Current Trends in Dental Morphology Research

NEW EVIDENCE FOR THE PERIODICITY OF INCREMENTAL STRUCTURES IN ENAMEL

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ABSTRACT

Tooth development is characterized by the rhythmic secretions of enamel- and dentine-forming cells, permanently recorded in the mineralizing tissues, which are analogous to the structural layers in marine organisms or tree trunks. Recent work has challenged the periodic nature of incremental features and the accuracy of histological analyses of dental development. In this study, experimentally labeled macaque (*Macaca nemestrina*) teeth were examined under regular and fluorescent light microscopy, and incremental features in the enamel were related to injection intervals. This study demonstrates the existence of sub-daily, daily, and multiple-day developmental rhythms. Cross-striations represent a daily rhythm in enamel secretion, which has been reported by several researchers and is confirmed in this study. Intradian lines, described as sub-divisions of cross-striations, appear to be the result of a 12-hour rhythm in enamel secretion. Long-period structures known as Retzius lines have a regular periodicity within individual dentitions. This was found to be 4 days in six individual macaques. Poorly known features termed laminations are the result of a daily rhythm in enamel secretion, which also appear to show 12-hour sub-divisions. Laminations should not be used to determine the periodicity of Retzius lines, as they may be obscured by the superimposition of Retzius lines, which run parallel, and may be formed in a similar manner. Identification of the periodicity of intradian lines and laminations within multiple individuals represents the first empirical evidence of these features in primates. These results provide important information about features that frequently complicate precise measurements of secretion rate and the periodicity of Retzius lines, key components for the determination of total crown formation time.

In a broader context, research on biological clocks demonstrates a large number of rhythmic cycles, ranging from a few hours to a yearly frequency. It is possible that long-period incremental features in dental tissues result from interactions between short-period rhythms. However, this does not explain the known range of periodicities among primates or within humans. Additional genetic, neurological, and hormonal research is needed to provide more insight into the physiological and structural basis of incremental feature formation.

INTRODUCTION

A major debate in Dental Anthropology has centered on the application of incremental dental development to studies of primate and human evolution, with several fundamental aspects being called into question (reviewed in Boyde, 1989; Risnes, 1990; FitzGerald, 1998). Earlier studies suggested that certain incremental structures are due to artifacts of imaging or preparation, and do not show consistent periodicities (e.g., Wilson and Schroff, 1970; Weber and Glick, 1975; Warshawsky and Bai, 1983; Warshawsky et al., 1984). These criticisms have continued to be revisited in the anthropological literature (e.g., Mann et al., 1990a,b, 1991; Skinner and Anderson, 1991; Huda and Bowman, 1994), as well as in the field of oral biology, including popular texts such as Berkovitz et al.'s (1992) *Color Atlas & Textbook of Oral Histology* and *Ten Cate's Oral Histology* (Nanci, ed., 2003). Several recent studies have attempted to refute criticisms by experimentally or deductively establishing the periodicity of daily features (e.g., Bromage, 1991; Dean et al., 1993; Antoine, 2000), as well as the regularity and equivalence of long-period features in enamel and dentine (e.g., Dean et al., 1993; Dean, 1995; Dean and Scandrett, 1996; FitzGerald, 1996). Despite these studies, it is evident that a lack of consensus exists regarding the daily nature of cross-striations and the regular periodicity of Retzius lines, as well as the methods used to characterize incremental development (e.g., Macho et al., 2003).

The aim of this study is to investigate the periodicity of incremental features of enamel microstructure. The repeat intervals of cross-striations, intradian lines, Retzius lines and laminations are examined in relation to multiple, known-period, fluorescent labels in a large sample of developing macaque (*Macaca nemestrina*) teeth. Cross-striations are defined as light and dark bands that cross enamel prisms perpendicularly with a common spacing of 3–6 µm. Smith et al. (2003, 2004) defined intradian lines as fine bands that appear between square/slightly rectangular light and dark bands (cross-striations). These latter two studies showed conclusively that they are genuine structural phenomena by demonstrating them with scanning electron microscopy (SEM) and tandem scanning reflected light microscopy (TSRLM), methods which are not influenced by optical artifacts that may be present in conventional transmitted or polarized light microscopy. However, the ratio of intradian lines to cross-striations is ambiguous; certain studies of enamel and dentine have reported multiple periodicities, including ones greater than a 2:1 ratio (Rosenberg and Simmons, 1980; Ohtsuka and Shinoda, 1995; FitzGerald, 1996), while others have suggested a precise 2:1 ratio (Kawasaki et al., 1977; Ohtsuka-Isoya et al., 2001).

Retzius lines are a prominent type of long-period feature found in primate enamel, which represent the successive positions of the developing enamel front and manifest on the tooth surface as perikymata. The consistent periodic nature of this feature has been one of the more contentious topics in the study of enamel microstructure (FitzGerald, 1998). Another class of incremental feature is known as laminations, which are often found specifically in association with sub-surface enamel and/or aprismatic enamel. Laminations appear parallel to Retzius lines, and have a similar spacing to cross-striations, but they do not generally cross prisms perpendicularly. It has been unclear how these features relate to cross-striations or intradian lines (Smith et al., 2003, 2004). Images shown in Bromage (1991) may be interpreted to suggest that these features are equivalent to cross-striations (Bromage, 1991: Figures 2, 4, 6, pp. 207–208, 210). However, work on the Miocene hominoids *Afropithecus turkanensis* and *Graecopithecus freybergi* suggested that laminations have a periodicity greater than cross-striations, as fewer laminations may be seen between pairs of Retzius lines than cross-striations (Smith et al., 2003, 2004). This study addresses some of these unresolved issues and tests the theoretical basis of numerous studies of enamel microstructure.

Labeling studies

An ideal study of the periodicity of incremental features in enamel requires a labeling protocol that leaves distinct markers (e.g., sodium fluoride or lead acetate) over known-period intervals (e.g., Mimura, 1939; Schour and Hoffman, 1939; Okada, 1943). In 1938, the Japanese researchers Mimura and Okada developed a 'time-marking procedure' that involved injecting a number of animals (including macaques) with lead acetate and sodium fluoride over certain intervals, which was used to illustrate a daily rhythm of enamel and dentine production (Mimura, 1939; Okada, 1943). Due to the nature of enamel development, this has proven difficult to do with antibiotic injections or fluorescent labels, as the markers tend to be lost during mineralization when the organic component is replaced by minerals (reviewed in Bromage, 1991; Dean and Scandrett, 1995). Dean and Scandrett (1995, 1996) have shown that large doses of tetracycline may be detected in enamel, and Bromage (1991) noted this for the fluorochrome DCAF. However, it is not practical to use fluorescent labels in enamel as the sole means to determine incremental periodicity, as they commonly appear as diffuse bands equal to or greater than the width of putative daily lines. Thus, the majority of fluorescent labeling studies have focused on dentine formation due, in part, to the relative ease of imaging labels.

Several studies have examined experimentally labeled macaque dentitions in the past few decades (Molnar et al., 1981; Bromage, 1991; Dean, 1993). Molnar et al. (1981) injected four juvenile rhesus macaques with a tetracycline series over 175 days, and subjected the animals to heat stress and cortisone injections in an attempt to look at their effects on dentine growth rates, as well as the existence of incremental features in the dentine. Newell-Morris and Sirianni (1982) injected 16 pigtailed macaques with three types of fluorescent labels (discussed in greater detail below) to examine rates of bone growth and craniofacial development. Two individuals from this sample were later used by Bromage (1991) to demonstrate the periodicity of daily lines in enamel and dentine. Dean (1993) gave four juvenile macaques a tetracycline series to document rates of root growth. The material originally used by Newell-Morris and Sirianni (1982) was considered to be most suitable for a comprehensive study of incremental formation, as the individuals were completing deciduous tooth formation and beginning permanent tooth development while the labels were administered; thus it was used as the basis of the current study.

METHODS

The dental material examined includes 98 histological sections of mandibular (dc, dp3, dp4, M1) and maxillary teeth (dp4, M1) from 17 pigtailed macaques (*Macaca nemestrina*), representing various developmental stages from birth to 443 days old. Approximately 100 thin sections of 16 embedded mandibles were generated in the late 1970's/early 1980's (Newell-Morris and Sirianni, 1982; Sirianni, 1985). During the original study, these individuals were injected three to five times with one to three fluorescent labels (minocycline hydrochloride, xylenol orange, and DCAF 2,4-Bis [N,N'-di-(carbomethyl)-aminomethyl] fluorescein) throughout the final two months of life. Dates of conception, injections, birth, and sacrifice are known. In addition, four sections of a mandibular first molar from a 374 day old individual were acquired, which did not undergo fluorescent labeling. Thin sections representing the mesial and distal cusps were prepared according to procedures described in Reid et al. (1998). Areas within sections that were determined to be oblique were not used to assess the periodicity of incremental features, due to the likelihood of interference artifacts.

The sections were examined under polarized, tandem scanning reflected, and fluorescent light microscopy. Although the three labels in the original study were chosen because of their minimal effect on bone growth, they are all apparent in the dentine when viewed under fluorescent light microscopy. The sections that showed clear growth disturbances in the enamel were identified, and the disturbances were matched to labels in the dentine using fluorescent light microscopy. Regions showing clear incremental features in association with confirmed labels were selected and imaged under high magnification light microscopy. The number of each specific feature (cross-striations, intradian lines, Retzius lines, laminations) was determined between markers, and then divided by the injection interval (in days) to yield a periodicity (number of features per day). Features were also related to one another to provide additional confirmation.

RESULTS

The three labeling agents minocycline, xylenol orange, and DCAF were apparent in the dentine of developing teeth using UV fluorescence microscopy and laser confocal microscopy as orange, red, and green lines, respectively. Additionally, DCAF, which showed the strongest fluorescence in dentine, was also apparent in the enamel of several postnatal labeled individuals, although it generally appeared as a hazy band rather than as a distinct line. Minocycline appeared to cause the greatest growth disturbance in both the enamel and dentine (Figure 1), although in these doses, these labels did not appear to disrupt the production of enamel increments for long, as daily increments within the injection intervals were present as expected (see below). Xylenol orange and DCAF did not appear to cause growth disturbances as frequently as did minocycline.

Incremental features, including cross-striations, intradian lines, Retzius lines, and laminations, were observed in teeth from all ages and labeling conditions, including deciduous and permanent teeth. Prenatal enamel frequently showed cross-striations and laminations. The two stillborn individuals did not show incremental features as clearly as those that were sacrificed several days after birth. When a neonatal line could be identified between labels, it did not appear to show an associated temporal delay. Ameloblasts (enamel-forming cells) were found attached to the developing enamel surface in many sections, and were observed at various secretory stages (tall columnar cells, secretory cells, reduced enamel epithelium). Differences were also noted in the clarity of incremental features in immature enamel as compared to mature (well mineralized) enamel, which often showed more clearly defined Retzius lines than the former. Retzius lines were more apparent in permanent first molars than in deciduous teeth, possibly also due to differences in mineralization.

This study provides additional support for the theory that features identified as cross-striations, light and dark bands that cross prisms perpendicularly, are the result of a 24-hour accretion rhythm. Lines in the enamel matched to labels in the dentine show the same number of cross-striations between them as days between respective injections (Figure 2). This relationship was observed in sections of prenatal labeled enamel of multiple individuals and sections.

This study also provides evidence that intradian lines, defined here as thin bands that sub-divide daily lines, are the result of a 12-hour rhythm in enamel production. Confocal light microscopy confirms that these closely spaced bands are not due to interference from adjacent layers. However, intradian lines are generally difficult to resolve clearly, as they are very closely spaced and require high magnification, which results in poorer definition of features. When using 50–60 × objectives and transmitted light microscopy, it appears that there are either two or three intradian lines between cross-striations; information from underlying layers may give the impression of additional structures in the focal plane. As one manually focuses through the section, features tend to shift position and number. When viewing regions under lower magnification (with 25–40 × objectives), it is clear that there is single sub-division located in the center of the interval between cross-striations (implying two evenly spaced 12-hour increments). It was also possible to show an inclusive series of 8 intradian lines between pairs of Retzius lines in two teeth with 4 day Retzius line periodicities (determined in several other areas), representing additional evidence that these features have a 12-hour periodicity (Figure 3).

No evidence was found in this study to suggest that Retzius lines do not have a regular periodicity. Where it was possible to make counts, the number of cross-striations between pairs of lines was consistent within a section, tooth, and/or individual. Six individuals were found to have a Retzius line periodicity of 4 days. It was difficult to test experimentally the consistent periodicity of Retzius lines, as few sections showed Retzius lines between labels. Retzius lines were often best defined near the enamel surface, while the labels were often clearest near the EDJ, and the two generally did not extend far enough into the mid-thickness of enamel to be related to one another. It was possible to relate Retzius lines to a known-period interval in one individual. This individual received a minocycline injection, followed two weeks later with a DCAF injection, two weeks after that with a minocycline injection, and was sacrificed shortly after the final injection. The minocycline lines were identified in the cervical enamel and traced to the surface, representing 28 days of enamel formation between them. Six complete Retzius line intervals (7 total lines) were counted between these two labels, plus 2–3 cross-striations (days) between the first label and the first Retzius line, and 1–2 cross-striations (days) between the 7^{th} Retzius line and the last label, totaling 6 intervals plus approximately 4 days. This suggests that each Retzius line interval represents 4 days on average, which is consistent with observations made on cross-striations between individual pairs of Retzius lines in this individual.

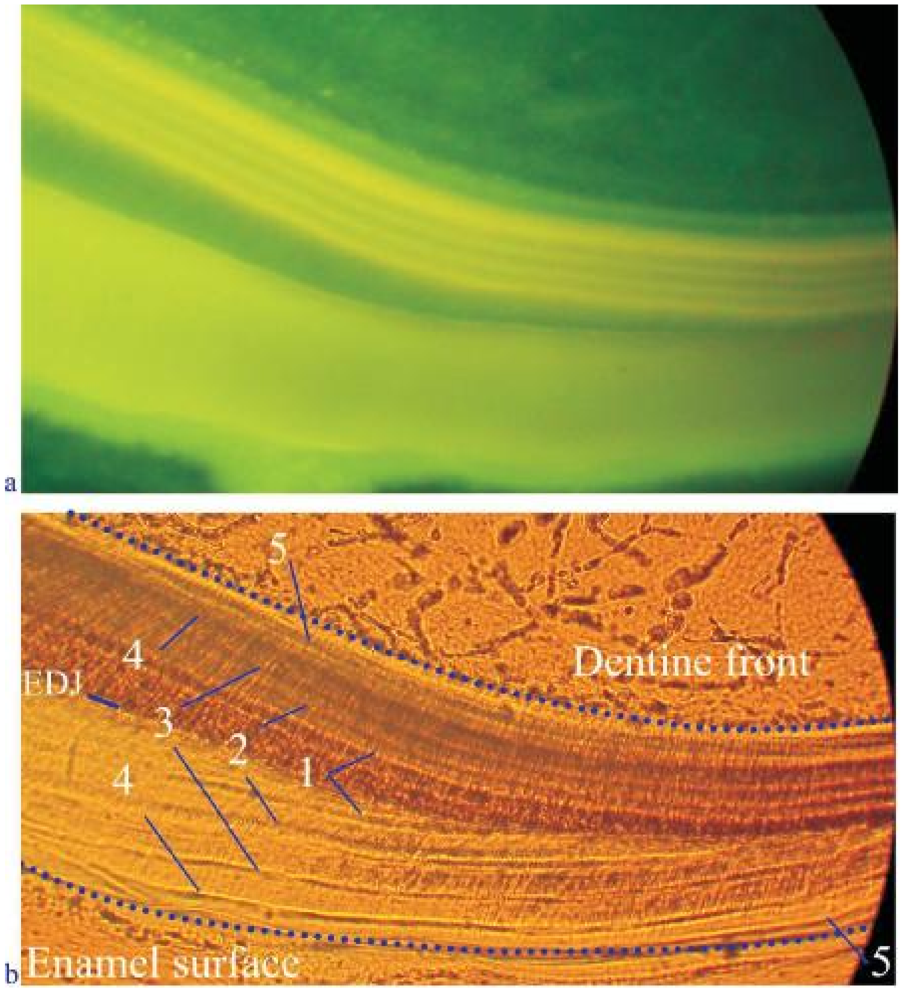

Figure 1. Fluorescence and transmitted light microscope images showing a series of accentuated lines (growth disturbances) related to minocycline injections; **a)** Fluorescence microscopy, and **b)** light microscopy of the same area showing five labels (numbered) in the dentine (above enamel dentine junction – EDJ), which correspond to the same five labels in the enamel (below EDJ). The EDJ is labeled on the left, and the cervix is to the right of the images

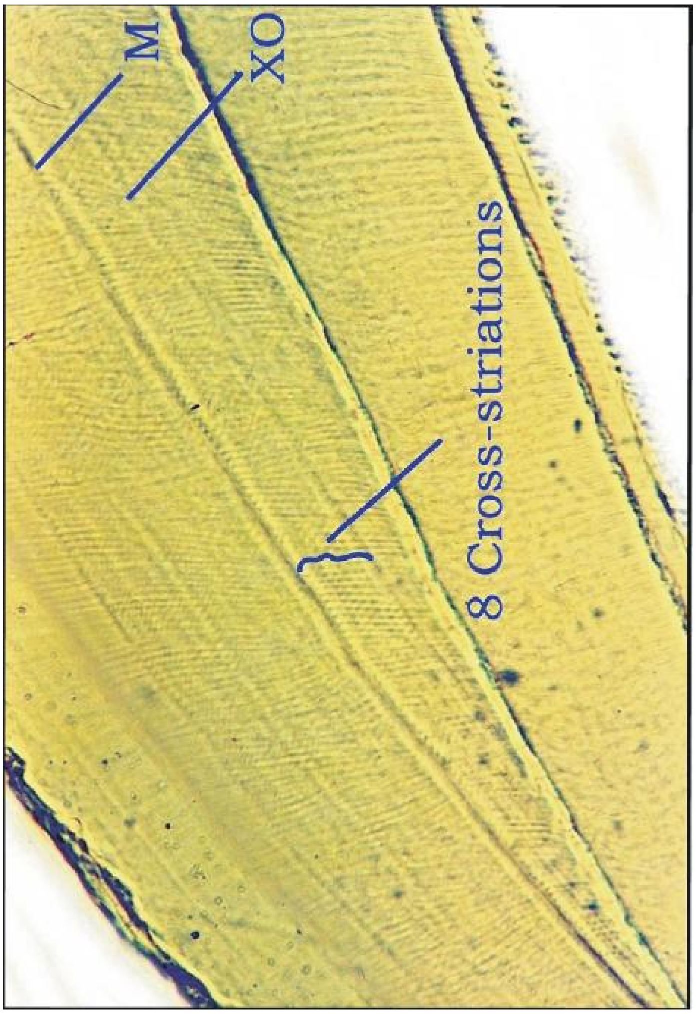

Figure 2. Light microscope image of cross-striations in cervical enamel. In this individual, a xylenol orange injection (XO) was followed eight days later by a minocycline injection (M). Eight cross-striations (paired light and dark bands) can be clearly distinguished between these two lines,confirming the daily nature of this feature. The cervix is to the lower left

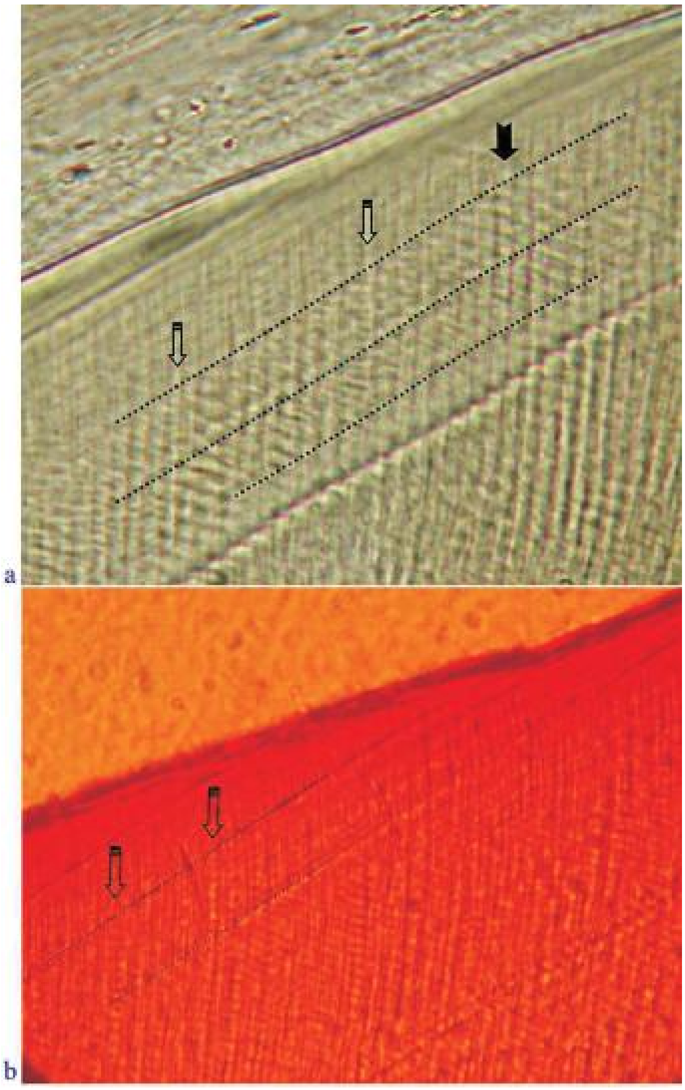

Figure 3. Transmitted light micrographs of intradian lines between Retzius lines; **a)** Four horizontal cross-striations are evident along a vertical prism (solid arrow) between a pair of Retzius lines (dotted lines), and eight intradian lines are present within the same interval (open arrows pointing down prisms). The dark line below the third Retzius line is an accentuated line related to a minocyclme injection; **b)** Eight intradian lines (open arrows) between a pair of Retzius lines (dotted lines). This tooth is stained red due to unrelated Alizarin red S staining. In both images the enamel surface is the dark diagonal line, and the cervix is to the lower left

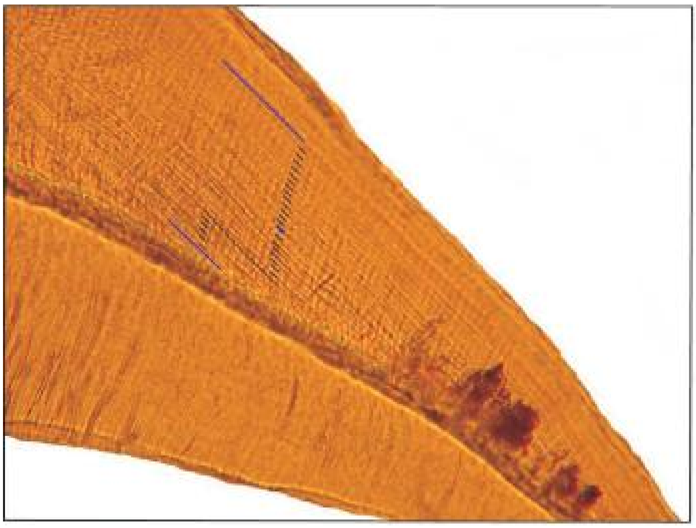

Figure 4. Transmitted light micrograph showing the daily nature of laminations. Laminations (labeled with black/blue lines) between injections (labeled in blue) at the cervix (to the right). This individual received a minocycline injection, followed two weeks later with a DCAF injection, two weeks after that with a minocycline injection, and was sacrificed shortly after the final injection. Twenty-eight laminations can be seen between the first and third labels, which are equal to 28 days of formation

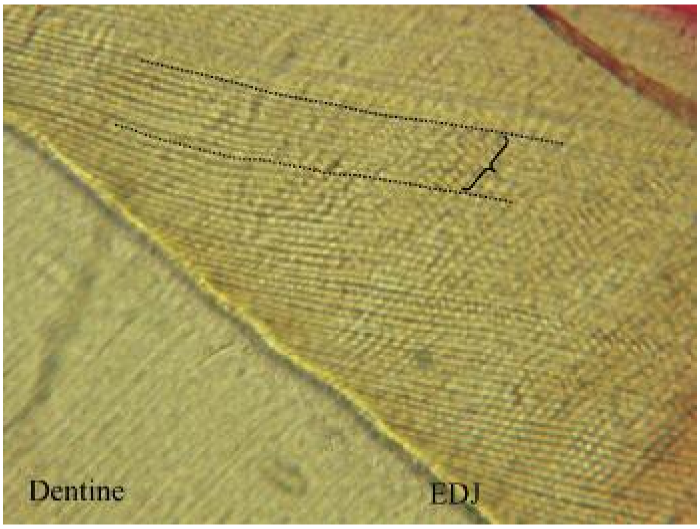

Figure 5. Transmitted light micrograph showing nine laminations in register with nine cross-striations (between the two dotted isochronous lines), confirming that these features are of equal periodicity

This study provides strong evidence that laminations show a daily periodicity, as the number of laminations between labels is equal to the injection interval in days (Figure 4). Additional evidence is present in several regions of cervical enamel, which show a number of laminations at the EDJ that is equivalent to the number of corresponding cross-striations (Figure 5). This correspondence has also been seen under confocal light microscopy, which also demonstrates that they are not artifacts of transmitted light microscopy. Laminations were observed to be most common in the enamel over the dentine horn, along the EDJ in the cervical region, and in the outer enamel in association with aprismatic enamel as well as between Retzius lines. Laminations also occasionally showed a sub-daily division. This was seen in several sections between features near the EDJ. When it was possible to image these structures, it consistently appeared that there was a single sub-division, representing additional evidence that a class of sub-daily feature is produced every 12 hours.

DISCUSSION

The current study demonstrates that cross-striations have a 24-hour repeat interval, which is consistent with experimental studies by Mimura (1939), Okada (1943), and Bromage (1991). As noted above, the incremental nature of cross-striations has been debated, with a few studies suggesting that these features are an artifact of sectioning with no true periodic nature, or that they are due to the optical phenomenon of cross-cut prisms viewed end-on (e.g., Wilson and Schroff, 1970; Weber and Glick, 1975; Warshawsky and Bai, 1983; Warshawsky et al., 1984; Skinner and Anderson, 1991). Previous criticisms suggesting that cross-striations result from prisms cut end-on, knife chatter, or optical superimposition have been shown to be unsubstantiated through the use of multiple forms of microscopy (Dean, 2000; Smith et al., 2003; Dean, 2004; Smith et al., 2004). Criticisms that postulated that these features do not show a temporal pattern have been refuted with experimentally labeled material such as in the present study. Given the consistent appearance and periodicity of cross-striations, counts and measurements of this feature may be used to establish the periodicity of other incremental features, as well as the rate and duration of enamel formation.

This study provides evidence that intradian lines are the result of a 12-hour rhythm in enamel secretion. Although they have been mentioned and debated in the literature since Gustafson's (1959) description (reviewed in Smith et al., 2003), their periodicity had yet to be demonstrated in enamel. As noted above, FitzGerald (1996) provided the most definitive statement about the existence and periodicity of intradian lines, reporting instances where two, or rarely three, intradian lines were found between cross-striations (FitzGerald, 1996: Figure 7-4A). He interpreted these observations to suggest that intradian lines have an 8- and/or 12-hour rhythm. Smith (2004, 2006) demonstrated that it is possible to image more than two sub-divisions between cross-striations using high magnification, but these can be 'focused through' to yield pairs of cross-striations. The majority of evidence in this study supports the existence of a single 12-hour feature, as intradian lines generally appear to sub-divide cross-striations into even halves. They are also found between Retzius lines in a ratio of 2 intradian lines for every 1 cross-striation. Further, daily laminations also show a single division (illustrated in Smith, 2004). Experimental work in dentine has also confirmed the presence of sub-daily features between daily features (Kawasaki et al., 1977; Rosenberg and Simmons, 1980; Ohtsuka and Shinoda, 1995; Ohtsuka-Isoya et al., 2001). Ohtsuka-Isoya et al. (2001) recently illustrated dentine lines that showed a 12-hour periodicity.

The current study provides no evidence to reject the hypothesis that Retzius lines have a consistent periodicity within an individual, shown here to be 4 days per line in six of the individuals examined. Given the meticulous study of FitzGerald (1996), which determined the periodicity in several areas of the same tooth and individual, as well as the concurrent observations of several other experienced researchers, it is unlikely that Retzius line periodicity is variable. Newman and Poole (1974, 1993) hypothesized that Retzius lines may result from interactions of multiple circadian oscillators. They suggested that a precise 24-hour rhythm and a free-running circadian rhythm may run in tandem, regularly producing a Retzius line when the two cycles were most offset from one another. A number of increasingly sophisticated studies from the past decade have brought us closer to a potential explanation (e.g., Roenneberg and Morse, 1993; Ohtsuka and Shinoda, 1995). The theory of interaction effects between multiple physiological circadian cycles is supported by the experimental work on single-celled organisms by Roenneberg and Morse (1993). They noted 'phase jumps' roughly every seven days, which occurred when a faster circadian rhythm corrected itself relative to a slower rhythm. They suggested that separate but coupled (approximately circadian) oscillators may produce a rhythm that appears to be controlled by a seven-day clock. Roenneberg and Morse (1993) also noted that an infradian (greater than a day) rhythm operated in this system, which provides support for Newman and Poole's (1974) theory of a 24-hour and a 27-hour rhythmic interplay. Ohtsuka and Shinoda (1995) also suggested that multiple intradian rhythms may provide the basis for Retzius lines resulting from an interaction of multiple short-period clocks. However, given the diversity of documented Retzius line periodicities, it is difficult to conceive of a simple 'interaction model' that will explain the known range among primates. Additional work on circadian and intradian clocks may shed more light on the development of long-period lines in dental tissues.

The class of feature that appears parallel to Retzius lines, known as laminations, is the result of a circadian rhythm in enamel production. Additional evidence for their daily nature comes from observations in the current study that cross-striations and laminations may be seen in register with one another. Despite this finding, laminations should not be primarily used to determine the periodicity of Retzius lines, particularly near the enamel surface. It is suggested that the common appearance of Retzius lines as broad, dark bands is often the result of optical superimposition of laminations (Smith, 2004). To date, a model of lamination formation has yet to be proposed, partially due to the fact that the periodicity of these features had not been proven. Given that they are daily features, Boyde's (1989) model of cross-striation formation does not adequately explain their formation, as laminations are structurally similar to Retzius lines, which have a different orientation than cross-striations. It is unknown how a short-period feature may be formed oblique to the secretory face of the Tomes' process, although Risnes' (1990, 1998) models of Retzius line formation may provide some insight.

Ohtsuka and Shinoda (1995) demonstrated that daily lines in rat dentine become apparent two to three weeks after birth, the same time other circadian rhythms including sleeping – waking, pituitary – adrenal, and pineal – melatonin cycles become apparent. However, they also noted the presence of a sub-daily increment with an 8–12-hour periodicity in the first week after birth, which was dominant before circadian increments and continued after their appearance. Their study also cited unpublished work noting that sub-daily increments have been found in rabbit dentine formed prior to birth. There is also evidence of incremental lines in primate prenatal enamel from both deciduous teeth (FitzGerald et al., 1999; Smith et al., 2002) and permanent teeth (Dirks, 1998; Reid et al., 1998). However, given the generally poor quality of increments in the first-formed enamel, and the difficulty of labeling enamel, it has not been possible to determine which type of increment appears first in primates. The present study suggests that laminations may be the first prominent incremental feature in macaque enamel, as they are common in the first-formed enamel over the dentine horn. However, this would benefit from additional study.

In closing, it is suggested that structural examples of biological rhythms, such as annual rings in the trunks of trees, or the daily, monthly, and annual ridges in shells of marine organisms, are fairly common (reviewed in Smith, 2004). Scrutton (1978) suggested that any organism with 'preservable hard parts' formed by a 'continually additive mode of growth' may provide evidence of rhythms. Structural evidence in dental enamel includes short-period cross-striations, intradian lines, laminations, and long-period Retzius lines. These features are known to have dentine analogues, and an annual ring is present in cementum as well. Given the diversity and complexity of cellular-levels rhythms (reviewed in Roenneberg and Merrow, 2001), it is entirely possible that multiple, independent rhythms are responsible for the production of different incremental features within a developmental system. However, additional work is needed to determine if and how interactions among incremental features relate to their periodicity and structural manifestations. It is hoped that research on the genetic, neurological, and hormonal aspects of physiological rhythms will provide more insight into the physiological and structural basis of incremental feature formation.

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