A C T A   T H E R I O L O G I C A

VOL. XV, 7: 111—131.   BIAŁOWIEŻA   30.IV.1970

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Development of the Teeth and Mandibles of Fallow Deer

[With 6 Tables & 3 Figs.]

Fallow deer, *Dama dama* (Linnaeus, 1758) have a diphyodont dentition comprising 20 deciduous and 32 permanent teeth. The best estimate of age is obtained by assuming a common date of birth and using the stage of tooth development only to decide the year group. The method is only applicable up to 3 years of age. Above that age the specimens are divided into arbitrary groups on the basis of the degree of wear of the third molar. The order of eruption of the permanent teeth is M_1, I_1, M_2, I_2, I_3, C, M_3, P_4, (P_3, P_2). The permanent molars start erupting at about 3 months and finish by 21—24 months although the third molar is not completely functional until 30 months. The permanent premolars start erupting at 17—20 months and are complete by 25—26 months whereas the permanent incisiform teeth start at about 7 months and finish at 17—20 months. The mandibles reach their maximum size by about 30 months although in males the diastema continues to grow after this time. The variation in size of mandibles both in and between populations is discussed.

I. INTRODUCTION

A knowledge of the age of the animals is a prerequisite for the successful study of mammalian populations. In many species, particularly wild ungulates, the eruption and wear of the teeth have been used widely as a means of determining the age of the specimens. The method usually employed is to sort the specimens into groups depending on the stage of eruption and wear of the teeth and to call these groups »age classes«. In many early studies, animals of known age were not available and it was assumed that specimens showing similar stages of eruption or wear had the same chronological age. The question of the variation which might occur in the eruption and wear of the teeth was usually ignored. In more recent studies, animals of known age have been included but the question of individual variation is still often ignored. In the preliminary stages of the present study, the mandibles for each sex were divided first into groups depending on the stage of eruption and wear of the molariform teeth. For example, mandibles in which only the first permanent molar had partially erupted were placed in one group, those in which they had fully erupted in a second group and so on. Mandibles in which all three molars had erupted were divided into four groups depending upon whether the distal cusps of the third molar was unworn (group 1), slightly worn (group 2), well worn (group 3) or very worn (group 4). These groups, although arbitrary, are useful as a means of classifying deer in which all the teeth have erupted.

On examining the mandibles in these groups it became apparent that there was a wide variation in the time taken for an animal to reach a particular stage of tooth eruption. For example, some of the deer which had been killed in July showed a very similar degree of eruption to some of the deer which had been killed in January. It could be argued that the two groups of deer were of the same chronological age and that one group had been born six months later than the other group. Fallow deer, however, are usually born in June and although it has been shown that the breeding period is more extended than is generally believed, it is very unlikely that a large number of deer would have been born as late as mid-winter and would have survived. Therefore, in attempting to classify deer into various age groups one has the choice of two possibilities. Either one can assume that the rate of development of a particular character, such as eruption of the teeth, is uniform in all the specimens and therefore, deer having the same degree of development are of the same chronological age, or one can assume that the deer were all born on a definite date and that variation in the rate of development of the character occurs. The truth no doubt, lies somewhere between these two extremes and one must now consider which view is likely to be more nearly correct. It is well known that in man eruption of a particular tooth occurs at varying chronological ages (Hurme, 1948; Moorrees, Fanning & Hunt, 1963). It has also been shown that in rats fed on various diets the rate of growth varies considerably although it is more marked in the bones than in the teeth (McCance, Ford & Brown, 1961; Widdowson & McCance, 1960). Quimby & Gaab (1957) have shown that in Elk, *Cervus canadensis* (Erxleben, 1777) tooth wear can vary enormously and they quote an example of a molar tooth of a two year old animal showing the same degree of wear as that of a ten year old animal. Also Mitchell (1967) refers to delayed development of the third molar in Red deer, *Cervus elaphus* (Linnaeus, 1758). We decided, therefore, that it was better to give a common date of birth to the deer and, in the case of the younger animals, to estimate their chronological age since the date of their death was known.

The present study describes the post-natal development of the mandibles and teeth of both wild and captive Fallow deer, *Dama dama* (L i n n a e u s, 1758) and gives an indication of the variation which occurs both within and between populations. Since adult animals of known age are not available, no attempt is made to determine the age of deer whose teeth have erupted fully and have started to wear. The mandibles of these animals were left in the four groups mentioned earlier. A preliminary report on part of this work has already been published (C h a p m a n & C h a p m a n, 1969).

II. MATERIALS AND METHODS

The mandibles of 185 wild and captive Fallow deer (111 ♂ 74 ♀) were available for study (Table 1).

The terminology used for the teeth is that proposed by R i n e y (1951).

The following four measurements, which are shown in Fig. 1, were made on the mandibles:

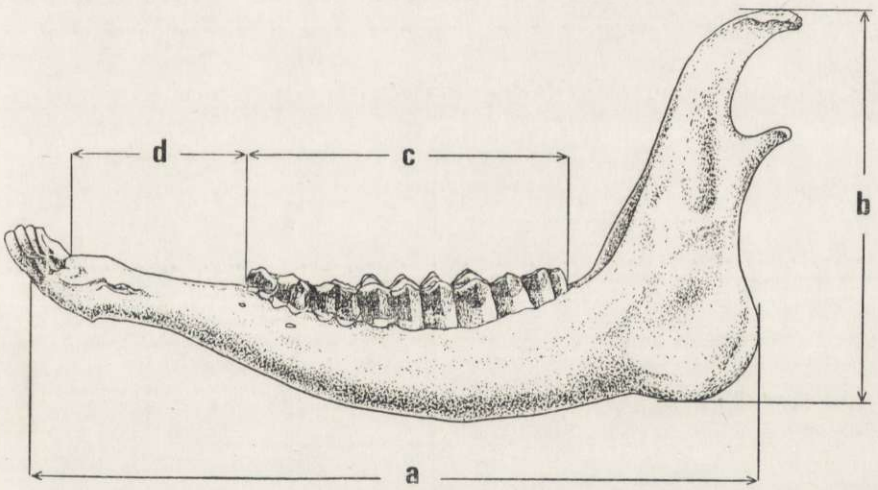

Fig. 1. Positions at which mandibular measurements were made.

a) The length of the mandible from the edge of the alveolus of the first incisor to the hind margin of the *ramus ascendens*.

b) The height of the mandible from the top of the coronoid process to the lowest point on the angle of the mandible.

c) The length of the cheek teeth (premolars and molars) from the distal end of the alveolus of the second premolar to the proximal end of the alveolus of the last molar erupted or erupting.

d) The length of the diastema from the proximal edge of the alveolus of the canine to the distal edge of the alveolus of the second premolar.

A few mandibles were too damaged for all four measurements to be made. Copies of the measurements have been deposited in the library of the British Museum (Natural History), London as they are too numerous to publish in full.

III. DENTITION

The Fallow deer is diphyodont having two successive dentitions, a deciduous dentition normally comprising 20 teeth and a permanent dentition normally comprising 32 teeth, although variations in the number of teeth have been observed.

The normal dental formula is:

$$\text{Deciduous} \quad i\,\frac{0}{3},\ c\,\frac{0}{1},\ pm\,\frac{3}{3} \times 2 = 20$$

$$\text{Permanent} \quad I\,\frac{0}{3},\ c\,\frac{0}{1},\ P\,\frac{3}{3},\ M\,\frac{3}{3} \times 2 = 32$$

The upper incisors and canines are absent but there is a thick pad of fibrous, connective tissue against which the lower incisors and canines bite.

Table 1.

The localities and number of 185 Fallow deer mandible examined.

Locality	Male	Female
Cannock Chase, Staffs.	3	1
Dumfriesshire	8	11
Essex	38	24
Forest of Dean, Glos.	1	11
Hampshire	9	10
New Forest, Hants.	0	1
Richmond Park, Surrey	45	14
Woburn Park, Beds.	7	2
Total	111	74

A large diastema exists between the canines and the premolars (Figs 2 A & B). The incisors and canines are spatulate.

The deciduous second and third premolars and all the permanent premolars are lophodont whereas the fourth deciduous premolar and all the permanent molars are selenodont. With the exception of the fourth deciduous premolar and the third molar, the molariform teeth are all quadritubercular and each has two roots. The fourth deciduous premolar and the third molar are sexitubercular, having an additional pair of cusps and three roots (Figs 2 A & B). The cheek teeth are hypsodont, continuing to erupt throughout life and thus compensating for the continued

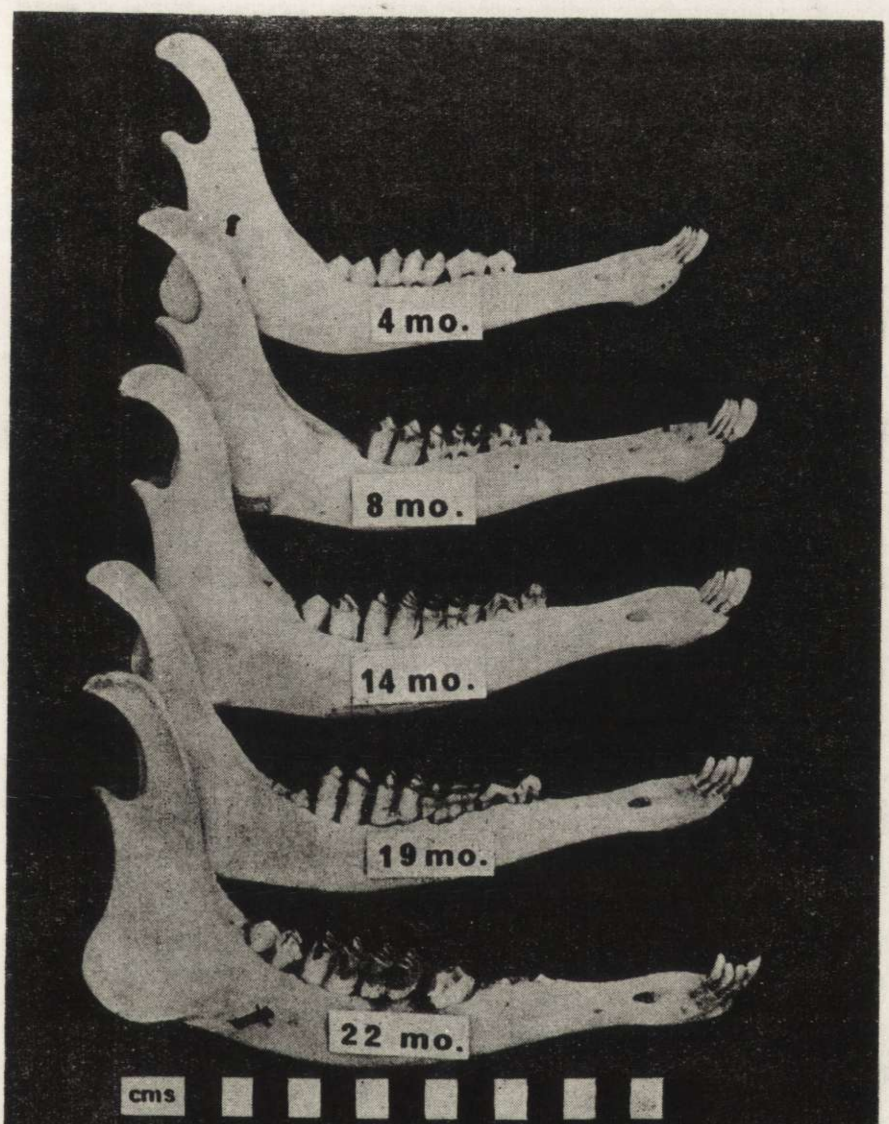

Fig. 2. Development of the mandible and eruption of the teeth up to two years (A) and above two years of age (B — page 116).

attrition of the surfaces. With the exception of the second premolar, the cheek teeth undergo a well defined mesial drift.

The molar rows in the mandibles are closer together than they are in the maxilla and they diverge distally in the shape of a slightly curved

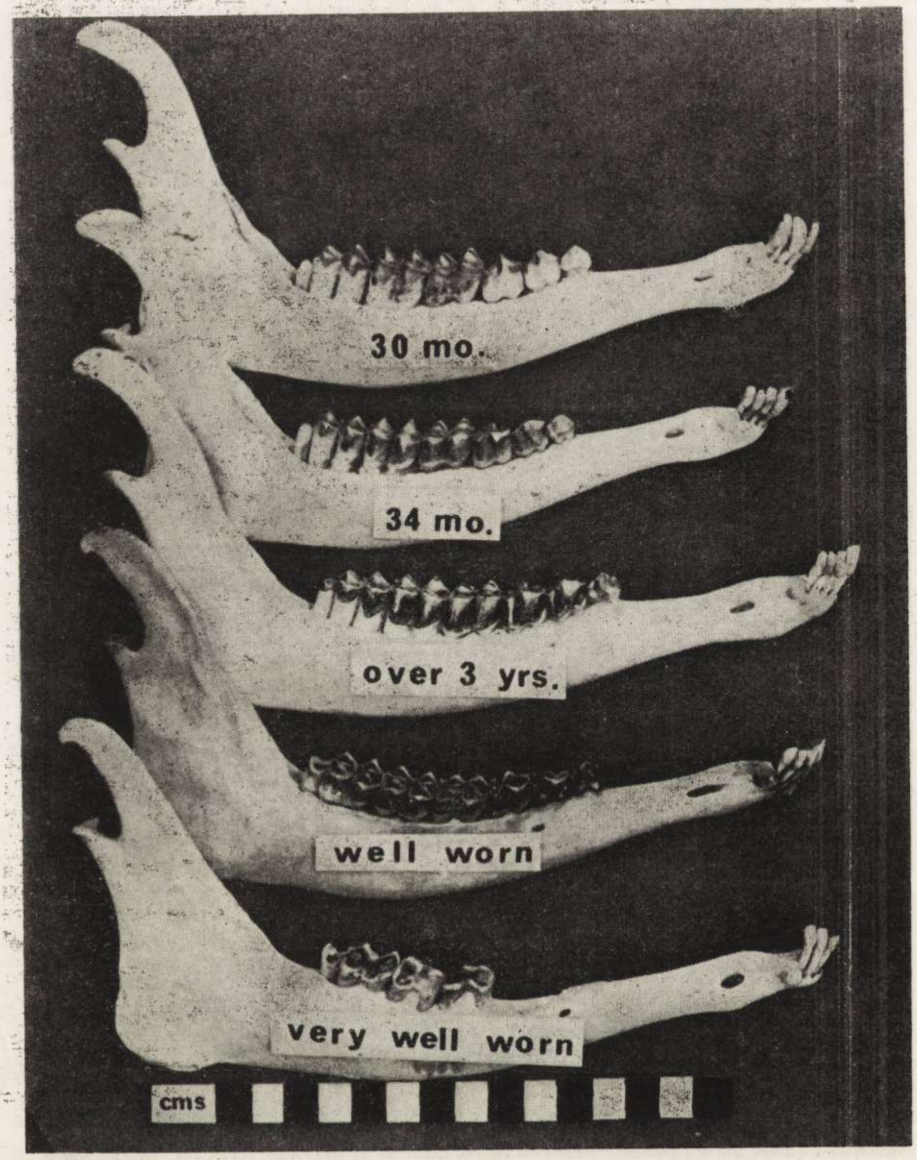

Fig. 2B

»V«. The lingual alveolar crest stands higher than the buccal so that the lower cheek teeth tilt slightly in a lingual direction. When chewing the animal's mandibles exhibit a lateral movement in relation to the maxilla. Therefore, when the lingual cusps of one side of the mandible are in contact with the maxillary teeth, it is the buccal cusps of the other side which are in contact and *vice versa*.

IV. ESTIMATION OF AGE

As mentioned earlier, it is assumed that all the deer were born on a given date. Since the majority of Fallow deer appear to be born in June (Armstrong, Chaplin, Chapman & Smith, 1969) the 15th, was chosen as the day of birth and all nominal ages have been calculated from that date. Having fixed the date of birth one must then determine whether an animal was in its first, second or subsequent year before its age can be estimated. This was achieved by arranging the mandibles in order of increasing amount of tooth eruption. In general it was found that with increasing amount of crown visible in the mouth, the number of months between the date of death and 15th June increased.

Table 2.

Mandibular dentition of Fallow deer of known-age as determined from cleaned specimens.

Age Months	Sex	Dentition
2.5	♂	i_{1-3}, c_1, $pm_{1-3} \times 2$ Alveolus of M_1 just forming
3.0	♂	i_{1-3}, c_1, $pm_{1-3} \times 2$ Alveolus of M_1 just forming
5.5	♀	i_{1-3}, c_1, pm_{1-3}, $M_1 \times 2$ Alveolus of M_2 just forming
6.5	♂	i_{1-3}, c_1, pm_{1-3}, $M_1 \times 2$ Alveolus of M_2 just forming
8.0	♀	i_{1-3}, c_1, pm_{1-3}, $M_1 \times 2$ Alveolus of M_2 just forming
9.0	♀	I_1 $i_{2,\,3}$, c_1 pm_{1-3}, $M_1 \times 2$ M_2 just visible in alveolus
13*	♂	I_{1-2}, i_3, c_0, pm_{1-3}, $M_{1-2} \times 2$
17	♂	I_{1-3}, C_1, pm_{1-3}, $M_{1-3} \times 2$ M_3 just showing
18*	♂	I_{1-3}, C_1, pm_{1-3}, $M_{1-3} \times 2$ M_3 just showing
18	♀	I_{1-3}, C_1, pm_{1-3}, $M_{1-2} \times 2$ Alveolus of M_3 just forming
27	♂	I_{1-3}, C_1, PM_{1-3}, $M_{1-3} \times 2$

* Wild deer from Essex; canine and its alveolus missing in one example.

Observations on the dentition of two wild and nine park deer of known-age have shown that the first molar has erupted and become functional by the December following birth, whilst the second molar has become functional by October of the following year. The age and mandibular dentition of the known-age deer, which were ear-tagged within a few days of birth, are given in Table 2.

Therefore animals in which the second molar has not completely erupted can be considered to be in their first year and those in which the third molar has not completely erupted can be considered to be in their second year. Similarly animals in which the third molar has erupted but in which the third pair of cusps is either unworn or only showing slight signs of wear are probably in their third year. Once an animal exhibits more than slight wear of the third cusp of its third molar then its age can only be stated as being over 3 years. This method does not necessarily give a precise estimate of age but is probably the best one available until more animals of known age can be studied. Further support for this method is provided in the section on the development of the mandible. The sizes of the mandibles are plotted against their estimated age and result in a smooth curve. Such a curve is unlikely to have resulted if some of the ages were greatly in error.

The difference between the actual and postulated dates of birth will cause a relatively larger error in the estimated age of young animals than in older animals. However, the reverse is true when tooth development and wear are considered, since the older the animal the more variation that is likely to have occurred. It is important, therefore, to consider both the date of death and tooth development when trying to estimate the animal's age. That quite appreciable variation does occur in the development of the teeth is shown later.

V. ORDER OF TOOTH ERUPTION

The dentition of five near full-term foetuses and two new-born fawns has been dissected and examined. The mandibles contained six deciduous incisors, two deciduous canines and three deciduous premolars. Fallow deer, therefore, are usually born with the deciduous dentition given on page 114. Determination of the order of eruption of the permanent teeth involved examination of all the mandibles in which the dentition was incomplete. The number was recorded for specimens in which one particular tooth, but not others, had erupted.

A tooth was considered to have erupted if any part of it was visible above the bone.

Inspection of Table 3 shows, for example, that in 13 specimens P_4 had erupted but that P_2 had not erupted: (see column 7, line 5) but the converse, that P_2 had erupted but P_4 had not erupted, (see column 5, line 7) was not found. Therefore it can be concluded that P_4 erupts before P_2. By comparing each tooth with every other tooth the order of eruption of the permanent teeth in male Fallow deer was found to be:

$$M_1,\ I_1,\ M_2,\ I_2,\ I_3,\ C,\ M_3,\ P_4,\ (P_3,\ P_2)$$

With regard to the second and third premolars only three specimens were available for examination, in two cases P_3 had erupted before P_2 and in the other case the reverse had occurred.

The order of eruption in female deer is similar except that in the six specimens available M_3 and P_4 had erupted at about the same time. In

Table 3.

Frequency of eruption of each pair of permanent teeth in 63 mandibles (38 ♂, 25 ♀) with incomplete dentition.

Not erupted	ERUPTED																													
	I_1			I_2			I_3			C			P_2			P_3			P_4			M_1			M_2			M_3		
	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total
I_1				0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	3	13	0	0	0	0	0	0
I_2	7	4	11				0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	7	24	2	1	3	0	0	0
I_3	9	3	12	2	0	2				0	0	0	0	0	0	0	0	0	0	0	0	19	7	26	4	1	5	0	0	0
C	9	5	14	2	1	3	0	1	1				0	0	0	0	0	0	0	0	0	19	8	27	4	2	6	0	0	0
P_2	20	17	37	12	12	24	11	12	23	11	11	22				1	1	2	4	9	13	38	25	63	21	15	36	8	9	17
P_3	19	16	35	11	11	22	10	11	21	10	10	20	1	0	1				3	8	11	37	23	60	20	14	34	7	8	15
P_4	15	10	25	7	5	12	6	5	11	6	4	10	0	0	0	0	0	0				34	15	49	17	6	23	4	3	7
M_1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				0	0	0	0	0	0
M_2	4	3	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	9	26				0	0	0
M_3	13	8	21	6	4	10	4	4	8	4	3	7	0	0	0	0	0	0	0	3	3	29	15	44	12	6	18			

three specimens M_3 had erupted before P_4 whereas the reverse was true for the other three specimens.

VI. AGE AT WHICH TOOTH ERUPTION OCCURS

The age of the 98 deer, (60 ♂, 38 ♀), in which either the dentition was incomplete or in which the third cusp of M_3 showed no signs of wear, was estimated by the method described earlier. The mandibles were then divided into groups and the number in which the various teeth had erupted was recorded. The numbers in each age group were small, consequently it was not possible to determine whether there was any difference between males and females in the age at which the teeth erupt. Therefore data for both sexes were combined (Table 4). Fractions of a month have been ignored, so that an animal whose estimated age is 16 months and 3 weeks is placed in the 13—16 month group, not in the 17—20 month group.

Table 4.

Per cent of animals in each age group with each tooth erupted.

Age Months	M_1	I_1	M_2	I_2	I_3	C	M_3	P_4	P_3	P_2
0—2	0									
3—4	50	0								
5—6	100	0	0							
7—8	100	83	0	0	0	0	0			
9—12		100	33	0	0	0	0	0	0	
13—16		100	100	100	17	20	17	0	0	0
17—20			100	100	100	100	61	50	6	0
21—24					100	100	100	100	100	75
25—26							100	100	100	100
27—30							100	100	100	100

Since the specimens were collected from several areas in England and Scotland, the variation in the age at which a particular tooth erupts is likely to be greater than in animals collected from a single herd.

The permanent molar teeth start erupting at about three months of age and the third molar has erupted by 21—24 months, although it does not become completely functional until about 30 months. The permanent incisors start erupting at about 7 months; the third incisor and canine are fully erupted by 17—20 months, so their development is much more rapid than in the molars. The permanent premolars start erupting between 17—20 months and are complete by 25—26 months, development being much more rapid than in either the molars or the incisiform teeth. These observations, which are illustrated in Fig. 2 A and B, are supported by the two wild and nine park deer of known-age mentioned earlier.

The length of the mandibular tooth row for deer from one area, viz. Essex, are plotted against age in Fig. 3 A. A stepwise graph results in which the vertical portions correspond with the eruption of the molar teeth and the horizontal portions with the growth of the teeth once they have erupted. In this population it can be seen that M_1 erupts at 4—6 months, M_2 at 12—14 months and M_3 at 20—24 months. Also included in Fig. 3 A are the mean, together with twice the standard deviation, for the adult deer from the same area which occur in groups 3 and 4 for the females and group 4 for the males (See page 112). The mean values for the adult deer appear to be slightly less than the values for the younger deer. If this is so, it would suggest that, once the premolars and molars have erupted, the length of the mandibular tooth row decreases with increasing wear and age.

In order to test this hypothesis, the length of the mandibular tooth row for those animals in groups 1 and 2 were compared with those in group 4 for the males and in groups 3 and 4 for the females; there being insufficient group 4 females to allow valid comparisons to be made. The difference was not significant for the females ($P > 0.1$) whereas it was probably significant for the males ($P = 0.02$). The differences in the length of the mandibular tooth row between male and female deer in groups 3 and 4 were not significant ($P > 0.1$). When the male deer in groups 1 and 4 from all localities were compared then the difference in the length of the tooth row was significant ($P < 0.01$). Hence it would appear that there is a tendency for the mandibular tooth row to decrease in length with increasing wear but the difference only becomes significant in animals with very well worn teeth.

VII. DEVELOPMENT OF THE MANDIBLE

The mandible of the adult Fallow deer is that of a typical ruminant and closely resembles that of other deer (Flerov, 1952; Gültekin, 1962; Mystkowska, 1966), cattle and sheep. The lower edge of the ramus is strongly bowed and in this respect it is more similar to cattle than to sheep (Hughes & Dransfield, 1953). The two halves of the mandible are not ossified at the symphysis. However, in deer with very worn teeth a certain amount of bony growth occurs in the symphysial region so that the two rami become attached by interlocking bony processes, though the two halves are easily separated.

Inspection of the mandibular measurements shows that there is a wide range of size for any given age both within and between populations. The variation between populations, which will be discussed more fully

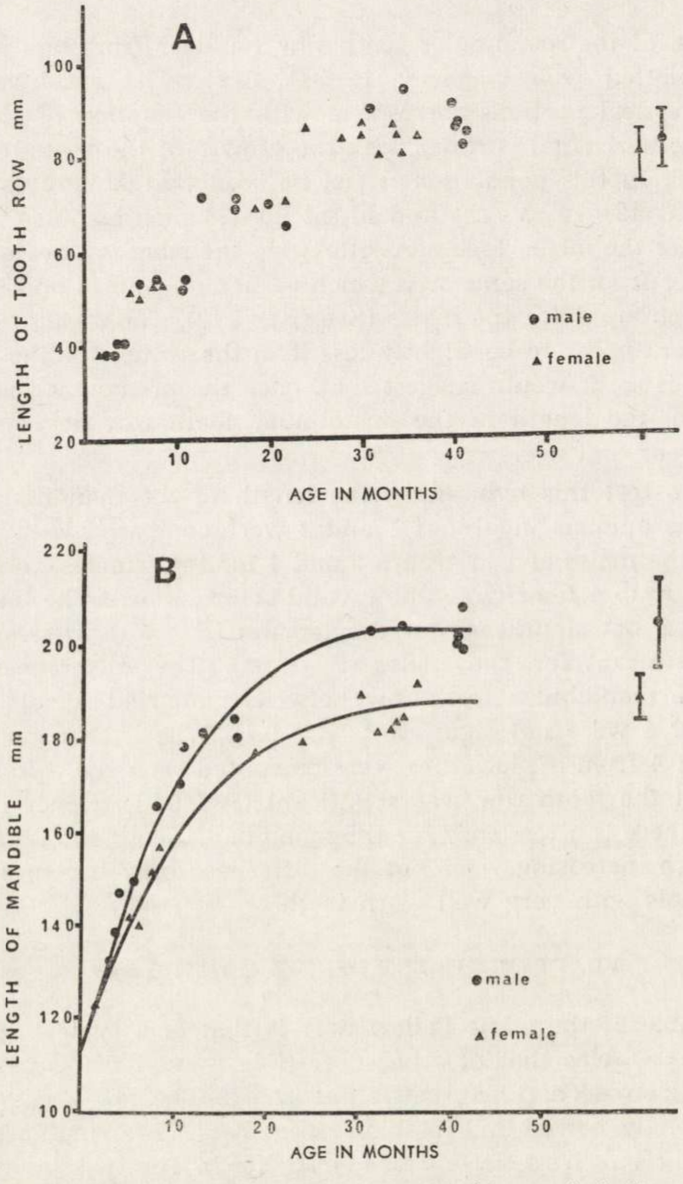

Fig. 3. Increase in the mandible measurements with age including the mean and twice the standard deviation of deer in groups 3 and 4.
A — length of the tooth row, the gaps correspond to the eruption of the molar teeth; B — length of the mandible; C — height of the mandible; D — length of the diastema.

later, tended to obscure the increase in size of the mandible with age if the specimens from all the areas were considered together. Therefore the changes are shown for the specimens from Essex alone (Fig. 3 B, C & D). Also included are the mean and twice the standard deviation of female deer from groups 3 and 4 and male deer from group 4.

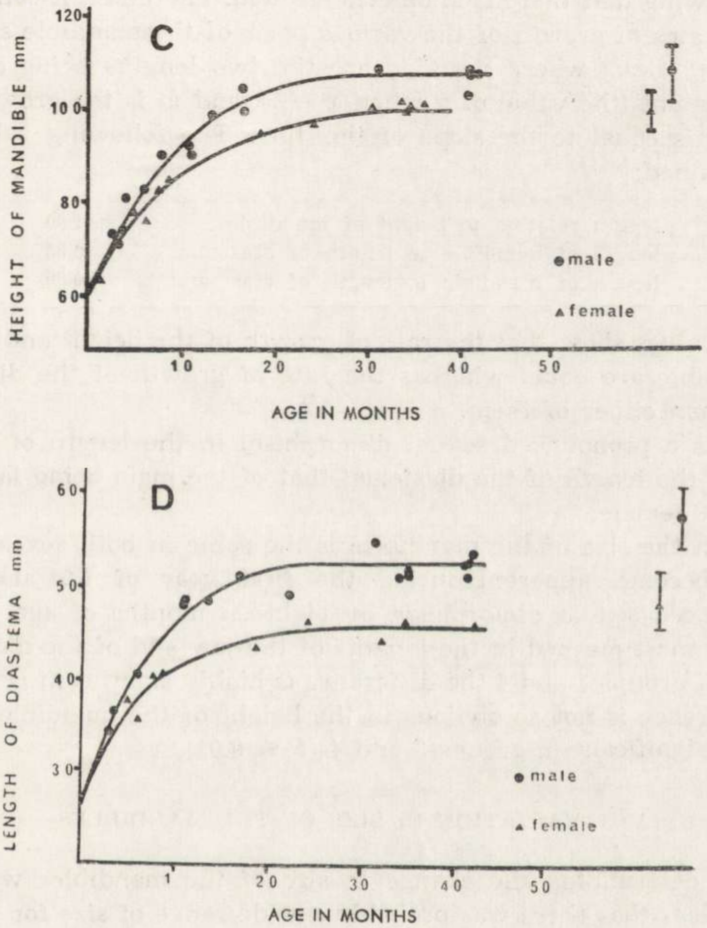

Fig. 3 (continued).

It can be seen that the rate of growth of the length and height of the mandible and the length of the diastema is very rapid during the first year of life, after which the rate gradually decreases until at about 30 months of age growth has almost ceased. This almost complete cessation of growth coincides with the time at which all the permanent teeth have erupted and become functional. The length and height of the mandible at this age do not differ significantly from that of the adults in groups 3 and/or 4 ($P > 0.01$ for both sexes). However, there is a highly significant increase in the length of the diastema in male deer after 30 months of age ($P < 0.001$) but not in the females ($P < 0.01$).

The logarithmic values of length, height and diastema length were plotted against each other in turn. Straight line graphs resulted in all cases, showing that there is allometric growth. Therefore, it can be taken that the rates of growth of the various parts of the mandible satisfy the equation $y = cx^m$ where x and y are the two lengths being compared, c is a constant (the value of y when $x = 1$), and m is the growth coefficient and is equal to the slope of the line. The following values of m were obtained:

length relative to height of mandible	= 1.00
length of mandible to length of diastema	= 0.88
height of mandible to length of diastema	= 0.89

These values show that the rate of growth of the height and length of the mandible are equal whereas the rate of growth of the diastema is greater than either of them.

There is a pronounced sexual dimorphism in the length of the mandible and the length of the diastema; that of the male being larger than that of the female.

At birth the size of the mandibles is the same in both sexes, but differences becomes apparent during the first year of life and there is a pronounced sexual dimorphism by eighteen months of age. This difference is most marked in the lengths of the jaw and of the diastema; in animals of groups 3 and 4 the difference is highly significant ($P < 0.001$). The difference is not so obvious in the height of the mandible although it is still significant in groups 3 and 4 ($P < 0.01$).

VIII. VARIATION IN SIZE OF THE MANDIBLES

Whilst determining the change in size of the mandibles with age it became clear that there was probably a wide range of size for any given age both within and between populations. With one exception there were insufficient specimens of like sex and age from a single locality to determine the variation in size within a population. The exception was twenty 27 month old male deer from Richmond Park. The mean and twice the standard deviation of the various lengths of these deer are:

length of mandible	193.9 ± 9.1 mm
height of mandible	103.8 ± 4.8 mm
length of diastema	50.4 ± 5.0 mm
length of cheek teeth	95.5 ± 4.0 mm

All dimensions of the mandible change with age and although these are almost negligible in adult animals, the precise rate of change is unknown. It is clear, therefore, that none of the actual measurements can be used directly to determine whether there is any difference in size between the samples unless a large number of deer of a particular age are available. The index obtained by expressing the length of the diastema as a percentage of mandibular length has been found to be independent of age and has been used to compare these samples of Fallow deer (Chapman & Chapman, 1969).

It is desirable to give an indication of the size of the mandibles of present-day Fallow deer in Great Britain, even though significant var-

Table 5.

Sizes of adult Fallow deer mandibles from Great Britain. Arithmetical means and twice the standard deviation (S.D.) are given.

	Sex	Mean±S. D. mm	Range mm	No. of Specimens
Length of mandible	♂ ♂	199.7±15.4	185—216	68
	♀ ♀	191.4±12.2	175—203	49
Height of mandible	♂ ♂	106.9± 8.0	99.5—115.5	63
	♀ ♀	102.7± 5.9	99.5—109.0	48
Lenght of diastema	♂ ♂	53.3±11.4	46.2— 62.0	68
	♀ ♀	48.8± 4.2	43.7— 54.5	50
Length of tooth-row	♂ ♂	85.6± 7.2	80 5— 93.8	69
	♀ ♀	84.2± 6.7	76.1— 89.3	50

iations occur between certain populations (Table 5). These measurements will enable comparisons to be made with specimens from other countries and with fossil and prehistoric material.

IX. DISCUSSION

The number and type of mandibular teeth in Fallow deer is similar to that of other species of *Cervidae* (Flerov, 1952). The fourth premolar, however, differs in different species of deer and is a character used in classifying fossil deer (Azzaroli, 1953). In Fallow deer this tooth is lophodont in that from the longitudinal buccal ridge there extends transverse ridges towards the lingual edge. The same appears to be true for elk (Quimby & Gaab, 1957) and Red deer (Ahlén, 1965) whereas in Mule deer, *Odocoileus hemionus* (Richardson, 1829) the tooth is selenodont (Rees, Kainer & Davis, 1966a). In artiodactyls the first premolar is usually considered to have taken on the form and function of a canine but in deer it is usually absent (L o o m i s, 1925). No evidence of this tooth was found in any of the 185 mandibles examined.

The majority of the mandibles examined had eight incisiform teeth (6 incisors and 2 canines), although in a small proportion of them either one or two of these teeth were absent, as were the alveoli. In each case the missing teeth were either the third incisors or the canines. These twc teeth are almost identical in Fallow deer and so far no decision has been made as to which tooth is missing. The only report we have been able to find of the absence of an incisiform tooth and its alveolus in deer is that of R o b i n e t t e (1958) who records two female Mule deer each having only six incisiform teeth. In one specimen those missing were permanent teeth whereas in the other the missing teeth were deciduous.

We feel that the most reliable estimate of age can be obtained by assuming the deer to be born in mid-June and calculating the number of months between then and death; the degree of tooth development being used only to determine the year class. This method is only applicable to animals less than three years old. Attempts to assign definite ages to deer above 3 years should be viewed with caution until animals of known age are available for comparison. Similar conclusions have been reached by M u r i e (1951) and Q u i m b y & G a a b (1957) for Elk and R o b i n e t t e, J o n e s, R o g e r s & G a s h w i l e r (1957) for Mule deer. However, L o w e (1967) comes to the conclusion that for Red deer the best method of determining age is by tooth replacement, eruption and wear.

The order of eruption of the permanent teeth of wild Artiodactyls is almost unknown. C a u g h l e y (1965) describes the sequence of eruption for the Himalayan thar, *Hemitragus jemlahicus* (S m i t h, 1826) and summarizes the information that was available to him for the families *Bovidae, Antilocapridae* and *Cervidae*. In none of the 13 species listed was the complete order of eruption known (cf. Table 6).

The first molar is the first permanent tooth to erupt in all the species and this is followed by the second molar or the first incisor. In Fallow deer the first incisor erupts before the second molar as it does in the white-tailed deer whereas in the other species listed in Table 6 the reverse procedure occurs. The second and third incisors are usually the next teeth to erupt, closely followed by the canine and the third molar. The premolars being usually the last to erupt, although M i t c h e l l (1963) states that in Scottish Red deer the premolars erupt between 21 and 28 months whilst the third molar does not erupt until 33 months. This is in contrast to the work of N a h l i k (1959) on Red deer and M u r i e (1951) and Q u i m b y & G a a b (1957) on the Elk. These last authors state that there is no particular order of replacement for deciduous molars in Elk and that in some instances they are replaced almost simultaneously. Although the deciduous molars in Fallow deer appear to be replaced over a short period of time, the fourth premolar is invariably the first to erupt. Some of these discrepancies may be due to different definitions of when a tooth has erupted and whether this is eruption above the jaw or through the gum. In the present work a tooth is considered to have erupted if the cusps are showing above the bone.

Comparison of the general order of tooth eruption in Cervids with other Artiodactyls is interesting. In the six species of *Bovidae* and one species of *Antilocapridae* listed by Caughley (1965), the first molar

Table 6.

Order of eruption of permanent mandibular teeth in deer.

Teeth are enclosed in square brackets where it was not possible to determine the order of eruption from the reference cited. Teeth enclosed in brackets erupt at about the same time.

Species	Order of Eruption	Reference
Dama dama	M_1 I_1 M_2 I_2 I_3 C M_3 P_4 (P_3 P_2)	Present Study
Cervus elaphus	M_1 [M_2 I_1] I_2 I_3 C [P_2 P_3 P_4] M_3	Mitchell (1963)
„ „	M_1 M_2 (P_2 M_3) P_3 P_4	Nahlik (1959)
Cervus canadensis	M_1 M_2 I_1 I_2 [I_3 M_3] [C P_2 P_3 P_4]	Murie (1951) Quimby and Gaab (1957)
Odocoileus hemionus	M_1 M_2 [I_1 I_2 I_3 C] M_3 P_4 P_2 P_3	Rees, Kainer and Davis (1966)
„ „	M_1 [I_1 M_2] I_2 [I_3 C M_3] [P_2 P_3 P_4]	Robinette, Jones, Rogers and Gashwiler (1957)
Odocoileus virginianus	M_1 I_1 M_2 I_2 [I_3 C] M_3 [P_2 P_3 P_4]	Severinghaus (1949)
Alces alces	M_1 [M_2 I_1] [I_2 I_3 C M_3 P_2 P_3 P_4]	Passmore, Peterson and Cringan (1955)
Rangifer articus	M_1 [M_2 I_1 I_2] [C M_3 P_2 P_3 P_4]	Banfield (1954)
Capreolus capreolus	M_1 M_2 I_1 I_2 [I_3 C] [M_3 P_2 P_3 P_4]	Baumann (1949)

is the first permanent tooth to erupt and this is usually followed by the second molar and the first incisor, as in the deer. The third molar, the second incisor and the premolars erupt next, followed by the third incisor and the canine; this order being the reverse to that which occurs in deer.

The first permanent tooth in Fallow deer (M_1) usually erupts between 3 and 6 months of age; a full complement of teeth is obtained by about two years although the third molars do not usually become functional until about 30 months. The eruption of the permanent incisors, canines and premolars occurs fairly rapidly whereas eruption of the molars is more prolonged. If allowances are made for different definitions of eruption then the ages at which the various permanent teeth erupt is similar to that quoted by Mitchell (1963) for Red deer, Quimby & Gaab (1957) for Elk and Rees, Kainer & Davis (1966b) for Mule deer. Tooth eruption in the Roe deer, *Capreolus capreolus* (Linnaeus, 1758) is quicker and a full set of teeth is usually obtained by 15 months (Raesfeld, 1923).

There is a tendency for the mandibular tooth row in male Fallow deer to decrease in length with increasing wear and, presumably, age. This tendency also appears to occur in Moose, *Alces alces* (Linnaeus, 1758) although no distinction is made between the sexes (Passmore, Peterson & Cringer, 1955). Lowe (1967) states that the length of the tooth row of Scottish Red deer declines with age after four years but again no distinction is made between the sexes. From measurements published by Mystkowska (1966) it would appear that there is a tendency for the length of the tooth row of male Polish Red deer to decrease with increasing tooth-wear.

Fallow deer mandibles reach their maximum length and height at about 30 months of age, although the length of the diastema continues to increase after this age. There is a pronounced sexual dimorphism in all these parameters; the male being appreciably larger than the female. The length of the mandible in Newfoundland Caribou, *Rangifer tarandus* (Linnaeus, 1758) reaches its maximum length between 3 and 4 years and increases little, if at all, after that age. The diastema, however, continues to grow until 7—9 years of age (Bergerud, 1964). In Scottish Red deer both the length of the mandible and of the diastema reach their maximum size at about three years (Lowe, 1967). However, Mystkowska (1966) claims that in Polish Red deer the mandibular length continues to increase throughout the animal's life and that the length of the diastema continues to grow until 12—16 years. Lowe was studying animals of known-age whereas Mystkowska estimated the ages of her specimens and so the former work is presumably more reliable. It also agrees with what is known of the growth of mammalian bones in general.

There is appreciable variation in the size of the mandibles from 20 deer of similar age and from an enclosed area, Richmond Park. Unfortunately it is very difficult to obtain large numbers of specimens of similar age from a single locality but the figures quoted give some idea of the degree of variation which can be expected.

The only measurements of Fallow deer mandibles which we have been able to find are those of Miller (1912) who examined only four specimens (1 ♂, 3 ♀). The male came from England whereas the females came from Sweden, Germany and a park in Washington D. C. in the United States of America. In all the specimens the third molar was either »moderately« or »much« worn and the measurements fall within the ranges given in Table 5.

Acknowledgements: We are most grateful to the following people who supplied the specimens: Mr. R J. P. Eden, Col. V. S. Laurie, Mr. A. Qvist, Superintendent of Epping Forest; Mr. D. Talbot, Deer Keeper to His Grace The Duke of Bedford at Woburn Park; Mr. G. J. Thomson, Superintendent of Richmond Park; Mr. V. Weir and to the following staff of the Forestry Commission, Messrs. K. W. Clark, D. E. Davis, E. Gwilliam and G. Springthorpe. Messrs. J. Caldwell, D. Corke, B. Eastcott, K. Hoy, M. Hum and W. Page helped to clean and prepare the specimens.

Our thanks are due also to the following firms who supplied materials and equipment: Bakelite Xylonite Ltd., Borax Consolidated Ltd., British Visqueen Ltd., Chemical Supply Co. Ltd., L. B. Holliday & Co. Ltd., Ilford Ltd., Imperial Chemical Industries Ltd., Agricultural and Mond Divisions and Southern Region, Laporte Chemicals Ltd., A. H. Marks & Co. Ltd., Shorko-Metal Box Ltd., Synthite Ltd., Transatlantic Plastics Ltd. and Walker Chemical Co. Ltd.

This work was carried out with the aid of grants from the Carnegie United Kingdom Trust and the Natural Environment Research Council to the Essex Field Club, to whom we express our grateful thanks.

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Received, November 25, 1969.

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ROZWÓJ ZĘBÓW I ŻUCHWY U DANIELA

Streszczenie

Daniel, *Dama dama* (Linnaeus, 1758) posiada uzębienie difiodontyczne, obejmujące 20 zębów mlecznych i 32 stałych. Wiek można oznaczyć najdokładniej posługując się znanym okresem urodzin oraz stopniem rozwoju zębów. Metoda ta daje się jednak zastosować tylko w odniesieniu do zwierząt w wieku poniżej 3 lat. Osobniki starsze podzielono na grupy na podstawie starcia trzeciego molara. Zęby stałe wyrzynają się w następującej kolejności: M_1, I_1, M_2, I_2, I_3, C, M_3, P_4, (P_3, P_2). Zęby trzonowe stałe zaczynają wyrzynać się w wieku około 3 miesięcy a kończą pomiędzy 21 a 24 miesiącem, jednakże trzeci molar spełnia swe funkcje dopiero po 30 miesiącu. Stałe zęby przedtrzonowe wyrzynają się między 17 a 20 miesiącem i są kompletne dopiero w 25—26 miesiącu, natomiast stałe siekacze rozpoczynają wyrzynanie w wieku około 7 miesięcy a kończą między 17 a 20 miesiącem. Żuchwa osiąga maksymalną wielkość w wieku około 30 miesięcy, chociaż diastema u samców zwiększa się jeszcze po tym okresie. Omówiono również zmienność wewnątrzpopulacyjną i międzypopulacyjną w wielkości żuchwy.