Geographical and Functional-Morphological Variations of the Skull in the Gray-Bellied Squirrel

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ABSTRACT. The geographical variations of the skulls were osteometrically examined in the gray-bellied squirrel (*Callosciurus caniceps*) from the populations of Korat, Ranong, southernmost Thailand, and Terutau Island. The skull size was larger in northern population than in the southern population in the continental mainland. The zoogeographical influences of the Isthmus of Kra remained unclear, since the plots from Korat population were intermingled with those from southernmost Thailand population in the principal component charts. Although Korat population has been thought to belong to north group, we suggest that Ranong and southernmost Thailand populations may contain individuals from both north and south groups separated by the ancient Kra barrier. Terutau Island population was similar to southernmost Thailand population in skull size, although Terutau population has been isolated in the island and separated from the south group of the Isthmus of Kra. In the proportional analysis the interorbital space was narrower and the binocular sense has been well-developed in Terutau population. It suggests that this population has been highly adapted to arboreal behavior. In contrast, the skull with larger interorbital space was more adaptive for terrestrial life in Korat population. The canonical discriminant analysis could clearly separate the four populations in the scattergrams of discriminant scores.

KEY WORDS: *Callosciurus caniceps*, geographical variation, gray-bellied squirrel, osteometry, skull.

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The Indomalayan Region includes about 10 species of the genus *Callosciurus* [2, 3, 13]. Among them the gray-bellied squirrel (*Callosciurus caniceps*) represents one of the most typical arbo-terrestrial squirrels in this region. The species is widely distributed in the north and central Thailand and the Malayan Peninsula, and shows complicated skin color variations in each locality [1, 8–12]. However, the osteometrical data have not been reported from the large distribution areas and the geographical variations have remained unclear in skull shape. We have expected that the skull shape has been functionally adapted to various natural environments within the species. In this study, therefore, the osteometrical and related statistical analysis were carried out in the skull to clarify the geographical variation among populations and to confirm the functional adaptation in each locality.

MATERIALS AND METHODS

We examined 74 skulls of the gray-bellied squirrel that have been stored in the Mammal Division in National Museum of Natural History of Smithsonian Institution. Museum numbers of each specimen are provided in Appendix 1. The skull specimens with fully erupted molars were used and considered as adult. Sex determination was dependent on the description of biological data of specimens. The

composition of origin and their abbreviations, and sex are shown in Table 1. We selected only four geographical populations (Table 1) from all subspecies of the gray-bellied squirrel, since relatively numerous specimens have been obtained from these four localities and stored as Museum Collection. Korat population was identified as *Callosciurus caniceps caniceps*, Ranong population as *Callosciurus caniceps bimaculatus*, Terutau Island population as *Callosciurus caniceps lacevensis* or *Callosciurus caniceps adangensis* in the biological record of the Museum specimens. Since the skin color variations from southernmost Thailand population are complicated, we considered them as one group in the osteometrical study. Skull measurement data were obtained with vernier calipers to the nearest 0.05 mm. Measurements are defined in Table 2, and were based on Driesch [4]. Differences of mean values among localities were examined by Student's *t*-test. We calculated the proportion indices as quotients of each measurement value divided by geometric mean of all measurement values. The significant differences of proportion indices were evaluated among populations by nonparametric U-test using software Statistica (Statsoft Inc., Tokyo, Japan). Principal component analysis and canonical discriminant analysis were carried out with all measurement data to clarify the geographical variation among localities by the use of the same software.

Table 1. Locality and sex composition of the specimens

Origin of Specimens	Symbols	Male	Female
Korat	K	4	2
Ranong	R	10	5
Southernmost Thailand (Trang, Nakhon Si Thammarat, Surat Thani, Songkla, Hat Yai)	S	21	24
Terutau Island	T	6	2
		41	33

Table 2. List of skull and mandibular measurements and their abbreviations

Cranium	
Profile length	PL
Maximum length	ML
Condylbasal length	CL
Short lateral facial length	SL
Maximum width of the nasal bone	MWN
Least breadth between the orbits	LBO
Least breadth of caudal point of zygomatic process of frontal bone	LBC
Greatest neurocranium breadth	GNB
Greatest occipital breadth	GOB
Median palatal length	MPL
Dental length	DL
Length of molar row	LMR1
Greatest palatal breadth	GPB
Length from Basion to Staphylion	LBS
Length from Basion to the most rostral point of zygomatic arch	LBR
Length from Basion to the most medial point of orbit	LBM
Length from Basion to the sagittal and rostral point of temporal bone	LBSR
Height from Akrokranium to Basion	HAB
Mandible	
Length from the condyle	LC
Length of molar row	LMR2
Thickness of mandible at middle point of M1	TM
Height of the mandible at M1	HM
Aboral height of the vertical ramus	AHR
Oral height of the vertical ramus	OHR

The measurement items were based on Driesch [4].

RESULTS

Mean values and standard errors of the 24 measurements are given in Table 3. Statistical differences in these measurements between all combinations of populations are shown in Table 4. We used the limit of 5% to evaluate the statistical differences. The statistical differences of mean values were obviously confirmed among the four populations. The skull size was larger in northern population than in the southern population among K, R, and S materials in mean values. The mean values of T population were obviously smaller than those of K population. The results of *t*-test showed significant size differences between many combination of localities, although the relationships between S-T in both sexes and K-R in female did not significantly indicate the differences in many measurements (Table 4). In the comparison between S and T populations, SL, DL, LMR1 and GPB were not different. It indicated that the size of the spranchocranium region was similar between the two pop-

ulations. The measurement values were also similar in mandibular size in these two populations.

The proportion indices are arranged in Table 5, and their significant differences confirmed by nonparametric U-test among localities are shown in Table 6. The significant differences were not observed in many indices in female. However, CL and LBS were larger and LBC smaller in T population than in the other populations. SL and LBO were larger and GNB and GOB smaller in K population. The tendency was statistically obvious in male, and the results of female in some locality combinations were consistent with those of male.

The principal component charts are shown in Fig. 1. The loading factors are arranged in each measurement (Table 7). The plots of the species were considered as four groups of K, R, S and T in charts of both sexes. However, the plot distribution of R was intermingled with S in both sexes, T with S in female. K plots in both sexes and T plots in male were completely separated from those of the other popula-

Table 3. Mean values (mm) and standard deviations for craniometric measurement in various populations

	PL	ML	CL	SL	MWN	LBO	LBC	GNB	GOB	MPL	DL	LMR1	GPB	LBS	LBR	LBM	LBSR	HAB	LC	LMR2	TM	HM	AHR	OHR
Korat																								
Male	56.83	56.53	50.43	24.20	7.86	20.95	19.58	21.91	23.78	29.03	28.08	10.96	13.29	21.55	41.84	33.90	25.73	14.70	37.41	11.36	4.06	9.19	19.50	18.69
	0.64	0.44	0.68	0.56	0.23	0.75	0.18	0.97	0.18	0.56	0.25	0.23	0.26	0.47	0.55	0.46	0.52	0.43	0.41	0.17	0.18	0.52	0.69	0.69
Female	55.65	55.55	49.28	23.60	7.65	20.25	19.28	22.00	23.73	28.43	26.93	11.48	13.20	21.20	40.48	33.25	24.58	14.03	35.50	11.23	4.08	8.93	19.08	17.83
	0.78	0.78	0.81	0.28	0.07	0.21	0.60	0.28	0.46	0.46	0.32	0.18	0.14	1.27	0.60	0.07	0.18	0.11	0.71	0.32	0.11	0.18	0.04	0.60
Ranong																								
Male	54.27	54.08	47.76	22.62	7.70	18.96	19.19	22.31	23.41	27.38	26.21	10.82	12.78	20.68	40.34	32.86	25.21	13.96	35.34	10.96	4.05	8.46	18.32	17.39
	1.45	1.39	1.33	0.74	0.46	1.11	0.76	0.85	0.90	0.77	0.85	0.27	0.32	0.73	1.38	1.03	0.74	0.43	0.92	0.28	0.33	0.30	0.52	0.49
Female	53.56	53.37	47.48	22.31	7.38	19.42	18.98	22.11	22.90	27.26	26.12	10.91	13.34	20.41	40.09	33.04	24.68	13.83	35.19	11.12	3.82	8.44	18.40	17.59
	0.43	0.58	0.80	0.25	0.44	0.81	0.48	0.47	0.59	0.46	0.47	0.31	0.46	0.47	1.26	0.85	0.39	0.26	0.49	0.31	0.25	0.12	1.01	0.99
Southernmost Thailand																								
Male	51.01	50.95	44.98	20.81	6.99	17.75	18.05	21.29	22.06	25.64	24.52	10.25	12.10	19.67	37.59	31.31	23.61	13.50	32.90	10.34	3.67	7.83	17.43	16.59
	2.00	2.02	1.90	1.03	0.53	1.46	0.74	0.69	0.92	1.12	0.90	0.53	0.39	1.11	1.72	1.50	0.94	0.49	1.46	0.44	0.33	0.51	0.88	0.91
Female	50.38	50.26	44.33	20.38	7.05	17.40	18.28	21.13	21.56	25.30	24.26	10.41	12.19	19.22	37.25	30.64	23.45	13.32	32.38	10.48	3.76	7.83	17.05	16.22
	2.01	1.97	1.99	1.22	0.36	1.11	0.69	0.89	0.91	1.04	0.94	0.41	0.30	1.09	1.56	1.25	0.87	0.56	1.56	0.40	0.19	0.44	0.89	0.94
Terutau Id.																								
Male	52.51	52.28	47.18	21.55	7.42	17.73	17.17	20.05	22.38	26.47	24.95	10.44	11.88	20.85	38.83	31.80	23.93	13.26	34.54	10.43	3.78	8.14	18.22	16.93
	0.72	0.62	0.65	0.61	0.16	0.28	0.23	0.27	0.54	0.39	0.33	0.53	0.31	0.34	0.38	0.40	0.46	0.24	0.57	0.48	0.23	0.24	0.17	0.20
Female	50.73	50.20	45.43	20.58	7.05	17.23	16.90	19.85	21.23	25.25	23.98	10.00	12.05	20.30	37.98	30.55	22.33	12.53	33.30	10.15	3.55	7.85	17.78	16.75
	1.17	0.92	0.74	0.60	0.49	1.45	0.28	0.42	0.32	0.42	0.46	0.07	0.35	0.21	0.74	0.28	0.04	0.18	0.21	0.14	0.07	0.21	0.46	0.14

Mean values are arranged in upper row, standard deviations in lower row.

Table 4. Significant differences of measurements among various populations

	PL	ML	CL	SL	MWN	LBO	LBC	GNB	GOB	MPL	DL	LMR1	GPB	LBS	LBR	LBM	LBSR	HAB	LC	LMR2	TM	HM	AHR	OHR
Male																								
KXR	0.003	0.003	0.001	0.001	0.253	0.003	0.172	0.233	0.224	0.001	0.001	0.181	0.008	0.025	0.030	0.039	0.113	0.006	0.001	0.010	0.473	0.003	0.002	0.001
KXS	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.066	0.001	0.000	0.000	0.008	0.000	0.002	0.000	0.001	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000
KXT	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.001	0.001	0.000	0.000	0.053	0.000	0.012	0.000	0.000	0.000	0.000	0.000	0.003	0.037	0.001	0.001	0.000
RXS	0.000	0.000	0.000	0.000	0.001	0.014	0.000	0.001	0.000	0.000	0.000	0.002	0.000	0.007	0.000	0.003	0.000	0.008	0.000	0.000	0.003	0.001	0.003	0.007
RXT	0.008	0.005	0.171	0.005	0.089	0.010	0.000	0.000	0.012	0.009	0.002	0.041	0.000	0.303	0.011	0.016	0.001	0.001	0.039	0.007	0.052	0.025	0.323	0.025
SXT	0.044	0.065	0.005	0.055	0.034	0.487	0.004	0.000	0.216	0.046	0.131	0.219	0.114	0.009	0.047	0.221	0.214	0.132	0.007	0.334	0.228	0.083	0.021	0.186
Female																								
KXR	0.002	0.004	0.022	0.001	0.227	0.117	0.258	0.389	0.071	0.015	0.040	0.034	0.352	0.121	0.354	0.377	0.368	0.183	0.261	0.352	0.117	0.004	0.207	0.387
KXS	0.001	0.001	0.001	0.001	0.016	0.001	0.030	0.092	0.002	0.000	0.000	0.001	0.000	0.011	0.004	0.004	0.043	0.047	0.005	0.010	0.016	0.001	0.002	0.013
KXT	0.019	0.012	0.019	0.012	0.116	0.050	0.018	0.013	0.012	0.009	0.009	0.004	0.025	0.214	0.033	0.003	0.002	0.005	0.026	0.024	0.014	0.016	0.029	0.066
RXS	0.001	0.001	0.001	0.001	0.043	0.000	0.020	0.012	0.002	0.000	0.000	0.008	0.000	0.013	0.000	0.000	0.003	0.030	0.000	0.001	0.268	0.003	0.003	0.003
RXT	0.002	0.001	0.013	0.001	0.212	0.021	0.001	0.001	0.007	0.002	0.001	0.006	0.009	0.387	0.042	0.006	0.000	0.001	0.002	0.005	0.104	0.002	0.228	0.155
SXT	0.406	0.483	0.226	0.415	0.500	0.419	0.005	0.029	0.305	0.474	0.336	0.092	0.269	0.091	0.264	0.462	0.044	0.030	0.209	0.133	0.073	0.472	0.138	0.218

Each value indicates the limit percentage in which the significant differences are confirmed between the two populations.

Table 5. The proportion indices in each measurement of various populations

		PL	ML	CL	SL	MWN	LBO	LBC	GNB	GOB	MPL	DL	LMR1
Male	Korat	2.711	2.696	2.405	1.154	0.375	0.999	0.934	1.045	1.134	1.385	1.339	0.523
	Ranong	2.702	2.692	2.378	1.126	0.383	0.943	0.956	1.111	1.166	1.363	1.305	0.539
	Southernmost Thailand	2.705	2.702	2.385	1.103	0.370	0.941	0.957	1.130	1.170	1.360	1.300	0.544
	Terutau Id.	2.732	2.720	2.455	1.121	0.386	0.922	0.893	1.043	1.164	1.377	1.298	0.543
Female	Korat	2.711	2.706	2.400	1.150	0.373	0.986	0.939	1.072	1.156	1.385	1.312	0.559
	Ranong	2.683	2.673	2.378	1.117	0.369	0.972	0.951	1.107	1.147	1.365	1.308	0.546
	Southernmost Thailand	2.691	2.685	2.368	1.088	0.377	0.929	0.977	1.129	1.152	1.352	1.297	0.557
	Terutau Id.	2.734	2.706	2.449	1.109	0.380	0.928	0.911	1.070	1.144	1.361	1.292	0.539
		GPB	LBS	LBR	LBM	LBSR	HAB	LC	LMR2	TM	HM	AHR	OHR
Male	Korat	0.634	1.028	1.996	1.617	1.227	0.701	1.785	0.542	0.194	0.438	0.930	0.891
	Ranong	0.637	1.030	2.009	1.636	1.255	0.695	1.760	0.546	0.202	0.421	0.912	0.866
	Southernmost Thailand	0.642	1.043	1.993	1.660	1.252	0.716	1.744	0.548	0.195	0.415	0.924	0.879
	Terutau Id.	0.618	1.085	2.021	1.655	1.245	0.690	1.797	0.542	0.197	0.424	0.948	0.881
Female	Korat	0.643	1.032	1.972	1.620	1.197	0.683	1.729	0.547	0.198	0.435	0.929	0.868
	Ranong	0.668	1.022	2.007	1.654	1.236	0.693	1.762	0.557	0.191	0.423	0.921	0.880
	Southernmost Thailand	0.652	1.027	1.990	1.637	1.253	0.712	1.730	0.561	0.201	0.418	0.911	0.866
	Terutau Id.	0.649	1.094	2.047	1.647	1.204	0.675	1.795	0.547	0.191	0.423	0.958	0.903

tions. The scattergrams from the canonical discriminant analysis are shown in Fig. 2, and the coefficients of the discriminant function are arranged in Table 8. The four popu-

lations were obviously distinguished in the plots of the discriminant scores unlike the principal component charts from the same osteometrical data.

Table 6. Significant differences of proportion indices among various populations

	PL	ML	CL	SL	MWN	LBO	LBC	GNB	GOB	MPL	DL	LMR1	GPB	LBS	LBR	LBM	LBSR	HAB	LC	LMR2	TM	HM	AHR	OHR
Male																								
KXR	0.480	0.777	0.120	0.024	0.480	0.034	0.258	0.034	0.024	0.203	0.048	0.157	0.888	0.777	0.671	0.396	0.066	0.396	0.258	0.671	0.480	0.157	0.258	0.090
KXS	0.657	0.824	0.505	0.003	0.824	0.032	0.103	0.008	0.008	0.138	0.018	0.088	0.335	0.415	0.604	0.088	0.088	0.159	0.054	0.335	0.941	0.032	0.459	0.505
KXT	0.201	0.136	0.033	0.055	0.088	0.011	0.011	0.831	0.088	0.831	0.033	0.201	0.088	0.011	0.286	0.201	0.286	0.136	0.670	0.522	0.670	0.136	0.136	0.670
RXS	0.899	0.526	0.291	0.009	0.205	0.866	0.499	0.190	0.767	0.704	0.767	0.331	0.353	0.311	0.331	0.031	0.767	0.002	0.375	0.704	0.254	0.176	0.118	0.139
RXT	0.023	0.017	0.002	0.745	0.515	0.329	0.001	0.002	0.664	0.129	0.664	0.664	0.051	0.001	0.386	0.104	0.329	0.448	0.065	0.745	0.588	0.828	0.013	0.051
SXT	0.071	0.199	0.002	0.162	0.129	0.221	0.000	0.000	0.771	0.199	0.953	1.000	0.012	0.003	0.036	0.953	0.484	0.006	0.005	0.683	0.560	0.115	0.009	1.000
Female																								
KXR	0.245	0.245	0.439	0.053	0.439	0.245	1.000	0.053	0.699	0.699	0.699	0.121	0.053	1.000	0.121	0.121	0.053	1.000	0.121	0.439	0.245	0.245	1.000	0.699
KXS	0.501	0.441	0.178	0.021	0.700	0.034	0.043	0.054	1.000	0.149	0.336	0.923	0.847	0.923	0.501	0.290	0.054	0.054	0.773	0.501	0.773	0.124	0.248	0.923
KXT	0.439	1.000	0.121	0.121	1.000	0.439	0.439	1.000	0.121	0.439	0.121	0.121	1.000	0.121	0.121	0.121	0.439	0.121	0.121	1.000	0.121	0.439	0.439	0.121
RXS	0.603	0.419	0.488	0.083	0.326	0.011	0.119	0.073	0.644	0.299	0.166	0.356	0.119	0.729	0.166	0.225	0.094	0.050	0.083	0.954	0.050	0.419	0.525	0.386
RXT	0.121	0.439	0.053	0.699	0.699	0.439	0.245	0.121	0.699	0.439	0.121	0.439	0.053	0.053	0.053	0.699	0.053	0.053	0.245	0.439	0.439	0.699	0.245	0.245
SXT	0.124	0.441	0.034	0.336	0.773	1.000	0.027	0.034	0.441	0.564	0.923	0.290	0.847	0.021	0.043	0.564	0.054	0.054	0.043	0.386	0.149	0.501	0.068	0.043

Each value indicates the limit percentage in which the significant differences are confirmed between the two populations.

Fig. 1. The principal component chart of skulls of the gray-bellied squirrel between the first and second transformed variables from 24 measurements. M) Male, F) Female. The symbols plotted in the chart are shown in Table 1. Horizontal axis, the first principal component. Vertical axis, the second principal component.

DISCUSSION

Since the important measurements as PL, ML and CL showed statistical difference between K, R, S populations (Tables 3 and 4), the traditional Bergmann's rule may be established among the three mainland populations. The influences of the Isthmus of Kra located in peninsular Thailand should be appreciated as an ancient zoogeographical barrier. We confirmed the sympatric distribution in the common tree shrew populations including the two independent species, *Tupaia glis* and *Tupaia belangeri*, in the south region of the Isthmus of Kra including original localities of R and S populations in the present study [5–7]. So, we can suggest that both R and S populations may contain the complicated genetic races influenced by the Isthmus of Kra. Indeed, the principal component charts did not separate R population from S population (Fig. 1). Although K population has been thought to belong simply to north group, we suggest that R and S population may contain individuals from both north and south groups separated by the ancient Kra barrier.

We noticed that the skull size of T population was not sta-

tistically different from that of S population in many measurements in each sex (Tables 3 and 4). The skin color of this population has been thought to be similar to that of *Callosciurus caniceps concolor* and *Callosciurus caniceps fallax*, the peninsular Thailand and related island populations in skin color character [2, 11]. Since Terutau Island is located near the border between Thailand and Malaysia, we think that the north group of the Isthmus of Kra may not be genetically related to this population. We suggest that the island-isolation effects in Terutau Island had influences on the skull size and shape of the ancestors in south group of mainland. Geographical factors of the size similarity between S and T populations should be examined in the future.

The present data in the proportional analysis (Tables 5 and 6) indicated the adaptational strategy in field behavior of each population. The smaller LBC indicated that the interorbital space was narrower and that the binocular sense has been well-developed in T population. It suggests that the skull has been highly adapted to arboreal behavior. In contrast, the large LBO suggests that the animal was more adaptive for terrestrial life in K population. The large GNB

Fig. 2. The visualized results of the canonical discriminant analysis among 4 populations. Scattergrams showing the individual scores on the discriminant axes 1 (horizontal) and 2 (vertical). The locality symbols are explained in Table 1. M) Male. The first function comprises 66.4% of the variance and the second function 26.9%. F) Female. The first function comprises 69.8% of the variance and the second function 20.3%.

Table 7. Character loading factors observed from the principal component analysis

		PL	ML	CL	SL	MWN	LBO	LBC	GNB	GOB	MPL	DL	LMR1
Male	PC1	0.979	0.980	0.933	0.954	0.750	0.709	0.765	0.534	0.876	0.936	0.928	0.666
	PC2	-0.043	-0.056	-0.243	-0.045	-0.024	0.233	0.569	0.751	-0.004	-0.129	-0.034	-0.030
Female	PC1	0.960	0.967	0.948	0.942	0.724	0.928	0.730	0.754	0.914	0.930	0.949	0.650
	PC2	-0.117	-0.102	-0.170	-0.154	-0.398	0.078	0.400	0.160	-0.060	-0.114	0.014	0.633

		GPB	LBS	LBR	LBM	LBSR	HAB	LC	LMR2	TM	HM	AHR	OHR	P.V.E
Male	PC1	0.809	0.842	0.951	0.905	0.926	0.836	0.914	0.775	0.571	0.893	0.879	0.870	72.13
	PC2	0.256	-0.315	-0.095	-0.046	0.027	0.295	-0.115	-0.039	-0.292	-0.113	-0.168	0.033	5.97
Female	PC1	0.702	0.826	0.939	0.941	0.827	0.736	0.898	0.588	0.329	0.888	0.878	0.886	70.53
	PC2	0.417	-0.212	-0.107	-0.033	0.223	0.127	-0.039	0.674	0.359	-0.262	-0.254	-0.261	8.03

Percentages of the variation explained by each factor (*).

and GOB indicated that the braincase has been enlarged bilaterally in this population, but the functional significance of the characters cannot be easily explained.

The positive loading factors and the explaining percentage of the first principal component scores suggest that the size factor contributes to the separation between the populations in this analysis (Table 7 and Fig. 1). The plots of R population could not be separated from those of S population in the principal component analysis, but the similarities were not so obvious that canonical discriminant analysis could distinguish these two populations (Figs. 1 and 2).

In this study, the sample size was smaller in female of K and T populations. The standard deviations were larger in female than in male at least in K and T populations. The number of skulls should be larger in the future. However, we can point out that the statistical tests and the multivariate analyses were valid also in female as well as in male in this examination.

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Table 8. Coefficients in each discriminant function

		PL	ML	CL	SL	MWN	LBO	LBC	GNB	GOB	MPL	DL	LMR1		
male	CAV1	-0.777	1.564	-1.731	0.579	-0.410	-0.048	-1.322	0.464	0.919	1.107	-1.312	0.093		
	CAV2	0.792	0.024	2.030	0.165	0.455	0.205	-0.279	-0.850	0.285	-2.203	-0.201	-0.442		
	CAV3	0.780	-0.640	0.165	0.598	1.018	-0.307	-0.199	0.543	0.422	-1.071	-0.209	1.139		
female	CAV1	-6.322	8.775	-0.100	-5.477	8.955	1.871	-0.062	0.715	-5.431	-4.013	-0.528	-0.811		
	CAV2	-3.387	5.345	-0.694	-0.641	0.337	-0.481	-0.410	0.663	2.386	1.602	0.305	-0.640		
	CAV3	0.072	0.079	0.081	0.817	-4.016	-0.848	-0.052	0.684	-1.224	-4.530	4.399	-6.781		
		GPB	LBS	LBR	LBM	LBSR	HAB	LC	LMR2	TM	HM	AHR	OHR	c. t.	e. v.
male	CAV1	-0.636	3.668	-1.427	0.814	-0.635	-1.674	-0.317	-0.744	-0.570	-1.909	-0.353	1.538	44.920	10.071
	CAV2	0.831	-0.201	-0.553	-0.758	-1.079	-1.862	0.414	-0.445	-0.907	-0.762	0.942	0.417	4.459	4.084
	CAV3	-0.891	-0.491	0.175	-0.022	0.977	-1.448	0.450	-1.326	1.449	0.202	-0.423	-0.924	0.135	1.018
female	CAV1	-9.240	1.441	0.792	-2.645	1.250	1.008	3.039	3.946	-3.549	1.389	-1.101	1.713	73.642	31.225
	CAV2	-2.668	0.935	-2.998	-0.821	0.846	0.170	-2.384	4.203	9.357	-0.101	-1.856	3.665	-46.237	9.090
	CAV2	2.675	-2.225	1.848	0.006	2.267	1.229	-0.718	0.768	0.606	1.672	-0.729	0.498	-17.417	4.421

F-values are 2.297 in male, and 2.922 in female. c.t.: constant term. e.g.: eigen values.

Appendix 1. Specimen No. (Mammal Division, Smithsonian Institution) used in this study

1. Male

Korat

221158 241436 241437 241438

Ranong

356707 356708 356709 356713 356716 356718 356719 356722 356727 356728

Southernmost Thailand

49467 83235 83238 83239 83496 251683 251686 251687 251697 254737

257770 257775 257777 257782 258914 259817 259818 355619 355625 355626

535166

Terutau Id.

123919 123920 123921 123923 123924 123926

2. Female

Korat

241439 255737

Ranong

356715 356717 356720 356723 356726

Southernmost Thailand

83495 251684 251685 253424 253560 254736 256869 256871 256872 257767

257768 257776 257779 257781 258915 258916 355620 355623 355632 356705

356706 535161 535163 535167

Terutau Id.

123922 123925

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