This page left intentionally blank

Proc. Univ. Bristol Spelaeol. Soc., 1987, **18** (1), 116-128

A PRELIMINARY REPORT ON INCREMENTAL BANDING AS AN INDICATOR OF SEASONALITY IN MAMMAL TEETH FROM GOUGH'S CAVE, CHEDDAR, SOMERSET

by

MARGARET J. BEASLEY

ABSTRACT

Incremental bands in the cementum and dentine of four teeth from horse (*Equus ferus*) and one tooth from red deer (*Cervus elephas*) from the late glacial site of Gough's Cave were investigated with a view to deciding whether preservation of these tissues was good enough to permit estimation of season of death of horse and red deer at this site. This report includes some background information on the principles and methods of tooth sectioning used in this preliminary investigation, followed by the results obtained. The results are encouraging, and suggest that the method can usefully be applied to such material.

INTRODUCTION

Samples from bones of mammalian fauna associated with human activity in Gough's Cave have been dated by radiocarbon to approximately 12,000 years b.p., correlating with the Lateglacial Interstadial of NW Europe (Burleigh *et.al.*, 1985; Currant, 1986; Jacobi, 1986).

The use of tooth sectioning as an aid to investigating season of death in mammals from Gough's Cave was first suggested by R. M. Jacobi, and A. P. Currant agreed to the specimens from the British Museum (Natural History) being investigated in this way. Specimens studied are listed in TABLE I.

TABLE I—*Specimens studied*

TEETH FROM HORSE *(EQUUS FERUS)*	
Mandibular tooth, probably P_3 or P_4	BM(NH) Palaeontology Dept. M 49749
Mandibular tooth, probably P_3	BM(NH) Palaeontology Dept. M 50038
Fragment of maxilla containing P^2 and P^3	Cheddar Caves Museum No. 1.2/11
TOOTH FROM RED DEER *((CERVUS ELEPHAS)*	
Maxillary tooth, M^1	BM(NH) Palaeontology Dept. M 50047

As early as the 1920s it was realized that growth periodicity in mammals might be analysed from incremental layers of periosteal bone (Kler, 1923), and by the late 1960s annually-deposited layers had been observed in the hard tissues of many species of marine mammals and terrestrial mammals (Kleinenberg & Klevezal, 1966; Klevezal & Kleinenberg, 1967). The original applicability of the study of incremental layers was to wildlife management schemes and in conservation, but it came to be realized that similar studies could be conducted on the faunal assemblages from archaeological sites (Saxon & Higham, 1968, 1969). A useful review of some of the major findings in studies of incremental layers in cementum, including some done on archaeological specimens, is by Stallibrass (1982).

DENTAL TISSUES WITH REFERENCE TO AGE AND SEASON OF DEATH DETERMINATIONS

The dental tissues, dentine and cementum, have been found to be generally more suitable for determination of age and season of death than periosteal bone which exhibits poor correspondence with age in some mammals, notably ungulates (Klebanova & Klevezal, 1966; Klevezal & Kleinenberg, op.cit.).

Dentine is a calcified tissue which forms the bulk of a tooth. The pulp in the interior of the tooth is always decreasing in volume and is gradually replaced by secondary dentine. Thus the volume of the pulp cavity puts a finite limit on the amount of secondary dentine that can be laid down. As a rule, incremental layers in the dentine of ungulates give an indication of a minimum probable age for the individual (Klevezal, pers. comm.; & personal observation) and the nature of the final band may be useful in determining the season of death.

Cementum is a bone-like calcified tissue which surrounds the dentine of the root of the tooth. In the high-crowned (hypsodont) teeth of certain ungulates the enamel of the crown is also surrounded by cementum. It should be noted that owing to the absence of detailed studies of the oral histology of the horse and red deer, some of what follows is based on extrapolation from other species. The tooth is attached to the surrounding bone by the fibres of the periodontal ligament which enter the cementum as Sharpey's fibres. Thus, cementum, as a functional component of both the tooth and the periodontium, supports the developing tooth during the process of eruption and after it has erupted into the mouth. It is thought that when the tooth has erupted and is in wear, any cementum of the root (radicular cementum) or of the crown (coronal cementum) which is below the bottom of the gingival sulcus retains its connection with the periodontal ligament and responds to minute changes in the position of the tooth so that correct occlusion is maintained. In the teeth of red deer only radicular cementum is involved, for cementum does not cover the crown. The crowns of the extremely hypsodont teeth of horse continue to grow for some considerable time, and migrate towards the occlusal plane in response to wear so that the correct relationship between the biting surfaces of the teeth can be maintained. At this stage the anatomical crown of the tooth fulfils the functions of both crown and roots, and it is likely that apposition of coronal cementum continues for as long as it surrounds a part of the crown below the gingival sulcus (or crevice). Root development is initiated relatively late in the life of the horse tooth. The timing of the development of roots is quoted variously as occurring between the ages of 2 and 7.8 years (Levine, 1982, appendix 1; after Barone 1954, Cornevin & Lesbre 1894, Axe 1905) or from the age of 5 years (Huidekoper (1891), after Girard) or between the ages of 5 and 12–14 (Sisson & Grosman, 1953). As indicated above, during root development, and after roots are fully formed, apposition of radicular cementum ensures continued attachment to the alveolar bone via the fibres of the periodontal ligament. It would appear, therefore, that radicular cementum of red deer and of horse, and coronal cementum below the gingival sulcus of horse may reasonably be expected to be suitable for season-of-death determination. The coronal cementum behind the free gingival margin and that visible above the gums is, however, no longer active and is unsuitable as a recording structure of age and season of death. Since it is less subject to spatial constraint, cementum is likely to exhibit more accurate correlation with age than dentine, but more detailed developmental data than is presently available for the species under consideration will be needed before accurate determinations can be achieved.

The cementum of teeth from archaeological sites may have suffered mechanical and/or chemical damage while buried. Thus in some cases, particularly where the cementum has been abraded or is very friable, the dentine from within the body of the tooth, may be in better condition. It is, therefore, advisable to study both tissues from each archaeological specimen.

INCREMENTAL BANDING

The terminology used in connection with studies of incremental banding can be confusing. The causes of the confusion are twofold. Firstly the words *layer, band* and *line* can be interchangeable in colloquial English and this causes problems when they are used to refer to specific zones of cementum or dentine. Secondly, zones of cementum or dentine have been referred to as *light* or *dark* in studies of seasonality but the same zone may look either light or dark depending on both the method of preparation and the type of microscopy used (see Table II). The terminology used here follows Klevezal and Kleinenberg (op.cit.) in that the word *layer* refers to the zone of cementum deposited in one year and the word *band* refers to the seasonal zones within the annual layer. In continental and temperate climates the annual layer typically comprises a broad band which appears opaque in thin ground sections viewed by transmitted light microscopy and a narrower band which is more translucent. As a general rule the opaque band is laid down in summer while the translucent band is formed in winter. Nevertheless the precise timing of the deposition of the seasonal bands is not known for all species of mammals and some studies indicate that it may vary somewhat within a single species (Grue & Jensen, 1979).

Table II—*The optical characteristics of cementum and dentine (adapted from Klevezal & Kleinenberg, 1967)*

Band of annual layer	*Transmitted light*		*Reflected light*	*Season*
	untreated section	*stained section*	*untreated ground section*	
Translucent	light	dark	dark	winter
Opaque	dark	light	light	summer

Within the seasonal bands of the annual layer of both these dental tissues supplementary *lines* and minor laminations can sometimes be observed.

METHODS OF SECTION PREPARATION AND STUDY

The standard histological techniques of section preparation used for modern teeth involve demineralization (decalcification) in either a dilute acid or a chelating agent, such as EDTA (ethylene diamene tetra-acetic acid). Demineralized teeth are then embedded in wax or frozen, sectioned on a microtome and stained. The sections are examined using transmitted light microscopy.

In an investigation of seasonality of reindeer at the French Upper Palaeolithic site of Abri Pataud, Speiss (1979) subjected 171 teeth to histological methods but obtained successful results on only a small percentage of them.

He concluded that 'Tooth sectioning by decalcification was not a great success, owing to the low collagen content and poor preservation of the protein structure of the teeth' (Speiss, op. cit. 188). More recently, Coy *et al.* (1982) described the use of decalcification followed by sectioning with a freeze microtome and staining, upon a collection of cattle teeth from an urban Anglo-Saxon site. They reported acceptable sections from 37 of 87 teeth. Saxon and Higham (op. cit.) used a simple petrological method for the thin sectioning of sheep molars from an Iron Age Site. They were able to show the dentine-cementum junction, and the presence of banding within the cementum.

In my experience incremental layers can be seen best in the cementum and dentine of archaeological tooth specimens when petrological, rather than histological techniques are used. The use of resin to support teeth during sectioning has been successfully applied to archaeological specimens of white tailed deer (*Odocoileus virginianus*) (Kay, 1974) and of sika deer (*Cervus nippon*) (Koike & Ohtaishi, 1985). A minimally-destructive method which combines the use of dental impression compound with an adaptation of the method used by Kay (op. cit.) has been used to obtain readable intact sections from a sample of 40 neolithic cattle teeth from the Stepleton causewayed enclosure in the Hambledon Hill complex (Beasley, 1984), on cattle teeth from Grimes Graves Bronze Age midden (Beasley, Brown & Legge, in progress) and on horse teeth from Perigordian levels at the French Palaeolithic site of Solutré (Beasley & Olsen, in progress). I have found that when teeth of horses and cattle have been bisected by diamond saw incremental bands can be seen in both the cementum and in the dentine without the necessity for further treatment but that study is easier after the bisected blocks of tooth have been ground and polished using fine wet-and-dry paper and water, followed by the use of a slurry of fine abrasive powder and water on a piece of plate glass. However, it is useful to examine the surface of the ground block of a tooth using reflected light and an intact thin section from the same tooth using both reflected and transmitted light because the translucent band of the annual layer becomes visible on ground sections slightly later in the season of its formation than on thin sections and may therefore pass unobserved on thick blocks until the following opaque band has started to form. (Klevezal, pers. comm.).

HORSE TEETH FROM GOUGH'S CAVE

Outlined below is the method of preparation which was used for two horse teeth (BM(NH) M 49749 and BM(NH) M 50038) from Gough's Cave:

1. The teeth were embedded in dental impression compound, but the upper part of the crown of each tooth was left exposed.
2. Using a water-cooled, rotary diamond-edged saw a transverse cut was made through the dental impression compound block. The transverse cut surfaces were examined by reflected (incident) light microscopy.
3. The section of the block enclosing the roots and the lower part of the crown was then bisected with the saw in bucco-lingual direction.
4. Dental impression compound was removed from one of these blocks which was then embedded in clear resin using an adaptation of the method of Kay (op. cit.).
5. Using the diamond saw, transverse and longitudinal thin sections (0.3–0.25 mm) were cut from the resin block.

6. The cut surfaces of the thick blocks of tooth were smoothed by grinding and polishing and re-examined by reflected light microscopy. The thin sections were examined under the microscope using transmitted light, polarized light and reflected light. Magnifications of between 10× and 40× were used to count the bands. At a magnification of 40× and above cementocyte lacunae and dentinal tubules were visible, particularly when the polarizer was used. These features are a useful aid to identification of the dentine-cementum junction.

The use of this method permits observation of a number of sections, both transverse and longitudinal, from each tooth, yet the method is minimally destructive as most of the tooth remains; much of the crown is intact, and the thin sections are cut from the centre of the tooth in such a way that one half of the embedded root and a sizeable piece of the other are retained.

The roots of two teeth (P^2 and P^3) in a fragment of maxilla from Cheddar Caves Museum (1.2/11) were broken, so, rather than attempting to extract the teeth or cut through both tooth and bone, the broken surfaces were flattened using the disc attachment on a dental drill and polished with fine wet-and-dry paper. This procedure gave in effect, transverse sections of the roots of each tooth and a tangental section of root and the lower part of the crown of P^3. Figs. 1 and 2 show specimen 1.2/11 before and after receiving this treatment. Note the minimal amount of alteration to the specimen. The sections were examined by reflected light microscopy at magnifications of between 10× and 40×.

The state of preservation of the horse teeth was good. All were in full wear and had roots. Crown heights were measured according to the system described by Levine (1982). Table III lists crown height and mesiodistal diameter for each of these teeth, together with its age estimated to the nearest year using Levine's curve adjusted with the fossil data (Levine, op. cit.) and details of incremental layers observed. The timing of the development of the roots of the permanent cheek teeth of horse is such that incremental layers in the cementum surrounding them must indicate a minimum age only, but, as indicated above, insufficient study has been made of dental development in modern equids for us to use layers for more accurate determination of age. Were more precise data available on the timing of the development and completion of roots of the teeth of horse, analagous to that obtained from radiographic examination of modern cattle (Brown, 1959, Brown *et al.* 1960), it would be feasible to count annual increments of radicular cementum and calculate the age in years of the horse by adding on the relevant age according to the developmental data. On the basis of the data cited above (page 117) concerning root development, an age of 5 years has been added to the cementum layer count to arrive at a provisional estimation of age for the Gough's teeth. It is reasonable to suppose that coronal cementum remains functional so long as it is below the gingival sulcus and might therefore give a more reliable indication of age than the cementum surrounding the later-formed roots, but it would be necessary to section a large sample of modern specimens to be sure of this. Interpretation of seasonality is only slightly less problematical, due to lack of modern comparative studies. Klevezal observed layers in sections of 9 incisors and 1 molar from *Equus hemionus* (Klevezal & Kleinenberg, op. cit.); Grue and Jensen (op. cit.) listed horse (*Equus caballus*) as a species of which fewer than 10 teeth had been sectioned; and I have found layers in a sectioned premolar from a 30-year-old Shetland pony killed in July 1986. More than 20 annual layers of cementum could be seen and the final band on both radicular and coronal cementum was opaque. On the basis of this one can suggest that the opaque band of cementum in horse teeth is formed in summer but obviously further study of modern specimens is required before this can be more than a working hypothesis. Interpretations of seasonality on the Gough's horse teeth are, therefore, provisional only. 'Summer' is used in the broadest possible sense, i.e. to mean 'not winter'.

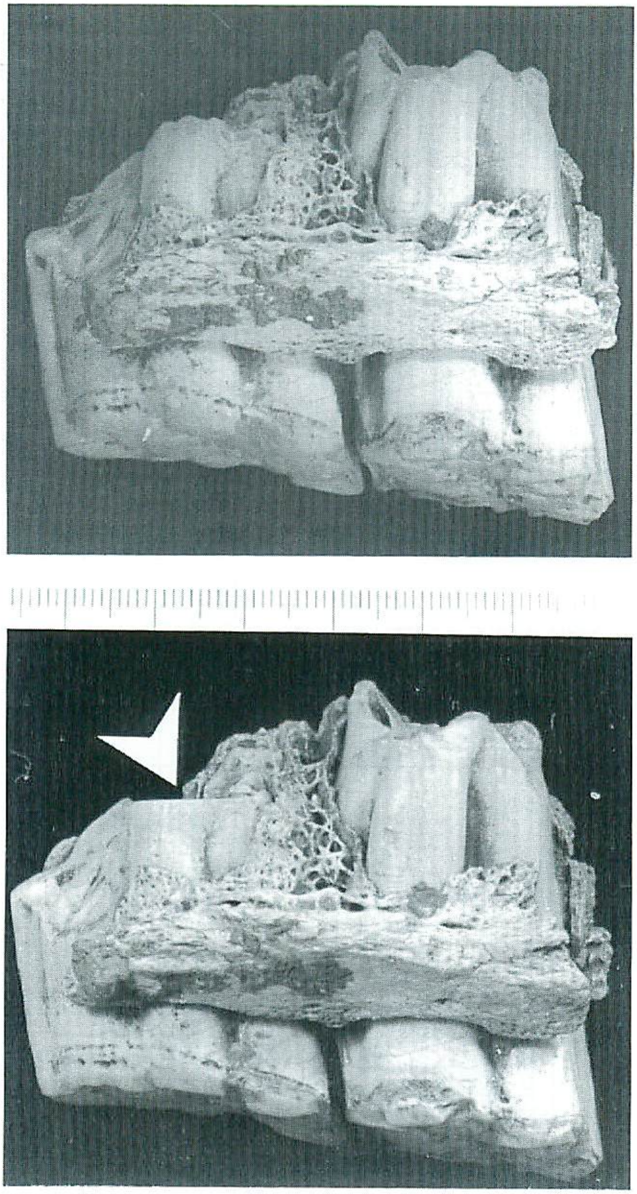

FIG. 1—FRAGMENT OF MAXILLA OF *EQUUS FERUS* CONTAINING TWO TEETH, P^2 AND P^3, FROM CHEDDAR CAVES MUSEUM, 1.2/11. THE MAXILLARY FRAGMENT IS SEEN BEFORE (ABOVE) AND AFTER (BELOW) SURFACES WERE FLATTENED TO PERMIT OBSERVATION OF INCREMENTAL BANDING. SCALE IN CM

TABLE III—*Mammal teeth from Gough's Cave, Cheddar, Somerset*

AGE DETERMINATION FROM CROWN HEIGHT (CH)								*AGE AND SEASON OF DEATH FROM CEMENTUM BANDING*				
				Mesio-distal diameter (0.1 mm)							*Readability*[6]	
Number	*Identification & Condition*		*CH* mm	*Gough's*	*Fossil Mean*	*New Forest Mean*	*Age*[1]	*Number of translucent bands in cementum and details of banding*[4]	*Age*[5]	*Character & 'season' of final band*	*Age*	*Season*
BM(NH) 49749 (from Parry's Level 18)	*Equus ferus* Fairly good condition. Posterior root present & completely formed. Anterior root broken off.	P_3 *or* P_4	41	270	— / 293	—[2] / 241	8 / 10	Up to 4 in roots H/(OT) OT OT OT O 4 or 5 more in the molar pad.	8+	Opaque broad 'summer'	3–	4
BM(NH) 50038 (from Parry's Level 10)	*Equus ferus* Fairly good condition. Roots present but broken.	P_3	56	274	—	—[2]	7	2 in roots H/OT OT O	7	Opaque broad 'summer'	3	4
Cheddar Caves Museum 1.2/11	*Equus ferus* 2 teeth in fragment of maxilla. Fairly good condition but roots broken.	P^2	38	366	374	325	Between 9 & 10	2 near base of crown and in roots. OT OT O	7	Opaque narrow early 'summer'	3	4
		P^3	50	285	—	—[2]	Between 9 & 10					
BM(NH) 50047	*Cervus elephas* Fairly good condition but buccal surface has several vertical fractures.	M^1	—	—	—	—	—[3]	2 along much of longitudinal section and on transverse section of root tip. H/OT OT O	2	Opaque band varying in width but mostly narrow 'summer' (possibly 'spring')	4	4

FIG. 2—FLATTENED ROOT SURFACE OF P^2 FROM 1.2/11 SEEN FROM ABOVE AT THE POSITION ARROWED IN FIG. 1

Notes for Table III opposite

1: Using Levine's curves adjusted with fossil data.
2: Measurements not available.
3: Age not estimated by crown height.
4: H = Hyaline layer between the granular layer of Tomes and the first-formed cementum; O = opaque; T = transparent.
5: Layer count + 5 to allow for timing of root formation (references cited in text).
6: Using the system of Klevezal, Grue & Mina (1981):
5 = best; 0 = worst. Readability evaluation is of the clarity of the banding. Note reservations on interpretation stated in text.

Results

In the two horse teeth (M 49749 and M 50038 (Fig. 3) sectioned using the method described above, the last-formed band in both coronal and radicular cementum of each tooth was opaque, considerably broader than the preceding transparent band and of approximately the same width as the previous opaque band. The dentine also ended on an opaque band on each tooth. This suggests that they were killed in summer.

The polished surfaces from 1.2/11 were examined using reflected light. Two annual layers of cementum were visible and on each surface the final band of cementum was light and opaque in appearance, but narrower than the previous opaque band, indicating that it was still under formation. This again suggests summer as the season of death but this horse may have been killed earlier in the season than M 49749 and M 50038.

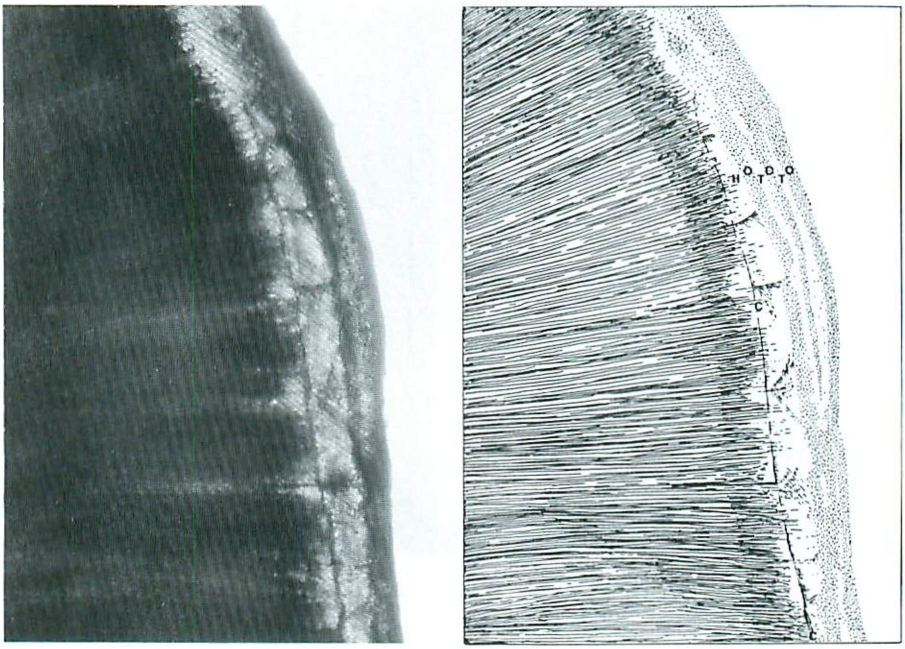

Fig. 3—Photomicrograph of transverse section of tooth of *Equus ferus*, P_3, BM(NH) 50038. (0) denotes opaque bands of cementum thought to represent summer; (T) denotes transparent bands thought to represent winter; and (H) denotes the hyaline layer at the dentine-cementum junction. C is a crack. Thickness of cementum = 0.17mm

RED DEER TOOTH FROM GOUGH'S CAVE

BM(NH) M 50047, 1st maxillary molar, in wear, with exposed dentine on all cusps but not quite at the stage where the infundibula would be islands of enamel surrounded by dentine i.e. almost , using a modification of Payne's diagrams for sheep and goat teeth (Payne, 1973; Deniz & Payne, 1982).

Natural fractures in the tooth enabled a portion of crown and root suitable for study to be prised from it, (FIG. 4). The edge of the fragment was smoothed down with fine wet-and-dry paper. The cementum of the root was then examined by reflected light and appeared to end on a light, opaque

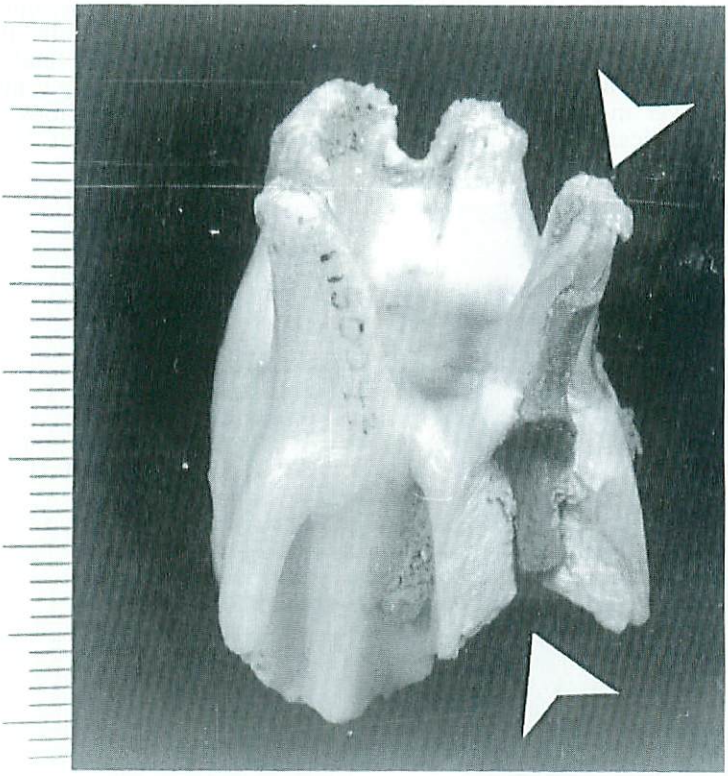

FIG. 4—FIRST MAXILLARY MOLAR OF *CERVUS ELEPHAS*, BM(NH) 50047. THE ARROWS POINT TO THE AREA WHERE NATURAL FRACTURES IN THE TOOTH FACILITATED THE REMOVAL OF THE FRAGMENT WHICH WAS SECTIONED. SCALE IN CM

band. The fragment was next embedded in clear resin and a thin section (0.25 mm) was cut, using the diamond saw. This was examined at magnifications from $10\times$ to $40\times$, under the microscope, using reflected, transmitted and polarized light. The use of polarized light on the thin section proved helpful in identifying the dentine-cementum junction because the hyaline layer adjacent to the granular layer of Tomes appeared blue in contrast to the brown and beige colouration of the bands in the cementum. The secondary dentine appeared opaque and banding was not discernable within

it. Banding in the cementum was clearly visible and is interpreted as follows:—
The first band of cementum is opaque, but only clearly differentiated from the layer of Tomes and the hyaline layer when observed by polarized light. The first band visible in other types of light is translucent. Although data on the precise timing of root development and completion in maxillary teeth are lacking one can suggest that this translucent cementum may represent the deer's first winter. This first winter band is followed by a broad opaque summer band. Only one further translucent (winter) band is present in the cementum. Opaque summer bands of cementum are, when fully formed, characteristically broader than the translucent winter bands. This final opaque band of cementum is, in some parts, narrower than the preceding translucent band and over most of its length it is narrower than the previous opaque band. This indicates that it was still in the process of formation at the season

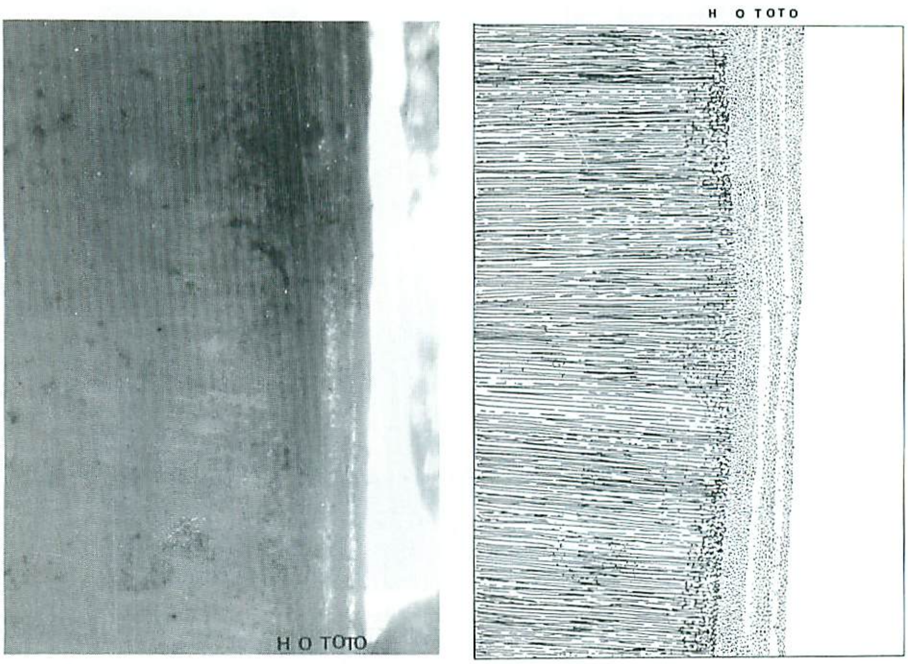

FIG. 5—PHOTOMICROGRAPH OF LONGITUDINAL SECTION OF TOOTH OF *CERVUS ELEPHAS*, M^1. (O), (T) AND (H) AS FOR FIG. 3. THICKNESS OF CEMENTUM = 0.09 MM

of death. Thus it is possible to suggest that this tooth came from a red deer which may have been killed in the spring or summer of its third year of life, i.e. at an age of 2+ (FIG. 5 & TABLE III). A note of caution is necessary because the exact timing of seasonal layers in modern populations of *Cervus elephas* is not fully understood. Although one can refer to summer and winter bands of the annual layer, studies in different countries (Mitchell, 1967; Almasan & Rieck, 1970; Smith, 1974) have shown that the timing of the bands is not always exactly the same, with winter band formation occurring later in Norway and Denmark than in Scotland (Grue & Jensen, op. cit.). Clearly we do not know the precise timing of seasonal bands during the Lateglacial Interstadial in southern Britain.

CONCLUSIONS

A recent study of immature red deer jaws (2 maxillae and 3 mandibles, representing 4 individuals) from Gough's Cave provides evidence which indicates that the cave was probably used in winter (Parkin, Rowley-Conwy & Sergeantson, 1986). On the other hand, four horse teeth, from three mature individuals, and one tooth from a mature red deer presented in this report all show a final opaque band, which is most likely to represent a summer kill. In my opinion, it would be foolhardy to pinpoint the time of death of either the horses or the deer represented by the sectioned teeth to a particular month of the year, although the general conclusion from the tooth sectioning experiments points to a summer occupation. Bearing in mind the indications for winter occupation found by Parkin *et al.*, a tentative conclusion would support the use of the site in both winter and summer, either continually or in a series of intermittment visits.

ACKNOWLEDGEMENTS

This work was carried out as part of a research investigation into cementum banding supported by the Science-based Archaeology Committee of the Science and Engineering Research Council. The grant is held by W. A. B. Brown, Dept. of Anatomy, King's College, London, and A. J. Legge, Department of Extra-Mural Studies, University of London.

Grateful thanks are extended to Roger Jacobi and Andrew Currant and to all colleagues who have helped in various ways with this project. I particularly thank Galina Klevezal for the invaluable training she gave me at N. K. Koltzov's Institute of Developmental Biology, USSR Academy of Science, Moscow, and the Central Research Fund of the University of London for funding my visit there; also Barry Brown, Tony Legge and Dale Serjeantson for helpful comments, and Pauline Howley and Peter Brinck for help with technical problems.

REFERENCES

ALMASAN, H. A. & RIECK, 1970. Untersuchungen der Zahnstruktur zur Altersbestimmung beim Rotwild (*Cervus elephas*). *Z. Jagdwiss.* **(16)**, 49–55.

AXE, J. W. 1905. *The horse, its treatment in health and disease*, Vol. VIII. Gresham Publishing Co., London.

BARONE, R. 1954. *Appareil digestif. Anatomie des equidées domestiques. Tome 2. Splanchnologie et angeiologie,* ed. TAGARD, R. & BARONE, R. Laboratoire d'Anatomie Ecole Nationale Veterinaire, Lyon.

BEASLEY, M. J. 1984. An investigation of incremental banding in cattle teeth from the neolothic causewayed camp of Hambledon Hill/Stepleton with a view to determining seasonality and ceremonial activity. Unpublished M.A. dissertation, University of London.

BROWN, W. A. B. 1959. Tooth development in cattle. M.Sc. Thesis, University of Illinois, Chicago.

BROWN, W. A. B., CHRISTOFFERSON, P. W., MASSLER, M. & WEISS, M. B. 1960. Postnatal tooth development in cattle. *American Journal of Veterinary Research*, **21**, (80), 7–34.

BURLEIGH, R., JACOBI, E. B. & JACOBI, R. M. 1985. Early human resettlement of the British Isles following the last glacial maximum: new evidence from Gough's Cave, Cheddar. *Quaternary Newsletter* **45**, 1–6.

CORNEVIN, C. & LESBRE, X. 1894. *Traité de l'age des animaux domestique d'après les dents et les productions epidermiques*. Libraire J.-B. Baillière et fils, Paris.

COY, J. P., JONES, R. T. & TURNER, K. A. 1982. Absolute ageing in cattle from tooth sections and its relevance to archaeology. In *B.A.R. British Series 109, Oxford—Ageing and sexing animal bones from archaeological sites*, ed. WILSON, B, GRIGSON, C. & PAYNE, S., 127–140.

CURRANT, A. J. 1986. The Lateglacial mammal fauna of Gough's Cave, Cheddar, Somerset. *Proc. Univ. Bristol Spelaeol. Soc.* **17**, (3), 286–304.

DENIZ, E. & PAYNE, S. 1982. Eruption and wear in the mandibular dentition as a guide to ageing Turkish Angora goats. In *Ageing and sexing animal bones from archaeological sites*, ed. WILSON, B., GRIGSON, C. & PAYNE, S. 155–205.

GRUE, H. & JENSEN, B. 1979. Review of the formation of incremental lines in tooth cementum of terrestrial mammals. *Danish Review of Game Biology*, **11**, (3), 1–48.

HUIDEKOPER, R. H. 1891. *Age of the domestic animals*. F. A. Davis, Philadelphia & London (citing GIRARD, N. F. *Traité de l'age du cheval*, 3rd ed., Bechat-Jeune, Paris).

JACOBI, R. M. 1986. A.M.S. results from Cheddar Gorge—trodden and untrodden 'lifeways', in *Archaeological results from accelerator dating*, ed. GOWLETT, J. A. J. & HEDGES, R. E. M., 81–86. Oxford University committee for Archaeology.

KAY. M. 1974. Dental annuli age determination on white-tailed deer from archaeological sites. *Plains Anthropologist*, **19**, 224–227.

KLEBANOVA, E. A. & KLEVEZAL, G. A. 1966. Lamination in the periosteal zone of the tubular bones of the extremities as a criterion of age determination in mammals. *Zool. Zh.* **45**, (3), 406–412 (In Russian with English summary).

KLEINENBERG, S. E. & KLEVEZAL, G. A. 1966. Age determination in mammals by the structure of tooth cement. A translation of *Zoologicheskii Zhurnal*, **45**, (5), 717–724. British Library Lending Division Programme, R.T.S. 3725.

KLER, V. O. 1923. *Proceedings of the first all-Russian meeting of Zoologists, Anatomists and Histologists in Petrograd, 1922*. (in Russian).

KLEVEZAL, G. A., GRUE, H. & MINA, M. B. 1981. A method of readability evaluation of recording structures in age determination of mammals. *Zool. Zh.* **60**, (12), 1869–1877.

KLEVEZAL, G. A. & KLEINENBERG, S. E. 1967. *Age determination in mammals from annual layers in teeth and bones*. (In Russian. English translation by Israel Program for Scientific Translations, Jerusalem, 1969).

KOIKE, H. & OHTAISHI, N. 1985. Prehistoric hunting pressure estimated by the age composition of excavated Sika deer (Cervus nippon) using the annual layer of tooth cement. *J.Arch.Sci.* **12**, 443–456.

LEVINE, M. 1982. The use of crown height measurements and eruption-wear sequences to age horse teeth. In WILSON, W., GRIGSON, C. & PAYNE, S. *Ageing and sexing animal bones from archaeological sites*, 223–250.

MITCHELL, B. 1967. Growth layers in dental cement for determining the age of red deer (*Cervus elephas*)—*J.Animal Ecol.* **36**, 279–293.

PARKIN, R. A. ROWLEY-CONWY, P. & SERJEANTSON, D. 1986. Late Palaeolithic exploitation of horse and red deer at Gough's Cave, Cheddar, Somerset. *Proc. Univ. Bristol Spelaeol. Soc..*, **17**, (3), 311–330.

PAYNE, S. 1973. Kill-off patterns in sheep and goats: the mandibles from Asvan Kale. *Anatolian Studies*, **23**, 281–303.

SAXON, A. & HIGHAM, C. W. F. 1968. Identification and interpretation of growth rings in the secondary dental cementum of Ovis aries. *Nature, London*, **219**, 634–635.

SAXON, A. & HIGHAM, C. W. F. 1969. A new research method for economic prehistorians. *Am. Antiq.*, **34**, (3), 303–311.

SISSON, S. & GROSSMAN, J. D. 1953. *The anatomy of the domestic animals*. 4th ed. W. B. Saunders, Philadelphia.

SMITH M. C. T. 1974. *Biology and management of the wapiti (Cervus elephas nelsoni) of Fiordland, New Zealand*. New Zealand Deerstalkers Assoc. Inc. Wellington, N.Z.

SPEISS, A. 1979. *Reindeer and caribou hunters*. Academic Press, New York.

STALLIBRASS S. 1982. The use of cement layers for absolute ageing of mammalian teeth. In *Ageing and sexing animal bones from archaeological sites*, ed. WILSON, B., GRIGSON, C. & PAYNE S., 109–126.

MARGARET J. BEASLEY, Department of Anatomy and Human Biology,
King's College London, Strand, London WC2R 2LS, U.K.