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Age determination of the West African buffalo *Syncerus coffer brachyceros* and the constancy of tooth wear

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Summary

Maxillae of 34 West African buffalo *Syncerus caffer brachyceros* were collected from three sites in Burkina Faso, West Africa, and age determined from tooth appearance and the enamel height of Ml according to the criteria of Grimsdell (1973) for Ugandan buffalo *Syncerus caffer caffer.* Good agreement between the two methods was found. Ground and decalcified sections were prepared from M 1 and the interradicular cementum lines counted. Although this gave inconsistent results in terms of assumed age compared with the other two methods, it is concluded that agreement was sufficiently close to suggest that the rate of attrition with age was similar in both populations.

Résumé

Les machoires de 34 buffles de 1'Ouest africain *(Syncerus caffer brachyceros)* ont été collectées en trois endroits au Burkina Faso en Afrique de 1'Ouest et on a déterminé leur age d'après 1'aspect des dents et Ie poids de 1'émail de Ml selon Ie critère de Grimsdell (1973) pour Ie buffle ougandais *(Syncerus caffer caffer).* On a trouvé une bonne correspondance entre les deux méthodes. La base et des sections décalcifiées de Ml sont preparées et les stries du cément interradiculaire sont comptées. Bien que cela donne des résultats peu intéressants pour l'estimation de 1'age en comparison avec les deux autres méthodes, on conclut que la concordance est sumsamment bonne pour suggérer que Ie taux d'usure en fonction de 1'age est semblance dans les deux populations.

Introduction

It is popularly asserted that tooth wear is not constant in a species but differs according to inheritance, nutrition, habitat and the severity of the seasons, the assumption being based upon evidence from domestic species (Deniz & Payne, 1982; Hillson, 1986). The validity of this assumption is open to question in view of the long evolutionary history of teeth and their importance in the survival of the species. The comparison of two widely separated populations of the same species would provide support for one or the other points of view in a definitive manner. With this object in view the authors have compared a sample of the morphologically very variable West African savannah buffalo *Syncerus caffer hrachyceros* (Grubb, 1972) with the results obtained by Grimsdell (1973) for a morphologically very variable Ugandan population of the East African cape buffalo *Syncerus caffer caffer.* The West African buffalo is subject to a unimodal rainfall regime with a harsh

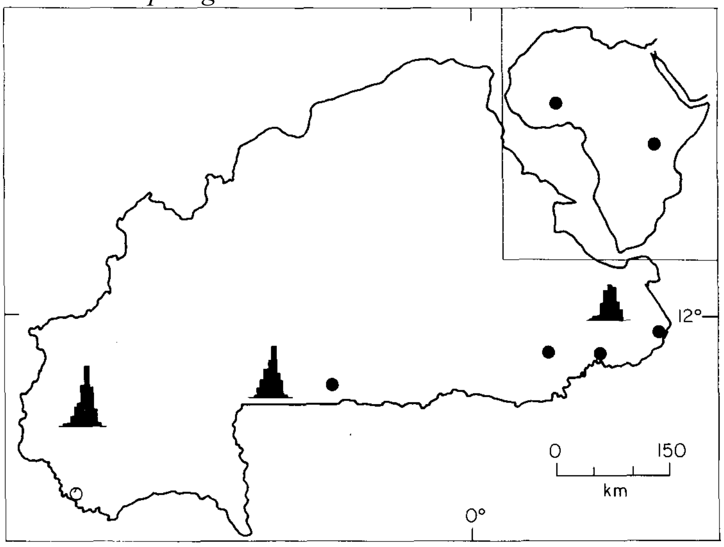

Fig. 1. Map of Burkina Faso showing skull collection sites with monthly rainfall histograms with (inset) the East and West African sites.

dry season and a long wet season; in contrast, the Ugandan buffalo, collected at lat. 0°, long. 30°E, is subject to a bimodal rainfall in a relatively benign environment. The two habitats differ markedly, the former with a grass layer dominated by coarse two-metre tall *Andropogonae,* and the latter by a grass layer of *Andropogonae* rarely exceeding half a metre in height and dominated by *Themeda triandra,* a species absent from the former habitat.

Spinage (1967) and Grimsdell (1973), studying the waterbuck *Kobus ellipsiprymnus* and the buffalo, respectively, found that in western Uganda apparently two prominent lines per year were produced in the tooth cementum. Under a unimodal rainfall regime Spinage (1976) concluded that the Grant's gazelle *Gazella granti* produced only one distinct line per year. The causative influence resulting in the rate or quality of cementum apposition still remains a subject of debate, but appears to have some relation to seasonal fluctuations in nutrition (Spinage, 1973, 1976a), although this does not seem to apply to *Canidae* in temperate zones (Grue & Jennsen, 1973). There are seemingly no hitherto published studies relating to age determination in large West African mammals.

The West African savannah buffalo differs considerably from the Cape buffalo, being much smaller and weighing from 300 to 500 kg (Roure, 1962) compared with 660-849 kg for the East African race (Ledger, 1968). It shows great variation in horn shape (Grubb, 1972), lacking the enhanced frontal boss of the Cape male, but, like the Ugandan population, shows all variations of coat colouration ranging from red to black.

Methods

Skulls of thirty-three buffalo were collected from three regions in Burkina Faso (formerly Upper Volta), West Africa, as follows: from the south-east (twenty-two);south-central (four) and south-west (six); in addition, one was of unknown provenance (Fig. 1). Skulls are difficult to find due to people collecting them for 'trophies', even inside national parks, and some use had to be made of material from animals which had died a good many years ago.

Ages were estimated according to the methods ofGrimsdell (1973) from the appearance of maxillary Ml, its enamel height, and the number of lines in the interradicular cementum of the tooth root. The molars were extracted randomly with respect to side for measuring and for sectioning, and no distinction was made between male and female. The major part of the crown was removed to aid decalci-fication. Thirty-three teeth were decalcified, sectioned at 15-20um, and thirty-one were stained using haematoxylin and eosin. Undecalcified ground sections were also prepared at 180 um.

Subjective visual examination of skulls and their teeth suggested that they might fall into two discrete size classes. The first molar was therefore measured with calipers in the cross-sectional plane (length x breadth) near the extremity of the crown, to give surface area; a measurement which is indicative although crude, allowance being made for the protuberance of the styles and lack of complete rectangularity. Mesial drift resulting in the approximal wear of the antero-postero surfaces of the teeth must also be taken into account in old animals.

Results

Variation in tooth size

Figure 2(a) shows the frequency distribution of tooth surface area divided into twelve classes, together with the calculated normal distribution, the difference between the distributions being significant (X^2 18.7, d.f. 9, 0.95 < P < 0.975).

When the distribution of size classes is compared with age determined from enamel height (Fig. 2b) among the largest tooth categories half were old animals (mean x = 10-5±2,4yr for *n=4,* based on enamel height), and half were young *(mean x* = 4-5 ±1-6). Among the smallest tooth categories one animal was young (5.5 yr),and three were old *(mean x* = 11.0 ±2.7 yr). Of the oldest animals (12-14 yr) the mean cross-sectional area was 521.9 ± 49.6 mm^2 for n = 10, in the range 440-600 mm^2. Three had teeth smaller than one standard deviation from the mean, and one had teeth greater than one standard deviation.

When the mean length and the mean width of teeth of animals of 12-14 years of age was compared with that of teeth of 5-8 years, the older classes had teeth significantly smaller in length but significantly greater in width (t = — 2-345, d.f. 20, 0.95 <P< 0.98 and t= 2.819, d.f. 20, 0.98 >P< 0.99 respectively), antero-postero wear being apparently compensated for by an increase in tooth width, the length declining by 10% and the width increasing by 9%.

Visual estimation of age

Could differences in tooth size lead to incorrect visual estimation of age? Examination of the data shows that animals in which age determined from visual estimation differed from that derived from enamel height by three years, were underestimated, and had a large mean tooth size (n = 3); but those differing by two years were overestimated (5 in 6) and also had a large mean tooth size 560 ±37 $^{mm-2}$ and 560 ±50-1 $^{mm-2}$, respectively). Difference in tooth size would

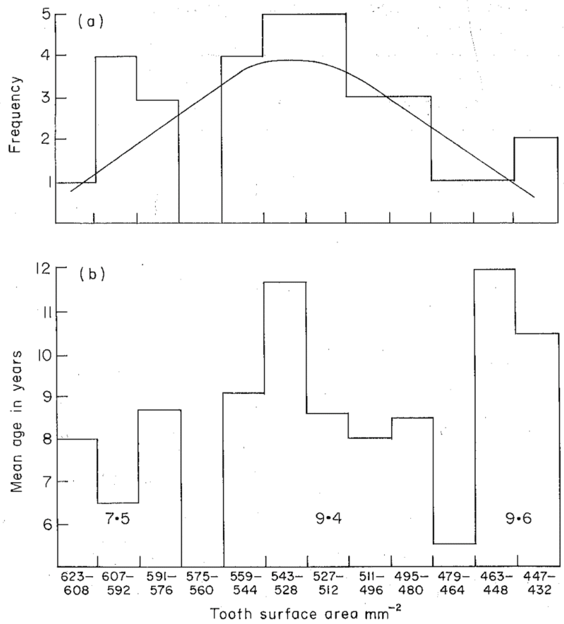

Fig. 2. (a) Frequency distribution of cross-sectional tooth area compared with the curve of normal distribution. (b) The distribution of tooth cross-sectional area related to age.

therefore apparently not lead to bias in age estimation. We have seen also that loss of tooth surface area resulting from interstitial wear is more or less compensated for in terms of tooth cross-sectional area. The ages assigned from visual appraisal are given in Table 1.

Age derived/rom cementum line counts

It was expected *a priori* that changes in the rhythm of cementum accretion would be much more clearly defined in these samples than in those from eastern Africa, due to the long and well-marked dry season. In fact the lines were very irregular in appearance and intensity and difficult to interpret. The number of lines was counted by three independent observers, only one of whom had previous experience, without reference to the assumed ages. None of the observers' results compared closely with ages assumed from enamel height, although linear regressions and paired correlations were significant (Mest for paired samples and Mann-Whitney U test). Differences did not increase with age, the lack of correlation being due to random ages having much higher line counts than expected. There were deviations of 4 years and more for two males and four females with two samples of unknown sex.

Table 1. Age determination of a sample of West African savannah buffalo expressed to the nearest year

Age from enamel height	Visual assessment	Cementum line count +1	Sex
3	5	5	F
4	5	5	M
4	6	5	F
5	5	5	F
5	7	5	?
6	5	4	F
6	5	7	M
6	6	7	F
6	6	9	M
7	6	')	M
7	7	7	F
7	8	4	M
7	8	II	F
S	7	10	F
8	7	9	F
8	8	5	M
9	11	9	M
10	10	6	F
10	10	8	?
10	10	16	F
11	10	9	M
11	10	10	F
12	9	13	M
12	10	7	F
12	11	12	?
12	11	5	?
12	13	5	M
13	12	7	?
14	11	14	M
14	14	17	F
14	14	14	M

Ages derived from the number ofcementum lines + 1 to equate with years, from the observer giving the highest correlation, are given in Table 1. Table 2 shows the scores for all three observers.

Comparison of methods

The two methods of determination, from visual appraisal and measurement of enamel height, showed good agreement, the paired samples not being significantly different at the 95% level of probability (Mann-Whitney U test

0.085 <*P*< 0.0858). This was in spite of the difficulty of assessing age from a single tooth which Grimsdell's criteria demand, a virtual impossibility in middle age classes without considerable experience of tooth wear patterns. Age can normally only be assigned by reference to wear on the premolars as well, which when present were taken into account when making decisions in this study. Where age was 0.5 yr in error for one

Table 2. Agreement of cementum line age with enamel height of three independent observers, as %

	Sections					
	H & E			Ground		
observer	within 1 yr.	within 2 yr.		within 1 yr.	within 2 yr.	
1	20-8	8-3	70-8	32-0	16-0	56-0
2	31-3	15-6	53-1	31-0	10-3	58-6
3*	45-2	16-1	38-7	—	—	—

"•Observer with previous experience.

Table 3. **Mean number of cementum lines per enamel height class**

Enamel height mm	Grimsdell's mean cementum line number divided by 2*	Mean cementum line number this study
40		
36	2-1	4-0
32	3-4	5-6
28	4.9	4-5
24	6-3	6-7
20	7-8	7-7
16	9.4	8-2
12	11-0	7-8
8	12-7	13-0
4	—	—
0	—	—

*Grimsdell's mean line number is divided by two as he found that on average two were laid down per year.

or the other method, the two ages were considered as equal, assessing age to the nearest half year from visual appraisal being impossible. Table 1 shows that 33% were correctly matched by these two methods; 36% were one year out; 18% were two years out and 12% were three years out. Age derived from cementum line counts showed relatively poor agreement with that derived from enamel height, only 22.5% being correctly matched; 22.7% one year out; 16-1% two years out and 35-5% more than two years out in the range 3-7 years. But the paired comparisons were not significantly different at the 95% level of probability (Mann-Whitney U test $0.1814 < P < 0.1788$). When the teeth were separated into enamel height classes of 4 mm, the mean number of cementum lines per class as calculated by Grimsdell (pers. comm.) when divided by two to equate with one hypothesised line per year in West Africa, gave a close correlation in the majority of cases with the mean number of lines per class calculated in this study (Table 3).

Attwell & Jeffrey (1980) note that in eland *Teurotragus oryx* from South Africa males of markedly different cementum line ages (7 and 12 years) from the same locality, were placed in the same wear class.

We are unable to say which provides the closest approximation to actual age, tooth appearance, enamel height or the number of cementum lines. But in spite of the differences between the methods an expected relationship of one cementum line per year of age provides the closest correlation with age derived from enamel height, and supports the concept that tooth wear is relatively constant within species despite wide differences in bodily size and environment, contrary to the assertion of many authors (Morris, 1978; Riney, 1982). That tooth wear is constant among wild species is hardly surprising when the long evolutionary history of teeth and their importance to the survival of the species is taken into consideration.

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