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VARIABILITY AND SYNCHRONY OF SEASONAL INDICATORS IN DENTAL CEMENTUM MICROSTRUCTURE OF THE KAMINURIAK CARIBOU POPULATION

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ABSTRACT: It has recently been established that microstructural variations in dental cementum indicate not only age, but also the season of death of mammals in highly seasonal environments. Because dental microstructure often remains intact in even fossilized teeth, these phenomena are of particular interest to zooarchaeologists. In this paper the degree to which these seasonal indications vary within one modern population of caribou is assessed. While broad temporal synchrony in cementum growth cycles within the population is demonstrated, variation is exhibited. The sources of variation derive from the mechanical error in specimen preparation and analysis and the different feeding behaviors of the socially segregated caribou.

KEY WORDS: DENTAL ANNULI ANALYSIS, CARIBOU, *Rangifer tarandus*, SEASONALITY, SKELETOCHRONOLOGY, TEETH

RESUMEN: Ha quedado recientemente demostrado que las variaciones microestructurales en el cemento dentario no sólo son indicadores de la edad sino también del momento de muerte de mamíferos que viven en ambientes con cambios estacionales marcados. Dado que con frecuencia la microestructura dentaria permanece intacta, incluso en dientes fosilizados, tales fenómenos resultan de especial interés en arqueozoología. En este estudio se calibra el grado de variación de estos indicadores estacionales dentro de una población extante de caribúes. Si bien se demuestra la existencia de una amplia sincronía en los ciclos de deposición del cemento dentro de dicha población, constatamos asimismo variaciones. Tales fuentes de variación derivan tanto de errores mecánicos en la preparación y análisis de las muestras como de las estrategias alimentarias evidenciadas por las diferentes agregaciones sociales que exhibe esta especie.

PALABRAS CLAVE: ANÁLISIS DE ANILLOS DENTARIOS, CARIBU, *Rangifer tarandus*, ESTACIONALIDAD, ESQUELETOCRONOLOGÍA, DIENTE

INTRODUCTION

Background to the Study

The skeletochronological study of the incremental structures in teeth has a long history in wildlife biology and paleontology. From the early 19th century work of Retzius (1837), to Laws's (1952) presentation of "a new method of age determination in mammals", to the pivotal works of Klevezal' and Kleinenberg (1967), Morris (1972), Spinage (1973), and Grue & Jensen (1979), to innumerable recent studies (see Gordon 1991 for bibliographic review) it has been recognized that variations in the microstructure of dental cementum and dentine may serve as a record of age at death in mammals. The fact that the same microstructural variations in cementum may unambiguously indicate the *season* of death has been more recently established. This information is of particular importance interest to archaeologists investigating prehistoric settlement and subsistence strategies (e.g., Saxon & Higham, 1969; Bourque *et al.*, 1975; Spiess, 1976, 1979; Gordon, 1982, 1988; Stallibrass, 1982; Savelle & Beattie, 1983; Koike & Ohtaishi, 1985, 1987; Pike-Tay, 1989, 1991a, 1991b, 1993; Beasley *et al.*, 1992; Burke, 1992, 1993; Lieberman & Meadow, 1992; Lieberman, 1993a, 1993b, 1994; O'Brien, 1994). Modern control samples of the same (or at least two closely related) species from broadly similar environmental and ecological conditions are a necessary prerequisite for any seasonality study of archaeofauna. However, the procurement of sufficient numbers of animals for appropriate control samples of known age and season-of-death is a difficult and time intensive undertaking. Therefore, when my colleagues at New York University and I were able to obtain a collection of right mandibular teeth of an entire population of *Rangifer tarandus* *groenlandicus* individuals from the Canadian Wildlife Service, a research project was designed to record skeletochronological and other metrical data (Pike-Tay *et al.*, n.d.) of relevance to zooarchaeology. In this report, I present the degree to which the seasonal indications gained from dental cementum vary within one population of barren-ground caribou, inhabitants of a highly seasonal environment.

Background to Dental Cementum Biology

Teeth are composed of three distinct types of mineralized tissue: dentine, cementum, and enamel. Each tissue is made up of two components: the inorganic crystallites of dahllite (a carbonate hydroxyapatite) and the proteins and lipids that comprise the organic matrix of the tissue. Each tissue is incremental in structure (Boyde & Jones, 1972; Hillson, 1986; Carlson, 1990). The physical and optical expressions of incremental "lines," or growth layers in teeth are due to differing patterns of collagen fiber organization and cell content (Castanet, 1981; Francillon-Vieillot *et al.*, 1990). In the case of dental cementum the differentiation of growth layers is the result of seasonal rhythms of cementoblast activity and quiescence, i.e., variable growth rates, and of occlusal strain (Lieberman, 1993a, 1993b). Generally, two types of growth increments are recognized in cementum: *annuli*, the narrow, relatively more mineralized increments that temporally correspond to "winter" and a physiological period of slow growth; and *zones*, the wider, relatively less mineralized increments that correspond to the onset and fruition of the warm season, a period of relatively rapid growth (Klevezal' & Kleinenberg, 1967; Castanet, 1981; Francillon-Vieillot *et al.*, 1990).

The Kaminuriak Control Sample

The study collection is comprised of the right mandibular teeth of 999 members of the Kaminuriak population of barren-ground caribou and is housed at New York University's Department of Anthropology. The caribou were collected by the Canadian Wildlife Service (CWS) during the months of April, May, June, July, September, November, and December, from the spring of 1966 through the summer of 1968 (Parker, 1972; Dauphiné, 1974; D.R. Miller, 1974; F.L. Miller, 1974). A major goal of the CWS project was to obtain animals during their major life history phases. A total of 563 females and 436 males were collected. The sexually mature segment (46 months and over) comprised 306 females and 178 males. Ages of the animals were determined by a combination of methods: 1) records of animals tagged at birth; 2) microscopic analysis of histologically prepared slides of cementum annuli of the mandibular incisors; and 3) eruption and wear estimates and linear dental measurements. Results from all three were in agreement (F.L. Miller, 1974). The demographic data was used by the CWS to assess the effects of natality and mortality on the population as well as the ages and sexes of the caribou grouping together during different seasons of the year. Observations of group structuring were made throughout the collection period. A high degree of segregation in the caribou bands was noted, particularly in spring, leading to the conclusion that caribou are socially cohesive (*Ibid*).

Changes in diet, specifically, hardness of food and its nutritional content, have been shown to effect dental cementum microstructure by causing variations in collagen fiber orientation and/or collagen mineralization in controlled laboratory experiments by Lieberman (1993a, 1993b, 1994). His study suggests that the two dietary variables may operate independently. The harder the substance chewed, the more vertically oriented relative to the dentine-cement border (Figure 1) the Sharpey's fibers (extrinsic collagen fibers of cementum that originate in the periodontal ligament) become in order to accommodate the higher tensile strains of mastication. This is consistent with cementum's primary function of anchoring the tooth in the alveolar socket. The lower the protein and mineral value of the food, the more mineralized (denser) is the cementum layer that is deposited. The rate of mineralization remains constant, but the rate of formation (the growth rate) of the collagen matrix is greatly reduced with poorer quality diet (Klevezal', 1980; Jones, 1981; Lieberman, 1993a, 1993b).

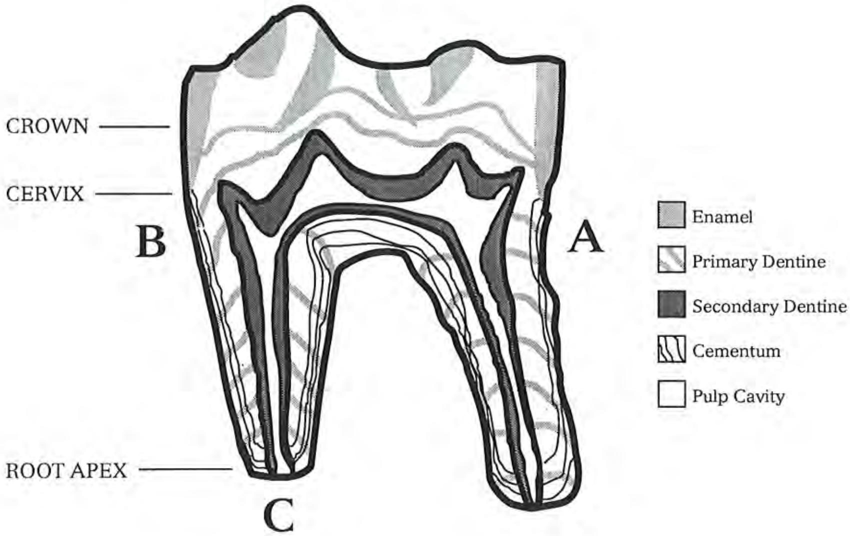

FIGURE 1. Drawing of a longitudinal section of a *Rangifer* molar indicating dental tissues and areas of cementum analyzed, where A and B are the distal side and mesial areas (respectively) of acellular cementum that extends from the root-enamel junction towards the root apices and C is the root apex area of cellular cementum. The interradicular arch ("root pad") is the other area of acellular cementum.

The diet of Kaminuriak caribou varies greatly with local geography and the seasons. The study area of the CWS project encompassed the total range of the Kaminuriak population, some 282,000 km^2 of northern Manitoba, northeastern Saskatchewan, and the southeastern district of Keewatin, Northwest Territories —- area covered with bogs and muskegs. Environmental and ecological aspects of various portions of the study area have been described in detail (Beckel, 1958a, 1958b; Rowe, 1959; D.R. Miller, 1974). The most pronounced difference in food quality is that of winter compared to the warmer months. Rowe (1959) places the range of the Kaminuriak population within three floristic types; tundra, forest-tundra, and the Northwestern Transition sections of the boreal forest. Winters are severe and long (temperatures consistently below -29°C, often below -40°C), springs are wet and cool, and summers are relatively dry and moderate (24-26). As a general rule, the animals seek out plants with the highest available protein and fat content wherever they range. In spring the caribou feed on herbaceous plants newly uncovered by snow, growing willow leaves (*Salix*) and other buds, and new sedge (primarily *Carex*) and grass shoots. In summer they feed on nearly all available growing green plants, especially willow shoots and leaves. The bases of sedges and grasses remain green for sometime after the arrival of the autumn frosts while herbaceous plants and willows lose most of their available protein. Thus, there is a notable dietary shift to a harder textured diet of grass and sedge during late fall into early winter for caribou still outside of the forest. Caribou that move into the boreal forest at this time search intensely for a range of fungi, which have substantially higher protein and fat content than other available plants. After the snow has covered the fungi and any remaining green plants the caribou wintering in the forest turn to (primarily arboreal) lichens including *Alectoria jubata* and *Cladonia*. While lichen protein content is lower than that of forage consumed in other seasons, it is higher than that of other winter-available plants which lie dormant (Kelsall, 1968; Dauphiné, 1974; D.R. Miller, 1974; F.L. Miller, 1974).

METHODS

Given the variable feeding behaviors among the sexes and ages of caribou, I tested for the synchrony of dental cementum growth rates among population members. Results of this initial skeletochronological study of the Kaminuriak collection are based on subsamples of 875 longitudinal (mesio-distal radial) ground thin sections of 677 teeth of 348 male and female animals. The breakdown of this sample is presented in Table 1. Initial preparation of the fresh mandibles by the CWS included soaking in hot water for several days to loosen soft tissue and any foreign material and allow easy removal. The molariform teeth were then gently removed with tooth extractors, fixed in 5% formalin solution, rinsed in H_2O, and dried. At NYU the teeth were embedded in epoxy, sectioned in the mesio-distal plane, ground to a thickness of 30-50 µm, and polished.

AGE CLASS	of thin sections	of teeth	of individuals	sex
Calves (0-9 months)	53	47	26	(11F, 15M)
Yearlings (10-23 months)	104	89	46	(21F, 25M)
Juveniles (24-35 months)	161	135	60	(25F, 35M)
Subadults (36-59 months)	78	61	34	(12F, 22M)
Prime adults (60-119 months)	407	287	158	(107F, 51M)
Post-prime (> 120 months)	72	58	24	(22F, 2M)
TOTAL	875	677	348	(198F, 150M)

TABLE 1. Sub-Sample of Right Mandibular Kaminuriak teeth for results discussed here.

Seasonal growth increments are clearly visible in the dental cementum of teeth of the Kaminuriak population with backscattered SEM (Figure 2), reflected light microscopy, white transmitted light, and polarized transmitted light (Figure 3). The wider increments of cementum were formed during the warmer months and appear light in color value and opaque under reflected light microscopy; light (bright) with backscattered SEM and transmitted polarized light (where increments are oriented at a 45° angle to the primary N-S axis of polarization), and dark under transmitted white light. The narrow increments of cementum were formed during the winter months and appear: dark in color value and transluscent under reflected light microscopy; dark with backscattered SEM and transmitted polarized light; and bright under transmitted white light. Because of its efficiency and cost effectiveness, I employed polarized transmitted light microscopy for the analysis of the 30-50 μm thick "dry" ground and polished longitudinal sections of teeth. Magnifications of 100x and 250x were most commonly employed. For image and data recording: 1) video images of the thin section were directly transferred from the microscope to the computer; 2) each cementum zone 's (i.e., growth layer's) width was measured in sequence at two or three transects per tooth; 3) measurements were then converted from pixels to microns and standardized so that different magnification scales could be compared. The mean, variance, and standard deviation were computed, and the relationship of the final cementum increment's width to the widths of the preceding increments was established. Since cementum grows in consecutive sheaths around the dentine core of a tooth, the final, outermost layer deposited is that which provides seasonal information.

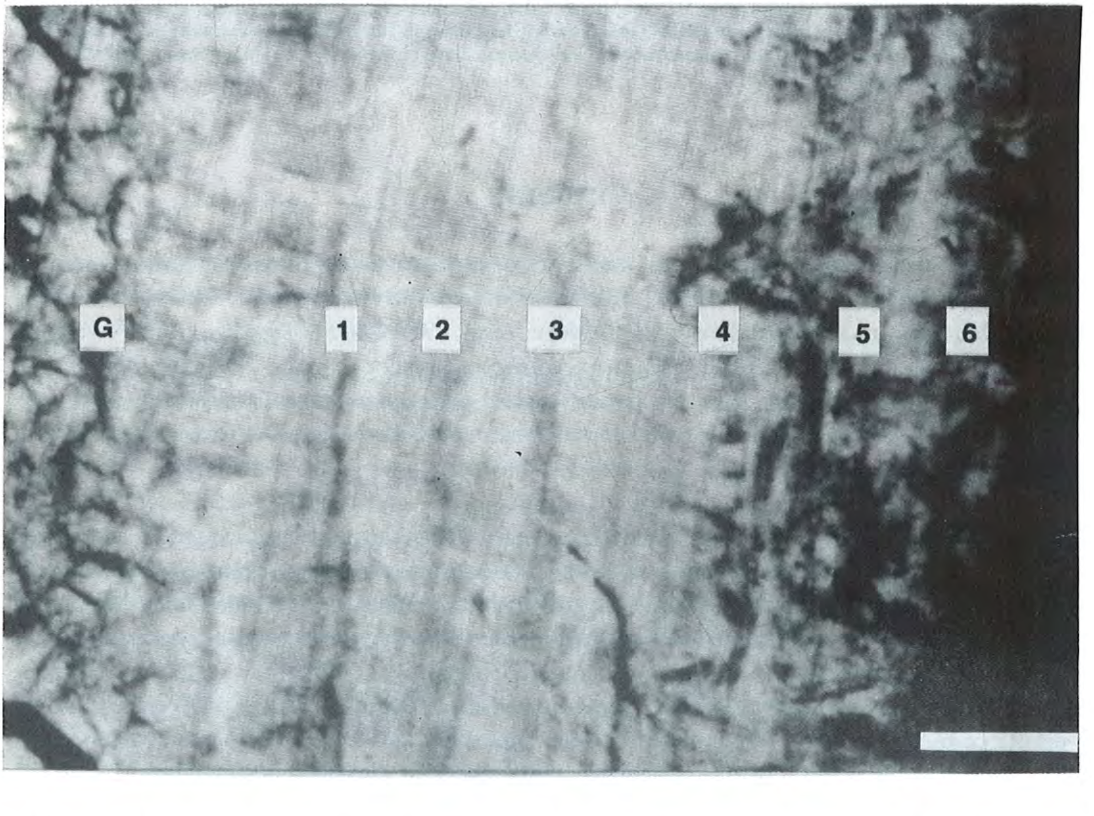

FIGURE 2. Backscattered Electron Image of a longitudinal thin section (40 μm thick) just below the root-enamel junction of an M_2 of a 7 year old female killed on June 20, 1966. Scale bar, 10 μm. Cementum-dentine border (granular layer of Tomes) (G); winter-formed *annuli* are numbered, with final growth *zone* just beginning after the 6th annuli.

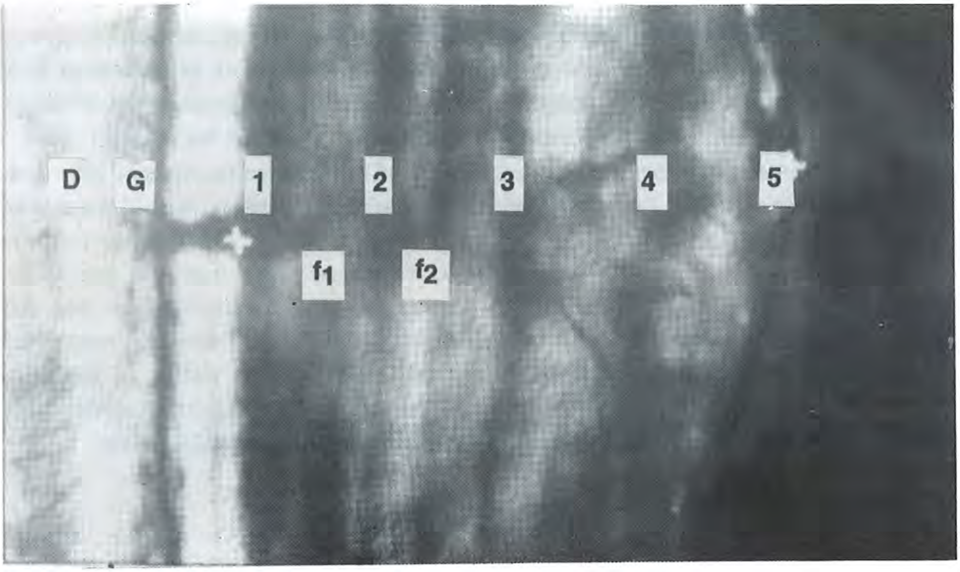

FIGURE 3. Transmitted polarized light micrograph (mag. 250X) of ground longitudinal thin section (40 µm thick) of the P_4 of a 6.4 year old female killed on November 25, 1966. Dentine (D), cementum-dentine border (granular layer of Tomes) (G), winter-formed annuli are numbered, the final (5^{th}) annuli is just beginning to form; "false" or secondary lines (f_1, f_2) are marked. The false lines are easily distinguished from the winter annuli because the former are discontinuous while the latter extend around the entire root.

RESULTS

Dental cementum is comprised of two types of collagen fibers: Sharpey's fibers, which are formed by fibroblasts of the periodontal membrane and are therefore extrinsic fibers and intrinsic fibers which are formed by the cementoblasts (Noyes *et al.*, 1938; Scott & Symons, 1977). Two types of cementum are recognized based upon the presence or absence of cells. Acellular (often called "primary") cementum extends from the cement-enamel junction and extends toward the root apex (Figure 1). Most of the collagen in acellular cementum consists of Sharpey's (extrinsic) fibers (3). Cellular ("secondary") cementum increases in thickness toward the root apices and at the interradicular arch, i.e., the "root pad". Lacunae are commonly and irregularly distributed throughout cellular cementum. Incremental layers may be counted in both types of cementum. Accurate age estimates of animals from examination of areas of cellular or acellular cementum are obtained by adding the age of the animal at the time the particular tooth erupts to the number of visible annuli. However, it is argued that accurate assessments of *season* of death, in ungulates at least, can only be taken from measurements of acellular cementum (Gordon, 1982; Pike-Tay, 1991a; Lieberman, 1993a). To test the latter, I took measurements from areas of cellular and acellular cementum from the teeth of forty-one adult caribou killed in June, September, and November. Measurements of the growth zone widths along transects of acellular cementum near the cement-enamel junction for site "A" on the distal side and site "B" on the mesial side, as well as of cellular cementum, at site "C," at the root apices (Figure 1) demonstrate that for *Rangifer*, cementum is deposited at a fairly regular seasonal rate only in areas of acellular cementum (Table 2).

A - Site	
Distal side	1.9
B - Site	
Mesial side	2.7
C - Site	
Root apex	16.8

TABLE 2. Mean Standard Deviation of Cementum Growth Zone Widths of teeth of 41 prime adult caribou killed in June, September & November.

To assess the role of mechanical error in the orientation and placement of the "cut" from which a thin section is made, three consecutive and longitudinally oriented slices of the tooth root were made and measurements of cementum growth zones from each were compared. 'A' was the buccal-most (cheek side) and superficial slice, 'B' next, and 'C' at, or nearest to, the mesio-distal midline of the tooth. The original thick sections of tooth were approximately 1 mm thick, and then were ground and polished to the 30-50 μ thickness. A standard error percent calculation was performed on the widths of final growth zone relative to the previous annual zone widths along two transects for each slice. Analysis of 24 thin sections comprised of 3 slices per tooth from 8 teeth revealed that the maximum width difference between final cementum zones from slice B and slice C (the midline) was 21%, while the maximum width difference between outermost buccal slice A and slice C was 33%. Therefore, in order to standardize results obtained, mesial-distal sections were taken only from the mid-line of each tooth for this study.

To test the assumption that any given tooth from an animal should reveal identical information regarding age and season of death, relative widths of the final cementum zone of two premolars and two molars from the same animals were compared to one another. Sections taken from the mid-line of 48 teeth, 4 each per 12 individuals, showed a range of variation of 3% to 19% in the percentage completeness of the outermost growth zone. In the teeth of ten out of twelve animals, however, the range of difference among the teeth of each animal was less than 10% (Table 3).

RANGE	3% - 19%
MEAN Standard Deviation of % Complete of Final Growth Zones:	
	mean = 3.49
	standard error = .6
	variance = 4.4

TABLE 3. Range of variation in % completeness of the final cementum zone among 4 teeth of the same animal based on 48 teeth from 12 individuals.

These results reveal that some difference does exist among the measured widths of increments at the sites of acellular cementum from the various teeth of an individual. The difference did not appear to be systematic or predictable and is assumed to be as much a result of the unavoidable mechanical error of specimen preparation and data recording as of actual variation among teeth. Important perhaps is the qualitative assessment that anomalous and very individual "fingerprints" such as false or secondary annuli can be identified in the same location on each tooth of an individual.

Within the total sample examined no sex-linked differences in the initiation of the 'true winter rest line' (annulus) or in the many occurrences of secondary or false annuli (Figure 3) (sometimes called rutlines) were detected. This is notable since rutting male caribou lose body weight and fat reserves from October to December and female caribou continue to gain weight and store fat during the same period (this confirms the observations of F.L. Miller, 1974).

In terms of the timing of initial cementogenesis, my findings concurred with those of F.L. Miller (1974) per his examination of the incisors of Kaminuriak juveniles. Miller notes that the apposition of 'light' cementum in the incisors begins by the fifth month of the *Rangifer* calves' life and the first annulus forms during the first winter of life. For Rangifer, i1 begins eruption at 9 months and is in occlusion by 13 months; with i2 and i3 beginning eruption at 11 months and in full occlusion by 15 months. Examination of the mandibular teeth revealed the pre-eruptive deposition of what has been called intermediate cementum at the dentine margin. This is a dense collagen-poor layer of cementum that is deposited at the dentine margin after formation of the tooth root but before the tooth is in occlusion. This pre-eruptive zone of irregular width has been reported for a wide range of mammals, including *Cervus* (Mitchell, 1963; Pike-Tay, 1989); *Rangifer (*Reimers & Nordby, 1968); and others cited in Lieberman (1993b). Formation of the first annulus of the Kaminuriak samples occurred during the first winter of the tooth's life.

A summary of the timing of cementum growth and annuli formation for the Kaminuriak sample and the variation observed among the teeth of 216 non-juvenile individuals (ages and sex per Table 1) is presented in Table 4. For statistical integrity this sub-sample was limited to sub-adult, adult, and post prime adult animals where cementum had more than three complete growth zones. It is important to note that cementum increments in the teeth of the post-prime adult caribou often (30% of sample) reveal substantial differences in width between the earlier deposited layers which become "compressed" and those that follow. When this phenomenon occurred it was after the seventh annuli that the increments became wider. This pattern has also noted by McEwan (1963) and F.L. Miller (1974) for *Rangifer*; Klevezal' & Pucek (1987) for *Bos/Bison* and Pike-Tay (1991) for *Cervus*. For this reason, season of death measurements from the teeth of post-prime adults in the Kaminuriak sample are restricted to the more recently formed, "un-compressed" increments of acellular cementum, which were of surprisingly even widths.

MONTH	MEAN	STANDARD DEVIATION	most commonly observed	total range	predicted growth*
April	6.5%	4	4% - 9%	0%- 17%	11%
May	-	-	-	-	22%
June	15%	10	16% - 25%	0%-32%	33%
July	-	-	-	-	44%
August	-	-	-	-	55%
September	68%	8	60% - 78%	53%-86%	66%
October	-	-	-	-	77%
November	93%	7.5	84% - 100%	78%-100%	88%
December	94%	6	94% - 100%	85%-100%	99%
January			*in winter annuli*		
February			*in winter annuli*		
March			*in winter annuli*		

TABLE 4. *Rangifer* Cementum: % Final Growth Zone Complete of the Kaminuriak Sample.
* **predicted growth:** if rate of growth is constant from April through December.

The seasonal indications gained from various members of the Kaminuriak population reveal a maximum difference of 33% in the widths of the final cementum zones of teeth from animals killed during the same month of the year (Table 4). If the hypothesis that dietary changes in food hardness and nutritional content effect dental cementum microstructure by causing variations in collagen fiber orientation and/or collagen mineralization (Lieberman, 1993a, 1993b) is valid, then the amount of variation observed is not surprising. As noted above, a high degree of social segregation was observed in the caribou bands. Therefore, dietary behaviors and geographic range of the caribou vary along sex and age lines at any given season. Nonetheless, the dramatic changes in cementum microstructure of teeth from caribou in the highly seasonal environment of the barren-grounds reveal no overlap between the early and late segments of the warm season. Moreover, the initiation of the winter annulus is fairly synchronized. The cessation of the winter annulus and initiation of the growth zone occurs most commonly in early April with 100% completion of the zone attained from mid-November through the end of December (It is not possible to subdivide the winter-formed annuli of this sample of *Rangifer* with the mechanical means employed; i.e., polarized transmitted light images measured with the National Institute of Health's public domain software IMAGE 1.43). If the rate of cementum deposition is constant across a zone, about 11% growth per month is expected. As can be seen in Table 4, the mean actual growth per month is close to the estimated constant rate with *all* predicted values falling within the observed range with the exception of the one percentile lag in June. Deposition of the growth zone is slightly slower in the beginning of the warm season but attains a fairly constant rate by mid-summer.

DISCUSSION

The seasonal indications gained from dental cementum of this population of barren-ground caribou were found to vary and concur along several lines. First, it was found that due to mechanical error involved in the orientation and slicing of the tooth, standardized results could only be obtained from longitudinal sections at the mesial-distal midline of a tooth.

Second, testing for the synchrony and constancy of cementum growth rates among the *Rangifer* population members revealed that: 1) cementum is deposited at a regular rate only in areas of acellular cementum; 2) the initiation of the growth zone is well synchronized with deposition being slightly slower early in the warm season but then assuming a roughly constant rate by mid-summer; 3) No overlap exists between the early and late segments of the warm season; 4) the initiation of the winter annulus is less well synchronized than its cessation and, 5) Multiple teeth from a given individual vary little from one another tooth in regard to the seasonal indications provided by cementum annuli analysis. Frequent occurrences of 'false' or 'secondary' annuli could not be linked to sex differences. Yet, these stigmata tend to occur in the same position on all the teeth of an individual. Such 'fingerprints' may prove useful in linking isolated archaeological teeth to the same individual.

Third, the teeth of the post-prime adult caribou often yield substantial differences in width between the earlier deposited cementum layers (which become "compressed") and those that follow. The same has been observed by other researchers of *Rangifer*, *Bos/Bison* and *Cervus* (McEwan, 1963; Miller, 1974; Klevezal' & Pucek, 1987; Pike-Tay, 1991). For this reason, season of death measurements from the teeth of post-prime adults should be restricted to the more recently formed, "un-compressed" increments of acellular cementum.

Fourth, evidence from the juveniles examined demonstrates that pre-eruptive cementogenesis yields intermediate cementum at the dentine margin and is followed by the apposition of the first annulus during the first winter of the tooth's existence.

If dietary changes including hardness of food and its nutritional content affect dental cementum microstructure by 1) causing variations in collagen fiber orientation as a result of the orientation and degree of tensile forces, and 2) affecting the rates of collagen matrix production (Lieberman, 1993a, 1993b); then, the variation in dental cementum growth rates observed among members of the Kaminuriak population is understandable.

CONCLUSIONS

Notable differences in feeding behaviors and local range of the two sexes and seasonally-changeable caribou social groupings exist, eventhough the caribou occupy a highly seasonal environment. At the same time the overall seasonal synchrony of cementum development among population members underscores the potential of cementum annuli analysis as an indicator of age, season of death, and related life history variables in both modern and archaeological faunas where the cementum microstructure is preserved. However, in addition to working with modern control samples the zooarchaeologist must take complex taphonomic variables into account when examining archaeological teeth. I have recently begun controlled taphonomic experiments assessing the impact of a range of variables (boiling, freezing, fire, trampling, etc.) on dental cementum. I hope that this work will contribute to the refinement of the investigative techniques of skeletochronology for archaeology.

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