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Incisor growth in voles

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Incisor growth was studied in three species of voles: *Clethrionomys glareolus* (Schreber, 1780) (*C. g.*), *Microtus agrestis* (Linnaeus, 1761) (*M. ag.*) and *Microtus arvalis* (Pallas, 1779) (*M. ar.*). All animals were given tetracycline hydrochloride intramusculary or per os, and were anaesthetized or killed on the 9–14 day after treatment. Longitudinal and cross ground sections and cross sections stained with hematoxyline were investigated. Incisor growth was expressed by eruption rate, the time of complete incisor reneval and rate of dentin apposition. The rate incisor eruption was greater in maxilla than in mandible and higher in *M. ar.*, and *M. ag.* than in *C. g.* It decreased with age in both studied voles (*M. ag.*, *C. g.*). The time of complete renewal of upper and lower incisors was similar. The rate of dentin apposition was different in upper and lower incisors, in different parts of the same tooth and in differen species of voles. In labial, lateral and lingual walls of upper incisors of the voles studied and in lower incisors of *M. ar.* an increase in the rate of dentin apposition was observed from the basal to the medial part of the tooth. In the medial wall of incisors a reverse tendency was seen in all voles. Daily layers of dentin were recognized in all incisors, but the greatest contrast was seen in *M. ar.* and the least visible, in *C. g.* Appositional layers in incisor dentin could be used for indirect determination of the rate of incisor eruption.

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Introduction

The incisors of voles continually grow. The growth area located in the basal part of the incisor produces odontoblasts that form a thin ring of dentin (Fig. 1). The dentin ring gradually moves apically, together with the odontoblasts. The continuous production of dentin by the odontoblasts results in a thickening of the tooth wall. With the thickening of the incisor walls, the pulp cavity narrows and when the incisor erupts it is virtually closed.

The apical movement of new dentin is continuous and compensates for the wearing down of the apical surface of the incisor. This constant movement, or as it is usually said, incisor eruption, has been studied thoroughly in laboratory voles (Schour 1960). In wild voles it is practically unknown. Therefore the use of vole incisors as a recording structure of growth in mammals (Klevezal 1988) requires an examination of their growth in various species.

The purpose of this study was to examine the growth mechanism of the upper and lower incisors in voles and to determine its changes with age, species and population.

Material and methods

We started with the examination of the upper and lower incisors of 107 bank voles, *Clethrionomys glareolus* (Schreber, 1780) [*C. g.*]. Voles came from the laboratory colony of the Mammal Research Institute, Polish Academy of Science in Białowieża and were from at least the 13th laboratory generation. The animals originated from two seasonal generations: autumn — born in August, 1981, and spring — born in April, 1982. These voles made up the 'Białowieża sample'. For comparative purposes animals from other research projects were also used. There were upper and lower incisors of 9 *C. g.* trapped near Moscow in December, 1987 ('Moscow sample') and lower incisors of 8 *C. g.* trapped in summer, 1980 near Volgograd ('Volgograd sample'). In addition there were pairs of both incisors of 10 *Microtus arvalis* (Pallas, 1778) (*M. ar.*), trapped in July, 1976 on the shores of the Markakol Lake (eastern Kazachstan) and the upper incisors of 20 *Microtus agrestis* (Linnaeus, 1761) (*M. ag.*), 1.5–10 months old from the laboratory colony of the Mammal Research Institute (13th–15th laboratory generations). The latter, as well as those *C. g.* of the Białowieża sample originated from parents that had been trapped in the Białowieża Primeval Forest during previous years.

Tetracycline was used as a vital marker. It is absorbed into growing teeth at the moment of introduction and can be seen as a yellow flourescent band in ultraviolet light (for review see Hansson 1967, Klevezal 1988). *C. g.* from the Białowieża and Moscow samples as well as *M. ag.* were given tetracycline intramuscularly (20 mg/kg body weight). After the injection they were kept in the laboratory for 10–14 days and then anasthetized (for details see Klevezal *et al.* 1984). *M. ar.* received in the field the same tetracycline doses in two portions at an interval of 3 to 14 days (see Klevezal 1981). *C. g.* from the Volgograd sample were given tetracycline in the field together with the bait (see Klevezal and Mina 1980, 1984). They were trapped with snap traps 9 — 12 days after treatment.

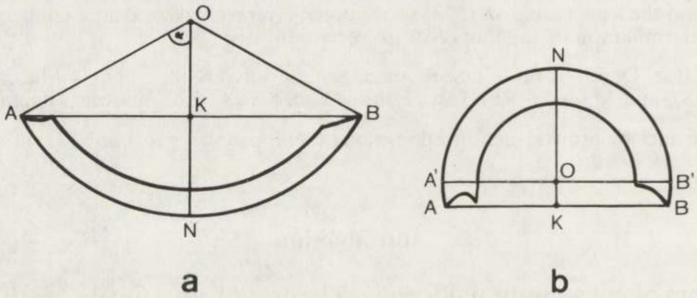

Fig. 1. Scheme of measuring the lower (a) and upper (b) incisors. See text for explanations.

Longitudinal and cross ground sections of the incisors were examined. The cross ground sections of the lower incisors of all *C. g.* from Białowieża were obtained from the other study. The cross sections of all incisors from the other voles, and the other lower incisors of 10 *C. g.* from Białowieża were prepared in the following manner: incisors, removed from the jaw, were cut transversely, perpendicularly to the longitudinal axis, into 3 parts, each of which were ground from both the apical and basal surfaces to the center. Longitudinal ground sections were made by grinding an incisor from both the lateral and medial sides until the pulp cavity was exposed. The ground sections, approximately 250 mkm thick, were examined under a microscope in normal and UV light. Before grinding the distance between the basal and apical points along a straight line (distance AB, Fig. 1a, b) was measured. All remaining measurements were done on the ground sections under microscope using an ocular micrometer.

Rodent incisor shape is approximated as a segment of logarithmic spiral (Thompson 1917). It was possible to treat it as an arc and to calculate the labial wall length using the equation for arc length. In the case of the lower incisor two equations (Fig. 1a) were used, the Hygen's equation:

$$\check{L}=2AN+\frac{1}{3}(2\,AN-AB) \qquad (1)$$

where $AN=\sqrt{AK^2+KN^2}$

or another one: $$\check{L}=\frac{\pi_{R\times n^\circ}}{180^\circ} \qquad (2)$$

where $R=\frac{AB^2}{8NK}+\frac{NK}{2}$ (at $R=AO=\sqrt{AK^2+KO^2}$; $KO=R-NK$, $AK=AB/2$),

$n^\circ=2\alpha$ and $\sin\alpha=\frac{AK}{R}$.

The upper incisor is more curved than the lower one, and with the increased arc angle, the error of the Huygen's equation increases. In the case of the upper incisors only equation (2) was used. Often in the upper incisors $NK=\frac{1}{2}AB$ which means that it was almost a half circle and that $\check{L}=\pi NK$. If the NK was larger than $\frac{1}{2}AB$, R was taken to be $\frac{AB}{2}$, $n^\circ=180$, the length of arc A' B' was calculated and the length of the missing AA' and BB' was added (Fig. 1b). In this case it meant that $\check{L}=\pi\frac{AB}{2}+2(NK-\frac{AB}{2})$.

Incisor growth was characterized with three parameters:
(1) Rate of incisor eruption — the rate in mm/day of moving of each established dentin or enamel point apically from the tooth base in the procees of continuous growth and wearing.
(2) Time of complete incisor renewal — the time (in days) in which each newly formed part of the basal dentin moves to the apical end of the incisor and wears out.
(3) The rate of dentin apposition — the rate in mkm/day at which the odontoblast ring, moving apically, produces dentin. It is the rate of tooth wall thickening.

Being injected intramuscularly, tetracycline marks the dentin growing within approximately 12 hours (Klevezal 1988). The newly marked dentin is found along the entire length of the pulp cavity, from the basal ring to the place of pulp cavity obliteration in the apical part of the tooth. As the incisor grows the tetracycline mark moves apically and in the ground section, in ultraviolet light, it can be seen as a narrow, yellow band, parallel to the pulp cavity and separating the dentin apposited after marking the animal (Fig. 2, A–C).

In order to determine the rate of incisor eruption the distance from its base to the place where the tetracycline mark reaches the enamel and disappears (Fig. 2, A — the place marked with a dot) was measured on the incisor labial side. The measured section was divided by the time that lapsed from the moment of tetracycline injection to the animal's death. The rate of complete incisor renewal was calculated as a quotient of the labial wall arc length and the rate of tooth eruption.

The rate of dentin apposition was determined on the longitudinal and cross sections of the tooth. Under the microscope the distance from the outside edge of the tetracycline band to the edge of the pulp cavity was measured (Fig. 2, B, C) and divided by the number of days between the moment of tetracycline injection and death of the animal. 'Error of measurement' was determined as a difference between the two independent measurements in per cent of half of their sum. It was on average 5% (n=50). Sometimes it happened that on the cross section through the entire mandible, the lingual and labial walls of the incisors were not cut perpendicularly. In measuring the rate of dentin apposition in such 'cross' sections some special correction was calculated.

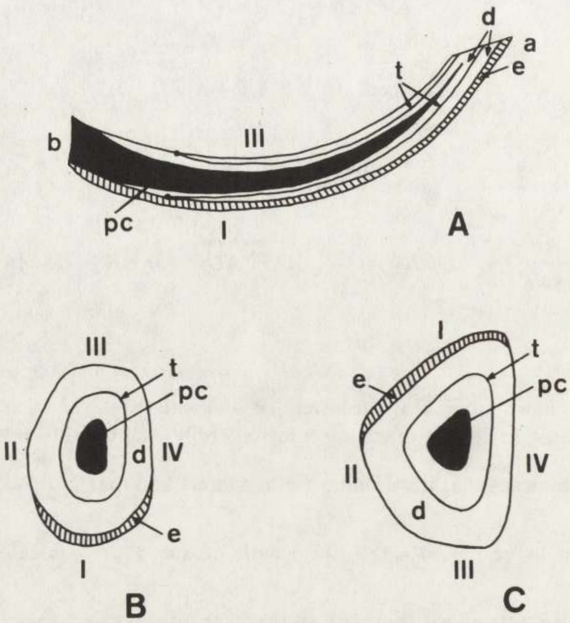

Fig. 2. Scheme of longitudinal (A) and transverse (B, C) sections of incisors. A, B — lower; C — upper. Explanation of symbols used: a — apical, b — basal parts of incisors; d — dentine; e — enamel; pc — pulp cavity; t — tetracycline mark; I — labial, II — lateral, III — lingual, IV — medial walls of incisor; dotts on Fig. A — means the place on labial and lingual walls, where tetracycline marks disappear.

To study the layered structure of dentin, 3–5 animals were chosen from each sample of voles. Their lower and upper incisors were decalcified, cut into sections 15–20 mkm thick and stained with Erlich hematoxyline.

Results

General size and shape of incisors

In all the examined voles the upper incisors were shorter than the lower ones and had slightly larger diameters. In *M. ag.* and *M. ar.* the upper and lower incisors are greater than those of *C. g.* (Table 1). Incisor size varied with age. The mean length of upper incisors (measured as length of chord) in *M. ag.* at 1.5 months was 7.4$\pm$0.35 mm (n=5) and at 8–18 months of age — 8.1$\pm$0.43 mm (n=7). The difference is statistically significant ($t=3.2$, $p<0.05$).

The mean length I_1 of *C. g.* from the Białowieża sample at 1 month of age was 12.2$\pm$0.33 mm (n=7) and at 8 — 18 months of age was 12.6$\pm$ 0.44 (n=19). The difference is statistically significant ($t=2.5$, $p<0.05$).

One to two month old spring generation *C. g.* from Białowieża had insignificantly longer incisors than animals of the same age but from the autumn generation (respectively: 12.5 ± 3.7 mm, n=8 and 12.2 ± 2.6 mm, n=9). In 8–10 month old animals no incisor size differences were noted between spring and autumn generation animals.

The thickness of the dentin wall is identical or almost identical on all sides in the basal part. It changes in accordance with movement towards the apex. From Table 1 it can be concluded that in all voles at the apical part of the incisors, the medial side is the thinnest and the labial or lateral is the thickest.

Rate of incisor eruption

Table 2 presents data concerning the rate of incisor eruption and the time of complete incisor renewal. In general incisors grew fastor in *M. ag.* and *M. ar.* than in *C. g.* A significant difference related to age in the rate of eruption of lower and upper incisors was observed in *C. g.* and *M. ag.* In 1–2 month old animals the rate of eruption was faster than in 8–10 month olds. The rate of eruption of lower and upper incisors also differed. Usually I_1 grew faster. The rate eruption of lower incisors in *C. g.* from the Moscow and Volgograd samples was significantly faster than in 8–10 month old voles from Białowieża but insignificantly faster than in 1–2 month old animals from the same sample.

When comparing the mean rate of eruption of upper and lower incisors within the same group of voles, we can see that the time of complete renewal of I^1 and I_1 is almost the same and that the rate of eruption of I^1 is significantly lower than I_1 (Table 2). The correlation between the rate of eruption of I^1 and I_1 is high and significant, $r=0.69$ ($p<0.01$). This is also true in the case of complete renewal of both incisors $r=0.88$ ($p<0.001$) (n=15 *C. g.* from the Białowieża sample).

The rate of dentin apposition

The rate of dentin apposition in identical parts of the same incisor in different groups of voles was compared. From Table 3 we see it is related to the rate of eruption of the incisors. In 1–2 month old animals the rate of dentin apposition is greater than in 8–10 month olds. In *C. g.* from the Moscow and Volgograd samples it was faster than in the Białowieża sample. Also the rate of dentin apposition was greater in *M. ag.* and *M. ar.* than in *C. g.* These relationships change when comparing the rate of dentin apposition in upper and lower incisors of these same voles. The rate is faster in the upper, slowly growing incisors. To determine the reason of these differences we calculated which portion of the overall thickness of the dentin wall is formed in the middle part of the incisor. From the data presented in Table 4 it can be concluded that in all cases the pulp cavity of I^1 is filled faster with dentin than in I_1.

In comparing the rate of dentin apposition in the same part of the tooth, but in different walls it can be seen that in all cases it is the least in the medial wall (Table 3). In the remaining walls it varies. However in most cases the faster rate of dentin apposition is in the labial or lateral tooth walls.

An explanation as to why the rate of dentin apposition differs in different parts of

Table 1. Average (±SD) measurements (in mm) of upper (u) and lower (l) incisors in adult voles. Sample sizes are given in brackets. LC – Length of chord from basal to apical points of incisor, LA – Length of incisor along outer arc of labial side, d – The diameter of incisor, [1/] – On labial, lateral, lingual, medial sides. Thickness of each of them expressed in relation to first one, [2/] – Acc. to Klevezal (1981), [3/] – Calculated on the basis of the average length of incisior chord and of arrow of labial arc (n=4).

Species	Incisor	LC	LA	d	Ratio of thickness of incisior walls[1/] in different parts: Basal	Medial	Apical
C. glareolus							
Białowieża	l	12.6±0.44(19)	15.2±0.5(8)	0.88±0.04(5)	1:1:1:1(2)	1:1.05:1:0.8(3)	1:0.9:0.9:0.6(3)
	u	6.4±1.86(13)	10.0±0.3(13)	1.00±0.04(5)			
Moscow region	l	13.0±0.45(9)	15.1±0.56(9)	0.85±0.04(8)	1:1:0.9:0.9(4)	1:1:0.9:0.8(2)	1:0.8:0.8:0.6(3)
	u	6.6±0.3(9)	9.8±0.3(9)	1.02±0.06(9)			
Volgograd region	l	13.9±0.3(5)	16.6±0.3(5)	0.99±0.06(5)			
	l	14.1[2/] (16)	16.6[3/]	0.94±0.08(4)	1:1:1:0.8(1)	1:1:1:0.9(2)	1:1.1:1.1:0.9(5)
M. arvalis	u	7.9±0.42(10)	12.0 (1)	1.26 (1)	1:1:0.8:0.8(3)	1:1:1:0.7(2)	1:1:1:0.6(2)
M. agrestis	u	8.1±0.43(7)	13.5±0.9(9)	1.28±0.03(5)	1:1:1:1:(6)	1:1:1:0.9(5)	1:1:0.9:0.6(6)

Table 2. Rate of incisior eruption (V) and time of complete incisior reneval (t_o) in voles. Averages ±SD and sample size (in brackets) are given. [1/] – avg length of arc on labial side divided by t_o, [2/] – Acc. to Klevezal (1981).

Species (age and locality)	Lower incisor: V mm/dy	Lower incisor: t_o, dys	Upper incisor: V mm/dy	Upper incisor: t_o, dys	Significance of differences of V
C. glareolus					
Białowieża					
1 – 2 mo.	0.30±0.04(8)	46±4.6(8)	0.23±0.03(16)	43±5.4(16)	$t=4.4$, $p<0.001$
8 – 10 mo.	0.24±0.02(10)	62±5.5(10)	0.17±0.03(17)	60±9.8(17)	$t=7.3$, $p<0.001$
	$t=6.7$, $p<0.001$	$t=4.3$, $p<0.001$	$t=7.7$, $p<0.001$	$t=6.4$, $p<0.001$	
Moscow region	0.33±0.04(9)	46±5.5(9)	0.21±0.04(9)	46±7.2(9)	$t=6.3$, $p<0.001$
Volgograd region	0.32 (2)	43(2)			
M. arvalis	0.60[1/]	27[2/]	0.36[1/]	33[2/]	
M. agrestis					
1.5 mo.			0.30±0.03(5)	39±5.5(5)	
8 – 10 mo.			0.25±0.02(6)	54±4.0(6)	
			$t=3.18$, $p<0.05$	$t=5.1$, $p<0.001$	

Table 3. The rate of dentine apposition (mkm/day) in defferent parts of incisior. Average values ±SD and sample size (in brackets) are given. [1] – Regression of daily increase of dentine in given wall of incisior in relation to total thickness of dentine on labial wall (in mkm), [2] – Acc. to Klevezal (1981), [3] – Both age classes joined together. Daily increase of dentine in relation to breadth of pulp cavity (in mkm).

Species (age, locality)		Wall of incisor	Part of incisor		Signi.		Slope (a) and intercept (b) of linear regression[1]
			basal	medial	*t*	*p*	
M. arvalis	l	lab.[2]	12.4±1.9(8)	14.4±2.2(14)	2.2	<.05	
		lat.	9.7±4.2(2)	15.6±1.5(7)			b=0.03
	u	lab.	20.2±1.5(4)	26.9±4.6(7)	3.5	<.01	a=11.4, b=0.04
		lat	21.6±1.9(4)	26.0±2.5(7)	3.3	<.01	a=15.2, b=0.03
		ling.	20.0±1.3(2)	24.9±2.7(7)	3.6	<.01	a=16.5, b=0.025
		med.	19.8±0.6(3)	19.2±2.8(6)			
M. agrestis	u	lab.	17.6±2.5(3)	22.9±3.2(6)	2.7	<.05	a=8.8, b=0.03
8–10 mo.		lat.	20.0±3.4(4)	23.2±3.2(8)			
		ling.		19.5±3.6(4)			
		med.	13.0 (1)				
C. glareolus							
Białowieża	l	lab.	7.0±1.4(12)	8.0±1.3(7)			
1–2 mo.		lat.	8.7±1.5(13)	7.3±2.1(8)			
		ling.	8.5±1.5(11)	8.9±2.0(7)			
		med.	6.7±1.4(11)	5.6±2.3(9)			
8–10 mo.		lab.	6.3±1.1(16)	7.3±1.3(11)	2.8	<.05	b=−0.005[3]
		lat.	7.6±1.0(16)	6.1±1.3(14)	3.5	<.01	b=0.009
		ling.	7.7±1.4(16)	7.9±1.0(12)			
		med.	5.8±1.2(15)	4.7±1.3(13)	2.3	<.05	
1–2 mo.	u	lab.	14.2±2.1(10)	16.4±1.7(10)	4.9	<.01	
		ling.	12.5±1.8(10)	13.7±1.7(10)			
·8–10 mo.		lab.	12.1±1.6(14)	13.5±1.5(14)	2.4	<.05	
		ling.	9.6±1.8(14)	11.2±1.4(14)	2.6	<.05	
Moscow	l	lab.	9.4±1.7(7)	9.6±1.6(8)			
region		lat.	9.9±1.8(5)	9.7±1.5(7)			
		ling.	9.7±1.2(6)	9.8±1.5(8)			
		med.	7.5±1.1(4)	6.8±1.4(7)			
	u	lab.	14.9±1.6(8)	16.5±2.5(7)			
		ling.	11.2±2.4(4)	14.2±3.0(8)			
Volgograd	l	lab.	9.9±1.3(5)	9.5±1.6(8)			
region		ling.	8.9±1.3(6)	8.6±0.4(4)			

the same wall is particularly interesting. In comparing the basal and the middle parts we see that only in the medial wall, both in the upper and lower incisors, in all voles the rate of dentin apposition decreases from the base to the middle of the tooth (Table 3). In the remaining walls it differs, depending on the type of tooth (upper or lower) and the place of origin of the vole sample.

In *M. ar.* — in both incisors, and in *M. ag.* and *C. g.* in the upper incisors there is a faster rate of dentin apposition from the basal part to the middle although the mean

Table 4. Relative thickness of dentin in medial part of incisor. Sum total of dentin thickness in labial and lateral walls expressed as *per cent* of incisor diameter, without enamel and cementum.

Species and locality	Incisor lower (n)	Incisor upper (n)
C. glareolus		
Białowieża	50 (5)	58 (5)
Moscow region	50 (6)	55 (8)
Volgograd region	50 (5)	–
M. arvalis	52 (3)	62 (1)
M. agrestis	–	64 (5)

Table 5. Indirect calculation of time of complete renewal if incisor (t). S_o – Average dentin thickness (mkm) in labial wall of middle point of incisor, measured on longitudinal ground sections, S_1 – Average dentin layer thickness (mkm), $t_1 = 2\frac{S_o}{S_1}$, t_2 – Time of complete renewal of incisor, estimated on movement of tetracycline marks (averages $\pm$SD). All age groups taken together.

Species and locality	Incisor	S_o	S_1 sections: ground	S_1 sections: stained	t_1	t_2
C. glareolus						
Białowieża	lower	220 (5)	8.0 (5)		55	55±9
	upper	362 (5)	12.6 (8)		57	50±10
Moscow region	lower	218 (6)	10.0 (2)		44	46±5
	upper	335 (8)	14.4 (4)	12.8 (4)	46; 52	46±7
Volgograd region	lower	257 (4)		12.8 (1)	40	43
M. arvalis	lower	248 (3)		17.7 (7)	28	27
	upper	372 (1)	24.8		30	33
M. agrestis	upper	436 (5)		20.5 (5)	42	47±9

differences are not always statistically significant.

In *C. g.* — in the majority of cases there is no difference in the rate of apposition in various parts of the lower incisors, but in the Białowieża sample — in the lateral wall. There is a small but visible decrease in rate, while in the labial wall — an increase from the base to the middle. The observed differences in the rate of dentin apposition from the basal part of the tooth towards the middle are confirmed also by the regression coefficients (Table 3). Admittedly they are not great, but significantly different from 0.

Daily layers in dentin

Layers in the dentin are visible both in ground and stained sections. Admittedly it was not always possible to differentiate them since the scale of distinctness could be from almost invisible to very distinct. According to the increase of distinctness of layers

incisors can be arranged in the following way:
I_1 *C. g.* Białowieża, Moscow and Volgograd Regions; I^1 *C. g.* from Białowieża and Moscow regions; I^1 — *M. ag.*; I^1 — *M. ar.* and I_1 *M. ar.*
In *C. g.* — the daily layers are poorly contrasted on the stained sections. On the ground sections they are irregular and visible only in certain parts of the incisor. They were somewhat more visible in the lower incisors in the apical section near the pulp cavity. Generally — more visible in I^1 than in I_1.
In *M. ag.* the dentin layers are more contrasted than in *C. g.* although both are considered difficult to see. The most distinct are in *M. ar.*, especially in the upper incisors.

The breadth of dentin layers in both incisors of *C. g.* and *M. ag.* and in the lower incisors of *M. ar.* completely agree with the daily growth of dentin (see Tables 3 and 5). In the upper incisors of *M. ar.* sometimes wider layers as well as narrower layers were clearly visible, the first one corresponding to the daily growth of dentin.

Indirect calculation of time of complete incisor renewal

When an incisor erupts more or less uniformly, the wall in the middle part is composed of daily increments of dentin. The amount of these increments equals half the time (in days) of complete renewal of the incisor. The daily increments can be presented as daily dentin layers. As a rule not the whole incisor wall is made up of layers and therefore it is not possible to use a simple counting to determine the number of daily increments. We determined this number by dividing wall thickness (without enamel) by the width of dentin layer (Table 5).

Considering the various rates of dentin apposition in different parts of the tooth the width of daily layers was measured only in the basal half of the incisor using the means of several measurements of layers from various places in this part of the incisor. Table 5 gives the results of indirect calculation of time of complete renewal of incisors, compared with the parameter obtained by tetracycline marking. The values obtained from this indirect method are close to the means obtained from marking and did not differ from them by more than 1 SD.

Discussion

The age and inter species differences in incisor size in voles are probably related to differences in skull size. This relationship was long ago noted in laboratory rats and appears to be obvious (Addison and Appleton 1915). However less obvious is the lack of a direct relationship between incisor size and rate of its eruption. On the one hand, the shorter upper incisors erupt slower than the lower ones. The lower incisors of *C. g.*, being the shortest in our material, erupt the slowest. On the other hand, the shorter incisors of voles 1 – 2 month old erupt faster than the longer incisors of 8 – 10 month old animals. In *M. ar.* the upper incisors are shorter but their rate of eruption is faster than in the upper incisors of *M. ag.* Ness (1963) confirmed Shadle's hypothesis as a whole that thinner incisors wear down faster than thicker ones, mentioning laboratory mice as an exception (Shadle 1944, refered acc. to Ness 1963). Our research does not confirm this relation. When comparing different species of voles another relationship comes to light. The lower incisors of *M. ar.* have a larger diameter and are renewed faster than the lower incisors of *C. g.* (Białowieża); the upper incisors of *M. ar.* and *M. ag.* have a significantly larger diameter and grow faster than *C. g.*'s upper incisors.

The literature data about changes with age in the rate of eruption of evergrowing teeth are not unequivocal. In laboratory mice a significantly slower rate of eruption of incisors from 6 to 17 weeks of age has been noted (Hwang and Tonna 1965). In rats this relationship was not found from 10 to 1000 days (Lavelle 1969). Our results indicate that the rate of eruption of lower and upper incisors in *C. g.* and of upper incisors in *M. ag.* at 1 – 2 months to 8 – 10 months of age slows down. These results agree with Golenishev and Koenigswald (1978) observations on evergrowing rootless cheek teeth in *Arvicolidae* and indicate that with age the proliferic activity in the growth area of evergrowing teeth lessens.

The eruption rate of lower incisors in *C. g.* from the Moscow and Volgograd samples is significantly greater than in the Białowieża voles 8 – 10 months old. The differences in the growth rate of *C. g.* incisors from these samples can not be explained by the differences in their age composition. They are most probably related to the fact that *C. g.* from Białowieża came from a laboratory colony and those from the remaining two samples were taken in the field. It is known that the growth rate of teeth is affected by various factors, including the type of diet (Ness 1963). Preventing normal grinding of the teeth by cutting one incisor does not decrease, but quite the opposite, increases the rate of eruption of the incisor (Michaeli and Weinreb 1968). So it is possible that the slow rate of eruption of the vole's incisors in Białowieża is not a direct result of the influence of breeding conditions but is the result of changes in their growth potential while breeding them in captivity for several generations.

Data from the literature indicate that often, but not always, the rate of eruption of upper incisors is slower than in the lower ones (Ness 1963). According to our observations these differences in voles are significant but the time of complete renewal of upper and lower incisors in these same animals is similar. Smith and Warshawsky (1976) got similar results in laboratory rats: the ring of odontoblast marked with isotope during the same time moves along the same portion of lower and of upper incisors.

The rate of dentin apposition in the walls of the incisors was proportional to the rate of their eruption. This is understandable since the faster the incisor moves apically, the faster should be the rate of filling the pulp cavity so that the pulp cavity would be closed when erupted through the gum. However, it was surprising that in the upper incisors, which erupt more slowly, the rate of apposition was significantly faster (sometimes even twice as fast) than in the lower incisors. This can perhaps be explained by the fact that the diameter of the upper incisors is slightly greater than that of the lower ones and their pulp cavity fills in faster (Table 4).

The changing rate of dentin apposition along with incisor eruption needs to be discussed separately. In nonevergrowing teeth the rate of dentin apposition decreases together with the filling up the pulp cavity. This also applies to the rat molars (Hoffman and Shour 1940). An analysis of our material reveals the same phenomenon in the apical part of the incisors, where the pulp cavity is rather small. The rate of dentin apposition in the apical part of the incisor was not dealt in this work. However the changes occurring in the basal part of the incisor should be discussed. In voles, not a slower but a faster rate of dentin apposition occurs from the base towards the apex of an incisor and together with a filling in of the pulp cavity. This does not occur in all species and not in all incisor walls. It is tempting to explain this occurrence by relating earlier results (Klevezal 1981) and our research.

It is not possible to relate the rate of dentin apposition with the known gradient of incisor growth determining specific incisor shape, *i.e.* segment of a logarithmic spiral (Thompson 1917). If such a relationship existed, the rate of dentine apposition would have to differ in the labial part (greater curvature of the tooth) and in the lingual part (smaller curvature) and in the same manner in the same walls in various species. This however was not observed.

An increase in the rate of dentin apposition can not be connected with odontoblast age, as it was previously done (Ahlgren 1968, Klevezal 1981). Odontoblast age increases from the basal part of the tooth towards the apex in all incisor walls in all species. An increased rate of apposition takes place only in some species, and up to date this has not been observed in any species in the medial wall of the incisor. Our results indicate that the faster mean rate of dentin apposition, the faster it increases from the basal part to the apex. In the incisor walls — labial, lingual and lateral, when the daily increment did not exceed 10 mkm (I_1 in *C. g.*) there is no increase in the rate of apposition or it is clearly extremely slow. If increment reaches 16 mkm, the daily rate of dentin apposition from the basal part to the medial part of the incisors increase by 1 – 3 mkm (I^1 in *C. g.*, I_1 in *M. ar.*). When the daily increment reaches a mean of 27 mkm (I^1 *M. ar.* and *M. ag.*) the daily rate of apposition increases by 3 – 6 mkm.

Smith and Warshawsky (1976) carefully followed the development of rat incisors and concluded that the development of each transverse segment is analogous to tooth development in man, if the crown is taken as the incisor part covered with enamel, and the root as the part covered with cementum. It is thus possible to imagine an incisor as a series of nonevergrowing teeth placed one after the other. The younger will be near the basal part and the older more apically. In light of the obtained results this analogy appears very probable, if we assume that homologous to the root is not the lingual but the medial wall, and to the crown — the labial and, partly, lateral walls. In teeth with limited growth (*e.g.* rat molars), the fastest rate of dentin apposition is seen in the crown and the slowest, in the root (Hoffman and Schour 1940). In incisors, both upper and lower, judging by our data, the fastest rate of dentin apposition is noted in the labial or lateral walls, and the slowest in the medial wall. Furthermore, in the upper incisors having a triangular shape, not only the labial but also the lateral walls are covered by enamel.

It is possible to imagine that the initial rate of dentin apposition, although different in different species, is in all species slow and does not exceed a certain speed. Even in the upper incisors of *M. ar.*, which are characterized by a fast mean rate of dentin apposition, the initial rate of apposition, calculated from regression (Table 3), was approximately 16 mkm/day. In these cases when a quick thickening of the wall is not necessary, the rate of dentin apposition maintains a typical tooth tendency — gradual slowing down. In our material this occurred in the medial wall (incisor 'root'), where the rate of dentin apposition in all incisors of all voles is in general low, as well as in the lateral wall of I_1 *C. g.* where the rate of wall thickening is slow. With its increase the initial tendency to decrease apposition can no longer take place since it would not be insured for normal filling in of the tooth pulp cavity. In these instances the initial rate of apposition is preserved (in the labial and lingual walls of I_1 *C. g.*) or it increases (in I_1 *M. ar.* and I^1 of all species studied) depending on how great is the need for wall thickening. Therefore increasing the rate of dentin apposition from the incisor base towards the middle which means a greater effectiveness in the activity of the odontoblasts along with their apical movement is a forced reaction of the incisor, related with the necessity of quickly forming tooth walls of a certain thickness.

In the lower incisors of *M. ar.* Klevezal (1981) did not find daily layers in the periferal dentin segments formed in the basal part of the incisor. She believed that the odontoblasts do not gain the ability to rhythmic production of dentin until a certain age. Further study of mice and birch mice did not confirm however this suggestion (Klevezal 1988) as well as the results presented above. Dentin layers easily seen in the incisors of *M. ar.*, in *C. g.* were significantly hard to see. In I_1 of *C. g.* the dentin mass, formed in the basal part of the tooth (young odontoblasts) do not have layers, while in dentin formed in the medial and apical parts (older odontoblasts) they are visible, although not distinct. At the same time in the incisors of some *M. ar.* and *M. ag.* the layers were visible in the entire breadth of the medial and lingual walls, and were more distinct in *M. ar.* than in *M. ag.* The reason for the differences in both location and distinctness are not clear and require further research.

A comparison of the width of dentin layers with their daily growth on a certain section of the tooth shows that those layers in vole incisors, are as a rule, daily. This agrees with earlier data for various rodents (Klevezal 1988). In the upper incisors of *M. ar.* 2 types of layers could be seen: (1) wider, daily and (2) narrow. The periods of formation of the latter is not clear.

A simple determination of the rate of incisor growth (with the help of a mechanical marking of the tooth or by using vital markers of the growing part of the dentin, as in this work) is time consuming and requires a special experiment under field or laboratory conditions. Our method of indirect calculation (Table 5) gives very satisfactory results. It is simple and can be used for determining the growth rate of incisors on any material. It is enough to make a thin, longitudinal section of an incisor, measure wall thickness of the dentin in the medial point of the tooth, divide the size by the mean thickness of the dentin layers in the basal part of the incisor, and then, doubling the value obtained, determine the entire time of complete incisor renewal. Knowing the tooth length it is possible to calculate the rate of its eruption. A weak point of this method is the assumption that the dentin layers are always daily. All data up to now (see Klevezal 1988) indicate that it is so, but deals only with lower incisors. The use of the lower incisors is also convenient as the change in the rate dentin apposition is not great. Error in measuring the width of daily layers, related with the changes in the rate of dentin apposition, is rather small. It can be lessened even more if for determination of the mean width of daily dentin layers it would be possible to measure a sufficient number of layers from various segments of the basal half of the incisor.

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