Geographical Variation of Skull Morphology and Its Functional Significances in the Red-Cheeked Squirrel

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ABSTRACT. Skulls of the red-cheeked squirrel (*Dremomys rufigenis*) from various geographical locations: Malaysia (peninsular area), Vietnam (south district)-Laos, and Thailand (north district) were osteometrically examined. The skull size of the squirrels in the southern (Malaysia) population was fundamentally larger than that in the northern (Vietnam, Laos and Thailand) populations. The proportion indices indicated that the splanchnocranium was relatively longer in the Malaysia population, and that the interorbital space was narrower in Vietnam-Laos, and Thailand populations. We suggest that the long nose and laterally-oriented orbits in the skull may be better adapted for terrestrial-insectivorous life in the Malaysia population and the binocular sense facilitated by rostrally-oriented eyes contributes to the arboreal-fruit eating behavior in the two northern populations. The Malaysia population was clearly distinguished from the other populations by the principal component analysis. We suggest that the geographical barrier of the Isthmus of Kra influences the morphological variation of the skull among the squirrel populations.

KEY WORDS: *Dremomys rufigenis*, geographical variation, osteometry, red-cheeked squirrel, skull.

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The Indomalayan Region has about 30 species of the Family Sciuridae with the geographical variations yielding different morphological characteristics [2, 3]. Among these species, the red-cheeked squirrel (*Dremomys rufigenis*) is an arbo-terrestrial species that is widely distributed in the southern part of China, and Indochinese region and Malayan Peninsula [2]. We thought that the geographical variations and adaptational strategies in diet and locomotion have been established in the skull morphology in each population of the red-cheeked squirrel since the species is largely distributed over various natural environments. In this study, therefore, the osteometrical study and statistical analysis were carried out in the skull of the red-cheeked squirrel to clarify the geographical variations and adaptational significances in diet and locomotion.

MATERIALS AND METHODS

We examined 77 skulls of the red-cheeked squirrel (*Dremomys rufigenis*) that have been stored in the Mammal Division of the National Museum of Natural History in the Smithsonian Institution. Sex determination was dependent on the description of biological data of specimens. Only specimens with fully erupted molars were considered to be adults. The composition of origin and sex, and locality symbols are shown in Table 1. Some skulls of Bornean mountain ground squirrel (*Dremomys everetti*) were also examined as a control to compare the interspecies variations

in the Genus *Dremomys* (Table 1). Skull measurements were obtained with vernier calipers to the nearest 0.05 mm. Measurements are defined in Table 2, and were based on Driesch [4]. Differences in mean values among localities were examined by Student's *t*-test. The proportion indices were the quotients of each measurement value divided by the geometric mean of all measurement values. The significant differences of proportion indices were examined among localities by nonparametric U-test using software Statistica (Statsoft Inc., Tokyo, Japan). The principal component analysis was carried out with all measurement data to clarify the geographical variation among localities. A package software for multivariate analysis (Shakai-Joho Service, Tokyo, Japan) added to Microsoft Excel 98 was used for this analysis.

RESULTS

Mean values and standard deviations of the 25 measurements are given in Table 3. Statistical differences in these measurements between all combinations of populations are shown in Table 4. The mean values of the important measurements such as PL, ML, CL, SL, ZW, and LC were significantly larger in M population than in the other two populations in many cases except for male LC between M and V-L populations, and female ML, CL, and LC between M and T populations. M population was from the southern side of the Isthmus of Kra, whereas V-L and T populations

Table 1. Locality and sex composition of the specimens

Species	Origin of Specimens	Symbols	Male	Female
<i>Dremomys rufigenis</i>	Malaysia (Pahang, Selangor)	M	15	7
	Vietnam (South District)	V	29	27
	Laos (Bolvane Plateau, Louangphrabang)	L	1	1
	Thailand (Chiang Mai Area)	T	3	7
<i>Dremomys everetti</i>	Borneo (Mt. Kinabalu)	☆	4	3
Total			32	45

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
Zygomatic width	ZW
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

were from the northern side, and we could conclude that the southern population had fundamentally larger skulls than the northern two populations. The measurements of GOB, LBS, LBR and LBM did not show the significant differences between M and the other V-L and T populations. The length and width related to the neurocranium were not different between northern and southern populations. The skull of *Dremomys everetti* was much smaller than that of the red-cheeked squirrel (*Dremomys rufigenis*) (Tables 3 and 4).

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 proportions of SL, LBO, LBC and MPL were larger in M population than in V-L and T populations. Some combinations did not show

the significant differences, however these population indices were the largest in M population. The large SL and MPL indicated that the splanchnocranium was relatively longer in M population. The small LBO and LBC indicated that interorbital space was narrower in V-L and T populations. In contrast, the indices LBS and LBR in both sexes and LBM in male were larger in V-L and T populations than in M population.

The principal component charts are shown in Fig. 1, and loading factors are arranged in each measurement (Table 7). The plots of *Dremomys rufigenis* were obviously separated into the two groups: 1) M and 2) V, L, and T. The plots were intermingled among V, L, and T populations in their distribution. *Dremomys everetti* was obviously separated from *Dremomys rufigenis* in the charts. The measurements, which contributed to the first principal component, are PL, ML and CL, and to the second principal component, are GNB, LBC, and LBSR in both sexes (Table 7).

DISCUSSION

The red-cheeked squirrel has actually been separated into the southern subspecies *Dremomys rufigenis rufigenis* from the Malayan Peninsula and the northern subspecies *Dremomys rufigenis belfieldi* from the Indochinese region by its skin color pattern [1]. The present results indicated that M population had larger values in PL, ML, CL, SL, ZW, and LC (Tables 3 and 4), and larger proportion indices in SL, LBO, LBC and MPL than in the northern populations (Tables 5 and 6). The large skull size in the southern population was consistent with the case of southern *Tupaia glis* and northern *Tupaia belangeri* [6, 8]. The principal component charts also showed the morphological distinction of M population from V, L and T populations. We suggest that the two subspecies distinction of the red-cheeked squirrel may be related to the geographical barrier of the Isthmus of Kra as shown in the two independent species, *Tupaia glis* and *Tupaia belangeri* by the osteometrical and karyological methods [6, 8, 9].

It was reported that the red-cheeked squirrel was arbo-terrestrial and fed on insects as well as plant matter from the data of stomach contents [10, 11], and we think that the long nose plays a role in searching for insects and invertebrates in the surface layer of the soil. The long splanchnocranium functionally helps and supports the terrestrial-insectivorous behavior, but is not adaptationally related to the arboreal-

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

	PL	ML	CL	SL	ZW	MWN	LBO	LBC	GNB	GOB	MPL	DL	LMR1	GPB	LBS	LBR	LBM	LBSR	HAB	LC	LMR2	TM	HM	AHR	OHR
<i>Dremomys rufigenis</i>																									
Malaysia																									
Male	51.65	51.47	45.33	24.15	29.35	6.59	16.15	18.94	21.17	20.85	27.55	25.19	10.19	11.43	18.02	35.29	28.55	23.02	14.05	31.80	9.96	3.47	6.95	16.09	15.38
	1.30	1.24	1.22	0.83	0.83	0.41	0.39	0.45	0.53	0.53	0.92	0.68	0.27	0.40	0.75	0.97	0.68	0.86	0.48	0.81	0.41	0.26	0.32	0.61	0.56
Female	52.36	52.01	45.64	24.70	30.03	6.56	16.68	19.16	21.56	20.96	27.84	25.17	10.09	11.51	18.16	35.54	28.90	23.51	14.14	32.12	9.90	3.48	6.90	16.30	15.34
	0.99	0.87	1.10	0.79	0.77	0.29	0.63	0.53	0.30	0.48	0.78	0.71	0.30	0.28	0.50	0.67	0.60	0.54	0.33	0.58	0.15	0.10	0.27	0.36	0.52
Vietnam and Laos																									
Male	50.39	50.32	44.52	23.02	28.93	6.43	15.30	17.63	20.26	20.69	26.60	24.71	9.68	11.13	18.14	35.03	28.25	22.39	13.84	31.33	9.85	3.52	7.17	16.20	15.32
	1.37	1.44	1.52	0.91	0.92	0.37	0.68	0.51	0.65	0.48	0.91	0.68	0.33	0.32	0.72	1.02	0.74	0.59	0.45	1.08	0.36	0.16	0.41	0.69	0.69
Female	50.39	50.21	44.61	23.15	29.00	6.46	15.28	17.44	19.88	20.38	26.65	24.89	9.93	11.16	18.14	34.83	28.05	22.12	13.50	31.44	9.95	3.54	7.11	16.16	15.37
	1.31	1.29	1.30	0.84	1.03	0.42	0.87	0.70	0.63	0.60	0.82	0.70	0.29	0.30	0.72	1.19	0.89	0.65	0.48	0.89	0.45	0.23	0.45	0.57	0.64
Thailand																									
Male	49.07	48.90	42.90	21.25	27.00	6.38	14.92	17.82	20.88	20.72	25.60	23.28	9.37	11.45	17.73	34.68	28.65	22.63	14.03	29.83	9.82	3.35	6.65	15.35	14.57
	2.25	2.32	3.08	1.94	2.16	0.54	1.75	0.65	0.49	0.64	1.00	1.61	0.32	0.35	1.79	2.20	1.57	0.67	0.36	2.18	0.38	0.43	0.58	1.50	1.52
Female	50.58	50.79	44.86	22.92	28.81	6.66	15.66	18.03	20.82	20.91	26.77	24.37	10.04	11.29	18.31	35.67	28.94	22.64	14.21	31.74	9.83	3.46	6.99	16.43	15.61
	1.76	1.76	1.80	1.04	1.14	0.28	0.68	0.47	0.51	0.77	0.91	0.94	0.39	0.27	1.02	1.39	1.09	0.77	0.51	1.03	0.51	0.22	0.47	0.72	0.61
<i>Dremomys everetti</i>																									
Borneo																									
Male	43.95	43.51	38.90	19.73	24.80	5.30	12.75	15.35	18.51	18.33	23.98	21.44	8.39	9.99	15.24	30.63	24.91	19.41	12.25	27.98	8.11	3.00	5.68	13.93	13.24
	1.75	1.94	2.41	0.95	1.73	0.27	0.80	0.40	0.57	0.44	0.86	1.09	0.32	0.17	1.52	2.34	0.96	0.52	0.16	1.57	0.14	0.11	0.43	0.81	0.91
Female	43.75	43.02	38.80	19.72	25.37	5.48	12.88	15.72	18.38	18.18	23.43	21.57	8.32	9.92	15.53	30.18	24.72	19.52	12.47	27.90	8.10	3.25	5.68	13.80	13.25
	1.78	1.98	2.08	0.68	1.14	0.41	0.14	0.12	0.14	0.64	1.08	1.07	0.15	0.10	0.88	1.34	0.90	0.10	0.25	1.01	0.28	0.33	0.08	0.68	0.78

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

Table 4. Significant differences of measurements among three populations in the red-cheeked squirrel

	PL	ML	CL	SL	ZW	MWN	LBO	LBC	GNB	GOB	MPL	DL	LMR1
Male													
Malaysia X Vietnam+Laos	0.003	0.006	0.040	0.000	0.071	0.101	0.000	0.000	0.000	0.163	0.001	0.016	0.000
Malaysia X Thailand	0.006	0.006	0.013	0.000	0.002	0.230	0.008	0.001	0.199	0.355	0.002	0.001	0.000
Vietnam+Laos X Thailand	0.071	0.065	0.059	0.003	0.002	0.419	0.214	0.282	0.060	0.467	0.042	0.002	0.063
Female													
Malaysia X Vietnam+Laos	0.000	0.001	0.032	0.000	0.010	0.276	0.000	0.000	0.000	0.011	0.001	0.179	0.109
Malaysia X Thailand	0.019	0.064	0.176	0.002	0.019	0.275	0.007	0.001	0.003	0.443	0.018	0.049	0.411
Vietnam+Laos X Thailand	0.378	0.163	0.338	0.269	0.341	0.129	0.142	0.022	0.000	0.027	0.364	0.054	0.200

	GPB	LBS	LBR	LBM	LBSR	HAB	LC	LMR2	TM	HM	AHR	OHR
Male												
Malaysia X Vietnam+Laos	0.004	0.298	0.204	0.094	0.003	0.075	0.073	0.174	0.223	0.036	0.315	0.386
Malaysia X Thailand	0.474	0.319	0.217	0.429	0.237	0.474	0.005	0.291	0.253	0.107	0.076	0.054
Vietnam+Laos X Thailand	0.056	0.210	0.311	0.213	0.255	0.238	0.022	0.446	0.072	0.025	0.039	0.060
Female												
Malaysia X Vietnam+Laos	0.004	0.468	0.072	0.011	0.000	0.001	0.032	0.383	0.236	0.125	0.263	0.452
Malaysia X Thailand	0.077	0.366	0.410	0.470	0.015	0.380	0.207	0.365	0.439	0.342	0.339	0.194
Vietnam+Laos X Thailand	0.154	0.302	0.058	0.015	0.039	0.001	0.220	0.265	0.206	0.264	0.143	0.191

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

fruit eating life in various Scandentia species [5, 7]. So, we suggest that the skull of M population with larger proportion indices in splanchnocranium (Tables 5 and 6) has been highly adapted for terrestrial-insectivorous life rather than arboreal-fruit-eating life, although both arboreal and terrestrial behaviors have been observed in the red-cheeked squirrel [2, 10]. In addition, the narrower interorbital space demonstrated that the binocular sense was facilitated in V-L and T populations (Tables 5 and 6). We also suggest that the higher arboreal and fruit-eating adaptation has been established in V-L and T populations rather than in M population.

The larger proportion indices of LBR in V-L and T populations indicated that the distances between the ventral margin of the foramen magnum and the dorsal surface points of the skull were relatively longer in V-L and T populations. It suggests that the opening angle of the foramen magnum

may be ventrally shifted. This character enables the animals to bend the skull rostral-ventrally and possess the visual sense in ventral direction on branches [12]. It is also consistent with the hypothesis that the behavior strategy is different between M and two other populations and that M population may be more adaptable to the terrestrial life than V-L and T populations. Since the behavior data have not been compared among populations in the red-cheeked squirrel, the comparative field study in this species will be needed in the future.

The principal component charts show the large skulls of the southern population in the horizontal axis (Fig. 1). The loading factors and the explaining percentage of the first principal component suggest that the size factor strongly contributes to the separation between the two groups in the charts (Table 7). Since we could not use the skulls from the

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

		PL	ML	CL	SL	ZW	MWN	LBO	LBC	GNB	GOB	MPL	DL	LMR1
<i>Dremomys rufigenis</i>														
Male	Malaysia	2.753	2.744	2.417	1.287	1.565	0.351	0.861	1.010	1.129	1.112	1.469	1.343	0.543
	Vietnam and Laos	2.740	2.736	2.421	1.251	1.573	0.350	0.832	0.959	1.102	1.125	1.446	1.344	0.526
	Thailand	2.736	2.726	2.389	1.183	1.503	0.355	0.830	0.994	1.165	1.156	1.428	1.297	0.523
Female	Malaysia	2.768	2.749	2.412	1.305	1.587	0.347	0.881	1.013	1.140	1.108	1.472	1.330	0.533
	Vietnam and Laos	2.744	2.734	2.429	1.260	1.579	0.352	0.831	0.950	1.083	1.110	1.451	1.356	0.541
	Thailand	2.721	2.732	2.413	1.233	1.550	0.358	0.843	0.970	1.121	1.125	1.440	1.311	0.541
<i>Dremomys everetti</i>														
Male	Borneo	2.765	2.737	2.446	1.241	1.559	0.333	0.802	0.967	1.166	1.154	1.509	1.348	0.528
Female	Borneo	2.739	2.693	2.429	1.235	1.589	0.343	0.807	0.985	1.152	1.139	1.467	1.350	0.521

		GPB	LBS	LBR	LBM	LBSR	HAB	LC	LMR2	TM	HM	AHR	OHR
<i>Dremomys rufigenis</i>													
Male	Malaysia	0.610	0.961	1.881	1.522	1.227	0.749	1.695	0.531	0.185	0.370	0.858	0.820
	Vietnam and Laos	0.605	0.986	1.904	1.536	1.218	0.753	1.703	0.536	0.192	0.390	0.880	0.833
	Thailand	0.640	0.987	1.932	1.597	1.263	0.783	1.662	0.549	0.186	0.370	0.854	0.810
Female	Malaysia	0.608	0.960	1.878	1.528	1.243	0.747	1.698	0.523	0.184	0.365	0.862	0.811
	Vietnam and Laos	0.608	0.988	1.896	1.527	1.205	0.735	1.712	0.542	0.193	0.387	0.880	0.837
	Thailand	0.607	0.985	1.919	1.557	1.218	0.764	1.708	0.529	0.186	0.376	0.884	0.840
<i>Dremomys everetti</i>													
Male	Borneo	0.629	0.957	1.925	1.567	1.222	0.772	1.759	0.511	0.189	0.357	0.876	0.832
Female	Borneo	0.621	0.972	1.890	1.548	1.223	0.781	1.747	0.507	0.203	0.356	0.864	0.829

Table 6. Significant differences of proportion indices among three populations of the red-cheeked squirrel

		PL	ML	CL	SL	ZW	MWN	LBO	LBC	GNB	GOB	MPL	DL	LMR1
Male														
	Malaysia X Vietnam+Laos	0.238	0.455	0.613	0.000	0.485	0.923	0.001	0.000	0.014	0.067	0.034	0.791	0.002
	Malaysia X Thailand	0.441	0.374	0.260	0.008	0.021	0.515	0.314	0.214	0.173	0.051	0.066	0.011	0.139
	Vietnam+Laos X Thailand	0.851	0.661	0.168	0.015	0.007	0.573	0.950	0.091	0.028	0.091	0.234	0.009	0.616
Female														
	Malaysia X Vietnam+Laos	0.053	0.076	0.343	0.002	0.364	0.536	0.001	0.000	0.001	0.741	0.187	0.026	0.284
	Malaysia X Thailand	0.025	0.110	0.848	0.003	0.048	0.142	0.013	0.009	0.180	0.277	0.064	0.110	0.949
	Vietnam+Laos X Thailand	0.099	0.967	0.174	0.011	0.021	0.458	0.433	0.063	0.021	0.138	0.303	0.000	0.621

		GPB	LBS	LBR	LBM	LBSR	HAB	LC	LMR2	TM	HM	AHR	OHR
Male													
	Malaysia X Vietnam+Laos	0.531	0.020	0.054	0.194	0.202	0.647	0.289	0.455	0.097	0.001	0.001	0.048
	Malaysia X Thailand	0.314	0.441	0.021	0.008	0.139	0.038	0.086	0.441	0.859	0.859	0.859	0.515
	Vietnam+Laos X Thailand	0.168	0.851	0.060	0.007	0.039	0.039	0.060	0.491	0.707	0.103	0.210	0.260
Female													
	Malaysia X Vietnam+Laos	0.837	0.007	0.058	0.621	0.012	0.266	0.174	0.035	0.012	0.004	0.011	0.021
	Malaysia X Thailand	0.655	0.142	0.025	0.110	0.225	0.064	0.277	0.848	0.749	0.338	0.048	0.085
	Vietnam+Laos X Thailand	0.967	0.967	0.063	0.026	0.266	0.008	0.592	0.248	0.083	0.149	0.564	0.564

localities close to the Isthmus of Kra but from Malaysia, Vietnam and North Thailand, the materials around the Isthmus of Kra will be needed to detail the geographical separation between the northern and southern groups in this species.

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Fig. 1. The principal component charts of skulls of the red-cheeked squirrel between the first and second transformed variables from 25 measurements. A) male, B) female. The symbols plotted in the charts are shown in Table 1. Horizontal axis, the first principal component. Vertical axis, the second principal component.

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

		PL	ML	CL	SL	ZW	MWN	LBO	LBC	GNB	GOB	MPL	DL	LMR1
Male	PC1	0.986	0.992	0.978	0.944	0.934	0.764	0.890	0.736	0.604	0.879	0.916	0.940	0.723
	PC2	0.083	0.048	-0.142	0.029	-0.144	-0.036	0.163	0.586	0.650	0.035	0.053	-0.097	0.427
Female	PC1	0.986	0.991	0.980	0.936	0.930	0.735	0.863	0.735	0.656	0.899	0.932	0.911	0.682
	PC2	0.038	0.009	-0.150	0.068	-0.037	-0.067	0.313	0.605	0.672	-0.024	0.029	-0.251	-0.043

		GPB	LBS	LBR	LBM	LBSR	HAB	LC	LMR2	TM	HM	AHR	OHR	P.V.E.*
Male	PC1	0.605	0.875	0.944	0.913	0.868	0.746	0.922	0.622	0.599	0.790	0.902	0.880	86.19
	PC2	0.408	-0.280	-0.114	0.028	0.318	0.318	-0.187	0.355	-0.137	-0.308	-0.214	-0.187	3.90
Female	PC1	0.816	0.878	0.942	0.904	0.864	0.712	0.932	0.539	0.498	0.766	0.895	0.809	85.41
	PC2	0.067	-0.278	-0.125	0.029	0.376	0.360	-0.090	-0.250	-0.368	-0.388	-0.216	-0.276	4.35

Percentages of the variation explained by each factor (*). PC1, the first principal component. PC2, the second principal component.

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