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GEOGRAPHIC VARIATION IN CRANIAL FEATURES OF THE POLYNESIAN RAT *RATTUS EXULANS* (PEALE, 1848) (MAMMALIA: RODENTIA: MURIDAE)

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ABSTRACT. **–** Geographic variation in skulls of the Polynesian rat, *Rattus exulans* (Peale, 1848) (Mammalia: Rodentia: Muridae) was examined based on 18 morphometric characters of 374 specimens collected from the Southeast and East Asia including the continent north of the Isthmus of Kra, the Malay Peninsula, Borneo, Sumatera, Jawa, Philippines, Sulawesi, Flores, Maluku, Taiwan, Ryukyus, New Guinea, and the Pacific Islands. The geographic variations among rats from the Southeast Asian islands were small and samples were similar to each other. The rats from New Guinea were similar to those from the Southeast Asian islands. The rats from the continent and the Malay Peninsula slightly differed from those from the Southeast Asian islands. The rats from the Pacific Islands were different from the rest. The rats from East Asia resembled those from the continent and the Malay Peninsula, but were characterised by the smaller molar size. The origin of the species was suggested to be on the continent north of the Isthmus of Kra. The dispersal may have occurred in association with prehistoric human activity, particularly the populations in New Guinea and the Pacific Islands. No subspecies were recognised regardless of the existence of the geographic differentiation, because *R. exulans* could be regarded a semi-domesticated animal.

KEY WORDS. **–** Taxonomy, morphometrics, *Rattus exulans*, *R. concolor*.

INTRODUCTION

The Polynesian rat *Rattus exulans* (Peale, 1848) is the smallest rat species of the genus *Rattus*, and was originally described from Tahiti, Society Islands (Tate, 1935; Taylor & Horner, 1973; Corbet & Hill, 1992; Musser & Carleton, 1993). This species is widely distributed in Southeast Asia including eastern Bangladesh, Myanmar (=Burma), Thailand, Laos, Cambodia, Vietnam, the Malay Peninsula, Christmas Island, Sumatera (=Sumatra), Jawa (=Java), Borneo, the Philippines, Sulawesi, the Lesser Sunda Islands, the Maluku (=the Moluccas); in New Guinea; on the majority of the tropical and subtropical Pacific Islands including New Zealand; and in East Asia including Taiwan and Miyakojima Island in the Ryukyus (Fig. 1; Corbet & Hill, 1992; Musser & Carleton, 1993; Motokawa et al., 2001). *Rattus exulans* occurs in houses, granaries, cultivated lands, gardens, plantations, scrub areas, second-growth forest, and forest edges (Musser & Newcomb, 1983; Corbet & Hill, 1992; Motokawa et al., 2001). These habits are maintained and disturbed by humans, thus *R. exulans* have been considered always associated with the human habitation (Chasen, 1940; Harrison, 1951, 1957, 1966, 1973; Davis, 1962; Medway, 1965, 1969; Taylor & Horner, 1973; Taylor et al., 1982; Musser & Newcomb, 1983; Payne et al., 1985; Rickart et al., 1993; Flannery, 1995a; Heaney et al., 1998, 1999). From its association with humans, *R. exulans* has been regarded as a commensal species. Most parts of its wide distribution range are thought to have been gained as a result of the transportation accompanying with the human agency such as ships and canoes (Musser & Newcomb, 1983; Roberts, 1991; Musser & Carleton, 1993; Matisoo-Smith et al., 1998).

The populations of *R. exulans* in the Pacific Islands and New Guinea are thought to have dispersed from somewhere in the Southeast Asian islands in association with the prehistorical human settlement (Taylor et al., 1982; Musser & Newcomb, 1983; Roberts, 1991; Flannery, 1995a; Matisoo-Smith et al., 1998) with the possibility of the intentional transport as a food item (Matisoo-Smith et al., 1998). Human settlements are presumed to have reached New Guinea by 40,000 years BP (=before present), the Solomon Islands by 30,000 years

BP, after 3,500 years BP into the islands of the Remote Oceania and around 1,000 years BP into New Zealand (Roberts, 1991; Matisoo-Smith et al., 1998). The dispersals of *R. exulans* are considered much later than the first human settlement in New Guinea and after 3,500 BP in the Pacific Islands, respectively (Flannery, 1995a, b), although the dispersal routes within the Pacific Islands are still controversial and have been discussed from distributional, morphological and genetic data obtained both from rats and human (Tate, 1935; Carter et al., 1945; Roberts, 1991; Matisoo-Smith et al., 1998; Matisoo-Smith & Allen, 2001). From the fact that *R. exulans* is known only from habitats around humans, most of the Southeast Asian populations have also been considered introduced with humans: the Malay Peninsula, Borneo, Jawa, Philippines, and Sulawesi (Chasen, 1940; Harrison, 1973; Musser, 1977; Musser & Newcomb, 1985; Rickart et al., 1993; Heaney et al., 1998, 1999). Only the populations in the north part of the Isthmus of Kra are suggested to be the original range of this rat (Tate, 1935; Musser & Newcomb, 1983). The human introduction of this species was thought to have occurred inadvertently in Southeast Asia (Musser & Carleton, 1993).

Although the importance of the human introduction in the distribution of *R. exulans* has been stressed, no comprehensive specimen-based study on the geographic variation of this species was carried out till now. In Southeast Asia, Musser & Newcomb (1983) have suggested the morphological features in skin and skull are uniform, but Chasen (1940) and Corbet & Hill (1992) expect them to show the slight geographic differences. Motokawa et al. (2001) recently reported *R. exulans* from Taiwan and an island (=Miyakojima Island) in the Ryukyus and suspected that those populations were recent introductions by human activity. Motokawa et al. (2001) also pointed out that the molar size of the specimens from Taiwan and the Ryukyus may be smaller than those from the Malay Peninsula, Philippines, and the Pacific Islands. If this is the case and if the East Asian populations have morphologically diverged from the conspecific populations, the hypothesis of recent introduction into the East Asian islands would be groundless.

We examined patterns of the geographic variation in skulls of *R. exulans* by using morphometric data. The specimens examined in this study covered the most of the known distributional range of *R. exulans*. We conducted univariate, bivariate, and multivariate analyses to clarify the patterns of the geographic variation among populations. We then tested whether the Southeast Asian populations were uniform in skull characteristics; and whether the East Asian populations had diverged from other conspecific populations. We also discuss the dispersal history and taxonomic implications of *R. exulans*.

MATERIALS AND METHODS

A total of 374 specimens were examined in this study (Appendix). Of them, 364 are deposited in the Natural History Museum, London. Identification was made based on skull characters following the key of Marshall (1977) and Motokawa et al. (2001). We also examined eight specimens from the Malay Peninsula (n=3), Taiwan (n=3) and Miyakojima of the Ryukyu Archipelago (n=2), which were previously reported by Motokawa et al. (2001) and deposited in the National Museum of Natural Science, Taichung and the National Science Museum, Tokyo. We obtained and examined two additional specimens from Taiwan, which are

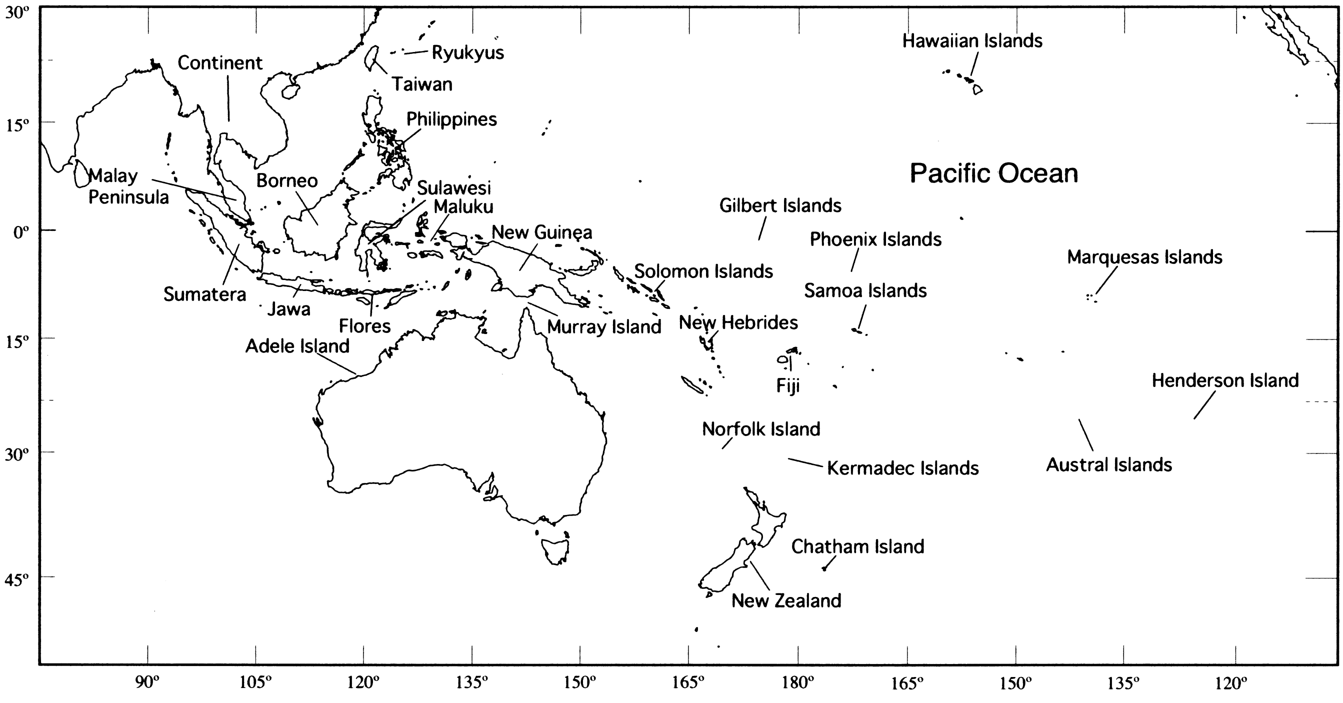

Fig. 1. Map of where *Rattus exulans* specimens were collected: Southeast and East Asia, and the Pacific Islands.

Table 1. Three cranial measurements (mm) of *Rattus exulans* from 13 localities: condylobasal length (CBL), alveolar length of the maxillary toothrow (ALM) and coronal width of the first upper molar (WM1). The upper row includes means±SD, followed by sample size. Ranges are given in the lower row.

Locality	CBL		ALM		WM1	
	Male	Female	Male	Female	Male	Female
Continent	27.40±2.13, 23	27.59±1.01, 13	4.85±0.21, 28	4.80±0.20, 18	1.47±0.06, 28	1.48±0.05, 18
	22.36-29.92	25.52-29.47	4.34-5.19	4.43-5.13	1.34-1.59	1.43-1.58
Malay Peninsula	28.19±1.53, 22	27.92±1.47, 14	5.10±0.30, 26	4.95±0.22, 18	1.52±0.08, 26	1.48±0.07, 18
	24.13-31.43	25.14-30.21	4.44-5.98	4.62-5.26	1.39-1.68	1.36-1.63
Borneo	28.12±1.42, 21	27.37±1.30, 28	5.13±0.23, 21	5.05±0.23, 29	1.54±0.05, 21	1.52±0.08, 29
	23.38-29.82	23.46-29.45	4.86-5.64	4.55-5.50	1.47-1.64	1.34-1.74
Sumatera	25.67, 1	25.42±1.91, 2	5.11±0.14, 3	5.00±0.09, 2	1.56±0.04, 3	1.56±0.08, 2
		24.07-26.77	4.99-5.26	4.93-5.06	1.52-1.59	1.50-1.62
Jawa	29.65±0.85, 16	28.19±1.39, 9	5.32±0.26, 21	5.36±0.22, 10	1.61±0.10, 21	1.63±0.07, 10
	28.05-31.27	26.31-30.22	4.90-6.11	5.08-5.78	1.45-1.86	1.51-1.73
Philippines	29.62±2.22, 7	27.78±1.92, 6	5.25±0.26, 8	5.22±0.14, 7	1.57±0.07, 8	1.58±0.10, 7
	24.97-31.48	25.09-29.62	4.86-5.58	5.00-5.40	1.46-1.66	1.46-1.77
Sulawesi	28.98±1.15, 6	28.15±1.66, 13	5.14±0.22, 7	5.17±0.21, 16	1.53±0.09, 7	1.56±0.07, 17
	27.16-30.46	24.04-29.80	4.78-5.49	4.67-5.48	1.40-1.67	1.40-1.70
Flores	26.90, 1	28.29±0.63, 3	5.10, 1	5.03±0.07, 3	1.41, 1	1.55±0.05, 3
		27.58-28.75		4.96-5.09		1.50-1.60
Maluku	29.08±2.60, 2	28.38±2.82, 2	5.46±0.13, 3	5.37±0.01, 2	1.63±0.09, 3	1.65±0.08, 2
	27.24-30.91	26.38-30.37	5.37-5.60	5.36-5.37	1.55-1.72	1.59-1.71
New Guinea	28.60±1.37, 27	27.67±1.59, 19	5.20±0.17, 30	5.04±0.24, 26	1.56±0.07, 30	1.56±0.08, 27
	23.85-30.69	24.23-29.62	4.88-5.50	4.62-5.47	1.39-1.69	1.46-1.78
Taiwan	29.33±0.38, 4	—	4.80±0.22, 4	4.96, 1	1.43±0.05, 4	1.48, 1
	28.77-29.60		4.52-5.01		1.38-1.47	
Ryukyus	—	26.51, 1	—	4.38±0.14, 2	—	1.43±0.04, 2
				4.28-4.48		1.40-1.45
Pacific Islands	30.93±2.19, 13	29.63±2.28, 17	5.65±0.27, 15	5.46±0.24, 21	1.65±0.08, 15	1.62±0.06, 21
	25.86-34.59	25.43-34.35	5.10-6.04	5.02-5.85	1.45-1.77	1.49-1.70

currently deposited in the National Museum of Natural Science.

We excluded juvenile and very old individuals, those with molars of the incomplete eruption or worn out, respectively, from statistical analysis. We also eliminated specimens lacking data for sex on the label attached to the skull. Consequently, we had 331 specimens for statistical analyses. These specimens, listed in the Appendix, were assigned into 13 locality samples: (1) continent, in the north part of the Isthmus of Kra (from Myanmar [=Burma] and Thailand), (2) the Malay Peninsula, in the south part of the Isthmus of Kra, (3) Borneo, (4) Sumatera, (5) Jawa (=Java), (6) Philippines, (7) Sulawesi, (=Celebes), (8) Flores, (9) Maluku (=Moluccas), (10) New Guinea, (11) Taiwan, (12) Ryukyus, and (13) Pacific Islands, including New Zealand (Fig. 1).

Eighteen cranial measurements were taken to the nearest 0.01 mm using digital callipers (Mitsutoyo Co.) by the first author following Motokawa et al. (2001): the occipitonasal length (ONL), the condylobasal length (CBL), the greatest zygomatic breadth (ZB), the breadth of the braincase (BBC), the breadth across the occipital condyles (BOC), the least interorbital breadth (LIF), the length of nasals (LN), the breadth of the rostrum (BR), the postpalatal length (PPL), the length of the bony palate (LBP), the length of the upper diastema (LD), the length of the incisive foramen (LIF), the breadth across the first upper molars (BM1s), the breadth of the zygomatic plate (BZP), the length of the auditory bulla (LAB), the alveolar length of the maxillary toothrow (ALM), the coronal width of the first upper molar (WM1), and the height of the braincase (HBC).

We distinguished sexes in all statistical analyses, because *R. exulans* might have shown sexual dimorphism. We selected CBL instead of ONL as an overall size indicator of skull. This was because the tip of nasal was often broken and we could not measure ONL in those specimens. Since molar size was assumed not to be affected by individual skull growth, the absolute value of the molar size is often used in the systematics of mice and rats (Corbet & Hill, 1992; Motokawa et al., 2003). Therefore, we compared three variables of CBL, ALM, and BM1, separately, by location using the analysis of variance (ANOVA) and the Tukey's multiple comparison test (when $p>0.05$ in Bartlett's test for homoscedasticity) or Dunn's multiple comparison test (when $p \leq 0.05$ in Bartlett's test) at a significant limit of 5%. For 14 variables, except ONL, CBL, ALM, and BM1, we compared samples among localities using the analysis of covariance (ANCOVA) with CBL as the covariable after log-transformation of all variables. If the slopes of the regression line of the variables did not differ among localities ($p>0.05$), the adjusted means calculated using the common slope and the common log-transformed CBL mean were compared at a significant limit of 5%. We conducted the ANOVA and the ANCOVA with the computer program made by T. Hikida of Kyoto University. To get reliable results, we eliminated samples with less than ten individuals.

To assess the overall pattern of the geographic variation, the principal component analysis (PCA) based on the correlation matrix of all of the log-transformed variables, except for ONL, was carried out with PRINCOMP procedure of SAS version 6 (SAS Inst., 1990). Specimens with missing values were excluded from the PCA. We included all locality samples, because the PCA is conducted based on the calculation at individual level, and is not dependant on the localities where specimens were obtained. Canonical discriminant analysis (CDA) was also carried out based on all of the log-transformed variables, except for ONL, with the CANDISC procedure of SAS to examine the level of discrimination among samples. In CDA, we used location with more than five individuals.

RESULTS

The mean, SD, sample size and minimum and maximum values of CBL, ALM, and WM1 for 13 locality samples are summarised in Table 1; and the ANOVA statistical comparison among the selected samples are given in Fig. 2. The CBL showed a slight but continuous change among localities; the rats from the Pacific Islands were the largest. The ALM and WM1 were the smallest in the rats from the continent, while were the largest in those from the Pacific Islands (Fig. 2). In male ALM, geographic variation was not continuous as indicated by the broken line in Fig. 2; the continental sample was the smallest, while the Pacific Islands sample was the largest. The ALM and WM1 of the rats from Taiwan and the Ryukyus were small; their ranges overlapping only with samples from the continent and the Malay Peninsula. We could not find a noticeable pattern in the geographic variation among the samples from the Southeast Asian islands and New Guinea.

The results of the ANCOVA among the selected localities are shown in Table 2. In males, no differences were found between rats from the continent and the Malay Peninsula, and between those from Borneo and Jawa. Several characters of the rats from the continent and the Malay Peninsula were relatively small (in relation to CBL) compared with the rats from the Southeast Asian islands, New Guinea, and the Pacific Islands. On the other hand, the rats from New Guinea and the Pacific Islands were relatively larger than rats from the continent, the Malay Peninsula, and the Southeast Asian islands. The rats from the Pacific Islands were larger in BOC and IOB than the rest. In females, the rats from the Malay Peninsula were characterised by relatively smaller IOB, and those from the Sulawesi had smaller LN.

The first three principal component axes explained 61.2%, 10.1%, and 5.4% of the total variation for males, and 60.1%, 10.4%, and 4.8% for females, respectively (Table 3). In both sexes, all variables in the first axis showed positive loading. The first axis was assumed to represent overall size variation. For males, the second and the third axes showed relatively large loading in WM1 (positive) and ALM (positive), and HBC (negative) and BBC (negative), respectively. The second and third axes showed relatively large loading for females in WM1 (positive) and ALM (positive), and LBP

Table 2. Results of the analysis of covariance (ANCOVA) with condylobasal length as the covariate performed on 14 cranial variables of *Rattus exulans* from selected localities in male (A) and female (B). Pairs of the different adjusted means ($p<0.05$) are shown; the uppercase and the lowercase indicate “larger” and “smaller”, respectively. See text for abbreviations of variables.

(A) Male*

Locality	Continent	Malay Peninsula	Borneo	Jawa	New Guinea	Pacific Islands
Continent	—		bbc,hbc	zb,bbc,bm1s,hbc	zb,bbc,boc,iob,hbc	zb,bbc,boc,iob,bm1s,hbc
Malay Peninsula		—	bbc,PPL,hbc	zb,bbc,PPL,hbc	zb,bbc,boc,iob,hbc	zb,boc,iob,PPL
Borneo	BBC,HBC	BBC,ppl,HBC	—		iob,ppl	boc,iob
Jawa	ZB,BBC,BM1S,HBC	ZB,BBC,ppl,HBC		—	iob,ppl,LIF	boc,iob,LIF
New Guinea	ZB,BBC,BOC,IOB,HBC	ZB,BBC,BOC,IOB,HBC	IOB,PPL	IOB,PPL,lif	—	boc,iob,PPL
Pacific Islands	ZB,BBC,BOC,IOB,BM1S,HBC	ZB,BOC,IOB,ppl	BOC,IOB	BOC,IOB,lif	BOC,IOB,ppl	—

*Slopes were differed among samples; and the adjusted means were not compared in BR, LD and BZP

(B) Female*

Locality	Continent	Malay Peninsula	Borneo	Sulawesi	New Guinea	Pacific Islands
Continent	—	IOB	lab,hbc	LN,hbc	hbc	iob,PPL
Malay Peninsula	iob	—	iob,bm1s,hbc	iob,LN,bm1s,hbcd	iob,br,bm1s,hbc	iob,PPL,bm1s
Borneo	LAB,HBC	IOB,BM1S,HBC	—	LN,LBP	LAB	iob,BZP
Sulawesi	ln,HBC	IOB,ln,BM1S,HBC	ln,lbp	—	ln	ln,lbp
New Guinea	HBC	IOB,BR,BM1S,HBC	lab	LN	—	iob,PPL,lbp,BZP
Pacific Islands	IOB,ppl	IOB,ppl,BM1S	IOB,bzp	LN,LBP	IOB,ppl,LBP,bzp	—

*Slopes were differed among samples; and the adjusted means were not compared in ZB, BBC and BOC.

Table 3. Eigenvectors of the first three principal component (PC) scores and the first two standardised canonical coefficients (CAN) based on 17 cranial variables in *Rattus exulans* from selected localities. See text for abbreviations of variables.

Variable	Male					Female				
	PC1	PC2	PC3	CAN1	CAN2	PC1	PC2	PC3	CAN1	CAN2
CBL	0.297	-0.142	0.086	0.949	-0.450	0.296	-0.191	0.066	0.218	0.434
ZB	0.286	-0.315	-0.164	0.438	0.524	0.288	-0.199	0.039	0.404	-1.198
BBC	0.247	-0.004	-0.463	-0.231	1.487	0.235	0.161	-0.348	0.579	1.519
BOC	0.194	0.296	0.029	0.191	-0.525	0.230	0.198	0.112	0.385	-0.589
IOB	0.213	0.219	-0.244	1.017	-0.938	0.200	0.167	-0.399	0.223	-0.626
LN	0.275	-0.098	0.094	0.461	-0.152	0.277	-0.188	0.042	-1.432	-0.875
BR	0.270	-0.127	-0.093	-0.314	0.315	0.264	-0.101	0.080	0.290	0.318
PPL	0.264	-0.231	0.070	-0.400	-0.241	0.258	-0.282	0.014	-1.040	-0.298
LBP	0.228	0.029	0.368	-0.022	-0.058	0.225	-0.012	0.618	-0.053	-0.384
LD	0.281	-0.212	0.086	0.058	-0.667	0.273	-0.252	-0.003	0.931	-0.391
LIF	0.231	-0.170	-0.096	-0.195	0.026	0.237	-0.151	-0.347	-0.103	-0.024
BM1s	0.271	0.144	0.108	0.427	1.032	0.269	0.196	0.065	0.742	0.620
BZP	0.220	-0.308	0.237	-1.032	0.280	0.210	-0.286	0.001	-0.155	0.757
LAB	0.248	-0.066	0.193	-0.341	-0.178	0.240	-0.052	-0.032	-0.331	0.811
ALM	0.182	0.497	0.176	0.223	0.191	0.210	0.403	-0.044	1.081	0.080
WM1	0.147	0.540	0.252	0.197	-0.155	0.148	0.545	0.310	-0.195	0.050
HBC	0.215	0.175	-0.563	-0.361	0.293	0.214	0.276	-0.496	-0.076	-0.311
Eigenvalue	10.405	1.723	0.913	2.245	1.786	10.222	1.763	0.823	3.152	2.018
Difference	8.682	0.809	0.217	0.459	1.194	8.459	0.940	0.027	1.134	1.003
Proportion	0.612	0.101	0.054	0.433	0.345	0.601	0.104	0.048	0.415	0.266

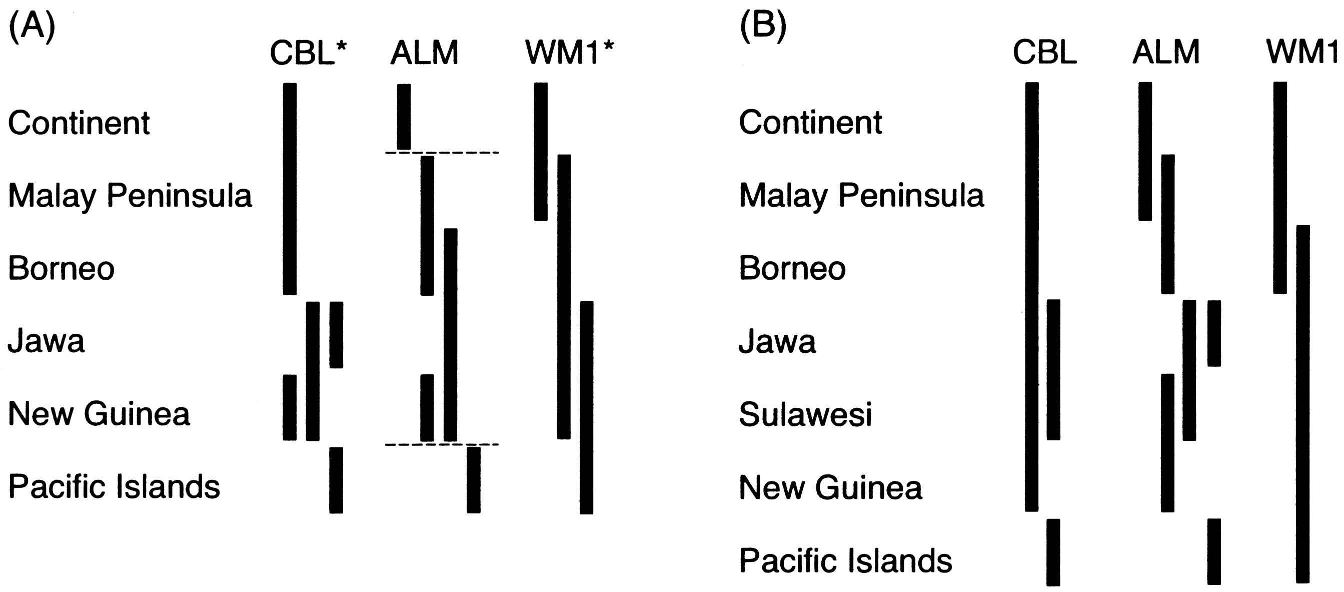

Fig. 2. Comparison of condylobasal length (CBL), alveolar length of the maxillary toothrow (ALM), and coronal width of the first upper molar (WM1) among *Rattus exulans* from the selected localities tested with the Tukey's or Dunn's (shown with asterisk) multiple comparison test. Vertical bars indicate subsets showing no significant difference among samples. The broken lines indicate discontinuities in variation.

(positive) and HBC (negative), respectively (Table 3). Individual scores for the second and the third axes (PC2 and PC3) are plotted in Fig. 3. The plots of the rats from the Southeast Asian islands and New Guinea showed large overlaps. Each of the plots of the rats from the Pacific Islands and those from the continent and the Malay Peninsula overlapped with samples from the Southeast Asian islands and New Guinea, but were only slightly different. One male individual from the Maluku was plotted without overlapping any of the others; it was characterised by large PC2 and small PC3. On the other hand, the males from Taiwan, characterised by the small PC2 and small PC3, showed little overlapping with other samples. One female from the Ryukyus was plotted outside the ranges of the remaining samples; characterised by the smallest PC2 of all the specimens examined.

The first and the second axes of the CDA explained 43.3% and 34.5%, respectively, of the total variation for males, and 41.5% and 26.6%, respectively, for females (Table 3). For males, in the first axis, BZP (negative) and IOB (positive) had a relatively large contribution. In the second axis, BBC (positive) and BM1s (positive) made a large contribution. For females, LN (negative), ALM (positive), and PPL (negative) contributed to the first axis, and BBC (positive) and ZB (negative) contributed to the second axis. Plots of the first two axes (CAN1 and CAN2, Fig. 4), showed rats from the Southeast Asian islands were largely overlapped for both males (Fig. 4A) and females (Fig. 4B). These samples were characterised by small CAN1 and large CAN2 in males, and large CAN1 and large CAN2 in females. The plots of rats from the continent were slightly separated from those from the Southeast Asian islands; they had small CAN1 and small CAN2 in males, and small CAN1 and medium CAN2 in females. The plots of rats from the Malay Peninsula were located between those from the continent and those from the Southeast Asian islands and New Guinea. The plots of rats from the Pacific Islands were isolated from the remaining samples without (in males) and with little (in females) overlapping; they were characterised by large CAN1 and medium CAN2 in males, and large CAN1 and small CAN2 in females.

DISCUSSION

The skulls of *R. exulans* did vary geographically. The Pacific Islands populations diverged from the remaining populations. The continental population, in the north part of the Isthmus of Kra, was slightly different from the Southeast Asian island populations. The Malay Peninsula populations seem intermediate between continent and the Southeast Asian island populations. The divergence among the populations in the Southeast Asian islands is probably low and the variation range may well overlap. The New Guinea population may have differentiated from the Pacific Islands populations, but not from the Southeast Asian island populations. The East Asian populations, those recently reported from Taiwan and an island in the Ryukyus (Motokawa et al., 2001) were more similar to the Southeast Asian populations than to the Pacific Islands populations. That they may have been diverged morphologically from the Southeast Asian populations is indicated in the PCA plots (Fig. 3). The East Asian populations were characterised by small molar size. This variation in molar size very slightly overlapped with the Southeast Asian island populations, but was almost completely included within the variation of the continental and Malay Peninsula populations.

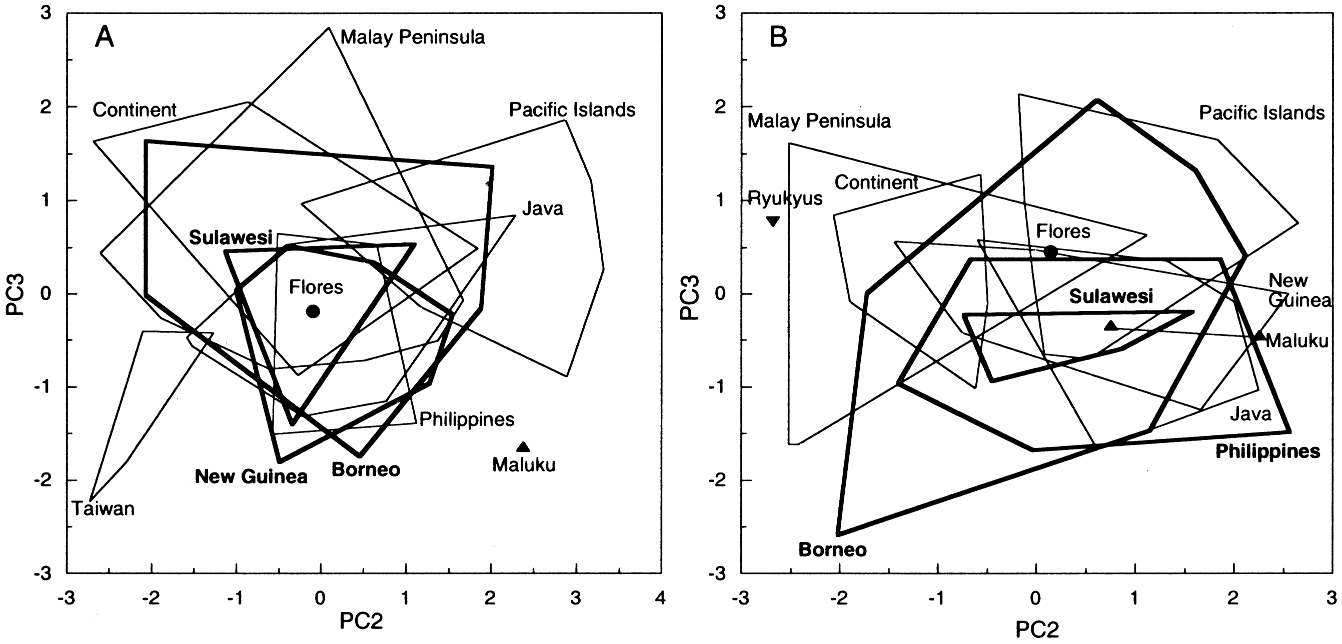

Fig. 3. Two-dimensional plots of the second against the third principal component scores of 17 cranial variables for male (A) and female (B) *Rattus exulans.*

Because geographic variation in Southeast Asia seemed to be continuous from the continent in the northern Isthmus of Kra, through the Malay Peninsula, to the islands of Sumatera, Jawa, Borneo, Philippines, and Sulawesi, it is possible that *R. exulans* originated somewhere in the north part of the Isthmus of Kra as suggested by Musser & Newcomb (1983), subsequently expanding its distribution southward through the Malay Peninsula into the Pacific Islands. We found little divergence among island populations in Southeast Asia. This implies that the rats moved at relatively high frequency among islands in association with human activity, resulting in interbreeding among different island populations and decreasing genetic and morphological divergence. With the present material, it is impossible to explore the initial and the past movements of rats among the Southeast Asian islands, because these materials only show the current pattern of divergence among the island populations. The past dispersal and divergence patterns can be determined only by dating the dispersal using the archaeological material, as suggested by Matisoo-Smith (2002), i.e. comparing DNA from archaeological rat specimens to present day specimens. Although we support the view of Musser & Newcomb (1983) that human agents played an important role in the dispersal of rats into the Malay Peninsula and the Southeast Asian islands, we doubt that the human introduction explains all of the initial dispersal events into these areas. In the late Pleistocene, the islands of Borneo, Sumatera, and Jawa were connected with the Malay Peninsula into “Sundaland” by the sea level lowering (Heaney, 1986). Migration through this land bridge formed in the late Pleistocene, may account for the *R. exulans* in some of these islands (Borneo, Sumatera, and Jawa). There is no question but that the populations in the Philippines, Sulawesi, Flores, and Maluku were introduced by humans, because there were no land bridge formations in the late Pleistocene (Heaney, 1986).

The initial introduction of the Pacific Islands populations of *R. exulans* are thought to have taken place about after 3,500 years BP and that of the New Guinea population is probably occurred not so much earlier than that time, by canoe along with the human settlement into the Pacific Islands (Roberts, 1991; Matisoo-Smith et al., 1998; Flannery, 1995a, b). The human dispersal from the Southeast Asian islands into the Pacific Islands was possibly restricted within a short time, limiting number of rats transported by canoe. Divergence between populations in the Pacific Islands and the Southeast Asian islands were possibly achieved by the isolation of 3,500 years at maximum. The bottleneck effect in the initial introduced rats may explain the high divergence, within a short period, of the Pacific Islands populations from those in Southeast Asia. In the Pacific Islands, the rat fauna are restricted to the several introduced species only (Matisoo-Smith & Allen, 2001). These faunal differences may also have contributed to the morphological differentiation of the Pacific Islands populations from the Southeast Asian populations. Therefore, the morphological divergence of the Pacific Islands populations probably occurred with strong human influence. On the other hand, the skulls of the New Guinea populations were not so different from the Southeast Asian populations, although they could be distinguished from the Pacific Islands populations. This may be explained by the different route of the prehistorical humans colonising New Guinea and the Pacific Islands, as suggested by Roberts (1991), and by the subsequent interaction between rat populations of New Guinea and the other Southeast Asian islands. The inadvertent movements of *R. exulans* among

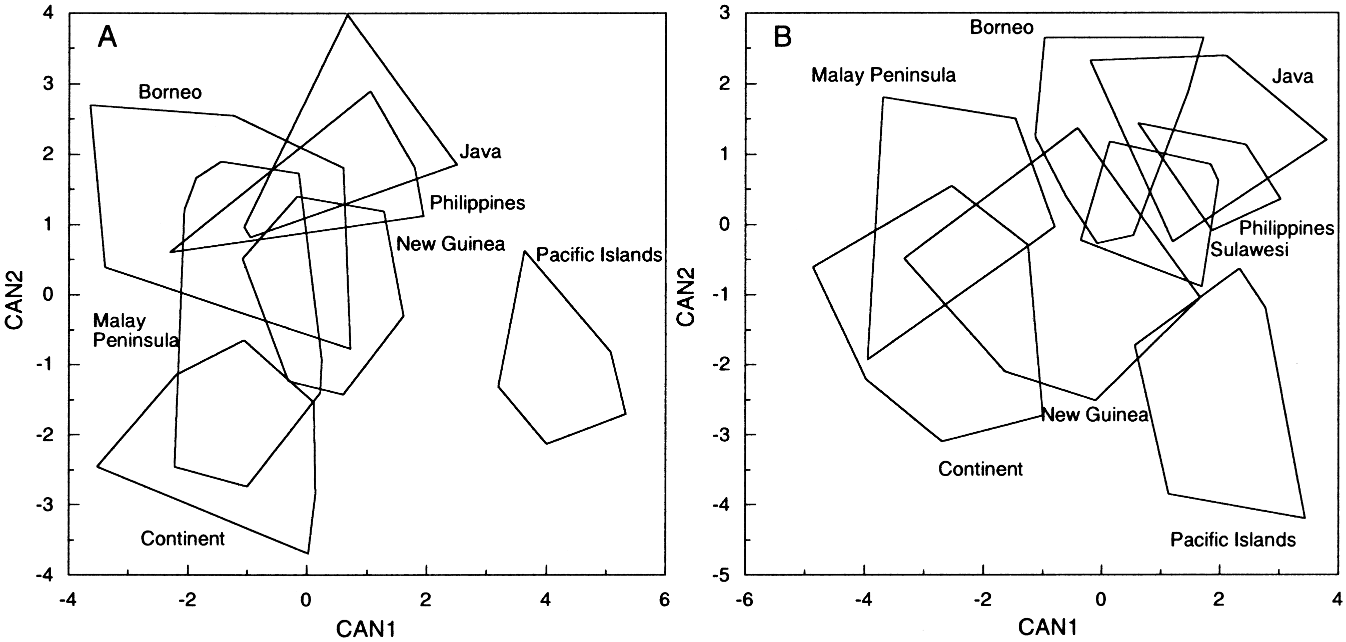

Fig. 4. Two-dimensional plots of the first against the second canonical scores of 17 cranial variables for male (A) and female (B) *Rattus exulans*.

the islands in Southeast Asia and New Guinea may have been taken place in various directions for thousands of years in association with human activity.

The East Asian populations from Taiwan and the Ryukyus had small molars and small PC2 values. The first recorded occurrence of *R. exulans* in Taiwan was in 1999. The first recorded occurrence in the Ryukyus was confirmed by two specimens collected in 1955 (Motokawa et al., 2001). Motokawa et al. (2001) suggests the recent colonisation of *R. exulans* in Taiwan and the Ryukyus was in association with human agents, such as ships. If so, these populations were likely to be morphologically similar to other populations in Southeast Asia. The morphological differences recognised in this study, suggest the rats were introduced into the East Asian islands earlier than suggested by Motokawa et al. (2001). *Rattus exulans* is not recorded from the continental China (Zhang, 1997), creating a distribution gap in between Vietnam and islands of Taiwan and the Ryukyus. We do not know the timing or dispersal methods of *R. exulans* into the East Asian islands. The future study using genetic markers may shed light on this question.

Many subspecies have been described for this rat (Ellerman, 1941, 1961), but most are currently considered junior synonyms of *R. exulans* (Corbet & Hill, 1992; Musser & Carleton, 1993). Ellerman & Morrison-Scott (1951) recognised two subspecies, *R. e. exulans* for the Pacific Islands populations and *R. e. concolor* for the Southeast Asian populations. Taylor et al. (1982) considered the New Guinea populations as a subspecies, *R. e. browni*. *Rattus e. concolor* was originally described by Blyth (1859) as *Mus concolor* from Schwegyin, Burma; and *R. e. browni* was described by Alston (1877) as *Mus browni* from the Duke of York Island or the adjacent parts of New Britain or New Ireland, Papua New Guinea (Taylor et al., 1982). We suggest that because the skulls of the Pacific Islands populations are distinguishable from the Southeast and the East Asian populations, the Pacific Islands *R. exulans* may have differentiated at the subspecies level. On the other hand, the New Guinea populations are suggested to be the same subspecies as the Southeast Asian populations. The morphological differences found in the Pacific Islands populations, however, is suggested to have formed as a result of transportation by human and the resulting bottleneck effect as discussed above. If these rats were transported as human food (Matisoo-Smith et al., 1998), then they were probably subject to human selection. As the rats in the Pacific Islands can be regarded as semi-domesticated animals, they should not be evaluated using the biological species concept. Therefore, we consider the Pacific Islands and New Guinea populations conspecific with and derived from the Southeast Asian populations. All of these populations are *R. exulans*; we do not recognise any subspecies.

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LITERATURE CITED

Alston, E. R., 1877. On the rodents and marsupials collected by the Rev. G. Brown in Duke-of-York Island, New Britain, and New Ireland. *Proceedings of the Zoological Society of London*, **1877:** 123-127.

Blyth, E., 1859. Reports of the Curator. *Journal of the Asiatic Society of Bengal*, **28:** 271-298.

Carter, T. D., J. E. Hill & G. H. H. Tate, 1945. *Mammals of the Pacific World*. The Macmillan Company, New York. 227 pp.

Chasen, F. N., 1940. A handlist of Malaysian mammals (a systematic list of the mammals of the Malay Peninsula, Sumatra, Borneo and Java, including the adjacent small islands). *Bulletin of the Raffles Museum*, **15:** 1-209.

Corbet, G. B. & J. E. Hill, 1992. *The Mammals of the Indomalayan Region*. Oxford University Press, New York. 488 pp.

Davis, D. D., 1962. Mammals of the lowland rain-forest of north Borneo. *Bulletin of the Singapore National Museum*, **31:** 1-129.

Ellerman, J. R., 1941. *The Families and Genera of Living Rodents. Volume II. Family Muridae.* British Museum (Natural History), London. 690 pp.

Ellerman, J. R., 1961. *The Fauna of India Including Pakistan, Burma and Ceylon. Mammalia (Second Edition) Vol. 3.* Zoological Survey of India, Calcutta. 884 pp.

Ellerman, J. R. & T. C. S. Morrison-Scott, 1951. *Checklist of Palaearctic and Indian Mammals 1758-1946.* British Museum (Natural History), London. 810 pp.

Flannery, T., 1995a. *Mammals of New Guinea.* Cornell University Press, New York. 568 pp.

Flannery, T., 1995b. *Mammals of the South-west Pacific & Moluccan Islands.* Cornell University Press, New York. 464 pp.

Harrison, J. L., 1951. Reproduction in rats of the subgenus *Rattus*. *Proceeding of the Zoological Society of London*, 121: 673-694.

Harrison, J. L., 1957. Habitat of some Malayan rats. *Proceeding of the Zoological Society of London*, 128: 1-21.

Harrison, J. L., 1966. *An Introduction to Mammals of Singapore and Malaya.* The Singapore Branch, Malayan Nature Society, Singapore. 340 pp.

Harrison, J. L., 1973. *An Introduction to the Mammals of Sabah.* The Sabah Society, Kota Kinabalu. 244 pp.

Heaney, L. R., 1986. Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction and speciation. *Biological Journal of the Linnean Society*, **28:** 127-165.

Heaney, L. R., D. S. Balete, M. L. Dolar, A. C. Alcala, A. T. L. Dans, P. C. Gonzales, N. R. Ingle, M. V. Lepten, W. L. R. Oliver, P. S. Ong, E. A. Rickart, B. R. Tabaranza, Jr. & R. C. B.

Utzurrum, 1998. A synopsis of the mammalian fauna of the Philippine Islands. *Fieldiana Zoology, New Series*, **88:** 1-61.

Heaney, L. R., D. S. Balete, E. A. Rickart, R. C. B. Utzurrum & P. C. Gonzales, 1999. Mammalian diversity on Mount Isarog, a threatened center of endemism on southern Luzon Island, Philippines. *Fieldiana Zoology, New Series*, **95:** 1-62.

Marshall, J. T., Jr., 1977. Family Muridae: rats and mice. In: Lekagul, B. & J. A. McNeely (eds.), *Mammals of Thailand*. Kurusapha Ladprao Press, Bangkok. Pp. 397-487.

Matisoo-Smith, E., 2002. Something old, something new: do genetic studies of contemporary populations reliably represent prehistoric populations of Pacific *Rattus exulans*?. *Human Biology*, **74:** 489-496.

Matisoo-Smith, E. & J. S. Allen, 2001. Name that rat: molecular and morphological identification of Pacific rodent remains. *International Journal of Osteoarchaeology*, **11:** 34-42.

Matisoo-Smith, E., R. M. Roberts, G. J. Irwin, J. S. Allen, D. Penny & D. M. Lambert, 1998. Patterns of prehistoric human mobility in Polynesia indicated by mtDNA from the Pacific rat. *Proceedings of the National Academy of Sciences of the United States of America*, **95:** 15145-15150.

Medway, L., 1965. *Mammals of Borneo. Field Keys and An Annotated Checklist.* Branch Royal Asiatic Society, Malaysia Printers, Singapore. 193 pp.

Medway, L., 1969. *The Wild Mammals of Malaya and Offshore Islands Including Singapore.* Oxford University Press, Kuala Lumper & Singapore. 127 pp.

Motokawa, M., K.-H. Lu, M. Harada & L.-K. Lin, 2001. New records of the Polynesian rat *Rattus exulans* (Mammalia: Rodentia) from Taiwan and the Ryukyus. *Zoological Studies*, **40:** 299-304.

Motokawa, M., L.-K. Lin & J. Motokawa, 2003. Morphological comparison of Ryukyu mouse *Mus caroli* (Rodentia: Muridae) populations from Okinawajima and Taiwan. *Zoological Studies*, **42:** 258-267.

Musser, G. G., 1977. *Epimys benguetensis*, a composite, and one zoogeographic view of rat and mouse faunas in the Philippines and Celebes. *American Museum Novitates*, **2624:** 1-15.

Musser, G. G. & M. D. Carleton, 1993. Family Muridae. In: Wilson, D. E. & D. M. Reeder (eds.), *Mammal Species of the World*, 2nd ed. Smithsonian Institution Press, Washington. Pp. 501-755.

Musser, G. G. & C. Newcomb, 1983. Malaysian murids and the giant rat of Sumatra. *Bulletin of the American Museum of Natural History*, **174:** 327-598.

Payne, J., C. M. Francis & K. Phillipps, 1985. *A Field Guide to the Mammals of Borneo.* The Sabah Society, Kota Kinabaru. 332 pp.

Peale, T. R., 1848. *United States Exploring Expedition During the Years 1838, 1839, 1840, 1841, 1842, Under the Command of Charles Wilkes. U. S. N., vol. 8. Mammalia and Ornithology*. C. Sherman, Philadelphia. 338 pp. (cited from Taylor & Horner [1973]).

Rickart, E. A., L. R. Heaney, P. D. Heideman & R. C. B. Utzurrum, 1993. The distribution and ecology of mammals on Leyte, Biliran, and Maripipi Islands, Philippines. *Fieldiana Zoology, New Series*, **72:** 1-62.

Roberts, M., 1991. Origin, dispersal routes, and geographic distribution of *Rattus exulans*, with special reference to New Zealand. *Pacific Science*, **45:** 123-130.

SAS Institute, 1990. *SAS/STAT User's Guide.* Version 6. SAS Institute, Cary, North Carolina. 1686 pp.

Tate, G. H. H., 1935. Rodents of the genera *Rattus* and *Mus* from the Pacific Islands, collected by the Whintney South Sea Expedition, with a discussion of the origin and races of the Pacific Island rat. *Bulletin of the American Museum of Natural History*, **68:** 145-178.

Taylor, J. M. & B. E. Horner, 1973. Results of the Archbold Expeditions. No. 98. Systematics of native Australian *Rattus* (Rodentia, Muridae). *Bulletin of the American Museum of Natural History*, **150:** 1-130.

Taylor, J. M., J. H. Calaby & H. M. Van Deusen, 1982. A revision of the genus *Rattus* (Rodentia, Muridae) in the New Guinean region. *Bulletin of the American Museum of Natural History*, **173:** 177-336.

Zhang, Y. (ed.), 1997. *Distribution of Mammalian Species in China.* China Forestry Publishing House, Beijing. 280 pp.

APPENDIX

Material examined. – The specimens with asterisk were not used for statistical analyses, either because their sexes were unknown or they were juvenile or much old (see text for criterion). BM: the Natural History Museum, London; NMNS: the National Museum of Natural Science, Taichung; NSMT: the National Science Museum, Tokyo.

Continent in the north of the Isthmus of Kra (n=56), BM 97.8.3.8, 98.10.5.43, —44*, —45 through —47, 1.7.7.11*, —12*, 14.6.18.31 through —34 (Thailand), 88.12.1.48*, 91.11.1.29*, 14.7.19.172 through —183, 14.12.8.186 through —191, 15.5.5.212*, —214 through —216, —217*, —218 through — 223, 27.11.18.31 through —34, 36.12.26.33*, 78.1243 through —1249, —1250* (Myanmar [=Burma]).

Malay Peninsula (n=47): BM 96.6.16.7*, 3.2.6.67 through —71, 5.12.7.76, —77*, —78, —79, 6.10.4.42, 9.4.1.453 through — 463, —473, —474*, 8.7.20.70, 55.3163, —3164, 3166 through —3169, —3171 through —77, 61.1205 through —1208, 62.740, —741, NSMT M7771 through 7773.

Borneo (n=54): BM 92.10.2.6, 93.6.3.2*, 94.6.12.6*, 11.1.19.3, — 4, 51.292*, 55.973 through —984, —986 through —989, 65.348, —349, 67.197, 71.2812 through —2838, —3051, — 3052.

Sumatera (n=5): BM 19.11.5.74, —75, —78, —92, —93.

Jawa (n=32): 9.1.5.786 through —789, 10.4.6.56, —58 through — 61, —63, —64, —66, 54.161 through 165, —167, —169 through —177, 57.308*, 61.1800, —1801, —1804, —1804 (duplicate number).

Philippines (n=19): 94.2.1.12*, 94.7.2.82, 52.91 through —94 (Palawan Island), 97.5.2.29 (Negros Island), 95.5.7.9* (Mindoro Island), 5.10.9.4, —5 (Mindanao Island), 95.8.2.11, 97.5.2.30, 52.87*, —88 through —90 (Luzon Island), 45.33.6.10*, 55.12.24.417, —418 (not specified).

Sulawesi (n=29): BM 97.1.2.33*, —34, —35*, 97.1.3.14, —30*, 21.2.9.13, —14*, 40.454 through —456, —458 through —475, -615.

Flores (n=4): BM 97.4.18.5 through —8.

Maluku (n=6): BM 10.3.4.52 (Seram), 10.3.4.112, —114, 11.7.12.33 through —35 (Ambon).

New Guinea (n=62): BM 3.7.6.1, 6.1.8.10*, 6.10.8.7, —8, —10 through 12, 7.2.1.5 through —8, 10.4.24.1 through —3, 15.2.18.11, —12, 29.5.27.19 through —21, 33.9.1.4, 34.6.1.7*, 47.1131 through —40, 50.1205, —1206, —1751 through — 1757, 53.231, 69.339, —340*, —341 through —345, 70.2011, 77.7.18.25-1*, 78.2136 through —2144, —3016, —3017, 81.1756.

Taiwan (n=5): NMNS 4520, 4521, 4524, 6833, 6836.

Ryukyus (n=2): NSMT M3334, 3335 (Miyakojima Island).

Pacific Islands (n=53): BM 99.9.10.2* (Murray Island), 91.10.9.2* (Adele Island), 93.4.30.1, —2, 9.8.10.1*, 51.7.18.51*, 56.502 through —511 (New Zealand), 92.9.3.2*, —3*, —4* (Chatham Island), 98.3.26.1 (Kermadec Islands), 58.12.27.12* (Norfolk Island), 35.9.2.1*, —2*, 54.904*, —905 (Solomon Islands), 25.6.4.5, 25.12.14.6 through —8, 50.1200*, —1201, —1202*, 56.11.12.1* (New Hebrides), 55.11.7.15, —17 (Fiji), 69.518 through —525 (Tarawa Island, Gilbert Islands), 90.12.10.6, —7 (Phoenix Islands), 26.2.7.1, 26.2.10.1* (Samoa Islands), 13.1.12.1, —2 (Henderson Island), 25.10.21.9 (Austral Islands), 25.10.21.12 (Marquesas Islands), 26.5.13.2, —3 (Hawaiian Islands).