

# Adaptive amelogenesis during unimpeded eruption of rat mandibular incisor

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## Abstract

The aim of the study was to see whether the length of the enamel secretion zone in unimpeded rat incisors, measured precisely, is in agreement with the observed decrease in enamel thickness. Unimpeded eruption of mandibular incisors of five experimental and two control rats was induced by cutting off the erupted part of the incisors three times per week for 5 weeks. The length of the zone of enamel secretion in unimpeded and impeded control incisors was measured on longitudinal and serial transverse histological sections of fixed, demineralised and embedded hemimandibles. Impeded contralateral incisors were also included in the study. The length of the zone of enamel secretion in unimpeded incisors showed an increase to  $8,398 \pm 558 \mu\text{m}$ , that is 161% of the length in control incisors ( $5,213 \pm 95 \mu\text{m}$ ). The contralateral incisor showed a reduction in eruption rate, in length of the secretion zone, and the whole tooth was shifted somewhat apically. The measured length of the secretion zone is in agreement with the observed thickness of enamel ( $98 \mu\text{m}$ ) in unimpeded incisors. The reduced eruption rate and the apical shift of the contralateral incisor are probably due to an increased occlusal load.

## KEYWORDS

amelogenesis, enamel thickness, rat incisor, unimpeded eruption

## 1 | INTRODUCTION

When the rat lower incisor is cut repeatedly out of occlusion, its rate of eruption is about doubled (Schour & Medak, 1951; Taylor & Butcher, 1951; Herrmann, 1953; Robinson, Kirkham, & Nutman, 1988; Steigman, Michaeli, Yitzhaki, & Weinreb, 1989; Risnes, Septier, & Goldberg, 1995; Gomes et al., 2013). Thus, the ameloblasts and odontoblasts, which are carried along with the erupting incisor as they produce enamel and dentin (Risnes, 1979), will, theoretically, only have about half the normal time available for their production. Dentin thickness is, accordingly, halved, but enamel thickness is only reduced to about 80% (Risnes, Møinichen,

Septier, & Goldberg, 1996; Risnes et al., 1995). This discrepancy could possibly be explained by a concomitant lengthening of the zone of enamel secretion. A lengthening of the enamel secretion zone has been observed; Robinson, Kirkham, and Nutman (1988) found a lengthening to 139%, Kirkham et al. (1993) to 142%, while Skobe et al. (1993) did not quantify the lengthening. None of these authors detected a decrease in enamel thickness in the unimpeded incisors and did not try to relate enamel thickness to length of the enamel secretion zone. The aim of the present study was to see whether the length of the enamel secretion zone in unimpeded incisors, measured precisely, is in agreement with the observed decrease in enamel thickness.

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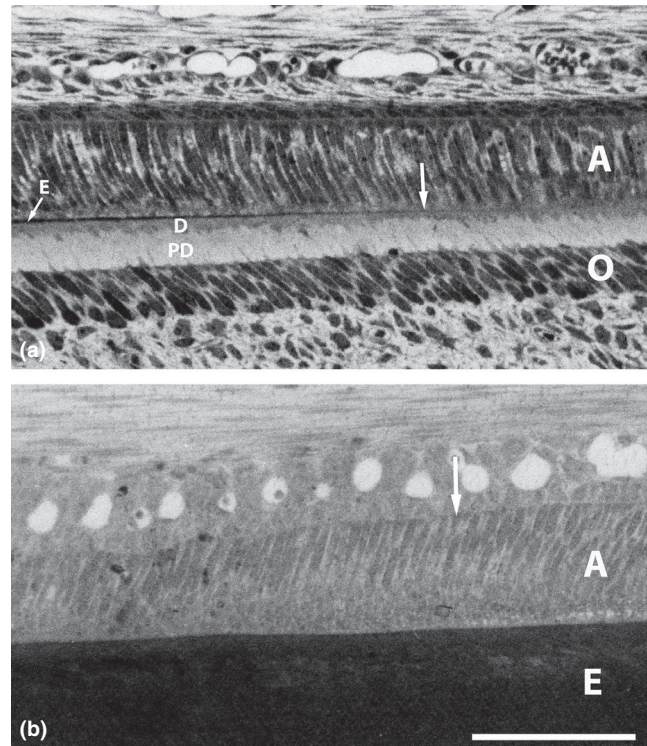
## 2 | MATERIALS AND METHODS

For the present investigation, only a small number of animals/teeth were available from the experiment described previously (Risnes et al., 1995). In short, unimpeded eruption of the left lower incisor of 6- to 7-week old (200–260 grams) male Sprague-Dawley rats was, under chloral hydrate anaesthesia, induced by cutting off the erupted part of the tooth at the gingival margin three times per week. The rats were given a standard pellet fodder and water *ad lib* throughout the experiment. The rats were kept and handled according to the standards of the time, in good accordance with the later adopted EU Directive 2010/63/EU for animal experiments. After an experimental period of 5 weeks, five experimental and two control rats were anaesthetised with chloral hydrate and sacrificed by perfusion fixation with a mixture of 2.5% glutaraldehyde and 2% paraformaldehyde buffered in 0.1 M sodium cacodylate, pH 7.2–7.4. Five left hemimandibles (with unimpeded incisors), three right hemimandibles (with contralateral impeded incisors) from the experimental rats and two left hemimandibles from the control rats were dissected out and fixation continued by immersion in the fixative overnight at 4°C. The specimens were demineralised in 4.13% ethylenediaminetetraacetic acid (EDTA, pH 7.2–7.4) at 4°C for 3 weeks and then post-fixed by OsO<sub>4</sub> in 0.1 M sodium cacodylate buffer, pH 7.2–7.4. The hemimandibles with the teeth in situ were divided into three segments, containing apical, middle and incisal parts of the incisor. After dehydration, the specimens were embedded in Epon and sectioned longitudinally or serially transversely with a Polycut E Microtome (Leica), the section thickness being 3 µm. The sections were stained with toluidine blue and observed in a Leitz Orthoplan light microscope.

The different functional zones of the ameloblast layer along the length of the rat incisor are defined and described by Warshawsky and Smith (1974). In the present study, the length of the zone of enamel secretion was measured directly on micrographs of the longitudinal sections or calculated by counting the number of serial transverse sections, in both instances between the points of start and end of enamel secretion according to Warshawsky and Smith (1974): the start of enamel secretion where there is a combination of development of Tomes' processes and elaboration of enamel matrix, and the end of enamel secretion where there is a clear reduction in ameloblast height in the transition zone. Examples of these stages are shown in Figure 1.

## 3 | RESULTS

The length of the zone of enamel secretion in unimpeded, in impeded control and in impeded contralateral rat mandibular incisors is shown in Table 1. Compared with control animals, the mean length of the zone of enamel secretion increased to 161% in unimpeded incisors, from 5,213 to 8,398 µm. The point of termination of enamel secretion moved incisally, from a position opposite the second molar in control animals to a position opposite the first molar in unimpeded



**FIGURE 1** Light microscopic images of longitudinally sectioned rat mandibular incisors. (a) Control incisor. Unlabelled arrow indicates the start of enamel secretion zone where first secreted enamel matrix is visible. (b) Unimpeded incisor. Unlabelled arrow indicates the end of enamel secretion zone where ameloblasts in the transition zone are reduced in height and lose their Tomes' processes. A = ameloblasts, O = odontoblasts, E = enamel, PD = predentin, D = dentin. Bar is 100 µm

erupting incisors (Figure 2). In the uncut contralateral incisors, the length of the zone of enamel secretion was reduced to 80% compared with control animals, from 5,213 to 4,189 µm. In these teeth, the point of termination of enamel secretion moved apically to a position opposite the third molar (Figure 2). This apical shift of the point of termination of enamel secretion was partly due to an apical shift of the whole incisor, increasing the distance between the third molar and the apex of the incisor (Figure 2).

## 4 | DISCUSSION

The present study is a follow-up to a previous study on the effects on enamel of unimpeded eruption of rat mandibular incisor (Risnes et al., 1995, 1996). In the present study, we measured the length of the enamel secretion zone in unimpeded and control incisors in order to be able to relate it to the previously measured enamel thickness.

The length of the zone of enamel secretion observed in control rats in the present study (Table 1) is in accordance with findings reported by Warshawsky and Smith (1974). Also, the position of the point of termination of enamel secretion relative to the molars corresponds with previous findings (Skobe et al., 1993; Smith & Nanci, 1989a). In our previous study (Risnes et al., 1995), the enamel

**TABLE 1** Length of zone of enamel secretion in unimpeded incisors, in impeded control incisors and in impeded contralateral incisors ( $\mu\text{m}$ )

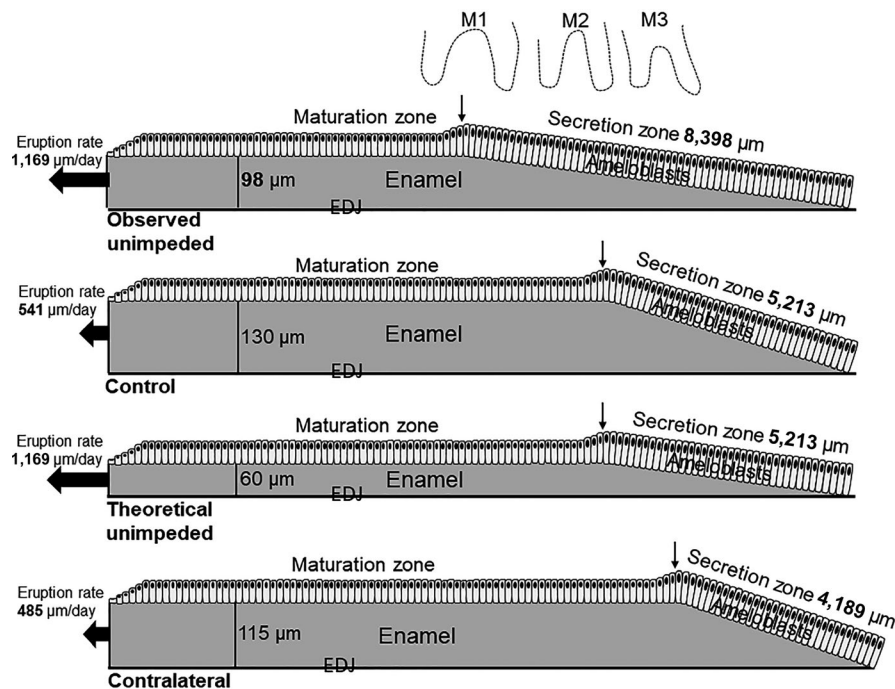
Rat #	Control impeded incisors	Experimental unimpeded incisors	Experimental impeded contralateral incisors
1		7,912 (L)	
2		9,024 (L)	
3		8,081 (L)	3,876 (L)
4		8,986 (L)	4,761 (L)
5		7,986 (T)	3,930 (T)
6	5,146 (L)		
7	5,280 (T)		
Mean	5,213	8,398	4,189
SD	$\pm 95$	$\pm 558$	$\pm 496$
<i>p</i> -values ( <i>t</i> test)	.00062*	.000039**	.071***

Abbreviations: L, sectioned longitudinally; T, sectioned serially transversely.

\*Unimpeded against control.

\*\*Unimpeded against contralateral.

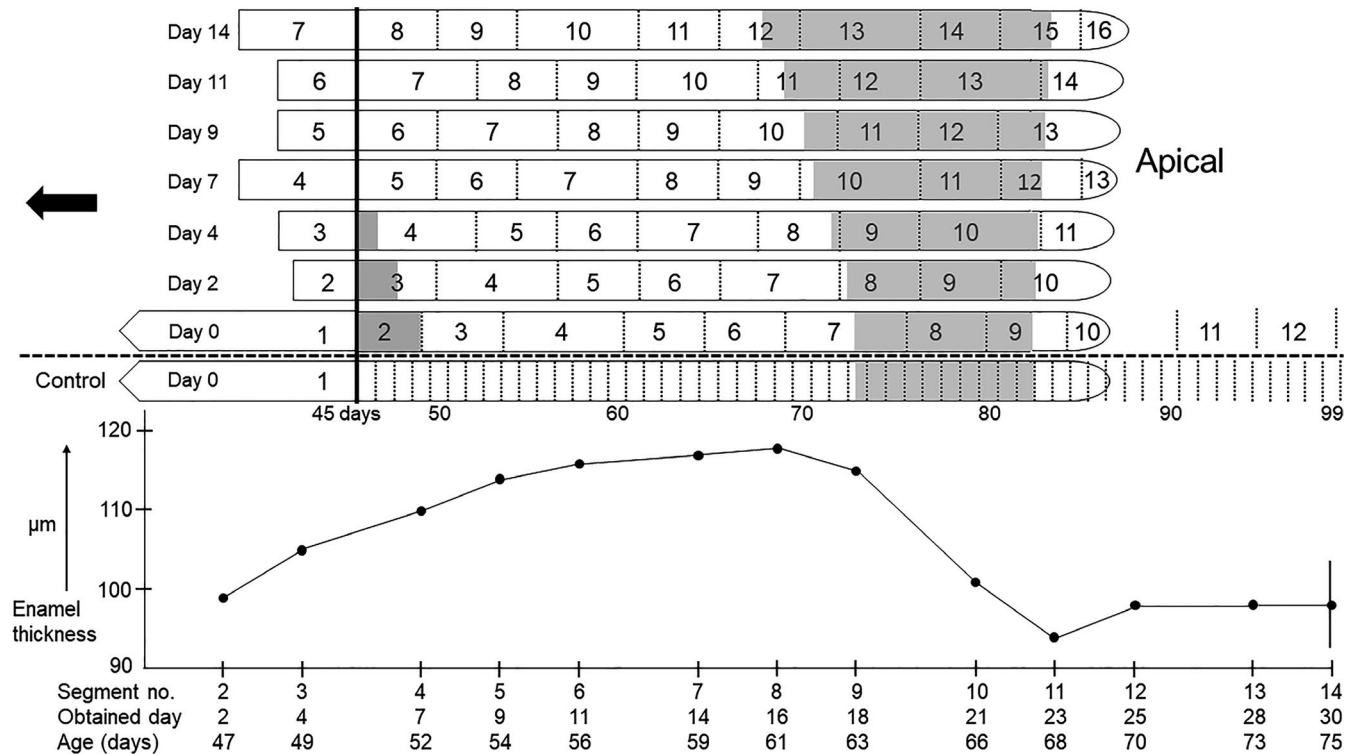
\*\*\*Contralateral against control.



**FIGURE 2** Schematic and theoretical representation of enamel and ameloblasts in rat mandibular incisors. Elements are not drawn to scale. Only the relative thickness of enamel and the relative length of the secretion and maturation zones are correct between the four situations. From top: observed unimpeded, control, theoretical unimpeded (enamel secretion zone not lengthened) and contralateral. Actual measured parameters are in bold: all eruption rates, length of enamel secretion zones and thickness of enamel in unimpeded incisors. The other parameters are calculated or stipulated (see text). The uncut contralateral incisor is somewhat shifted apically. Arrows indicate the position of end of enamel secretion. The position of the roots of the three molars (M1–M3) is indicated at top. EDJ = enamel–dentin junction

thickness was measured in consecutive, erupted segments cut off from the unimpeded incisor; the enamel thickness increased from 97  $\mu\text{m}$  in the first segment to 118  $\mu\text{m}$  in the 8th segment, whereafter it was reduced gradually to a thickness of 94  $\mu\text{m}$  in the 11th segment and then increased to 98  $\mu\text{m}$  from the 12th segment onwards (Figure 3). Since the eruption rate was increased to 216% (1,169  $\mu\text{m}/\text{day}$ ) of the baseline rate (541  $\mu\text{m}/\text{day}$ ), one would, with other

parameters constant, have expected a reduction in enamel thickness to 46%, since the unimpeded ameloblasts would only spend 46% of the normal time in enamel secretion (541·100/1169). However, the reduced enamel thickness observed from the 12th segment onwards (98  $\mu\text{m}$ ) should not be related to the observed maximum thickness in the 8th segment (118  $\mu\text{m}$ ), but to the thickness that the enamel in the 12th segment would have had if it had erupted at a normal impeded



**FIGURE 3** Schematic representation of movement of successive segments (numbered from 1 to 16) of rat mandibular incisors during unimpeded eruption (upper part above stippled line), and graph showing thickness of enamel in these segments (lower part) (Risnes et al., 1995, 1996). The vertical bar to the right on the graph indicates mean standard deviation. All dimensions, except tooth width, are in correct proportions to each other. The length of the intrabony part of the incisor was set to 22,000 µm (Warshawsky & Smith, 1974; Smith & Warshawsky, 1975). The bold vertical line to the left marks transition from intrabony to erupted part of incisors, and the black arrow indicates direction of eruption. The position and length of segments are shown at different time intervals from day 0 to day 14 in accordance with cutting schedule, total intrabony incisor length, eruption rate and enamel thickness (see text). Imaginary segments that will eventually be created and incorporated in the erupting incisors are indicated apical to the unimpeded and the control incisor at day 0. The length of segment 2 has been made somewhat shorter than subsequent segments obtained after 2 days of eruption (i.e. segments 3, 5 and 6), since it erupted before full unimpeded eruption rate had been attained. The shaded areas to the right indicate the zone of enamel secretion at the various time intervals. Initial length (5,213 µm) and final length (8,398 µm) are from the present study. Full lengthening of the secretion zone seems to be achieved within 13–14 days. The rate of lengthening of the secretion zone is slower than the rate of unimpeded eruption. The shaded areas to the left indicate the enamel pigmentation zone, being reduced in length at the same rate as the secretion zone is increased in length, giving total loss of pigmentation from the 5th segment onwards (Risnes et al., 1996). A control incisor with daily increments at normal eruption rate is shown below the stippled line at the bottom of the series of incisors. The segment of this tooth that will erupt at an age of 99 days corresponds to the 12th segment of the unimpeded tooth erupting at an age of 70 days. An apical extension of the incisor with age has been introduced according to Smith and Nanci (1989a)

rate (541 µm/day). The enamel thickness in rat incisors increases with age (Herzberg & Schour, 1941; Schour & Massler, 1949). The 12th segment, which was obtained at day 25 into the experiment, at an age of about 70 days ( $\approx 45$  days at start + 25 days), would have been obtained at a higher age in normal impeded eruption, since the segment would need longer time to reach the erupted position, that is at an age of about 99 days ( $\approx 45$  days at start + 2.16.25 days) (Figure 3). At this age, the enamel thickness in the erupted part of the rat mandibular incisor is about 130 µm (Herzberg & Schour, 1941; Schour & Massler, 1949). Steigman et al. (1989) found a comparable difference in enamel thickness between unimpeded and impeded incisors. Thus, compared with the normal impeded incisor, the reduction in enamel thickness in the 12th segment is to 75% ( $98 \cdot 100/130$ ), not to 46% (60 µm) as would be expected if the length of enamel secretion zone had not increased in length (Figure 2).

It may be shown that the stipulated reduction in enamel thickness to 75% (98 µm) in unimpeded incisors is consistent with the lengthening of the zone of enamel secretion observed in the present study. The rationale for this is as follows, using the available data: in control rats, an ameloblast passes through the zone of enamel secretion in 9.6 days ( $5213/541$ ). The enamel apposition rate is then 13.5 µm/day ( $130/9.6$ ), which corresponds well with other findings (Risnes, 1979; Smith & Nanci, 1989b). If the enamel apposition rate remains constant during unimpeded eruption, an enamel thickness of 98 µm will be elaborated in 7.3 days ( $98/13.5$ ). In this time (7.3 days), an ameloblast moving at the speed of the unimpeded eruption rate (1,169 µm/day) will build the observed enamel thicknesses of 98 µm if the length of the secretion zone is 8,534 µm ( $1,169 \cdot 7.3$ ), that is an increase to 164% of the control situation (5,213 µm). The length of the zone

of enamel secretion was in the present study measured to be  $8,398 \pm 558$  (Table 1), somewhat less than what would be needed to explain the observed enamel thickness ( $98 \mu\text{m}$ ). This discrepancy may possibly be explained if there also is an increase in ameloblast secretion rate. Such an increase is supported by the fact that while the thickness of enamel increases with age (Herzberg & Schour, 1941; Schour & Massler, 1949), the length of the enamel secretion zone does not increase with age (Smith & Warshawsky, 1975). Based on these premises, the enamel secretion rate would increase from  $8.3 \mu\text{m/day}$  in 10-day-old rats ( $5213/541 = 9.6$ ;  $80 \mu\text{m}$  enamel thickness/ $9.6$ ) to  $13.5$ – $16.1 \mu\text{m/day}$  in 100- to 150-day-old rats ( $130$ – $155 \mu\text{m}$  enamel thickness/ $9.6$ ). An increase in ameloblast secretion rate from  $13.5 \mu\text{m/day}$  to  $13.6 \mu\text{m/day}$  ( $8398/1169 = 7.2$  days;  $98/7.2 = 13.6 \mu\text{m/day}$ ) would be enough to explain the length of the enamel secretion zone in unimpeded incisors observed in the present study. A decrease in the eruption rate with age, as has been noted by Herrmann (1953), providing more time for enamel production in a secretion zone of stable length, would reduce the need for an increase in enamel production rate as an explanation for the resulting enamel thickness. However, in the experiment from which the present animals were obtained, the eruption rate of unimpeded incisors was not reduced during the duration of the experiment (5 weeks), in agreement with observations of Harari, Hermolin & Harari (2005). Theoretically, in control rats, the eruption rate in old rats would have to be reduced to about 50%–60% of the rate in young rats in order for the thicker enamel to be produced without an increase in secretion rate, far more than 87% observed by Herrmann (1953) and 82% observed by Harari, Hermolin, and Harari (2005).

The reason why Robinson et al. (1988) and Kirkham et al. (1993) found a shorter lengthening of the enamel secretion zone than our 161%, that is 139% and 142%, respectively, is probably their different and less precise method of defining and measuring the zone, that is from apex to white opaque zone (maturation).

The length of the enamel secretion zone increases from  $5,213 \mu\text{m}$  in control incisors to  $8,398 \mu\text{m}$  in unimpeded incisors, but the rate at which this lengthening occurs is unknown. However, from a schematic reconstruction of unimpeded incisors (Figure 3), it appears that the observed enamel thickness in the erupted and cut-off segments may be explained if the secretion zone attains its maximum length within 13–14 days, with a rate of lengthening slower than the rate of unimpeded eruption: the maximum decrease in enamel thickness is found in the 11th segment because it passes through the whole secretion zone in a state of accelerated eruption, but does not benefit from the full lengthening of the zone of enamel secretion. This, however, befalls the 12th segment, and the subsequent segments, which, therefore, attains a somewhat increased enamel thickness compared with the 11th segment. The decrease in enamel thickness in the 9th and 10th segments is due to a combination of accelerated eruption and only a small lengthening of the enamel secretion zone, less so for the 9th segment, since full unimpeded eruption is not attained until day 4 (Risnes et al., 1995). The diminished rate of increase in enamel thickness observed in the 7th and

8th segments probably primarily reflects a diminished general rate of increase in enamel thickness with age (Herzberg & Schour, 1941; Schour & Massler, 1949). It appears that the length of the zone of enamel pigmentation is reduced at a rate comparable to the rate of increase in length of the enamel secretion zone, resulting in total loss of pigmentation from the 5th segment onwards (Risnes et al., 1996). A lengthening of the enamel secretion zone reduces the length of the maturation zone correspondingly. The maturation process, thus, suffers, both from a reduced length of the maturation zone and from the increased speed at which the ameloblasts pass through it, resulting in hypomineralised enamel (Risnes et al., 1996). Also, the increased speed at which the ameloblasts pass through the secretion zone affects the orientation of the prisms, that is the path of the secretory ameloblasts (Risnes et al., 1996).

When a rat incisor is immobilised and prevented from erupting, the length of the zone of enamel secretion is reduced (Kirkham et al., 1993). This indicates that the reduction in length of the zone of enamel secretion in the uncut contralaterals observed in the present study is due to an increased occlusal load on the contralateral. The reduction in its eruption rate to about 90% (Risnes et al., 1995) and the apical shift of the whole contralateral incisor support this assumption. The changes induced in the contralateral incisor demonstrate that it may not serve as an adequate control for the unimpeded incisor. The thickness of the enamel in the contralateral incisors was calculated to  $115 \mu\text{m}$  (Figure 2), based on length of enamel secretion zone ( $4,189 \mu\text{m}$ ), rate of eruption ( $485 \mu\text{m/day}$ ) (Risnes et al., 1995) and rate of enamel secretion ( $13.5 \mu\text{m/day}$ ).

Whatever forces cause the rat incisor to erupt in the normal situation (e.g. tissue proliferation, tissue/blood pressure, periodontal ligament remodelling; see for instance Gomes et al., 2013), the lack of antagonistic contact in the unimpeded situation seems to allow an increased expression of the potential of these forces. The resulting increased length of the enamel secretion zone, decreased length of the enamel maturation zone and abolition of the enamel pigmentation zone create an aberrant enamel with reduced thickness, reduced degree of mineralisation and absent pigmentation (Risnes et al., 1995, 1996). Which processes and/or signals allow and govern the new balance of division between ameloblast functions along the ameloblastoma in the unimpeded situation is not known.

The small sample sizes, especially of control incisors ( $N = 2$ ), could possibly weaken the conclusions of the present study. However, this problem is to a large extent solved by the fact that the length of the enamel secretion zone measured in our sample is in close agreement with that of Warshawsky and Smith (1974), that is  $5,213 \mu\text{m}$  and  $5,142 \mu\text{m}$ , respectively, using comparable methods. Furthermore, the agreement demonstrated between length of enamel secretion zone and enamel thickness suggests that the samples represent the populations adequately. However, since it has been shown that Student's *t* test may be applied to extremely small sample sizes (de Winter, 2013), we still performed a statistical analysis. Assuming that the variances of the three samples are equal, and finding that the effect sizes are large (Coe, 2002), *p*-values of .00062 and .000039 were obtained for unimpeded incisors against impeded control

incisors and impeded contralateral incisors, respectively, while impeded contralateral incisors against impeded control incisors gave a *p*-value of .071 (Table 1).

## 5 | CONCLUSIONS

The observed lengthening to 161% of the zone of enamel secretion, together with a slight increase in ameloblast secretion rate, can explain a reduction in enamel thickness to 75% in unimpeded mandibular incisors. The contralateral has to bear an increased occlusal load, resulting in reduced eruption rate, reduced length of the zone of enamel secretion and an apical shift of the whole incisor.

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