

Biological Clocks and the Formation of Human Tooth Enamel ^[1]

By: MacCord, Kate Keywords: Evolution ^[2] Teeth ^[3] Human development ^[4]

Tooth enamel contains relics of its formation process, in the form of microstructures, which indicate the incremental way in which it forms during enamel formation on teeth (). These microstructures, called cross-striations and striae of Retzius, develop as enamel-forming cells called ameloblasts, which cyclically deposit enamel on developing teeth in accordance with two different biological clocks. Cross-striations result from a twenty-four-hour cycle, called a Circadian rhythm, in the enamel deposition process, while striae of Retzius have a longer periodicity. Unlike other tissues, enamel does not remodel after it forms, leaving those microstructures intact after deposition. Cross-striations and striae of Retzius thus provide evidence of the timing and processes of tooth development, and they indicate how organisms in a lineage differently grow and develop across generations. Researchers have examined these microstructures to investigate human [evolution](#) ^[5].

Teeth begin to form in [humans](#) ^[6] during the third month of fetal development. During the enamel formation process, called amelogenesis, all baby teeth mineralize *in utero*, completing enamel formation within the first year of life. During amelogenesis, ameloblasts go through two stages to form enamel. First, the ameloblasts produce an organic matrix that creates a scaffold-like structure. Then the ameloblasts enter the maturation phase, during which they absorb the organic matrix and replace it with minerals. Amelogenesis produces the hardest tissue in the body, allowing enamel to withstand chewing forces during its organism's life and giving teeth the ability to fossilize easily.

Amelogenesis begins at the cusp of the developing tooth, and the ameloblasts produce enamel in waves that stretch down towards the tooth root. Amelogenesis forms a single layer of enamel at a time, and builds enamel thickness by depositing one layer on top of another in a process called appositional growth. During a twenty-four-hour period, the ameloblasts go through a cycle of growth that results in a daily layer, called a cross-striation, along the length of their outgrowing path. The cross-striation forms by differing rates of enamel deposition during the circadian cycle. These layers form appositionally, and are separated by more clearly defined microscopic structures called striae of Retzius. Retzius lines are regularly spaced disturbances in the enamel that represent a slowing of matrix secretion, and are usually separated by seven to nine cross-striations. Thus, the striae of Retzius represent on average a week of enamel formation.

Anatomist [Richard Owen](#) ^[7] in England first described enamel microstructures in his 1840 treatise, *Odontography*. Throughout the nineteenth century, scientists investigated these microstructures as part of a debate about whether ameloblasts secreted enamel or mineralized themselves to become part of enamel, but they didn't see that the structures resulted from a temporal rhythm. Cross-striations became associated with a daily rhythm in 1916, in the doctoral thesis of Hans Asper at Universität Zürich, in Zurich, Switzerland. Asper

used sections of canine teeth from [humans](#) [6] to estimate the periodicity of both striae of Retzius and cross-striations. His estimations, five to ten days for Retzius lines and twenty-four hours for cross-striations, came close to current estimates of formation times.

Following Asper's work, incremental enamel growth remained largely uninvestigated until the late 1930s. In 1937, Isaac Schour and Henry George Poncher of the [University of Illinois](#) [8] at Chicago in Illinois published their findings on the incremental rate of enamel growth in [humans](#) [6]. Schour and Poncher injected a terminally ill infant with a sodium fluoride solution at regular time intervals for four months in order to determine the growth rate of enamel. Following the death of the child, Schour and Poncher sectioned the teeth and compared the discolorations left by the sodium fluoride in the enamel layers with their records of injection. The pair used this association to conclude an enamel apposition rate of nearly four micrometers per day in [humans](#) [6]. Schour and Poncher's work provided experimental evidence for Asper's association of cross-striations with a Circadian rhythm.

Scientists studied the periodicity of enamel microstructures throughout the twentieth century, adding further evidence for a Circadian rhythm influence on enamel deposition. Many of the mechanisms that govern the biological clocks of enamel remain unknown. Research on rats points to [hormones](#) [9] that trigger or maintain the appositional growth of enamel. Several researchers have also suggested that daily variations in the circulating levels of calcium and carbonate control enamel increments. Correlations between varying levels of calcium and carbonate in blood plasma and the time of day support a day/night cycle, a correlation for future studies.

Despite the lack of explicit mechanistic models of the biological clocks that control enamel apposition, research using dental microstructures has increased over the past twenty-five years. In the mid-1980s, scientists realized that the cross-striations and striae of Retzius preserved in the enamel provide a comparative framework of dental development for living and for long-extinct species, enabling growth and development to be compared on evolutionary timescales. Studies of human [evolution](#) [5] in particular have resulted from this research. As of 2011, scientists have studied the incremental dental development of every extant hominoid species, and they have sampled from nearly every extinct hominoid genus. They have also been able to infer the rate at which organisms within a taxon grow by counting the total number of cross-striations and striae of Retzius in the teeth of those organisms. When researchers have compared the widths of cross-striations across taxa, they have found variation in the rates of enamel formation, showing how fast or how slow organisms within one taxon grow when compared to the organisms in another. This information about developmental differences between taxa can then be used to establish the evolutionary histories of growth rates, and enrich our understanding of evolutionary relationships within the hominoid clade.

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Subject

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Publisher

Arizona State University. School of Life Sciences. Center for Biology and Society. Embryo Project Encyclopedia.

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Format

Articles [24]

Last Modified

Wednesday, July 4, 2018 - 04:40

DC Date Accessioned

Monday, March 18, 2013 - 23:34

DC Date Available

Monday, March 18, 2013 - 23:34

DC Date Created

2013-01-31

DC Date Created Standard

Thursday, January 31, 2013 - 07:00

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