Acta Theriologica 35 (3–4): 345–356, 1990.
PL ISSN 0001–7051

Daily layers and hibernation marks in incisor dentin of *Sicista pseudonapaea* and some biological remarks

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Klevezal G. A. and Mina M. V. 1990. Daily layers and hibernation marks in incisor dentin of *Sicista pseudonapaea* and some biological remarks. Acta theriol. 35: 345–356.

The structure of the dentin of Altai gray birch mouse *Sicista pseudonapaea* Strautman, 1949 incisors was studied. The birch mice were caught in July 1976 (3 individuals) and in June 1988 (33 individuals) in southwest Altai near Markakol Lake (about 1800 m a.s.l.). The labelling of animals with tetracycline was carried out in 1988. Animals' age was determined by the number of layers of periosteal bone in the mandible. The dentin of incisors was studied in longitudinal ground sections and in longitudinal and cross sections stained with Ehrlich hematoxylin. Distinct daily layers in the dentin were revealed. Moreover, strongly contrasting bands were found which are believed to be formed during hibernation. The presence of these hibernation marks makes it possible to estimate the time of waking up of birch mice from hibernation. This is possible as long as the mark does not disappear in the course of growth and the wearing out of an incisor. It was speculated that males of birch mice wake up approximately two weeks before females. Methods of estimating eruption rate and the time of complete replacement of incisors are offered. The time of complete renewal of upper and lower incisors of the same individuals proved to be approximately the same. In one year for old birch mice it is significantly shorter than in older individuals ($T_1 = 49.6 \pm 1.17$; $T_2 = 57.6 \pm 1.72$ respectively). It is supposed that hibernation marks are formed not only in birch mice but also in other hibernating rodents.

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Key words: dentin, daily layers, hibernation marks, *Sicista pseudonapaea*

Introduction

An interest in the microstructure of mammalian teeth increases drastically after it was shown that the age of animals could be determined by the number of growth layers in tooth tissues. However the incisors of rodents did not draw much attention in this respect since it was clear that annual layers could not be accumulated in them because of their rapid renewal thus making them unfit for age determination. However, it has been shown that one can judge retrospectively about various events in an animal's life using structural characteristics of layers in tooth tissues (Klevezal 1988). Therefore the incisors of rodents as recording structures (for the definition of the term see: Mina and Klevezal 1970, Klevezal 1988) should be reconsidered.

It has been shown by oral biologists that as an incisor wears out a new dentin formed in the basal part of the incisor shifts to the apex of the incisor and then disappears (wears out). The rate of shifting (= rate of eruption) determines the rate of dentin formation. Since the rate of eruption can be rather fast, the incisor dentin in rodents is the most sensitive recording structure. The use of recording structure in ecological studies of rodents was began by tetracycline labelling of nonhibernating rodents (Klevezal and Mina 1980, 1984). The purpose of this presentation was to demonstrate possibilities of using dentin in ecological studies of hibernating rodents taking Altai gray birch mouse as an example.

Material and methods

All the Altai gray birch mice *Sicista pseudonapaea* Strautman, 1949 under study were caught by snap traps near Markakol Lake (southwest Altai, about 1800 m a.s.l.) on mountain slopes covered with shrubs and forest. Three animals were caught in July 1976 and 33 were caught in June 1988. In 1988 bait with tetracycline was put at two plots on a southern exposed slope covered mostly with shrubs. Steamed oats flakes with sunflower oil were used as the bait (Klevezal and Mina 1980, 1984). The bait on one plot was arranged in 5 rows with 20 bait points in a row. The distance between points in a row and between rows was 5 m and 10 m, respectively. The bait was left at plots for two days, then all the uneaten bait was removed and 4–9 days later snap traps were set on every second bait points and in lines 10 m, 30 m and 50 m around the plots.

One upper and one lower incisor were taken from each animals and lateral and medial sides of each of the incisors were ground till the pulp cavity was exposed. These longitudinal ground sections were stored in glycerine. The remaining upper and lower incisors were decalcified and cross sections through basal, middle and apical parts of the teeth were prepared using freezing microtome. The cross sections were stained with Ehrlich hematoxylin and mounted in glycerine. The upper incisors of four individuals were used to make longitudinal stained sections through the basal and the apical halves of the tooth.

All the ground sections were studied in UV light (the source OU- 18). In sections where tetracycline lines were found we measured under the microscope, using an ocular micrometer, the distance from the basal margin of a section up to the point where the dentin band labelled with tetracycline contacted the enamel and also the width of the dentin between the tetracycline line and the pulp cavity in different parts of the section.

The direct line distance from an incisor base up to its apex (AB, Fig. 1) was measured with a caliper rule or with an ocular micrometer before grinding the tooth. Measurements of distance OK, KM (sagittal width of an incisor) and KN (width of the labial wall) (Fig. 1) were made with an ocular micrometer on ground sections.

Ground sections of six upper and six lower incisors were photographed. Their pictures were enlarged (× 37.7) and using them the width of the tooth wall was analysed as a function of distance measured along the outer arc of an incisor outline from the basal margin of the section.

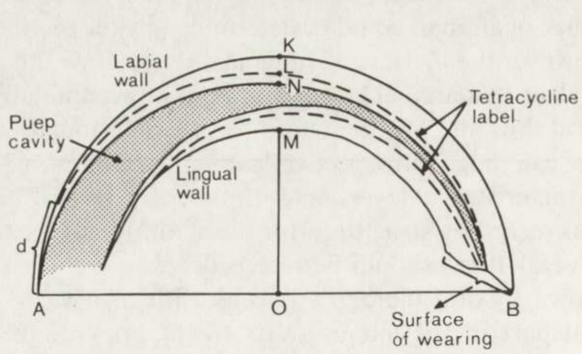

Fig. 1. Scheme of measurements of birch mouse incisors.

All the stained sections were studied under the microscope, the measurements being made with an ocular micrometer.

The following main characteristics of the incisors were used: incisor length (L) measured along the outer arc outlining the labial margin of the longitudinal sections of the incisor; rate of eruption (R) estimated by the speed of shifting of a fixed point in dentin along the incisor; time of complete renewal of an incisor (T) estimated as the time (days) from the moment when a dentin unit is formed at the base of the incisor, in its labial wall, up to the time when the dentin unit disappears at the apex due to incisor wear; rate of dentin apposition estimated as the rate of width increase of the incisor wall.

Incisor length (L) was calculated as:

$$L = \pi r n^\circ / 180^\circ; \; r = AB^2/8OK + OK/2$$

n° was estimated while taking into account that $\sin n^\circ/2 = AB/2r$ (Fig. 1).

Rate of eruption was estimated as $R = d/t$, where d – distance from the basal margin of an incisor up to the point where the tetracycline line contacts enamel on the labial wall of an incisor (Fig. 1), t – period (days) from consuming tetracycline bait by an animal up to the time when the animal was caught. Since the bait was offered to animals during two days we got minimal and maximal possible values of t which gave us maximal and minimal, respectively, possible values of R.

Rate of dentin apposition in the middle part of an incisor was estimated in a similar way, as $= LN/t$, where LN – distance from tetracycline line to the edge of the pulp cavity (Fig. 1). Age was determined by the number of growth layers in the mandibles (Ivanter 1973) of 13 birch mice caught in June and for 3 individuals caught in July. In dubious cases the counts of layers in dentin and cementum of molar were used. These individuals served as standards when the age of other animals in the sample was estimated by the upper molars wear.

Results

Sex and age composition of the sample

In 1988 the birch mice were sampled on June 8 – 9 beyond the labelling plots and on June 13 – 16 and June 18 – 19 at both the plots and beyond them. There was only 1 female among 21 birch mice caught before June 18, but there were 5 females among 12 individuals caught on June 18 – 19.

Age of birch mice in the sample can be conveniently expressed as the number of winters survived by the animals. Studying mandible cross sections of animals caught in June we found one cement line on some of them very near to the margin of the bone. It was clear that those animals survived one winter. There were also specimens where no cement lines were formed but because they were adult we included them into the same age group as overwintered. The group of birch mice which survived one winter was thus represented in the sample of 1988 by 15 individuals. We also distinguished 15 animals which survived two winters, 2 animals which survived three and 1 animal which survived four winters. All three birch mice sampled in 1976 had survived two winters.

There were not only primary but also additional lines in the bone tissue of birch mice which survived two and more winters. Distinct layers could sometimes be seen in cementum of lateral parts of cheek teeth roots and in secondary dentin of their crowns. These layers were used as a subsidiary criterium of age in dubious cases.

Size of the incisors

Mean upper incisor length (mm) was estimated as $L_u = 8.9 \pm 0.96$ (n=23), mean lower incisor length $L_l = 11.7 \pm 0.111$ (n=11), mean sagittal width estimates of the incisors were $W_u = 0.88 \pm 1.225$ (n=6) and $W_l = 0.99 \pm 2.449$ (n=6), respectively. Mean width of labial wall (mm) in the middle of incisor was $m_u = 0.257 \pm 0.029$ (n=22) and $m_l = 0.210 \pm 0.031$ (n=16). Width of the labial wall in the middle of the upper and the lower incisors makes up 67 and 52 per cent, respectively, of their maximal width. Measurements of the labial wall in different parts of an incisor from its base to the apex show that an increase of the wall width proceeds at a fairly constant rate until a little more than 1/2 of the interval in the upper incisor and about 2/3 of the interval in the lower one is reached (Fig. 2).

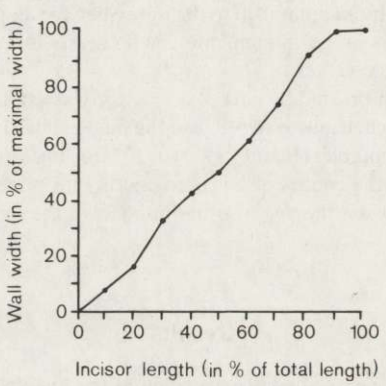

Fig. 2. Increase of maximal width of the labial wall in a lower incisor of a two-year old birch mouse from the base to the apex.

Tetracycline labelling

Five birch mice were caught which had tetracycline lines in the dentin of their incisors. We could measure shifting of the label from basal margin (Fig. 1, d) of both the upper and the lower incisors in one individual only, which was one year old. For five or six days from consuming the tetracycline bait by the animal up to its death the basal point of the tetracycline line shifted for 900 mkm in the upper incisor and for 1239 mkm in the lower one. Thus the minimal and maximal possible rate of tooth eruption can be estimated for the upper incisor as $R_u = 150 - 180$ mkm/day and for the lower incisor as $R_l = 207 - 248$ mkm/day. As for this birch mouse $L_u = 9.4$ mm and $L_l = 12.2$ mm, we estimate minimal and maximal time of the complete renovation as $T_u = 52 - 63$ days and $T_l = 49 - 59$ days. In all five labelled individuals the distance from the tetracycline line up to the pulp cavity in the basal part of the tooth was somewhat bigger than in the middle one. The rate of dentin apposition in the middle of the upper and lower incisors was estimated as 7.0 – 8.9 mkm/day and 6.3 – 8.3 mkm/day, respectively.

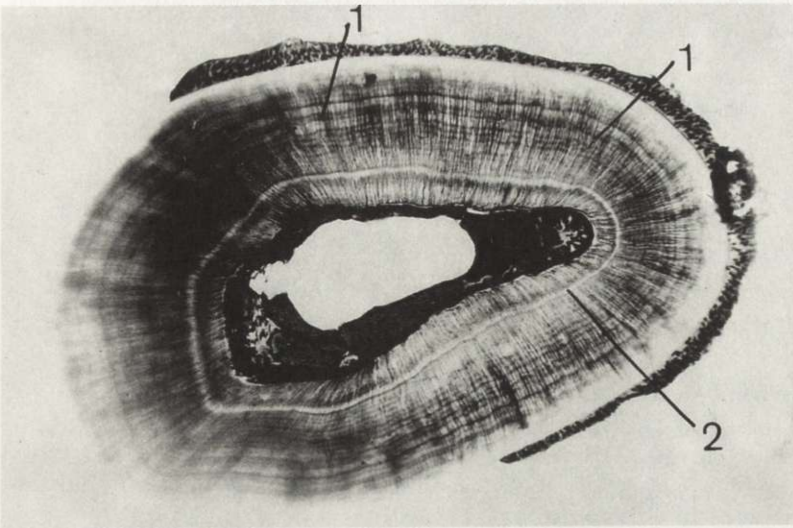

Fig. 3. Cross section through the middle part of the upper incisor of a two-year old birch mouse (male, caught on June 14). 1 — daily layers, 2 — strongly contrasting band (hibernation mark).

Table 1. The number of dentin layers in the labial wall of the middle of the incisors of birch mice. [1/]number of survived winters, [2/]the value was determined by dividing the width of the wall by mean width of one layer, [3/]for the higher values of the *T*, [4/]for the lesser values of the *T*, u – upper, l – lower.

Coll. No.	Sex	Age[1/]	Length of the incisor (L), mm		Number of dentin layers in the incisor		Time of complete renovation of the incisor (*T*), days		
			u	l	u	l	u	l	mean (u+l)
38	m	1	9.76		24	23–24	48	46–48	
39	m	1		12.21	23	24	46	48	
62	m	1	8.63	11.08	25–26	25	50–52	50	49.6 ± 1.17[3/]
77	m	1	8.83		25	24	50	48	
80	m	1	8.50		26	24	52	48	
									$t_d = 3.84$ $p < 0.01$
82	m	2	8.31	11.24	28	27	56	54	
501	m	2	8.30		31		62		
567	m	2			30[2/]		60		57.6 ± 1.72[4/]
568	m	2			29		58		
41	f	3	9.58	12.00	26–27		52–54		

Structure of the dentin

The dentin of the birch mouse incisors looks homogenous in the ground sections. Rarely, bands more transparent than the adjacent ones can be seen. Distinct narrow layers are visible on the stained sections (Fig. 3, 4). They often can be distinguished on all the sections of an incisor being especially well seen in the sections through the middle

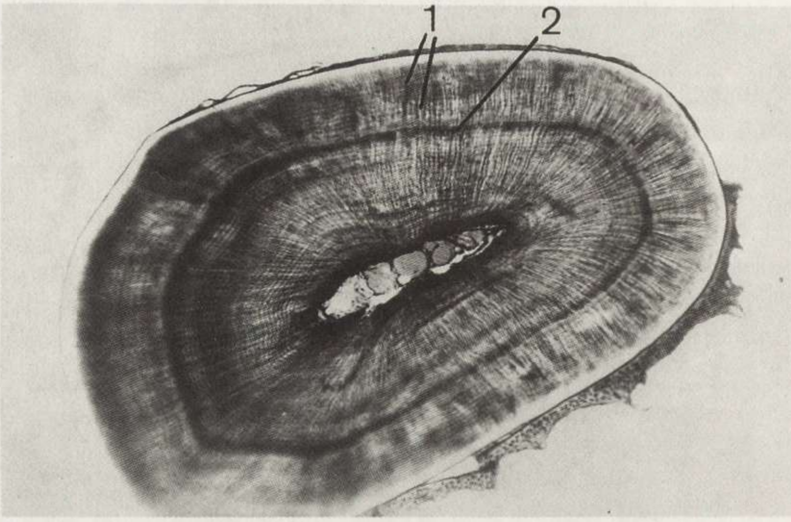

Fig. 4. Cross section through the apical part of the upper incisor of a two-year old birch mouse (male, caught on July 9). 1 and 2 are the same as in Fig. 3.

and through the apical thirds of the tooth. In the basal and the middle parts of the incisor all its walls are layered in structure. The numbers of layers in the middle parts of the upper and of the lower incisors are basically the same (Table 1).

In the apical third of the incisors the layers are visible in the outer and middle parts of the wall and gradually disappear near the pulp cavity where they are substituted by nonlayered dentin and then by secondary dentin with several wide, dark bands. It is difficult to determine exactly when the layers disappear but it appears to happen when the labial wall has a width of no less than 300 mkm in the upper incisor and no less than 260 mkm in the lower one. The secondary dentin appears in the lower incisor when the width of its wall makes up approximately 2/3rds of its final width (the mean final width being 325 mkm, n = 5).

The layers formed in the basal third of an incisor are somewhat wider than those formed in the middle third near the pulp cavity, and layers become quite narrow in the

Table 2. Width of dentin layers in different parts of the incisors of birch mice.

	Basal third		Middle		Apical third	
	mkm	n	mkm	n	mkm	n
Upper incisor						
labial wall	9.4±0.8	6	8.9±1.1	11	6.8±1.2	6
lingual wall			6.9±0.8	7		
Lower incisor						
labial wall	8.6±0.6	3	8.1±0.5	4	6,5	1
lingual wall	9.2±0.8	4	8.1±0.8	11	5.6±1.1	3

apical part before they completely disappear (Table 2). The same trend can be followed looking at cross sections through the apical part of the incisors of 9 out of 10 specimens: the peripheral layers which were formed in the basal part of the tooth are just a bit wider than the layers in the middle zone of the cross section (formed in the middle part of the tooth) and layers in the inner zone of the cross section formed in the apical part of the tooth are the narrowest. The width of a layer in the lingual wall on a cross section through the apical third of a lower incisor was 8.7 mkm on the periphery, 8.0 mkm in the middle zone and 6.0 mkm near the pulp cavity.

On the stained sections of birch mouse incisors not only layers described above were visible in dentin but also a strongly contrasting light band with dark borders (Fig. 3). Sometimes the band was dark and the borders were lighter (Fig. 4). In females caught in June the band was found in all parts of the incisors near the pulp cavity. In

Table 3. Position of strongly contrasting band in cross sections through the middle of the incisor of birch mice sampled in1988. *age was determined using cross sections of mandible. See text for an explanation.

Coll. No.	Sex	Date of sampling	Age	Number of dentin layers formed after contrasting band in the incisor		Calculated date of waking up
				upper	lower	
19	m	9.06	4*	6	6	3.06
20	m	9.06	2	6	6–8	3.06
31	m	14.06	2*	25	25	20.05
32	m	14.06	1*	14	13	31.05–1.06
34	m	14.06	2	15	16	29–30.05
36	m	14.06	2	15	?	30.5
37	m	14.06	3*	12	13	1–2.06
38	m	14.06	1*	3	3	11.06
39	m	14.06	1*	11	11	3.06
40	m	14.06	2*	5	6	8–9.06
41	f	14.06	3*	1	1	13.06
48	m	14.06	2*	12–13	12	2.06
53	m	15.06	1	4	4	11.06
55	m	15.06	1	11	15	31.05–4.06
62	m	17.06	1*	12	12	5.06
77	m	19.06	1*	16	18–19	1–3.06
78	f	19.06	1	0–1	0–1	18.06
79	m	19.06	2	20	20	30.05
80	m	19.06	1*	16	19	31.05–3.06
81	f	19.06	1	3	3	16.06
82	m	19.06	2*	21	21–22	29.05
83	m	19.06	2	?	27	23.05
85	f	19.06	1	1	1	18.06
86	f	19.06	1	1	1	18.06
87	f	19.06	2	3–4	?	15–16.06
88	m	19.06	2	15	19	31.05–4.06
89	m	19.06	2	14–15	14	5.06

Table 4. Position of strongly contrasting band in sections of the apical part of the upper incisors of birch mice sampled in 1976. *from Tables 1 and 5.

Coll. No.	Sex	Date of sampling	Number of dentin layers in a cross section formed: before strongly contrasting band	after strongly contrasting band	Number of dentin layers in a longitudinal section near the wearing surface between contrasting band and labial margin of the incisor	Time of complete renovation of the incisor (T)*	Number of days after waking up	Calculated date of waking up
501	m	9.07	14	28+?	27	58–60	31–33	6–8.06
567	m	26.07	16	33+?	21	61	40	16.06
568	m	26.07	8–9	39+?	no such section	58	40–50	7–16.06

Table 5. Growth characteristics of the upper incisior of birch mice.

Coll. No.	Sex	Age	Rate of eruption of the incisor (R), mkm/layer, estimated in its basal part	apical part	Length of the incisor (L), mm	Time of complete renovation (T), days
33	m	1	178	171	9.26	52–54
54	m	2	153	153	8.4	55
501	m	2		139–142	8.3	58–60
567	m	2		120	7.3	61

males caught at the same time the band could be seen in the middle and apical parts of the incisor far from the pulp cavity. In incisors of animals caught in June the band was visible only in the apical parts of the teeth. The position of the band in relation to the pulp cavity was quite similar in the lower and in the upper incisors of the same individual. The width of the band was estimated as 9.8 ± 4.2 mkm (n = 18) in I^1 and as 10 ± 3.3 mkm (n = 13) in I_1.

On the sections through the basal and the middle parts of the incisors it was possible to count layers which formed after the band. If not all the layers were distinct enough, their number could be calculated by taking into account the mean width of the layer and the distance from the band to the pulp cavity (Table 3). On the cross sections through the apical part of the incisors we could count the layers formed before the band and the layers formed after the band but before the appearance of the nonlayered dentin. On the longitudinal sections we could determine where the band came to the wearing surface of the incisor and how many layers there were between the band and the outer margin of the dentin (Table 4).

The presence of the band allowed us to estimate the distance of shifting of an incisor during the formation of one layer. For that it was only necessary to choose two points on the outline of the outer surface of the incisor, then to measure the distance between them along the outline and to count the layers from the outer surface of the incisor up to the band in each point. The difference in the numbers of layers indicates how many layers were formed during the time of shifting of the incisor at the distance between the two points. Such data were analyzed for four individuals. For two of them the calculations were done using two points; first in the basal, then in the apical parts of an upper incisor. Results proved to be identical (Table 5).

Discussion

The daily increment of dentin in the middle part of an incisor evaluated using tetracycline labelling both for the upper and for the lower incisors turend out to be equal to the mean width of a dentin layer in the same part of the tooth. It proves that the layers in the incisors of birch mice are daily layers as previously described in other rodents (Klevezal 1988). These layers in birch mice incisors are very clear in all parts of the teeth and therefore differ from previously observed common and bank voles (Klevezal *et al.* 1990).

The strongly contrasting band we found in the incisors of birch mice has not been described in other rodents. The band is a little wider than a daily layer and is probably formed during hibernation. Assuming that the number of layers formed this 'hibernation mark' is equal to the number of days after waking up of the given individual we have to conclude that birch mice in the vicinity of Markakol Lake wake up after hibernation at the end of May or during the first half of June. Males wake up approximately two weeks before females (Tables 3 and 4). The situation seems to be typical for birch mice. It was noted for *Sicista betulina* by a number of scientists (Kubik

1952, Sorokin and Sokolov 1960, Ivanter 1975, Pucek 1982) and for *S. tianshanica* by Zimina and Merkova (1960) that in early spring males only (or predominantly) were caught. On that ground Zimina and Merkova (1960) came to a logical conclusion that males wake up in spring earlier than females. No correlation between time of waking up and age of an animals could be revealed in our limited material.

We tried to estimate the time of waking up by means of counting daily layers which were formed after a hibernation mark. As any other layer in the incisor dentin this mark shifts to the apex and then disappears. According to our data the mark can be observed in the middle of an incisor for 25 days after it is formed then it could be seen only in the apical half of the tooth. When the mark is in this position it is possible to count layers formed before the mark but we can not say how many layers were formed after it as there are no daily layers near the pulp cavity in the apical part of an incisor. If there is a longitudinal section of an incisor we can count layers near the wearing surface between hibernation mark and the labial margin of the tooth. Then it is possible to estimate the number of days the animal lived after waking up as the difference between the time (in days) of complete renewal of an incisor (T) and the number of counted layers. When there is a cross section through the apical part of an incisor only, we can not estimate the number of days after waking up precisely. However it is possible to evaluate limits of this parameter. The number of countable layers from the hibernation mark up to the pulp cavity gives a lower limit. The difference between the T (in days) and number of layers from outer surface up to hibernation mark gives an upper limit (Table 5, No. 568).

From what has been said above it is evident that evaluation of T is very important and the accuracy of estimates of the number of days an animal lived after waking up depends mostly upon the error in estimation of T.

Now when we know that the layers in dentin of birch mouse incisors are daily ones we can estimate T rather easily on a longitudinal section of an incisor. It is only necessary to calculate the distance of shifting of the incisor during the time of formation of one layer and then to divide the length of the incisor by the distance.

Another way to estimate T was suggested (Klevezal *et al.* 1990) by using the number of layers in the middle section of an incisor. If eruption of an incisor and increase in the width of its walls proceed in parallels then the number of daily layers in the middle of the incisor is equal to 0.5 T.

However, the eruption is not directly connected with the activity of odontoblasts and depends on the action of periodontal ligaments. In experiments on rats it was shown that when the basal part of an incisor, where odontoblasts are formed, is removed, the apical part still shifted into the oral cavity (Bhaskar 1980). Since processes of incisor eruption and increase in width of its walls are determined by different mechanisms it is necessary to prove that these two processes proceed parallelly. In the case of birch mouse the increase in the width of an incisor wall proceeds uninterruptedly in relation to the distance from the base of the tooth at least up to its middle part (Fig. 2). Some interruptions of the process take place in the apical third of the incisor, *i.e.* just in the part where secondary dentin begins to form and odontoblasts rearrange. As evidence of the consistant rate of shifting along an incisor we consider the fact that eruption rate estimated in the apical and in the basal parts of the same incisor is practically identical (Table 5).

Thus it seems that estimation of *T* using the number of layers in the middle of an incisor is justified. The value of *T* estimated in such a way proved to be similar to the values received using eruption rate (*R*) estimated in longitudinal sections (Tables 1 and 5, animals No. 501 and 567). The difference between the values received by different methods can be attributed to errors of measurements and countings.

It was previously shown for voles (Klevezal *et al.* 1990) that the upper and the lower incisors were characterized by different values of *R* but the values of *T* were similar. This conclusion agrees with the results of Smith and Warshawsky (1976) who found that rat odontoblasts labelled with a radioactive isotope shifted during the same time at the same part of the tooth length in both the upper and lower incisors. Taking into account the possible errors of countings and measurements we can conclude that in birch mice also the values of *T* for the upper and lower incisors are approximately the same (Table 1).

The values of *T* for birch mice which survived one winter are lower than the values for older animals. The difference in mean *T* values is significant (Table 1). It means that *T* really increases with age in an animal. It was also found in voles that *T* values for young individuals were less than for old ones (Klevezal *et al.* 1990).

Comparing incisors of birch mice with those of voles we can conclude that they differ in size, in eruption rate, and in rate of dentin apposition. The incisors of voles are bigger than those of birch mice, the rate of their eruption and dentin apposition being higher. In voles the rate of dentin apposition in an incisor increases with age of odontoblasts and consequently the width of daily layers increases from the base to the apex of the incisor. In birch mouse incisors the rate of dentin apposition decreases with age of odontoblasts as is typical for nonevergrowing teeth. Just like in these teeth odontoblasts of birch mouse incisors terminate their existance forming secondary dentin.

In principle the formation of a hibernation mark in dentin of birch mouse incisors appears to be the same phenomenon as the formation of a winter band of annual growth layers in nonevergrowing teeth. We can expect to find hibernation marks similar to those found in birch mice in the dentin incisors of other hibernating rodents. Some preliminary data (G. Klevezal, unpubl.) allow us to suppose that there are hibernation marks in incisors of sousliks (*Spermophilus undulatus*, *S. pygmaeus*).

A peculiar feature of incisors of birch mice is the extraordinary distinctness of daily layers in their dentin. These layers are much more distinct that the daily layers in incisors of voles. It would be interesting to study other species of *Sicista* and other populations of the same species to decide whether the distinctness of daily layers is due to same biological peculiarities of *Sicista* or is it connected with a wide range of daily temperatures in the mountains where the animals we studied were sampled.

Acknowledgement: Many thanks are due to M. A. Ritus for her technical assistance and to two anonymous reviewers for invaluable remarks.

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Received 19 February 1990, accepted 9 November 1990.