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23. Recent experiments by N. M. Ribe and U. R. Christensen [*Eos* **73** (suppl.), 578 (1992)] with three-dimensional numerical convection models suggest that plumes do not penetrate the lithosphere to a great degree and so may not reset fossil anisotropy. However, large-scale lateral motion in the asthenosphere occurs in their calculations as the plume material spreads at the base of the lithosphere. Lateral gradients in anisotropic properties may exist near the Hawaii plume because quasi-Love waves, coeval with the Love wave, can be observed on several seismic records that approach station KIP (Kipapa, Hawaii) from the west.
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27. Earthquake locations and magnitudes are from the daily bulletins of the U.S. National Earthquake Information Center.
28. Data from several broadband seismic networks contributed to our study: the Global Digital Seismograph Network (GDSN), the Global Seismographic Network of the Incorporated Research Institutions for Seismology (IRIS), in cooperation with the International Deployment of Accelerometers (IDA) at the University of California, San Diego, and the U.S. Geological Survey, Project Geoscope, Mednet, and the Chinese Digital Seismic Network. Seismic data were obtained through the IRIS Data Management Center. The source mechanisms for the Landers and Balleny Islands earthquakes were provided by the Harvard centroid moment tensor Project, courtesy of G. Ekstrom and M. Salgalnik. D. M. Rye offered useful comments on the manuscript. Supported by NSF grant EAR-9018215.

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Life History Variables Preserved in Dental Cementum Microstructure

Daniel E. Lieberman

The age and season of death of mammals, as well as other aspects of their life history, can be estimated from seasonal bands in dental cementum that result from variations in microstructure. Scanning electron micrographs of goats fed controlled diets demonstrate that cementum bands preserve variations in the relative orientation of collagen fibers that reflect changes in the magnitude and frequency of occlusal forces from chewing different quality diets. Changes in the rate of tissue growth are also reflected in cementum bands as variations in the degree of mineralization.

Cementum is an avascular, bone-like tissue that anchors tooth roots by mineralizing extrinsic collagen fiber bundles (Sharpey's fibers) produced in the periodontal ligament (*1, 2*). Cementum, which is continuously deposited and rarely remodeled or resorbed, grows in incremental bands (Fig. 1) that are visible in cross sections through tooth roots in polarized light or stained sections (*3*). Correlations between cementum bands and the age and season of death of mammals have been recognized for more than 30 years (*4–6*), but the underlying causes of the bands have been unknown. In most mammals, opaque acellular bands tend to be deposited during seasons of reduced tissue growth (such as winter), and translucent bands (cellular or acellular) tend to be deposited during seasons of rapid tissue growth (such as spring and summer) (*7–10*). In this report, I demonstrate that bands in cementum are caused by two different phenomena, occlusal strain and growth rate, that can be used to reconstruct significant life history variables of mammals after death.

Cementum has a complex three-dimensional microstructure that reflects its function to maintain teeth in position for effective occlusion in spite of the high strains caused by chewing (*11*). Scanning electron microscope (SEM) micrographs of fractured tooth roots (Fig. 2A) show that cementum microstructure is influenced principally by Sharpey's fiber orientation. Sharpey's fibers in cellular and acellular cementum tend to be oriented parallel to one another at an oblique angle relative to the dentine-cementum border. Sharpey's fibers in cementum are therefore aligned so as to counter the tensile forces that tend to depress teeth in their alveoli during occlusion. In addition, the predominant orientation of intrinsic collagen fibers within the cementum matrix is perpendicular to the Sharpey's fiber bundles (Fig. 2B). These fibers also appear to wrap around Sharpey's fibers (*13*). Cementum microstructure is thus analogous to other mineralized tissues, such as bone or tendon, in which collagen fibers are generally aligned at right angles to each other (*13–16*). However, unlike bone or tendon, cementum microstructure is determined primarily by extrinsic collagen.

I tested the effects of changes in diet on cementum microstructure in a controlled

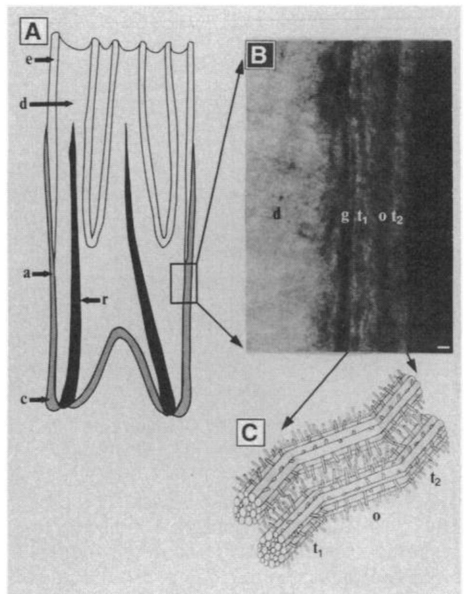

Fig. 1. Cross section of goat tooth showing location of tissues, increments, and collagen fiber orientation in increments. (**A**) Schematic cross section of lower first molar (M_1) showing location of enamel (e), dentine (d), acellular cementum (a), cellular cementum (c), and root canal (r). (**B**) Transmitted polarized light micrograph of ground section (50 μm thick) of M_1 from lingual surface near enamel-dentine-cementum junction. The goat was fed hard food for 4 months, soft food for 4 months, and hard food for 4 months. Dentine (d), first translucent increment corresponding to harder food diet for first 4 months (t_1), opaque increment corresponding to softer food diet for middle 4 months (o), second translucent increment corresponding to harder food diet for last 4 months (t_2), and granular layer of Tomes (the cementum-dentine border) (g). Tissue deposited during each phase was labeled with calcein (20 mg per kilogram of body weight), oxytetracycline (50 mg/kg), and alizarin red (50 mg/kg). Scale bar represents 10 μm. (**C**) Idealized reconstruction of collagen orientation in cementum bands in (B), depicting larger Sharpey's fiber bundles, which vary in orientation between bands, and the smaller fibers of intrinsic collagen that are aligned at right angles to the Sharpey's fibers. Sharpey's fiber bundles mineralized under conditions of higher bite force (increments t_1 and t_2) are more vertically oriented than those mineralized under conditions of lower bite force (increment o).

Department of Anthropology and the Society of Fellows, Harvard University, 11 Divinity Avenue, Cambridge, MA 02138.

experiment on goats that demonstrates that cementum bands can result from variations in either collagen orientation or collagen mineralization. Six goats (*Capra hircus*) were kept for 12 months under identical conditions with the exception of their diets. Two goats were fed for the entire experiment a control diet of hay and pellets that provided maintenance-level nutrition; two were fed the same food as that of the control group, but the food was ground and softened during the middle 4 months; and the final two were fed food of the same hardness as the control group, but the food was 33% lower in protein and 55% lower in mineral (including calcium and phosphorus) and vitamin content during the middle 4 months. Tissue deposited during different phases was labeled with fluorochrome dyes (oxytetracycline, calcein, and alizarin).

SEM micrographs of fractured sections of the goats' cementum (Fig. 3) show that Sharpey's fibers became more vertically oriented (relative to the dentine-cementum border) during the process of mineralization under higher and more frequent tensile strains. As shown by measurements made on the lingual surface of the first molars just below the dentine-cementum-enamel junction (Fig. 1A), the two animals fed a softer diet during the middle phase of the experiment had Sharpey's fibers that were oriented less vertically ($x = 75.6° \pm 1.7°$, $n = 18$) in those 4 months than during the periods when the food was harder ($x = 52.3° \pm 3.5°$, $n = 36$) (*17*). The four animals fed food of the same hardness (regardless of nutritional content) all year had no change in Sharpey's fiber orientation ($x = 56.0° \pm 2.2°$, $n = 36$). In vivo strain-gauge analyses (*18*) revealed that the strain in the mandible just below the molars while eating the hard food was approximately 1.5 times that while eating the softened food. In addition, the harder food required six times as many masticatory cycles to chew as the softer food. Cementum bands therefore preserve seasonal variations in Sharpey's fiber orientation (Fig. 1C): Acellular cementum bands with different Sharpey's fiber orientations appear alternately opaque or translucent in ground thin sections under transmitted polarized light because regions of cementum with different collagen orientation refract light in different directions (*19*).

Changes in the rate of acellular and cellular cementum deposition also result in bands that are visible in transmitted light because of differences in mineral density. Microradiographs (Fig. 4) indicate that hypermineralized (denser) cementum bands were deposited during periods of reduced cementogenesis. The animals fed a low protein and mineral diet during the middle 4 months of the experiment ceased growing (as measured in body weight); cementum deposited during this period was more mineralized and 70% as thick as the tissue deposited during periods of maintenance-level diet [as measured in the lower first molar (M_1)]. The control sample and the goats fed a soft food diet exhibited no change in the rate of cementum deposition or mineralization. Variations in the rate of cementogenesis thus affect the rate of formation of the collagen matrix, but the rate of mineralization remains constant. Similar effects of growth rate on mineralization have been documented in cementum (*12, 20*), bone (*21, 22*), and dentine (*23*).

Cementum bands are useful for estimating the age and season of death of goats and other mammals as well as other aspects of their life history (*12*). The number of bands records the number of seasons since a tooth erupted, and the nature of the outermost band records the season of death. Changes in collagen fiber orientation and relative

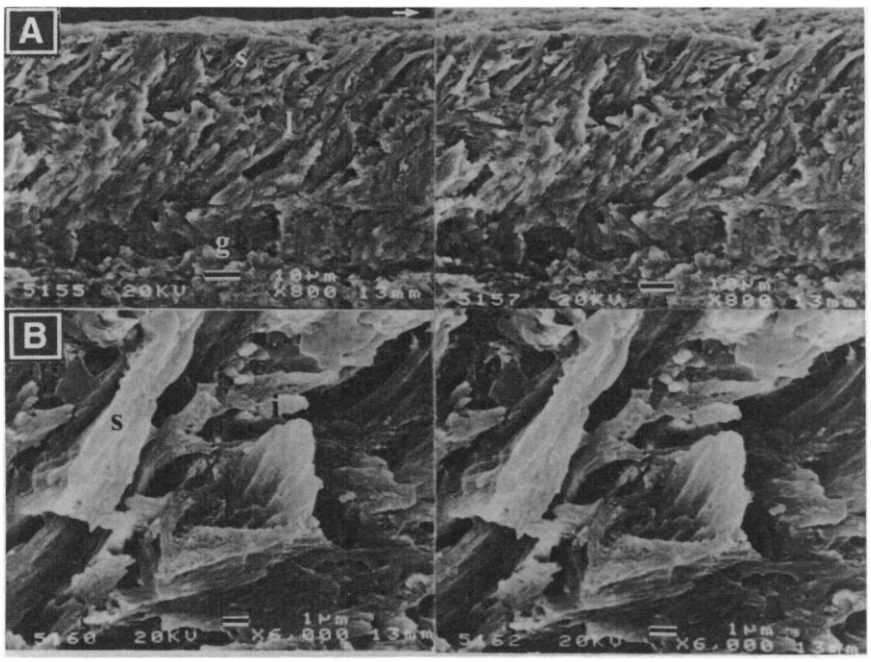

Fig. 2. Stereomicrographs of extrinsic and intrinsic collagen orientation in cementum on a fractured section just below the enamel-dentine-cementum junction on the lingual surface of a goat M_1. The goat was fed a hard, maintenance-level diet for the first and last 4 months and a hard, low protein and mineral diet for the middle 4 months. (**A**) Sharpey's fiber bundles (s) are oriented obliquely to the cementum-dentine border (g); the more mineralized region (l) corresponds to the period when the goat was fed a low protein diet. The arrow points toward the crown. The scale bar represents 10 μm. (**B**) High magnification view of (A). Intrinsic collagen fibers (i) are oriented perpendicular to Sharpey's fiber bundle (s) in a radiating fashion. The tooth was prepared for SEM as described (*27*).

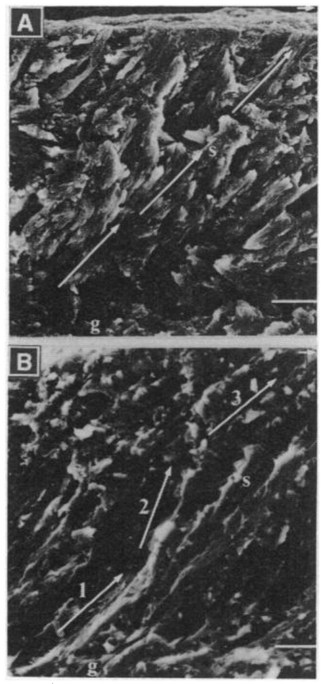

Fig. 3. SEM micrographs of variations in extrinsic collagen orientation in acellular cementum in fractured sections through goat M_1's just below the enamel-dentine-cementum junction on the lingual surface. Scale bar, 10 μm; small arrow at the upper right points toward the tooth crown. (**A**) Goat fed a hard, maintenance-level diet for the first and last 4 months and a hard, low protein and mineral diet for the middle 4 months (same as in Fig. 2). The orientation of the mineralized Sharpey's fiber bundles (s) is constant. (**B**) Goat fed hard food for 4 months, soft food for 4 months, and hard food for 4 months (with maintenance-level nutrition held constant). The angle of the Sharpey's fibers mineralized during the period the goat was fed soft food (2) are on average 23.2° less oblique relative to the dentine-cementum border (g) than those mineralized during the periods in which the goat was fed hard food (1 and 2). The teeth were prepared as described (*27*).

mineralization can also be used to reconstruct variations in seasonal diet quality and growth rate over the course of an animal's life. This technique has many applications. Cementum bands appear in a wide variety of mammals with both grazing and nongrazing diets (*7, 8*), and aspects of cementum microstructure are visible in many fossils because Sharpey's fiber orientation is sometimes preserved through either collagen preservation or mineral replacement. In addition, because cementum is rarely remodeled or resorbed, it can be used for longitudinal studies of the effects of growth rate and mechanical stress on the structure of mineralized tissues. These results support the hypotheses that collagen orientation in mineralized tissues can be affected by the orientation and degree of tensile forces (*24, 25*) and that the rates of collagen matrix production and collagen mineralization may be relatively independent (*26*).

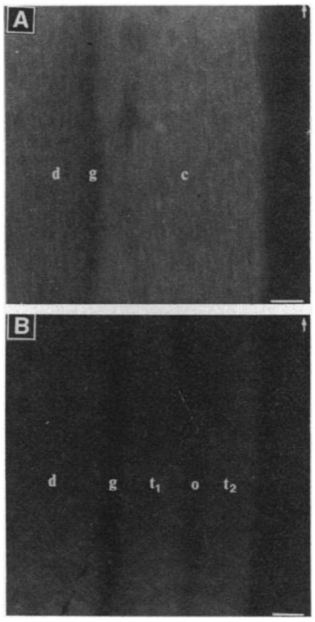

Fig. 4. X-ray microradiographs of variation in acellular cementum mineralization on ground thin sections (50 μm) through goat M_1's just below the enamel-dentine-cementum junction on the lingual surface. Scale bar, 10 μm; the arrow points toward the tooth crown. (**A**) Goat fed the control diet for the entire experiment. The density of the cementum (c) is constant. Cementum-dentine border (granular layer of Tomes) (g) and dentine (d). (**B**) Goat fed a hard food, maintenance-level diet for the first and last 4 months and a hard, low protein and mineral diet for the middle 4 months. First band corresponding to control diet for first 4 months (t_1); more opaque band corresponding to reduced nutrition diet for middle 4 months (o); and band corresponding to control diet for last 4 months (t_2). The more opaque band has a higher density and is relatively more narrow. The teeth were prepared for the micrographs as described (*28*).

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17. For consistency and comparability, nine measurements were taken on each individual at 10-μm intervals on the lingual surface of M_1 near the enamel-dentine-cementum junction. Differences are statistically significant (t test = −34.06, $P < 0.0001$, $n = 18$). Correlations between diet phases and cementum bands were made with fluorochrome dyes.
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27. A fresh tooth was cut out of the mandible with a rotary saw and the periodontal ligament was stripped. The tooth was then immersed in 1 M acetone for 10 min, fractured in the mesio-distal plane through the tooth root, rinsed with distilled H_2O, air-dried, coated with 200 nm of gold, and photographed at 20 kV.
28. Fresh teeth were cut out of the mandible with a rotary saw, and the periodontal ligaments were stripped. Teeth were fixed in 10% formaldehyde for 24 hours, rinsed in distilled H_2O for 1 hour, dehydrated in 1 M ethanol, embedded in epoxy, sectioned in the mesio-distal plane, ground to a thickness of 50 μm, and polished. Specimens were photographed at 110 KV for 20 min.

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Repair of DNA Methylphosphotriesters Through a Metalloactivated Cysteine Nucleophile

Lawrence C. Myers, Michael P. Terranova, Ann E. Ferentz, Gerhard Wagner,* Gregory L. Verdine*

The *Escherichia coli* Ada protein repairs methylphosphotriesters in DNA by direct, irreversible methyl transfer to one of its own cysteines. Upon methyl transfer, Ada acquires the ability to bind specific DNA sequences and thereby to induce genes that confer resistance to methylating agents. The amino-terminal domain of Ada, which comprises the methylphosphotriester repair and sequence-specific DNA binding elements, contains a tightly bound zinc ion. Analysis of the zinc binding site by cadmium-113 nuclear magnetic resonance and site-directed mutagenesis revealed that zinc participates in the autocatalytic activation of the active site cysteine and may also function as a conformational switch.

Methylation of DNA can occur enzymatically and nonenzymatically. Whereas enzymatic methylation fulfills an essential role in many organisms, nonenzymatic methylation insults the genome with a variety of toxic and mutagenic adducts (*1, 2*). To counter this threat, cells express a variety of proteins that recognize and repair aberrantly methylated DNA. A noteworthy example is *Escherichia coli* Ada, which repairs the mutagenic adduct 6-O-methylguanine by direct, irreversible methyl transfer to a cysteine residue in the COOH-terminal domain (*3*). Ada also repairs the S_p diastereomer of DNA methylphosphotriesters (MePs) by direct methyl transfer to a second cysteine, Cys^{69}, located in the NH_2-

L. C. Myers, Program for Higher Degrees in Biophysics, Harvard University, Cambridge, MA 02138.
M. P. Terranova and A. E. Ferentz, Department of Chemistry, Harvard University, Cambridge, MA 02138.
G. Wagner, Program for Higher Degrees in Biophysics, Harvard University, and Department of Biological Chemistry and Molecular Pharmacology, Harvard Medical School, Boston, MA 02115.
G. L. Verdine, Program for Higher Degrees in Biophysics and Department of Chemistry, Harvard University, Cambridge, MA 02138.

*To whom correspondence should be addressed.