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Digital Cementum Luminance Analysis (DCLA): A Tool for the Analysis of Climatic and Seasonal Signals in Dental Cementum

C. M. WALL-SCHEFFLER* AND **R. A. FOLEY**

Leverhulme Centre for Human Evolutionary Studies, University of Cambridge, Downing Street CB2 3DZ, Cambridge, UK

ABSTRACT Cementum banding patterns have been used by archaeozoologists and wildlife managers for a number of decades to assess the season and age at death of mammalian populations. However, the observation and measurement of the nature of cementum banding, especially that of the final band, has proved to be difficult except under conditions of excellent preservation and advanced microscopy. The research presented here details a method for extracting luminance data from the banding patterns of cementum in order to quantify the optical properties of cementum tissue. By doing so, analysis of the relationship between cementum deposition and environmental variables is achieved. We present the results of a digital cementum luminance analysis (DCLA) on a sample of first molars from two species, *Ovis aries*, Soay and *Capra ibex.* The results indicate that significant relationships occur between seasonal temperature changes and cementum histology. Furthermore, we show that luminance values can be used to assess the geographical range of genetically similar populations. Our results demonstrate that the study of luminance is a vital tool for the quantitative study of dental cementum for both archaeological and ecological studies. Copyright © 2007 John Wiley & Sons, Ltd.

Key words: cementum; seasonality; Soay sheep; alpine ibex; digital image analysis

Introduction

It has long been recognised that the analysis of banding in the cementum of mammalian teeth can be used to infer both age and season of death (Fisher & MacKenzie, 1954; Sergeant & Pimlott, 1959; Aho *et al.*, 1981; Hamlin *et al.*, 2000). Such research, although it has been applied to archaeological and contemporary ecological situations, has been troubled by problems of analytical robusticity and replicability. In simple terms, the observation and measurement of the nature of cementum banding, especially that of the final band, has proved to be difficult except under conditions of excellent preservation and advanced microscopy. Furthermore, various authors (Lieberman, 1994; Burke & Castanet, 1995; Pike-Tay, 1995) have also questioned what factors underlie the formation of bands, and therefore how they should be interpreted in terms of development and environment.

In this paper we attempt to advance the methodology for the analysis of cementum banding by the application of digital luminance analysis. We present a method for using high resolution digital imagery in the measurement of banding patterns, and explore patterns of

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* Correspondence to: Leverhulme Centre for Human Evolutionary Studies, The Henry Wellcome Building, University of Cambridge, Fitzwilliam Street, Cambridge CB2 1QH, UK (current address). e-mail: cscheff@gmail.com

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banding using these techniques given known environmental and developmental conditions. The study samples are drawn from populations of Soay sheep (*Ovis aries,* Soay) and Alpine ibex from Italy and Switzerland (*Capra ibex*). The Caprinae were extensively exploited by prehistoric populations, and so these species offer potential models for archaeological applications. The proposed method offers a greater possibility of quantification, and therefore the ability to place interpretations of seasonality into a statistical framework.

Environment, cementum deposition and quantification

Cementum is a primarily calcified tissue which covers the entire exposed dentine surface of teeth. Cementum is highly developed in mammals but can occur in lower vertebrates (Schmidt & Keil, 1971: 296). Its properties are similar to that of bone in that it contains branching cells lying in lacunae and it is penetrated by collagenous fibre bundles (which attach a tooth to the alveolus) (Manley *et al.*, 1955; Shroff, 1966: 137). Unlike bone, however, cementum is more stable and is only reabsorbed under extreme and rare circumstances (Manley *et al.*, 1955; Lieberman & Meadow, 1992; Lieberman, 1993). Much of this is due to the fact that cementum does not receive nutrients from the tooth pulp (Jenkins, 1978: 193); even if a tooth dies, the cementum will continue to function, remain stable, and ensure that the tooth remains attached to the periodontal fibres – cementum has a tendency to form regardless of circumstances (Shroff, 1966: 146). Furthermore, cementum will not be readily reabsorbed due to the density of Sharpey's fibres, the proximity of epithelial cells to the root surface, and the position of blood vessels near to the alveolar bone (Berkovitz *et al.*, 1992: 155).

The function of cementum is to attach principal fibres of the periodontal membrane to the root surface, thus supporting (anchoring) the tooth in the jaw (Manley *et al.*, 1955; Schmidt & Keil, 1971; Jenkins, 1978; Gordon, 1988; Berkovitz *et al.*, 1992). Cementum extends from the edge of the cervical enamel to the apex of a tooth. The thickness of cementum varies around a tooth and is generally most thick at the root apex (on average 50–200 μm) and most thin at the cervical region (on average 10–50 μm) (Berkovitz *et al.*, 1992: 155). Cementum is immediately adjoined with the periodontal ligament on its outer side and is adhered to dentine on its inner surface. As cementum grows continuously throughout the life of the tooth, the newest cementum is being continually reattached to the periodontal ligament fibres (Shroff, 1966: 251; Scott & Symons, 1974; Berkovitz *et al.*, 1992: 155). The earliest cementum growth is nearest the cemento-dentine junction (see Figure 1).

When the dentine of a root begins to form, it is covered with the epithelial sheath of Hertwig – this covering separates the dentine from the surrounding tissues of the dental follicle (Scott & Symons, 1974: 251). As a tooth erupts, the

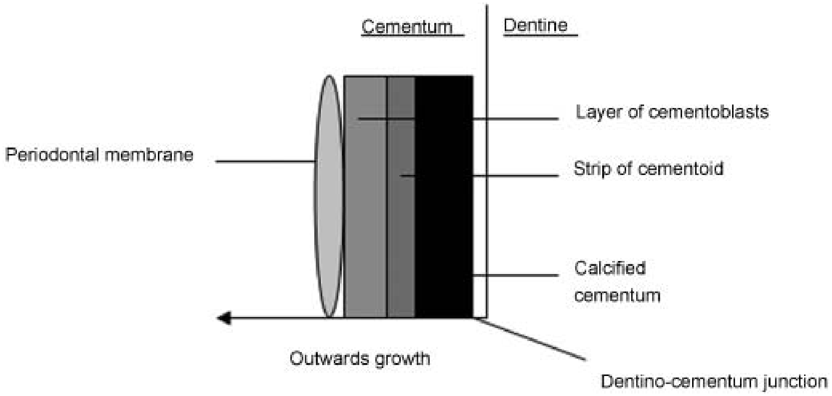

Figure 1. An idealised (not to scale) portrait of the pattern of cementum deposition. Throughout the tooth's growth, the calcified cementum (shown in black) will continue growing to maintain connection with the periodontal membrane.

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disintegration of Hertwig's sheath begins and the inner vascular layer of the mesodermal dental follicle begins to come into contact with dentine. The cells of the mesodermal dental follicle differentiate to form cementoblasts, the cells which form cementum. Cementoblasts are large cells with vesicular nuclei and prominent nucleoli.

During the early stages of cementum development, cementoblasts are cubical cells which form a single layer in contact with dentine. Once the dentine surface is covered fully with differentiated cementoblasts, the cementoblasts lay down fibres and amorphous material and attach the amorphous material – with embedded fibres – to dentine's surface. Calcific material which forms the inorganic element of cement is then deposited into the amorphous substance (Scott & Symons, 1974: 251; Moss-Salentijn & Klyvert, 1980: 260). As cement forms, it attaches to the principal fibres of the periodontal membrane. These principal fibres are known as 'Sharpey's fibres' or more specifically 'embedded parts' of the principal fibres. After the cementum is deposited, the cementoblasts become mixed into the periodontal ligament fibroblast population and are no longer identifiable along the root surface (Cho & Garant, 1989). The tooth is thus securely attached to the alveolar bone. Cementum is deposited in these layers throughout life and this process repeats itself. The progressive nature of cementum ensures that the attachment of the periodontal fibres to a tooth's root can be altered or shifted according to the functional needs of the tooth: teeth which receive more wear (or which move more in the jaw) necessarily have thicker cementum (Mitchell, 1967; Schmidt & Keil, 1971: 296). This is necessary for erupting teeth and for mesial movements due to approximal wear (Scott & Symons, 1974: 256). Increases in the thickness of cementum are compensated for by reductions in the thickness of the periodontal membrane and not by reabsorption of bone (Jenkins, 1978: 192).

There are two types of cementum, acellular (or primary) and cellular (or secondary). Although they both fulfil the same function of attaching the principal fibres of the periodontal membrane to the root surface, they have a number of significant differences which are important in their identification. Both types of cementum consist of two types of collagen fibrils. The first is an intrinsic group of collagenous fibres running parallel to the surface of the tooth and embedded in a calcified ground substance. These are formed by cementoblasts and are found between Sharpey's fibres. They are arranged randomly or parallel to the surface of cement (Shroff, 1966: 140; Scott & Symons, 1974: 252–3). The second group of fibres are Sharpey's fibres which, as described earlier, are fibres of the periodontal membrane embedded into cementum tissue with a more perpendicular direction than the intrinsic fibres. Most of the collagen in acellular cementum is provided by Sharpey's fibres (Scott & Symons, 1974: 253). They are formed by fibroblasts of the periomembrane (Scott & Symons, 1974: 252).

Acellular cementum is the preferred cementum type for seasonality studies of Artiodactyla ungulates, because of evidence suggesting that acellular cementum is an accurate measure of season-of-death and age-at-death (Gordon, 1988; Pike-Tay, 1991, 2000; Lieberman & Meadow, 1992; O'Brien, 1994). Cellular cementum conversely forms directly in response to tooth growth and displacement and may be less accurate as a measure of season of death amongst ungulates (Lieberman & Meadow, 1992; O'Brien, 1994), although some evidence suggests it is still a valid source of information on the age at death (Lieberman & Shea, 1994). Furthermore, the distinction between cellular and acellular cementum may not be relevant for all species. For example, among *Equus* samples, Burke & Castanet (1995) found evidence of cementocytes throughout the cementum and found no evidence for acellular cementum.

Cementum build-up has visible lines representing intervals between successive deposits of cement. These lines often alternate between thicker zones and thinner zones. The thick zones – which have an increased number of cementocyte lacunae – have been generally understood to indicate faster growth and greater intensity of dental attrition (Sergeant & Pimlott, 1959; Hillson, 1986: 226). This relates to cementum maintaining an increased grip on the periodontal membrane and the tooth staying in place. The faster-growing band is further characterised by a highly organised arrangement of its collagen

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fibrils (Stutz, 2002). The thinner zones – build-up of fibre-free amorphous substance (Scott & Symons, 1974: 254) – are often more prominent in higher latitudes and more seasonal environments. In such locations, winters are longer and more pronounced and the restricted food intake can lessen the intensity of dental attrition (Hillson, 1986: 229). These thinner zones are generally characterised by a more poorly organised arrangement of collagen fibrils, typically associated with a higher density of biogenic apatite crystallites (Stutz, 2002). In some populations, however, the distinction between fast- and slow-growth (acellular) cementum may also be caused by differences in the angles of collagen fibre orientation. Within such populations, contrast between bands is enhanced.

While genetic factors have often been suspected as controlling the 'rhythm' of cementum growth, cementum deposition is also 'triggered' by external environmental factors (Burke & Castanet, 1995). Fine-tuning the relationship between cementum growth and the environment has been demonstrated by a number of previous studies, including those by Lieberman (1994), Pike-Tay (1995) and Mitchell (1967). Klevezal & Kleinenberg (1967: 25) further suggested that cementum banding patterns reflect the seasonal environmental conditions in which growth occurred and may record dietary information (Klevezal, 1996: 202. In addition, Klevezal (1996: 194) suspected that life history factors, including pregnancy, parturition and lactation (anything, in fact, that would alter an individual's metabolism) would also influence the growth of cementum, and provided evidence from studies on bears as well as Beluga whales (p. 195) that changes in cementum do occur in females raising young.

The optical distinctions of the 'seasonal' bands of cement have been found to be the result of two primary factors: the orientation of collagen and variable mineralisation patterns. Lieberman (1993) demonstrated that collagen-fibre orientation varies with seasonal changes in diet, which place variable occlusal stress on the teeth. Under higher, more tensile strain, Sharpey's fibres become more vertically oriented relative to the dentine-cementum border (Lieberman, 1993). The opposite is true under conditions of a softer diet. Lieberman's (1993) conclusion was that the different orientations cause the appearance of dark or light bands under polarised light.

In addition to orientation, mineralisation differences also contribute to the appearance of cementum under polarised light. Whilst mineralisation always follows the same pattern, the rate of mineralisation differs. This is variously understood as a consequence of the age of the mineralisation front (which relates to the age of the element) and to the age of the individual organism. It is possible that the health of the individual may also contribute to mineralisation rate. By controlling for nutrient intake, Lieberman was able to show that cementum deposited during a period of stilted body growth was more mineralised and less thick than cementum deposited during a period of normal growth: while the rate of mineralisation remained constant, the rate of formation of the collagen matrix varied. Lieberman (1993) thus concluded that the differences in collagen orientation and mineralisation, which contribute to the appearance of cementum under polarised light, can be used 'to reconstruct variations in seasonal diet quality'.

In this context, the research we report analyses differences in the expression of cementum banding between populations with known reproductive, environmental and developmental histories. Detection of cementum variation is a key problem that has emerged in dental cementum studies, and not simply due to its relationship with the environment. Difficulties in counting bands, and identifying the outermost band that relates directly to the season of death, makes robust analysis in cementum studies impossible. Difficulties can arise due to the examination of distorted areas of the root, differences in preparation methods, a lack of knowledge of cementum formation, 'false' or 'split' slow growth lines, and subjectivity owing to poor resolution of increments (Lieberman *et al.*, 1990; Pike-Tay, 1991). A number of methodological issues have consequently arisen for archaeologists and zoologists concerning the replicability and precision of season-of-death estimates, and the ability to measure the optical variation which could be a quantifiable variable of environment, or at the very least, a measure of nutritional intake and food hardness.

A possible means to solving some of these problems is through digital image analysis, which over the past 15 years has been used by dental cementum researchers to enhance the detail in thin-section images that might be lost through sectioning methods, and to create a means of looking more closely at patterns of cementum formation. Particularly notable was work accomplished in the early and mid-1990s which utilised graphical representations of cementum bands using NIH Image (Lieberman *et al.*, 1990; Lieberman & Meadow, 1992; Lieberman, 1994; Burke, 1995). However, as noted in Wall & Wall (2006), the 640 × 480 pixel resolution probably did not allow for numerical analysis of the luminance graphs, but simply graphical representations of 'relative' luminance.Therefore, two problems exist that we seek to resolve. The first is to measure the intensity of light variation and to quantify this intensity on a continuous scale of variation. Past research has shown band width to be variable within an individual (Foley, 1986). Furthermore, there exist substantial width differences between 'earlier deposited layers' and later layers (Pike-Tay, 1995); earlier bands appear to be compressed, while later bands are much wider. We therefore also seek to quantify band width in both a relative and an absolute sense.

The use of higher resolutions, such as the 2560 × 1920 pixels used in this study, allows for the quantitative analysis of true luminance values of cementum bands. With thin-sections of similar thickness and utilising the same microscope for consistent light intensity, the photos of the sections can be assessed not simply for band-width values, but also for the resultant 'luminance' of elements of the tissue structure (fibre density and orientation). This should offer information to answer important questions, including whether luminance (and thus cementum formation) might be an assessment of health or the surrounding environment, in conjunction with providing useful information about season of death. Furthermore, using a computer-assisted program to extract luminance information should alleviate the pressures of error between observers and between assessments by the main observer.

The first step in this study is to verify that DCLA provides accurate estimates of season-of-death and age-at-death. Next, the relationship between the environment and cementum growth, as assessed by digital cementum luminance analysis (DCLA), will be studied in two different species. The first study analyses *Ovis aries*, Soay in order to test whether the optical properties of cementum can be quantified absolutely (rather than relatively – see Lieberman *et al.*, 1990) and correlated with ecological variables. To control for as many factors as possible, half of the population is from a single birth and death cohort and the entire population is from one area. The second analysis compares two genetically similar populations of *Capra ibex* which live in highly different environments: a group of *C. ibex* entirely from the Valsavarenche region of Gran Paradiso, Italy, and five small groups from multiple habitats in Switzerland.

Materials

Two Caprinae species were utilised for this study and each species was chosen for a number of reasons. The first study species, *Ovis aries*, Soay was chosen because, as mentioned previously, it was a highly utilised prey species among *Homo* sp., and a better understanding of the Soay sheep can offer important information to zoologists and archaeozoologists. Furthermore, this particular population has been well-studied for over 50 years. The ongoing study allowed us access to detailed records of individuals' life history variables, as well as information pertaining to the climate and environment.

The *Ovis aries*, Soay samples ($n = 27$) from the island of Hirta off the west coast of Scotland (57°49′N, 08°34′W) are a remnant of a Bronze Age population introduced to Hirta and the St. Kilda archipelago 4000 years ago (Boyd & Jewell, 1974). The Soay sheep have been the focus of a number of studies and are tagged at birth (Clutton-Brock *et al.*, 1991). Genotyping of family groups and data collection on parity and offspring are also collected throughout the life of the individual and have been for numerous decades (Bancroft *et al.*, 1995). During most of the winter months when the majority of deaths

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occur, animals are collected every day so the date of death is generally exact.

The second species utilised for this study is *Capra ibex*. All living *C. ibex* populations are descendants of the Gran Paradiso population from Italy. After being hunted to near extinction during the 19th century, ibex were rescued and vigilantly protected on Gran Paradiso National Park land. After a number of years, new ibex populations were started in both Austria and Switzerland. Because of this recent ancestry of European alpine ibex from the Gran Paradiso population, there is low genetic variability between the populations (Gauthier *et al*., 1991). As genetic similarity between populations would prove useful in allowing the impact of differential environmental effects on cementum banding patterns to be assessed, we decided to choose two populations from different environmental situations (see Figure 2).

Samples ($n = 15$) were firstly obtained from the valley of Valsavarenche in Gran Paradiso National Park in Italy (45°31′N, 07°16′E), one of the oldest populations of alpine ibex in the world. The Valsavarenche valley is located in the northwestern Italian Alps, in the Valle d'Aosta. The elevation of the valley is 1951 m. The lower valleys of Gran Paradiso contain forests primarily of larch, above which are alpine pastures.

We then gathered samples ($n = 9$) from five distinct *C. ibex* colonies in the Berner Oberland region of Switzerland (centred around 46°41′N, 07°51′E). The areas are southeast of the city of Bern and reach an elevation of 4274 m (Zuber *et al*., 2001). The environments of the colonies differed from each other in the location of water (some on river systems, some near lakes) as well as altitude. The colonies most near the lakes especially vary in altitude as the lakes are at a level of 558 m above sea level but the ibex range into the mountains.

While the *C. ibex* samples do not have the detailed life histories of the Soay sheep, they all have known seasons of death and many have known ages at death.

Methods

Twenty-seven Soay specimens, nine Swiss ibex and 15 Italian ibex of varying age and sex were analysed, and lower M1s were extracted,

Figure 2. Google map of the Swiss and Italian locations of the *Capra ibex* specimens. This image provided courtesy of Google Earth. Reproduced with permission of Google Earth. This figure is available in colour online at www.interscience.wiley.com/journal/oa.

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encapsulated, and made into ground thin-sections using established techniques (Lieberman *et al.*, 1990; Pike-Tay, 1991; O'Brien, 2001; Wall, 2004). Once extracted, each molar was embedded in resin, sliced longitudinally down the centre, and each face was polished. Each half was then adhered to a frosted slide with more of the same resin (Buehler Epo-thin epoxy) and left to dry overnight. Once dry, the remaining tooth was sliced off and the thin-section ground down and polished to 70 ± 10 μm (this range of section width does not have a significant effect on the luminance values).

Upon completion, each thin-section was viewed using a polarising microscope. Polarising light microscopes which utilise transmitted light are regarded as superior to reflected light microscopes as they allow finer histological details to be seen (Hillson, 1986); in addition, previous researchers have had problems using a reflected light microscope for the analysis of cement (McCullough, 1996). Reflected light reveals superficial detail, whilst polarised light transmitted through the specimen is scattered by the structural properties of the cementum, thus revealing more detail than the reflected light microscope (see further description in Burke, 1993). Furthermore, a polarising set-up is crucial for Palaeolithic zooarchaeologists in assessing the appearance of diagenetic samples among faunal remains (Stutz, 2002).

The microscope used for this research is a Leica DM EP with 10× and 20× objectives. It has a rotating stage that can be used to align the sample with the polarising lenses. The optical properties of cementum can vary depending upon the orientation of the sample relative to the polarisers (see Stutz, 2002, for a detailed explanation). To create consistency in the way in which the optical properties of our samples were observed, our protocol consisted of lining each sample up to one of the perpendicularly oriented polarisers, so the first cementum band after the layer of Tommes would appear bright (Lieberman, 1994). Under polarised light, bands of high luminance (HL bands) tend to represent summer, or fast-growth periods, while bands of low luminance values (LL bands) tend to represent winter, or slow-growth periods (Morris, 1978; Lieberman & Meadow, 1992). In northern latitude ungulates, the fast-growth period is generally between April–November and the slow-growth period is between December and March (Grue & Jensen, 1979; Klevezal, 1996). Previous research on both of the study species has indicated that they follow this general trend (Clutton-Brock *et al.*, 1991; Serrano *et al.*, 2004).

A Nikon Coolpix 5000 with 12× magnification was attached to the microscope. The entire edge of cementum on each tooth was assessed for areas of complete cementum (e.g. no damage to the outer edges) which also exhibited high contrast between HL and LL bands. All areas of high contrast were photographed and assigned unique numbers to ensure proper cross-referencing with the photographs.

The program used to extract the luminance data from the cementum was MATLAB 6.5, for which a custom graphical user interface (GUI) could be written (Wall & Wall, 2006). The luminance data are a relative measure of the intensity of light; a luminance value of $255 = 100\%$ and represents the most intense light possible, whilst a value of $0 = 0\%$ and is the darkest light possible. Intermediate values could then be measured on a continuous scale.

Each photographed region was then analysed to determine the strength of contrast; the region that demonstrated the highest contrast was chosen to represent that particular thin-section. The region was then graphed and the numerical values of each pixel and luminance reading from the cementum region were copied into a spreadsheet. The minimum luminance value of each LL band and the maximum value of each HL band were then entered into a database, with the corresponding band-widths (see also Wall & Wall, 2006, for further image capture details). To prevent the inclusion of false peaks or troughs in the graph, no minimum or maximum point which was within two luminance values of the previous maximum or minimum was recorded. A range of two luminance values was chosen because it was large enough for those situations in which there was not a great difference between the luminance of HL and LL bands in a particular individual, and thus specific bands could still be recognised. In addition, the range was small enough to ensure that the height or depth of luminance points were not being interfered with by other marks

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(i.e. mineral deposits; see Gordon, 1988) within the cementum. Both band-by-band luminance and width, as well as luminance and width averages across an individual, were used throughout this analysis.

In order to evaluate the effect of seasonality and the environment on cementum growth, data from specific climatic variables had to be collected. Temperature and precipitation data were thus gathered from a weather station near the Hirta island population of *Ovis aries*, Soay. The monthly averages used in this study are data provided by the Large Animal Research Group at the University of Cambridge (Clutton-Brock & Pemberton, 2004). Temperature and precipitation data were not generally available for the regions which the *Capra ibex* sample inhabited.

Results

Life history and cementum: Ovis aries*, Soay*

Can DCLA provide accurate readings of season of death? All of the *Ovis aries* specimens lived under the same general environmental conditions. An end-of-winter date of death for all individuals ($n = 27$) was established blind on the basis of the DCLA, a result that was confirmed by demographic records. As previous research has shown, cementum bands can be used to assess the season of death accurately (Pike-Tay, 1991; Lieberman & Meadow, 1992; Burke & Castanet, 1995; O'Brien, 2001); for the Soay sheep this further proves to be the case, and the season of death was correctly assessed 100% of the time (see Table 3), confirming Saxon & Higham's (1968) pioneering research on sheep.

As can be seen from Figure 3a and b, utilising both the width of the bands and the luminance profile gives more complete evidence than the band-widths alone, and the high-resolution luminance profiles can detect evidence that might be lost with standard digital imaging. As the thin-sections are made to the same thickness, shifts in the intensity of band luminance are indicators of individual variation (although whether of collagen structure or of the degree of mineralisation, we are unsure at this point) and not differential section preparation. A further utility of DCLA is that differences between users are reduced and similarities quantified. Using a paired *t*-test, similarities between graphs taken by experienced and inexperienced observers are significant ($P < 0.01$) at the 99% level (see Figure 4).

Can DCLA provide accurate readings of age at death? Age estimates were produced by counting the numbers of cementum bands. Small differences were found between the known ages and the observed band numbers, though they remain highly significantly correlated ($P < 0.001$; R^2 is 0.890; see Table 3). The variation is an unexpected result, given the perfect relationship between expected and observed seasons of death. The two results taken together imply that high luminance (HL) and low luminance (LL) cementum bands are either added or are never lain down in some years, but possible causes for the addition or exclusion of bands are still unclear. As other studies have also found minor variations in band number and known age (Morris, 1978), it is likely that this finding has more to do with the animals' biology than with the method.

Indeed, using DCLA to test for a correlation between the strength of the luminance values and errors in estimation gave informative results. Significant differences do exist between the luminance values of LL bands and the actual occurrence of incorrect age estimates ($P = 0.003$). Furthermore, the luminance of LL bands has a significant effect on the total number of bands observed ($P < 0.001$; $\beta = 0.592$); this relationship was also seen to a lesser extent among the luminance values of HL bands ($P = 0.012$; $\beta = 0.239$). These results indicate that the reaction of Soay sheep to their particularly harsh winter environments (Clutton-Brock *et al.*, 1991) may leave specific signals in their dental cementum in terms of band number, band structure and band mineralisation.

Furthermore, as suspected and mentioned in past work (Pike-Tay, 1995), age does have a significant effect on band width and there is a significant difference between the widths of bands laid down in the first three years of life and later bands ($P = 0.027$ for HL widths; $P = 0.025$ for LL widths). In addition, the total

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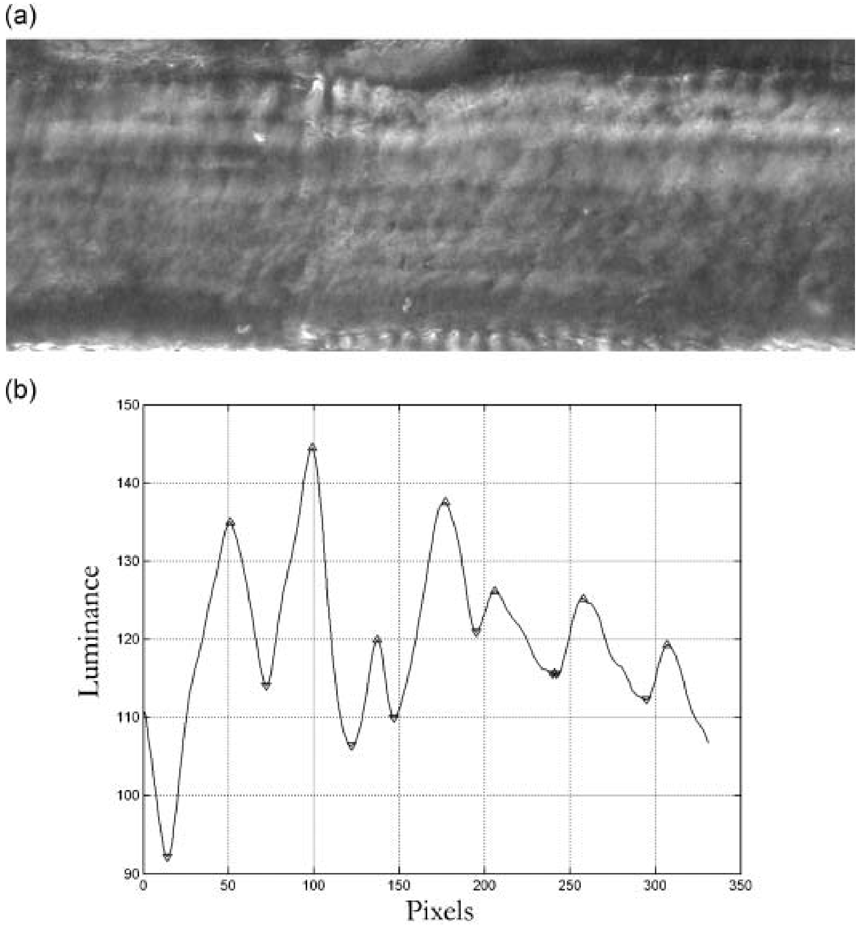

Figure 3. (a) A photo of the thin-section for *Ovis aries*, Soay individual 14, in black and white. The most recent cementum bands are located at the top of the photo and correspond to a pixel value of 15 in (b). (b) Luminance graph of *Ovis aries*, Soay individual 14. The most recent cementum is located around 15 pixels and the oldest cementum is located at 300 pixels.

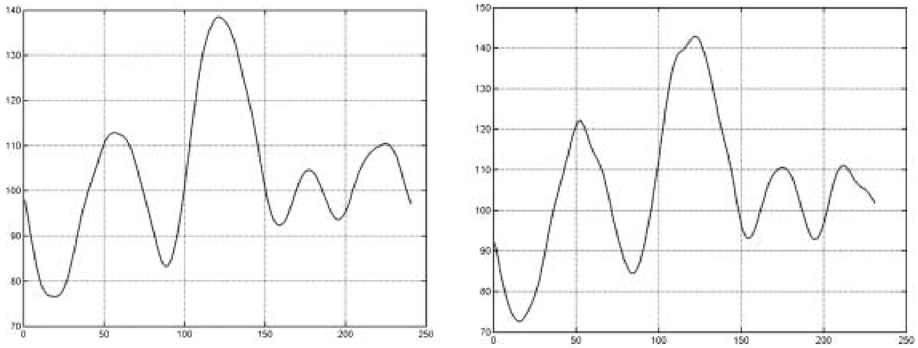

Figure 4. Two graphs of *Capra ibex* individual 10. The graphs were taken at different times by different observers. All graphs taken by both experienced and inexperienced observers were significantly correlated ($P < 0.01$).

number of LL and HL band pairs that are laid down in a given tooth also has a highly significant positive effect on the *luminance* of LL bands ($P < 0.001$; $\beta = 0.343$). As more bands are laid down, the luminance values of LL bands increase. The obvious next step in this research will be to obtain scanning electron microscope (SEM) micrographs so it can be determined whether the luminance is increasing because of the density of the bundles, the orientation of the bundles or the degree of mineralisation. The general consensus has been that the organisation and orientation of the bundles is highly important to the optical properties of cementum (Stutz, 2002).

Do life history events alter banding patterns?

Evidence that suggests that the stress of reproduction may alter banding patterns (Mitchell, 1967) initiated our interest in the predictive values of life history variables, especially considering the small differences between known age, and age as observed through the cementum bands. To test the relationship between reproduction and cementum histology, a regression was run using life history variables, including sex, age at death, how many times the individual produced twins, the age at first reproduction, and the total number of offspring produced (see data in Table 1).

No single life history variable had a significant predictive effect on the *extent* of differences between known and observed ages (i.e. one year or four years different); however, life history variables do influence the *accuracy* of age at death and season of death estimates. The accuracy of age estimates are specifically correlated with those life history variables that relate to reproduction. These variables include age at first successful reproduction ($P = 0.016$, Pearson

Table 1. Life history data and luminance results for each *Ovis aries*, Soay sample

Sample no.	Sex	Age at first offspring	No. of twin sets	Total offspring	Total pregnancies	Av. HL value	Av. HL width	Av. LL value	Av. LL width
1	F	1	3	9	6	142.52	20.43	112.30	20.50
2	M	4	0	3	3	137.86	31.00	99.15	29.54
3	F	2	0	4	4	107.28	16.89	86.52	15.93
4	M	1	0	3	3	150.35	55.00	110.51	54.83
5	F	—	0	1	1	138.30	28.97	112.52	30.00
6	F	1	0	8	8	104.89	20.71	76.32	23.75
7	M	0	0	0	0	154.53	40.71	82.28	36.43
8	F	0	0	0	0	139.38	40.67	105.06	40.00
9	F	0	0	0	0	112.46	30.17	82.02	28.17
10	F	1	1	11	10	163.80	20.71	133.69	20.38
11	M	0	0	0	0	136.96	35.67	95.06	29.33
12	F	0	0	0	0	168.04	23.67	94.72	16.00
13	M	4	0	15	15	118.06	27.65	102.62	25.71
14	F	2	3	8	5	129.64	15.52	110.19	15.00
15	F	0	0	0	0	193.99	63.57	79.22	49.29
16	F	1	2	9	7	110.43	16.55	85.74	16.07
17	F	0	0	0	0	116.34	27.33	42.02	27.00
18	F	2	3	9	6	126.01	26.96	110.75	26.79
19	M	—	—	—	—	110.69	11.47	87.41	11.27
20	F	0	0	0	0	126.78	29.00	65.31	40.67
21	F	0	0	0	0	166.20	40.00	88.72	33.00
22	F	0	0	0	0	159.98	26.00	85.73	27.33
23	M	0	0	0	0	144.87	36.67	79.77	20.67
24	M	0	0	0	0	159.03	27.00	92.53	24.00
25	M	0	0	0	0	91.16	21.89	59.49	20.67
26	F	1	3	9	6	120.88	13.13	107.03	13.80
27	F	3	0	4	4	124.99	15.71	104.29	16.25

In order to save space, the average luminance and width values are listed; both averages and band-by-band values were used in this study.
Widths are in micrometers.
For males, 'total pregnancies' refers to total successful pregnancies caused.

Table 2. Location of *Capra ibex* samples and each sample's average luminance and width by band type

Sample no.	Location	Sex	Average HL value	Average HL width	Average LL value	Average LL width
Switzerland						
1	Justistal	F	125.51	24.42	70.25	23.92
2	Schwarzmonch	F	142.39	18.52	97.07	18.33
3	Brienzer Rothorn	F	135.03	16.64	110.71	16.36
4	Tscharzis	M	149.91	14.17	110.40	13.58
5	Tscharzis	F	113.52	14.09	99.67	15.44
6	Brienzer Rothorn	M	122.06	18.08	96.84	20.78
7	Brienzer Rothorn	M	123.60	15.39	108.24	14.72
8	Salibiel	M	173.91	23.19	139.19	23.87
9	Salibiel	M	163.92	25.95	112.94	24.71
Italy						
10	Gran Paradiso	M	119.29	16.83	79.29	16.25
11	Gran Paradiso	M	139.15	22.62	130.77	22.38
13	Gran Paradiso	M	138.39	14.49	106.10	14.54
14	Gran Paradiso	M	112.62	11.50	90.88	10.92
15	Gran Paradiso	F	115.12	28.12	80.83	30.14
16	Gran Paradiso	M	168.38	21.12	128.42	21.02
17	Gran Paradiso	M	144.78	14.48	123.83	15.22
18	Gran Paradiso	M	160.56	8.85	133.86	8.81
19	Gran Paradiso	M	106.36	20.00	77.52	20.89
21	Gran Paradiso	M	96.83	14.00	84.99	14.25
22	Gran Paradiso	M	85.84	27.14	72.38	27.43
23	Gran Paradiso	M	109.27	10.50	103.24	11.78
24	Gran Paradiso	M	105.95	14.50	91.79	15.26
25	Gran Paradiso	M	104.89	17.75	92.48	16.92
26	Gran Paradiso	M	142.33	18.86	98.70	17.95

correlation = 0.592), total number of offspring ($P = 0.003$, Pearson correlation = 0.687), and total number of pregnancies ($P = 0.001$, Pearson correlation = 0.729). These correlations are inclusive of female data only ($n = 16$). While these numbers remain significant if males are included, running the tests with only male data return no significant values. It may be possible that the highly significant relationships between females and reproductive cost overwhelm the male data (see data in Table 1). None the less, energy depletion associated with the rut may still warrant further research. Among the Soay sheep, the increased amount of energy used during the rut, combined with decreased nutritional intake, makes males far more susceptible to death from malnutrition than females (Boyd, 1974; Boyd & Jewell, 1974). The males may in fact be more susceptible to reproductive under-nourishment than females, and in future a larger sample should be used to test for such effects on cementum.

Despite the potential influence of life history variables on the accuracy of age estimates, the quantitative signal of band luminance shows no correlation with any life history variables. Furthermore, the average width of bands also shows no significant relationship with any life history variables, other than increasing age. These results imply that while actual banding number may indicate energy drain due to reproduction, the physical properties of collagen orientation are probably constrained by genetics and/or biomechanical factors, or related to other factors such as environment and climate.

Environment and cementum

Do environmental variables, such as temperature and precipitation, alter cementum deposition and thus its luminance? Low luminance bands, laid down during the winter months, show a highly significant negative relationship with the temperature of the summer prior to the winter of band growth (linear regression: $P = 0.003$; $\beta = -0.376$). Similarly, HL values – laid down during the summer months – are positively

Table 3. The known age and season of death of *Ovis aries*, Soay, and the season of death as observed with DCLA; outer bands which displayed a low luminance value were interpreted as a winter season of death

Subject number	Known season of death	Observed season of death	Expected age	Observed age
1	Winter	Winter	7	10
2	Winter	Winter	9	10
3	Winter	Winter	8	9
4	Winter	Winter	4	2
5	Winter	Winter	Unknown	9
6	Winter	Winter	12	Early years unreadable
7	Winter	Winter	1	1
8	Winter	Winter	1	1
9	Winter	Winter	1	2
10	Winter	Winter	12	13
11	Winter	Winter	1	1
12	Winter	Winter	1	1
13	Winter	Winter	7	7
14	Winter	Winter	7	7
15	Winter	Winter	1	1
16	Winter	Winter	8	6
17	Winter	Winter	1	1
18	Winter	Winter	8	4
19	Winter	Winter	Unknown	5
20	Winter	Winter	1	1
21	Winter	Winter	1	1
22	Winter	Winter	1	1
23	Winter	Winter	1	1
24	Winter	Winter	1	1
25	Winter	Winter	3	3
26	Winter	Winter	7	5
27	Winter	Winter	7	8

correlated with the temperature of the previous winter ($P = 0.036$; $\beta = 0.277$). The β-value improves, however, when both LL bands and winter temperature are included in the model predicting HL banding patterns ($\beta = 0.443$). These findings indicate that environmental factors may in fact influence cementum deposition, and more specifically, mineralisation or orientation of collagen fibres may be influenced by the temperature of the season prior to the band being laid down.

Even more intriguing for studies of seasonality is that the difference between two successive HL and LL values is significantly correlated to the difference between summer and winter temperatures (linear regression: $P < 0.001$ at 99%; $\beta = 0.473$). The positive correlation implies that as the difference between summer and winter temperatures increases, so does the difference between HL and LL values. As Lieberman (1994) suggested, the seasonal changes in the quality of diet, especially in terms of the hardness of available foods, may be expected to change cementum deposition. In response to such variation, cementum is likely to either increase the number of collagen fibre bundles, have slower growth which will result in increased mineralisation, or attain a more vertical orientation of Sharpey's fibres during the periods of increased stress (Lieberman, 1993, 1994). (This correlation does not hold true for the differences between HL and LL band widths – although because the widths are so closely related to each other (linear regression: $P < 0.001$; $\beta = .906$), this is not particularly surprising.)

Precipitation shows no significant relationships with luminance or width, which is somewhat unanticipated considering it is in fact precipitation and storms that wipe out food and therefore sheep populations on Hirta (Clutton-Brock *et al.*, 1991). Such a significant variable might be expected to have correlations with luminance, but it is not apparent in this particular sample. While the deaths are caused virtually exclusively by starvation (Clutton-Brock *et al.*, 1991), it remains unclear whether deaths occur directly following the storms (and thus perhaps the effect is too rapid to detect in the cementum bands), or whether starvation occurs gradually over the course of a winter filled with storms (which would then be more surprising). Further data on the grouping of deaths and on the strength of individual storms will be necessary to understand the role of precipitation.

Variation between populations and cementum: Capra ibex

The analysis of *Capra ibex* cementum utilised:

(1) a regression approach in order that relationships between luminance and the environment could be modelled to determine predictive effects;
(2) *t*-tests to detect significant differences between the two populations.

For age and season of death it was useful to consider the populations together, as it allowed a greater number of individuals to be compared. All regressions were run at a 99% confidence interval.

Does DCLA provide accurate readings of season of and age at death for caprids?

As expected, based on previous research and the above results, regional populations of *Capra ibex* show highly significant relationships between the known season of death and the season of death as predicted by the cementum bands ($P = 0.002$ for the entire sample, $\beta = 0.655$, $n = 19$ (individuals who died in April are not included)). It does appear that individuals who died in April show an increased variation in the luminance of the final band than those who died in other months. This could perhaps be because spring occurs at different times in different years: the Italian individuals who show the final band as an HL band died in years in which the average April temperatures were over 5°C higher than March temperatures, while the individual whose final band was an LL band (and for whom we had temperature data) died in a year in which the April temperatures were barely 4°C higher than March temperatures. With such a small sample, none of these differences are significant, but the data do show a trend.

Unfortunately a lack of known-age samples, combined with differences in cementum deposition in early versus late life, precluded a proper analysis of age at death; the results, however, are listed in Table 4. For those samples that can be analysed, age at death shows a significant positive predictive effect on the number of cementum bands of a sample ($P = 0.007$, $\beta = 0.857$; $n = 16$).

Does a quantitative measure of cementum luminance provide a means to test intra-population variability?

The results showed that luminance values of the HL bands of the Italian versus the Swiss populations were significantly different from each other (using an independent *t*-test: $P = 0.002$) (Figure 5). The HL values of the Swiss population showed an increased range of values compared with the Italian samples, despite the larger sample size from the Italian site. As the Italian samples were from a single alpine valley, while the Swiss samples were from five distinct regions (see Table 2 and Figure 2), it would appear that luminance range mirrors geographical range.

Discussion and conclusions

The quantitative analysis of digital luminance profiles thus offers the possibility of collecting intriguing information about individual and group cementum patterns that cannot be obtained from standard pictorial measurements alone. DCLA is not meant as a substitution for the educated understanding and viewing of cementum bands, but as an important complement to the study of seasonal environments and histological growth patterns. The digital analysis of luminance offers important insights for the quantitative measurement of cementum variation between populations: work that should support other comparative studies such as those by Pike-Tay (1995; Pike-Tay & Cosgrove, 2002), Lam (2002) and O'Brien (1994).

Furthermore, whilst absolute luminance values do not show predictive correlations with life history variables, luminance contrasts are in fact significantly predicted by yearly temperature

Table 4. The known and expected ages and season of death for *Capra ibex* from the two discrete environments

Sample no.	Location	Known season of death	Observed season of death	Known age	Observed age
Switzerland					
1	Justistal	Summer	Winter	Adult	8
2	Schwarzmonch	Winter	Winter	Adult	7
3	Brienzer Rothorn	April	Winter	Adult	10
4	Tscharzis	Winter	Winter	8.5	8
5	Tscharzis	Summer	Summer	3.5	3.5
6	Brienzer Rothorn	Summer	Summer	5.5	3.5
7	Brienzer Rothorn	Summer	Winter	5.5	6
8	Salibiel	Summer	Summer	Adult	12.5
9	Salibiel	Summer	Summer	Adult	5.5
Italy					
10	Gran Paradiso	Winter	Winter	6	4
11	Gran Paradiso	Winter	Winter	12	6*
13	Gran Paradiso	Winter	Winter	15	14
14	Gran Paradiso	Winter	Winter	12	4*
15	Gran Paradiso	April	Summer	Adult	15.5
16	Gran Paradiso	April	Winter	10	14
17	Gran Paradiso	Winter	Summer	14	6.5*
18	Gran Paradiso	Winter	Winter	13	9*
19	Gran Paradiso	Summer	Summer	12	8.5*
21	Gran Paradiso	Winter	Winter	8	4
22	Gran Paradiso	Winter	Winter	15	5*
23	Gran Paradiso	April	Summer	12	3.5*
24	Gran Paradiso	April	Summer	12	9.5*
25	Gran Paradiso	Winter	Winter	Adult	4
26	Gran Paradiso	Winter	Winter	Adult	7

* Unreadable beginning of cementum.

variations. The relationship of HL and LL values with seasonal temperature variations implies that increases in the seasonal variation of temperature are indicated through increased differences between HL and LL bands. The importance of this correlation for understanding past populations and the effects of climate change on cementum formation cannot be stated too strongly. What this implies is that the information to be gleaned from the 'destruction' of archaeological faunal remains is more than data on seasonal site use; long-term climatic data for a discrete region might also be obtainable (Wall-Scheffler, in press). Indeed, while luminance values for *Ovis aries* are predicted by temperature values, the exact environmental variable(s) which trigger differences in luminance values in other species may well be different and complementary.

Furthermore, using luminance profiles allows for the vigorous testing of relationships between banding patterns and life history variables. The

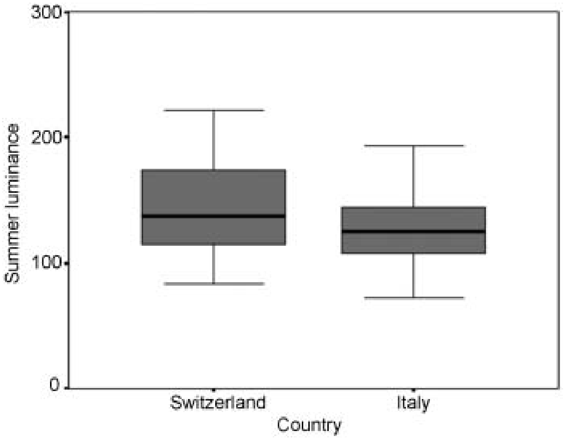

Figure 5. Variation in the luminance of HL bands of alpine ibex cementum by country. The Italian specimens ($n = 15$) from a small regional area show darker luminance and smaller variation than the Swiss specimens ($n = 9$) which come from a variety of areas. The Swiss specimens further show a broader range of luminance and overall brighter bands. The difference between the two populations is significant ($P = 0.002$).

significant correlations between whether observed and expected ages are equal and female reproductive variables provide evidence that female reproductive drain may have an effect on cementum banding patterns. While the occurrence of 'rut-lines' in male ungulates (not found in this population) has led researchers to suspect that energetic drain or lack of eating causes cementum changes (Mitchell, 1967; but see Pike-Tay, 1995), few studies prior to this have been able to detect cementum changes in reproductive females (but see Lockard, 1972).

The results from the Swiss and Italian *Capra ibex* samples demonstrate that the variation in luminance profiles can be used to understand further the range of habitats that genetically similar populations may utilise. Our findings support our hypothesis that, by quantifying cementum luminance, we should have some measure of the environmental range of populations: this capability could prove highly useful in studies of prehistoric ranging strategies and in studying the same species through time.

In addition to these findings, the most useful aspect of DCLA is its design for quantitative analysis of cementum variation between and within populations. Unlike previous research in which qualitative differences are drawn between 'obscure' and 'clear' banding patterns (Klevezal, 1996), DCLA can be used to analyse banding patterns quantitatively, regardless of the strength of seasonal indicators. Further study to uncover the mechanistic relationship between environmental fluctuation and cementum banding patterns must be accomplished in order to define exactly what makes up the variation detected by DCLA (mineralisation and/or orientation); the most likely route to do this is through SEM micrographs. In addition, the relationship between luminance and climatic variables, in addition to temperature, should be investigated in other species and populations.

Use of DCLA by archaeologists should not be undertaken without following the detailed protocol set forth by Stutz (2002) in order to recognise and consider the extent of chemical diagenesis of a sample before embarking on any large-scale analysis of ancient dental cement. While the results from the study of a deeply stratified site have shown how informative DCLA can be to archaeological studies (Wall, 2004; Wall-Scheffler, in press), the use of a polarising microscope to detect the effects of diagenetic change in the samples must occur before any analysis of luminance can proceed successfully.

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