GROWTH AND DEVELOPMENT IN TWO FORMS OF *CLETHRIONOMYS*

III. Cranial characters, with special reference to phylogenetic relationships

Hisashi ABE

Institute of Applied Zoology, Faculty of Agriculture,
Hokkaido University, Sapporo

Received October 20, 1972

In earlier papers (ABE 1968, 1973), the growth and development of some external characters, body weight, behavior, and tooth characteristics of *Clethrionomys sikotanensis* (TOKUDA) were compared with those of *C. rufocanus bedfordiae* (THOMAS). It has been determined that some of the above characters show marked divergence between the two forms. In the present work a similar comparison was extended to the characters of the skull.

Material and Methods

All the specimens used in this work were the same as those studied previously (ABE 1973), namely, about 840 animals taken from laboratory stock, the original of which has been collected on Daikoku Island (*Clethrionomys sikotanensis* (TOKUDA)=D-form)* and in the suburbs of Sapporo on the mainland of Hokkaido (*C. rufocanus bedfordiae* (THOMAS)=M-form). The samples of both forms consisted of 14 age-groups, each of which contained 15 males and 15 females. In addition to these, a few specimens of *C. rex* IMAIZUMI taken from Rebun Island and the Daisetsu Mountains on Hokkaido were employed for the phylogenetic comparison.

Cranial measurements were taken as follows:

Condylobasal length (CBL): from the condyle to the front of the premaxila.

Palatal length (PL): from a point immediately posterior to the incisor to the anteriormost point of the posterior border of the palate.

Depth of braincase (DB): from the basisphenoid to the dorsal top of the braincase.

[Jour. Facul. Agr., Hokkaido Univ., Sapporo, Vol. 57, Pt. 2, 1973]

* Voles from Daikoku Island are different in certain characters from those from Sikotan Island, but the present author provisionally used this name for the former.

Length of braincase (LB): from the occipital condyle to the anteriormost point of the posterior border of the palate.

Length of rostrum (LR): from the anterior margin of the zygomatic arches to the anterior tip of the nasals.

Width of rostrum (WR): width of rostrum at the front of the infraorbital foramina.

Posterior length of nasals (PLN): from a line connecting the anterior margin of the zygomatic arches to the posterior tip of nasals.

Measurements of zygomatic width (ZW), mastoid width (MW), nasal length (NL), nasal width (NW), palatal foramina (PF), diastema (D), width of tympanic bulla (WT), interorbital width (IW), length of mandible without incisor (M), upper tooth row (UT), and lower tooth row (LT) were as usual.

For the study of variation in the shape of the zygomatic arches, the position of a line crossing the widest point of the arches was measured according to the following five grades:

1. The line across the postero-outer angles of the arches.
2. The line situated between the postero-outer angles and the postorbital crests.
3. The line on the tips of the postorbital crests.
4. The line situated between the postorbital crests and the antero-onter angles of the arches.
5. The line at the antero-outer angles of the arches.

Results

1. Growth of cranial dimensions.

Except for the DB, IW, and PLN, in all measurements the dimension was observed to increase rapidly until 50 to 60 days of age, when most of the individuals attained sexual maturity (Fig. 1–4). After this stage of age, a gradual increase was observed, which continued into the last stage of age. The pattern of each growth curve was basically similar to that of the head and body (ABE 1968).

The DB showed a little increase and the IW decreased gradually after the 15th day (Fig. 1, 2).

The PLN of the M-form indicated no growth from early to last stage of age, while that of the D-form increased until around the 40th day after birth (Fig. 4).

Proportions such as ZW/CBL, MW/CBL, NW/CBL, UT/CBL, LT/CBL, M/CBL, WR/CBL, and WR/LR decreased until 30 to 50 days of age, after

which there were no great variations (Fig. 5–9). The PL/CBL also indicated no great variation after the 20th day (Fig. 6).

The IW/CBL continued to decrease from the early stage of age towards the last stage (Fig. 7). The growth curves of the DB/CBL and WT/CBL had a peak at the 10th day after birth, respectively, after which they decreased through the life of the animals (Fig. 6, 10).

The D/CBL and LB/CBL showed almost no variation throughout life Fig. 7, 10). The PF/CBL, NL/CBL, and LR/CBL increased to the 30th day and the LB/MW to the 40th day, but there were no great variations after these stages. The values of the PLN/CBL were similar to each other in the earliest stage of growth (Fig. 8). In the D-form, however, the value increased to about the 40th day, while that of the M-from decreased rapidly to the 20th day. After these stages they did not show great variation.

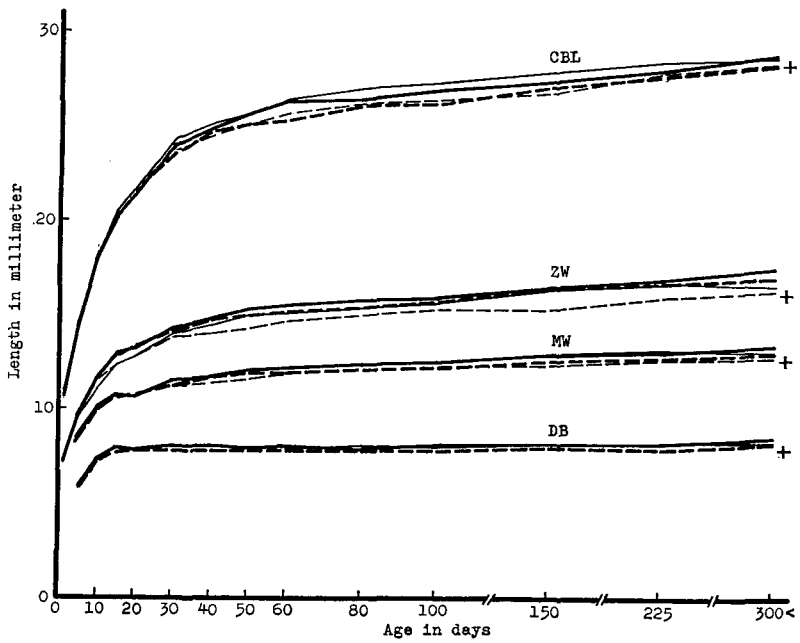

Fig. 1. Growth curves of the condylobasal length, the zygomatic width, the mastoid width, and the depth of braincase. Narrow lines indicate M-form, thick ones D-form, solid ones males, and broken ones females. Cross marks represent the average size in over-wintered very old specimens of *C. rex*.

The retardation of the growth which was observed in dimensions such as ZW, MW, M, and WT at the 20th day of age may be attributable to the physiological and ecological crisis at this age, when the weaning of the juvenile is completed and the young begin to fend for themselves (ABE 1968). Similar retardation has been shown in the growth curves of these dimensions in *C. glareolus* as shown by MAZÁK (1962).

Many of the cranial characters complete their growth at the stage of sexual maturity. This suggests an antagonistic relationship between the onset of sexual maturity and growth in size in morphogenesis. Major growth in the proportions of the dimensions, however, is undertaken in stages earlier than the occurrence of sexual maturity, and the onset of a decrease in the growth rate coincides with the onset of sexual maturity. This indicates that the overall features of the skull become adult-like as early as the stage of sexual maturity, though some change in the features of the skull occurs thereafter with advancing age.

2. Differences of cranial dimensions between sexes.

As shown in Table 1, cranial dimension does not always indicate a sta-

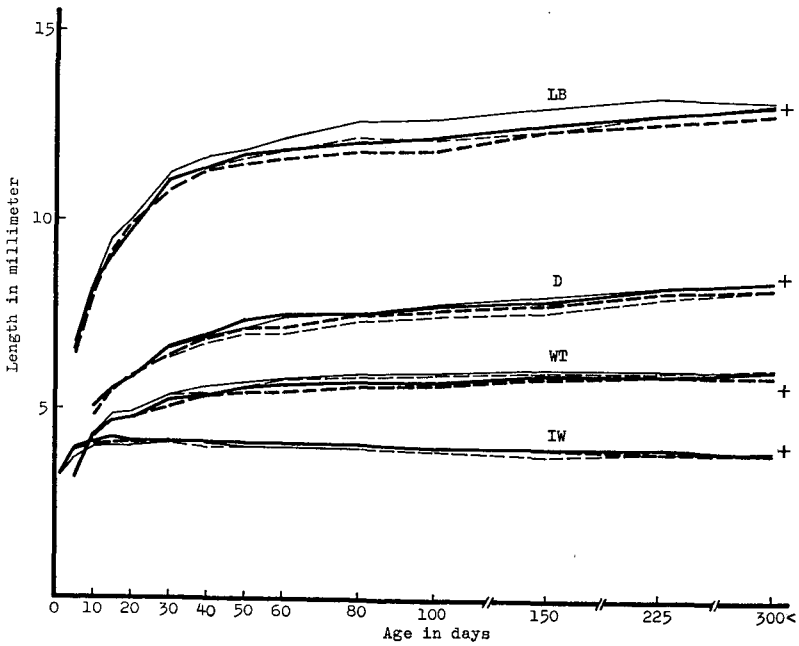

Fig. 2. Growth curves of the length of braincase, the diastema, the width of tympanic bullae, and the interorbital width. Cf. Fig. 1.

tistically significant difference between the sexes. Many of the dimensions, however, are usually larger in average in the male than in the female, as shown in Fig. 1–4. These differences, therefore, may have a biological significance. For example, there are no significant sexual differences of the PF in many of the age stages, but in the male, the PF is always larger, on an average, than in the female (Fig. 3).

Dimensions in which significant differences have been observed in adult stage are the MB, DB, and LB (M-form only) which are related to the size of braincase.

In proportions, the M/CBL, UT/CBL, and LT/CBL are larger in females than in males in many stages of age (Fig. 5–7). Other proportions, however, showed no great sexual differences. This observation indicated that the masticatory organs of the female are relatively larger than those of the male.

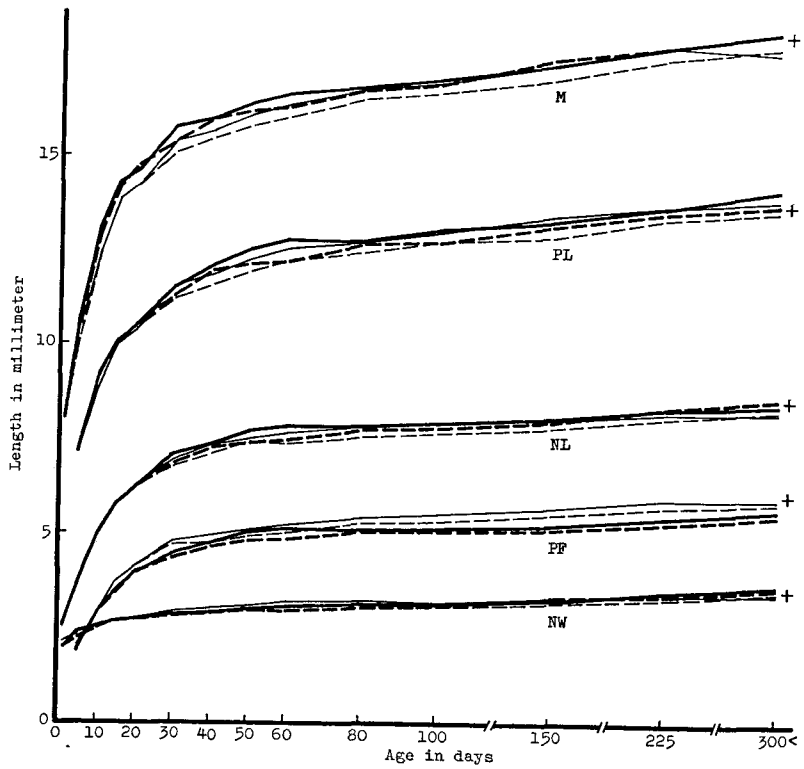

Fig. 3. Growth curves of the mandible, the palatal length, the nasal length, the palatal foramina, and the nasal width. Cg. Fig. 1.

3. Differences of cranial dimensions between the two forms.

There are significant inter-form differences in dimensions such as ZW, PF, WT, LR, WR, and PLN from relatively early stages of age to later stages, while others show no apparent differences (Table 1). The ZW, WR, and PLN are larger in the D-form, but the others are larger in the M-form.

Inter-form differences of cranial dimensions are well indicated in their proportions: namely ZW/CBL, D/CBL, PL/CBL, NL/CBL, PLN/CBL, WR/CBL, WR/LR, M/CBL, LT/CBL, IW/CBL, WT/CBL, PF/CBL, LR/CBL, LB/CBL, LB/MW, and UT/CBL diverge to each other's form from relatively early stages of age. The first nine are distinctly larger in the D-form than in the M-form. These characters showed the following overall features of the skull: Generally, the skull of the M-form is long but narrow, although the diastema, mandible, and tooth row are relatively short. On the other hand, the D-form has a relatively short but wide skull, with a relatively long diastema, mandible, and tooth row. The skull of the latter form, therefore, is very strong and heavy in appearance.

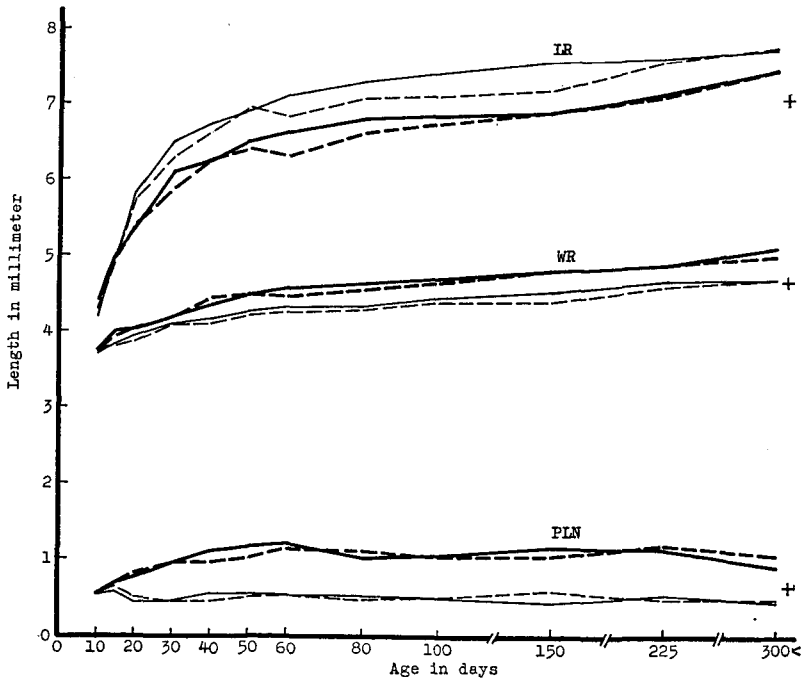

Fig. 4. Growth curves of the length of rostrum, the width of rostrum, and the posterior length of nasals. Cf. Eig. 1.

Notwithstanding the proportion of NL/CBL of the D-form, which is larger than that of the M-form, the LR (=anterior length of nasals) is distinctly shorter than that of the M-form (Fig. 7, 8, 4). In the D-form, the nasals are shifted, as a whole, more posteriorly. The longer PLN of this form is also indicative of such a shift (Fig. 4). In contrast with the short anterior length of nasals, the diastema of the D-form is longer than that of the M-form (Fig. 10). The combination of these characters may have induced a proodont type of incisors in the D-form (ABE 1973).

One of the most characteristic dimensions of the D-form is the very wide zygomatic arches. In addition to this, the vole has another distinguishable cranial feature. Before the 30th day of age, all zygomatic arches are widest at the postero-outer angles (Table 2). In the D-form, however, the line crossing the widest points of the arches rapidly moves forwards with advancing age and reaches grade 4 in a few specimens as early as the 30th

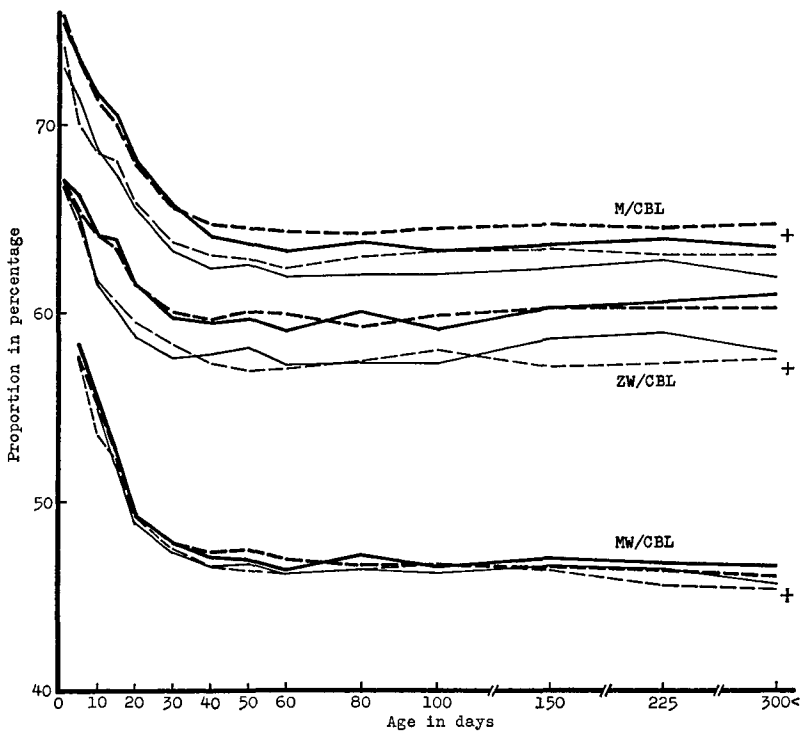

Fig. 5. Growth curves of the proportions of the mandible, the zygomatic width, and the mastoid width to the condylobasal length. Cf. Fig. 1.

day. After the 50th day the line is shifted to grade 3 or 4 in many individuals and even to grade 5 in a few old specimens. From these changes, the D-form in old stage comes to have zygomatic arches which are wide anteriorly. On the other hand, the line in the M-form reaches grade 3 at first as late as the 40th day of age, but about one-third of the individuals is still in grade 2 even after the 50th day. There are only a few individuals reaching, in the position of the line, grade 4, and none reaches grade 5. The M-form, therefore, retains the zygomatic arches which are usually widest at the central or posterior part even in the old stages of age.

The profile of the skull is also different between the two forms. The variation of the angle which is made with the profiles of the nasals and the frontal is given in Table 3. The angle increases with advancing age, but the change is more rapid and stronger in the D-form than in the M-form. That of the latter increases little after the 30th day.

In the formation of posterior palatine bridges is also a difference between the two forms (Table 4). The bridges of the D-form are made rapidly and almost completed by around the 80th day of age in many individuals.

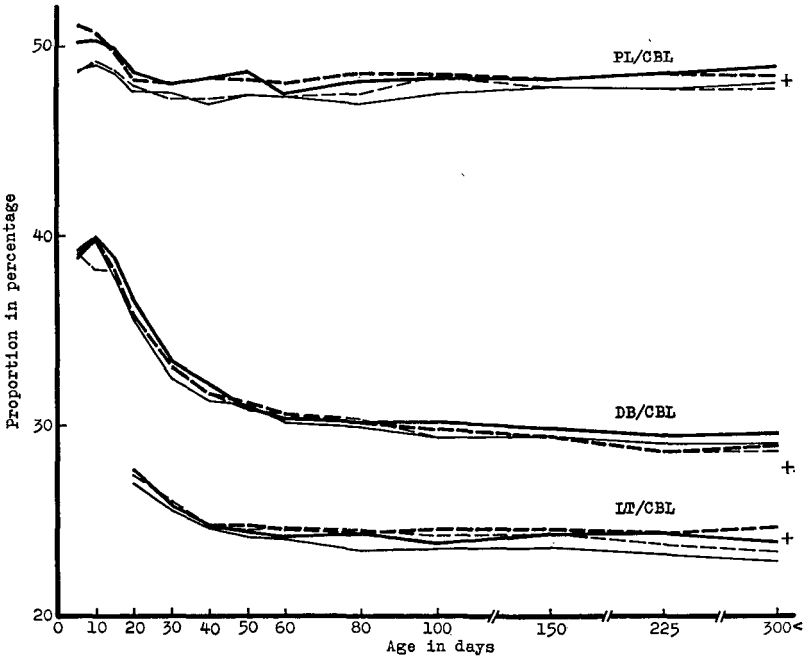

Fig. 6. Growth curves of the proportions of the palatal length, the depth of braincase, and the lower tooth row to the condylobasal length. Cf. Fig. 1.

The bridges are strong and heavy, and the average width is 0.49 ± 0.0979 mm at the last stage. On the other hand, those of the M-form show an apparent retardation in the growth, and only two-thirds of them are completed at the last age stage. Moreover, the bridges are very weak and the average width, if completed, is 0.24 ± 0.0748 mm at the last stage. Their suture is usually not fused in the M-form.

Discussion

General features in the growth and development of cranial dimensions are very similar in *C. sikotanensis* and *C. rufocanus bedfordiae.* Some dimensions, however, are slightly different between the two forms of vole at

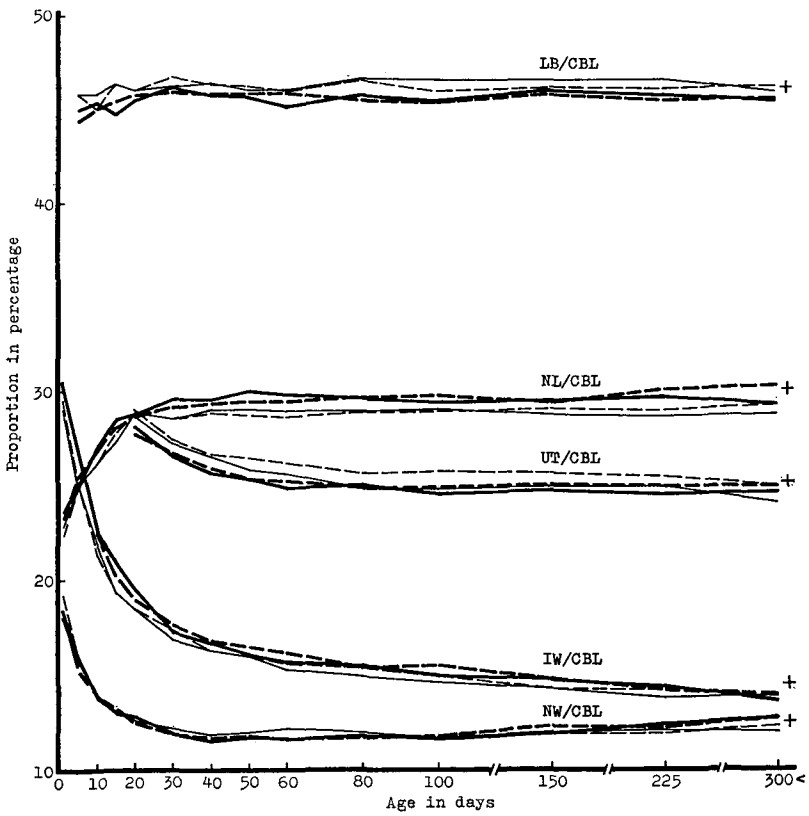

Fig. 7. Growth curves of the proportions of the length of braincase, the nasal length, the upper tooth row, the interorbital width, and the nasal width, to the condylobasal length. Cf. Fig. 1.

many growth stages. Consequently some relatively distinct differences in their proportions can be seen.

Characters which are slightly different between the two forms are divided into two groups as follows:

1. Characters which are similar to each other in early stages of the postnatal growth and diverge in later stages are ZW/CBL, PF/CBL, NL/CBL, PLN/CBL, LR/CBL, WR/CBL, MW/CBL, palatine bridges, the profile of nasals, and the position of the widest points of zygomatic arches.

2. Characters which have already diverged to the respective form of vole at birth or at early stages of growth but show similar modes of growth at later stages are D/CBL, LB/CBL, PL/CBL, UT/CBL, M/CBL, LT/CBL, IW/CBL, and WT/CBL.

The former group of the characters is likely more adaptively changeable than the latter, which may have strongly affected the overall features of the skulls of the two forms. The characters of group 2 seem to have diverged in earlier, i.e. prenatal, stages of the ontogeny. Although the change occurs at a different age, it is presumed that the mode of the

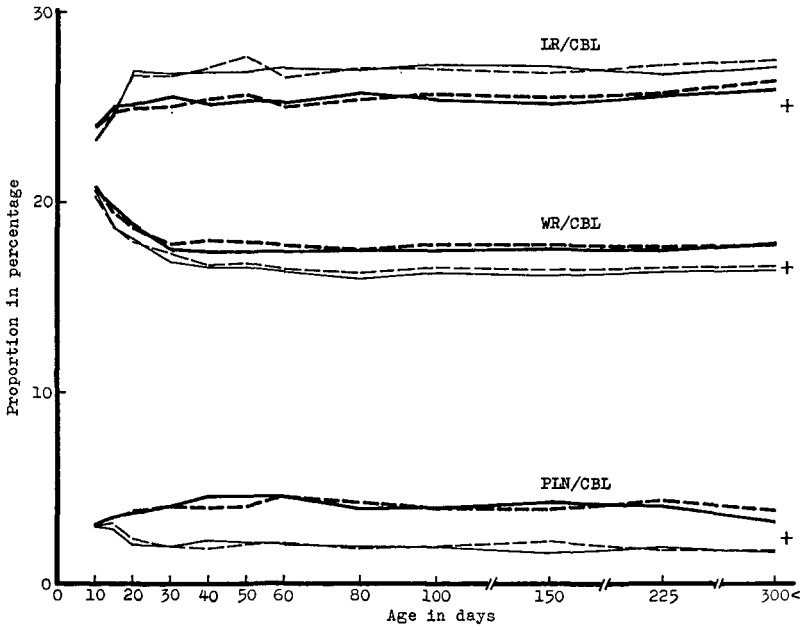

Fig. 8. Growth curves of the proportions of the length of rostrum, the width of rostrum, and the posterior length of nasals to the condylobasal length. Cf. Fig. 1.

divergence may be similar to that of group 1. There are usually no great variations in growth and development after the differences have appeared.

Excluding from consideration the proportions LR/CBL, LB/CBL, WT/CBL, PF/CBL, and UT/CBL, some specific observations can be made: The

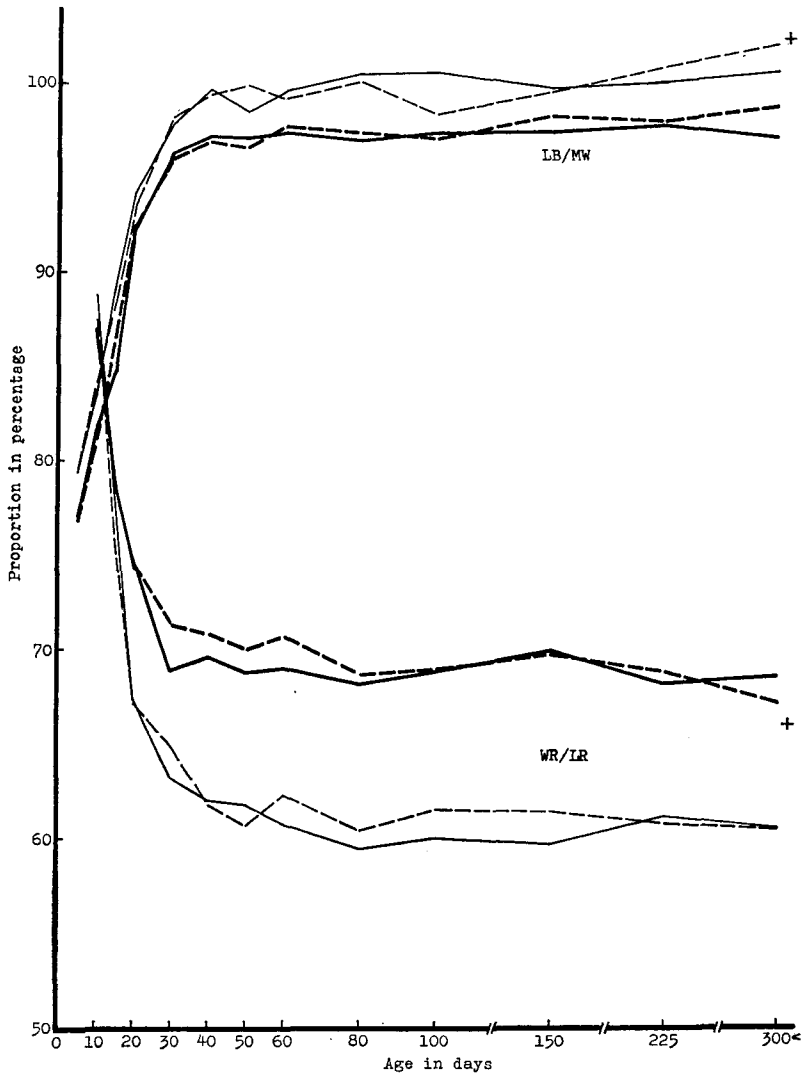

Fig. 9. Growth curves of the proportion of the length of braincase to the mastoid width and that of the width of rostrum to the length of the latter. Cf. Fig. 1.

cranial characters of the M-form remain at relatively earlier stages in the general age variation, compared with those of the D-form ; in the D-form, they reach a more advanced state in the general age variation. The characters of the M-form in the last stage of the growth, however, are not the same as those of earlier stages in the D-form, which correspond to the former. An example of this disparity is clearly shown by the completed palatal bridge of the M-form, which is much weaker than that of the D-form. The skull of the D-form, therefore, may be regarded as having, as a whole, more advanced features in morphogenesis than that of the M-form*. In other words, the M-form is neotenous in comparison with the D-form.

It is interesting to compare measurements of the skull of the two forms with *C. rex*, another vole in Hokkaido. Average values of the measurement and its proportion in over-wintered very old specimens of *C. rex* taken from the field are given in Figures 1–10 in whicn the average is shown by (+). When those of *C. rex* are compared with those of the D- and M-forms an interesting difference is seen.

In characters of the first group given above, two, i. e. NL/CBL and LR/CBL, of *C. rex* are close to those of the D-form while the remaining seven, i. e. PF/CBL, WR/CBL, ZW/CBL, MW/CBL, the profile of nasals,

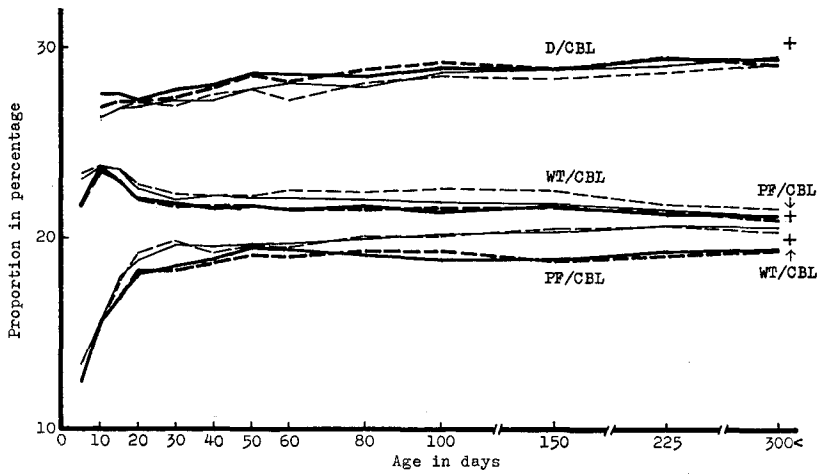

Fig. 10. Growth curves of the proportions of the diastema, the width of tympanic bullae, and the the palatal foramina to the condylobasal length. Cf. Fig. 1.

* This phenomenon corresponds with "Acceleration" in the classification of variations by DE BEER (1954)

TABLE 1. Results of the significance test in the differences between two averages. Only the significant ones at the levels of P=0.05 (+) and P=less than 0.02 (++) have been set out.

Dimensions	Pairs for comparison	Age in days													
		1	5	10	15	20	30	40	50	60	80	100	150	225	300<
CBL	M♂:M♀			++			++	++	++		++	++	++	+	
	D♂:D♀						+		++	++		+			++
	M♂:D♂										+		+		
	M♀:D♀	++		++											
ZW	M♂:M♀			++				++	++	+			++	++	
	D♂:D♀								++						++
	M♂:D♂			++	++	+	+		+	++					++
	M♀:D♀	+			++	++	+	++	++	++			++	++	++
IW	M♂:M♀												++		
	D♂:D♀			++	++	+					+				
	M♂:D♂		++	++	++	++				+					
	M♀:D♀		++		+	+		++	+			+	++		
MW	M♂:M♀							++	++		++	+	++	++	++
	D♂:D♀						+		+	++	+	++	++		++
	M♂:D♂			+											++
	M♀:D♀							+	++				++		
DB	M♂:M♀							+	++		+	++	++	++	
	D♂:D♀						++	++		++		++		++	++
	M♂:D♂														
	M♀:D♀														
NL	M♂:M♀										+	++			
	D♂:D♀						++		++	++					
	M♂:D♂														
	M♀:D♀													+	+
NW	M♂:M♀							++	++	++	++		++		
	D♂:D♀														
	M♂:D♂	++					+	++		+					++
	M♀:D♀	++					++								
PLN	M♂:M♀				+								+		
	D♂:D♀							++	++						+
	M♂:D♂				++	++	++	++	++	++	++	++	++	++	++
	M♀:D♀					++	++	++	++	++	++	++	++	++	++

Dimensions	Pairs for comparison	Age in days													
		1	5	10	15	20	30	40	50	60	80	100	150	225	300<
LR	M♂:M♀											+	++		
	D♂:D♀						++				+				
	M♂:D♂					++	++	++	++	++	++	++	++	++	++
	M♀:D♀					++	++	++	++	++	++	++	++	++	++
WR	M♂:M♀												+		
	D♂:D♀									+					+
	M♂:D♂				++		+	++	++	++	++	++	++	++	++
	M♀:D♀				+	++	++	++	++	++	++	++	++	++	++
PF	M♂:M♀														
	D♂:D♀								++	++					
	M♂:D♂		+		+	+	++	++			++	++	++	++	++
	M♀:D♀					+	++			+	++	++	++	++	++
D	M♂:M♀						++			++		++	++	++	
	D♂:D♀						+		++	++					+
	M♂:D♂			+					+						
	M♀:D♀														
PL	M♂:M♀						++	+	++				++		
	D♂:D♀								++	++					++
	M♂:D♂			+					+						
	M♀:D♀							++					+		
LB	M♂:M♀							++		+	++	++	++	++	
	D♂:D♀								++			+			
	M♂:D♂				++			++			++	++	++	++	
	M♀:D♀			+							++				
M	M♂:M♀			+			+		+				++	+	
	D♂:D♀						++			+					
	M♂:D♂			++	++	+	++	+	+	++					++
	M♀:D♀					++	+	++	++				++	+	+
WT	M♂:M♀							+							
	D♂:D♀						++		++	++	+				++
	M♂:D♂		++		++	+	+	++		++	++	++	++		
	M♀:D♀		++	++	+	+	++		++	++	++	++	++		++

TABLE 2. Age variation in the position of the widest points of zygomatic arches.

Age \ Grade*	1	2	3	4	5
C. rex					
Old	2	4	3		
M-form					
20	30				
30	9	22			
40	4	23	3		
50		11	18	1	
60	2	11	16	1	
80	2	9	17	2	
100		17	12	1	
150	2	10	19		
225		5	21	4	
300		4	18	8	
D-form					
20	30				
30	17	9	2	2	
40	7	2	8	12	
50			5	25	
60	1		4	25	
80			16	14	
100			15	15	
150		1	6	23	
225			3	27	
300			4	25	2

* See text

TABLE 3. Age variation in the bending-degree of the profile of nasals

Age \ Degree*	2.6–5	5.1–7.5	7.6–10	10.1–12.5	12.6–15	15.1–17.5	17.6–20	20.1–22.5	22.6–25
C. rex									
Old				2	4	3			
M-form									
15	1	4	14	6	5				
20		3	5	16	4	1			
30			2	12	11	6			
40			3	13	10	4			
50			3	7	13	7			
60			2	10	8	9	1		
80			2	6	12	9	1		
100				13	7	10			
150			1	10	9	10			
225			3	5	10	10	2		
300			1	11	9	6	4		
D-form									
15	1	5	20	2					
20		2	4	14	5	5			
30				4	9	16	1		
40				3	2	15	9		
50					5	16	8	1	
60				1	6	13	8	2	
80						10	14	5	1
100						11	14	4	1
150				1	2	6	14	7	
225						8	14	8	
300					2	8	14	5	1

* See text

TABLE 4. Growth of the posterior palatine bridges.

Form	Age	Both bridges uncompleted	One side bridged	Both sides bridged
C. rex	Old	6	1	
M-form	10	30		
	15	30		
	20	30		
	30	30	1	
	40	28	2	
	50	22	4	4
	60	25	3	2
	80	23	5	2
	100	14	8	8
	150	12	5	13
	225	12	8	10
	300	5	6	19
D-form	10	31		
	15	26	3	
	20	23	6	
	30	11	8	11
	40	3	3	23
	50		4	26
	60		2	28
	80		1	29
	100			30
	150			30
	225		2	28
	300			30

the palatine bridges, and the position of the widest points of zygomatic arches, of *C. rex* are similar to those of the M-form rather than to those of the D-form. The PL/CBL of *C. rex* is intermediate to both M and D-forms. *C. rex*, therefore, appears to have close relationship with the M-form, so far as can be judged from the characters in which an inter-form divergence occurs at the middle or later stage of postnatal growth. Moreover, some of the characters of *C. rex* appear to be more primitive than those of the M-form. From these observations, therefore, a phylogenetic arrangement such as *rex*—M-form—D-form may be supposed.

Of 8 characters of the second group, however, five, i.e. D/CBL, WT/CBL, LT/CBL, IW/CBL, and M/CBL, are closer in *C. rex* to those of the

D-form, while the character, LB/CBL, is similar to that of the M-form. UT/CBL and PL/CBL of *C. rex* are intermediate.

It is generally believed that in some animals, similarities in the characters which are formed in earlier stages of the ontogeny indicate their closer relationship in phylogeny. Therefore, it seems reasonable to conclude that the D-form (*C. sikotanensis*) is closer, in phylogeny, to the primitive *C. rex* than to the M-form (*C. rufocanus bedfordiae*), in spite of the highly advanced overall features, morphogenetically, of the skull of form D. The same conclusion was drawn from the study of tooth characters (ABE 1973).

The present distribution of the three forms is as follows: The M-form ranges to Kunashiri Island and Hokkaido with its adjacent small islands, namely Rebun, Rishiri, Teuri, and Yagishiri. The D-form is known from Daikoku Island which is adjacent to Hokkaido. Up to the present, relic populations of *C. rex* have been recorded from Rishiri and Rebun, which are much larger in size than Teuri, Yagishiri, and Daikoku, and also from relatively high altitudes of Daisetsu and Hidaka Mountains in Hokkaido.

There is a possibility that *C. rex* occurs on the mainland of Asia and on Sakhalin, but it has not been recorded from these areas. According to the description and figures given by HINTON 1926 and OGNEV 1950, *C. rufocanus regulus* of Korea and some specimens of *C. rufocanus* from Sakhalin retain characters which are similar to those of *C. rex*. From the examination of some specimens of *C. rufocanus regulus* preserved in the Yamashina Institute of Ornithology (Tokyo), however, it has been seen that the vole is apparently different in systematic relation from *rex*.

Judging from the characters of the skull, teeth, tail, and coat color (ABE et al. 1971; IMAIZUMI 1971), *C. rex* appears to be most primitive among the three forms. Hence it is most tenable to establish a hypothesis that the D-form and the M-form might have been separately derived from the ancestral stock of *C. rex* or from a stock related to it.

From phylogenetic and distributional observations, it is assumed that a vole similar to *C. rex* might have been distributed through the whole of Hokkaido in some time of the past, and that population of the vole might have diverged to the D-form in the small island of Daikoku, which was isolated from the mainland after the the retreat of the last glacier about 10,000 years ago (MINATO and IJIRI 1966). On the other hand, the M-form which might have diverged from the original stock on the Continent or on small island such as Teuri and Yagishiri, may have invaded Hokkaido. After the invasion, it may have driven the vole of *C. rex* stock into its present distribution in Hokkaido.

Very rapid development (an advanced morphogenesis) of the skull characters of the D-form may be a correlate of the rapid development of sexual maturity (ABE 1968). It is possible that the development of those characters which are formed at relatively later stages in the ontogeny may have been accelerated by or with the rapid sexual development, and consequently may have induced the comparatively highly advanced state in the D-form. Analyses of geographical variation in morphology together with physiological and ecological variations of the voles are needed.

As stated earlier, PL/CBL, M/CBL, LT/CBL, and the proportions of width to length in many cranial dimensions are larger, stronger, and heavier in the D-form than in the M-form. These may be a result of adaptation to the coarse foods on the inhabited island. A similar observation has been reported in insular forms of *C. glareolus* of the British Isles (STEVEN 1953).

Generally the proportions of the width to the length in cranial dimensions are greater in each of the two forms in early stages of growth but rapidly decrease towards the levels at the 40th to 60th day of age. In contrast, except for the upper and lower tooth rows and the mandible, the proportions of the length of each dimension to the CBL are usually less in early stages of growth, but rapidly increase towards the levels of proportion at the 30th to 40th day of age. Contrary to the general accounts, the fact that the value of M/CBL is larger from early stages of growth suggests that the mandible has an important role in the sucking activity of young. The large value of this proportion indicates an adaptation to sucking activity as seen also in the rapid growth of the fore feet in this stage (ABE 1968). The fact that the length of the tooth row is large at the weaning stage may also indicate an adaptation for taking solid foods in independent life thereafter.

Summary

1. *Clethrionomys rufocanus bedfordiae* (THOMAS) (M-form) collected from the suburbs of Sapporo, and *C. sikotanensis* (TOKUDA) (D-form) from Daikoku Island, were reared in the laboratory, and the growth and development of the cranial dimensions were studied.

2. Except for the depth of braincase, the interorbital width, and the posterior length of nasals, all other dimensions increase rapily until the 50th to 60th day of age, after which they gradually increase towards the last stage of age. Proportions such as ZW/CBL, MW/CBL, NW/CBL, UT/CBL, LT/CBL, M/CBL, WR/CBL, and WR/LR decrease until the 30th to 50th day of age, after which there are no great variations. The IW/CBL con-

tinues to decrease from the early stage of age to the last. The growth curves of the DB/CBL and WT/CBL each have a peak at the 10th day, and thereafter they decrease. The D/CBL and LB/CBL show almost no variation through out the life of the animal. The PF/CBL, NL/CBL, LR/CBL, and LB/MW increase to the 30th or 40th day, with no great variations thereafter. The PLN/CBL of the D-form increases to about the 40th day, while that of the M-form decreases rapidly to the 20th day.

3. Many of the cranial dimensions are larger in average in males than in females. The most distinctive differences between sexes are expressed in the size of braincase. Proportions such as M/CBL, UT/CBL, and LT/CBL are usually larger in females than in males. The other proportions show no great sexual differences.

4. The ZW, PF, WT, LR, WR, and PLN indicate a significant interform difference, respectively, while the CBL, MW, DB, LB, D, IW, M, PL, NL, and NW do not show such a difference. Many of the proportions of the dimensions diverge to each other's form in relatively early stage of the growth. The shape of the zygomatic arches, the profile of the skull, and the feature of the formation of posterior palatine bridges are clearly different between the two forms.

5. As a whole, the skull of the M-form is long but narrow in shape, except for the relatively short diastema, mandible, and tooth row. On the other hand, the D-form has a relativey short but wide skull, except for the relatively long diastema, mandible, and tooth row. The skull of the latter is very strong and heavy in structure.

6. Cranial characters of *C. rex* obtained from the field were compared with those of the two forms. The result suggests that M- and D-forms may have been derived from *C. rex* or a primitive stock related to it.

Acknowledgment

The author wishes to express his sincere appreciation to Professor Emeritus Dr. T. Inukai, the Historical Museum of Hokkaido, and Dr. R. L. Rausch, Arctic Health Research Center, Fairbanks, Alaska, for reviewing the manuscript and offering their valuable suggestions.

Literature

ABE, H. 1968. Growth and development in two forms of *Clethrionomys*. 1. External characters, body weight, sexual maturity, and behavior. Bull. Hokkaido Forest Exp. St. 6: 69–89 (in Jap. with Engl. Summ).

ABE. H. 1973. Ditto. 2. Tooth characters, with special reference to phylogenetic rela-

tionships. Jour. Fac. Agr. Hokkaido Univ. 57 (2):

——, T. KOBAYASHI, K. MAEDA, and I. HAYATA 1971. Results of the small mammal survey on the Daisetsu Area. Ann. Rep. JIBP/CT-S Fisc. Year 1970. pp. 13–22.

DE BEER, G. 1954. Embryos and ancestors. Oxford. pp. 159.

HINTON, M. A. C. 1926. Monograph of the voles and lemmings (Microtinae). British Museum (N. H.) pp. 448.

IMAIZUMI, Y. 1971. A new vole of the *Clethrionomys rufocanus* group from Rishiri Island, Japan. Jour. Mamm. Soc. Jap. 5 (3): 99–103.

MAZÁK, V. 1962. Wachstum und Entwicklung des Schädels von *Clethrionomys glareolus* SCHREBER 1780 (Mammalia, Microtidae) im Laufe des postnatalen Lebens. Věstnik Čsl. Zool. Spol. 26: 257–270.

MINATO, M., and S. IJIRI 1966. The Japanese Islands. Tokyo (in Jap).

OGNEV, S. I. 1950. Mammals of the USSR and adjacent countries. VII. Rodents. Israel Progr. Sci. Trans. Jerusalem 1964.

STEVEN, D. M. 1953. Recent evolution in the genus *Clethrionomys*. Symp. Soc. Exp. Biol. VII pp. 310–319.