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Temporal Nature of Periradicular Bands ('Striae Periradicales') on Mammalian Tooth Roots

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Abstract

Periradicular bands, or fine circumferential lines on tooth roots, have received attention recently due to their prominence on hominin fossils and their potential utility for informing studies of root formation. In 1938, Komai and Miyauti [Dtsch Zahn Mund Kieferheilkd 1938;5:791–795] demonstrated that periradicular bands are related to dentine growth rather than cementum, suggesting that they were equal to accentuated lines in dentine ('dentine lamellae' or 'contour lines'). More recent indirect evidence from band spacing on primate roots suggests that they are temporally equal to other long-period lines in enamel (Retzius lines, perikymata) and dentine (Andresen lines). One of the main complications in understanding the relationship between Andresen lines and periradicular bands is the layer of cementum found on erupted teeth, which often obscures bands. Here we present both direct and indirect evidence that periradicular bands are temporally equivalent to internal long-period lines in the enamel and dentine. A sample of modern human teeth showing periradicular bands and accentuated rings was externally notched, molded, and sectioned; in one instance it was possible to show an equal number of long-period lines (internal Andresen lines and external periradicular bands) between isochrons (internal accentuated lines and external accentuated rings), confirming the temporal equivalence of these features. Furthermore, counts of long-period lines on crown and root surfaces of a Neanderthal anterior dentition showed approximately equal numbers of lines (113 ± 1) between matching hypoplasias and accentuated rings across teeth. Despite their potential for studies of primate root growth, the etiology of these lines in mammalian roots requires further study.

Dental histologists have recognized the existence of incremental lines on tooth crown surfaces and within enamel and dentine for hundreds of years [1]. The structure of enamel is more often studied than dentine, due to anthropological interest in primate enamel thickness, taxonomy, phylogeny, and life history [1, 2]. It is well known that incremental features exist within dental hard tissues that range from sub-daily to annual rhythms [1–4]. Enamel shows long-period markings known as Retzius lines that run from the enamel-dentine junction to the tooth surface, terminating as circumferential ridges on the crown termed perikymata. The direct correspondence between internal and external long-period enamel lines has been demonstrated in the teeth of several primate taxa [5–7]. Dentine also shows long-period lines termed Andresen lines, which are temporally equal to Retzius lines in enamel [1]. In contrast to Retzius lines, it is less clear if Andresen lines terminate on the surface of the dentine, although regularly spaced circumferential features known as periradicular bands are present on mammalian root surfaces (fig. 1).

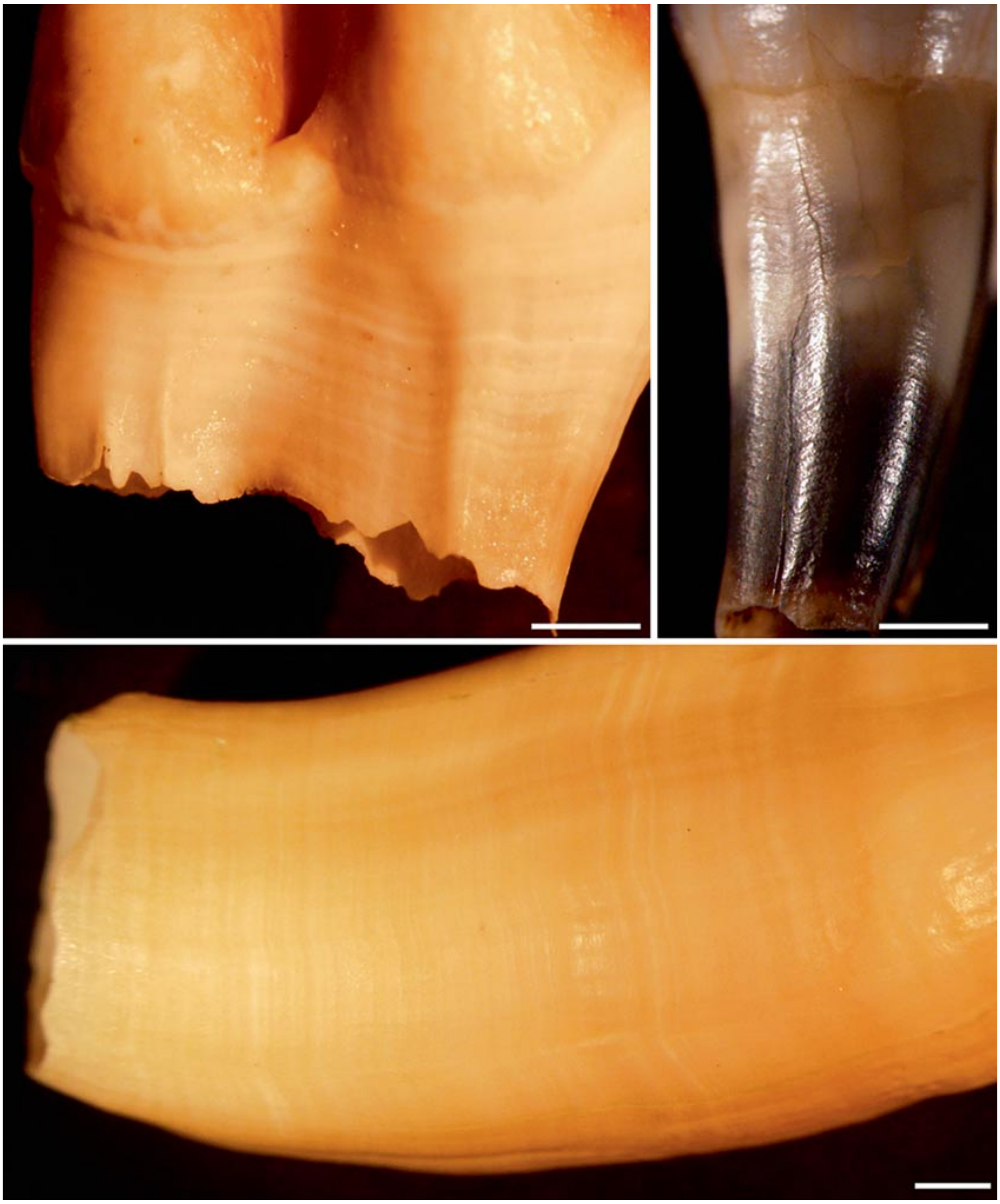
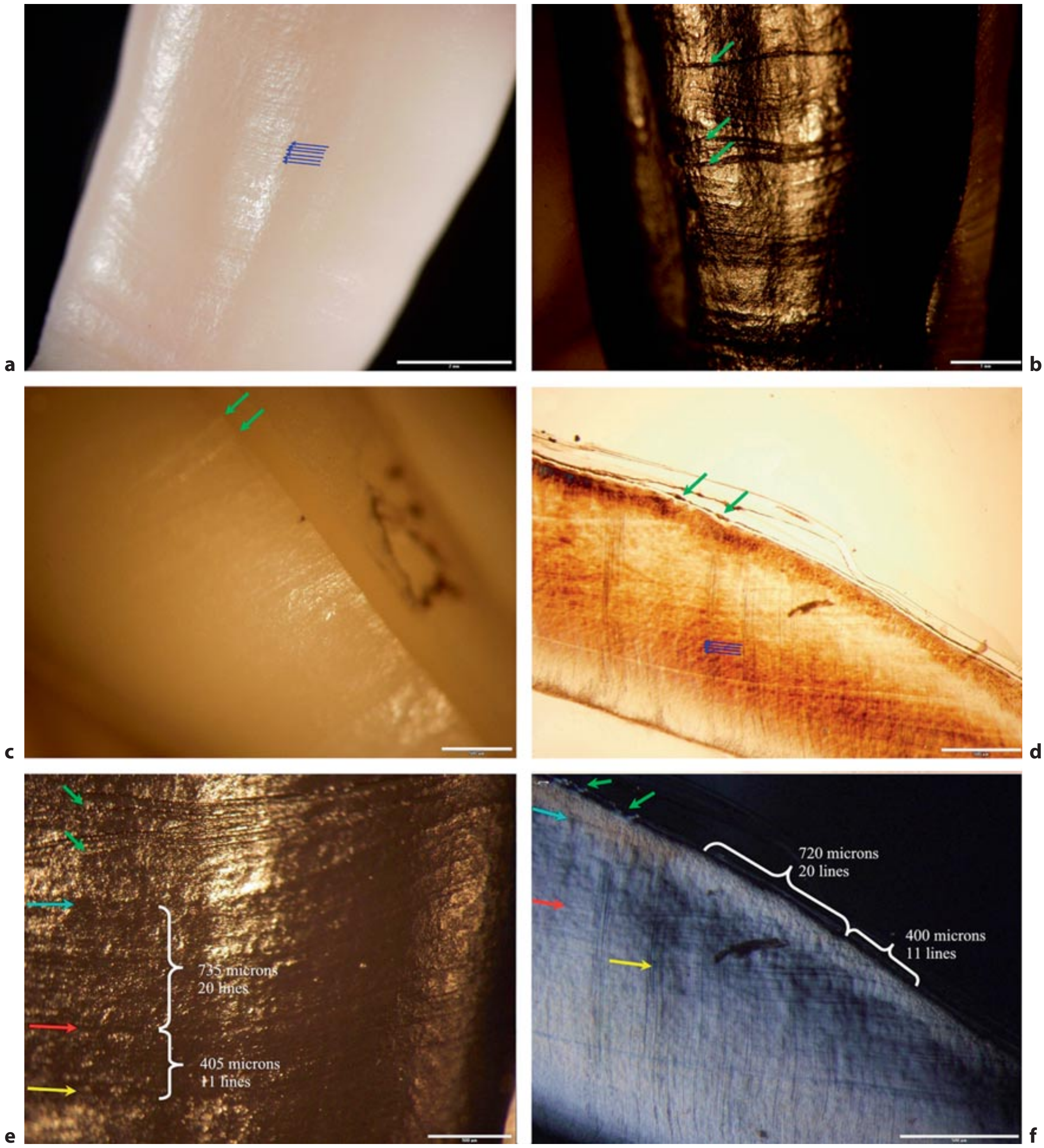


Fig. 1. Fine periradicular bands encircling developing tooth roots in reindeer molar (**a**), Neanderthal premolar (**b**), and chimpanzee canine (**c**). Particularly marked accentuated rings (parallel to regular periradicular bands) are likely caused by an unknown physiological stressor [12, 13]. Scale bars = 2 mm.


a
b
c
d
735 microns
20 lines
405 microns
11 lines
e
720 microns
20 lines
400 microns
11 lines
f

Komai and Miyauti [8] note that Fujita suggested that these external root lines be termed 'striae periradicales', which translates as 'depressions or furrows around the root'. (Here we refer to these features by the contemporary convention 'periradicular bands' [1, 9–11].) Additional irregular rings also encircle tooth roots that represent non-specific stress markers [12], which are similar to hypoplasias on crowns [13], here termed 'accentuated rings'. This study aims to present data on the relationship between long-period lines (Retzius lines, perikymata, Andresen lines) and periradicular bands, permitting more accurate assessment of root formation.

Materials and Methods

Approximately 100 clinically extracted teeth were obtained from European dentists; the sample was primarily comprised of developing and fully formed premolars. Notes were made on the presence of accentuated rings and periradicular bands observed under low magnification stereomicroscopy. Accentuated rings were distinguished from periradicular bands as the former were typically more widely spaced, slightly discolored, and/or slightly raised or depressed relative to the root surface. Impressions of five roots were made with Struers Repliset impression material, followed by photography and histological sectioning along the long axis of the root (detailed in Reid et al. [14]). Roots were notched with a razor above and below distinct areas of periradicular bands prior to molding and sectioning. Impressions and thin sections were imaged with stereomicroscopy and polarized light microscopy, respectively, to compare periradicular bands on the external aspect of teeth with internal Andresen lines in the corresponding region. Root regions were registering by matching external accentuated rings (and notches) with internal accentuated lines (and profiles of notches).

Results

Periradicular bands are rare on clinically extracted teeth, particularly fully formed teeth with residual connective tissue or thick cementum. Approximately 15% of the teeth examined were found to show some banding; only ~5% showed bands for more than 3/4 of the root length. Roots with broad accentuated rings were most likely to show adjacent fine periradicular bands, most often in the middle of the root. Histological sections revealed that, even in those few teeth that expressed clear periradicular bands, Andresen lines were rare in dentine below the cervix, particularly in the lower 2/3 of the root. Roots that showed clear external accentuated rings often showed a corresponding internal accentuated line in the dentine.

In one tooth it was possible to relate periradicular bands on the root surface with an equal number of long-period Andresen lines in the corresponding dentine (fig. 2), demonstrating temporal equivalence. The tooth had been extracted

Fig. 2. **a** Human lower premolar root with evenly spaced periradicular bands encircling the tooth root (blue arrows). Scale bar = 2 mm. **b** Impression of root surface after notching with a razor blade (green arrows). Notches are oriented slightly oblique to the direction of periradicular bands. Scale bar = 1 mm. **c** Tooth after sectioning showing the paired notches (green arrows), with an area of clear periradicular bands running perpendicular to the cut surface (diagonal through the image). Scale bar = 0.5 mm. **d** Histological section showing the perpendicular orientation of **b** and **c**. Notches (green arrows) are equal to the lower pair in **b** (and **c**). Several horizontal accentuated lines may be seen, as well as regularly spaced Andresen lines (blue arrows). Scale bar = 0.5 mm. **e** Magnified image of the negative impression shown in **b**. The same pair of notches are indicated with green arrows, followed by three horizontal accentuated lines (light blue, red, and yellow). The distances between accentuated lines and the number of periradicular bands in the two intervals are indicated to the right of the brackets. Numbers represent the average of several counts taken on the original tooth and negative impression. Scale bar = 0.5 mm. **f** Magnified polarized image of the histological section in **d**, showing the same pair of notches (green arrows), as well as the three corresponding accentuated lines. The distances between accentuated lines and the number of Andresen lines in the two intervals are indicated to the right of the brackets. The number of periradicular bands and Andresen lines between the accentuated lines is equal, confirming the temporal equivalence of these features. Scale bar = 0.5 mm. Image reproduced courtesy of *Proceedings of the National Academy of Sciences USA*.

prior to extensive cellular cementum deposition, which was only apparent histologically in the most apical aspect of the root. The long-period line periodicity in this individual (determined from enamel) was 9 days. The average extension rate in the lower third of the root (fig. 2b–f) was ~3.8 μm/day, and the dentine daily section rate ranged from ~1.5–2.0 μm/day in the first 300 μm deep to the root surface.

Discussion

History of Study

Komai and Miyauti [8] report that Hanazawa and Masaki first described periradicular bands in an experiment published in 1931, regarding them as regular cementum growth lines equivalent to perikymata. Komai and Miyauti [8] illustrate these bands in numerous mammalian taxa, noting variation in band thickness and spacing, and their more frequent appearance near the cervix (relative to root apices). They show that periradicular bands are difficult to see in root areas covered with thick cementum, which they state is due to the fact that periradicular bands are dentine surface configuration lines, commonly overlaid (and obscured) by cementum. These authors conclude that periradicular bands represent the termination of 'contour lines' related to the lamellar structure of dentine. From their illustrations it appears that they are referring to irregular accentuated lines sometimes called contour lines of Owen (see Dean [1]). We advocate that two classes of root surface lines be distinguished: long-period incremental lines commonly termed periradicular bands, and irregular accentuated rings (misleadingly termed root hypoplasias [12]).

Observations of regular concentric lines on mammalian root surfaces have also been made on seal canines [15] and beaver incisors [11]. In the former case they were interpreted to represent annual dentine growth lines formed during the winter, while in the later case they were used to calculate dentine growth rates, which were related to environmental conditions. Rinaldi and Cole [11] review Rinaldi's experimental work that demonstrated circadian periradicular bands in marmots and laboratory rats, stating 'periradicular bands are the external manifestation of von Ebner lines' [p. 290]. However, one difficulty in identifying dentine incremental features is the parallel nature of Andresen and von Ebner's lines (see images in [2, 3]), and it is unclear if these increments are distinguishable (or of separate etiology) in an organism with a circadian Andresen line periodicity.

Newman and Poole [9, 10] were some of the first to suggest that periradicular bands are equivalent to perikymata in primate enamel. Dean [1] provided indirect evidence by documenting the spacing and number of periradicular bands on a *Homo habilis* juvenile's roots (OH 16). He observed that periradicular band spacing did not vary greatly from cervix to apex, but anterior teeth showed more widely spaced bands than posterior teeth. Using a range of likely periodicities and total periradicular band numbers, Dean estimated formation times and extension rates that would result if periradicular bands represented long-period lines, finding a pattern akin to modern great apes. In a similar approach, Berkovitz et al. [16] measured the spacing of periradicular bands in a modern human child, which were similar to extension rates derived from radiographic studies.

Most recently, Smith et al. [17–19] observed and counted these fine lines on several Middle Paleolithic fossil hominin teeth, making predictions of root formation duration and age at death by assuming periradicular bands were equivalent to other long-period lines. In their study of the Scladina Neanderthal's dentition, Smith et al. [17] found equal numbers of perikymata and periradicular bands (113 ± 1 line) between a pair of hypoplasias/accentuated rings on tooth crowns/roots in 5 of 6 anterior teeth (see Smith et al. [17]:

fig. 1, p. 20222). This strongly suggests that these features represent equivalent periods of time, given that varying proportions of crowns and roots yielded essentially equal counts.

Appearance and Etiology
Dean [20] suggested that periradicular bands are difficult to see due to overlying cementum, as well as their more tightly packed and less prominent appearance relative to perikymata. However, a number of unresolved issues remain concerning cement formation [21]. During cementogenesis and prior to tooth eruption, acellular cementum is deposited on a thin layer of unmineralized predentine [22]. It is likely that the clarity of periradicular bands in developing teeth is due to the fact that a significant amount of cellular cementum has yet to be deposited. Given the appearance of periradicular bands on high-resolution developing root impressions, it appears that the dentine surface is not initially blanketed and flattened by cementum. A thin layer of initial acellular cementum may adhere to the dentine surface in a manner that preserves the underlying dentine topography. Periradicular bands are less evident in fully erupted and root complete teeth, which tend to possess more cementum, although they may be seen where the cementum has been removed [8].

In addition to the difficulties associated with resolving periradicular bands, section obliquity may influence the appearance of Andresen lines in histological sections of tooth roots (also noted by Dean [1]), which may explain the direct correlation of Andresen lines and periradicular bands in only a single tooth in this study. Dean [20] also suggested that Andresen lines may be difficult to resolve below the dentine surface due to dentine microanatomy and subsurface mantle dentine formation. However, there is some debate over whether mantle dentine is found along the cementum-dentine junction, or if it is only found near the enamel-dentine junction [22]. In roots the outermost layer of dentine, the hyaline layer, mineralizes after the bulk of radicular dentine. It is unknown how this layer relates to the underlying dentine, although dentine tubules can be identified that are continuous with the deeper dentine [23]. We concur with Dean's [20] statement that the subsurface dentine revealed in histological sections does not typically display incremental features, although we note that it is possible in some instances (e.g. fig. 2f).

In closing, we have demonstrated that periradicular bands on tooth root surfaces are equivalent to long-period Andresen lines in root dentine. Given Dean's [1] demonstration that internal long-period lines in enamel and dentine are equivalent, we suggest that the periodicity of long-period lines on the external surfaces of primate tooth crowns and roots, and within the enamel and dentine, is also equivalent. The same long-period rhythm has also recently been identified in bone [24]. Incremental features on tooth roots may compliment information derived from tooth crowns; however, additional research is needed to understand the diversity of mammalian incremental features, the formation of the interface between dentine and cementum, and the etiology of long-period lines.

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