

*The dentition of fallow deer (Dama dama):*

*a scoring scheme to assess age from wear of the permanent molariform teeth*

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The sequence of tooth wear was determined from skulls of fallow deer of known age. A system for scoring molariform tooth wear has been devised so that small but readily recognizable wear changes of the individual cusps may be recorded and used to assess the age of animals of unknown birth dates. The technique can be readily adapted for other ruminant species with the appropriate database.

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### Introduction

A knowledge of the age of a live or dead animal is an important aid for domestic livestock and wildlife management and can give archaeologists invaluable insights into the socio-economic and ritual activities of prehistory. In the past, ages of animals have been routinely assessed by evaluating stages of tooth eruption and tooth wear, but often the justification for these estimates has been insufficiently validated by examining samples of known age.

Brown *et al.* (1960) established a chronology of tooth eruption and tooth development from over 800 cattle (*Bovis*) of known age. They claimed the latter was a more reliable indication of age than tooth eruption. No analysis was made of tooth wear. Chapman & Chapman (1970, 1975) provided guidelines for estimating the age of fallow deer (*Dama dama* L.) from an appraisal of tooth eruption in animals of known age. However, there are limitations to using stages of eruption for determining age because there are comparatively few detectable events to observe and by two years of age when the teeth of opposing jaws are in occlusion there is nothing more to evaluate. Because of these restrictions, attempting to age animals from the amounts their teeth have worn has been an obvious line of enquiry to follow. Rieck (1973) recognized that the age of fallow deer could be estimated by the wear on the cheek teeth and be determined according to the number of 'annual zones' in the regenerative-dentine of the first incisor, but he does not demonstrate exactly how his system was used as he had no animals of known age. Grue & Jensen (1979) investigated incremental lines in cementum of many species, but examination of incisors from our known-age fallow deer specimens gave a poor correlation between estimated and actual age (H. Grue, *pers. comm.*, 1980). However, other reports on different species do not find this inconsistency between known age and the number of cementum increments or annuli. Keiss (1969) and Gilbert & Stolt (1970) make it apparent that more detailed analyses need to be made of the different ways of assessing an animal's age from its teeth. Keiss found for elk (*Cervus canadensis*) that comparing age assessed from cementum annuli with eruption-wear patterns gave only a 50% agreement between the two methods, but he gave no indication which the more reliable method was. Gilbert & Stolt (1970) made a comparison of the two ageing methods for Maine white-tailed deer (*Odocoileus virginianus*) and reported that the percentage difference between deer assigned to each of four age classes increased from 6-3% for yearlings to 100% for six and a half-year-old and older animals. Precise age was not known, 'correct age' being assumed when there was agreement between the cementum annuli count and tooth-wear pattern.

Chapman & Chapman (1975) briefly described the wear appearance up to the seventh year of the teeth of fallow deer from one population and gave an outline guide to assessing age. Ueckermann & Hansen (1968), Rieck (1973) and Szabolics (1975) published photographs of molariform teeth *in situ* in fallow deer up to 14, 12 and 20 years, respectively. However, no method of scoring the wear patterns has been described for this species. Recording schemes have been very well established and illustrated by Payne (1973) for goats (*Capra*) and by Grant (1982) for cattle (*Bovis*). But Payne's original work was based on animals of imprecisely known ages, though in a later publication this was largely remedied (Deniz & Payne, 1982). Furthermore, some of the wear-state symbols represent a level of wear that may prevail for very many months and even years. Likewise, Grant's illustrations, though based on a logical rank ordering from the appearance of worn teeth, are not on data from animals of known age and there is no way of evaluating how accurately the wear symbols represent any particular age range. Levitan (1982) has indicated how borderline patterns in Payne's technique may be incorrectly observed, causing errors during the recording of wear patterns. He also found ambiguities in Grant's wear stages. Hamilton (1982),

examining a sample of Iron Age sheep mandibles, found that there was a degree of age overlap using both Payne's and Grant's stages, a finding that stresses the need for separate databases for all species.

Carter (1975) assessed age of sheep (*Ovis*) from crown height measurements and believed that with a jaw containing three molar teeth he was able to age the animal to a month with 80% confidence, but he had no means of making an independent check. Robinette *et al.* (1957) examined 91 mule deer (*Odocoileus hemionus hemionus*) believing that wear of the molars offered the best means of ageing mule deer older than two years. They devised a quantitative approach measuring surface wear and crown height to form a ratio, but found that there was obvious age overlap in molar ratio values for animals 2-4 years old. Lowe (1967) investigated four different techniques for assessing age of red deer (*Cervus elaphus*) from a selected series of imprecisely known-aged mandibles: correlating jaw and tooth measurements, examining secondary dentine depositions within the first incisor crowns, analysing cementum lines and lastly assessing tooth replacement, eruption and wear, which he found the most reliable.

It is apparent that these different approaches are not precise enough to establish objective criteria for assessing age from tooth wear. To achieve that, there must be easily recognizable and consistent features altering with wear, which are easy to see, simple to record and for which the range of variability for a particular age can be established, and so animals of a precisely known age are an essential prerequisite.

Separate assessments need to be made for each species because there are minor differences in tooth wear patterns and rates of wear, as is already apparent from our study of red deer (In prep.). Also, there are minor morphological differences; the teeth of Cervidae, though they have the same cuspal and infundibulum arrangement for the molars, differ in certain important aspects from those of Caprinae and Bovidae. The crown is not as tall and is clearly demarcated from the root.

These assessments of age are possible because tooth wear of the cheek teeth takes place in a strictly sequential manner. This follows the order of eruption which is normally an invariable sequence for the molars and the fourth premolar, but with some variation in the sequence for the second and third premolar, (Chapman & Chapman, 1970, 1975). It is assumed, and not unreasonably, that the more worn the teeth of the animals, the older the animals are likely to be;

but the extent to which the rate of wear may vary for individual animals of a particular species living under comparable conditions is not known. It must be apparent that the speed of attrition must vary according to the season and the nature of the herbage, including any soil contamination, which they consume, and the conditions in which it is found, as Ludwig, Healey & Cutress (1966) confirm. For incisor teeth in sheep they found that 70% of the wear took place between July and October when the largest amounts of soil were ingested. Deniz & Payne (1982) also noted different rates of tooth wear from their analyses of three herds of goats which were maintained on different levels of management and grazing. They also observed in their sample that the teeth of males erupted sooner and wore more rapidly than the females. It is therefore essential to study animals of known age and, if the sample is large enough, males separately from females so the extent of the variation in wear patterns with age can be correctly appraised; but it is equally important that the animals to be studied should have had the same diet, though assessments of different wear patterns made by Chaplin & White (1969) found only minimal differences in matched age groups between deer from Richmond Park and wild deer in Essex. A final refinement would be to study the same animals over a number of years.

For this analysis of wear patterns in fallow deer teeth, to enable comparisons to be made, attempts were made to use existing tooth wear recording systems devised for sheep and goats by

Payne (1973) and cattle by Grant (1982), but they proved to be unsuitable. In this study, very careful selection has been made of readily observable progressive changes to the crown's morphological features and particularly the detailed changes that occur on the individual cusps and of the subsequent events that occur in the life history of a tooth. A system for scoring small but readily recognizable wear changes has been devised to record exactly how extensive the changes are for different age groups. In this way it will be possible to predict the likely age at death of an animal from a healthy and isolated population of wild animals'.

### Materials and methods

#### *Sample*

The sample consisted of 53 fallow deer, 34 males and 19 females of known age from 4 months to 91 months (Table I). Because of the uneven numbers of male and female animals in the different age groups and small numbers in the older groups, it was decided to analyse the teeth of both sexes together. The animals were assigned to groups arranged in yearly increments according to their age. The spread of ages within a group is necessarily restricted by the fact that all the fawns are born within a short 4-week period and are mostly culled around the same time each year. As part of the normal culling programme, 40 deer of the sample were shot within the appropriate legal seasons (males: mostly during August and September and females: mostly during November, December and January). Thirteen deer were the victims of a variety of accidents throughout the year. One mandible was too severely damaged to be analysed.

All the animals were pastured in Richmond Park, Surrey between the years 1965 and 1975. For 11 years during the month of June, fawns were ear-tagged with plastic jumbo tags (Dalton Supplies Ltd., Nettlebed, Oxon. RG9 5AB) within a few days of birth. The tag in the left ear was numbered and colour coded for the year. The male and female halves of the right ear tag gave a colour combination specific to an individual animal within a year group. Upon the death of marked animals, the skulls and mandibles were prepared by bleaching with sodium borate tetrahydrate [NaBo<sub>3</sub>4H<sub>2</sub>O] (Chapman & Chapman, 1969).

#### *Teeth examined*

Only the permanent mandibular molariform teeth have been examined in depth for this study (Fig. 1); but the same principles for analysis and interpretation apply equally to the teeth of the maxilla. The permanent incisors and canines were excluded from the analysis because there are very few qualitative changes to observe and record once the teeth come into wear. The deciduous teeth have also been excluded from the tooth wear analysis because they are all lost by 1½ years. The wear stages have been determined from the time of eruption of the first molar which erupts and comes into wear around 4-5 months of age.

TABLE I *Fallow deer (Damn dama) sample: numbers, age and sex*

Age (months)	Males	Females	Totals
4-11	5	3	8
18-22	2	8	10
26-35	17	2	19
38-43	5	3	8
48-59	4	1	5
67-91	1	2	3
	<b>34</b>	<b>19</b>	<b>53</b>



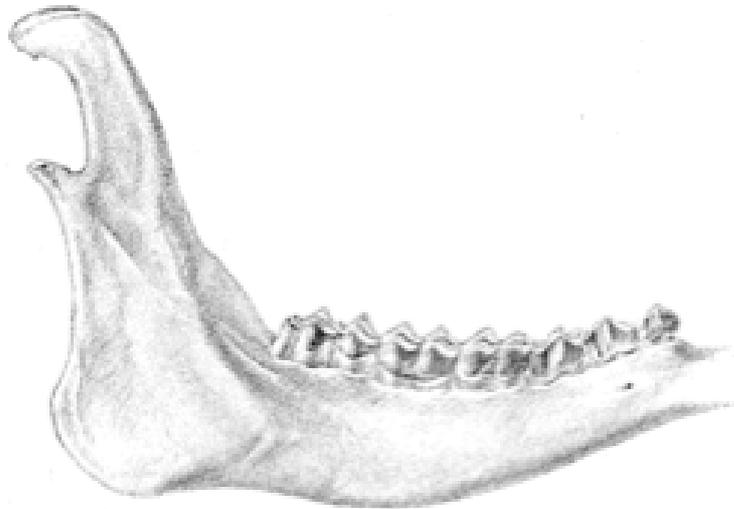


FIG. 1. The right side of the mandible of fallow deer (*Dama dama*) showing the premolars and molars ( $\times 5/6$ ).

FIG. 1. The right side of the mandible of fallow deer (*Dama dama*) showing the premolars and molars (x 5/6).

*Dentitions* Fallow deer have a deciduous and a permanent dentition.

*Deciduous* 0/3.0/1.3/3. *Permanent* 0/3.0/1.3/3.3/3.

The molars are *selenodont* with crescent-shaped cusps (Figs 1 & 4). The first and second *mandibular* molars are composed of a crown made up of mesial and distal pairs of cusps and a mesial and distal root. The third molar has an additional distal cusp and a root which is fused to the main distal root (Fig. 2). The space that separates the paired mesial or distal cusps is the *infundibulum*. The cusps are named along the principles defined by *Osborn* (1907), discussed in depth by *Peyer* (1968) and illustrated for 'teeth with *infoldings* and *infundibulums*' by *Hillson* (1986). Therefore, on the lingual side the mesial cusp is the *paraconid* and the distal cusp the *metaconid*; these are flattened in appearance each with a centrally placed vertically rounded ridge and pointed cusp tip; the mesial cusp appears to overlap the distal cusp; on the *buccal* or cheek side, the mesial cusp is the *protoconid* and the distal cusp is the *hypoconid*; both are rounded and arise from pillar-like structures. It should be noted that the evolutionary origin of the most distal cusp of the third mandibular molar does not appear to have been precisely defined. Though we are not aware of any direct evidence, we have decided to refer to it for convenience, as the *hypoconulid*, on the basis that this is the cusp next to the hypoconid in the *talonid* which forms the distal part of the molar in the *Osborn* scheme (Fig. 2). The permanent premolars are *lophodont* with well-marked ridges (Fig. 4). As in all *Cervidae*, the first permanent premolars are absent, the most anterior ones therefore being the second premolars (*Riney*, 1951). The premolars have a mesial and a distal root.

Additional or absent teeth have been noted; *Whitehead* (1972) reported the presence of an upper canine in a three-year-old buck and the incidence of the presence of maxillary canine and the absence of *ofincisiform* teeth has been described by *Chapman & Chapman* (1969, 1973).

#### *Histology and wear patterns*

To interpret the characteristic tooth wear patterns, it is necessary to understand the simple histology of the tooth and the way the several tissues of which it is composed are formed and related to each other (Figs 3a, b).

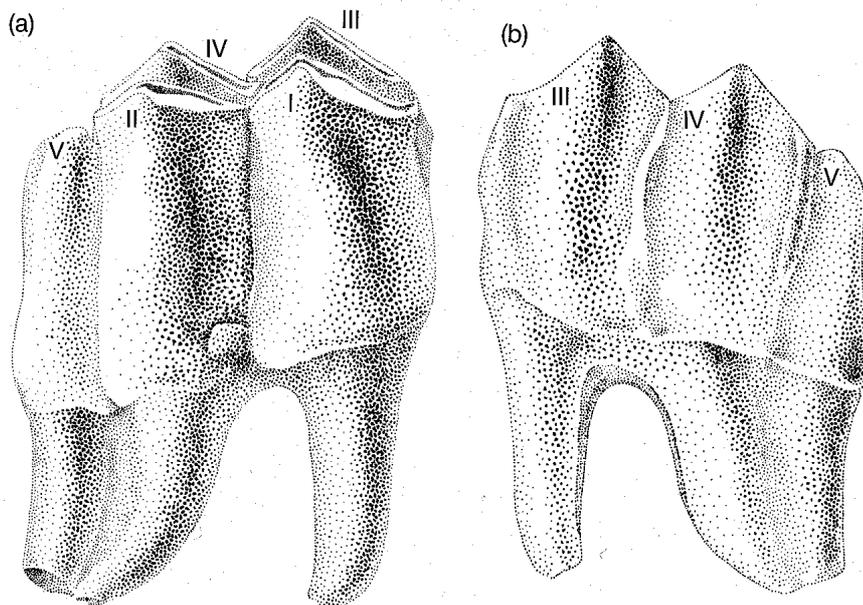


FIG. 2. The right **mandibular** third molar (x 4-5). (a) **Buccal** aspect showing the pillar-like appearance of I, the mesial **protoconid**; II, the **hypoconid**; and V, the distal **hypoconulid** cusps of the crown. The two distal roots are fused, (b) Lingual aspect with III, the flattened mesial **paraconid**; IV, the **metaconid**; and V, the distal hypoconulid cusps. As the tooth is worn the vertical grooved features are lost. The first and second molars are very similar, but without **V** the distal hypoconulid cusp and fused distal root.

A tooth is composed of a core of soft tissue, the pulp, which is completely surrounded by dentine. The dentine of the crown is covered by enamel and of the root by **cementum**. The enamel of the **Ruminantia** is usually covered by a thin layer of cementum, but this is not readily observable in fallow deer. Dentine and cementum which are mineralized tissues are formed slowly throughout life by **odontoblasts** and **cementoblasts**, respectively. Enamel, one of the hardest mineralized tissues known, is completely formed by **ameloblasts** before root formation begins and afterwards, because the enamel forming cells are lost, no more enamel can be added. As the dentine, known as secondary dentine, is laid down sequentially and **incrementally** in layers, the pulp chamber is slowly filled in from the tip region of the cusps towards the root apices. In this way a barrier is formed and the pulp tissues are protected from direct contact with the environment of the oral cavity; and incidentally this dentine gives teeth with the contrasting appearance of enamel the characteristic tooth wear patterns (Fig. 3b).

#### *Eruption*

Chapman & Chapman (1970) have given the age and order for the eruption of the mandibular permanent teeth of fallow deer as follows: **M** 1,11, M2,12,13, **C**, M3, P4, P3 or P2. It is this order which brings teeth into sequential wear and enables the wear patterns to be scored and used as an indication of age. In dried skeletal material a tooth was considered to have erupted if any part of it was visible above the bone. In a living animal, because of the covering epithelial tissues of the oral cavity, there would be an apparent slight delay in the time a tooth became visible in the mouth and counted as erupted, but this would not alter the sequence of eruption. Table II gives the ages when the teeth in this sample come into wear. These ages are slightly later than the times given for eruption by Chapman & Chapman (1970) because there is a short interval between eruption of the tooth into the mouth and the time it comes into wear against the teeth in the opposing jaw.

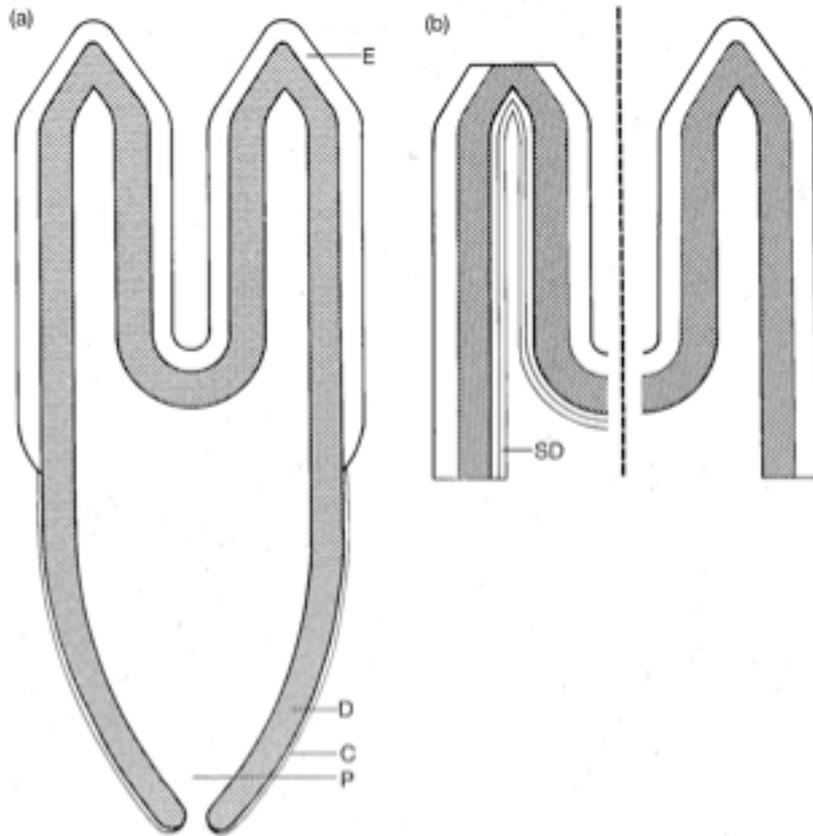


FIG. 3. (a) A schematized representation of the crown and root of a tooth to show the relationship of the enamel, E; dentine, D; cementum, C and pulp, P to each other. The enamel of the Ruminantia is usually covered by a thin layer of cementum, but it is not readily observable in fallow deer. (b) The sequential nature of secondary dentine SD deposition (left side) which will eventually replace most of the crown and root pulpal tissue. On the right the tooth is shown before cuspal wear.

*Wear stages* Several stages of wear for the molars may be noted:

1. For each molar in turn, shortly after it comes in contact with the tooth in the opposite jaw, the enamel on the slopes of the cusp becomes worn first and when it is worn away the underlying dentine is exposed; it is yellow in colour compared with the white enamel. The mesial cusps start to wear before the distal, its mesial slope being the first to come into wear followed soon after by the distal slope, as has taken place in the first and second molar (Fig. 4b). For the third molar, the additional distal cusp, the hypoconulid, is the last to be worn.

2. The wearing down of the cusp and the exposure of the dentine leads to the formation of secondary dentine with the slow incremental filling in of the pulp chamber. The amount of dentine that is formed by this process is identifiable by rings of well-marked stained bands or lines, the centrally located secondary deposition, the last to be formed, shows as a white spot or 'eye', to be seen in the three molars (Fig. 4d).

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TABLE II

*Fallow deer (**Dama dama**) age by which the molars and premolars are erupted and come into wear in the sample. Ages for fallow deer eruption from Chapman & Chapman (1970) are given in parentheses*

	AGE	
	(months)	(months)
Molars		
1st	5	(3-5)
2nd	18	(9-13)
3rd	26	(13-21)
Premolars		
2nd	27-43	(21-25)
3rd	26	(17-21)
4th	22	(17-21)

3. Eventually, all the enamel that surrounds the **infundibulum** is completely worn away, and the tooth's **occlusal** surface consists entirely of dentine surrounded by a thin but distinct covering of enamel. None of the animals in this sample was old enough to demonstrate this.

4. At the same time as attrition proceeds on the occlusal surfaces, wear takes place **interstitially** between neighbouring teeth and the thin enamel covering may be lost from the mesial and distal surfaces, exposing the underlying dentine which in turn becomes worn. No attempt was made to score this wear. The original boundaries of the pulp chamber remain clearly demarcated by the lines and bands of the secondary dentine.

For the **premolars** whose crowns are characterized by ridges, similar wearing away of the outer enamel and exposure of the underlying dentine takes place, but not in the same distinct sequential pattern as for the molars (Fig. 4c, d).

#### *Wear scores and how they were recorded*

**Molars** (Table IIa): To score the molar wear patterns, each slope of a tooth cusp that had only enamel worn was given a score of one (a). When the underlying dentine was exposed score of 2 was given. An **additional** score of one was given when:

1. The dentine between mesial and distal slopes showed a central white 'eye' (b), indicating the central zone of secondary dentine in the pulp.
2. The dentine was exposed to link the dentine of the lingual and **buccal** cusps (c, d, e). This could be between mesial and/or distal cusps. There were five locations where this could take place: the mesial and distal marginal ridges and the dentine between the paired mesial and distal cusps.
3. The mesial and distal cusps were worn so that there was a continuous joining line of exposed dentine between the two cusps on either the lingual or buccal aspect of the tooth (f, g).
4. The exposed dentine linking the lingual and buccal cusps and the exposed dentine linking the mesial and distal cusps were stained dark brown.

The small size and unique shape of the third cusp, the **hypoconulid**, of the third **mandibular** molars presented special problems. One point each was given for wear on the lingual or buccal sides (h, i), and an additional point when the two wear sites were joined together. A further point was given when the lingual or buccal dentine was linked with that of the **metaconid** or **hypoconid**.

THE DENTITION OF FALLOW DEER (*DAMA*)

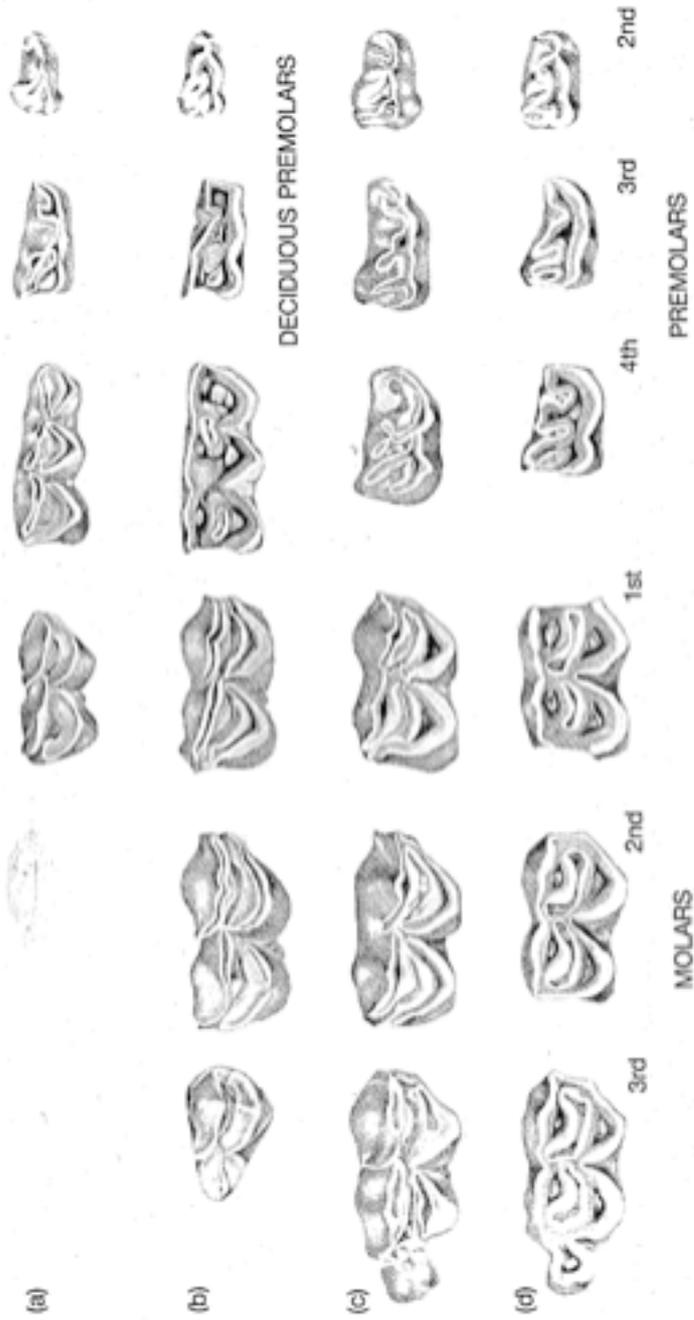
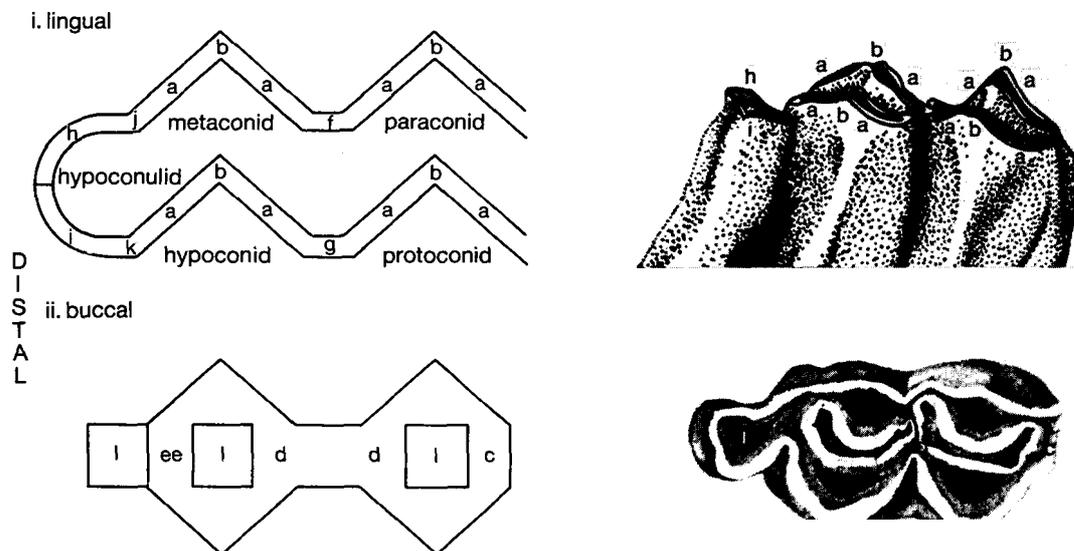




FIG. 4. Fallow deer (*Dama dama*) stages of molar and premolar wear shown for the right side of the mandible. For clarification the illustrations of the teeth have been idealized and the individual teeth separated from each other, (a) 4 months old, (DIC 103). The three deciduous and first molars are present. There is no wear on the first molar. There is wear on the deciduous premolars, but no deciduous teeth have been used to assess wear scores as these teeth are all shed by 47 months and will be replaced by the premolars (Table II). (b) 18 months old (N 25). Considerable additional wear of the deciduous premolars is apparent. The first and second molars are in wear and the third molar erupting. For the first molar the mesial and distal slopes of all four cusps are worn with the paired mesial cusps showing the first sign of an 'eye' at the tip of their cusps. The dentine of the mesial marginal ridge has been exposed, and as is frequently found has already been partially worn away by interstitial wear. For the second molar all the slopes except the distal slopes of the distal cusps are in wear. The exposed lingual and buccal dentine are not continuous with each other. There is no wear on the cusps of the third molar, (c) 26 months old (H4). The three premolars 2nd, 3rd and 4th have erupted and replaced the deciduous premolars. Their ridges all show varying degrees of wear. The first molar has worn to reveal extensive secondary dentine formation in each of its cusps. Wear of the second molar is very similar to, but less extensive than, the first molar. The mesial marginal ridge dentine is exposed and is continuous with that of the mesial slope dentine of the mesial cusps, but it has not been worn away by interstitial wear as it has in (b). The third molar shows wear on the mesial slopes of the mesial and distal cusps, (d) 75 months old (H11). All the teeth show extensive wear. In addition to the wear seen on the teeth of the younger animals, there is for the first and second molars exposed dentine on the distal marginal ridges which links that of the lingual and buccal distal cusps. Most of the heights of the infundibular are lost for the first molar.

TABLE IIa

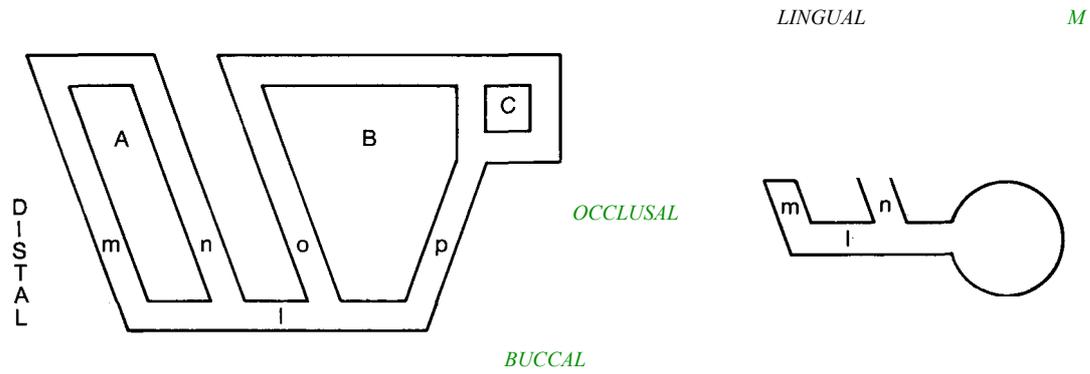
The locations for scoring the third molar. The first and second molar are identical but without the distal hypoconulid. Though the representations of the cusps and other features are very diagrammatic, they proved to be a very effective way of recording the wear locations



ill. occlusal

Type of wear	Location	Score
Enamel wear on cusp slopes	a	1
Dentine wear on cusp slopes	a	2
Central 'eye' between slopes	b	1
Dentine links between lingual and buccal cusps:		
(i) mesial ridge	c	1
(ii) between mesial and distal cusps	d	1
(iii) distal ridge	e	1
Dentine links between mesial and buccal cusps:		
(i) lingual aspect	f	1
(ii) buccal aspect	g	1
Third molar hypoconulid dentine exposed:		
(i) lingual aspect	h	1
(ii) buccal aspect	I	1
(iii) distal linking of (i) and (ii)	h & I	1
(iv) link with lingual cusp	j	1
(v) link with buccal cusp	k	1
(vi) link between lingual and buccal cusps	e	1
All infundibulum worn away	l	1
Black staining of exposed dentine		1

The locations/or scoring the second and third premolar. The fourth premolar is very similar to the third premolar. Though the representations of the premolar ridges are very diagrammatic, they proved a very satisfactory way of recording wear locations



	<i>3rd or 4th premolars</i>	<i>2nd premolar</i>
Type of wear	Location	Score
Enamel or dentine wear on ridges	1, m, n, o & p	1
Continuous linking wear on all ridges	1, m, n, o & p	1
Continuous wear round A to join m and n		1
Continuous wear round B to join o and p		1
Continuous wear round C		1

When all the enamel that lines the **infundibulum** was worn away (1) so that there was a continuous core of dentine surrounded by the tooth's peripheral enamel, a further point would have been given; there were no animals in this sample old enough to demonstrate this. The scores for wear of the individual molars and premolars are given in Table IV and the total molar scores, are shown in a scatter plot (Fig. 5).

To assist in the recording of the molar scores, a diagrammatic representation was made of: (i) the lingual cusps; (ii) the **buccal** cusps; and (iii) the **occlusal** surfaces for each tooth, so that sites of wear could be marked as shown on the chart in Table IIIa. Though these representations may appear to be very crude, they proved very effective in use, enabling a quick visualization of the wear sites to be seen and scored. A separate chart was completed for each animal. Each molar tooth was scored on three aspects, (a) The mesial and distal slopes and tip of the paired lingual cusps, the **paraconid** and **metaconid**. (b) The mesial and distal slopes and tip of the paired buccal cusps, the **protoconid** and the **hypoconid**; and additionally, for the third molar the most distal cusp, the **hypoconulid**. (c) The occlusal surfaces on which the dentine linking the lingual and buccal cusps was exposed. Scores were also recorded for exposure of the dentine linking the paired lingual or buccal cusps to each other and the hypoconulid. Altogether for the first and second molars there are 20 locations on each tooth for which a wear pattern may be recognized and recorded and an additional seven locations that can be scored for the hypoconulid of the third molar (Table III).

*Premolars* (Table IIIb): Because of the different morphology of the premolars with their distinct ridges, the following scoring system was devised. A point was given for each ridge that was independently worn and an additional point was given when all the ridges were joined together (1, m, n, o, p), and a final point when all the underlying dentine was exposed around A, B, or C. There are a number of ways that points could be awarded for stages of wear, but the one described here gave the most consistent and **repeatable** results.

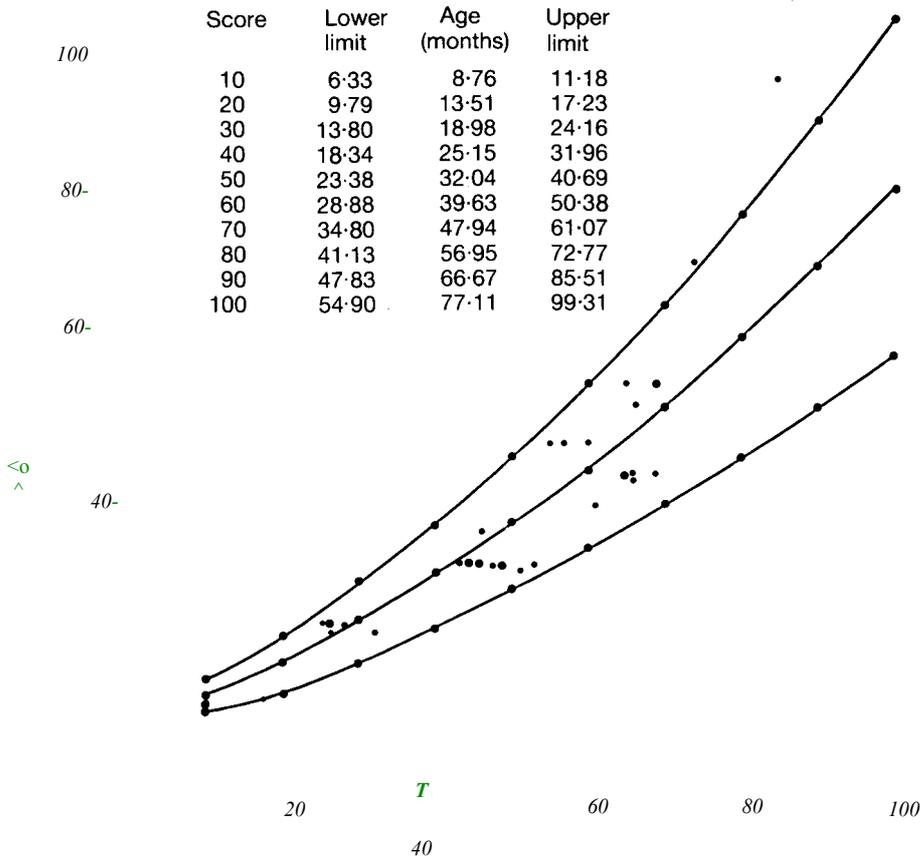
Each tooth was examined several times with the aid of a minimum x 10 lens.

TABLE IV

Wear scores for molars and premolars of fallow deer **Duma damm** arranged in order of age, n = 52. A bar (—) indicates that the tooth is not yet functional

Age (months)	Molar wear score			Totals	Premolars			Totals
	3rd	2nd	1st		4th	3rd	2nd	
4								
5			1	1				
7	—	—	4	4	—	—	—	—
8	—	—	10	10	—	—	—	—
8	—	—	10	10	—	—	—	—
9	—	—	8	8	—	—	—	—
9	—	—	10	10	—	—	—	—
11	—	—	13	13	—	—	—	—
18	—	10	22	32	—	—	—	—
18	—	6	20	26	—	—	—	—
18	—	7	21	28	—	—	—	—
19	—	8	18	26	—	—	—	—
19	—	8	18	26	—	—	—	—
19	—	9	21	30	—	—	—	—
19	—	11	18	29	—	—	—	—
19	—	9	19	28	—	—	—	—
19	—	8	17	25	—	—	—	—
22	—	13	21	34	1	—	—	1
26	6	22	23	51	4	5	—	9
27	2	19	22	43	5	5	—	10
27	3	19	22	44	6	3	1	10
27	4	18	22	44	6	5	—	11
27	6	18	22	46	3	3	1	7
27	3	18	21	42	3	3	1	7
27	5	21	23	49	6	4	—	10
27	6	21	22	49	4	4	1	9
27	2	20	22	44	3	—	—	4
27	5	22	22	49	4	4	—	8
27	5	19	22	46	5	3	2	10
27	5	21	22	48	6	4	—	10
27	9	22	22	53	5	5	—	10
27	5	22	22	49	6	2	—	8
27	6	17	21	44	5	4	—	9
27	4	17	23	44	3	2	—	5
27	4	20	22	46	7	4	1	12
31	4	20	22	46	6	5	—	11
35	16	21	24	61	8	5	1	14
38	20	21	25	66	7	6	2	15
39	16	22	28	66	8	6	2	16
39	17	22	30	69	11	7	3	21
39	18	22	25	65	10	5	2	17
39	20	21	24	65	7	6	1	14
43	12	21	22	55	8	6	—	14
43	12	21	27	60	5	4	1	10
43	12	20	25	57	8	5	1	14
48	21	20	25	66	10	8	2	20
51	21	22	26	69	8	7	3	18
51	21	22	22	65	9	7	2	18
51	22	22	25	69	10	6	3	19
67	24	23	27	74	9	7	2	18
75	38	31	33	102	10	8	6	24
91	25	26	34	85	13	8	4	25

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### Score

FIG. 5. A scatter plot of the data, together with the age (months) with 95% prediction intervals obtained from a regression of age on total molar scores for fallow deer,  $n=52$ . For the latter, scores at intervals of 10 have been plotted against age. The inset table gives the age with upper and lower limits for these scores.

### *Statistical analysis of the wear scores*

The analysis of the data is presented in three parts, the first identifies the ages by which specific wear patterns may be found (Tables V, VI, VII & VIII), the second gives the ages by which for each molariform tooth a particular score is likely to be found (Tables IX, X, XI, XII, XIII, XIV) and the third gives the predicted age together with 95% prediction intervals obtained from a regression of age on total molar wear scores (Fig. 5). Before deciding to confine the regression analysis only to the total molar scores, an initial evaluation was made of the scores for the molars and the premolars separately, then the total molar scores, total premolar scores and finally the combined total molar and premolar scores (Feldman & Gagnon, 1985). It was found that only the total molar wear scores gave results with a range of ages for predicted values that were usable. The data shown in Fig. 5 suggest a curved relationship between age and total molar wear score. The same plot also suggests an increasing variability in age as total score increases. For these reasons, a weighted multiple (i.e. curvilinear) regression of age on score and (score)<sup>2</sup> was done. The weights were based on the assumption that the residual standard deviation was proportional to the value on the fitted line. The calculations were performed using GLIM (Payne, 1986) and the fitted regression was:

$$\text{predicted age} = 4.7 + 0.37 \times (\text{score}) + 0.0035 \times (\text{score})^2.$$

(Similar, and arguably more appropriate, calculations were done using a curvilinear regression of score against age. However, they were more awkward to obtain and are not included as the results they gave are qualitatively similar to the ones reported here.)

#### *The prediction of age*

To determine the age of an animal of unknown provenance, the following procedure is suggested:

1. If all the molars are present, score for each tooth as described and then read off the predicted age from the regression line (Fig. 5).
2. If only a single **molariform** tooth is available, an assessment of age may be made first from looking at the particular wear pattern and referring to the age group in which it is likely to be found (Tables V, VI, VII or VIII). Secondly, a score may be derived for the tooth and this matched against scores for the appropriate tooth (Tables IX, X, XII, XIII or XIV).

### **Results**

#### *Eruption and the age when the molariform teeth become functional*

Details of the eruption sequences are an integral part of the understanding of tooth wear patterns and because the times they may erupt, though not usually the sequences, may vary from one population to another, they are given for this sample of fallow deer from Richmond Park (Table II).

By five months the first molar is erupted and functional; a year later the second molar has erupted and by 22 months the third molars have erupted and are functional. The fourth, third and second **premolars**, which replace the deciduous **premolars**, are erupted and functional by 22, 26 and by 27 to 43 months, respectively.

#### *Wear patterns of the molars*

The sequential pattern of molar tooth eruption and their functional contact with teeth in the opposing jaw is also reflected in the orderly and sequential pattern of tooth wear. The precise locations of tooth wear are given in Table IIIa. Ages are given by which selected wear events commenced or are always found to be present (Tables V, VI, VII & VIII).

For the first molar, wear of the mesial and distal slopes of the paired mesial and distal cusps had begun between five and eleven months, and all these sites were found to be worn by 18 months. For the second molar, wear of these cusps began some time after 11 months and before 18 months, but not until 26 months were all the slopes of the distal cusps found to be in wear. Wear of the third molar cusps begins from 26 months and, except for the distal slope of the distal cusp, all the cusp slopes are in wear by 38 months (Table V).

The exposure of dentine on the mesial marginal ridge is readily identified. For the first molar it is found between four and 11 months, and is always found by 18 months. The marginal ridge dentine is exposed for the second molar by, and is always visible from, 26 months. Not until 51 months does the marginal ridge become worn in the third molar, and even after seven years may be found unworn (Table VI).

The linking of exposed dentine between the lingual mesial and distal cusps or the **buccal** mesial and distal cusps is readily observable. It is first seen at 27 months, but may not become worn until



TABLE V

Percentage of fallow deer (*Dama dama*) in each age group with wear started on paired mesial and distal cusps of the permanent mandibular molars

Age range (months)	Number	Wear pattern	M3	M2	M1
4-11	8	mesial cusps: mesial slopes			75
		distal slopes			75
		distal cusps: mesial slope			63
		distal slope			63
18-22	10	mesial cusps: mesial slope		100	100
		distal slope		100	100
		distal cusps: mesial slope		100	100
		distal slope		50	100
26-35	19	mesial cusps: mesial slope	94	100	100
		distal slope	15	100	100
		distal cusps: mesial slope	73	100	100
		distal slope	9	100	100
38-43	8	mesial cusps: mesial slope	100	100	100
		distal slope	100	100	100
		distal cusps: mesial slope	100	100	100
		distal slope	63	100	100
48-59	5	mesial cusps: mesial slope	100	100	100
		distal slope	100	100	100
		distal cusps: mesial slope	100	100	100
		distal slope	100	100	100

TABLE VI

Percentage of fallow deer (*Dama dama*) in each age group in which the dentine of the lingual and buccal cusps of the permanent mandibular molars is exposed and continuous on the mesial marginal ridge

Age range (months)	Number	M3	M2	M1
4-11	8			13
18-22	10			100
26-35	19		100	100
38-43	8		100	100
48-59	5	40	100	100
67-91	3	33	100	100

67 months. Neither the second nor third molars show any wear at this site (Table VII). The ranges of age by which wear of the cuspal slopes and the mesial marginal ridge and the hypoconulid of the third molar begins and is always present are summarized in Table VIII.

#### *Wear patterns of the premolars*

The wearing of the premolar ridges proved too variable to relate them convincingly to a specific wear pattern.

#### *Wear scores*

These are given for the individual molars for the different age groups (Table IX) and for the combined molar scores (Table X). The scores for the individual molars give a well-defined range of scores to distinguish the early years after eruption. For instance, no first molar scores more than 14 up to 11 months of age; and the lowest score for the 18–22 month group is 17. When the molar scores are combined, they separate distinctly the three younger age groups. Table XI summarizes the score ranges for the three molars up to the age of 35 months after which the scores overlap.

Tables XII and XIII give the individual and combined premolar scores, respectively. There is too much overlap of the scores to be confident that the premolars on their own can be a reliable guide to age.

TABLE VII

*Percentage of fallow deer (Dama dama) in each age group in which the dentine of the lingual and buccal mesial and distal cusps is exposed and continuous*

Age range (months)	Number	M3	M2	M1
26–35	19			10
38–43	8			75
48–59	5			80
67–91	3			100

TABLE VIII

*Ages by which specific wear characteristics take place in fallow deer (Dama dama)*

Wear characteristic	3rd molar (months)	2nd molar (months)	1st molar (months)
Mesial cusps begin to wear	26–35	after 11	4–11
Distal cusps begin to wear	26–35	18–22	4–11
Mesial cusps begin to wear	38–43	18–22	18–22
Distal cusps begin to wear	48–59	26–35	18–22
Mesial marginal ridge wear begins	48–59	after 22	4–11
Mesial marginal ridge wear always present	after 91	26–35	18–22
Hypoconulid wear begins	24		
Hypoconulid wear always present	48		

TABLE IX  
Scores for individual mandibular molar wear for different age groups of fallow deer (*Dama dama*)

Age group (months)	4-11		18-22		26-35		38-43		48-59		67-91	
	Score	n	Score	n	Score	n	Score	n	Score	n	Score	n
1st Molar	0	1	17	1	21	2	22	1	22	1	27	1
	1	1	18	3	22	11	25	3	25	1	33	1
	4	1	21	5	23	4	27	3	26	2	34	1
	8	1	22	1	24	1	30	1	27	1		
	10	3			28	1						
	14	1										
2nd Molar			6	1	17	2	19	2	21	1	21	1
			7	1	18	2	21	3	22	4	26	1
			8	3	19	2	22	3			27	1
			9	2	20	4						
			10	1	21	5						
			11	1	22	4						
3rd Molar					2	2	12	3	21	2	24	1
					3	2	15	1	23	2	28	1
					4	3	18	2	24	1	35	1
					5	4	19	2				
					6	6						
					9	1						
				14	1							

TABLE X  
Combined scores for mandibular molar wear for different age groups of fallow deer (*Dama dama*)

Age group (months)	4-11		18-22		26-35		38-43		48-59		67-91	
	Score	n										
	0	1	25	1	42	1	55	1	65	1	74	1
	1	1	26	2	44	6	56	1	68	1	88	1
	4	1	27	1	46	2	58	1	70	1	95	1
	8	1	28	1	48	2	64	1	72	2		
	10	1	29	1	49	3	65	2				
	14	1	30	2	50	1	67	1				
			32	1	51	1	70	1				
			34	1	59	2						

When the molar and premolar scores are combined together, they confirm that scores are indicative of age for the younger groups of animals (Table XIV).

*Regression analysis of age on wear scores*

The curved regression line was constructed by plotting total molar scores against individual known age (Fig. 5). It is apparent from the graph that the ranges on either side of the predicted

TABLE XI  
Age by which a particular score will be achieved for fallow deer  
(*Dama dama*)

Age (months)	3rd Molar scores	2nd Molar scores	1st Molar scores	Total Molar scores
4-11	zero	zero	0-14	0-14
18-22	zero	6-13	17-22	25-34
26-35	2-14	17-22	21-28	42-59
38-43	overlap	overlap	overlap	overlap

TABLE XII  
Scores for individual mandibular premolar wear for different age groups of  
fallow deer (*Dama dama*)

Age group (months)	4-11		26-35		38-43		48-59		67-91	
	Score	n	Score	n	Score	n	Score	n	Score	n
4th Premolar	1	1	3	4	5	1	7	1	9	1
			4	3	7	2	8	1	10	1
			5	4	8	3	9	1	13	1
			6	6	10	1	10	2		
			7	1	11	1				
3rd Premolar			8	1						
			1	1	4	1	6	2	7	1
			2	2	5	2	7	2	8	2
			3	4	6	4	8	1		
2nd Premolar			4	6	7	7				
			0	12	0	1	2	3	2	1
			1	6	1	2	3	2	4	1
			2	1	2	4			6	1
		3	1							

values for a 95% prediction interval increase markedly with increased scores, giving, for instance, with a score of 10, a predicted age of 8.76 months  $\pm$  2.42 months, with a score of 50, a predicted age of 32 months  $\pm$  8.66 months and with a score of 90, a predicted age of 66 months  $\pm$  18 months.

### Discussion

Three approaches have been followed to determine at what age for fallow deer a particular wear state or score may be found. First there is the age by which a particular wear pattern may be present, secondly the scores that may be calculated for the individual molariform teeth, and lastly, for total molar scores, the predicted age and 95% prediction intervals from the regression analysis. The first approach allows for a rapid characterization of a sample of unknown provenance. The second analysis, especially if the scores of the molars are combined, will give a reasonable assessment of age up to three years. The regression analysis will give the best guide to age when all the left or right mandibular molars are available for examination. The method to use will depend

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TABLE XIII  
 Combined scores for mandibular premolar wear for different age groups  
 of fallow deer (*Dama dama*)

Age group (months)	18-22		26-35		38-43		48-59		67-91	
	Score	n	Score	n	Score	n	Score	n	Score	n
	0	27	0	12	0	1	2	3	2	1
	1	1	1	7	1	2	3	2	4	1
	2	3	2	4	6	2	6	1		
	3	8	3	1	7	3	7	1		
	4	9	4	1	8	2	8	2		
	5	10	5	3	9	1	9	1		
	6	6	6	4	10	2	10	1		
	7	1	7	9			13	1		
	8	1	8	3						
			10	1						
			11	1						

TABLE XIV  
 Combined scores for mandibular molar and premolar wear for different age groups  
 of fallow deer (*Dama dama*)

Age group (months)	4-11		18-22		26-35		38-43		48-59		67-91	
	Score	n										
1st Molar	0	1	25	1	48	1	69	2	80	1	92	1
	1	1	26	2	49	2	70	1	80	1	113	1
	4	1	27	1	53	1	79	1	90	1	119	1
	8	1	28	1	54	2	80	1	91	1		
	10	3	29	1	55	2	82	2				
	14	1	30	2	56	1	91	1				
			32	1	57	3						
			35	1	58	2						
					60	2						
					62	1						
					69	1						
					73	1						

on whether all the molariform teeth of one side of the mandible are available for examination or only a single tooth. All three procedures can be used to assess age, but the regression analysis, especially, will allow better comparisons to be made with other techniques currently in use.

*Wear patterns of the molars*

Distinct patterns of tooth wear are apparent in fallow deer, and with this Richmond Park sample it is possible to state, with varying degrees of confidence, by what age group any particular wear event takes place. Tables V, VI and VII give the ages for the initial wearing of the mesial and distal cusps, the exposure of the lingual and buccal dentine continuous with that of the mesial

marginal ridge, and when exposure of the dentine takes place to link the paired lingual or buccal cusps. Therefore, a first molar that does not have a worn distal cusp slope is likely to be from an animal less than 18 months old. Similarly, an unworn distal cusp slope on a second molar would be from an animal less than 26 months, and on a third molar from an animal less than 48 months old (Table V). Equally, with assessing dentine exposure on the mesial marginal ridge (Table VI), or linking of exposed dentine between the mesial and buccal cusps on either the lingual or buccal aspects (Table VII), can place an animal into an age bracket. Table VIII summarizes these events and can be used to locate the age group into which a particular tooth may be placed or excluded.

#### *Wear patterns of the premolars*

The wearing of the premolar ridges does not follow a sufficiently consistent sequential order from one ridge to the next that can readily be related to increasing wear with increasing age.

#### *Wear scores*

The summed scores derived from all the sites on a tooth where wear may have taken place give a good indication of overall wear.

1. *For individual molars:* The range of wear scores for the individual permanent molars (Table IX) showed that up to the age of 22 months, 35 months and 43 months for the first, second and third molars, respectively, they were a very good indication of an animal's age. After these respective ages, the scores begin to overlap and so they could not be regarded as a reliable enough way of assessing age. For instance, for the first molar a wear score of 22 might be measured for any age from 18 to 48 months and for the second molar a wear score of 21 might be measured from 26 to 48 months. The third molar wear scores look reliable for distinguishing between animals younger and older than 48 months.
2. *For combined molar scores:* By combining together the scores for the three molars, a much clearer indication of age was obtained up to 43 months (Table X).
3. *For individual premolar scores:* The scores do not increase evenly with age (Table III), and it can readily be seen that the ranges of wear scores for the three premolars all overlap and therefore were not a suitable indication of age (Table XII).
4. *For combined premolar wear scores:* As for the individual teeth, there was too much overlap of the combined scores for them to serve any purpose in attempting to age animals (Table XIII).
5. *For combined molar and premolar scores:* These scores gave a useful guide to age up to 35 months; but they are not as secure as the combined molar scores on their own (Table XIV).

These findings suggest that an age derived from a high score cannot be an absolute statement of age but more an indication of how long the teeth have been functional in relation to a particular diet; and this is especially true for the older age groups. The overall scores for wear given in Tables IX, X, XI, XII, XIII and XIV show that a wide range is possible. This is partly a reflection of the age spread of the sample which is to some extent restricted by all the fawns being born in the same 4-6 weeks of the year and being culled for any one year during the same month. Only accidental death allowed a wider spread of ages. The scores by themselves are useful as they enable comparisons to be made, but for practical purposes the best interpretation of the extent of wear and how old an animal may be is when the scores are totalled for all the molars.

The use of a collective description of a definite pattern of wear to assess age as described by

Payne (1973) may be misleading. It is apparent that as sequential as wear patterns usually are, they do not always follow the expected pattern. It is why the score system presented here is seen as an additional aid to estimating age from the state of wear of the teeth. However, certain caveats must be made. The data presented here is only strictly applicable to animals living under the same regimen as those in Richmond Park, but it appears from Chaplin & White (1969) that wild deer living in Essex are not too different from the Richmond Park deer; and furthermore allowance must be made for animals that existed under different nutritional regimens. Deniz & Payne (1982) have reported on the eruption and tooth wear variations to be found among three different flocks of Turkish angora goats; and there is no reason to doubt that similar differences would be found among different populations of *Dama dama*.

#### *Regressions analysis of age on wear scores*

The evidence from the regression analysis shows that the total molar wear scores give the best indication of age from score. From the 95% prediction intervals it can be seen that, as the scores become higher, the range of possible age from the predicted values increases so that, for instance, with a wear score of 70, the predicted age of an animal would be 48 months  $+ / -$  13-4 months (Fig. 5). Higher scores are of decreasing value for the prediction of age, a score of 100 would give a predicted age of 78 months  $+ / -$  22 months. These wide limits at the higher scores mainly reflect the increasing variability of score at the older ages rather than the small sample size at those ages. This increase in variability presumably reflects the fact that inherent individual variations have had more time to manifest themselves. There are several possible explanations for these variations:

they could be due to slight morphological differences in the cusps; the tooth's inclination might be slightly abnormal in relation to the teeth of the opposing jaw, thus modifying the wear pattern;

acquired or inherent variations in the teeth against which a tooth occludes may disturb a wear pattern. The wider range of variation for the older ages may reflect that with every season that passes there is an increasing chance that the individual experience of any one animal may be very different and this would be accumulative over the years. This variation is largely masked by the fact that this is a cross-sectional sample and only by examining the same animals over a period of years will individual variation be properly elucidated. An additional consideration in explaining variation is that the wear stages are not of an equal duration of time, so an unavoidable subjective element comes into the scoring. There can be a long period of wear when a particular score could represent a considerable wear period. This suggests that a useful adjunct to this scoring technique would be the measurement of total crown height which could be used to modify the scores, and this would be especially true for the older animals.

One important way in which the regression graph with its prediction intervals may be of special value is in the assessment of other methods of age determination. If there is with increasing wear an ever-increasing widening range of possible age, is there a range beyond which there is little justification for making an assessment at all (Fig. 5). Is an age range of  $+ / -$  24 months informative in any way?

There is no other similar data on *Dama dama* available with which to make comparisons, so it is only possible to look at studies on closely related animals. Our current studies on red deer (In prep.) give a very similar regression curve, except that, for a given total wear score, red deer are predicted to be younger. This confirms that each species will need its own database from which to predict age; and that it is misleading to rely on methods of ageing derived for other species. Robinette *et al.* (1957) described a quantitative method for evaluating age of mule deer and stated

that they found with their method that there was an obvious overlap of 2-year-olds with 3- and even 4-year-olds. Payne (1973) provides a very helpful visual guide to tooth wear patterns in goats, but goats differ from deer in certain important aspects. Furthermore, his system does not allow an animal's age to be identified within a precise enough range. Payne recently (1987) added reference codes to his original wear stages for sheep and goats which has increased the value of the first published descriptions. The same reservations must be made about Grant's analysis (1982) of cattle's teeth which has not yet been tested against animals of known age.

The scoring scheme that is described here has been specifically related to the sample that has been studied in which the oldest animal is 91 months, but there is no reason why the ages of much older animals should not be estimated by adding additional points to the score for particular events such as, for instance, the complete wearing away of the *infundibulum*.

The provenance of this sample necessarily influences the results, and these need to be interpreted with the understanding that it was obtained within the framework of a well-established management pattern, so that the range of ages within any age group is, especially the older ones, unavoidably small. More animals in the older range would increase the reliability of the data and it would also be valuable to have animals of ages to represent every month in the year. Do fallow deer teeth wear quicker in the warmer months, when there is usually a plentiful supply of herbage, or during the winter months when there is less to eat, but what there is to eat may be of a rougher texture? We do not know with absolute certainty the answer to this question; but it has been reported that tooth rate wear in bison (*Bison bison*) is significantly slower if the animals are fed high protein concentrates in winter (Prison & Stanford, 1982), though it may be reassuring when comparing deer from a variety of provenances that Chaplin & White (1969) found minimal differences in tooth wear patterns between park and wild deer. Also, the sample was not large enough to provide details for the male and female deer separately; and this needs to be borne in mind when making comparisons with other samples.

However good the claims are for assessing age from *cementum* increments, the procedures are lengthy and cannot be carried out in the 'field'; and further validation of the technique is still necessary for fallow deer. The results presented here derived from a detailed analysis of *cuspal* wear will provide a readily usable and improved method for assessing fallow deer of unknown age, especially when all the molar teeth are available for analysis; and that taken with all the other age assessing criteria when a live animal or a whole body is available for examination, this scoring technique will enhance the evaluation of age. Where teeth may be found on their own as part of an archaeological investigation, it will be possible, even if it is only a single molar tooth, to make an appraisal of likely age, but the range of possible age will be much larger than with a complete molar tooth series. Certainly, if a number of teeth from different animals are found, comparisons will be easily made to determine how similar or disparate in age the sample may be.

### Summary

The nature of tooth wear and the sequential nature of the wear with the identification of specific morphological features have been described. A scoring system has been devised to evaluate stages of wear. Chronology tables have been constructed to show the age by which any event in the sequence may have taken place; and to indicate for each age group the range of scores that may be found. The linear regression of age on total molar scores gives the predicted age, together with the 95% prediction intervals associated with any particular score, which can be used to assess the age of an animal of unknown provenance. Wear of the *premolar* teeth is not a good guide to age and

allows for only the crudest assessment. The data on the *premolar* teeth has been included to provide a baseline and comparison for future studies. The several analyses presented enable assessments of age to be made, with varying degrees of confidence, of animals of unknown birth dates.

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#### REFERENCES

- Brown, W. A. B., Christofferson, D. V. M., Massler, M. & Weiss, M. B. (1960). Postnatal tooth development in cattle. *Am. J. Vet. Res.* **21**: 7-34.
- Carter, H. H. (1975). Guide to rates of tooth wear in English lowland sheep. *J. Archaeol. Sci.* **2**: 231-333.
- Chaplin, R. E. & White, R. W. G. (1969). The use of tooth eruption and wear, body weight and antler characteristics in the age estimation of male wild and park Fallow deer (*Dama dama*). *J. Zool., Lond.* **157**: 125-132.
- Chapman, D. I. & Chapman, N. G. (1969). The use of sodium perborate tetrahydrate (NaB<sub>3</sub>O<sub>4</sub>H<sub>2</sub>O) in the preparation of mammalian skeletons. *J. Zool., Lond.* **159**: 522-523.
- Chapman, D. I. & Chapman, N. G. (1970). Development of the teeth and mandibles of fallow deer. *Acta theriol.* **15**: 111-131.
- Chapman, D. I. & Chapman, N. G. (1973). Maxillary canine teeth in Fallow deer, *Dama dama*. *J. Zool., Lond.* **170**: 143-147.
- Chapman, D. I. & Chapman, N. G. (1975). *Fallow deer: Their history, distribution and biology*. Lavenham, Suffolk: Terence Dalton.
- Deniz, E. & Payne, S. (1982). Eruption and wear in the mandibular dentition as a guide to ageing in Turkish Angora goats. In *Ageing and sexing animal bones from archaeological sites*: 155-205. Wilson, R., Grigson, C. & Payne, S. (Eds). Oxford: B. A. R. British Series 109.
- Feldman, D. & Gagnon, J. (1985). Statview, Brainpower Inc., 24009 Ventura Blvd, Suite 250, Calabasas, CA 91302, USA.
- Frison, G. C. & Stanford, D. F. (1982). *The Agate Basin Site*. New York: Academic Press.
- Gilbert, P. F. & Stolt, S. L. (1970). Variability in aging Maine White-tailed deer by tooth-wear characteristics. *J. Wildl. Mgmt* **34**: 532-535.
- Grant, A. (1982). The use of tooth wear as a guide to the age of domestic animals. In *Ageing and sexing animal bones from archaeological sites*: 91-108. Wilson, R., Grigson, C. & Payne, S. (Eds). Oxford: B.A.R. British Series 109.
- Grue, H. & Jensen, B. (1979). Review of the formation of incremental lines in tooth cementum of terrestrial mammals. *Dan. Rev. Game Biol.* **11** (3): 1-48.
- Hamilton, J. (1982). Re-examination of a sample of Iron Age sheep mandibles from Ashville Trading Estate, Abingdon, Oxfordshire. In *Ageing and sexing animal bones from archaeological sites*: 215-222. Wilson, R., Grigson, C. & Payne, S. (Eds). Oxford: B.A.R. British Series 109.
- Hillson, S. (1986). *Teeth*. Cambridge: Cambridge University Press.
- Keiss, R. E. (1969). Comparison of eruption-wear patterns and cementum annuli as age criteria in elk. *J. Wildl. Mgmt* **33**: 175-180.
- Levitan, B. (1982). Errors in recording tooth wear in ovicaprid mandibles at different speeds. In *Ageing and sexing animal bones from archaeological sites*: 223-250. Wilson, R., Grigson, C. & Payne, S. (Eds). Oxford: B.A.R. Series 109.
- Lowe, V. P. W. (1967). Teeth as indicators of age with special reference to Red deer (*Cervus elaphus*) of known age from Rhum. *J. Zool., Lond.* **152**: 137-153.
- Ludwig, T. G., Healey, W. B. & Cutress, T. W. (1966). Wear of sheep's teeth III. Seasonal variation in wear and ingested soil. *N.Z. J. Agric. Res.* **9**: 157-164.

- Osborn, H. F. (1907). *Evolution of mammalian molar teeth*. New York: Macmillan.
- Payne, C. D. (Ed.) (1986). *The GUM System: Release 3.77*. Oxford: Numerical Algorithms Group.
- Payne, S. (1973). Kill-off patterns in sheep and goats: the mandibles from Asvan Kale. *Anatolian Studies* **23**: 281-303.
- Payne, S. (1987). Reference codes for wear states in the mandibular cheek teeth of sheep and goats. *J. Archaeol. Sci.* **14**: 609-614.
- Peyer, B. (1968). *Comparative odontology*. (Transl. & Ed. R. Zangeri). Chicago: The University of Chicago Press.
- Rieck, W. (1973). *Damwildalter-Merkblatt*. Herausgegeben vom Schalenwildausschu [B] des Deutschen Jagdschutz-Verbandes.
- Riney, T. (1951). Standard terminology for deer teeth. *J. Wildl. Mgmt* **15**: 99-101.
- Robinette, W. L., Jones, D. A., Rogers, G. & Gashwiler, J. S. (1957). Notes on tooth development and wear for Rocky Mountain Mule deer. *J. Wildl. Mgmt* **21**: 134-153.
- Szabolics, J. (1975). *A damvad*. Budapest: Mezogazdasagi Kiado.
- Ueckermann, E. & Hansen, P. (1968). *Das Damwild*. Hamburg and Berlin: Verlag Paul Parey. Whitehead, G. K. (1972). *Deer of the world*. London: Constable.