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Growth and Development of the Smith's Red-backed Vole, *Eothenomys smithi*

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The postnatal growth and development of the Smith's red-backed vole, *Eothenomys smithi*, were investigated from birth to day 120 in captivity. Seven litters with a total of 26 individuals (14 males : 12 females) were used in the present study. The body weight increased rapidly until day 34, and afterwards continued to grow gradually even to day 120. The total, head and body, and tail lengths almost ceased to increase at about day 50, attaining to more than 90 % of their adult size (measurements at day 120). The hind foot and ear lengths reached almost their adult size at day 28 and day 25, respectively. No sexual difference was observed in the growth curve patterns of the body weight and the above five measurements. Principal events of the development arranged in order of age in days are as follws : The ear pinnae began to erect at day 4.1 ; the dorsum was fully covered with hairs by days 7-8 ; the juvenile pelage was completed by days 10-11 ; the fore and hind digits separated perfectly at day 9.2 and 11.7, respectively ; the auditory meatus opened at day 12.3 and the eyes at day 13.8. Compared with *Clethrionomys rufocanus bedfordiae* and *Microtus montebelli* in the developmental pattern, *E. smithi* fundamentally resembles *C. r. bedfordiae*, but is much the same as in *M. montebelli* only in the age of incisor eruption, Accordingly, it can be said that *E. smithi* possesses the developmental pattern having the property of *C. r. bedfordiae* in the major part and of *M. montebelli* in part.

INTRODUCTION

The genus *Eothenomys* (Microtinae) consists of 11 species occurring mainly in China, Taiwan and Japan (Corbet, 1978). The Smith's red-backed vole, *Eothenomys smithi* which is an endemic species of Japan inhabits the western half of Honshu, east to the Toyama Prefecture, Shikoku, Kyushu and Dogo of the Oki Islands (Imaizumi, 1957), but this species is said to occur also in the central Honshu (Miyao, 1967a). The northernmost limit of its distribution is in the Niigata Prefecture (Imaizumi, 1972).

This species was first described as *Evotomys (Phaulomys) smithii* by Thomas (1905) ; then, it was included in *Clethrionomys* by Hanaoka (1937), *Eothenomys* by Imaizumi (1949) and Aimi (1980), *Anteliomys* by Tokuda (1955) and *Phaulomys* by Tanaka (1971). Imaizumi (1957) regarded the mammal formula "1+0+2=6" as *smithi*'s and "0 + 0 + 2 = 4" as *kageus*'s one, separating *E. kageus* from *E. smithi* by the difference. However, Miyao (1967b) and Kaneko (1985) did not agree with Imaizumi's (1957) opinion, because the difference in the number of mammae depends on mere individual variation. Tanaka (1971) and Aimi (1980) dealt with the morphological and geographical variations in *Eothenomys*, respectively, concluding that *E. kageus* is a synonym of *E. smithi*. As mentioned above, the classification of this species has much remains to be investigated.

In *E. smithi*, the reproductive activity in the field has been fragmentarily reported by Miyao (1967b), Yoshida (1973), Yukawa (1976) and Igarashi (1980) ; however, no information has been published on the growth and development. We recently succeeded in breeding it in captivity and could obtain detailed data on the growth and development. The purpose of this study is to describe the pattern of the growth and development in this species and to discuss the specific characters of this species by a comparison with those of *Microtus montebelli* and *Clethrionomys rufocanus bedfordiae*, etc. (Microtinae) well investigated.

MATERIALS AND METHODS

Ten adults of *E. smithi* (five males and five females), all of which were paired up for breeding, and one pregnant female were trapped in Mt. Wakasugi near Fukuoka from November 1981 to January 1983. Four pairs were kept in outdoor concrete pens (60 x 60 X90 cm), and one pair and a pregnant female were housed in stainless cages (43X25X23 cm) placed in an environment-controlled room (20±2°C, LD 13 : 11). The four females which were pregnant in the pens were allowed to give birth in the stainless cages in the controlled room. As the result, five litters (litter size : 2, 2, 4, 5 and 6) were obtained from the females kept in the pens, one litter (litter size : 4) from a female kept in the controlled room, and another litter (litter size : 3) from a gravid female captured in the field ; a total of 26 young from seven litters were used in this study. All animals were given *ad libitum* a commercial diet (CMF, Oriental Yeast Co., Ltd., Tokyo) and water.

The body weight and five external characters were measured without anaesthetization every other day from birthday (day 0) to 14 day after birth, at two- to seven-day intervals to 50 days and at 10-day intervals to 120 days when measuring was ceased. The five external characters involved the total length, and the lengths of the head and body, tail (from the anus to the tip of the tail), hind foot (without claw) and ear ; the tail ratio also was calculated. Measuring was made to the nearest 0.1 mm with a ruler and/or a pair of dividers, and weighing was read to the nearest 0.01 g on an electronic balance (PC 220, Mettler). Changes in the external characters and the development of behaviour were observed everyday until 30 days of age.

The significant difference ($P < 0.05$) between two means given with 95 % confidence interval was examined by Student's t-test in case of equal variances and by Cochran-Cox's t-test in case of unequal variances. With respect to the growth, the fittest growth equation was estimated in accordance with Yamagishi (1977), i.e. the Gompertz equation :

$$W = Ke^{-ae^{-\lambda t}}$$

for the body weight and the logistic equation :

$$L=\frac{K}{1+e^{a-\lambda t}}$$

for the total length, and the lengths of the head and body, and tail ; where e is the base of the natural logarithm, t the age in days, K the asymptotic size, λ the growth rate constant, and a the coefficient depending on the size at birth.

RESULTS

Phenomena relating to the postnatal growth and development progress simultaneously, but are described separately according to the following three aspects — growth, changes in external characters, and behavioural changes and weaning. The growth stages before eye opening is shown in Fig. 1.

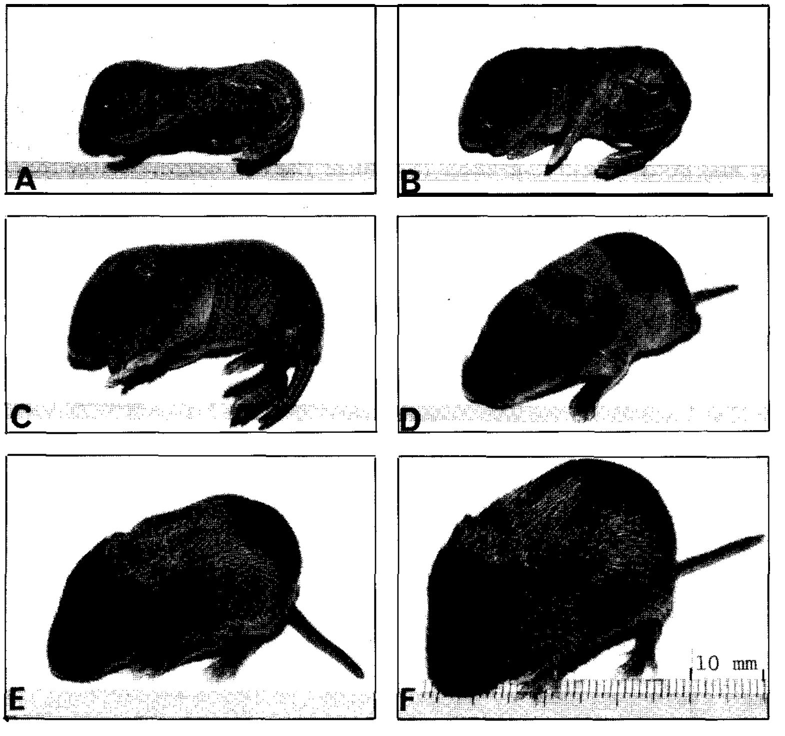

Fig. 1. Growth stages before eye opening in *Eothenomys smithi*. A, newborn stage — there are many wrinkles on the surface of the body ; B, day S-stage-the ear pinnae begin to erect ; C, day 5-stage -the ear pinnae erect as an adult ; D, day 'I-stage — the dorsum is completely covered with hairs ; E, day Y-stage -the fore digits separate completely ; F, day 13-stage — the eyes open.

1. Growth

1) Body weight

The average weight in both sexes combined was 2.13±0.06 g (N=16, range 1.98-2.26 g) at birth (day 0), and afterwards increased rapidly until day 34 (Fig. 2). During this period, the growth rate in the male (0.50 g/day) was a little greater than that in the female (0.44 g/day) ; speaking in detail, both growth rates after weaning, which is initiated at day 14 (0.52 g/day in the male, 0.49 g/day in the female), were slightly high compared with those before weaning (0.49 g/day in the male, 0.42 g/day in the female). The average weight at day 34 reached 18.65± 1.81 g (N = 13) in the male and 16.90± 1.67 g (N= 11) in the female. After day 34, the weight tended to increase at a relatively low rate on the whole. The male and the female attained 25.71f6.15 g (N =4) and 24.18± 6.14 g (N=5) in the body weight at day 120, respectively. Although the male always exceeded the female in the mean weight after day 8, the differences between the sexes were not significant except for day 60. Coefficients of the Gompertz equation for the body weight are shown in Table 1.

2) *Total, head and body, and tail lengths*

The three lengths in both sexes (Fig. 3) increased rapidly and linearly from birth until days 21-23. The growth rates of males and females during this period were 3.16 and 3.04 mm/day in the total length, 2.06 and 2.04 mm/day in the head and body length, and 1.13 and 1.09 mm/day in the tail length, respectively, showing that the growth rate of the head and body length is greater to that of the tail length. After that, the three lengths continued to increase until about day 50 during which the growth rates gradually decreased daily. At day 50, males and females were 141.6f4.76 mm (N= 11)

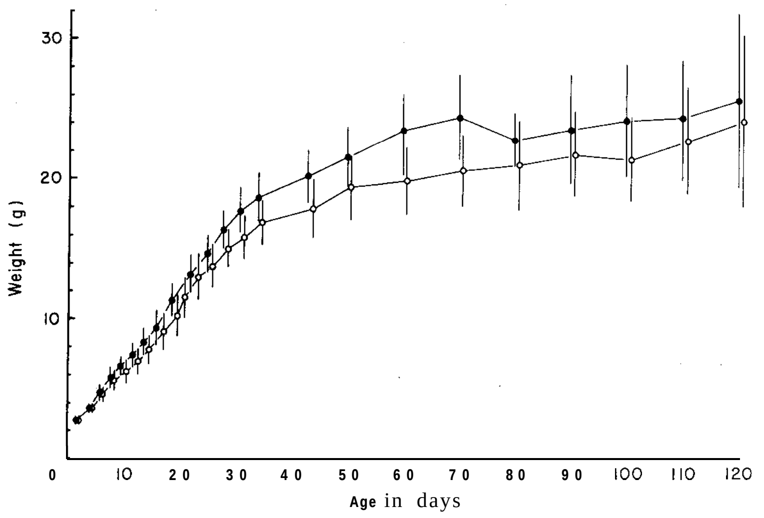

Fig. 2. Growth in the body weight in *Eothenomys smithi*. Solid and open circles represent the mean values of males and females, respectively. Vertical lines indicate 95 per cent confidence intervals. N = 4 to 14 for males and N = 5 to 12 for females.

Table 1. Coefficients of the Gompertz epuations* for the body weight in *Eothenomys smithi.*

	Sex	K	a	λ
Body weight	♂	24.64	2.4481	0.0618
	♀	22.34	2.3502	0.0600

* $W = Ke^{-ae^{-\lambda t}}$

and 136.2±4.10 mm (N=10) in the total length, 96.2f2.44 mm (N=13) and 92.9k2.63 mm (N = 11) in the head and body length, and 46.2 ± 2.35 mm (N = 12) and 43.8 ± 2.76 mm (N = 10) in the tail length, respectively. Each measurement at day 50 attained more than 90 % of that at day 120. The increases in these lengths nearly ceased at about day 50, so that the growth curves became parallel to the abscissa. The significant differences between both sexes were transiently recognized in the head and body length, but not detectable in the total and tail lengths. Coefficients of the logistic equation for each measurement are shown in Table 2.

3) Tail ratio

The tail ratios in both sexes (Fig. 4), in which significant differences were not detected between them, showed a similar tendency with age. The values of males and females increased from 24.59f1.07 %(N=14) and 25.34±1.00%(N=8) at day 2 to 48.18± 1.78 % (N = 12) and 47.16±2.71%(N = 10) at day 50, respectively, with a temporary hiatus (day 12 to 19). The maximum ratios in the male and the female were 49.11± 1.62 % (N = 9) at day 80 and 49.44k2.88 % (N =7) at day 90, respectively.

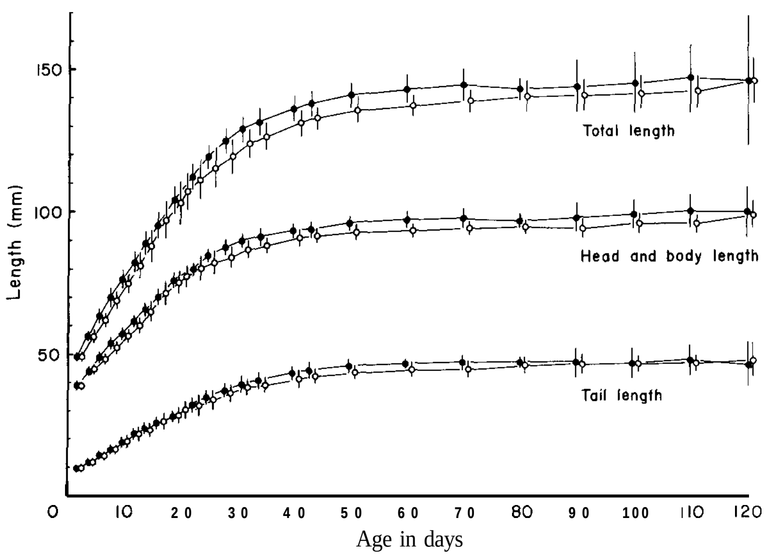

Fig. 3. Growth in the total length, head and body length, and tail length in *Eothenomys smithi*. Symbols are the same as in Fig. 2. N =3 to 14 for males and N =4 to 12 for females.

Table 2. Coefficients of the logistic equation* for the total length, head and body length, and tail length in *Eothenomys smithi*.

	Sex	K	a	λ
Total length	♂	145.44	0.8201	0.0920
	♀	141.73	0.7944	0.0906
Head and body length	♂	98.83	0.6462	0.0961
	♀	95.62	0.9394	0.0986
Tail length	♂	47.60	1.2690	0.0893
	♀	46.64	1.2216	0.0881

* $L=\frac{K}{1+e^{a-\lambda t}}$

Afterwards, although the tail ratios in both sexes fell slightly, they still kept 46.87± 3.07 % (N = 3) in the male and 48.38± 5.96 % (N = 4) in the female at day 120.

4) *Hind foot and ear lengths*

The hind foot lengths in both sexes (Fig. 5) increased rapidly until day 14 during which the growth rate was 0.63 mm/day in the male and 0.57 mm/day in the female, and subsequently their growth rates decreased gradually. The hind foot length at day 28, which was 17.06±0.43 mm (N=13) in the male and 16.81-t0.54 mm (N-11) in the female, almost attained adult size. The difference between the sexes was significant only at day 40 and 50.

The ear lengths in both sexes (Fig. 5), in which no significant difference was detectable, had a similar tendency. The rapid increases in the ear length occurred within the first 20 days after the ear pinnae unfolded. The ear length was 10.75±0.34 mm (N=13) in the male and 10.65f0.30 mm (N-11) in the female at day 25. The growth curves after this age were nearly parallel to the abscissa.

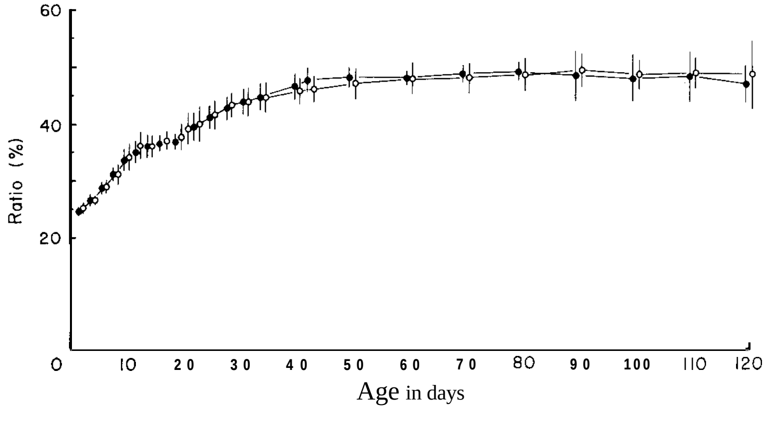

Fig. 4. Change in the tail ratio in *Eothenomys smithi*. Symbols are the same as in Fig. 2. N = 3 to 14 for males and N = 4 to 12 for females.

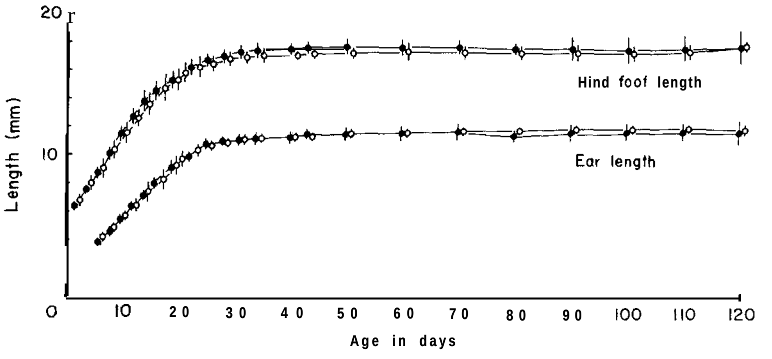

Fig. 5. Growth in the hind foot length and ear length in *Eotkenomys smitki.* Symbols are the same *as* in Fig. 2. N=4 to 14 for males and N=5 to 12 for females.

2. Changes in external characters

1) Pelage

The neonates at birthday were bright reddish pink in colour, and the eyes were visible as dark spots under the skin. No hair was detectable except for the mystacial vibrissae on the snout. However, fine short hairs were sparsely distributed on the dorsum with a binocular dissecting microscope. At day 1, the brightness became faint all over the body, and especially the dorsal colour changed to dark pink, because grey pigmentation developed at that time. At day 2, the ventral colour also turned into sombre one. At day 3, the dorsum became blackish grey as the pigmentation increased, which resulted in a sharp contrast with the belly in colour. At day 4, sparse and dark grey hairs became obvious on the dorsum with the naked eye. At days 5-6, the hairs grew thick and lengthened ; at this time, dandruff-like epidermal flakes appeared on the dorsum. By days 7-8, the dorsum was overspread with dark grey hairs, whereas the belly became covered with whitish grey hairs except for the hairless inguinal region. The teats were detectable in the female after that time. By days 10-11, the juvenile pelage was completely arranged. Thereafter, the post-juvenile moult began at days 31-32, occurring in a regular sequence (Fig. 6). Replacement occurred first in the pectoral region, and then it spread cephalad, caudad and dorsad at about day 40, so that the areas of the juvenile pelage formed into a long and narrow belt from the head to the rump. As the moult progressed, the areas of new hairs were dorsally joined with the exception of the head and rump regions, which were retained to be last replaced.

2) *Ears, digits, incisors and eyes*

The ear pinnae at birth were folded and fused with the skin of the head, covering the auditory meatus; they began to erect at day 4.1 $\pm$0.3 (N =24) with a range of 3-5 days, and were completely unfolded at day 5.2f0.3 (N=24), and the auditory meatus opened at day 12.3$\pm$0.6 (N =24). The fore and hind digits, with tiny claws, were fused each other throughout their overall length at birth. Separation of the digits occurred first between the digit I and the digit II and between the IV and the V, then between the II and the III, and finally between the III and the IV, finishing at day 9.2$\pm$0.5 (N= 24) in the fore-limb and 11.7$\pm$0.6 (N = 24) in the hind-leg.

The mean age of incisor eruption was day 4.8 ± 0.3 (N = 22) in the upper and day 5.0 ± 0.3 (N = 22) in the lower ; the upper and lower incisors penetrated the gums at the same day in most of instances (17 of 22 young), but in one the lower incisors erupted before the upper ones did. The eyes were completely sealed at birth; the eye slits appeared at days 4-5 and became apparent with age in days, and the eyes opened at day 13.8 ± 0.5 (N = 23).

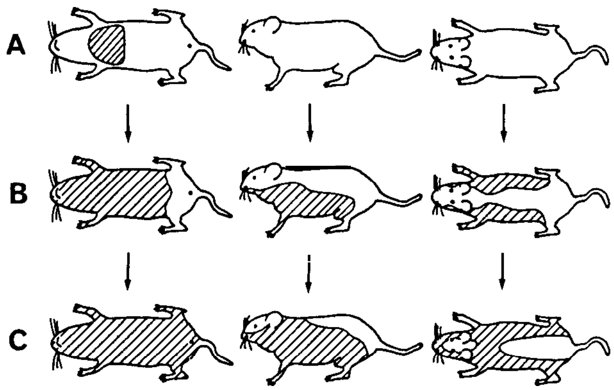

Fig. 6. Post-juvenile moult pattern in *Eothenomys smithi*. Lefthand, ventral view ; Middle, lateral view ; Righthand, dorsal view. A, 31-32 days old ; B, about 40 days old ; C, about 50 days old.

3. **Behavioural changes and Weaning**

The neonates remained lying down, and sometimes wriggled slowly or moved feebly their fore-limbs and hind-legs during the first 3 days. Afterwards, by days 4–5 the young voles were able to keep lying in a normal dorsum-up posture, and by days 5–6 they could crawl with the jaw and venter dragging. In this stage, the young often lost their balance and laid down on the floor, owing to little coordinated movement of the fore- and hind-legs. At about 8 days, the young began to walk lifting their body although they were still unsteady. They could walk steadily by day 11 and walked about in the nest box at day 12 when the hind digits separated completely, in spite of their still sealed eyes. Once eyes opened, the young moved around vigorously, and sometimes went out of the nest box.

The young started to take solid food at the day followed by eye opening, which means the initiation of weaning. Thereafter, the young still suckled every day although the frequency of suckling decreased gradually. The age when the young ceased suckling was about 25 days (30 days in the latest individual).

The development and behavioural changes from birth to 20 days of age are summarized in Fig. 7.

DISCUSSION

This is the first report on the growth and development in the genus *Eothenomys*. The developmental pattern of a given species is considered to indicate an aspect of the specific characters. In *Mus musculus* (8 inbred strains), the differences in the age when each developmental event occurs are recognized even between the strains (Goto *et al.*, 1980). The growth and development are closely related with a mode of life such as habitats, reproductive patterns and so forth (Layne, 1968 ; Miyao, 1974). Thus, it is of great importance to investigate the condition of neonates at birth and the age bringing about the subsequent developmental events.

Principal events in the development of *E. smithi* are arranged in order of age in days as follows : Erection of the ear pinnae, eruption of the incisors, separation of the fore and hind digits, and opening of the auditory meatus and the eyes. With respect to the age at which these events occurred, Table 3 shows a comparison between *E. smithi* and other three microtine rodents ; *Microtus montebelli* (Tasumi, 1959 ; Shiraishi, 1969 ; Obara, 1975), *Clethrionomys rufocanus bedfordiae* (Abe, 1968, 1973) and *C. rutilus mikado* (Mizushima, pers. comm.). First, eruption of the incisors in this species (the upper incisors, day 4.8; the lower ones, day 5.0) was earlier than that in C.

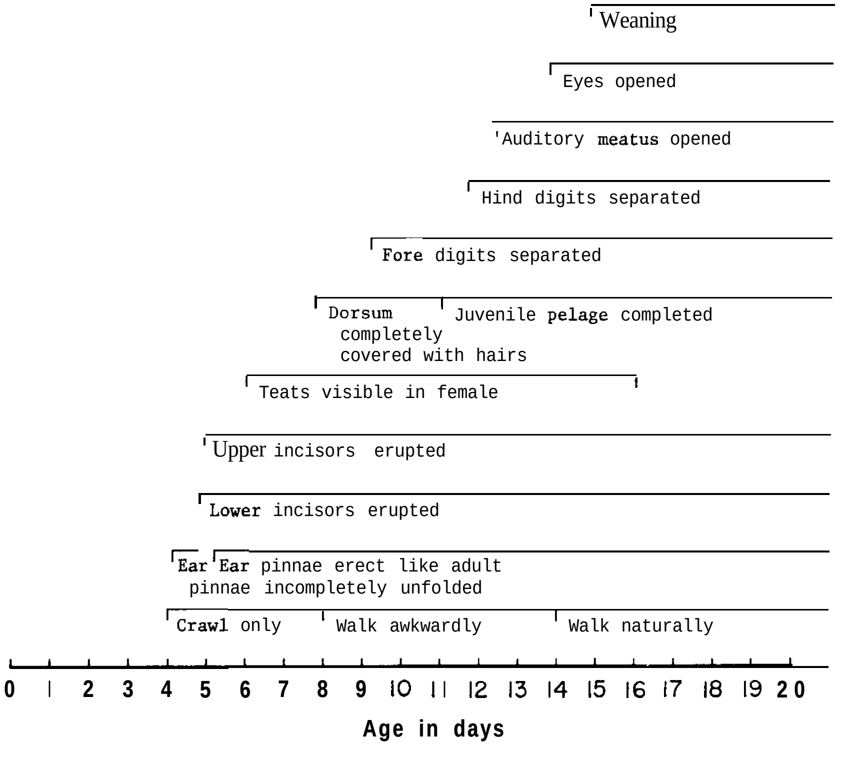

Fig. 7. Diagram showing principal events in the postnatal development in *Eothenomys smithi*.

Table 3. Comparison of the developmental pattern among four microtine species.*

Species	EP	EI	SFD	SHD	OAM	OE	References
E. smithi	4.1	4.8(U) 5.0(L)	9.2	11.7	12.3	13.8	Present work
M. montebelli	2.0	5.3(U) 4.8(L)	7.1	8.4	7.1	7.9	Obara (1975)
	3	6	–	–	7	10	Shiraishi (1969)
	–	5(U) 4(L)	–	–	–	7 - 8	Tasumi (1959)
C. rufocanus bedfordiae	4 - 5	7 - 8	9 -10	9 -11	10–11	12 - 13	Abe (1968, 1973)
C. rutilus mikado	5	7 - 8	–	–	12	14	Mizushima (pers. comm.)

* The developmental pattern is represented by age in days when the following involved principal events occur.
EP, erection of ear pinnae; EI, eruption of incisors (U, upper incisors; L, lower incisors); SFD, separation of fore digits; SHD, separation of hind digits; OAM, opening of auditory meatus; OE, opening of eyes.

rufocanus bedfordiae (days 7-8) and C. *rutilus mikado* (days 7-8) ; it occurred at about the same age as in *M. montebelli* (the upper incisors, day 5.3 ; the lower ones, day 4.8). Regarding the relation between the times of incisor eruption and eye opening, the incisors of *E. smitki* erupt relatively earlier than that of *M. montebelli*. On the other hand, the occurrence of each event, excluding eruption of the incisors, is earliest in *M. montebelli*, and the time in *E. smitki* was much the same as in C. r. *bedfordiae* and C. r. *mikado*. The statistically significant differences ($P<0.01$) between *E. smitki* and *M. montebelli* (Obara, 1975) are recognized in erection of the ear pinnae (a difference of 2.1 days), separation of the fore digits (2.1 days) and the hind ones (3.3 days), opening of the auditory meatus (5.2 days) and the eyes (5.9 days). In addition, the differences in the age giving rise to the developmental events between both the species had a tendency to become greater in the later events.

As pointed out by Tasumi (1959) in *Mus musculus* and *M. montebelli* and Abe (1968) in C. r. *bedfordiae*, the eyes opening coincides with an initiation of weaning, which is also one of the important turning points on the growth and development, i. e., as the eye opening occurs earlier, the weaning and self-supporting stages come earlier. In the Superfamily Muroidea, the most precocial species, *Otomys denti* (Otomyinae, Muridae) is born with opened eyes (Dieterlen, 1968), while the most altricial ones, *Dendromus melanotis* (Dendromurinae, Muridae) and *Peromyscus megalops* (Cricetinae, Cricetidae) open the eyes at day 22 (Dieterlen, 1971) and at day 22.8 (Layne, 1968), respectively. Therefore, even in the same Superfamily, there is a great disparity (about three weeks) in the age of eyes opening between the above two extremes. Judging from the age of the eyes opening (*E. smitki*, day 13.8 ; *M. montebelli*, day 7.9), the former young were more altricial in the development than the latter young although the neonates of both species were hairless and blind. The time of the eyes opening is days 10-11 in *Microtus oregoni* (Cowan and Arsenault, 1954), day 9 in *M*.

oeconomus (Morrison *et al.*, 1954), days 6-10 in *M. ochrogaster* (Kruckenberg *et al.*, 1973), and days 8-9 (Lee and Horvath, 1969) or 9.76 (Innes and Millar, 1979) in *M. pennsylvanicus*. Furthermore, the time of eye opening in other than *Clethrionomys* species listed in Table 3 is day 12.82 in *C. gapperi* (Innes and Millar, 1979) and 10-11 in *C. rutilus dowsoni* (Morrison *et al.*, 1954). Accordingly, it is revealed at the generic level that the period from birth to the day of eye opening is relatively shorter in *Microtus* than in *Eothenomys* and *Clethrionomys*.

Eothenomys is an intermediate form which combines characters of both *Microtus* and *Clethrionomys* (Jameson, 1961; Nowak and Paradiso, 1983). Also, *Eothenomys* is closely related to *Clethrionomys*, although the former is devoid of the rooted cheek-teeth, while the latter have them (Corbet, 1978). On the whole, the developmental pattern in *E. smithi* is similar to that in *C. r. bedfordiae* and *C. r. mikado*, but only the time of the incisor eruption in *E. smithi* is much the same as in *M. montebelli*. The facts suggest that *E. smithi* possesses the developmental pattern of *C. r. bedfordiae* in the greater part, and of *M. montebelli* partially, and produce one of circumstantial evidence that *Eothenomys* is an intermediate genus between *Clethrionomys* and *Microtus*.

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