, 361-366, 375, 376, 388-395, 397-399, 426-439, 450-452, 1200-1210, 1474-1491, and 1493-1502; Taiwan NMNS 136, 185, 187, 191, 196, 268, 274, 282, 284, 291, 314, 364, 370, 422, 425, 456, 741, 1024, 1028, 1053, 1057, 1062, 1064, 1068, 1069, 1072, 1103, 1105, 1110, 1112, 1116, 1124, 1130, 1372, 1928, 1929, 1932, 1957, 1985, 2269, 2277, 2280, 2285, 2286, 2359, 2360, 2365, 2392, 2410, 2441, 2444, 2992, 2994, 2996, 2998-3002, 3015-3023, 3025-3028, 3030, 3033, and KUZ-M 1136.

Since both *M. caroli* and *M. musculus* are distributed in similar habitats in Okinawajima and Taiwan (Aoki and Tanaka 1941, Tokuda 1941, Kaneko 1994, Motokawa 1995), species were carefully identified using morphological features. All of the specimens used in this study were identified as *M. caroli*, with a tail as long as the head and body length, a short nasal, proodont upper incisors, and a narrow zygomatic plate with an S-shaped anterior border. All of these character states differ from those of *M. musculus*, as given by Marshall (1977a b). Specimens were collected using various mouse traps, and all were considered to be individuals after weaning.

The following standard external measurements (in mm) taken by the collector of the specimen were recorded from attached labels or from the museum specimen database: tail length (T), head and body length (HB) by subtracting T from total length, hind foot length exclusive of claws (HF), and ear length (E). Seventeen cranial measurements (in mm) were used in this study: condylobasal length (CBL) from the occipital condyles to the anterior edge of the incisor, length of the nasals (LN), length of the diastema (LD), length of the incisive foramen (LIF), length of the bony palate (LBP), postpalatal length (PPL), length of the auditory bulla (LAB), breadth of the rostrum (BR), breadth of the zygomatic plate (BZP), breadth across the 1st upper molars (BM1s), least interorbital breadth (IOB), greatest zygomatic breadth (ZB), breadth of the braincase (BBC), breadth across the occipital condyles (BOC), height of the braincase (HBC), alveolar length of the maxillary toothrow (ALM), and coronal width of the 1st upper molar (WM1). All variables followed Carleton and Straeten (1997), except for CBL, which was substituted for occipitonasal length to maintain the sample size, because the anterior nasal tip was often broken; and HBC, an additional variable. All measurements were made by MM to the nearest 0.01 mm using digital calipers. The age of all specimens was determined from the pattern of tooth wears on the occlusal surface under a microscope. Specimens were classified into 6 age classes, age classes 1-6, from younger to older individuals following the method used by Chou et al. (1998) for the house mouse, *M. musculus*.

All variables were log-transformed before the bivariate and multivariate analyses. Univariate and bivariate analyses were conducted on a personal computer using programs provided by T. Hikida of Kyoto University. Multivariate analyses were conducted using SAS vers. 6 (SAS Inst. 1990). We selected 1% as the limit of significance to exclude the possibility that sampling bias affected the results. Differences between sexes were tested with multivariate analysis of covariance (MANCOVA) with HB for external variables and CBL for cranial variables as covariates using the GLM procedure of SAS. The MANCOVA revealed no significant differences between sexes in external (Wilk's lambda 0.969, $F = 0.76$, $p = 0.520$ in the Okinawajima sample; Wilk's lambda 0.960, $F = 0.90$, $p = 0.447$ in the Taiwan sample) or cranial (Wilk's lambda 0.615, $F = 1.72$, $p = 0.077$ in the Okinawajima sample; Wilk's lambda 0.614, $F =$

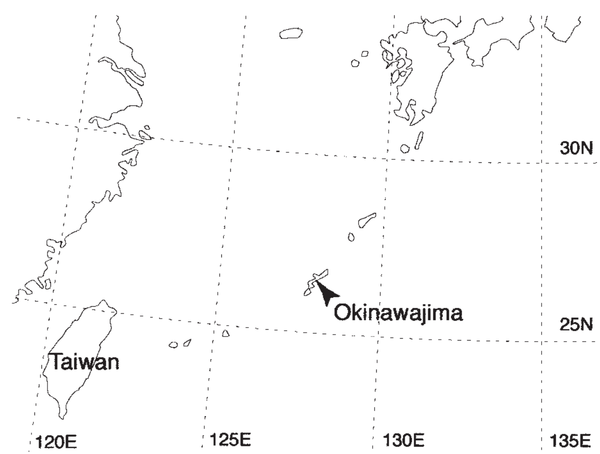

Fig. 1. Map of East Asia showing Okinawajima and Taiwan, where *Mus caroli* specimens were collected.

Table 1. Sample size and CBL (mean ± SD, in mm) for each age class of *Mus caroli* from Okinawajima and Taiwan. The CBL for samples from Okinawajima and Taiwan was compared using Student's *t*-test

Age	Okinawajima			Taiwan			Difference[a]
class	♂	♀	CBL	♂	♀	CBL	
1	4	4	18.79 ± 1.22	1	0	19.99	—
2	13	12	19.58 ± 0.83	3	2	19.64 ± 1.18	ns
3	13	17	19.97 ± 0.93	18	12	19.99 ± 0.81	ns
4	11	7	20.51 ± 0.69	6	9	20.98 ± 0.80	ns
5	7	4	20.53 ± 0.52	14	10	21.09 ± 0.66	ns
6	2	3	21.24 ± 0.52	3	1	21.74 ± 0.61	ns
Total	50	48		45	34		

[a]ns, not significant ($p > 0.01$).

1.73, $p = 0.076$ in the Taiwan sample) variables. Therefore, we combined specimens of both sexes in subsequent analyses.

The mean CBL in each age class was tested using Student's *t*-test to determine the overall size differences between the samples from Okinawajima and Taiwan. External and cranial variables were compared between samples in the analysis of covariance (ANCOVA) covaried with HB and CBL, respectively. The variables, which had no significant correlation with HB or CBL in either sample, were tested using Student's *t*-test in a univariate analysis, because these variables are thought to be unaffected by overall size growth. In the ANCOVA, when slopes of the regression line of the variable differed between samples, the pattern of geographic variation was determined by examining a 2-dimensional plot of that variable and HB or CBL. When the slopes of the regression line of the variable did not differ significantly between samples, the adjusted means calculated using the common slope and common log-transformed mean of HB or CBL were compared.

To assess the pattern of geographic variation, principal component analysis (PCA) based on the correlation matrix of log-transformed cranial variables was carried out with the PRINCOMP procedure of SAS. Specimens with missing values due to partial breaks in the relevant portions were excluded from the PCA; consequently there were complete sets of variables for 62 specimens from Okinawajima and 62 from Taiwan. Canonical discriminant analysis (CDA) based on log-transformed cranial variables was conducted with the CANDISC procedure of SAS to examine discrimination between samples. External variables were not used for the PCA or CDA, because they might have included the effects of minor methodological differences among observers.

RESULTS

The age composition of the samples is summarized in table 1 with CBL values calculated by combining the sexes. Both samples involve all age classes, and the sampling bias between localities was thought to be small. Student's *t*-test revealed no differences between the samples from Okinawajima and Taiwan in all age classes, except for age class 1, which could not be compared statistically due to the small size of the Taiwan sample. The sample size, mean, SD, and minimum and maximum values of the external and cranial variables (all age classes combined) of the samples from Okinawajima and Taiwan are summarized in table 2.

Of the external variables, T was correlated with HB in both samples. According to the ANCOVA, the slopes differed between samples: $\log(T) = 0.583 \times \log(HB) + 0.796$ in the Okinawajima sample ($n = 78$), and $\log(T) = 0.289 \times \log(HB) + 1.372$ in the Taiwan sample ($n = 75$). Two-dimensional plots of HB and T are shown in figure 2a. The Taiwan sample had a larger relative value of T compared to HB than did the Okinawajima sample, but with some overlap. The difference between samples decreased with increasing HB. HF was significantly correlated with HB in the Okinawajima sample only. In the ANCOVA, the slopes did not differ, and a significant difference in the adjusted mean HB (1.231 in the Okinawajima sample and 1.240 in the Taiwan sample; $p < 0.01$) was detected between samples (Fig. 2b). E was correlated with HB. In the ANCOVA, the slopes did not differ, and a significant difference in the adjusted mean

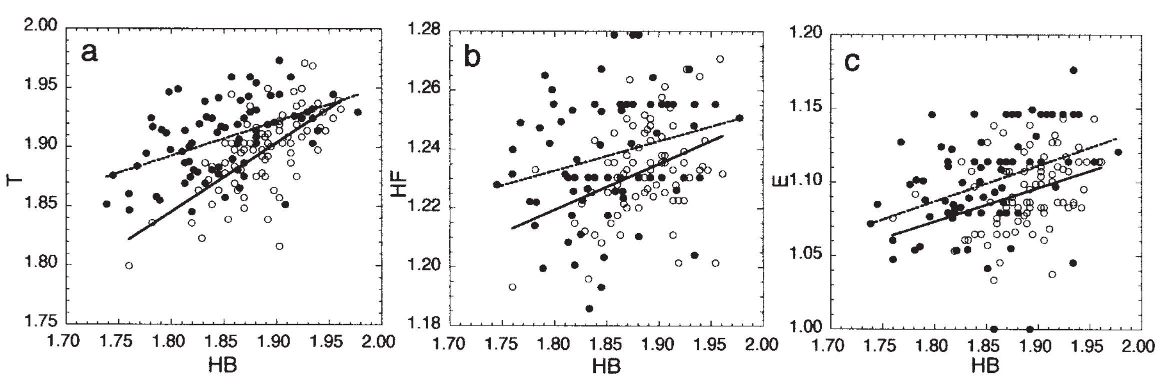

Fig. 2. Plots of head and body length (HB) against tail length (T; a), hind foot length (HF; b), and ear length (E; c) of *Mus caroli* from Okinawajima and Taiwan. Both variables (mm) were log-transformed. Open and closed circles represent samples from Okinawajima and Taiwan, respectively. Solid and broken lines are regression lines for samples from Okinawajima and Taiwan, respectively.

HB (1.089 in the Okinawajima sample and 1.104 in the Taiwan sample; $p < 0.01$) was detected between samples (Fig. 2c).

The cranial variables were compared between samples using ANCOVA with CBL as the covariate (Table 3). Of the 16 variables examined, fourteen were significantly correlated with CBL in both or in only 1 population. Of these, only BZP showed a difference in slopes between populations: log (BZP) = 1.631 × log (CBL) - 1.765 in the Okinawajima sample (n = 94) and log (BZP) = 1.073 × log (CBL) - 1.036 in the Taiwan sample (n = 79), whereas the remaining variables showed no slope differences and were compared using the adjusted means. Two-dimensional plots of BZP against CBL are shown in figure 3. Although the slopes differ, the plots largely overlap between populations.

Of the 13 variables with no slope differences, six showed significant differences in the adjusted means between samples (Table 3; Fig. 4). LIF, LAB, BR, IOB, and ZB had significantly larger adjusted means in the Taiwan sample compared to the Okinawajima sample (Fig. 4a, c-f). By contrast, PPL was larger in the Okinawajima sample than in the Taiwan sample (Fig. 4b). ALM and WM1 were not correlated with CBL, and were tested by a univariate analysis using Student's t-test between samples (Table 2). ALM and WM1 were

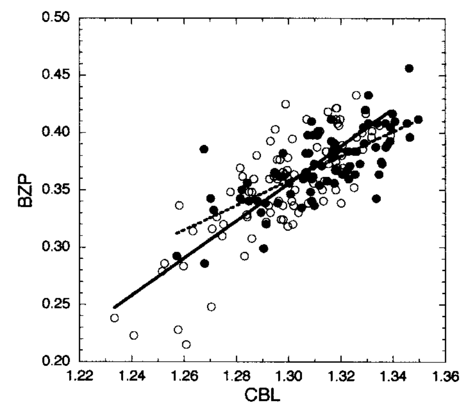

Fig. 3. Plots of condylobasal length (CBL) against breadth of the zygomatic plate (BZP) of *Mus caroli* from Okinawajima and Taiwan. Both variables (mm) were log-transformed. The symbols are the same as those in figure 2.

Table 2. External and cranial measurements (mm) of *Mus caroli* from Okinawajima and Taiwan

Variable	Okinawajima					Taiwan				
	n	mean	SD	min	max	n	mean	SD	min	max
HB	82	77.67	6.67	57.50	91.50	76	71.30	8.55	54.77	95.00
T	78	78.97	6.16	63.00	93.50	75	80.94	5.73	70.00	94.00
HF	97	17.05	0.73	14.65	18.65	73	17.31	0.82	15.34	19.00
E	98	12.28	0.83	9.90	14.00	75	12.60	0.98	10.00	15.00
BW	96	11.22	2.63	5.20	16.80	75	12.93	3.14	8.10	23.00
ONL	76	20.69	0.91	17.77	22.53	70	20.91	0.79	18.99	23.02
CBL	96	20.01	1.00	17.12	21.83	79	20.58	0.97	18.08	22.37
LN	77	7.47	0.56	5.95	8.76	70	7.64	0.49	6.82	9.03
LD	98	5.93	0.45	4.70	6.88	78	6.23	0.46	5.08	7.38
LIF	98	4.30	0.31	3.13	5.02	79	4.61	0.30	4.04	5.36
LBP	92	3.63	0.24	3.11	4.33	79	3.70	0.25	2.93	4.43
PPL	89	7.58	0.46	6.31	8.43	79	7.63	0.46	6.33	8.54
LAB	97	3.78	0.31	3.00	4.53	78	4.15	0.26	3.43	4.69
BR	98	3.59	0.20	3.08	4.09	78	3.87	0.22	3.39	4.48
BZP	96	2.28	0.23	1.64	2.71	79	2.36	0.17	1.93	2.86
BM1s	97	4.46	0.14	4.11	4.90	79	4.53	0.16	4.11	5.02
IOB	98	3.77	0.11	3.42	4.08	79	3.89	0.12	3.63	4.15
ZB	89	10.65	0.48	9.23	11.47	74	11.03	0.48	9.92	12.04
BBC	98	9.43	0.22	8.78	9.96	79	9.45	0.28	8.87	10.03
BOC	91	5.28	0.17	4.88	5.61	79	5.35	0.20	4.92	5.88
HBC	96	6.82	0.24	6.10	7.48	79	6.97	0.29	6.40	7.78
ALM	98	3.54	0.16	3.16	4.02	79	3.41	0.16	3.04	3.83
WM1	98	1.19	0.07	1.00	1.36	78	1.20	0.08	0.98	1.43

The sample size (n), mean, SD, and minimum (min) and maximum (max) values are given. See text for abbreviations of variables.

larger in the sample from Okinawajima than in that from Taiwan.

In the PCA, the first 3 principal component axes explained 47.8%, 8.5%, and 7.2% of the total variation, respectively (Table 4). The eigenvectors of the PCA for each variable are listed in table 4. In the 1st axis, all variables showed a positive loading. In the 2nd axis, WM1, ALM, and BBC had relatively large positive loadings. In the 3rd axis, ALM (positive) and LAB (negative) had relatively large loadings. Individual scores for the 1st and 2nd (PC1 and PC2) and for the 2nd and 3rd (PC2 and PC3) principal component variables are plotted in figure 5. In the plots of PC1 and PC2, the Taiwan sample largely overlapped the Okinawajima sample, although the mean PC1 and

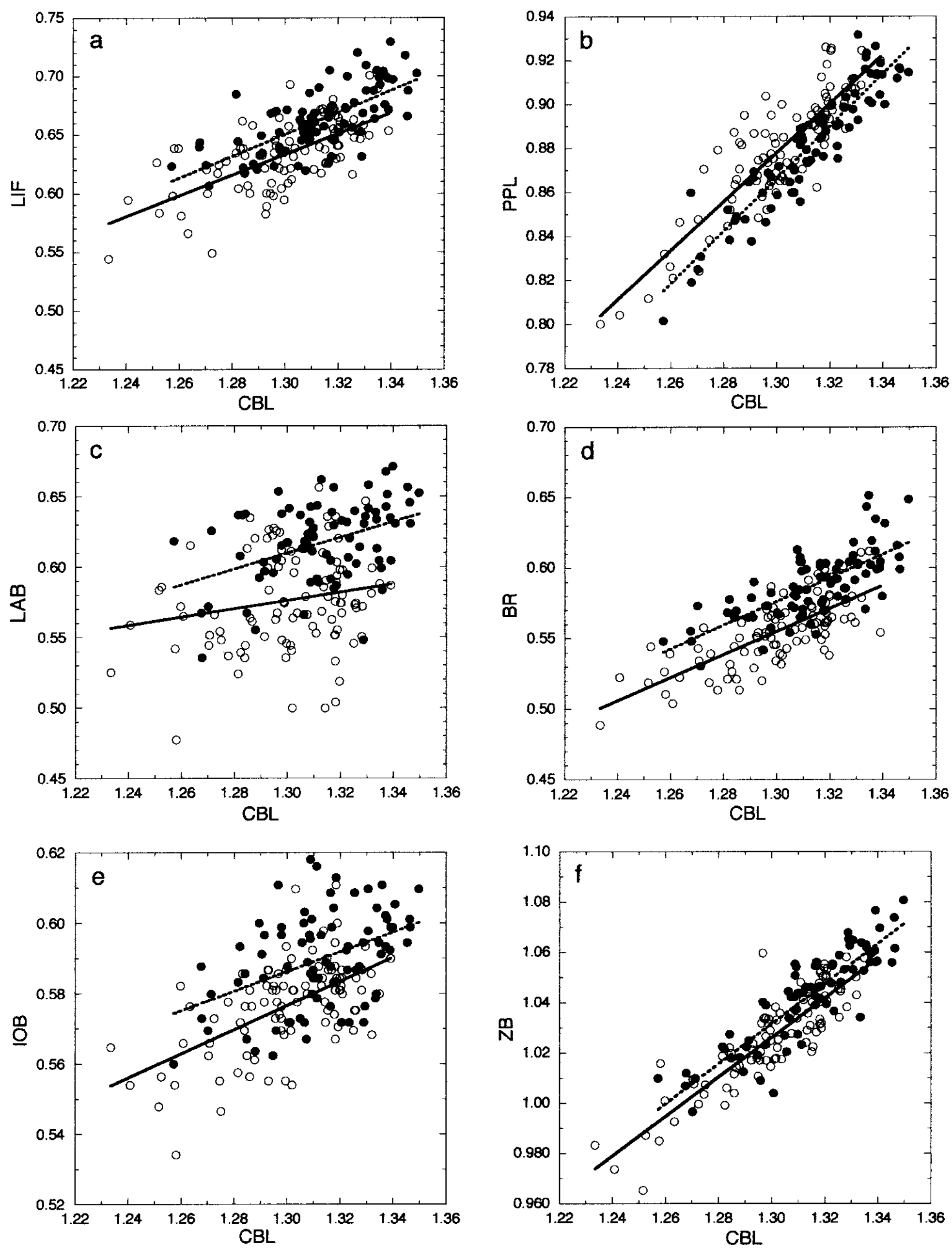

Fig. 4. Plots of condylobasal length (CBL) against the length of the incisive foramen (LIF; a), postpalatal length (PPL; b), length of the auditory bulla (LAB; c), breadth of the rostrum (BR; d), least interorbital breadth (IOB; e), and greatest zygomatic breadth (ZB; f) of *Mus caroli* from Okinawajima and Taiwan. Both variables (mm) were log-transformed. The symbols are the same as those in figure 2.

PC2 scores of the Taiwan sample were larger and smaller, respectively, than the Okinawajima samples ($p < 0.01$, Student's *t*-test). In plots of PC2 and PC3, the Okinawajima sample was characterized by larger PC3 values than the Taiwan sample with some overlap ($p < 0.01$, Student's *t*-test).

Table 3. Results of the analysis of covariance (ANCOVA) with CBL as the covariate performed on cranial variables of *Mus caroli* from Okinawajima and Taiwan

Variable	Okinawajima (O)		Taiwan (T)		Difference[a]
	n	Mean	*n*	Mean	
LN	75	0.876	70	0.877	ns
LD	96	0.779	78	0.785	ns
LIF	96	0.639	79	0.656	T > O
LBP	90	0.563	79	0.563	ns
PPL	89	0.885	79	0.874	O > T
LAB	96	0.578	78	0.614	T > O
BR	96	0.560	78	0.581	T > O
BM1s	95	0.652	79	0.653	ns
IOB	96	0.579	79	0.588	T > O
ZB	88	1.031	74	1.037	T > O
BBC	96	0.976	79	0.973	ns
BOC	91	0.724	79	0.726	ns
HBC	96	0.835	79	0.841	ns

[a]ns, not significant ($p > 0.01$).
Only the variables with significant correlations with CBL in both or individual samples and non-significant differences in the slopes between samples are shown with sample sizes (*n*) and adjusted means (mm, log-transformed). See text for abbreviations of variables.

Table 4. Eigenvectors of the first 3 principal component (PC) scores and the 1st standardized canonical coefficients (CAN1) based on 17 cranial variables in *Mus caroli* from Okinawajima and Taiwan

Variable	PC1	PC2	PC3	CAN1
CBL	0.332	-0.089	0.150	-0.377
LN	0.274	-0.135	0.215	-0.354
LD	0.293	-0.238	0.071	0.359
LIF	0.261	-0.084	-0.101	0.929
LBP	0.170	0.063	0.353	-0.019
PPL	0.292	-0.086	0.253	-1.292
LAB	0.165	0.023	-0.441	0.673
BR	0.286	-0.184	-0.044	0.808
BZP	0.284	-0.088	0.080	0.349
BM1s	0.257	0.079	-0.099	0.020
IOB	0.226	0.010	-0.320	0.135
ZB	0.329	-0.019	-0.001	0.413
BBC	0.219	0.416	0.046	-0.490
BOC	0.190	0.277	-0.128	0.208
HBC	0.204	0.179	-0.280	0.230
ALM	0.023	0.528	0.507	-0.487
WM1	0.070	0.539	-0.243	-0.096
Eigenvalue	8.118	1.452	1.221	
Difference	6.666	0.231	0.254	
Proportion	0.478	0.085	0.072	
Cumulative proportion	0.478	0.563	0.635	

See text for abbreviations of variables.

The CDA of the specimens from Okinawajima and Taiwan revealed significant variation (Wilk's lambda 0.240, F = 19.77, p < 0.01). Most of the specimens from the Okinawajima sample had negative 1st canonical variables (CAN1), whereas those from the Taiwan sample had positive ones. Only 3 Okinawajima specimens had positive CAN1 values, and only 1 Taiwan specimen had a negative one. Therefore, samples from Okinawajima and Taiwan were well discriminated using CAN1 in most specimens (96.8%, 59 of 62 specimens in the Okinawajima sample and 61 of 62 in the Taiwan sample). The standardized canonical coefficients of CAN1 are given in table 4. PPL and LIF made large negative and positive contributions, respectively, to CAN1.

DISCUSSION

Our results indicate that the morphometric characters of *Mus caroli* from the Okinawajima and Taiwan populations differ. These differences are characterized mainly by differences in external factors and relative cranial values (shape factor) rather than in overall size differences.

The tail length ratios to head and body length and hind foot length have been used as the most important characters in mouse systematics (Marshall 1977a b). In this study, the relative lengths of the tail and hind foot differed between the Okinawajima and Taiwan populations, being shorter in the former. This probably characterizes both populations, although one must be careful because many different collectors were involved, which might have resulted in interobserver measurement errors.

The relative values of the cranial variables LIF, LAB, BR, IOB, and ZB were greater in the Taiwan population than in the Okinawajima population. BR was taken at the root of the incisors and may have been affected by the robustness of the incisors, while LIF is an indicator of incisor length. Therefore, the greater values of BR and LIF suggest more-developed incisors in the Taiwan population compared with the Okinawajima population. Since both IOB and ZB reflect the width of the orbital region, the Taiwan population may have a broader cranium. The larger LAB in the Taiwan population may be related to a larger ear (E), which differed between the populations relative to HB. In contrast, the Okinawajima population had a larger relative PPL, which may have been affected by elongation of the braincase. ALM and WM1 showed no correlation with CBL, and were larger in the Okinawajima population than in the Taiwan population. Cranial growth in mice is not thought to affect molar size; consequently, the absolute value of molar size is often used in mouse systematics (Corbet and Hill 1992).

The PCA also showed shape factor differences between the 2 populations, as expressed in PC2 and PC3, as well as by a slight difference in overall size, as expressed in PC1. The CDA suggests that the Okinawajima and Taiwan populations can be discriminated using cranial variables

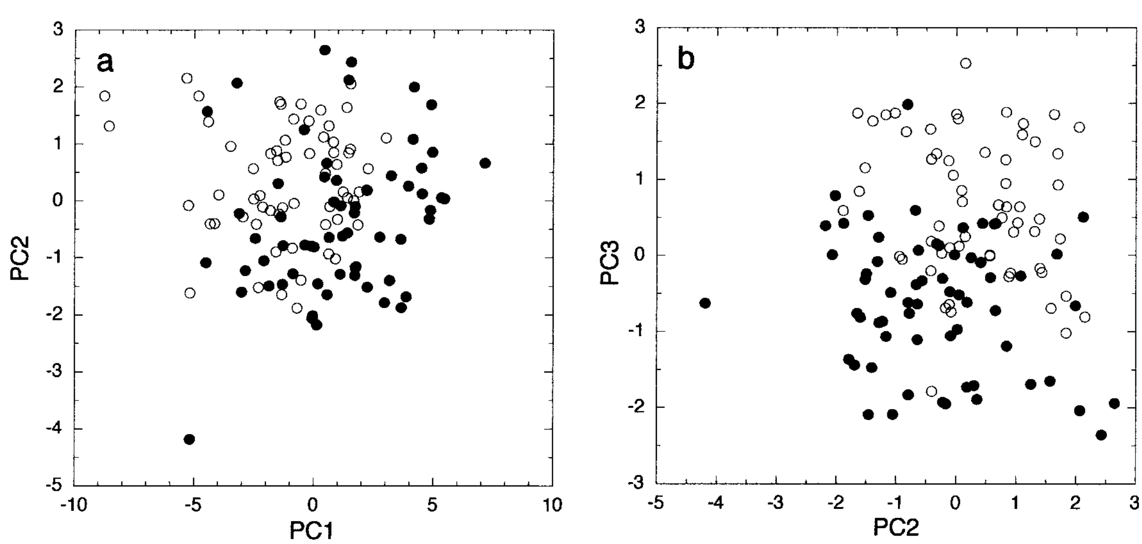

Fig. 5. Plots of the 1st against the 2nd (a), and the 2nd against the 3rd (b) principal component (PC) scores for the 17 cranial morphometric variables in *Mus caroli* from Okinawajima and Taiwan. The symbols are the same as those in figure 2.

with an error of less than 5%. Our univariate, bivariate, and multivariate analyses strongly suggest morphological divergence between the *M. caroli* populations from Okinawajima and Taiwan.

Marshall (1977a) classified the Okinawajima and Taiwan populations into the same geographic group and subspecies. Since the Okinawajima population is thought to have originated from the Taiwan or Fujian populations via human introduction, these morphological differences have occurred within a relatively short time. Okinawajima is located about 700 km northeast of Taiwan. It has been suggested that the tail, hind foot, and ear become larger at higher temperatures (Arai and Shiraishi 1978); therefore, the larger T, HF, and E of the Taiwan population compared to those of Okinawajima may be due to climatic differences. Cranial changes, however, are thought to have no relationship to climatic changes, and probably resulted from morphological changes in the Okinawajima population. It is likely that the initial population introduced to Okinawajima was small, and the rapid genetic changes and subsequent morphological changes occurred as a result of the founder effect.

The human introduction of *M. caroli* onto Okinawajima probably resulted from transporting animals from Taiwan or Fujian. The immigration of *M. caroli* to the other Ryukyu Islands from Taiwan, Fujian, or Okinawajima is also possible, and may have actually occurred. Nevertheless, the occurrence of *M. caroli* in the Ryukyus is restricted to Okinawajima. We postulate that *M. caroli* cannot maintain populations on the islands north of Okinawajima due to the much colder climate, or on the islands south of and around Okinawajima due to their small areas. Evidence that this species is known only from the continental mainland and larger islands in its natural and introduced range (Corbet and Hill 1992) indirectly supports the latter interpretation.

This pattern greatly differs from that of *M. musculus*, which has successfully colonized many islands via human introduction (e.g., Moriwaki et al. 1994), and is distributed on most of the small islands in the Ryukyus (Motokawa 1995). This difference in the ability to colonize small islands between *M. caroli* and *M. musculus* may be attributable to differences in habits: *M. caroli* lives outside human residences, while *M. musculus* lives inside and near human residences and has a much stronger relationship with humans. In Okinawajima and Taiwan, these 2 species seem to show habitat segregation (Aoki and Tanaka 1941, Motokawa 1995, Chou et al. 1998), which suggests strong ecological competition between them. On small islands, the coexistence of *M. musculus* and *M. caroli* is probably impossible and only *M. musculus*, which can be regarded as the best colonizer in mice, likely survives.

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REFERENCES

Aoki B, R Tanaka. 1941. The rats and mice of Formosa illustrated. Mem. Fac. Sci. Agric. Taihoku Imp. Univ. **23:** 121-191.

Arai S, S Shiraishi. 1978. Growth and development of the Charles' mouse, *Mus caroli caroli* Bonhote. Zool. Mag. **87:** 274-282. (in Japanese with English abstract)

Bonhomme F, N Miyashita, P Boursot, J Catalan, K Moriwaki. 1989. Genetic variation and polyphyletic origin in Japanese *Mus musculus*. Heredity **63:** 299-308.

Bonhote JL. 1902. On some mammals obtained by the Hon N. Charles Rothschild, from Okinawa, Liu-Kiu Islands. Nov. Zool. **9:** 626-628.

Carleton MD, EV der Straeten. 1997. Morphological differentiation among Subsaharan and North African populations of the *Lemniscomys barbarus* complex (Rodentia: Muridae). Proc. Biol. Soc. Wash. **110:** 640-680.

Chou CW, PF Lee, KH Lu, HT Yu. 1998. A population study of house mice (*Mus musculus castaneus*) inhabiting rice granaries in Taiwan. Zool. Stud. **37:** 201-212.

Corbet GB, JE Hill. 1992. The mammals of the Indomalayan region. New York: Oxford Univ. Press.

Kaneko Y. 1994. Family Muridae. *In* Japan Wildlife Research Center, ed. A pictorial guide to the mammals of Japan. Tokyo: Tokai Univ. Press, pp. 90-109, 168-183. (in Japanese)

Kloss CB. 1921. Some rats and mice of the Malay Archipelago. Treubia **2:** 115-124.

Kuroda N. 1925. Description of a new species of the genus *Mus* from Formosa. Zool. Mag. (Tokyo) **37:** 1-16.

Kuroda N. 1930. The geographical distribution of mammals in the Bonin Islands. Bull. Biogeogr. Soc. Jpn. **1:** 81-88. (in Japanese with English abstract)

Lin JY, LK Lin. 1983. A note on the zoogeography of the mammals in Taiwan. Ann. Taiwan Mus. **26:** 53-62. (in Chinese with English abstract)

Marshall JT Jr. 1977a. A synopsis of Asian species of *Mus* (Rodentia, Muridae). Bull. Am. Mus. Nat. Hist. **158:** 173-220.

Marshall JT Jr. 1977b. Family Muridae: rats and mice. *In* B Lekagul, JA McNeely, eds. Mammals of Thailand. Bangkok: Association for the Conservation of Wildlife, pp. 397-487.

Moriwaki K, T Shiroishi, H Yonekawa, eds. 1994. Genetics in wild mice. Tokyo: Japan Scientific Societies Press.

Motokawa M. 1995. External measurements and ecological distribution of mice of the genus *Mus* in Amami Islands and Okinawajima Island. Chirimosu **6:** 10-14. (in Japanese)

Motokawa M. 2000. Biogeography of living mammals in the Ryukyu Islands. Tropics **10:** 63-71.

Musser GG, C Newcomb. 1983. Malaysian murids and the giant rat of Sumatra. Bull. Am. Mus. Nat. Hist. **174:** 327-598.

Musser GG, MD Carleton. 1993. Family Muridae. *In* DE Wilson, DM Reeder, eds. Mammal species of the world. 2nd ed. Washington, DC: Smithsonian Institution Press, pp. 501-755.

Ota H. 1998. Geographic patterns of endemism and speciation in amphibians and reptiles of the Ryukyu Archipelago, Japan, with special reference to their paleogeographical implications. Res. Popul. Ecol. **40:** 189-204.

SAS Inst. 1990. SAS/STAT user's guide. Ver. 6. Cary, NC: SAS Institute.

Takada Y, H Yamada, T Tateishi. 1994. Morphometric variation of Japanese wild mice on islands. J. Mamm. Soc. Jpn. **19:** 113-128.

Tokuda M. 1941. A revised monograph of the Japanese and Manchou-Korean Muridae. Trans. Biogeogr. Soc. Japan **4:** 1-155.