Relative Growth of the Skull in the Laboratory-reared Smith's Red-backed Vole, Eothenomys smithii and So-called "Kage" Red-backed Vole, E. kugeus

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Relative Growth of the Skull in the Laboratory-reared Smith's Red-backed Vole, *Eothenomys smithii* and So-called "Kage" Red-backed Vole, *E. kageus**

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The relative growth of the skull was analyzed in laboratory-reared *E. smithii* and *E. Kageus*. For 15 dimensions, the relative growth coefficients (α) of the allometry formula were calculated against the condylobasal length. Regarding the dimensions parallel to the long axis of the *E. smithii* skull (the nasal, frontal, parietal, interparietal and occipital lengths) and those parallel to the short axis (the rostral, zygomatic, parietal and cranial widths), the α was lowest in the interparietal length and parietal width, and highest in the nasal length and zygomatic width. The highest α value among all dimensions existed in the mandibular height. The α values in *E. kageus* had the same tendency as in *E. smithii,* except for the insignificance of the correlation in some dimensions with a low correlation coefficient. In particular, comparisons of the nine dimensions having a relatively high correlation coefficient showed no significant difference between *E. smithii* and *E. kageus*. Therefore, it is concluded from the viewpoint of the relative growth that *E. kageus* is not distinguished from *E. smithii*.

INTRODUCTION

The Smith's red-backed vole, *Eothenomys smithii* and "Kage" red-backed vole, *E. kugeus* are said to occur in the western and central parts of Japan, respectively (Imaizumi, 1957). However, the taxonomic validity of *E. kageus* has been debated from the viewpoint of the morphology (Jameson, 1961; Miyao *et al.*, 1964 ; Miyao, 1967a ; Tanaka, 1971; Aimi, 1980 ; Kaneko, 1985) and the karyology by a conventional staining method (Tsuchiya, 1970, 1981) ; but the dispute on the taxonomic position of these two "species" has still remained unsolved. In this connection, comparisons of the growth and development patterns and the karyotypes (G- and C-band patterns) between *E. smithii* and *E. kugeus* revealed that the characteristics of both the patterns in *E. kugeus* were essentially identical with those in *E. smithii* (Ando *et al.*, 1987, 1988b ; Ando and Shiraishi, 1988).

Morphological differences between species are interpreted as discrepancies in ratio of the size (the length, weight, volume, etc.) in each part of the body ; such differences in ratio are brought about by different growth rates, and closely related

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with a mode of life of the species concerned (Miyao et *al.*, 1962a ; Miyao, 1967b). In other words, morphological characteristics of a given species reflect the mode of life of the species. The relative growth is the most useful method for an analysis of changes in ratio of the size (Shimizu, 1957 ; Miyao and Yanagidaira, 1967). The aim of this study is to analyze the relative growth of the skull in *E. smithii* and *E. kageus*, and to compare the relative growth coefficients (α) of *E. smithii* with those of *E. kageus*.

MATERIALS AND METHODS

A total of 139 *E. smithii (sexes* combined) and 56 *E. kageus (sexes* combined) used in the present study were obtained from laboratory colonies which were derived from wild voles live-trapped in Kyushu and central Honshu, respectively (Ando *et al.*, 1988a ; Ando and Shiraishi, 1988). The age ranged from day 20 to day 1,280 in the former species, and from day '20 to day 350 in the latter species. After skulls were cleaned and dried up, the following 16 dimensions were measured (Fig. 1). The dimensions included

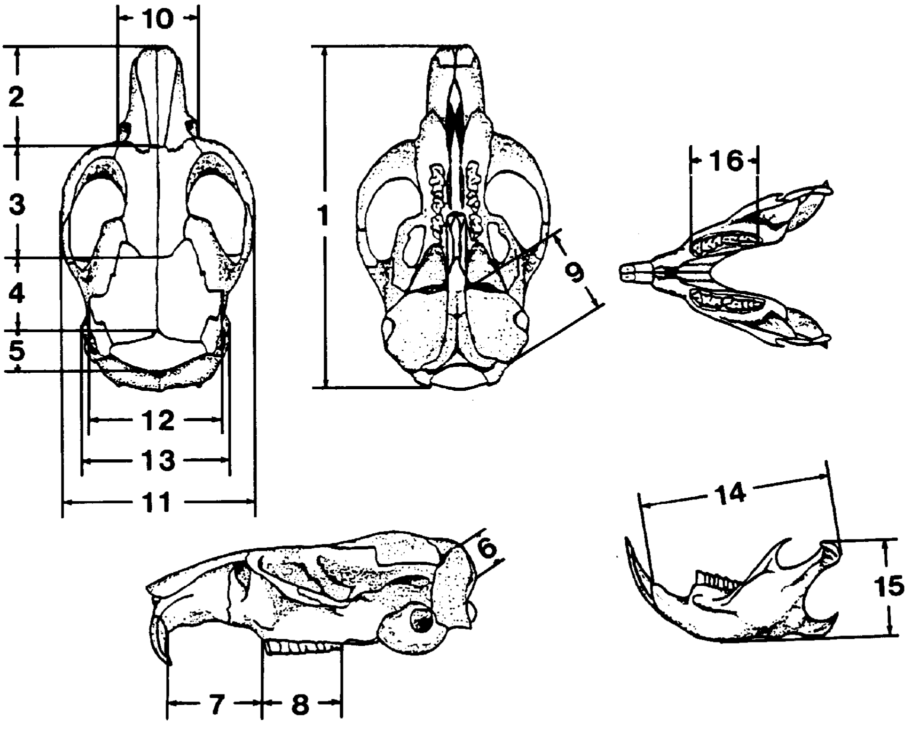

Fig. 1. The skull of *Eothenomys smithii* showing the cranial and mandibular measurements. 1, Condylobasal length; 2, Nasal length; 3, Frontal length; 4, Parietal length ; 5, Interparietal length ; 6, Occipital length ; 7, Diastema length ; 8, Length of upper molar series ; 9, Auditory bulla length ; 10, Rostra1 width ; 11, Zygomatic width ; 12, Parietal width ; 13, Cranial width ; 14, Mandibular length ; 15, Mandibular height ; 16, Length of lower molar series.

the condylobasal length, nasal length, frontal length, parietal length, interparietal length, occipital length, diastema length, length of upper molar series, auditory bulla length, rostra1 width, zygomatic width, parietal width, cranial width, mandibular length, mandibular height and length of lower molar series. Measurements were taken with sharp-pointed vernier calipers and recorded to the nearest 1/20 mm.

Applying the allometry formula $y = bx^{a}$ to our data, relative growth coefficients (a) and initial growth indices (log b) of the 15 dimensions against the condylobasal length were calculated. The biphasic allometry was determined using the method of Takai and Akiyoshi (1981). Out of 139 specimens of *E. smithii,* 76 specimens whose ages were less than or equal to day 350 were used for a comparison of a between *E. smithii* and *E. kageus*, in accordance with the oldest specimen (day 350) of *E. kageus*. The significant difference in a between both species were tested at the 5% significance level by the method of Zar (1984).

RESULTS

1. *Eothenomys smithii*

The relative growth coefficients (a), initial growth indices (log b) and correlation coefficients (r) of the 15 dimensions against the condylobasal length (a range of 17.05-26.10 mm) are given in Table 1. The correlation coefficients were high (0.8388-0.9529) in the seven dimensions of the skull, i. e. the nasal length, frontal length, diastema length, auditory bulla length, rostra1 width, zygomatic width and cranial width. On the

Table 1. Relative growth coefficients (a), initial growth indices (log b) and correlation coefficients (Y) of 15 dimensions against the condylobasal length in 139 laboratory-reared ***Eothenomys smithii*** (from day 20 to day 1,230).

Dimensions	a	log b	r
Nasal length	0.9895	-0.5053	0.8908
Frontal length	0.7204	-0.0741	0.8388
Parietal length	0.4633	-0.0099	0.4011
Interparietal length	0.3923	0.0224	0.3140
Occipital length	0.6251	-0.4267	0.4219
Diastema length	1.1111	-0.6912	0.9459
Length of upper molar series			
1st phase	0.4403	0.1076	0.6517
2nd phase	0.9188	-0.5248	0.6984
Auditory bulla length	0.7171	-0.1667	0.8694
Rostra1 width	1.1079	-0.8244	0.8898
Zygomatic width	1.1346	-0.4274	0.9529
Parietal width	0.2680	0.6417	0.4672
Cranial width	0.7809	-0.0090	0.9323
Mandibular length	0.8394	-0.0032	0.9598
Mandibular height	1.3009	-0.9531	0.9170
Length of lower molar series			
1st phase	0.4390	0.0954	0.7398
2nd phase	1.2193	−0.9454	0.6314

other hand, in the parietal length, interparietal length, occipital length and parietal width, the correlation coefficients were low (0.3140-0.4672) because of their wide individual variations, but the correlation was significant for these dimensions. Regarding the dimensions along the long axis of the skull, the relative growth coefficients (or) became lower in the following order : the nasal (0.9895), frontal (0.7204), parietal (0.4633) and interparietal (0.3923) lengths, followed by a slight increase in the occipital length (0.6251). As to the dimensions parallel to the short axis of the skull, the a was lowest in the parietal width (0.2680), and highest in the zygomatic width (1.1346). In addition, the α values of the mandibular length and height were 0.8394 and 1.3009, respectively; the latter value was highest in the 15 dimensions of the skull. The lengths of upper and lower molar series showed a biphasic allometry.

2. *Eothenomys kageus*

The range of the condylobasal length on the basis of our limited data in *E. kageus* (18.95-23.00 mm) was narrow. Table 2 shows the relative growth coefficients (α), initial growth indices (log b) and correlation coefficients (r) of the 15 dimensions against the condylobasal length. The values in *E. kageus* had the same tendency as in

Table 2. Relative growth coefficients (a), initial growth indices (log b) and correlation coefficients (r) of 15 dimensions against the condylobasal length in 56 laboratory-reared *Eothenomys kageus* (from day 20 to day 350).

Dimensions	α	log b	r
Nasal length	1.0477	−0.5579	0.7603
Frontal length	0.6654	-0.0052	0.6069
Parietal length	−	−	0.0345'
Interparietal length			-0.2276'
Occipital length			0.2389'
Diastema length	1.0827	-0.6384	0.8894
Length of upper molar series †	0.9272	-0.5199	0.8515
Auditory bulla length	0.9140	-0.4384	0.7906
Rostral width	0.8145	-0.4190	0.6454
Zygomatic width	1.1342	-0.4238	0.8971
Parietal width	0.2845	0.6118	0.5017
Cranial width	0.8523	-0.1156	0.8744
Mandibular length	0.7496	0.1201	0.8764
Mandibular height	1.3655	-1.0302	0.8416
Length of lower molar series †	0.7197	-0.2579	0.7727

*The correlation coefficient was not significant at the 0.05 level.
†The biphasic allometry was not recognized on the basis of our limited data, unlike *E. smithii*.

E. smithii. However, the significance of the correlation was not recognized in the parietal, interparietal and occipital lengths, all of which indicated low correlation coefficients in *E. smithii*. Unlike *E. smithii*, the biphasic allometry was not found in the lengths of upper and lower molar series.

DISCUSSION

The skulls of members belonging to the Microtinae are characterized by the short rostrum, the zygomatic arches which are strongly built and widely bowed laterally, the large and rounded auditory bulla, the hypsodont cheekteeth with a prismatic coronal pattern, and so forth (Hinton, 1926 ; Carleton and Musser, 1984), and they exhibit a stocky appearance as compared with slender skulls of the Murinae. Such characteristics are due to differences in growth rate of bones which compose the skull. In general, an interspecific comparison of the relative growth coefficients (α) has a taxonomical significance, because the a is an important index representing species specific characteristics in growth patterns (Shimizu, 1957).

The relative growth coefficients in *E. smithii* ranged from 0.2680 to 1.3009, suggesting the existence of various dimensions showing from a remarkably negative allometry to a positive allometry. As for the dimensions parallel to the long axis (the nasal, frontal, parietal, interparietal and occipital lengths) and those parallel to the short axis (the rostral, zygomatic, parietal and cranial widths), the α was lowest in the interparietal length and parietal width, so that the dead center of the skull resides apparently in the parietal and interparietal parts of the braincase. It has been known that the dimensions relevant to the braincase show a markedly negative allometry in *Microtus* ***mon** tebelli* (Watanabe, pers. comm.) and *Clethrionomys andersoni* (Miyao and Yanagidaira, 1967), supporting our results.

In Fig. 2 showing the dorsal view of the skulls of ***E. smithii, M. montebelli*** and *Rattus* ***norvegicus*** drawn to identical size, it is characteristic of *E. smithii* that the zygomatic arches are bowed laterally and the zygomatic width is rather broader-than the cranial width. In this connection, although *E. smithii* has the α of the cranial width which is almost equal to that of ***M. montebelli,*** the α of the zygomatic width is slightly higher in the former species than in the latter species (Table 3). Further, ***E. smithii (0.9895)*** is closer to ***M. montebelli*** (♂1.100, ♀1.011) in the α of the nasal length than ***R. norvegicus*** (♂ 1.327, ♀ 1.236). The α of the mandibular height is approximately 0.93 in ***M. montebelli,*** while it was highest among all dimensions in ***E. smithii*** (1.3009). Development of the zygomatic arches and the mandible is closely related to that of the

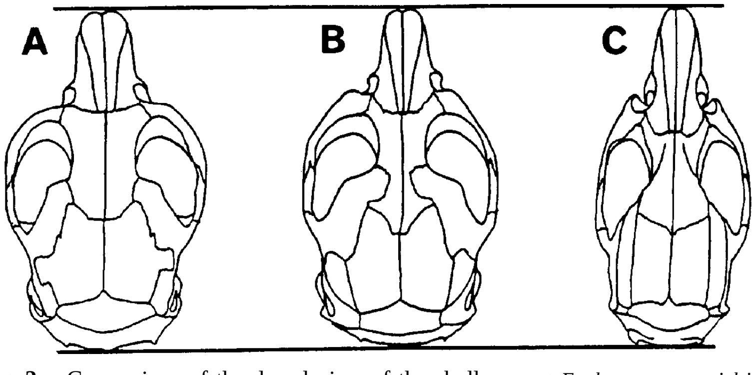

Fig. 2. Comparison of the dorsal view of the skull among *Eothenomys smithii* (A), *Microtus montebelli* (B) and *Rattus norvegicus (C).* The skulls were drawn to identical size for the benefit of easy comparison.

Table 3. Relative growth coefficients (a) of ten dimensions in three murid species (*Eothenomys* ***smithii,*** *Microtus* ***montebelli*** and *Rattus* ***norvegicus).***

Dimensions	*E.* ***smithii***	*M.* ***montebelli****		***R.*** *norvegicus* †	
	Sexes combined	♂	♀	♂	♀
Nasal length	0.9895	1.100	1.011	1.327	1.236
Frontal length	0.7204	0.528	0.767	0.827	0.856
Occipital length	0.6251			1.440	1.155
Diastema length	1.1111	1.050	1.177	1.264	1.252
Auditory bulla length	0.7171	0.823	0.977	—	
Rostral width	1.1079	0.974	0.946	—	
Zygomatic width	1.1346	0.878	0.833	0.948	1.036
Cranial width	0.7809	0.621	0.460		—
Mandibular length	0.8394	0.706	0.847	0.958	1.023
Mandibular height	1.3009	0.935	0.939		

*After Watanabe (pers. comm.), who adopted the basal length as a standard dimension instead of the condylobasal length.
†After Shimizu (1942).

masseter ; e. g. the ratio of the wet weight of the *musculus* ***masseter*** *lateralis* to the **dry** weight of the cranium has been reported to be larger in *E.* ***smithii*** and *M. montebelli* than in R. *norvegicus* (Miyao et ***al.,*** 1962b). From the above consideration, it can be said that the skull of *E.* ***smithii*** possesses the characteristics of the Microtinae from the standpoint of the relative growth. However, since the dimensions with the small α value in *E.* ***smithii*** show a low correlation coefficient (the parietal length, interparietal length, occipital length and parietal width), it may be necessary to examine more deeply the application of the allometry formula to such dimensions.

In order to compare the *E.* ***kageus*** skull with the *E.* ***smithii*** skull (less than or equal to 350 days of age ; 56 specimens in the former and 76 in the latter), differences in the relative growth coefficients (α) were examined statistically in the following nine dimensions having a relatively high correlation coefficient : the nasal length, frontal length, diastema length, auditory bulla length, rostral width, zygomatic width, cranial width, and mandibular length and height (Table 4). Diet conditions (a hard or soft diet) affect growth of the skull and development of the masseter in rats (Moore, 1965), but the specimens of both ***E. smithii*** and ***E. kageus*** used in this study were reared under about the same conditions (Ando ***et al.,*** 1988a ; Ando and Shiraishi, 1988). As given in Table 4, the difference in the relative growth coefficients are not significant between both species in the above nine dimensions ($p > 0.05$). In particular, it is noteworthy that the a value of ***E. smithii*** is not significantly different from that of ***E. kageus*** in the cranial length, zygomatic width, nasal length and mandibular height. In an analysis of the relative growth of the six dimensions (the nasal length, rostral width, zygomatic width, braincase length, auditory bulla width and length of upper molar series) against the condylobasal length in wild specimens of both the species en ***bloc*** collected from five localities including Kyushu and central Honshu, the relative growth coefficients show no significant difference among these five localities (Aimi, 1980).

In conclusion, the growth pattern of the *E.* kageus skull is identical with the *E.*

Table 4. Comparison of the relative growth coefficients ($a\pm$ SE) in nine dimensions between *Eothenomys smithii* (N = 76) and *E. kageus* (N = 56). The age in both species ranged from day 20 to day 350.

Dimensions	*E. smithii*	*E. kageus*	Significance of the difference
Nasal length	1.0024±0.0547	1.0484±0.1218	NS
Frontal length	0.7208±0.0514	0.6653±0.1186	NS
Diastema length	1.1250±0.0419	1.0828±0.0757	NS
Auditory bulla length	0.8614±0.0429	0.9150±0.0963	NS
Rostra1 width	1.0142±0.0609	0.8149±0.1311	NS
Zygomatic width	1.0981±0.0377	1.1364f0.0760	NS
Cranial width	0.8100f0.0361	0.8512t0.0643	NS
Mandibular length	0.8063t0.0258	0.7499±0.0561	NS
Mandibular height	1.4321±0.0597	1.3665f0.1193	NS

NS, not significant at the 0.05 level.

smithii skull in the relative growth coefficient. It is thus elucidated from the viewpoint of the relative growth that *E. kageus* is not distinguished from *E. smithii*.

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