GROWTH AND DEVELOPMENT IN TWO FORMS OF *CLETHRIONOMYS*

II. Tooth characters, with special reference to phylogenetic relationships

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1. Introduction

The study of living organisms on islands has offered much of interest to evolutionary science, while the results of such studies have often confused taxonomists. One of the insular forms of the red-backed vole which occurs in Daikoku Island adjacent to Hokkaido has been identified as *Clethrionomys sikotanensis* (TOKUDA) by IMAIZUMI (1960).* OTA (1956), however, has regarded it as a synonym of *C. rufocanus bedfordiae* (THOMAS) from the main island of Hokkaido. On Hokkaido, where it is abundant, the red-backed vole shows fairly distinct local variations in morphology and ecology. A comparison of the patterns of growth and development between the above local variants is necessary in order to understand the phylogenetic relationships involved.

In a previous paper (ABE 1968), external characters, body weight, sexual maturity, and behavior were compared, and it was indicated that the voles in some characters had achieved distinct divergence. The present paper gives accounts of dental characters of the two variants from Daikoku and Hokkaido Islands.

2. Material and Methods

Most of the animals studied in this work were those examined previously (ABE 1968); namely the approximately 840 specimens were the descendants of the original stocks which had been taken alive from Daikoku Island, off Akkeshi in eastern Hokkaido (D-form), and which had been captured in the suburbs of Sapporo, Hokkaido Island (M-form). They were

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* 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.

reared in out-door cages in Sapporo. None of the laboratory-reared individuals of several generations showed any noticeable deviation in tooth characters from the wild types, although retardation in the attrition rate of teeth and in the growth rate of roots was noted; this effect was probably due to the artificial diet supplied.

The sample of each of the two forms contained specimens grouped by age into 14 stages, each of which, in principle, consisted of 15 females and 15 males. The 14 age-stages were as follows: 1, 5, 10, 15, 20, 30, 40, 50, 60, 80, 100, 130–170 (150 in average), 200–250 (225 in average), and 300–600 days.

The sample of the D-form belonging to the last age stage contained 10 specimens which were older than 425 days, while that of the M-form consisted of individuals between 300 and 400 days in age.

For determination of the period in which the teeth erupt and become fully formed, a number of young specimens were examined. These were intermediate to the age-stages listed.

In addition to the above samples, some specimens of *C. rex* IMAIZUMI from Rebun Island off northern Hokkaido, and some from areas of high altitude of the Daisetsu Mountains were used for the comparison.

Slide calipers (1/20 mm) were used for measuring the length of the tooth row. Measurements of finer parts of the teeth were made through a binocular microscope with an ocular micrometer accurate to 1/16 mm or 1/40 mm.

The following measurements were taken:

Length of tooth row: The distance between the outer margins of alveoli of the first and third molars.

Total crown length of M^3 and M_1.

Anterior length of M^3: Length from the rear margin of the tip of the second inner re-entrant angle to the frontal margin of anterior loop on the crown (Fig. 4).

Posterior length of M^3: Length from the rear margin of the tip of the second inner re-entrant angle to the rear margin of the posterior loop on the crown.

Width of anterior loop of M^3.

Anterior length of M_1: Length from the frontal margin of the tip of the third inner re-entrant angle to the frontal margin of anterior loop on the crown (Fig. 5).

Posterior length of M_1: Length from the frontal margin of the tip of the third inner re-entrant angle to the rear margin of posterior loop on the crown.

Width of M_1: Width between the outer tips of the 5th inner and the 4th outer salient angles.

Forward-projection degree of upper incisors was measured according to the method shown in Fig. 1, with universal projector (an optical measuring instrument).

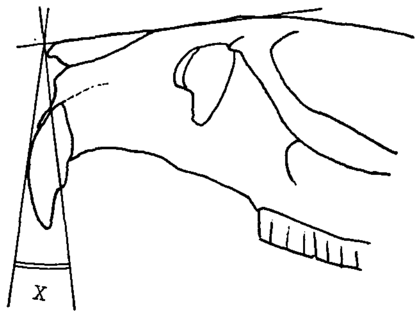

Fig. 1. Method of measurement of the projection degree of upper incisors.

Concerning the types of enamel pattern and the isthmus of dentinal space, there occur occasional animals in which the teeth of the left and right sides of the jaw are of different types. In such cases, the teeth of the right jaw were examined so far as it was not incomplete.

The second upper molar was most appropriate for measuring the growth of the root, because it is straight and the outer bone cover was easily removed.

The formation of neck and roots in the M^2 was classified according to the standard shown in Fig. 2. Two kinds of measurements were applied for the measurement of root length, i. e. the combined root length (root length-1) and the length of separate roots (root length-2). The former included the combined length of the neck and the separate roots, which was measured from the innermost base of the groove to the center of the

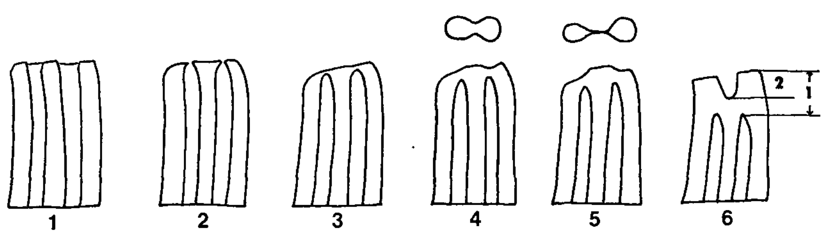

Fig. 2. Stages of root formation. 1. No trace of neck formation. 2. Cement spaces are closing at the basal tip. 3. The cement spaces have been just closed at the basal tip. 4. After the closing of the cement spaces, the "neck" grows. Pulp cavities are broadly confluent with each other or the side walls are approaching to each other at the central part of the basal tip. 5. The neck increases in length. The pulp cavities are divided into two parts by the closing of the side walls. Roots are not yet separated. 6. Separate two roots are formed and increase in length.

anterior root tip. The latter was measured according to the method of LOWE (1971), i. e. the length from the transverse line at the crutch to the center of the anterior root tip, along a line drawn between the point at which the posterior edge of the first prism meets the occlusal surface and the center of the anterior root tip.

3. Results

a. The time and the order of the eruption of the teeth

Incisors cut the gum at the 7th or 8th day after birth and grow vigorously to the time of eye-opening (at about the 12th day).

Some of the first molars, both the upper and lower, cut the gum at the central part of the crown on the 11th day. On the 12th day, when many individuals began to eat solid food, most of the crown of the first molar and the anterior part of the second molar appeared above the gum. On the 13th day, most of the crown of the second molar appeared above the gum line, but the third molars still remained unerupted. On the 15th day, wear extended to the anterior parts of M^3 in about 10 per cent of individuals of the D-form, but all M_3 of this form were within the gum. In the M-form about 17 per cent of M^3 and about 3.5 per cent of M_3 cut the gum at the anterior part of the crown on the 15th day.

On the 20th day, about 90 per cent of M^3 in the D-form showed wear on the anterior parts, and the crowns of the other 10 per cent were still distinctly lower than the level of M^1 and M^2. The M^3 of the M-form showed more advanced growth than that of the D-form, and about 20 per cent of the teeth had more or less worn out parts on the occlusal surface. More than 70 per cent of M_3 in the D-form were still very much lower than the level of M_1 and M_2 at this age, and hence no wear was seen on those teeth. In contrast with this, the teeth of the M-form grew faster, and about 80 per cent of them indicated a certain amount of wear on the crown. In this form on the 20th day, less than 20 per cent had no trace of wear.

On the 30th day, about 20 per cent of M^3 in the respective forms almost formed the perfect occlusal surface; the remaining had incomplete posterior ends, of which the posterior margin, when viewed from the side, was convex posteriad. All M_3 of the two forms had a perfect occlusal surface at this age and the posterior margin was nearly straight.

On the 40th day, a majority of the specimens in the two forms had developed M^3 with perfect occulusal surfaces.

The growth change of the teeth was rather rapid in the M-form until the 20th day of age. However, that of the D-form soon increased and reached a stage similar to that of the M-form at the 30th day of age. The above-mentioned is referred to the early feature of the change observed in the enamel pattern of the lower molars.

The occlusal surface of M^3 was formed latest among the upper and lower molars.

b. Growth of molar tooth row

Growth curves of the length of tooth row are given in Fig. 3. The length of the upper and lower tooth rows of the D-form increased until the latest stage of age. The upper tooth row of the M-from was significantly longer ($P=0.001$–0.05) in average than that of the D-form in many stages of age, but the averages of the two forms approached each other at the last stage of age, because of the reduced growth rate in the former. There was no significant difference in the average length of the lower tooth row between the two forms in the early four-fifths of the age stages, after which, however, that of the M-form showed no increase at all. There appeared significant differences ($P=0.001$–0.01) between these dimensions in the two forms at the last age stage. No significant difference between males or females was observed in this measurement.

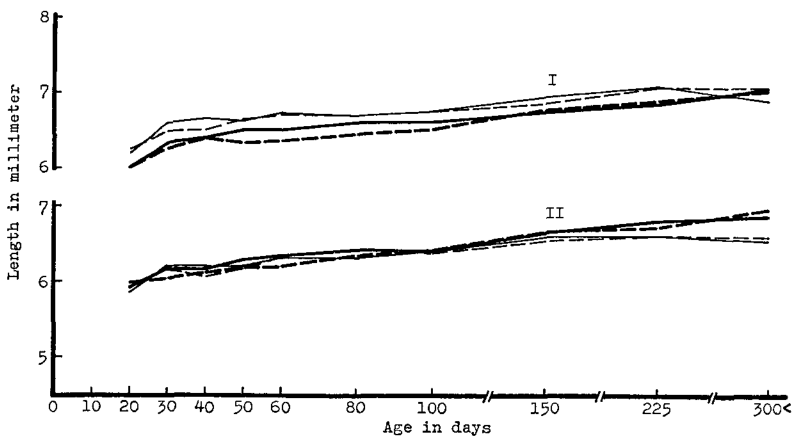

Fig. 3. Growth of molar tooth rows. I: Upper tooth row. II: Lower tooth row. Narrow lines indicate M-form, thick ones D-form, solid ones males, broken ones females.

c. Change in the occlusal surface of molars

Common change of enamel pattern. As is well-known, in many microtine rodents (HINTON 1926) the enamel of molar teeth is thin and weak in

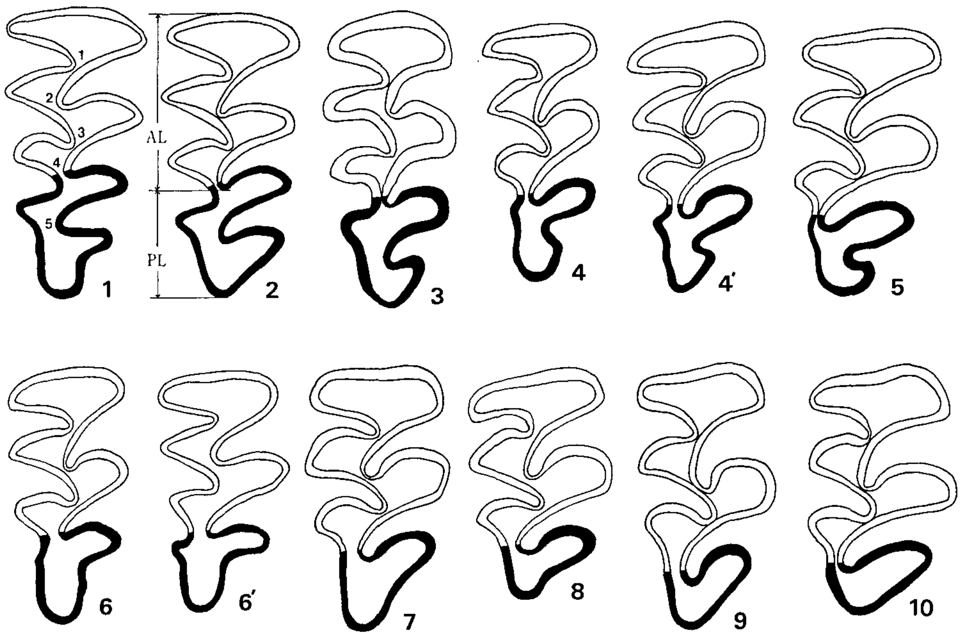

Fig. 4. Variation in the enamel pattern of the third upper molar. AL: Anterior length. PL: Posterior length.

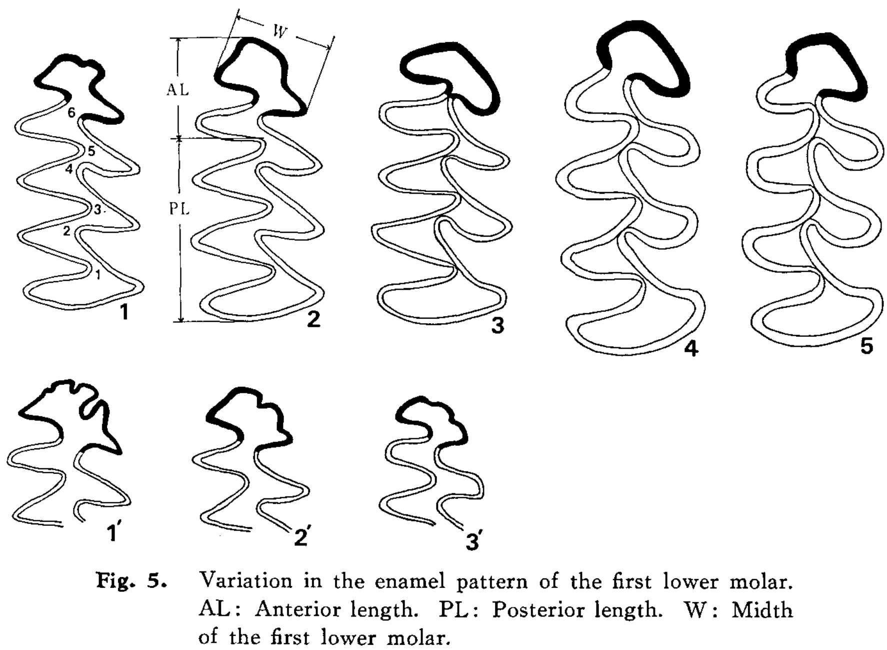

Fig. 5. Variation in the enamel pattern of the first lower molar. AL: Anterior length. PL: Posterior length. W: Midth of the first lower molar.

younger stages but becomes thick and heavy with advancing age. The prisms which are formed with rather flat plates of enamel are apparently angular in the young, but the salient angles become rounded in senile animals.

Isthmus of dentinal space. Dentinal spaces are broadly confluent with each other at isthmuses in younger stages of age. The isthmuses, however, decrease in width with advancing age and are usually closed at later stages of age.

In all specimens measured, each isthmus was numbered from front to back in the upper molars and from the back to front in lower molars (Fig. 4

TABLE 1. Growth of the closed isthmus of dentinal space in upper molars

No. isthmus / Age	M1				M2			M3				
	1	2	3	4	1	2	3	1	2	3	4	5
C. rex												
Old (9*)	8	9	9	9	9	9	7	9	4	8	8	1
M-form												
30	0	0	0	0	0	0	0	0	0	0	0	0
40	0	1	1	3	2	2	2	0	1	0	0	0
50	3	3	3	5	6	3	3	1	1	0	0	0
60	0	1	6	9	13	15	13	3	6	1	0	0
80	6	10	15	21	24	24	23	7	9	5	1	0
100	20	21	29	28	30	28	26	24	25	14	0	0
150	25	27	30	30	30	30	30	29	28	28	5	0
225	27	28	30	29	29	30	29	27	29	28	5	0
300	27	29	30	27	30	30	27	27	29	29	12	0
D-form												
30	0	0	0	0	0	0	0	0	0	0	0	—
40	1	3	3	5	4	4	5	1	2	2	0	0
50	1	2	2	4	4	3	3	0	1	0	0	—
60	3	4	4	7	7	5	6	2	4	4	0	—
80	17	18	18	25	24	22	25	14	21	18	0	0
100	21	26	27	30	30	29	30	22	28	27	0	—
150	30	30	30	30	30	30	30	28	30	30	1	—
225	30	28	30	30	30	30	30	30	30	30	4	—
300	28	30	30	30	30	30	30	30	30	30	13	—

* Sample size

and 5), and the width of the dentinal space between enamels at isthmus was measured under a microscope with a micrometer. When the width was less than one space in the micrometer scale (=0.025 mm), the isthmus was regarded as "closed". Table 1 and 2 represent the growth of the closed isthmus numbered according to the above method.

As shown in this table, the closing in M^1 proceeded from behind forwards. Closing in the D-form occurred in an earlier stage of age than in the M-form, being completed at the 150th day of age; in the M-form some individuals still had open anterior isthmuses even at the last age stage.

In M^2 there was no difference in the time of closing of isthmus among

TABLE 2. Growth of the closed isthmus of dentinal space in lower molars

No. isthmus / Age	M_1						M_2				M_3		
	1	2	3	4	5	6	1	2	3	4	1	1′	2
C. rex													
Old (9*)	9	2	9	2	7	0	9	0	9	0	9	—	9
M-form													
30	1	1	0	0	0	1	1	0	0	0	2	—	1
40	5	3	1	2	0	2	12	1	9	0	15	—	14
50	10	4	3	3	0	0	19	0	13	0	29	—	27
60	17	15	7	12	0	0	24	0	22	0	29	—	29
80	25	24	14	22	2	4	29	3	27	0	30	—	30
100	29	29	28	28	10	8	30	7	30	0	30	—	30
150	30	30	30	30	16	14	30	17	30	0	30	—	30
225	30	28	30	28	18	11	30	18	30	0	30	—	30
300	30	28	30	29	16	6	30	18	30	1	30	—	30
D-form													
30	0	0	0	0	0	0	0	0	0	0	0	—	2
40	5	5	5	4	0	1	13	0	10	0	17	—	20
50	3	3	1	2	0	1	16	0	16	0	28	—	28
60	11	7	5	5	2	0	17	0	16	0	29	—	30
80	22	24	21	23	14	7	25	7	23	0	30	—	30
100	30	30	30	30	23	11	30	16	30	0	30	—	30
150	30	30	30	30	25	12	30	29	30	0	30	4	30
225	30	30	30	30	30	16	30	29	30	1	30	8	30
300	30	30	30	30	30	14	30	29	30	0	30	3	30

* Sample size

the isthmuses of the tooth and also between the two forms. The isthmuses of this tooth closed most rapidly in upper molars.

The anterior three isthmuses of M^3 closed somewhat earlier in the D-form; in a few individuals of the M-form, these were not closed even at the last stage of age. The width of the fourth isthmus also decreased with advancing age (Fig. 6–V) but the closing was retarded in many individuals. In the M-form, the fifth isthmus, retained only by molars belonging to the types 4, 4′, and 5 (Fig. 4), never closed. As explained later, the D-form lacked the fifth isthmus in many individuals, except for those with the type 5 crown pattern. As a whole, the closing of the isthmuses of M^3 occurred latest in all molar teeth.

Isthmuses of M_1 began to close first in the posterior and the closing proceed anteriad; many of the anterior isthmuses remained open until relatively late stages of age. The decrease in the number of the closed sixth isthmus, at the last stage of age, is due to the secondary opening caused by degeneration of the anterior loop at later stages (Table 2). The closing in M_1 was latest generally in the lower teeth. A difference in time of closing between the two forms appeared in the anterior isthmuses, i. e. more individuals of the D-form than those of the M-form achieved the closing in late stages of age.

The first and third isthmuses of M_2 which closed in early stages of age showed no inter-form difference, but in the second isthmus which shows a slower closing the D-form undertook more frequent closing than in the M-form.

Isthmuses of M_3 are closed generally at the earliest stage of age in all the molar teeth. This molar has usually two isthmuses which are made with two pairs of the tips of outer and inner re-entrant folds. In a few old individuals of the D-form, however, the tip of the first outer re-entrant fold of M_3 touched the rear edge of the second inner re-entrant fold and the tip of the first inner fold touched the rear edge of the first outer fold (as did those of M_2), then formed an additional closed isthmus corresponding to the second one of M_2. Such a case was not found in the M-form.

From the observations given above, the change in the isthmuses of the M-form may be regarded as having remained at a younger or more primitive stage in the general age variation of these voles as compared with that of the D-form. When isthmusal change of *C. rex* were taken into account, the situation is further interesting: the latter seemed to be the most primitive in this character among these three forms, since the overwintered, very old specimens that were trapped in the summer often retained isthmuses which are not closed, especially in lower molars.

Enamel pattern of M^1 and M^2. Enamel patterns of M^1 and M^2 did not show so great variation as in M^3 but did show a general age variation. Few differences were observed between the two forms.

Crown length and enamel pattern of M^3. The growth pattern of the crown length of M^3 fitted a curve similar to that of the upper tooth row (Fig. 6). The length in the D-form, which averaged shorter than that of the M-form, continued to grow until the last age-stage, while that of the M-form showed little increase after 225 days of age. Hence the significant differences ($P=0.001$–0.05) between the two forms at early stages of age become insignificant at the last age stage. There was no significant differ-

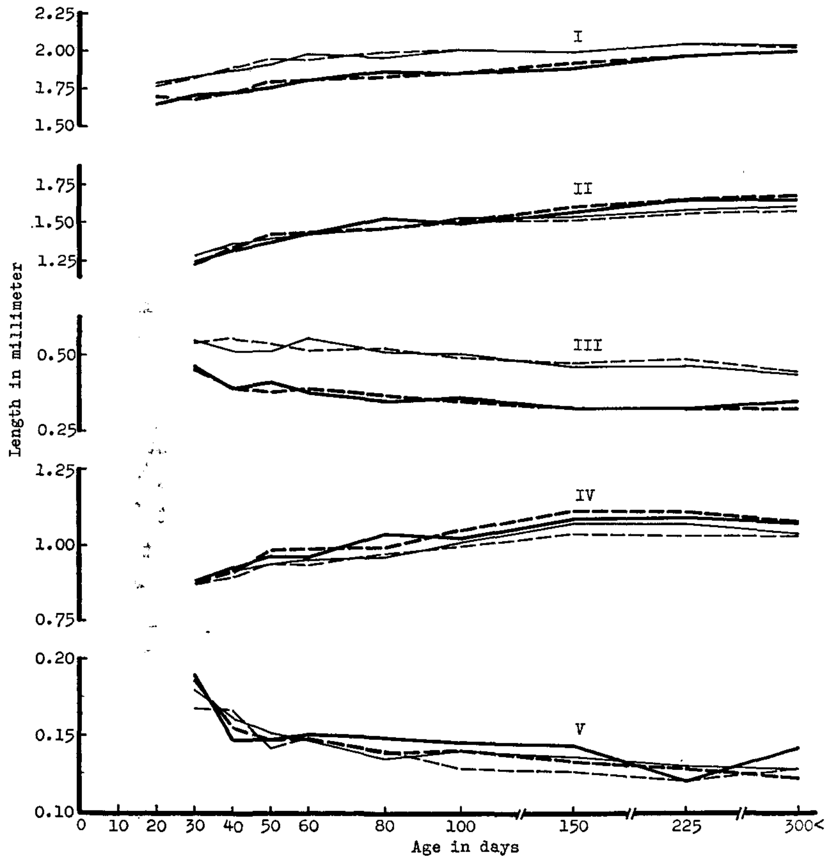

Fig. 6. Growth of five parts of the third upper molar. I: Crown length. II: Anterior length. III: Posterior length. IV: Width of anterior loop. V: Width of the fourth isthmus.

ence observed between the sexes.

As shown in Fig. 6–II and III, the growth of the crown length of M^3 can be attributed completely to the increase of the anterior length of the tooth, since the prosterior length decreases distinctly with advancing age. Though the anterior length of the D-form is greater, on an average, than that of the M-form in later stages of age, there are only a little differences between the two forms. The posterior length, on the other hand, showed very significant difference ($P=0.001$) on an average between the two forms. These observations indicate that the difference of the crown length of M^3 in the two forms can be attributed to the length of the posterior portion.

The closeness of crown length of the two forms at the last age stage (Fig. 6–I) may be a result of the difference in rate of growth of the anterior length.

The anterior parts of the enamel pattern are also very similar to each other between the forms, but it was noted that the most apparent difference in enamel pattern appeared on the posterior parts of the tooth.

In general, variation with age of the posterior parts of the enamel pattern is attributed to the degeneration of the posterior loop which simplifies in structure. This has been observed in many kinds of voles (HINTON 1926 ; ZEJDA 1960).

As shown in Table 3, a few young individuals of the M-form had the types 4 and 4′ of enamel pattern while the others were of the type 6 with 6′. The former changed to type 5 with advancing age and the latter to type 7 or type 9. Voles of the M-form have usually a very long posterior loop, and in the latter two types the loop is much longer than that of the D-form which belongs to the same categories (Fig 6–III).

The D-form lacked the types 4 and 4′ which were observed only in young individuals of the M-form, but contained a few individuals with the advanced type "type 5" which was observed in older individuals of the latter form. Type 6 was most common in the young animals of the D-form, but as stated above, the posterior loop was much shorter than that of the M-form (Fig. 6–III). Forty per cent of juveniles of the D-form had the enamel pattern of type 7 which in the M-form appeared only in older stages. The change in the enamel pattern of the D-form progressed in the last stages of age to type 9 in which the posterior loop was extremely reduced, becoming sometimes closer to type 10 in which the teeth almost completely lacked the posterior loop. The latter was not observed in the M-form. In some very old individuals of the D-form which had heavily worn and narrow-crowned teeth (often seen in wild voles), there occurred

TABLE 3. Age variation in the enamel pattern of the third upper molar

Age \ Type*	1	2	3	4	4′	5	6	6′	7	8	9	10
C. rex												
Young	6											
Old		2	7									
M-form												
20				3	1		22	4				
30				2			29					
40					3		22	4	1			
50				1			27	2				
60				2			24		4			
80	1			5	1		12		9		2	
100				1		2	18		5		4	
150						2	12		8		8	
225				1		2	7		8		12	
300						1			10		19	
D-form												
20							18		12			
30							18		12			
40							9		16		3	1
50						1	10		15	4		
60							6		14	4	4	2
80						2	2		8	5	8	5
100							3		7	6	8	6
150										7	2	21
225											4	26
300											4	27

* Cf. Fig. 4.

a secondary change of the pattern from the type 10 to 9. Individuals classified as type 9 of the last age stage in table 3 and 5, therefore, contained a few examples applicable to this case.

Summarizing these phenomena, the whole age variation in the enamel pattern of the M-form remains in a relatively primitive stage in general tendency of variation, while that of the D-form starts from a relatively advanced stage and reaches in old individuals to a stage of variation in which the change is further strengthened or oversteps the last stage of the M-form.

It should be noted that M^3 tooth showed the slowest growth and that its posterior end was slowest in speed of completion and most variable in shape.

The width of M^3 grows until 150 days of age, after which it indicates no increase but rather decreases on account of wearing at the last stage of age. In M^3 in females there are seen significant inter-form differences ($P=0.001-0.05$) but none in males.

Crown length and enamel pattern of M_1. The crown length of M_1

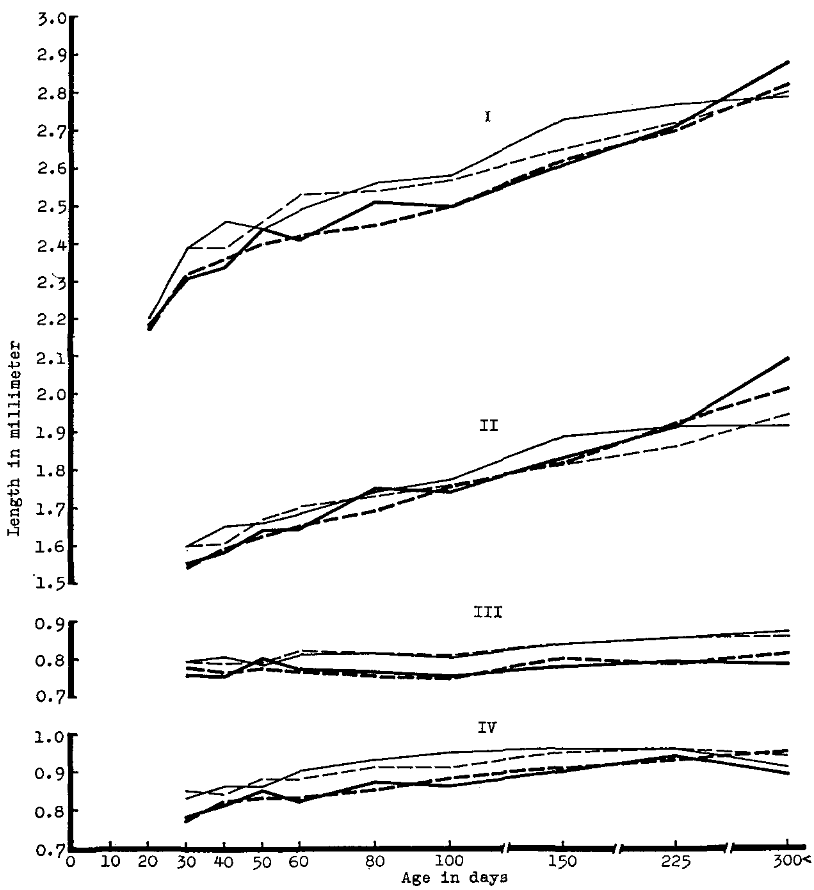

Fig. 7. Growth of four parts of the first lower molar. I: Crown length. II: Posterior length. III: Anterior length. IV: Width of the first lower molar.

grows rapidly until the 30th days of age and then increases gradually to the last age stage (Fig. 7–I). The crown length in the M-form is significantly larger than that of the D-form in many stages of age except for the eariest and the last ones. There was no significant difference between the sexes.

In the posterior length of M_1, the M-form slightly predominates over the D-form in early age stages, but the latter predominates over the former in the later stages. The retarded growth of the total crown length in the former at later age stages is attributable to the retardation of the growth of the posterior length. This type of growth resembles that of the anterior length of M^3 shown above.

The anterior length of M_1 which corresponds to the posterior length of M^3 showed little increase with age, and there were significant differences ($P=0.01$–0.05) in the average lengths between the two forms at many stages of age (Fig. 7–III).

There was no great difference in the posterior enamel pattern between the two forms, but there occurred general age variation. The anterior part, especially the anterior loop, however, varied greatly in form with advancing age and there was only a slight difference in the character of the two forms. This part also undergoes the change from the complex to the simple form, in that about a half of the juveniles at the 20th day have complex enamel patterns (Fig. 5 and Table 4) but most of the adults have simpler ones. The most complex one (type 1) retains a clear fifth outer salient angle. In the second most complex, however, the fifth outer salient angle becomes weak and vestigial. After the 30th day, some of the voles that have the second type of the pattern may come from those that retained the type 1 in earlier stage, and some with type 3 from those with type 2.

Some individuals that had an anterior loop with several vestiges of a primitive ridge, which suggested a complex prototype of the tooth, appear in the youngest short period (around or before the 20th day), but they completely disappeared in the next stage of age (type 1′, 2′, and 3′ in Table 4). The transformation from these complex types to the simple common type (3) appeared to occur a little more rapidly in the M-form than in the D-form. Many individuals with the common type of the enamel retained it throughout life, but a few senile animals underwent further simplification in the enamel pattern. In these cases the dentinal space in the anterior loop of the type 3 was combined with that of the neighbouring triangle, with the weakening of the fifth inner salient angle and the fourth inner re-entrant fold. Then a new anterior loop (type 5) was formed. Along

TABLE 4. Age variation in the enamel pattern of the first lower molar

Age \ Type*	1	1′	2	2′	3	3′	4	5
C. rex								
Young	1		1		9			
Old					3		5	2
M-form								
20	2	2	11	3	12			
30			4	1	26			
40			4		26			
50					29		1	
60					30			
80					30			
100			1		29			
150					30			
225					30			
300					30			
D-form								
20	4		9	2	14	1		
30	3		6		20		1	
40			2		27			
50			2		28			
60					30			
80					28		2	
100					30			
150					30			
225					27		2	
300					28		1	2

* Cf. Fig. 5.

with this process, the combination of the two re-entrant folds which constituted the neck of the anterior loop was changed, i.e. the neck in type 3 consisted of the fourth inner and the third outer re-entrant folds, but the neck in type 5 was formed by both the third inner and outer re-entrant folds.

M-form, as shown in Table 4, had a few individuals belonging to types 4 and 5. The lack of these types in the sample may not indicate the original nature of this form but may be attributable to the fact that the sample from the last age stage contained no old specimens as those of D-form, some of which were older than 400 days; very old ones in the original stock of the M-form (Table 5) and some senile animals taken from the field had those types of M_1. Then, the enamel pattern of M_1 did not show so great an inter-form difference as that in M^3.

It is interesting that there appeared a few individuals with a simplified M_1 at later stages of age. Such a fact was also observed in *Mimomys intermedius* by HINTON (1926).

The width of the anterior loop of M_1 increases with advancing age, but decreases slightly at later stages of age due to wear. The average

TABLE 5. Variation in the enamel pattern of the original stock from which the sample used in the present work has been descended. Almost all the specimens are regarded to be older than 12 months of age according to the date of trapping and the period of rearing

Type*	M^3 7	M^3 9	M^3 10	M_1 3	M_1 4	M_1 5
M-form	5 (23.8)	16 (76.2)		13 (76.5)	3 (17.6)	1 (5.9)
D-form		4**(28.6)	10 (71.4)	9 (64.3)	3 (21.4)	2 (14.3)

* Cf. Fig. 4 and 5. ** See text.

TABLE 6. Age variation in the enamel patterns of the second and third lower molars

Age \ Type*	M_2 1	M_2 2	M_2 3	M_3 1	M_3 2	M_3 3
M-form						
20	28		2	20	9	1
30		1	30	11	5	15
40			30		6	24
50			30			30
D-form						
20	30			20	10	
30	10	10	10	16	14	
40		1	28	10	19	
50			30		1	29

* Cf. Fig. 8.

width is always larger in the M-form than in the D-form. This suggests a more advanced degeneration of the anterior part of M_1 in the D-form.

Enamel pattern of M_2 and M_3. M_2 and M_3 have a distinct anterior loop in early stages of age, but the loop is reduced to a round and simple anterior edge with advancing age. As shown in Table 6, the rate of change in this part is a little more rapid in the M-form (Fig. 8).

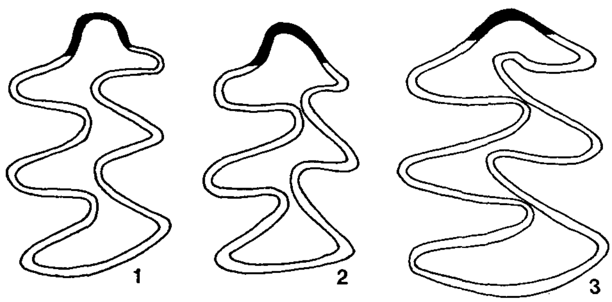

Fig. 8. Variation in the enamel patterns of the second and third lower molars.

d. Length of M^2 and the growth of roots

The length of M^2 continued to grow to the 60th day in the M-form, while in the D-form it grew until the 80th or 100th day (Fig. 9). After these stages of age, the respective lengths gradually decrease to the last stage of age. The average length is always larger ($P=0.001$–0.02) in the D-form than in the M-form after the 40th day. Sexual differences in the length are seen in many of the age stages in the D-form, but not in the M-form.

Figures shown in Table 7 represent a process of root formation along with the day-age, being counted according to the classification shown in Fig. 2. In this classification stages 2, 3, and 5 are rapidly passed through and hence the individuals having the characters assigned to these stages are very few. Stage 6 contains all individuals with divergent roots. The growth curve of root length in this stage is given in Fig. 10.

The time of the root formation is slightly earlier in the M-form than in the D-form. At 100 days of age, for example, the mode of variants in the both forms is situated at the 4th stage, but the other variants of the D-form range to earlier stages, i. e., 2 and 3, while those of the M-form range to advanced stages, i. e., 5 and 6. The mode in the M-form moves to the 6th stage at the next age category while that of the D-form is still at the same stage (4) even at this advanced age.

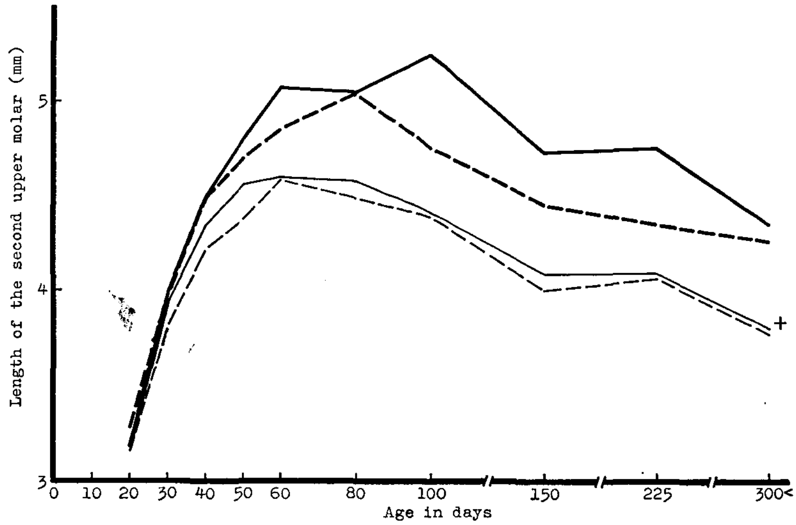

Fig. 9. Growth of the length of the second upper molar. The cross mark indicates the average length in over-wintered very old secimens of *C. rex*.

TABLE 7. Growth of the root of the second upper molar

Age \ Stage*	1	2	3	4	5	6
M-form						
50	27	3				
60	17	7	6			
80	2		11	16	1	
100				24	3	3
150				6	4	20
225				1		29
300						30
D-form						
50	30					
60	29	1				
80	6	10	5	9		
100		1	4	25		
150				17	9	4
225				1		29
300						31

* Cf. Fig. 2.

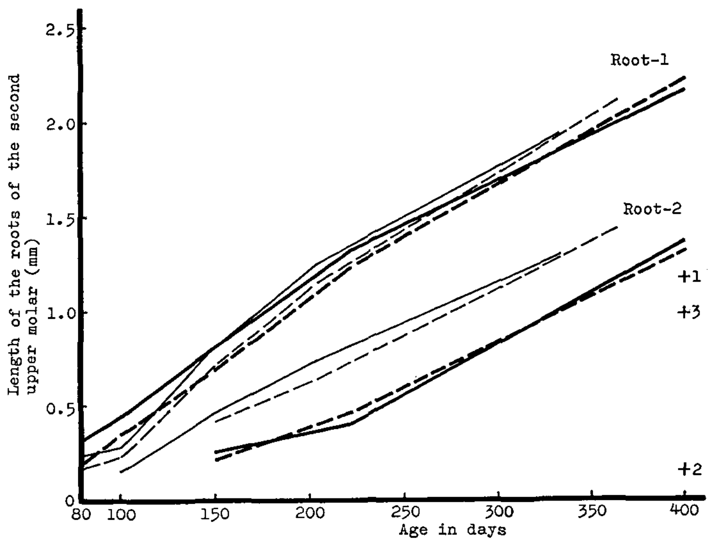

Fig. 10. Growth of roots of the second upper molar. The last two age stages have baen modified so as to represent the real average age in the respective sample. The cross marks indicate the average lengths in 9 specimens of *C. rex* that have been estimated to be older than at least 300 days of age. +1: Root-1, +2: Root-2, +3: See text.

The retarded root formation in the D-form and the rapid one in the M-form may have a close correlation with the duration of growth in the length of M^2. In the former growth occurs over a relatively long time, while in the latter duration of growth is rather short (Table 7 and Fig. 9).

As seen in Fig. 10 there was no significant difference in root-1 between the two forms, but root-2 showed a clear difference ($P=0.01$–0.1). From these facts it is seen that the D-form has usually shorter roots, on an average, for the age, in comparison with individuals of the same age in the M-form.

Except for root-2 of D-form, the growth rate of roots of females becomes greater than that of males in later stages of age. A similar result has been given by VIITALA (1971), who studied *C. rufocanus* from Finnish Lapland.

e. Projection degree of upper incisors

The projection degree of upper incisors showed little age variation except during the last stage of age when it slightly decreased on the average

(Table 8). There was no significant difference between the features of age variation in the two forms. The projection degree of the M-form, however, is apparently smaller on an average than that of the D-form in which the teeth are of proodont type. The prominent upper incisors of the D-form is seemed to be a character occurred in relation to the relatively long mandible of this vole.

TABLE 8. Variation in the projection degree of upper incisors

Age \ Degree*	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								
Young				1	2	4	4	1
Old						4	4	1
M-form								
20	1	6	9	7	6			
40	1	7	9	7	5	1		
80	1	3	7	14	5			
150		2	8	13	6	1		
300		3	12	9	3	3		
D-form								
20				2	13	7	6	2
40			1	2	12	10	4	
80			1	3	12	9	4	1
150			2	4	10	10	3	1
300			4	10	8	5	3	1

* Cf. Fig. 1.

5. Discussion

The characters of teeth including tooth row length, root formation, projection degree of incisors, and basic enamel pattern show an inter-form difference from relatively early stage of the growth. The change in the isthmuses of dentinal space and the general age variation in the enamel pattern of M^3, however, occur in the middle or later stages of growth.

STEVEN (1953) stated that the enmel pattern of *C. glareolus* is probably controlled by a single gene. Therefore, in the present study, the pattern should be referable to that of the original stock from which the sample was derived, as is given in Table 5. All the individuals shown in this table are old, and their character corresponds well with that of descendants (Table 3 and 4), as the latter shows no special deviation in the phenotypic composition.

It is very interesting to compare the enamel pattern of *C. rex* with those of the two forms. *C. rex* was recently described by IMAIZUMI (1971) from Rishiri Island, off the coast of Wakkanai, the northernmost part of Hokkaido. The M^3 of *C. rex* has a very complex type of enamel at an early stage of the growth, and the posterior loop is reduced with advancing age, approaching type 3 in Fig. 4 (Table 3). So far as known, there is no further simplification of M^3 than the type in this form.

In the M-form (*C. rufocanus bedfordiae*), a few individuals retain complex patterns (type 4 and 4′) of M^3, which are even somewhat simpler than those observed in *C. rex*, i. e. the 4th inner and outer salient angles are weaker (Table 3 and Fig. 4). The tendency of variation with age in this form resembles that of *C. rex*.

The enamel pattern of M_1 of *C. rex* also varies with advancing age, in ways that are very similar to those of form M and form D (*C. sikotanensis*) (Table 4). These observations suggest that the enamel pattern of M_1 is fairly constant in this group of voles, though there is distinct variation with age. OGNEV (1950) also gave a similar account regarding *C. glareolus* and the continental *C. rufocanus*.

In the upper molars, M^3 undergoes the slowest growth and shows the greatest amount of intra- and inter-form variations. In the lower molars, M_1 which grows earliest is most variable ontogenically but not so, phylogenetically. It must also be noticed that M_3, showing the slowest growth in the lower teeth, represents an inter-form variation. GUTHRIE (1964) has given a similar result in which the greatest amount of variation in the crown patterns of two species of *Microtus* is present in the anterior end of M_1 and the posterior end of M^3.

According to TUPIKOVA et al. (1968), who studied *C. glareolus*, the formation of roots of M^2 correlates with that of the other teeth, e. g. the roots of M_1, and shows little geographic variation. The time and the rate of the root formation, therefore, appear to be fairly constant within one species of red-backed vole. On the other hand, LOWE (1971) presented data on *C. glareolus* indicating that the growth rate of roots is somewhat different between sexes and among individuals born in different seasons. VIITALA (1971) obtained a similar result in *C. rufocanus*. LOWE (l. c.) also showed that an apparent retardation in the growth rate and the time of root formation occurred in voles reared in his laboratory. The present samples which have been taken from laboratory stocks also indicate a retardation in growth rate which is different from that of wild voles. The time of the beginning of the root formation in the present samples, however, appears not to have been greatly modified in the captive animals, as shown by the comparisons with wild voles that were marked, released, and recaptured later. Therefore, the difference in the features of root formation shown in the two forms of voles studied herein may be significant. The further retarded root formation in the D-form as compared with that of the M-form is of a very distinctive character for form D; the other characters such as enamel pattern of M^3, the isthmus of dentinal space, structures of the skull (ABE 1973), body weight, and sexual maturity (ABE 1968), all change more rapidly than do those of the M-form. As shown by ABE et al. (1971), the roots of molars of *C. rex* are formed very slowly in comparison with those of the M-form. In addition to the marked retardation in the growth of roots, it is noted that the cementum is deposited between the roots in *C. rex*. The separate parts of the roots, therefore are very short in this species, as shown in the Fig. 10 (+2). The real root length (+3 in the figure), however, is almost similar to but slightly shorter than that of the D-form. This suggests a close phylogenetic relationship between the D-form and *C. rex*.

HINTON (1926) stated that "*Evotomys* (=*Clethrionomys*) has descended from an ancestor with a more complex M_1 than that now normal in the genus. Much more definite evidence pointing in the same direction is afforded by the M^3, which in practically all members of the genus is more complex in early stages of wear than it is in ordinary adult specimens". The features of the present samples well fit this statement.

The general tendency of age variations which are shown in such characters as enamel pattern of M^3 and isthmus of dentinal space is very similar in the present three forms, and the inter-form differences are those of the stage of morphogenesis which each form has reached in general age variation. Namely, of the three forms, the characters of *C. rex* are at the most primitive stage in general variation with age. Those of the M-form indicate that they are in a stage overstepped by *C. rex*, but are intermediate between *C. rex* and the D-form. Those of the D-form have reached the most advanced stage of the variables seen.

One may refer to HAECKEL's Theory of Recapitulation for an explanation of the above facts. However, when the case is carefully examined, the theory will not be applicable. It appears rather reasonable that the situation is applicable to the "acceleration" or "hypermorphosis combined with acceleration" in the classification of variations according to DE BEER (1954). Moreover, the three forms have not always such a phylogenetic relationship as a line of *rex*—M-form—D-form which may be expected in applying the theory, but are actually in a line of *rex*—M-form and a line of *rex*—D-form, respectively. The D-form and M-form appear to have descended separately or in the different age from *C. rex* or from a generalized stock that might have had primitive characters probably similar to those of *C. rex*. One of the reasons for the latter is seen in a character of the upper incisors which does not show great age variation. Namely, the teeth of *C. rex* are of proodont type, and the D-form has also a similar, although slightly distinct, type of teeth. The M-form, however, has not such a type, but usual one (Table 8). The feature of root formation shows also a closer relationship between the D-form and *C. rex* than that between the other combinations (Fig. 10). As will be shown in a separate paper (ABE 1973), the tympanic bullae and the diastema of the D-form are similar to those of *C. rex* rather than to those of the M-form.

It is very interesting and very meaningful for the study of phylogenetic relationships between the D-form and *C. rex* to note that all the characters given above show little variation with age, i.e., they are basically formed in early stages of the ontogeny.

The longer teeth (Fig. 9) and the slower growth of root in the D-form appear to be an adaptation for using the coarser food on the native island, which has relatively simple vegetation consisting mainly of *Polygonum sachalinense* FR. SCHMIDT, *Calamagrostis canadensis* var. *lengsdorffii* (LINK), *Sasa amphitricha* KOIDZ., *Artemisia montana* PAMP., and *Coelopleurum lucidum* L. etc. The longer life span of *C. sikotanensis* (D-form), which might have been developed along with the shortening of breeding season owing to the severe climatic conditions, may be also responsible. The breeding cycle has been observed by Mr. T. TAKAYASU (pers. comm.), who has undertaken a long term census-study of this vole on Daikoku Island.

The duration of the increase of length in M^2 of the M-and D-forms is much shorter, as a whole, than that of M_1 of *C. glareolus* as given by MAZÁK (1963). Though the sequence in the growth of the length may be different with each tooth, the differential sequence in the duration of the growth shown by the former two and *C. glareolus* suggests that the teeth of the former two forms have a larger growth rate, respectively, because the absolute length of the teeth is much longer in the former than in *C. glareolus*.

The age at which roots of the teeth begin to be formed appears to be basically not different between the present two forms and *C. glareolus* (MAZÁK 1963; TUPIKOVA et al. 1968), or slightly earlier in the latter (KOSHKINA 1955), but the growth rate in the length of the teeth and the age at which the growth of the length ceases are greatly different between the two. The relationship which has been found between the duration of the growth of M^2 and the time of the root formation in D- and M-forms is not likely to be applicable to *C. glareolus*. In the latter, the increase in the length of the tooth continues to a later stage than does the onset of root formation. The observations presented suggest many lines of research on the evolution of rootless molars and phylogenetic relationships among the microtine rodents. However, the data are too few, at present, to discuss the question generally.

Summary

1. *Clethrionomys rufocanus bedfordiae* (THOMAS) (M-form), taken 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 teeth were studied.

2. The eruption of teeth and the change in enamel pattern of lower molars in early stages of age occur a little more rapidly in the M-form than in the D-form.

3. The length of the upper and lower tooth rows continues to grow in the D-form up to the last stage of age, while those of the M-form increase little after the 150th or 225th day of age. There are significant differences in the length of the upper tooth rows between the two forms.

4. The isthmuses of dentinal spaces of each molar tooth are closed in different stages of age, respectively, but as a whole those of the D-form are closed more rapidly than in the M-form.

5. Growth pattern of the crown length of M^3 resembles that of the upper tooth row. The anterior length of this tooth grows with age, while the posterior length distinctly decreases with it. There is no great inter-form difference in the anterior length, but a significant difference in the posterior length between the two forms. The enamel pattern of M^3 shows a great age variation, changing from the complex to the simple. The variation in the D-form ranges from that of the advanced stage in the M-form to an overstepped simpler one in old age. The enamel pattern of the D-form is simpler as a whole than that of the M-form.

6. The growth of the crown length of M_1 is similar to that of the lower tooth row. The posterior length of this tooth grows with advancing

age, but the anterior one shows little age variation. There is a significant difference in the anterior length between the two forms. The structure of enamel pattern of M_1 changes from the complex to the simple with age, but it shows no great inter-form differences.

7. The total length of M^2 is significantly longer in the D-form than in the M-form. On the other hand, the growth of diverged roots is much stronger in the M-form.

8. Tooth characters of *C. rex*, taken from the field, were compared with those of the two forms. Phylogenetic relationships among these three forms are discussed. It is suggested that the M-form and the D-form might have been derived from *C. rex* or some original stock similar to *C. rex*.

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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.).

——— 1973. Ditto. 3. Cranial characters, with special reference to phylogenetic relationships. 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.

GUTHRIE, R. D. 1965. Variability in characters undergoing rapid evolution, an analysis of *Microtus* molars. Evolution 19: 214-233.

HINTON, M. A. C. 1926. Monograph of the voles and lemmings (Microtinae). British Museum (N. H.) pp. 488.

IMAIZUMI, Y. 1960. Col. Illustr. Mamm. Jap. Osaka pp. 196 (in Jap.).

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

KOSHKINA, T. 1955. Method of age determination in the bank vole and its application. Zool. Zhurn., Moscow 34: 631-639 (in Russian).

LOWE, V. P. W. 1971. Root development of molar teeth in the bank vole (*Clethrionomys glareolus*). Jour. Anim. Ecol. 40 (1): 49-61.

MAZÁK, V. 1963. Notes on the dentition in *Clethrionomys glareolus* SCHREBER, 1780, in the course of postnatal life. Säuget. Mitt. 11 (1): 1–11.

OGNEV, S. I. 1950. Mammals of the USSR and adjacent countries. VII. Rodents. Israel Progr. Sci. Trans. Jerusalem 1964. pp. 626.

OTA, K. 1956. The Muridae of the islands adjacent to Hokkaido. Mem. Fac. Agr. Hokkaido Univ. 2 (4): 123–136. (in Jap. with Engl. Summ.).

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

TUPIKOVA, N. V., G. A. SIDOROVA, and E. A. KONOVALOVA 1968. A method of age determination in *Clethrionomys*. Acta Theriol. XIII (8): 99–115.

VIITALA, J. 1971. Age determination in *Clethrionomys rufocanus* (SUNDEVALL). Ann. Zool. Fennici 8: 63–67.

ZEJDA, J. 1960. The influence of age on the formation of third upper molar in bank vole, *Clethrionomys glareolus* (SCHREBER, 1780) (Mammalia, Rodentia). Zool. Listy 9 (23): 159–166.